Bibliography on CO_2 Effects on Vegetation and Ecosystems: 1990-1999 Literature

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1

Abarzua, S., R. Altenburger, R. Callies, L.H. Grimme, A. Mayer, D. Leibfritz, and U. Schiewer. 1993. Ammonium rhythm in cultures of the cyanobacterium microcystis- firma. *Physiologia Plantarum 89(3):659-663.*

Over a period of several days, rhythmic changes in extracellular NH4+ concentration take place in cultures of the cyanobacterium Microcystis firma (Breb et Lenorm.) Schmidle, strain Gromov/St. Petersb. 398, under conditions of restricted CO2 supply and light/dark alternation. The changes are enhanced by nitrate supply. Among the various processes generating intracellular NH4+ (NH4+ uptake, NO3- reduction, protein and amino acid degradation, photorespiration), NO3- reduction appears as the one most important. This can be concluded from experiments with and without nitrate and/or ammonium in the medium. In the presence of saturating CO2, continuous light, or continuous darkness, rhythmic NH4+ oscillations are not induced. Studies of the incorporation of NH4+ nitrogen by in vivo N-15-NMR show that if CO2 is supplied, N-15 is accumulated in several components with the following time course: in the first hour in Gln (delta), in the second hour in the alpha- amino groups of most nonbranched amino acids, in the third hour in gamma-aminobutyric acid (GABA), Orn (delta) and Lys (epsilon), and in the sixth hour in Ala. Carbon limitation, however, results in accumulation of label in the amide nitrogen of glutamine only.

KEYWORDS: METABOLISM, N-15, NMR-SPECTROSCOPY, NUCLEAR MAGNETIC-RESONANCE

2

Abdin, O.A., X.M. Zhou, B.E. Coulman, D. Cloutier, M.A. Faris, and D.L. Smith. 1998. Effect of sucrose supplementation by stem injection on the development of soybean plants. *Journal of Experimental Botany 49(329):2013-2018.*

Over the past half decade several stem injection methods have been developed for cereal plants. These methods allow researchers to administer solutions to cereal plants to study their effects on plant physiology. However, little work has been done to extend this technique to non-cereals. An experiment was conducted to test an injection technique that could be suitable for soybean plants (Glycine max [L.] Merr.), and to study the effect of long-term injection of sucrose on the growth of soybean plants. An injection setup comprising a supporting stand and a fluid injection system was established. Pressure was applied to the plunger of a 5 ml syringe using ceramic bricks to force test solutions into the plants. Solutions of 0, 150, and 300 g sucrose I-1 were injected into soybean plants for 8 weeks starting at the seedling VC stage. Distilled water had the greatest uptake rate, followed by the 150, and then the 300 g sucrose I-1 solutions. The overall average uptake during the injection period was 77.3 ml. Average sucrose uptake values were 11.8 and 13.5 g per plant for the 150 and 300 g sucrose I-1 treatments. This represented approximately 65% of the total dry weight of the plants. Sucrose injection increased leaf area and pod number relative to the control plants. Nodule numbers were lower for sucrose injected treatments, but their dry weights were higher than the control. Above-soil dry matter was higher for the plants injected with 300 g sucrose I-1 than those injected with water. The injection system tested was able to administer concentrated solutions into soybean plants for most of their period of growth and development. The sucrose supplementation had positive effects on soybean growth but suppressed photosynthesis.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, LEAVES, MAIZE, NITROGEN, PEDUNCLE PERFUSION, PHOTOSYNTHESIS, WHEAT, YIELD

3

Abdullaev, A.A., B.B. Dzhumaev, Z.N. Abdurakhmanova, V.L. Kaler, and I.M. Magmedov. 1992. Integral effect of environmental-factors on photosynthetic metabolism of carbon in cotton leaves. *Soviet Plant Physiology 39(2):140-144.*

We used the method of mathematical experiment planning (a 2(3) scheme) to study the influence of environmental factors separately or in combination on the photosynthetic rate and distribution of C-14 among products of photosynthetic carbon metabolism in the cotton (Gossypium hirsutum L.) leaf Increase of light intensity during cultivation accelerated photosynthesis and stimulated incorporation of C-14 into phosphoglyceric acid (PGA), sugar diphosphate (SDP), fructose monophosphate (FMP), and malate, but suppressed incorporation of C-14 into sucrose, glucose monophosphate (GMP), and glycerate. Temperature increase by itself and in any combination with other factors at the upper level suppressed photosynthesis. Elevated temperature increased accumulation of the label in PGA, sucrose, and malate, but lowered it in GMP, alanine, glycine, and serine. Growing plants at enhanced CO2 concentration led to acceleration of photosynthesis and increase of the share of C-14 in SDP, GMP, and malate, but decrease of it in sucrose, alanine, glycine, and serine. Very perceptible effects of interaction are discernible in different combinations of factors. All three factors at the upper level appreciably induced activity of phosphoenolpyruvate carboxylase (PEPCase) in cotton leaves.

KEYWORDS: PHYSIOLOGY

4

Aben, S.K., S.P. Seneweera, O. Ghannoum, and J.P. Conroy. 1999.

Nitrogen requirements for maximum growth and photosynthesis of rice, Oryza sativa L-cv. Jarrah grown at 36 And 70 Pa CO2. *Australian Journal of Plant Physiology 26(8):759-766.*

The hypothesis that growth of rice (Oryza sativa L. cv. Jarrah) at elevated atmospheric CO2 partial pressure alters leaf nitrogen (N) concentrations required to support maximum dry mass production and photosynthetic rates during the period of rapid tiller initiation was tested by growing plants for 30 days in unstirred sand/hydroponic culture with N concentrations of 5, 20, 40, 60 and 100 mg N L-1. Maximum growth and photosynthetic potential was greater at 70 than 36 Pa CO2 at all N concentrations in the solution. Elevated CO2 reduced leaf N concentrations required to support 90% of maximum growth and photosynthetic rates (critical concentration) from 40 to 27 g kg(-1) for growth and from 45 to 30 g kg(-1) for photosynthesis. Morphological changes at elevated CO2 included increased tiller numbers and reduced leaf area ratio. The latter could be explained by lower plant N concentrations which occurred at high CO2 at each N concentration in the solution, primarily due to lower leaf blade and root N concentrations. Changes in tiller numbers at high CO2 were unrelated to leaf or plant N but were strongly correlated with leaf soluble carbohydrate concentrations. We conclude that elevated CO2 alters the nutritional physiology of rice during the rapid tillering phase in a way that increases the efficiency of N utilisation for growth and photosynthesis.

KEYWORDS: ACCLIMATION, CAPACITY, COTTON, ELEVATED CO2, LEAVES, NUTRITION, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, WHEAT

5

Aber, J.D., S.V. Ollinger, C.A. Federer, P.B. Reich, M.L. Goulden, D.W. Kicklighter, J.M. Melillo, and R.G. Lathrop. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research 5(3):207-222.*

Rapid and simultaneous changes in temperature, precipitation and the atmospheric concentration of CO2 are predicted to occur over the next century. Simple, well-validated models of ecosystem function are required to predict the effects of these changes. This paper describes an improved version of a forest carbon and water balance model (PnET-II) and the application of the model to predict stand- and regional-level effects of changes in temperature, precipitation and atmospheric CO2 concentration. PnET-II is a simple, generalized, monthly time- step model of water and carbon balances (gross and net) driven by nitrogen availability as expressed through foliar N concentration. Improvements from the original model include a complete carbon balance and improvements in the prediction of canopy phenology, as well as in the computation of canopy structure and photosynthesis. The model was parameterized and run for 4 forest/site combinations and validated against available data for water yield, gross and net carbon exchange and biomass production. The validation exercise suggests that the determination of actual water availability to stands and the occurrence or non-occurrence of soil-based water stress are critical to accurate modeling of forest net primary production (NPP) and net ecosystem production (NEP). The model was then run for the entire NewEngland/New York (USA) region using a 1 km resolution geographic information system. predicted long- term NEP ranged from -85 to + 275 g Cm-2 yr(-1) for the 4 forest/site combinations, and from -150 to 350 g C m(-2) yr(-1) for the region, with a regional average of 76 g Cm-2 yr(-1). A combination of increased temperature (+6 degrees C), decreased precipitation (-15%) and increased water use efficiency (2x, due to doubling of CO2) resulted generally in increases in NPP and decreases in water yield over the region.

KEYWORDS: DEPOSITION, ECOSYSTEMS, ELEVATED CO2, MODEL, REGIONAL-ANALYSIS, RESPONSES

6

Ackerly, D.D., and F.A. Bazzaz. 1995. Plant-growth and reproduction along co2 gradients - nonlinear responses and implications for community change. *Global Change Biology 1(3):199-207.*

The effects of rising atmospheric CO2 concentrations on natural plant communities will depend upon the cumulative responses of plant growth and reproduction to gradual, incremental changes in climatic conditions. We analysed published studies of plant responses to elevated CO2 to address whether reproductive and total biomass exhibit similar enhancement to elevated vs. ambient CO2 concentrations, and to assess the patterns of plant response along gradients of CO2 concentrations. In six annual plant species, mean enhancement at double ambient vs. ambient CO2 was 1.13 for total biomass and 1.30 for reproductive biomass. The two measures were significantly correlated, but there was considerable scatter in the relationship, indicating that reproductive responses cannot be consistently predicted from enhancement of total biomass. Along experimental CO2 gradients utilizing three concentrations, there was a great diversity of response patterns, including positive, negative, non-monotonic and non-significant (nat) responses. The distribution of response patterns differed for plants grown in stands compared to those grown individually. Positive responses were less frequent in competitive environments, and non- monotonic responses were more frequent. These results emphasize that interpolation of plant response based on enhancement ratios measured at elevated vs. ambient CO2 concentrations is not sufficient to predict community responses to incremental changes in atmospheric conditions. The consequences of differential response patterns were assessed in a simulation of community dynamics for four species of annual plants. The model illustrates that the final community composition at a future point in time depends critically on both the magnitude and the rate of increase of atmospheric CO2.

KEYWORDS: ANNUALS, ATMOSPHERIC CO2, CO2-INDUCED CLIMATE CHANGE, COMPETITION, ELEVATED CO2, ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PINUS-TAEDA SEEDLINGS, RESOURCE USE

7

Ackerly, D.D., J.S. Coleman, S.R. Morse, and F.A. Bazzaz. 1992. Co2 and temperature effects on leaf-area production in 2 annual plant-species. *Ecology 73(4):1260-1269.*

We studied leaf area production in two annual plant species, Abutilon theophrasti and Amaranthus retroflexus, under three day/night temperature regimes (18-degrees/14-degrees, 28- degrees/22-degrees, and 38-degrees/31-degrees-C) and two concentrations of carbon dioxide (400 and 700-mu-L/L). The production of whole-plant leaf area during the first 30 d of growth was analyzed in terms of the leaf initiation rate, leaf expansion, individual leaf area, and, in Amaranthus, production of branch leaves. Temperature and CO2 influenced leaf area production through effects on the rate of development, determined by the production of nodes on the main stem (the plastochron index), and through shifts in the relationship between whole-plant leaf area and the number of main stem nodes. In Abutilon, leaf initiation rate was highest at 38- degrees, but area of individual leaves was greatest at 28- degrees. Total leaf area was greatly reduced at 18-degrees due to slow leaf initiation rates. Elevated CO2 concentration increased leaf initiation rate at 28-degrees, resulting in an increase in whole-plant leaf area. In Amaranthus, leaf initiation rate increased with temperature, and was increased by elevated CO2 at 28-degrees. Individual leaf area was greatest at 28-degrees, and was increased by elevated CO2 at 28-degrees but decreased at 38-degrees. Branch leaf area displayed a similar response to CO2, but was greater at 38- degrees. Overall, whole-plant leaf area was slightly increased at 38-degrees relative to 28-degrees, and elevated CO2 levels resulted in increased leaf area at 28-degrees but decreased leaf area at 38-degrees. The effects on leaf area closely parallel rates of biomass

accumulation in the same experiment, suggesting that responses of developmental processes to elevated CO2 and interacting factors may play an important role in mediating effects on plant growth.

KEYWORDS: C-3, CANOPY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, LEAVES, LIGHT, PHOTOSYNTHESIS, RESPONSES, SUNFLOWER

8

Acock, B., M.C. Acock, and D. Pasternak. 1990. Interactions of CO2 enrichment and temperature on carbohydrate production and accumulation in muskmelon leaves. *Journal of the American Society for Horticultural Science 115(4):525-529.*

9

Acock, B., and G.W. Wall. 1995. A simple conductimetric co2 analyzer with automatic recalibration .1. Design, implementation, and functionality. *Agronomy Journal 87(1):70-75.*

Controlled-environment plant growth cabinets may be used to investigate the long-term effect of elevated carbon dioxide concentration ([CO2]) on plant growth. Infrared gas analyzers (IRGAs) are normally used to monitor and control [CO2] in plant cabinets. With many cabinets in use, however, it soon becomes impractical to purchase an individual IRGA for each cabinet, A more economical method of monitoring and controlling [CO2] relies on the change in electrical conductivity when CO2 is dissolved in demineralized water, This work describes the design, implementation, and functionality of an inexpensive conductimetric system for controlling [CO2] in plant growth cabinets, Regressing electrical conductivity against [CO2] over the range 0 to 1000 mu L L(-1) yields a quadratic response. Calibration drift inherent in the conductimetric CO2 analyzer requires that each analyzer be recalibrated periodically. Automatically recalibrating with an IRGA every 900 s gave control of the [CO2] within the plant enclosures to within 10 to 15 mu L L(-1) of the set point, The [CO2] control system is robust enough to maintain this accuracy regardless of the desired [CO2] set point or the mass of plant material within the plant growth cabinet, In this approach, only one IRGA is required to control [CO2] in many plant growth cabinets if each cabinet has a dedicated conductimetric CO2 analyzer.

10

Adams, R.M., R.A. Fleming, C.C. Chang, B.A. McCarl, and C. Rosenzweig. 1995. A reassessment of the economic-effects of global climate-change on US agriculture. *Climatic Change 30(2):147-167.*

This study uses recent GCM forecasts, improved plant science and water supply data and refined economic modeling capabilities to reassess the economic consequences of long-term climate change on U.S. agriculture. Changes in crop yields, crop water demand and irrigation water arising from climate change result in changes in economic welfare. Economic consequences of the three GCM scenarios are mixed; GISS and GFDL-QFlux result in aggregate economic gains, UKMO implies losses. As in previous studies, the yield enhancing effects of atmospheric CO2 are an important determinant of potential economic consequences. Inclusion of changes in world food production and associated export changes generally have a positive affect on U.S. agriculture. As with previous studies, the magnitude of economic effects estimated here are a small percentage of U. S. agricultural value.

11

Adamse, P., and S.J. Britz. 1992. Amelioration of uv-b damage under high irradiance .1. Role of photosynthesis. *Photochemistry and photobiology 56(5):645-650.*

Sensitivity to ultraviolet-B radiation (UV-B, 280-315 nm) is generally reduced when background irradiance is high. We tested the involvement of photosynthesis in the amelioration of UV-B damage by treating plants at high PAR (photosynthetically- active radiation. 400-700 nm; 1000 mumol m-2 s-1) with supplemental UV-B at double ambient levels of biologically- effective radiation (18 kJ m-2 d-1) and either "ambient" (450 mumol mol-1) or short term elevated (750 mumol mol-1) CO2 levels. Responses to UV-B were assessed by photosynthetic gas exchange, leaf expansion and production of UV-absorbing compounds (presumptive flavonoids) in cultivars of cucumber (Cucumis sativus L.) previously demonstrated to be relatively sensitive (cv. Poinsett) and insensitive (cv. Ashley) to UV-B. Except for marginal leaf interveinal chlorosis observed in Poinsett, both cultivars responded similarly. UV-B had little direct effect on leaf photosynthesis, but it did cause reductions in leaf area and corresponding increases in leaf dry matter per area. Increased CO2 stimulated plant growth, counteracting the effect of UV-B on leaf growth and indicating an important role for photosynthesis. In contrast, the accumulation of UV-absorbing flavonoid compounds was enhanced by UV-B exposure but was not affected by CO2 enrichment.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CELL-SUSPENSION CULTURES, LIGHT, PETROSELINUM- HORTENSE, PHOTON FLUX- DENSITY, PHYTOCHROME, PLANTS, RADIATION, SENSITIVITY

12

Adamsen, F.J., P.J. Pinter, E.M. Barnes, R.L. LaMorte, G.W. Wall, S.W. Leavitt, and B.A. Kimball. 1999. Measuring wheat senescence with a digital camera. *Crop Science 39(3):719-724.*

Documenting crop senescence rates is often difficult because of the need for frequent sampling during periods of rapid change and the subjective nature of human visual observations. The purpose of this study was to determine the feasibility of using images produced by a digital camera to measure the senescence rate of wheat and to compare the results with changes in greenness determined by two established methods. Measurements were made as part of an experiment to determine the effects of elevated CO2 and limited soil nitrogen on spring wheat (Triticum aestivum L.) at the University of Arizona's Maricopa Agricultural Center, near Phoenix, AZ. "Greenness" measurements were made during senescence of the crop with a color digital camera, a hand-held radiometer, and a SPAD chlorophyll meter. The green to red (GIR) for each pixel in an image was calculated and the average GIR computed for cropped images from a digital camera representing 1 m(2) for each treatment and sample date. The normalized difference vegetation index (NDVI) was calculated from the red and near-infrared canopy reflectances measured with a hand held radiometer. A SPAD reading was obtained from randomly selected flag leaves. All three methods of measuring plant greenness showed similar temporal trends. The relationships between GIR with NDVI and SPAD were linear over most of the range of GIR. However, NDVI was more sensitive at low values than GIR. GIR was more sensitive above G/R values of 1.2 than SPAD because the upper limits of SPAD measurements were constrained by the amount of chlorophyll in the leaf, while GIR responded to both chlorophyll concentration in the leaves as well as the number of leaves present. Color digital imaging appears useful for quantifying the senescence of crop canopies. The cost of color digital cameras is expected to decrease and the quality and convenience of use to improve.

KEYWORDS: CHLOROPHYLL METER, CROP, EFFICIENCY, RED, VEGETATION INDEXES, WINTER-WHEAT, YIELD

13

Agar, I.T., J. Streif, and F. Bangerth. 1997. Effect of high CO2 and controlled atmosphere (CA) on the ascorbic and dehydroascorbic acid content of some berry fruits. *Postharvest Biology and Technology 11(1):47-55.*

High CO2 concentrations as well as controlled atmosphere storage are widely used to extend the storage and shelf-life of many fruits. To investigate the effect of these storage procedures on several berry fruits, strawberries, raspberries, currants and blackberries were stored at three different elevated CO2 concentrations, with or without a parallel reduction in O-2. Vitamin C content (ascorbic acid plus dehydroascorbic acid) was reduced by high CO2 concentrations (10-30% CO2), particularly in strawberries. This reduction in vitamin C was moderate in black currants and blackberries and almost absent in raspberries and red currants when compared with strawberries. Reducing the O-2 concentration in the storage atmosphere in the presence of high CO2 had little effect on the vitamin C content. Ascorbic acid was more diminished al high CO2 than dehydroascorbic acid. This suggests a stimulating effect of high CO2 concentrations on the oxidation of ascorbic acid and/or an inhibition of mono- or dehydroascorbic acid reduction to ascorbic acid. (C) 1997 Elsevier Science B.V.

KEYWORDS: HYDROGEN- PEROXIDE, O2, PLANTS

14

Aggangan, R.T., A.M. O'Connell, J.F. McGrath, and B. Dell. 1999. The effects of Eucalyptus globulus Labill. leaf letter on C and N mineralization in soils from pasture and native forest. *Soil Biology and Biochemistry 31(11):1481-1487.*

The effects of addition of Eucalyptus globulus leaf litter on carbon and nitrogen mineralization in soils from a pasture and a native forest were evaluated using a long-term laboratory aerobic incubation assay (29 weeks at 20 degrees C) in leaching microlysimeters, The amount of added leaf litter significantly influenced microbial respiration, microbial biomass and N turnover in both the native forest and pasture soils. Cumulative CO2-C respired increased with increasing rate of leaf litter addition when leaf litter was mixed through the soil or placed on the soil surface. These increases were associated with increases in microbial biomass C content. Cumulative net N mineralization declined in ail treatments when litter was added and was lowest when leaf litter was mixed with soil. When leaf litter was added in increasing amounts to the soil surface, there was a concomitant increase in microbial biomass N content (r(2) = 0.79, n = 8), indicating that the reduction in net N mineralization was primarily due to immobilization of N in microbial tissues. In contrast, when litter was mixed with soil in increasing amounts, there was a decrease in microbial biomass N in forest soil and an increase in pasture soil. Consequently, changes in the rate of net N mineralization were not well related to changes in microbial biomass N content. It is suggested that this may be due to the greater activity and more rapid turnover of microorganisms where litter was incorporated resulting in more of the immobilized N being partitioned into metabolic products or dead microbial cells. Incorporation of litter may also have enhanced loss N through denitrification, (C) 1999 Published by Elsevier Science Ltd. All rights reserved.

KEYWORDS: DECOMPOSITION, DENITRIFICATION, EXTRACTION METHOD, IMMOBILIZATION, LITTER, MICROBIAL BIOMASS CARBON, NITROGEN MINERALIZATION, PLANT RESIDUES, RESPIRATION, WESTERN-AUSTRALIA

15

Agren, G.I. 1996. Nitrogen productivity or photosynthesis minus respiration to calculate plant growth? *Oikos 76(3):529-535.*

One approach to calculate plant growth rate is from models of photosynthesis, respiration and allocation. This requires that processes with characteristic time constants of seconds to minutes be scaled to hours or days. Another approach is to use aggregate models defined at the time scale of growth, hours and days. I use such an aggregate model, the nutrient productivity, to compare the performance of the two approaches on growth experiments with small, nitrogen-limited birch plants. The problems of error aggregation when using the large number of parameters required to scale from the detailed level of photosynthesis and respiration to the aggregate level of growth are in this case such that whole plant growth rate is more accurately predicted with the nutrient productivity model.

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, BIOMASS, BIRCH SEEDLINGS, CARBON, CLIMATE, ECOSYSTEMS, ELEVATED CO2, NUTRITION, STRESS

16

Agren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor, and H.H. Shugart. 1991. State-of-the-art of models of production decomposition linkages in conifer and grassland ecosystems. *Ecological Applications 1(2):118-138.*

We review the state-of-the-art of models of forests and grasslands that could be used to predict the impact of a future climate change arising from increased atmospheric carbon dioxide concentration. Four levels of resolution are recognized: physiologically based models, population models, ecosystem models, and regional or global models. At the physiological level a number of important processes can be described in great detail, but these models often treat inadequately interactions with nutrient cycles, which operate on longer time scales. Population and ecosystem models can, on the other hand, encapsulate relationships between the plants and the soil system, but at the expense of requiring more ad hoc formulations of processes. At the regional and global scale we have so far only steady-state models, which cannot be used to predict transients caused by climate change. However, our conclusion is that, in spite of the gaps in knowledge, there are several models based on dominant processes that are well enough understood for the predictions of those models to be taken seriously.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BOUTELOUA-GRACILIS, CARBON DIOXIDE, CO2-INDUCED CLIMATE CHANGE, EVEN- AGED STANDS, LOLIUM-PERENNE L, NITROGEN PRODUCTIVITY, PLANT GROWTH, SIMULATION-MODEL, THEORETICAL- ANALYSIS

17

Ahmadi, H., W.V. Biasi, and E.J. Mitcham. 1999. Control of brown rot decay of nectarines with 15% carbon dioxide atmospheres. *Journal of the American Society for Horticultural Science 124(6):708-712.*

Effects of short-term exposure to a 15% CO2 atmosphere on nectarines [Prunus persica (L.) Batsch (Nectarine Group) 'Summer Red'] inoculated with Monilinia fructicola (Wint.) Honey (causal agent of brown rot) were investigated, Nectarines were inoculated with spores of M.fructicola and incubated at 20 degrees C for 24, 48 or 72 hours and then transferred to storage in either air or air enriched with 15% CO2 at 5 degrees C. Fruit were removed from storage after 5 and 16 days and were examined for brown rot decay immediately and after ripening in air for 3 days at 20 degrees C. Noninoculated nectarines were stored and treated likewise for evaluation of postharvest fruit attributes to determine their tolerance to 15% CO2. Incubation period after inoculation, storage duration, and storage atmosphere had highly significant effects on fruit decay, 'Summer Red' nectarines tolerated a 15% CO2 atmosphere for 16 days at 5 degrees C. Development of brown rot decay in fruit inoculated 24 hours before 5 or 16 days storage in 15% CO2 at 5 OC was arrested.

After 3 days ripening in air at 20 degrees C, the progression of brown rot disease was rapid in all inoculated nectarines, demonstrating the fungistatic effect of 15% CO2. The quantity of fungal cell wall materials (estimated by glucosamine concentration) was compared to visual estimation of decayed area and visual rating of fungal sporulation. The glucosamine assay defined the onset and progress of brown rot infection more precisely than either of the two visual tests.

KEYWORDS: FRUIT, IPRODIONE, MOLD, SUPPRESSION, SWEET CHERRIES, TISSUE, TOMATO PRODUCTS

18

Ahmed, F.E., A.E. Hall, and M.A. Madore. 1993. Interactive effects of high-temperature and elevated carbon- dioxide concentration on cowpea [vigna-unguiculata (L) walp]. *Plant, Cell and Environment 16(7):835-842.*

Limitations in carbohydrate supplies have been implicated as a factor responsible for reproductive failure under heat stress. Heat stress affects two stages of reproductive development in cowpea [Vigna unguiculata (L.) Walp.], and genotypes are available with tolerance and sensitivity to heat during these different stages. The objectives of this study were to determine the responses of these cowpea lines to ambient and elevated [CO2], under heat stress and optimal temperature, and test whether differences in carbohydrate supplies due to genotypes, CO2 enrichment and heat stress are associated with differences in sensitivity to heat during reproductive development. Plants were grown in reach-in growth chambers and subjected to day/night temperatures of either 33/20 or 33/30- degrees-C, and [CO2] levels of either 350 or 700 mumol mol-1. Under intermediate night temperature (33/20-degrees-C), all lines set substantial numbers of pods. Under high night temperature (33/30-degrees-C) with either ambient or elevated [CO2], one heat-sensitive line produced no flowers and the other set no pods, whereas the heat-tolerant line abundantly set pods. High night temperature reduced the overall carbohydrate content of the plants, especially peduncle sugars, and caused decreases in photosynthetic rates. The high pod set of the heat-tolerant line, under high night temperature, was associated with higher levels of sugars in peduncles compared with the heat-sensitive lines. The heat-tolerant line accumulated substantial shoot biomass, exhibited less accumulation of starch in leaves, and possibly had less down- regulation of photosynthesis in response to CO2 enrichment and heat stress than the heat-sensitive lines. Elevated [CO2] resulted in higher overall carbohydrate levels in heat- sensitive lines (starch in leaves, stems and peduncles), but it did not increase their heat tolerance with respect to flower production or pod set. Heat-induced damage to floral buds and anthers in the sensitive lines was associated with low sugars levels in peduncles, indicating that heat had greater effects on assimilate demand than on leaf assimilate supply. The heat- tolerant line was the most responsive genotype to elevated [CO2] with respect to pod production under either high or intermediate temperatures.

KEYWORDS: ABSCISSION, ACCLIMATION, AIR- TEMPERATURE, CO2, COTTON, HEAT-STRESS, LEAVES, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, REPRODUCTIVE RESPONSES

19

Aikman, D.P. 1996. A procedure for optimizing carbon dioxide enrichment of a glasshouse tomato crop. *Journal of Agricultural Engineering Research 63(2):171-183.*

The procedure consists of two parts. A Gompertz model for the kinetics of fruit growth is used predict the time distribution of photosynthate subsequent harvests. This is combined with predictions of future market prices to compute estimates, one for each day from first anthesis, of a factor to convert CO2 assimilate to expected financial value, based on the worth anticipated from partitioning to fruit. A model of the climate and the crop regime is used to predict temperatures and hence allow for the temperature dependence of fruit growth. The conversion estimates are revised to include the deferred benefit given by additional photosynthesis through increasing early vegetative growth, and hence subsequent photosynthesis and yield. This revision also extends the set of conversion factors to include any period before first anthesis. Given the current environmental variables and conversion factor for that day, a real-time system can use a crop photosynthesis model to predict the cash benefit for any CO2 concentration. The cost of maintaining a concentration can be obtained from a prediction of the ventilation air exchange rate and the unit price of CO2. The CO2 set-point is evaluated as the concentration that maximizes the net profit rate. (C) 1996 Silsoe Research Institute

KEYWORDS: CO2- ENRICHMENT, CUCUMBER, FRUIT- GROWTH, GREENHOUSES, LYCOPERSICON-ESCULENTUM MILL, MODEL, PLANTS, TEMPERATURE, VENTILATION

20

Akimoto, M., A. Shirai, K. Ohtaguchi, and K. Koide. 1998. Carbon dioxide fixation and polyunsaturated fatty acid production by the red alga Porphyridium cruentum. *Applied Biochemistry and Biotechnology 73(2-3):269-278.*

Focusing on CO2 fixation, photoautotrophic cultivation of the red alga Porphyridium cruentum was investigated by means of a batch culture under a 5% CO2-enriched atmosphere. The alg-al growth kinetics was successfully described with a logistic model, and simulation of a continuous culture under the optimum growth conditions (30 degrees C, 12 klux and 1.18 g-cells/L) showed that the algal CO2-fixation activity could reach 0.66 g- CO2/(L X d). Under the same growth conditions, eicosapentaenoic acid (20:5 n-3, EPA) and arachidonic acid (20:4 n-6, ARA) yields were similarly calculated to be 3.6 mg-EPA/(L X d) and 6.5 mg-ARA/(L X d), respectively.

KEYWORDS: CULTIVATION, GROWTH, LIGHT-INTENSITY, TEMPERATURE

21

Akin, D.E., B.A. Kimball, J.R. Mauney, R.L. Lamorte, G.R. Hendrey, K. Lewin, J. Nagy, and R.N. Gates. 1994. Influence of enhanced co2 concentration and irrigation on sudangrass digestibility. *Agricultural and Forest Meteorology 70(1-4):279-287.*

An experimental line of sudangrass (Sorghum bicolor L. Moench) was included in the free-air CO2 enrichment (FACE) project in 1991 at the University of Arizona Maricopa Agricultural Center to evaluate the effect of ambient (approximately 370 mumol mol- 1) and enriched (550 mumol mol-1) CO2 in well-watered or water- stressed plots. Our specific objective was to determine modifications caused by these environmental effects on the percentages of morphological parts and the fiber components, and on the in vitro digestibility in vegetative and mature harvests. Enrichment with CO2 did not ($P > 0.05$) change the percentages of morphological parts or fiber components, or the digestibility of any of the morphological components. Protein levels tended to be lower in CO2-enriched plants. However, water-stressed plants tended to have a higher proportion of leaves (blades and sheaths) and a lower proportion of stems, were more digestible, and had lower amounts of anti-quality, aromatic compounds within the plant cell. Stems had the highest digestibility of all morphological components (about 75% in vegetative plants) despite the lowest levels of protein. Stems also showed the greatest changes caused by all treatments, including a 20% decline in digestibility from vegetative to mature samples. The results indicate that enriching CO2 to 550 mumol mol-1 did not reduce digestibility of sudangrass.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT

22

Akin, D.E., B.A. Kimball, W.R. Windham, P.J. Pinter, G.W. Wall, R.L. Garcia, R.L. Lamorte, and W.H. Morrison. 1995. Effect of free-air co2 enrichment (face) on forage quality of wheat. *Animal Feed Science and Technology 53(1):29-43.*

Wheat (Triticum aestivum L., cultivar 'Yecora rojo') was grown in ambient (370 mu mol mol(-1)) or enriched (550 mu mol mol(- 1)) concentrations of CO2 in the free-air CO2 enrichment (FACE) project, and components were analyzed for in vitro digestibility, fiber constituents, and crude protein. Four replicated plots of each CO2 treatment were split for irrigation: 'wet' regions received 60 cm of water and 'dry' regions received 30 cm of water through underground tubes. Enriched CO2 concentrations had no effect on in vitro digestion of intact sections of young (26-32-day-old plants) leaf blades except at 24-27 h incubation, at which time enriched leaves were lower in digestibility than control ones. Enriched CO2 concentrations increased the content of acid detergent fiber (ADF) and cellulose of young wet leaves, Sections of main shoots at 26 days tended to have increased digestibility with elevated CO2 levels. Enriched CO2 concentrations did not alter the digestibility of flag leaves from 105-day-old plants or of flag leaves, uppermost stems, and sheaths from plants at full grain maturity, Enriched CO2 levels reduced the acid detergent lignin (ADL) and tended to reduce the protein of leaves from 105-day-old plants. For mature leaf blades, neutral detergent fiber, ADF, and cellulose were, or tended to be, higher while protein content tended to be lower in elevated CO2-grown plants; for both CO2 treatments, 'dry' leaves were higher in digestibility and lower in ADL than 'wet' samples. Mature stems plus sheaths had lower protein contents in plants grown in elevated CO2. Results indicated that enriched CO2 concentrations to 550 mu mol mol(-1) did not substantially alter wheat in vitro digestibility, regardless of irrigation treatment. Elevated CO2 altered fiber components and protein, but these were not consistent among parts and harvests.

KEYWORDS: CELL-WALLS, ECOSYSTEMS, MICROSPECTROPHOTOMETRY, PHENOLIC CONSTITUENTS

23

Akin, D.E., L.L. Rigsby, G.R. Gamble, W.H. Morrison, B.A. Kimball, P.J. Pinter, G.W. Wall, R.L. Garcia, and R.L. Lamorte. 1995. Biodegradation of plant-cell walls, wall carbohydrates, and wall aromatics in wheat grown in ambient or enriched co2 concentrations. *Journal of the Science of Food and Agriculture 67(3):399-406.*

Mature internodes from wheat (Triticum aestivum L) grown in control (ambient at c 370 mu mol mol(-1)) or enriched (to 550 mu mol mol(-1)) concentrations of atmospheric CO2 in the free- air CO2 enrichment (FACE) system were analyzed for potential changes in biodegradation of constituents due to predicted increases in atmospheric levels of CO2. The first internodes below the grain were incubated with the lignocellulose- degrading white rot fungus, Phanerochaete chrysosporium K-3, or incubated without microorganisms. Plant samples were then analyzed for dry weight loss, disposition of specific cell types to biodegradation using electron microscopy, carbohydrates and lignin using solid state NMR spectroscopy, and ester- and ether-linked aromatics using gas chromatography. Phanerochaete chrysosporium extensively degraded stems cells (c 75%) and both carbohydrate and aromatic portions of the wheat stems proportionately more carbohydrates were removed by the fungus from the stems. Enriched CO2 did not affect the chemical composition of wheat stems or the biodegradation by P chrysosporium of plant cell walls or wall components for the most part. Data from various methods all indicated that enriched CO2 did not substantially alter the biodegradation of wheat cell wall internodes or wall components. Evidence was not found for an influence on C cycling due to CO2 concentrations in this study.

KEYWORDS: ECOSYSTEMS, LIGNINS, PHENOLIC CONSTITUENTS

24

Alagusundaram, K., D.S. Jayas, N.D.G. White, W.E. Muir, and R.N. Sinha. 1995. Controlling cryptolestes-ferrugineus (stephens) adults in wheat stored in bolted-metal bins using elevated carbon-dioxide. *Canadian Agricultural Engineering 37(3):217-223.*

Experiments were conducted in two 5.56 m-diameter farm bins to determine the mortality of caged adult rusty grain beetles, Cryptolestes ferrugineus (Stephens) (Coleoptera: cucujidae), under elevated carbon dioxide (CO2) concentrations. The bins were filled with wheat to a depth of 2.5 m. Dry ice was used to create high CO2 concentrations in the wheat bulks. Two different modes of application of dry ice were used: (i) pellets on the grain surface and in the aeration duct and (ii) pellets on the grain surface and blocks in insulated boxes on the grain surface. The pellets exposed to the ambient conditions on the grain surface and in the aeration duct sublimated quickly and had to be replenished at frequent intervals. Dry ice blocks in insulated boxes, however, maintained high CO2 concentrations without replenishment for over 15 d. In both modes of application, the observed CO2 concentrations in the intergranular gas were about 15% and 30% (all the CO2 concentrations given in this article are on a volume basis) at 2.05 m and 0.55 m above the floor, respectively. At 0.55 m above the floor, the mortality of rusty grain beetle adults was more than 90% while in the top portions of the bulk (2.05 m above the floor) the mortality was only 30%. On an average about two thirds of the insects were killed. The use of controlled atmosphere treatment within an integrated pest management context is outlined.

KEYWORDS: INSECTS

25

Alberto, A.M.P., L.H. Ziska, C.R. Cervancia, and P.A. Manalo. 1996. The influence of increasing carbon dioxide and temperature on competitive interactions between a C3 crop, rice (Oryza sativa) and a C-4 weed (Echinochloa glabrescens). *Australian Journal of Plant Physiology 23(6):795-802.*

Many of the most troublesome weeds in agricultural systems are C-4 plants. As atmospheric CO2 increases it is conceivable that competitive ability of these weeds could be reduced relative to C-3 crops such as rice. At the International Rice Research Institute (IRRI) in the Philippines, rice (IR72) and one of its associated C-4 weeds, Echinochloa glabrescens, were grown from seeding to maturity using replacement series mixtures (100:0, 75:25, 50:50, 25:75, and 0:100, % rice:%weed) at two different CO2 concentrations (393 and 594 mu L L(-1)) in naturally sunlit glasshouses. Since increasing CO2 may also result in elevated growth temperatures, the response of rice to each CO2 concentration was also examined at day/night temperatures of 27/21 and 37/29 degrees C. At 27/21 degrees C, increasing the CO2 concentration resulted in a significant increase in above ground biomass (+47%) and seed yield (+55%) of rice when averaged over all mixtures. For E. glabrescens, the C-4 species, no significant effect of CO2 concentration on biomass or yield was observed. When grown in mixture, the proportion of rice biomass increased significantly relative to that of the C- 4 weed at all mixtures at elevated CO2. Evaluation of changes in competitiveness (by calculation of plant relative yield (PRY) and replacement series diagrams) of the two species demonstrated that, at elevated CO2, the competitiveness of rice was increased relative to that of E. glabrescens. However, at the higher growth temperature (37/29 degrees C), growth and reproductive stimulation of rice by elevated CO2 was reduced compared to the lower growth temperature. This resulted in a reduction in the proportion of rice:weed biomass present in all

mixtures relative to 27/21 degrees C and a greater reduction in PRY in rice relative to E. glabrescens. Data from this experiment suggest that competitiveness could be enhanced in a C-3 crop (rice) relative to a C-4 weed (E. glabrescens) with elevated CO2 alone, but that simultaneous increases in CO2 and temperature could still favour a C-4 species.

KEYWORDS: DRY-MATTER, ENRICHMENT, GROWTH, NITROGEN, PLANTS, WHEAT

26

Alcamo, J., G.J.J. Kreileman, M.S. Krol, and G. Zuidema. 1994. Modeling the global society-biosphere-climate system .1. Model description and testing. *Water, Air, and Soil Pollution 76(1-2):1-35.*

This paper describes the IMAGE 2.0 model, a multi-disciplinary, integrated model designed to simulate the dynamics of the global society-biosphere-climate system. The objectives of the model are to investigate linkages and feedbacks in the system, and to evaluate consequences of climate policies. Dynamic calculations are performed to year 2100, with a spatial scale ranging from grid (0.5-degrees x 0.5-degrees latitude- longitude) to world regional level, depending on the sub-model. The model consists of three fully linked sub-systems: Energy- Industry, Terrestrial Environment, and Atmosphere-Ocean. The Energy-Industry models compute the emissions of greenhouse gases in 13 world regions as a function of energy consumption and industrial production. End use energy consumption is computed from var-ious economic/demographic driving forces. The Terrestrial Environment models simulate the changes in global land cover on a grid-scale based on climatic and economic factors, and the flux of CO2 and other greenhouse gases from the biosphere to the atmosphere. The Atmosphere-Ocean models compute the buildup of greenhouse gases in the atmosphere and the resulting zonal-average temperature and precipitation patterns. The fully linked model has been tested against data from 1970 to 1990, and after calibration can reproduce the following observed trends: regional energy consumption and energy-related emissions, terrestrial flux of CO2 and emissions of greenhouse gases, concentrations of greenhouse gases in the atmosphere, and transformation of land cover. The model can also simulate long term zonal average surface and vertical temperatures.

KEYWORDS: CARBON-CYCLE, CO2, SENSITIVITY

27

Alcamo, J., G.J. Vandenborn, A.F. Bouwman, B.J. Dehaan, K.K. Goldewijk, O. Klepper, J. Krabec, R. Leemans, J.G.J. Olivier, A.M.C. Toet, H.J.M. Devries, and H.J. Vanderwoerd. 1994. Modeling the global society-biosphere-climate system .2. Computed scenarios. *Water, Air, and Soil Pollution 76(1-2):37-78.*

This paper presents scenarios computed with IMAGE 2.0, an integrated model of the global environment and climate change. Results are presented for selected aspects of the society- biosphere-climate system including primary energy consumption, emissions of various greenhouse gases, atmospheric concentrations of gases, temperature, precipitation, land cover and other indicators. Included are a "Conventional Wisdom" scenario, and three variations of this scenario: (i) the Conventional Wisdom scenario is a reference case which is partly based on the input assumptions of the IPCC's IS92a scenario; (ii) the "Biofuel Crops" scenario assumes that most biofuels will be derived from new cropland; (iii) the "No Biofuels" scenario examines the sensitivity of the system to the use of biofuels; and (iv) the "Ocean Realignment" scenario investigates the effect of a large-scale change in ocean circulation on the biosphere and climate. Results of the biofuel scenarios illustrate the importance of examining the impact of biofuels on the full range of greenhouse gases, rather than only CO2. These scenarios also indicate possible side effects of the land requirements for energy crops. The Ocean Realignment scenario shows that an unexpected, low probability event can both enhance the build-up of greenhouse gases, and at the same time cause a temporary cooling of surface air temperatures in the Northern Hemisphere. However, warming of the atmosphere is only delayed, not avoided.

28

Allen, D.J., I.F. McKee, P.K. Farage, and N.R. Baker. 1997. Analysis of limitations to CO2 assimilation on exposure of leaves of two Brassica napus cultivars to UV-B. *Plant, Cell and Environment 20(5):633-640.*

Apex and Bristol cultivars of oilseed rape (Brassica napus) were irradiated with 0.63 W m(-2) of UV-B over 5 d. Analyses of the response of net leaf carbon assimilation to intercellular CO2 concentration were used to examine the potential limitations imposed by stomata, carboxylation velocity and capacity for regeneration of ribulose 1,5-bisphosphate on leaf photosynthesis. Simultaneous measurements of chlorophyll fluorescence were used to estimate the maximum quantum efficiency of photosystem II (PSII) photochemistry, the quantum efficiency of linear electron transport at steady-state photosynthesis, and the light and CO2-saturated rate of linear electron transport. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) content and activities were assayed in vitro. In both cultivars the UV-B treatment resulted in decreases in the light-saturated rate of CO2 assimilation, which were accompanied by decreases in carboxylation velocity and Rubisco content and activity. No major effects of UV-B were observed on end-product inhibition and stomatal limitation of photosynthesis or the rate of photorespiration relative to CO2 assimilation. In the Bristol cultivar, photoinhibition of PSII and loss of linear electron transport activity were observed when CO2 assimilation was severely inhibited, However, the Apex cultivar exhibited no major inhibition of PSII photochemistry or linear electron transport as the rate of CO2 assimilation decreased. It is concluded that loss of Rubisco is a primary factor in UV-B inhibition of CO2 assimilation.

KEYWORDS: ENHANCED RADIATION, HIGHER-PLANTS, ORYZA-SATIVA, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PHOTOSYSTEM, PISUM-SATIVUM, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, ULTRAVIOLET-RADIATION, VIGNA-SINENSIS L

29

Allen, L.H. 1992. Free-air co-2 enrichment field experiments - an historical overview. *Critical Reviews in Plant Sciences 11(2-3):121-134.*

KEYWORDS: CARBON DIOXIDE, CO2, COTTON, CROPS, FUMIGATION, GROWN SOYBEANS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SULFUR-DIOXIDE, SYSTEM

30

Allen, L.H., E.C. Bisbal, and K.J. Boote. 1998. Nonstructural carbohydrates of soybean plants grown in subambient and superambient levels of CO2. *Photosynthesis Research 56(2):143-155.*

Elevated carbon dioxide (CO2) concentration increases plant photosynthesis, biomass and carbohydrate accumulation. Since plants have grown in low CO2 (200 to 300 mu mol mol(-1)) for the last several million years, how will they use extra photoassimilate as the atmospheric CO(2)continues to rise? The objectives were to determine the effects of past, present and projected future levels of CO2 on diurnal and seasonal patterns of total nonstructural carbohydrate (TNC) concentration of soybean [Glycine max (L.) Merr.] tissues. Plants were grown at 160, 220, 280, 330, 660 and 990 mu mol mol(-1) CO2 in outdoor, sunlit chambers wherein CO2 uptake rates were measured continuously. Early morning and fate afternoon plant samples were taken at eight dates. The

TNC concentration of leaves, petioles and stems increased as CO:! increased. Canopy photosynthetic rates also increased with increasing CO2, apparently without any negative impact of increased leaf TNC. Concentrations of TNC in all vegetative tissues were lower in the morning than the afternoon, which indicates overnight mobilization and utilization of carbohydrates for growth processes. The concentration of TNC was lowest in ail plant components during rapid vegetative growth at Vg to R2 developmental stages. Leaves of all plants, especially those grown in superambient CO2, contained large pools of TNC at plant maturity, which indicated that not all of the reserves were utilized for seed yield. Soybean cultivars for the future should be designed to utilize carbohydrates more readily for seed production so that greater benefit can be realized from rising atmospheric CO2.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, EXPORT, L MERR PLANTS, LEAF, LEAVES, LIGHT, PHOTOSYNTHETIC RESPONSE, REPRODUCTIVE GROWTH, STARCH CONCENTRATION, TEMPERATURE

31

Allen, L.H., E.C. Bisbal, K.J. Boote, and P.H. Jones. 1991. Soybean dry-matter allocation under subambient and superambient levels of carbon-dioxide. *Agronomy Journal 83(5):875-883.*

Rising atmospheric carbon dioxide concentration [CO2] is expected to cause increases in crop growth and yield. The objective of this study was to investigate effects of subambient, as well as superambient, [CO2] on soybean [Glycine max (L.) Merr.] dry matter production and allocation for two reasons: to assess response of plants to prehistoric as well as future expected CO2 levels and to increase confidence in [CO2] response curves by imposing a wide range of [CO2] treatments. Soybean was grown in outdoor, sunlit, controlled- environment chambers at CO2 levels of 160, 220, 280, 330, 660, and 990-mu-mol (CO2) mol-1 (air). Total dry matter growth rates during the linear phase of vegetative growth were 5.0, 8.4, 10.9, 12.5, 18.2, and 20.7 g m-2 d-1 for the above respective [CO2]. Samples taken from 24 to 94 d after planting showed that the percentage of total plant mass in leaf trifoliolates decreased with increasing [CO2] whereas the percentage in structural components (petioles and stems) increased. At final harvest the respective [CO2] treatments resulted in 38, 53, 62, 100, 120, and 92% seed yield with respect to the 330-mu-mol mol-1 treatment. Total dry weight responses were similar. Late season spider mite damage of the 990 and 280-mu-mol mol-1 treatments reduced yields. These data confirm not only that rising CO2 should increase plant growth, but also that plant growth was probably seriously limited by atmospheric [CO2] in preindustrial revolution times back to the previous global glaciation.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CHAMBERS, DEVELOPMENTAL STAGES, PHOTOSYNTHESIS, PLANT GROWTH, TRANSPIRATION RESPONSES, WATER-USE, WEIGHT, YIELD

32

Allen, L.H., B.G. Drake, H.H. Rogers, and J.H. Shinn. 1992. Field techniques for exposure of plants and ecosystems to elevated co-2 and other trace gases. *Critical Reviews in Plant Sciences 11(2-3):85-119.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON-DIOXIDE CONCENTRATIONS, ESTUARINE MARSH, OPEN-AIR FUMIGATION, OPEN-TOP CHAMBERS, PORTABLE CHAMBER, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES, VENTILATED CHAMBER, WATER-VAPOR EXCHANGE

33

Allen, L.H., R.R. Valle, J.W. Jones, and P.H. Jones. 1998. Soybean leaf water potential responses to carbon dioxide and drought. *Agronomy Journal 90(3):375-383.*

Rising CO2 can have direct effects on crop water relations and indirect effects on water available for growth. We studied the effects of elevated CO2 and drought on leaf water relations of soybean [Glycine max (L.) Merr. cv. Bragg] and considered the hypothesis of osmotic adjustment mediated by increased photosynthesis (Hypothesis 1) vs. the hypothesis of water conservation mediated by decreased stomatal conductance (Hypothesis 2) to explain improved water relations of plants growing under elevated CO2. In Exp. 1, soybean was grown at 330, 450, 660, and 800 mu mol mol(-1) CO2 in sunlit, closed- circulation, controlled-environment chambers under well-watered conditions. Leaf total water potential (WP), osmotic potential (OP), and turgor potential (TP) were measured at midday during V4 to R6 stages of development. In Exp. 2 (well-watered, R1-R3) and Exp. 3 (13-d drying cycle, R6 seed filling), soybean was grown at 330 and 660 mu mol mol(-1) CO2 and WP, OP, and TP were measured five times per day on sunlit and shaded leaves. In Exp. 3, stomatal conductance (g(s)) and transpiration rate (TR) of leaves were also measured. Experiments 1 and 2 showed that elevated CO2 increased TP and decreased OP, but did not affect leaf WP, thus favoring Hypothesis 1. In Exp. 3, leaf WP was higher in elevated than ambient CO2. Diurnal TP was higher in elevated than ambient CO2 at the beginning of drought, and was maintained longer each day as drought progressed. At the end of drought, TP and WP was higher in elevated than ambient CO2. Elevated CO2 leaves had lower TR because of lower g(s) than ambient CO2 counterparts. Thus, Exp. 3 supported Hypothesis 2, that both stressed and nonstressed plants in elevated CO2 have a better water status (e.g., higher TP) than plants in ambient CO2 due to water conservation mediated by decreased g(s). Remobilization of leaf nutrients during seed filling may limit the capability for osmotic adjustment. Regardless of the mechanisms, growth of plants in elevated CO2 should be less affected by drought than plants in ambient CO2.

KEYWORDS: DIFFERENT CO2 ENVIRONMENTS, FIELD, LEAVES, MAIZE, NITROGEN, OSMOTIC ADJUSTMENT, PLANT GROWTH, STRESS, USE EFFICIENCY, YIELD

34

Allen, L.H., R.R. Valle, J.W. Mishoe, and J.W. Jones. 1994. Soybean leaf gas-exchange responses to carbon-dioxide and water-stress. *Agronomy Journal 86(4):625-636.*

As global carbon dioxide concentrations rise, we need to understand the combination of direct effects of this gas and the anticipated effects of climate change, including drought, on physiology and growth of all crops. Effects Of CO2 on plants begin at the leaf level; our objectives, therefore, were to determine interrelationships among factors governing gas exchange responses of soybean [Glycine max (L.) Merr.] leaves to elevated CO2 and water stress. Photosynthetic CO2 assimilation and transpiration rates were measured in cuvettes on leaflets of soybean (cv. Bragg) grown in controlled- environment chambers at 330 and 660 mumol CO2 Mol-1 air. Leaflets at high CO2, either water-stressed or well-watered, had higher photosynthetic and lower transpiration rates, and therefore higher water-use efficiencies (WUE), than those at Control CO2 levels. As irrigation was withheld during an 11-d period, WUE decreased about 30 to 50% with respect to the well- watered treatments. Midday leaf temperature and leaf-to-air vapor pressure gradient levels increased as the water stress progressed. For water stress treatments, midday leaf conductance (G(lw)) was generally higher and residual internal conductance (G(r)) was generally lower in low than in high CO2. Ratios of midday G(r)/G(lc), were nearly constant throughout the period in both the stressed and the well-watered treatments. The ratios of intercellular C(i), to ambient C(a), CO2 concentration (i.e., C(i)/C(a)) during the water stress period remained similar to the respective nonstressed treatments within each CO2 level. These findings support the concept that leaf conductances are governed by CO2 assimilation rates under water-stressed as well as unstressed conditions.

KEYWORDS: ABSCISIC- ACID, CARBOXYLASE, DIFFERENT CO2 ENVIRONMENTS, FIELD, GROWTH, LEAVES, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION RATE, WHEAT

35

Allen, L.H., R.R. Valle, J.W. Mishoe, J.W. Jones, and P.H. Jones. 1990. Soybean leaf gas-exchange responses to CO2 enrichment. *Soil and Crop Science Society of Florida Proceedings 49:192-198.*

36

Almeida, J.P.F., A. Luscher, M. Frehner, A. Oberson, and J. Nosberger. 1999. Partitioning of P and the activity of root acid phosphatase in white clover (Trifolium repens L.) are modified by increased atmospheric CO2 and P fertilisation. *Plant and Soil 210(2):159-166.*

The growth response of white clover (Trifolium repens L.) to the expected increase in atmospheric partial pressure of CO2 (p(CO2)) may depend on P availability. A decrease in the rate of transpiration due to increased p(CO2) may reduce the amount of P transported to the shoot, thereby causing a change in the partitioning of P between the root and shoot. To test these hypotheses, four concentrations of P in the nutrient solution, combined with two p(CO2) treatments, were applied to nodulated white clover plants. Compared to ambient p(CO2) (35 Pa), twice ambient p(CO2) (70 Pa) reduced the rate of transpiration but did not impair the total P uptake per plant. However, at twice ambient p(CO2) and a moderate to high supply of P, concentrations of structural P and soluble P (Pi) were lower in the leaves and higher in the roots. The activity of root acid phosphatase was lower at twice ambient p(CO2) than at ambient p(CO2); it depended on the Pi concentration in the roots. At the highest P concentration, twice ambient p(CO2) stimulated photosynthesis and the growth rate of the plant without affecting the concentration of nonstructural carbohydrates in the leaves. However, at the lower P concentrations, plants at twice ambient p(CO2) lost their stimulation of photosynthesis in the afternoon, they accumulated nonstructural carbohydrates in the leaves and their growth rate was not stimulated; indicating C-sink limitation of growth. P nutrition will be crucial to the growth of white clover under the expected future conditions of increased p(CO2).

KEYWORDS: AIR, BEAN-PLANTS, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, MAGNESIUM-DEFICIENCY, PHOSPHORUS, SOURCE-SINK RELATIONS, SUBTERRANEUM L

37

Alvarez, R., M. Alconada, and R. Lavado. 1999. Sewage sludge effects on carbon dioxide-carbon production from a desurfaced soil. *Communications in Soil Science and Plant Analysis 30(13-14):1861-1866.*

Desurfaced soils are found near cities in the Pampean Region of Argentina because A horizons were used for brick production. These soils are not suitable for agriculture. Application of sewage sludge is a tool for improving soil productivity, but its effects on the environment are not thoroughly understood. Production of carbon dioxide (CO2)-carbon (C) in the field from a desurfaced soil in which 25 Mg dry matter ha(-1) of sewage sludge were applied the first year and 10 Mg dry matter ha(-1), the second year was evaluated during a corn (Zea mays L.) growing cycle. Microbial biomass and metabolic activity were also measured. Sludge applications produced an increase of the CO2-C efflux in the field of 30-50% during summer. Microbial biomass was not affected by sludge some months after the application, but metabolic activity and organic matter mineralization were enhanced. The increase of the CO2-C emission from the soil represented 21% of the sludge C applied the year of the experiment and 15% of the C applied the year before. Consequently, an important quantity of the sludge C was retained in the soil.

KEYWORDS: CROPS, GLUCOSE, HEAVY-METALS, MAIZE, MANURE, MICROBIAL BIOMASS DYNAMICS, RESIDUE

38

Ambus, P., and G.P. Robertson. 1999. Fluxes of CH4 and N2O in aspen stands grown under ambient and twice-ambient CO2. *Plant and Soil 209(1):1-8.*

Elevated atmospheric CO2 has the potential to change below- ground nutrient cycling and thereby alter the soil-atmosphere exchange of biogenic trace gases. We measured fluxes of CH4 and N2O in trembling aspen (Populus tremuloides Michx.) stands grown in open-top chambers under ambient and twice-ambient CO2 concentrations crossed with `high' and low soil-N conditions. Flux measurements with small static chambers indicated net CH4 oxidation in the open-top chambers. Across dates, CH4 oxidation activity was significantly (P < 0.05) greater with ambient CO2 (8.7 mu g CH4-C m(-2) h(-1)) than with elevated CO2 (6.5 mu g CH4-C m(-2) h(-1)) in the low N soil. Likewise, across dates and soil N treatments CH4 was oxidized more rapidly (P < 0.05) in chambers with ambient CO2 (9.5 mu g CH4-C m(-2) h(-1)) than in chambers with elevated CO2 (8.8 mu g CH4-C m(-2) h(-1)). Methane oxidation in soils incubated in serum bottles did not show any response to the CO2 treatment. We suggest that the depressed CH4 oxidation under elevated CO2 in the field chambers is due to soil moisture which tended to be higher in the twice-ambient CO2 treatment than in the ambient CO2 treatment. Phase I denitrification (denitrification enzyme activity) was 12-26% greater under elevated CO2 than under ambient CO2 in the `high' N soil; one sampling, however, showed a 39% lower enzyme activity with elevated CO2. In both soil N treatments, denitrification potentials measured after 24 or 48 h were between 11% and 21% greater (P < 0.05) with twice- ambient CO2 than with ambient CO2. Fluxes of N2O in the open- top chambers and in separate 44 cm(2) cores +/-N fertilization were not affected by CO2 treatment and soil N status. Our data show that elevated atmospheric CO2 may have a negative effect on terrestrial CH4 oxidation. The data also indicated temporary greater denitrification with elevated CO2 than with ambient CO2. In contrast, we found no evidence for altered fluxes of N2O in response to increases in atmospheric CO2.

KEYWORDS: ATMOSPHERIC METHANE CONSUMPTION, DENITRIFICATION, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GAS FLUXES, GRASSLAND, NITROUS-OXIDE, RESPONSES, TALLGRASS PRAIRIE, TEMPERATE FOREST SOILS

39

Amiro, B.D., J.I. MacPherson, and R.L. Desjardins. 1999. BOREAS flight measurements of forest-fire effects on carbon dioxide and energy fluxes. *Agricultural and Forest Meteorology 96(4):199-208.*

Fire is the dominant stand-replacing agent in the Canadian boreal forest, but few quantitative measurements are available on the micrometeorological effects of fire. Airborne flux measurements during the BOREAS experiment were referenced to age of burn along a 500-km transect through Saskatchewan and Manitoba, Canada. These data for 1-, 5-, and 7-year-old burns were supplemented with 15- and 30-year-old-burn data from the BOREAS northern study site near Thompson, Manitoba. Data were available near midday only and included the June, July and September campaigns during 1994, and July of 1996. Surface radiometric temperature increased by up to 6 degrees C and remained elevated even 15 years after fire. Net radiation was largely unaffected whereas albedo decreased in the first year post-fire but recovered by the fifth year. Sensible heat flux increased by 10-20% for the first few years

after the fire and then decreased. Latent heat flux slightly decreased after the fire, causing the Bowen ratio to increase by ca. 50% for 7 years post-fire. The CO2 flux was reduced for the 15-year period after fire with the greatest reduction to ca. 25% of control areas during the year following fire. However, diurnal and annual data are needed to determine the total impact of fire on the boreal-forest carbon balance.

KEYWORDS: ASPEN FOREST, ATMOSPHERE, ECOSYSTEMS, EXCHANGES, MICROBIAL BIOMASS, NORTHERN, PINE FOREST, SOIL RESPIRATION, WATER-VAPOR, WILDFIRE

40

Amoroso, G., C. Weber, D. Sultemeyer, and H. Fock. 1996. Intracellular carbonic anhydrase activities in Dunaliella tertiolecta (Butcher) and Chlamydomonas reinhardtii (Dangeard) in relation to inorganic carbon concentration during growth: Further evidence for the existence of two distinct carbonic anhydrases associated with the chloroplasts. *Planta 199(2):177-184.*

Using mass-spectrometric measurements of O-18 exchange from (CO2)-C-13-O-18 intracellular carbonic anhydrase (CA) activity was investigated in the unicellular green algae Dunaliella tertiolecta and Chlamydomonas reinhardtii which were either grown on air enriched with 5% CO2 (high-C-i cells) or on air (low-C-i cells). In D. tertiolecta high- and low-C-i cells had detectable levels of internal CA activity when measured under in-vivo conditions and this activity could be split up into three distinct forms. One CA was not associated with the chloroplasts, while two isozymes were found to be located within the plastids. The activities of all intracellular CAs were always about twofold higher in low than in high -C-i cells of D. tertiolecta and the chloroplastic enzymes were completely induced within 4 h of adaptation to air. One of the chloroplastic CAs was found to be soluble the other was insoluble. In addition to the physical differences, MgSO4 in vitro caused a more than twofold stimulation of the soluble activity while the insoluble form of CA remained rather unaffected. In C. reinhardtii, MgSO4 increased the soluble CA activity by 346% and the concentration of MgSO4 required for half-maximum stimulation was between 10 and 15 mM. Again, the insoluble CA activity was not affected by MgSO4. Furthermore, the soluble isoenzyme was considerably more sensitive to ethoxyzolamide, a potent inhibitor of CA, than the insoluble enzyme. The concentration of inhibitor causing 50% inhibition of soluble CA activity was 110 and 85 mu M ethoxyzolamide for D. tertiolecta and C. reinhardtii, respectively. From these data we conclude that the two chloroplast-associated CAs are distinct enzymes.

KEYWORDS: CELL-SURFACE, CO2, CYANOBACTERIUM SYNECHOCOCCUS PCC7942, INCREASES, INTACT CHLOROPLASTS, MICROALGAE, O-18 EXCHANGE, PHOTOSYNTHESIS, SALINA, TRANSPORT

41

Amthor, J.S. 1991. Respiration in a future, higher-CO2 world. *Plant, Cell and Environment 14(1):13-20.*

Apart from its impact on global warming, the annually increasing atmospheric [CO2] is of interest to plant scientists primarily because of its direct influence on photosynthesis and photorespiration in C3 species. But in addition, 'dark' respiration, another major component of the carbon budget of higher plants, may be affected by a change in [CO2] independent of an increase in temperature. Literature pertaining to an impact of [CO2] on respiration rate is reviewed. With an increase in [CO2], respiration rate is increased in some cases, but decreased in others. The effects of [CO2] on respiration rate may be direct or indirect. Mechanisms responsible for various observations are proposed. These proposed mechanisms relate to changes in: (1) levels of nonstructural carbohydrates, (2) growth rate and structural phytomass accumulation, (3) composition of phytomass, (4) direct chemical interactions between CO2 and respiratory enzymes, (5) direct chemical interactions between CO2 and other cellular components, (6) dark CO2 fixation rate, and (7) ethylene biosynthesis rate. Because a range of (possibly interactive) effects exist, and present knowledge is limited, the impact of future [CO2] on respiration rate cannot be predicted. Theoretical considerations and types of experiments that can lead to an increase in the understanding of this issue are outlined.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, DARK RESPIRATION, ENERGY OVERFLOW, GAS-EXCHANGE, GROWTH, LEAF, PHOTOSYNTHESIS, PLANTS, TEMPERATURE

42

Amthor, J.S. 1994. Scaling co2-photosynthesis relationships from the leaf to the canopy. *Photosynthesis Research 39(3):321-350.*

Responses of individual leaves to short-term changes in CO2 partial pressure have been relatively well studied. Whole-plant and plant community responses to elevated CO2 are less well understood and scaling up from leaves to canopies will be complicated if feedbacks at the small scale differ from feedbacks at the large scale. Mathematical models of leaf, canopy, and ecosystem processes are important tools in the study of effects on plants and ecosystems of global environmental change, and in particular increasing atmospheric CO2, and might be used to scale from leaves to canopies. Models are also important in assessing effects of the biosphere on the atmosphere. Presently, multilayer and big leaf models of canopy photosynthesis and energy exchange exist. Big leaf models - which are advocated here as being applicable to the evaluation of impacts of 'global change' on the biosphere - simplify much of the underlying leaf-level physics, physiology, and biochemistry, yet can retain the important features of plant- environment interactions with respect to leaf CO2 exchange processes and are able to make useful, quantitative predictions of canopy and community responses to environmental change. The basis of some big leaf models of photosynthesis, including a new model described herein, is that photosynthetic capacity and activity are scaled vertically within a canopy (by plants themselves) to match approximately the vertical profile of PPFD. The new big leaf model combines physically based models of leaf and canopy level transport processes with a biochemically based model of CO2 assimilation. Predictions made by the model are consistent with canopy CO2 exchange measurements, although a need exists for further testing of this and other canopy physiology models with independent measurements of canopy mass and energy exchange at the time scale of 1 h or less.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, LIGHT-INTENSITY, PHOTOSYNTHETIC CO2 FIXATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOURCE-SINK RELATIONS, STOMATAL CONDUCTANCE, SUNFLOWER LEAVES, WATER-USE EFFICIENCY

43

Amthor, J.S. 1995. Predicting effects of atmospheric CO2 partial pressure on forest photosynthesis. *Journal of Biogeography 22(2-3):269-280.*

A mechanistic (i.e. hierarchic or explanatory) model of forest canopy mass and energy exchange that has been previously tested with eddy-correlation measurements in the field - albeit only at present ambient CO2 partial pressure - was used to predict photosynthetic response of a deciduous Quercus-Acer forest in eastern North America to atmospheric CO2 partial pressure. Four partial pressures of CO2 were used in simulations: 28 (pre- industrial), 36 (present), 54 and 72 Pa. This is (one of) the first set(s) of predictions of forest photosynthetic response to

CO2 partial pressure made by a mechanistic forest physiology model shown to accurately predict independent field measurements of whole-forest CO2 exchange at the hourly time scale. The model includes a biochemically based Farquhar-type model of leaf mesophyll CO2 assimilation, which is central to its ability to predict photosynthetic response to different CO2 partial pressures. Whole-forest photosynthesis was positively related to CO2 partial pressure, as expected. This was the case under both clear and cloudy skies, but the relative response to CO2 was greater under a clear sky compared to a cloudy sky (the clear sky day was also warmer). Instantaneous water use efficiency (mel CO2 assimilated per mol H2O transpired) was positively related to atmospheric CO2 partial pressure for all conditions included in the simulations. Model predictions indicate that (1) present forest photosynthesis and water use efficiency may be significantly greater than they were in pre- industrial times (per unit ground area of forest) and (2) future higher CO2 partial pressures could further stimulate forest photosynthesis and water use efficiency, unless future climatic changes have significant negative effects on photosynthesis or acclimation and adaptation processes markedly downregulate photosynthesis in response to greater CO2 partial pressure.

KEYWORDS: C-3 PLANTS, CANOPY, DECIDUOUS FOREST, ELEVATED CO2, GAS-EXCHANGE, GROWTH, MODELS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RISING CO2, SOLAR RADIATION

44

Amthor, J.S. 1995. Terrestrial higher-plant response to increasing atmospheric [co2] in relation to the global carbon-cycle. *Global Change Biology 1(4):243-274.*

Terrestrial higher plants exchange large amounts of CO2 with the atmosphere each year; c. 15% of the atmospheric pool of C is assimilated in terrestrial-plant photosynthesis each year, with an about equal amount returned to the atmosphere as CO2 in plant respiration and the decomposition of soil organic matter and plant litter. Any global change in plant C metabolism can potentially affect atmospheric CO2 content during the course of years to decades. In particular, plant responses to the presently increasing atmospheric CO2 concentration might influence the rate of atmospheric CO2 increase through various biotic feedbacks. Climatic changes caused by increasing atmospheric CO2 concentration may modulate plant and ecosystem responses to CO2 concentration. Climatic changes and increases in pollution associated with increasing atmospheric CO2 concentration may be as significant to plant and ecosystem C balance as CO2 concentration itself. Moreover, human activities such as deforestation and livestock grazing can have impacts on the C balance and structure of individual terrestrial ecosystems that far outweigh effects of increasing CO2 concentration and climatic change. In short-term experiments, which in this case means on the order of 10 years or less, elevated atmospheric CO2 concentration affects terrestrial higher plants in several ways. Elevated CO2 can stimulate photosynthesis, but plants may acclimate and (or) adapt to a change in atmospheric CO2 concentration. Acclimation and adaptation of photosynthesis to increasing CO2 concentration is unlikely to be complete, however. Plant water-use efficiency is positively related to CO2 concentration, implying the potential for more plant growth per unit of precipitation or soil moisture with increasing atmospheric CO2 concentration. Plant respiration may be inhibited by elevated CO2 concentration, and although a naive C balance perspective would count this as a benefit to a plant, because respiration is essential for plant growth and health, an inhibition of respiration can be detrimental. The net effect on terrestrial plants of elevated atmospheric CO2 concentration is generally an increase in growth and C accumulation in phytomass. Published estimations, and speculations about, the magnitude of global terrestrial- plant growth responses to increasing atmospheric CO2 concentration range from negligible to fantastic. Well-reasoned analyses point to moderate global plant responses to CO2 concentration. Transfer of C from plants to soils is likely to increase with elevated CO2 concentrations because of greater plant growth, but quantitative effects of those increased inputs to soils on soil C pool sizes are unknown. Whether increases in leaf-level photosynthesis and short-term plant growth stimulations caused by elevated atmospheric CO2 concentration will have, by themselves, significant long-term (tens to hundreds of years) effects on ecosystem C storage and atmospheric CO2 concentration is a matter for speculation, not firm conclusion. Longterm field studies of plant responses to elevated atmospheric CO2 are needed. These will be expensive, difficult, and by definition, results will not be forthcoming for at least decades. Analyses of plants and ecosystems surrounding natural geological CO2 degassing vents may provide the best surrogates for long-term controlled experiments, and therefore the most relevant information pertaining to long-term terrestrial-plant responses to elevated CO2 concentration, but pollutants associated with the vents are a concern in some cases, and quantitative knowledge of the history of atmospheric CO2 concentrations near vents is limited. On the whole, terrestrial higher-plant responses to increasing atmospheric CO2 concentration probably act as negative feedbacks on atmospheric CO2 concentration increases, but they cannot by themselves stop the fossil-fuel-oxidation-driven increase in atmospheric CO2 concentration. And, in the very long-term, atmospheric CO2 concentration is controlled by atmosphere-ocean C equilibrium rather than by terrestrial plant and ecosystem responses to atmospheric CO2 concentration.

KEYWORDS: DIOXIDE CONCENTRATION, ELEVATED CO2, GAS-EXCHANGE, PARTIAL-PRESSURE, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STOMATAL DENSITY, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

45

Amthor, J.S. 1998. Perspective on the relative insignificance of increasing atmospheric CO2 concentration to crop yield. *Field Crops Research 58(2):109-127.*

Average yield of most crops in many countries increased significantly during the past 50 to 100 years. Although atmospheric CO2 concentration, [CO2](a), also increased during that time period, and although crop growth and yield can respond positively to [CO2](a) increase, yield increases were due mainly to factors other than increasing [CO2](a). Similarly, some yield increases prior to 1900 were also associated primarily with factors other than changes in [CO2](a). In particular, past national average yield increases were the result chiefly of technological advances such as nitrogen fertilization; selection of genotypes with increased harvest index and disease resistance; mechanization of planting, cultivation, and harvesting; and chemical weed and pest control. If technology continues to increase average yields at recent rates, near-future increases in [CO2](a) will have only small impacts on yield in comparison to technology in many countries. Conversely, if future increases in [CO2](a) are the main drivers of future yield increases, those yield increases will be small. These points are demonstrated through a comparison of (i) long-term records of yield, (ii) data from key controlled-[CO2] experiments, and (iii) records of past [CO2](a). Finally, it is noted that continued [CO2](a) increase may bring with it climatic changes that could have negative or positive impacts on future yield.

KEYWORDS: 18TH-CENTURY ENGLAND, AGRICULTURAL PRODUCTIVITY, CARBON DIOXIDE, CLIMATE, ENRICHMENT, PHOTOSYNTHESIS, RESPONSES, SPECULATIONS, TRENDS, WHEAT

46

Amthor, J.S., R.J. Mitchell, G.B. Runion, H.H. Rogers, S.A. Prior, and C.W. Wood. 1994. Energy content, construction cost and

phytomass accumulation of glycine-max (L) merr and sorghum-bicolor (L) moench grown in elevated co2 in the field. *New Phytologist 128(3):443-450.*

Grain sorghum [Sorghum] bicolor (L.) Moench, a C-4 crop] and soybean [Glycine max (L.) Merr. cv. Stonewall, a C-3 crop] plants were grown in ambient (c. 360 mu l l(-1)) and twice- ambient (c. 720 mu l l(-1)) CO2 levels in open-top chambers in soil without root constriction. Plant dry mass, energy content, composition and construction cost (i.e. amount of carbohydrate required to synthesize a unit of plant dry mass) were assessed at the end of the growing season. Elevated CO2 (a) increased phytomass accumulation (kg per plant) in both species, (b) had little affect on energy concentration (MJ kg(-1) plant) but caused large increases in the amount of plant energy per ground area (MJ m(-2) ground), and (c) did not alter specific growth cost (kg carbohydrate kg(-1) plant growth) but greatly increased growth cost per ground area (kg carbohydrate m(-2) ground) because growth was enhanced. For soybean, twice-ambient CO2 resulted in a 50 % increase in the amount of nitrogen and energy in grain (seed plus pod) per ground area. This response to elevated CO2 has important implications for agricultural productivity during the next century because the rate of human population growth is exceeding the rate of increase of land used for agriculture so that future food demands can only be met by greater production per ground area.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LEAVES, MAINTENANCE, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPIRATION, RESPONSES, YIELD

47

Andalo, C., B. Godelle, M. Lefranc, M. Mousseau, and I. TillBottraud. 1996. Elevated CO2 decreases seed germination in Arabidopsis thaliana. *Global Change Biology 2(2):129-135.*

The impact of elevated [CO2] on seed germination was studied in different genotypes of Arabidopsis thaliana from natural populations. Two generations of seeds were studied: the maternal generation was produced in the greenhouse (present-day conditions), the offspring generation was produced in two chambers where the CO2 concentration was either the present atmospheric concentration (about 350 ppm) or elevated (700 ppm). The seeds were tested for proportion of germinated seeds and mean germination time in both chambers to study the impact of elevated [CO2] during seed production and germination. Elevated [CO2] during maturation of seeds on the mother-plants decreased the proportion of germinated seeds, while elevated [CO2] during germination had no effect on the proportion of germinated seeds. However, when seeds were both produced and germinated under elevated [CO2] (situation expected by the end of next century), germination was slow and low. Moreover, the effect of the [CO2] treatment differs among genotypes of Arabidopsis: there is a strong treatment x genotype interaction. This means that there is ample genetic variance for a selective response modiying the effects of high levels of [COP] in natural populations of Arabidopsis thaliana. The outcome at the community level will depend on what seeds are available, when they germinate and the resulting competition following germination.

KEYWORDS: GROWTH, PLANTS

48

Andalo, C., C. Raquin, N. Machon, B. Godelle, and M. Mousseau. 1998. Direct and maternal effects of elevated CO2 on early root growth of germinating Arabidopsis thaliana seedlings. *Annals of Botany 81(3):405-411.*

Individuals of Arabidopsis thaliana, collected in different natural populations, were grown in controlled and elevated CO2 in a glasshouse. Following germination, root growth of progeny of different lines of these populations was studied in control and elevated atmospheric CO2. No significant direct effect of atmospheric CO2 concentration could be demonstrated on root growth. An important parental effect was apparent, namely that root length and branching were decreased in seeds collected from a mother plant which had been grown in elevated CO2. This was correlated with smaller seeds, containing less nitrogen. These parental effects were genetically variable. We conclude that CO2 may affect plant fitness via parental effects on seed size and early root growth and that the genetic variability shown in our study demonstrates that Arabidopsis populations will evolve in the face of this new selective pressure. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELONGATION, ENRICHMENT, PLANT, QUALITY, SEED-GERMINATION, SENECIO-VULGARIS, TEMPERATURE, TRITICUM-AESTIVUM L, WHEAT

49

Anderson, J.M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications 1(3):326-347.*

Current models of climate change predict a reduction of area covered by northern coniferous forests and tundra, and an increase in grasslands. These scenarios also indicate a northerly shift in agricultural regions, bringing virgin soils under cultivation. The direct effects of man on tundra,boreal forest, and temperate grassland ecosystems are likely to result in less carbon mobilization from soils and vegetation than from tropical forests. However, as a consequence of climate change, carbon mineralization rates from arctic and sub-arctic soils could be very rapid under warmer and drier conditions because of low stabilization of soil organic matter (SOM) and enhanced microbial responses to small changes in soil moisture and temperature. Predicting the response of these systems to climate change is complicated where the edaphic environment regulating SOM dynamics is not a direct function of macroclimatic conditions. Grasslands contain a greater proportion of highly stabilized SOM than coniferous forests, distributed over greater depth in the soil profile, which is less susceptible to changes in mineralization rates. It is concluded that short-term responses of soil processes to climate change are more predictable in well-drained grassland and forest soils than in waterlogged soils of the tundra and boreal region. Over longer periods of time, however, plant species and soil types will alter in response to new temperature and moisture regimes above- and belowground interacting with the effects of carbon enrichment and changes in nutrient availability. The dynamics of these plant-soil interactions and the future status of soils in different life zones as sources or sinks of carbon is poorly understood. More data are also needed on the distribution of waterlogged forest soils in the boreal zone and responses to warming, which include the production of methane as well as CO2. The primary recommendation for future research is for integrated studies on plant and soil processes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DOUGLAS-FIR, LEAF-LITTER DECOMPOSITION, LONG-TERM DECOMPOSITION, NITROGEN-AVAILABILITY, NORTHERN HARDWOODS, SCOTS PINE FOREST, SOIL ORGANIC MATTER, SPRUCE-LICHEN WOODLAND, TEMPERATE ECOSYSTEMS

50

Anderson, P.D., and P.T. Tomlinson. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO2 and water stress - I. Carbon assimilation and biomass production. *New Phytologist 140(3):477-491.*

The interactive influences of elevated carbon dioxide, water stress, and ontogeny on carbon assimilation and biomass production were

investigated in northern red oak, a species having episodic shoot growth characteristics. Seedlings were grown from acorns through three shoot-growth hushes (8-11 wk) in controlled-environment chambers at 400, 530 or 700 mu mol mol(-1) CO2 and under well watered or water-stressed soil- moisture regimes. Increasing CO2 growth concentration from 400 to 700 mu mol mol(-1) resulted in a 34 % increase in net assimilation rate (A), a 31 % decrease in stomatal conductance to water vapour (g(s)) and a 141 % increase in water use efficiency (WUE) in well watered seedlings. In contrast, water- stressed seedlings grown at 700 mu mol mol(-1) CO2 demonstrated a 69 % increase in A, a 23 % decrease in g(s), and a 104 % increase in WUE. However, physiological responses to increased CO2 and water stress were strongly modified by ontogeny. During active third-flush shoot growth, A in first-flush and second- flush foliage of water-stressed seedlings increased relative to the quiescent phase following cessation of second-flush growth by an average of 115 %; g(s) increased by an average of 74 %. In contrast, neither A nor gs in comparable foliage of well watered seedlings changed in response to active third-flush growth. Whereas seedling growth was continuous through three flushes in well watered seedlings, growth of water-stressed seedlings was minimal following the leaf-expansion stage of the third flush. Through three growth flushes total seedling biomass and biomass allocation to root, shoot and foliage components were very similar in water-stressed seedlings grown at 700 mu mol mol(-1) CO2 and well watered seedlings grown at 400 mu mol mol(-1) CO2. Enhancement effects of elevated CO2 on seedling carbon (C) assimilation and biomass production may offset the negative impact of moderate water stress and are likely to be determined by ontogeny and stress impacts on carbon sink demand.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE ENRICHMENT, DROUGHT, GAS-EXCHANGE, GROWTH-RESPONSE, LEAVES, PHOTOSYSTEM, QUERCUS-RUBRA L, RISING CO2, USE EFFICIENCY

51

Andersson, N.E. 1991. The influence of constant and diurnally changing CO2 concentrations on plant-growth and development. *Journal of Horticultural Science 66(5):569-574.*

Plants of Ficus benjamina and miniature rose (Rosa hybrida cv. Red Minimo) were grown under four CO2 treatments. Two had constant CO2 levels (600 and 900 ppm) and the other two had diurnal changes in CO2 levels, one increasing from 600 to 1500 ppm and one decreasing from 1500 to 600 ppm, each in four steps of 300 ppm during the day-time. In all treatments 900 ppm CO2 was maintained during the night when supplementary light was used, except in the treatment with constant 600 ppm where 600 ppm was also continued throughout the night. Plant growth was monitored under both decreasing and increasing natural daylength and irradiance. The tallest plants and greatest increment in height for Ficus occurred with plants grown under constant CO2 concentration at 600 ppm and also with increasing CO2 concentration. In both experiments the dry weight per pot was lowest when plants were grown under a constant CO2 concentration at 900 ppm. In both experiments with miniature roses the number of flower buds was significantly increased under diurnally changing CO2 concentration or when the CO2 level was constant at 600 ppm compared with a constant 900 ppm. Time to flowering was decreased by constant CO2 at 900 ppm as compared with the other treatments.

KEYWORDS: ATMOSPHERES, CARBON-DIOXIDE ENRICHMENT, DURATION, EXCHANGE, LIGHT-INTENSITY, ROSE, YIELD

52

Andrade, J.L., and P.S. Nobel. 1996. Habitat, CO2 uptake and growth for the CAM epiphytic cactus Epiphyllum phyllanthus in a Panamanian tropical forest. *Journal of Tropical Ecology 12:291-306.*

In the tropical forest of Barro Colorado Island, habitat characteristics, diel acidity changes, CO2 uptake and growth were investigated for the epiphytic cactus Epiphyllum phyllanthus (L.) Haw. It occurred most frequently in tree cavities with its roots in canopy soil and was especially abundant on two tree species: Platypodium elegans J. Vogel and Tabebuia guayacan (Seem.) Hemsl. Its maximum net CO2 uptake rates were low under natural conditions (1.4 mu mol m(-2) s(- 1)) but were comparable to those of other CAM and C-3 epiphytes under wet conditions in a screenhouse. Under both natural conditions and in the screenhouse, partial shade enhanced growth and CAM activity. When plants grew under a photosynthetic photon flux of c. 4 mol m(-2) d(-1), their nocturnal acidity increase and total net CO2 uptake were twice as much as for plants growing at lower (an average of 2.4 mol m(-2) d(-1)) and higher (7.7 mol m(-2) d(-1)) photosynthetic photon fluxes. Stem elongation was 27% greater at the intermediate photosynthetic photon flux. Seedlings of E. phyllanthus survived three months of drought and responded rapidly to rewetting, recovering fully within three days. Transpiration rates and nocturnal acidity increases also recovered to the values of well-watered plants a few days after rewetting, indicating that this species can take advantage of episodic rainfall during the dry season.

KEYWORDS: ACCUMULATION, C-3 BROMELIADS, COMPARATIVE ECOPHYSIOLOGY, CRASSULACEAN ACID METABOLISM, LEAF, OPUNTIA FICUS INDICA, SHADE, VASCULAR EPIPHYTES

53

Andre, M., and H. Ducloux. 1993. Interaction of co2 enrichment and water limitations on photosynthesis and water efficiency in wheat. *Plant Physiology and Biochemistry 31(1):103-112.*

Wheat plants (Triticum aestivum L. cv. Capitole) were grown in twin closed growth chambers with continuous monitoring of CO2 and water exchanges. During the vegetative stage the effect Of CO2 enrichment, from 330 to 660 mul-1, was studied under irradiance of 660 muE m-2 s-1 with an optimum watering. Comparisons were made with successive experiments in which daily water supply was fixed to a fraction (0.62-0.50-0.25) of the maximal transpiration of previous experiments. In a well- watered canopy, doubling CO2 decreased transpiration by only 8%. Water use efficiency was increased (factor 1.45) mainly by the stimulation of photosynthesis. Under restricted water supply, photosynthesis of plants was more limited than transpiration. The inhibition of photosynthesis and the increase of water use efficiency can be predicted by a simple diffusion model applied to the response curve of photosynthesis to CO2, measured on canopy in standard conditions of watering. The main hypothesis is that the equivalent stomatal conductance is reduced proportionally to the water availability, without closure by patching. Under enriched CO2, the same reduction of leaf surface by water limitation was observed. Photosynthesis was less affected. Therefore, water-use-efficiency was again increased. Doubling CO2 concentration can compensate for water stress inhibition on CO2 assimilation. That model also predicts interactions of CO2 and water stress observed on water-use- efficiency which was increased by a factor up to 5 in comparison with well-watered plants in standard atmosphere. The implications of this study for global change models are discussed.

KEYWORDS: ASSIMILATION, CARBON-DIOXIDE ENRICHMENT, CONDUCTANCE, EXCHANGES, GROWTH, PHASEOLUS-VULGARIS L, PLANTS, SEEDLINGS, STRESS, YIELD

54

Andrews, J.A., K.G. Harrison, R. Matamala, and W.H. Schlesinger. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during Free-Air Carbon Dioxide Enrichment (FACE). *Soil Science Society of America Journal 63(5):1429-1435.*

Soil respiration constitutes a major component of the global carbon cycle and is likely to be altered by climatic change. However, there is an incomplete understanding of the extent to which various processes contribute to total soil respiration, especially the contributions of root and rhizosphere respiration. Here, using a stable carbon isotope tracer, we separate thf relative contributions of root and soil heterotrophic respiration to total soil respiration in situ. The Free-Air Carbon dioxide Enrichment (FACE) facility in the Duke University Forest (NC) fumigates plots of an undisturbed loblolly pine (Pinus taeda L.) forest with CO2 that is strongly depleted in C-13. This labeled CO2 is found in the soil pore space through live root and mycorrhizal respiration and soil heterotroph respiration of labile root exudates. By measuring the depletion of (CO2)-C-13 in the soil system, we found that the rhizosphere contribution to soil CO2 reflected the distribution of fine roots in the soil and that late in the growing season roots contributed 55% of total soil respiration at the surface, This estimate may represent an upper limit on the contribution of roots to soil respiration because high atmospheric CO2 often increases in root density and/or root activity in the soil.

KEYWORDS: CO2, DECIDUOUS FOREST, FATE, FLUXES, LITTER, ORGANIC-MATTER, PONDEROSA PINE, RHIZOSPHERE, SEEDLINGS

55

Andrews, T.J., G.S. Hudson, C.J. Mate, S. Voncaemmerer, J.R. Evans, and Y.B.C. Arvidsson. 1995. Rubisco - the consequences of altering its expression and activation in transgenic plants. *Journal of Experimental Botany 46:1293-1300.*

Transgenic tobacco (Nicotiana tabacum W38) hemizygous for a single antisense gene directed against Rubisco's small subunit had 35% of the Rubisco content of control leaves (15% when homozygous). CO2 assimilation (at 1000 mu mol quanta m(-2) s(- 1) and 350 mu bar CO2) by the hemizygous leaves was reduced to 40% of that of the controls without material effect on stomatal conductance, chlorophyll content or other photosynthetic components. Leaf soluble protein was reduced commensurately with the reduction in Rubisco. CO2 assimilation rate in the hemizygous leaves remained limited by Rubisco activity at all, even very high, CO2 concentrations. This led to a simple, hyperbolic response of photosynthesis to intraplastid CO2 concentration from which the in vivo catalytic properties of Rubisco were inferred and compared with those of isolated Rubisco in vitro. Using a similar approach, the content of Rubisco activase was suppressed by incorporating a partial cDNA for activase into the tobacco genome in the antisense orientation with respect to a cauliflower mosaic virus 35S promoter. The progeny of a primary transformant with two anti- activase inserts had from <1% to 20% of the activase content of control plants. Quite severe suppression of activase, to less than 5% of the amount present in control leaves, was required before effects on photosynthesis and growth became apparent, indicating that one activase tetramer must be able to service, continuously, as many as 200 Rubisco octamers. Plants with lower activase contents could not grow unless the atmosphere was enriched with CO2. Their Rubisco was less carbamylated and they had lower CO2 assimilation rates than the controls. The rate of release of 2'-carboxyarabinitol-1-phosphate from Rubisco after illumination of the anti-activase leaves was also impaired. Older anti-activase plants accumulated increasing amounts of Rubisco in their younger leaves, but were unable to carbamylate it. The photosynthetic rate per carbamylated Rubisco active site in the strongly suppressed anti-activase leaves was only approximately 25% of that seen in control leaves, suggesting that activase may not only promote carbamylation of uncarbamylated Rubisco sites, but also accelerate turnover at carbamylated sites.

KEYWORDS: 2-CARBOXYARABINITOL 1-PHOSPHATE, ACTIVITY INVIVO, ANTISENSE GENE, CATALYSIS, GROWTH, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SLOW INACTIVATION, TOBACCO NICOTIANA-TABACUM

56

Andriolo, J.L., J. LeBot, C. Gary, G. Sappe, P. Orlando, B. Brunel, and C. Sarrouy. 1996. An experimental set-up to study carbon, water and nitrate uptake rates by hydroponically grown plants. *Journal of Plant Nutrition 19(10-11):1441-1462.*

The experimental system described allows concomitant hourly measurements of CO2, H2O, and NO3 uptake rates by plants grown hydroponically in a greenhouse. Plants are enclosed in an airtight chamber through which air flows at a controlled speed. Carbon dioxide exchange and transpiration rates are determined from respective differences of concentrations of CO2 and water vapor of the air at the system inlet and outlet. This set-up is based on the "open-system" principle with improvements made on existing systems. For instance, propeller anemometers are used to monitor air flow rates in the chamber. From their signal it is possible to continuously adjust air speed to changing environmental conditions and plant activity. The air temperature inside the system therefore never rises above that outside. Water and NO3 uptake rates are calculated at time intervals from changes in the volume and the NO3 concentration of the nutrient solution in contact with the roots. The precise measurement of the volume of solution is achieved using a balance which has a higher precision than any liquid level sensors. Nitrate concentration is determined in the laboratory from aliquots of solution sampled at time intervals. A number of test runs are reported which validate the measurements and confirm undisturbed conditions within the system. Results of typical diurnal changes in CO2, H2O, and NO3 uptake rates by fruiting tomato plants are also presented.

KEYWORDS: CROP, DIOXIDE, ELEVATED CO2, GAS-EXCHANGE, LIFE-CYCLE, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, SYSTEM, TOMATO, TRANSPIRATION

57

Angell, R., and T. Svejcar. 1999. A chamber design for measuring net CO2 exchange on rangeland. *Journal of Range Management 52(1):27-31.*

Net carbon exchange of terrestrial ecosystems will likely change as atmospheric CO2 concentration increases, Currently, little is known of the annual dynamics or magnitude of CO2 flux on many native and agricultural ecosystems. Remoteness of many ecosystems has limited our ability to measure CO2 flux on undisturbed vegetation. Today, many plant ecologists have portable photosynthesis systems with which they make single- leaf photosynthesis measurements. Utility of this equipment is enhanced when canopy-level CO2 flux is also measured. We designed a portable 1-m(3) closed chamber for use in measuring CO2 exchange in short statured vegetation with widely varied canopy structure. The design includes external ductwork equipped with doors which are used to open the chamber for ventilation with outside air between measurements. The chamber was tested on a Wyoming big sagebrush (Artemisia tridentata ssp. Wyomingensis Nutt.)/Thurber's needlegrass (Stipa thurberiana Piper) community using 10 plots equally divided between shrub and interspace, The ductwork and doors provided adequate ventilation to allow consecutive measurements of CO2 nux without removing the chamber from the plot. The chamber could differentiate CO2 flux between plots with sagebrush and those with grass only, even at relatively low fluxes, Net CO2 uptake per unit ground area was greater (P = 0.04) on sagebrush-grass plots (7.6 +/- 1.4 mu mol m(-2) s(-1)) than on interspace plots without sagebrush (3.1 +/- 1.0 pmol m(-2) s(- 1)). Chamber and leaf temperature increased by an average of 0.5 and 1.2 degrees C, respectively, during measurements.

KEYWORDS: CARBON-CYCLE, FLUXES, SYSTEM, TUNDRA ECOSYSTEMS

58

Apel, P., and M. Peisker. 1995. Variability of photosynthetic gas exchange parameters, dark respiration, and stomatal numbers in species of Polygonum. *Physiologia Plantarum 95(3):365-372.*

Within the genus Polygonum a large variation was found between species with regard to stomatal number, gas phase resistance, intracellular resistance and dark respiration. Interspecific variation in CO2 compensation concentration and intercellular CO2 concentration at constant external concentration were comparatively small. Correlations were found between stomatal number and gas phase resistance, stomatal number and Gamma, and Gamma and the product of dark respiration rate and intracellular resistance. The influence of dark respiration and stomatal number on photosynthetic gas exchange is discussed. It was concluded that dark respiration in light was enhanced by 22% as a mean value in 9 Polygonum species and by 62% in Polygonum lapathifolium.

KEYWORDS: CONDUCTANCE, LEAVES, PLANTS

59

Apple, M.E., M.S. Lucash, D.M. Olszyk, and D.T. Tingey. 1998. Morphogenesis of Douglas-fir buds is altered at elevated temperature but not at elevated CO2. *Environmental and Experimental Botany 40(2):159-172.*

Global climatic change as expressed by increased CO2 and temperature has the potential for dramatic effects on trees. To determine what its effects may be on Pacific Northwest forests, Douglas-fir (Pseudotsuga menziesii) seedlings were grown in sun-lit controlled environment chambers at ambient or elevated (+ 4 degrees C above ambient) temperature, and at ambient or elevated (+ 200 ppm above ambient) CO2. In 1995-1996 and 1996- 1997, elevated CO2 had no effect on vegetative bud morphology, while the following unusual morphological characteristics were found with greater frequency at elevated temperature than at ambient: rosetted buds with reflexed and loosened outer scales, convoluted inner scales, clusters of small buds, needles elongating between scales, needle primordia with white, hyaline apical extensions, and buds with hardened scales inside of unbroken buds. Buds became rosetted in elevated temperature chambers after temperatures exceeded 40 degrees C in July, 1996. Rosettes were induced within 48-h in buds placed in a 40 degrees C oven; fewer rosettes formed at 20 degrees C. Induction was reversible in buds transferred from 40 to 20 degrees C, implying that resetting is a physical rather than a growth phenomenon. It appears that rosettes form after long- term exposure to elevated temperature and after shorter periods of exposure to intense heat. Elevated temperature influences bud morphology and may therefore influence the overall branching structure of Douglas-fir seedlings. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCUMULATION, BUDBURST, CHILLING REQUIREMENT, DORMANCY, FROST DAMAGE, HEAT-SHOCK PROTEINS, INTERIOR, POPULATIONS, SEEDLINGS, SHOOT

60

Arakelyan, V.V., G.B. Ibragimova, and Y.S. Nasyrov. 1993. Effects of light, co2, and temperature on carbonic-anhydrase activity in C3-plants. *Russian Journal of Plant Physiology 40(6):759-767.*

Carbonic anhydrase activity was studied in cotton (Gossypium hirsutum L.) and Triticale plants exposed to various light intensities, temperatures, and CO2 concentrations in the air. The activity was measured using an original method based on the HCO3- dehydration reaction, which is carried out in conditions resembling those occurring in the chloroplast stroma in vivo. Carbonic anhydrase activity in stromal fractions from cotton and triticale plant chloroplasts appears to respond to environmental changes. Plant exposure to increased light intensities and temperatures results in increased activity, whereas high ambient CO2 concentrations lower carbonic anhydrase activity. After examining in vitro the HCO3- dehydration reaction, which in vivo is catalyzed by carbonic anhydrase, we concluded that the physiological role of the stromal enzyme consists of preventing local CO2 depletion in the carboxylation sites. Thus, high temperatures and low ambient CO2 concentrations enhance carbonic anhydrase activity, while impeding CO2 transport from the air to the carboxylation sites in the leaf. This accelerates HCO3- dehydration and reduces its concentration in the stroma, thereby producing an additional driving force for HCO3- transport to the chloroplast.

61

Archer, S., D.S. Schimel, and E.A. Holland. 1995. Mechanisms of shrubland expansion - land-use, climate or co-2. *Climatic Change 29(1):91-99.*

Encroachment of trees and shrubs into grasslands and the 'thicketization' of savannas has occurred worldwide over the past century. These changes in vegetation structure are potentially relevant to climatic change as they may be indicative of historical shifts in climate and as they may influence biophysical aspects of land surface-atmosphere interactions and alter carbon and nitro en cycles. Traditional explanations offered to account for the historic displacement of grasses by woody plants in many arid and semi-arid ecosystems have centered around changes in climatic, livestock grazing and fire regimes. More recently, it has been suggested that the increase in atmospheric CO2 since the industrial revolution has been the driving force. In this paper we evaluate the CO2 enrichment hypotheses and argue that historic, positive correlations between woody plant expansion and atmospheric CO2 are not cause and effect.

KEYWORDS: AMERICAN SOUTHWEST, ATMOSPHERIC CO2, CARBON DIOXIDE, DESERTIFICATION, ECOSYSTEMS, ELEVATED CO2, GROWTH, INCREASING CO2, NATURAL VEGETATION, PAST 2 CENTURIES

62

Arienzo, M., G. Basile, R. Dandria, V. Magliulo, and A. Zena. 1995. Irrigation with carbonated water and nutrient availability - tests on strawberry plants. *Agrochimica 39(1):61-72.*

A research was carried out to study the nutrient availability and yield performances of a strawberry crop cv. 'Chandler' in response to equivalent depths (100% of ETM) of CO2 enriched water and plain water applied with different irrigation frequencies. Plots were arranged in a complete randomized block design replicated four times, using mulch and a drip irrigation system adopting 4 1/h emitters. The crop was covered by a plastic tunnel following treatment differentiation. The statistical analysis revealed an increased availability of Cu, Zn, Ca, Mg, and Mn for the CO2 treatment, probably linked with the pH reduction (from 7,5 to 6,5). The increased nutrient uptake in the CO2 enriched water treatment may be the cause of the commercial yield enhancement (8,6 %) and reduction in the weight of deformed berries (-12,1 %).

KEYWORDS: DIOXIDE

63

Arisi, A.C.M., G. Cornic, L. Jouanin, and C.H. Foyer. 1998.

Overexpression of iron superoxide dismutase in transformed poplar modifies the regulation of photosynthesis at low CO2 partial pressures or following exposure to the prooxidant herbicide methyl viologen. *Plant Physiology 117(2):565-574.*

Chloroplast-targeted overexpression of an Fe superoxide dismutase (SOD) from Arabidopsis thaliana resulted in substantially increased foliar SOD activities. Ascorbate peroxidase, glutathione reductase, and monodehydroascorbate reductase activities were similar in the leaves from all of the lines, but dehydroascorbate reductase activity was increased in the leaves of the FeSOD transformants relative to untransformed controls. Foliar H2O2, ascorbate, and glutathione contents were comparable in all lines of plants. Irradiance-dependent changes in net CO, assimilation and chlorophyll a fluorescence quenching parameters were similar in all lines both in air (21% O-2) and at low (1%) O-2. CO2-response curves for photosynthesis showed similar net CO2-exchange characteristics in all lines. In contrast, values of photochemical quenching declined in leaves from untransformed controls at intercellular CO2 (Ci) values below 200 mu L L-1 but remained constant with decreasing Ci in leaves of FeSOD transformants. When the O-2 concentration was decreased from 21 to 1%, the effect of FeSOD overexpression on photochemical quenching at limiting Ci was abolished. At high light (1000 mu mol m(-2) s(-1)) a progressive decrease in the ratio of variable (F-v) to maximal (F-m) fluorescence was observed with decreasing temperature. At 6 degrees C the high-light-induced decrease in the F-v/F-m ratio was partially prevented by low O-2 but values were comparable in all lines. Methyl viologen caused decreased F- v/F-m ratios, but this was less marked in the FeSOD transformants than in the untransformed controls. These observations suggest that the rate of superoxide dismutation limits flux through the Mehler-peroxidase cycle in certain conditions.

KEYWORDS: ASCORBATE PEROXIDASE, CHLOROPHYLL FLUORESCENCE, ELEVATED LEVELS, HYDROGEN- PEROXIDE, OXIDATIVE STRESS TOLERANCE, PHOTOINHIBITION, QUANTUM YIELD, SPINACH-CHLOROPLASTS, TEMPERATURE, TRANSGENIC PLANTS

64

Arnone, J.A. 1997. Indices of plant N availability in an alpine grassland under elevated atmospheric CO2. *Plant and Soil 190(1):61-66.*

The objective of this study was to estimate whether elevated atmospheric [CO2] alters plant N availability in a native high- elevation grassland in the Swiss Alps using two integrative, relatively non-disruptive methods. Estimates based on seasonal net plant N uptake, and those based on the amounts of NH4+-N plus NO3--N captured by ion exchange resin (IER) bags, did not differ in plots treated with ambient (355 mu L L-1) and elevated (680 mu L L-1) [CO2] in either the second (1993) or third (1994) growing season under treatment with elevated [CO2]. The results of this study suggest that the effects of rising atmospheric [CO2] on plant N availability may be negligible in this grassland. The results also contrast the relatively large effects of elevated atmospheric [CO2] (increases and decreases) reported for highly disturbed artificial systems.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, EXCHANGE, FEEDBACK, GROWTH FORMS, NITROGEN-AVAILABILITY, NUTRIENT AVAILABILITY, RESPONSES, SOIL-NITROGEN, TUNDRA

65

Arnone, J.A. 1997. Temporal responses of community fine root populations to long- term elevated atmospheric CO2 and soil nutrient patches in model tropical ecosystems. *Acta Oecologica-International Journal of Ecology 18(3):367-376.*

Biomass and length density of fine roots, as well as overall allocation of dry matter to root growth, of C-3 plants has been shown to increase under elevated CO2. However, it is uncertain whether the stimulatory effect of elevated CO2 on fine root population size in plant communities will persist, or whether fine root populations at high CO2 simply reach their maximum sooner (or possibly later) than those produced under ambient CO2. It is also unclear whether increased nutrient demand at the stand-level under elevated CO2 will lead to more intense nutrient foraging via enhanced fine root proliferation into relatively nutrient-rich soil microsites. I addressed these questions in a 530 day experiment with model tropical plant communities established in four equivalent ecosystem (17 m(3)) in which plants shared a common low fertility soil. Fine root (less than or equal to 2 mm empty set) populations (biomass and length density) in ecosystems maintained at elevated CO2 (610 mu l l(-1)) increased more rapidly than those in ecosystems maintained at ambient CO2 (340 mu l l(-1)) during the first half of the experiment and also remained greater over the entire experiment. The data also indicate that: (1) fine root populations at both CO2 levels eventually stabilize, (2) stabilization occurs sooner under elevated CO2 (occupation of the soil volume), and (3) steady-state populations under elevated CO2 may be slightly larger than those maintained under ambient CO2. Fine root proliferation into artifically nutrient- enriched microsites was dramatic in all ecosystems (22% to 75% greater than into non-enriched soil). However, proliferation into enriched microsites was not enhanced by elevated CO2. Thus, elevated CO2 may not enhance exploitation of nutrient- rich microsites even in low fertility soils, suggesting that increased plant nutrient capture under elevated CO2 also may be unlikely.

KEYWORDS: AMAZONIAN FORESTS, BIOMASS, CARBON DIOXIDE, ENRICHMENT, GROWTH, MICROSITES, PLANT-COMMUNITIES, PROLIFERATION, RAIN-FOREST, UPTAKE KINETICS

66

Arnone, J.A. 1999. Symbiotic N-2 fixation in a high Alpine grassland: effects of four growing seasons of elevated CO2. *Functional Ecology 13(3):383-387.*

1. Increasing carbon dioxide concentration (E: 680 mu l CO2 litre(-1) vs ambient, A: 355 mu l CO2 litre(-1)) around late- successional Alpine sedge communities of the Swiss Central Alps (2450 m) for four growing seasons (1992-1995) had no detectable effect on symbiotic N-2 fixation in Trifolium alpinum-the sole N-2-fixing plant species in these communities (74 +/- 30 mg N m(-2) year(-1), A and E plots pooled). 2. This result is based on data collected in the fourth growing season showing that elevated CO2 had no effect on Trifolium above-ground biomass (4.4 +/- 1.7 g m(-2), A and E plots pooled, n = 24) or N content per unit land area (124 +/- 51 mg N m(-2), A and E pooled), or on the percentage of N Trifolium derived from the atmosphere through symbiotic N-2 fixation (%Ndfa: 61.0 +/- 4.1 across A and E plots) estimated using the N-15 dilution method. 3. Thus, it appears that N inputs to this ecosystem via symbiotic N-2 fixation will not be dramatically affected in the foreseeable future even as atmospheric CO2 continues to rise.

KEYWORDS: ATMOSPHERIC CO2, ECOSYSTEM, ENRICHMENT, GAS-EXCHANGE, NITROGENASE ACTIVITY, NODULATION, REDUCTION, RESPONSES, TRIFOLIUM-REPENS L, TUNDRA

67

Arnone, J.A., and P.J. Bohlen. 1998. Stimulated N2O flux from intact grassland monoliths after two growing seasons under elevated atmospheric CO2. *Oecologia 116(3):331-335.*

Long-term exposure of native vegetation to elevated atmospheric CO2 concentrations is expected to increase C inputs to the soil and, in

ecosystems with seasonally dry periods, to increase soil moisture. We tested the hypothesis that these indirect effects of elevated CO2 (600 mu l l(-1) vs 350 mu l l(-1)) would improve conditions for microbial activity and stimulate emissions of nitrous oxide (N2O), a very potent and long-lived greenhouse gas. After two growing seasons, the mean N2O efflux from monoliths of calcareous grassland maintained at elevated CO2 was twice as high as that measured from monoliths maintained at current ambient CO2 (70 +/- 9 vs 37 +/- 4 mu g N2O m(-2) h(-1) in October, 27 +/- 5 vs 13 +/- 3 mu g N2O m(-2) h(-1) in November after aboveground harvest). The higher N2O emission rates at elevated CO2 were associated with increases in soil moisture, soil heterotrophic respiration, and plant biomass production, but appear to be mainly attributable to higher soil moisture. Our results suggest that rising atmospheric CO2 may contribute more to the total greenhouse effect than is currently estimated because of its plant- mediated effects on soil processes which may ultimately lead to increased N2O emissions from native grasslands.

KEYWORDS: CALCAREOUS GRASSLAND, CARBON-DIOXIDE ENRICHMENT, DENITRIFICATION, ECOSYSTEMS, INCREASE, METHANE, NITROUS-OXIDE PRODUCTION, SHORTGRASS STEPPE, SOIL-NITROGEN, STOMATAL RESPONSES

68

Arnone, J.A., and J.C. Gordon. 1990. Effect of nodulation, nitrogen-fixation and CO2 enrichment on the physiology, growth and dry mass allocation of seedlings of alnus-rubra bong. *New Phytologist 116(1):55-66.*

69

Arnone, J.A., and G. Hirschel. 1997. Does fertilizer application alter the effects of elevated CO2 on Carex leaf litter quality and in situ decomposition in an alpine grassland? *Acta Oecologica-International Journal of Ecology 18(3):201-206.*

The purpose of our investigation was to determine: (1) whether fertilization with NPK would result in an improvement in leaf litter quality of the dominant species (Carer curvula) in a high alpine grassland in Switzerland; and especially (2) if fertilization improves the quality of leaf litter produced under elevated atmospheric CO2 and compensates for the suppressive effects of high CO2 on the in situ decomposition rates of C. curvula litter, observed at this site in an earlier study. Fertilizer application (40 k(g) N ha(-1) yr(-1)) resulted in 34% higher leaf litter [N] but did not change C:N or lignin N ratios, when viewed across both CO2 treatments. Improvement in the mean N quality of litter produced under elevated CO2 resulting from fertilization appeared to lead to a significantly faster mean decomposition rate (+ 60%), but fertilization had no significant effect on decomposition of litter produced under ambient CO2. We conclude that the potential stimulatory effect of an increase in atmospheric N deposition on litter quality and decomposition rates may partially compensate for the inhibitory effects of rising atmospheric CO2 in these high alpine grassland ecosystems.

KEYWORDS: ECOSYSTEMS, NITROGEN, RESPONSES

70

Arnone, J.A., and C. Kestenholz. 1997. Root competition and elevated CO2: Effects on seedling growth in Linum usitatissimum populations and Linum Silene cretica mixtures. *Functional Ecology 11(2):209-214.*

1. Root competition can be an important determinant of the performance of neighbours within plant populations and communities. Because plants often maintain larger root systems and allocate more of their carbon to root systems under elevated atmospheric CO2 than they do at lower CO2 concentrations, root-root interactions could play an increasingly important role in determining competitive outcomes among individuals and plant species as global CO2 concentration continues to rise. 2. We established 12 pure stands of Linum usitatissimum (flax) and 12 mixed stands of Linum and its naturally co-occurring weed species Silene cretica in opaque plastic trays each filled with the same amount of nutrient-rich soil mix. In half of the trays from each of these stand types, vertical waterproof partitions separated the root systems of individual plants from each other to prevent root competition, while in the other half no partitions were present. Half of the trays from all treatments were allowed to grow under low atmospheric CO2 concentration (320 mu ll(-1)) and the other half under elevated CO2 (600 mu ll(-1)), in daylight growth: chambers for 30 days from seedling emergence until harvest in mid-June. All trays received equal amounts of water so that soils in the low CO2 treatment were maintained at field capacity. 3. Our results indicate that under high soil fertilities: (1) intra-specific root-root interactions alone play a relatively insignificant role in determining plant biomass production within pure Linum populations and (2) the impact of an aggressive species (Silene) on co-occurring less aggressive species (Linum) becomes more severe under elevated CO2 as a result of amplified interspecific root competition.

KEYWORDS: AMBIENT, ANNUALS, ATMOSPHERIC CO2, C-3, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENRICHMENT, PLANTS, RESPONSES

71

Arnone, J.A., and C. Korner. 1993. Influence of elevated co2 on canopy development and red - far- red ratios in 2-storied stands of ricinus-communis. *Oecologia 94(4):510-515.*

Vertical structure of plant stands and canopies may change under conditions of elevated CO2 due to differential responses of overstory and understory plants or plant parts. In the long term, seedling recruitment, competition, and thus population or community structure may be affected. Aside from the possible differential direct effects of elevated CO2 on photosynthesis and growth, both the quantity and quality of the light below the overstory canopy could be indirectly affected by CO2-induced changes in overstory leaf area index (LAI) and/or changes in overstory leaf quality. In order to explore such possible interactions, we compared canopy leaf area development, canopy light extinction and the quality of light beneath overstory leaves of two-storied monospecific stands of Ricinus communis exposed to ambient (340 mul-1) and elevated (610 mul-1) CO2. Plants in each stand were grown in a common soil as closed "artificial ecosystems" with a ground area of 6.7 m2. LAI of overstory plants in all ecosystems more than doubled during the experiment but was not different between CO2 treatments at the end. As a consequence, extinction of photosynthetically active radiation (PAR) was also not altered. However, under elevated CO2 the red to far-red ratio (R: FR) measured beneath overstory leaves was 10% lower than in ecosystems treated with ambient CO2. This reduction was associated with increased thickness of palisade layers of overstory leaves and appears to be a plausible explanation for the specific enhancement of stem elongation of understory plants (without a corresponding biomass response) under elevated CO2. Col enrichment led to increased biomass of overstory plants (mainly stem biomass) but had no effect on understory biomass. The results of this study raise the possibility of an important indirect effect of elevated CO2 at the stand-level. We suggest that, under elevated CO2, reductions in the R:FR ratio beneath overstory canopies may affect understory plant development independently of the effects of PAR extinction.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL CONTENT, CLOVER TRIFOLIUM-REPENS, GROWTH, LEAF ANATOMY, LIGHT-QUALITY, PLANTS, RAIN-FOREST, RESPONSES

72

Arnone, J.A., and C. Korner. 1995. Soil and biomass carbon pools in model communities of tropical plants under elevated co2. *Oecologia 104(1):61-71.*

The experimental data presented here relate to the question of whether terrestrial ecosystems will sequester more C in their soils, litter and biomass as atmospheric CO2 concentrations rise. Similar to our previous study with relatively fertile growth conditions (Korner and Arnone 1992), we constructed four rather nutrient-limited model communities of moist tropical plant species in greenhouses (approximately 7 m(2) each). Plant communities were composed of seven species (77 individuals per community) representing major taxonomic groups and various life forms found in the moist tropics. Two ecosystems were exposed to 340 mu l CO2 l(-1) and two to 610 mu l l(-1) for 530 days of humid tropical growth conditions. In order to permit precise determination of C deposition in the soil, plant communities were initially established in C-free unwashed quartz sand. Soils were then amended with known amounts of organic matter (containing C and nutrients). Mineral nutrients were also supplied over the course of the experiment as timed-release full-balance fertilizer pellets. Soils represented by far the largest repositories for fixed C in all ecosystems. Almost 5 times more C (ca. 80% of net C fixation) was sequestered in the soil than in the biomass, but this did not differ between CO2 treatments. In addition, at the whole-ecosystem level we found a remarkably small and statistically non-significant increase in C sequestration (+4%; the sum of C accretion in the soil, biomass, litter and necromass). Total community biomass more than quadrupled during the experiment, but at harvest was, on average, only 8% greater (i.e. 6% per year; n.s.) under elevated CO2, mainly due to increased root biomass (+15%, P = 0.12). Time courses of leaf area index of all ecosystems suggested that canopy expansion was approaching steady state by the time systems were harvested. Net primary productivity (NPP) of all ecosystems - i.e. annual accumulation of biomass, necromass, and leaf litter (but not plant-derived soil organic matter) - averaged 815 and 910 g m(-2) year(-1) at ambient and elevated CO2, respectively. These NPPs are remarkably similar to those of many natural moist tropical forested ecosystems. At the same time net productivity of soil organic matter reached 7000 g dry matter equivalent per m(2) and year (i.e. 3500 g C m(-2) year(-1)). Very slight yet statistically significant CO2- induced shifts in the abundance of groups of species occurred by the end of the experiment, with one group of species (Elettaria cardamomum, Ficus benjamina, F: pumila, Epipremnum pinnatum) gaining slightly, and another group (Ctenanthe lubbersiana, Heliconia humilis, Cecropia peltata) losing. Our results show that: (1) enormous amounts of C can be deposited in the ground which are normally not accounted for in estimates of NPP and net ecosystem productivity; (2) any enhancement of C sequestration under elevated atmospheric CO2 may be substantially smaller than is believed will occur (yet still very important), especially under growth conditions which permit close to natural NPP; and (3) species dominance in plant communities is likely to change under elevated CO2, but that changes may occur rather slowly.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, C-3, COMPETITION, DIOXIDE, ENRICHMENT, ESTUARINE MARSH, GROWTH, NITROGEN, TUSSOCK TUNDRA

73

Arnone, J.A., J.G. Zaller, C. Ziegler, H. Zandt, and C. Korner. 1995. Leaf quality and insect herbivory in model tropical plant-communities after long-term exposure to elevated atmospheric co2. *Oecologia 104(1):72-78.*

Results from laboratory feeding experiments have shown that elevated atmospheric carbon dioxide can affect interactions between plants and insect herbivores, primarily through changes in leaf nutritional quality occurring at elevated CO2. Very few data are available on insect herbivory in plant communities where insects can choose among species and positions in the canopy in which to feed. Our objectives were to determine the extent to which CO2-induced changes in plant communities and leaf nutritional quality may affect herbivory at the level of the entire canopy. We introduced equivalent populations of fourth instar Spodoptera eridania, a lepidopteran generalist, to complex model ecosystems containing seven species of moist tropical plants maintained under low mineral nutrient supply. Larvae were allowed to feed freely for 14 days, by which time they had reached the seventh instar. Prior to larval introductions, plant communities had been continuously exposed to either 340 mu l CO2 l(-1) or to 610 mu l CO2 l(-1) for 1.5 years. No major shifts in leaf nutritional quality [concentrations of N, total non-structural carbohydrates (TNC), sugar, and starch; ratios of: C/N, TNC/N, sugar/N, starch/N; leaf toughness] were observed between CO2 treatments for any of the species. Furthermore, no correlations were observed between these measures of leaf quality and leaf biomass consumption. Total leaf area and biomass of all plant communities were similar when caterpillars were introduced. However, leaf biomass of some species was slightly greater - and for other species slightly less (e.g. Cecropia peltata) - in communities exposed to elevated CO2. Larvae showed the strongest preference for C. peltata leaves, the plant species that was least abundant in all communities, and fed relatively littie on plants species which were more abundant. Thus, our results indicate that leaf tissue quality, as described by these parameters, is not necessarily affected by elevated CO2 under relatively low nutrient conditions. Hence, the potential importance of CO2-induced shifts in leaf nutritional quality, as determinants of herbivory, may be overestimated for many plant communities growing on nutrient-poor sites if estimates are based on traditional laboratory feeding studies. Finally, slight shifts in the abundance of leaf tissue of various species occurring under elevated CO2 will probably not significantly affect herbivory by generalist insects. However, generalist insect herbivores appear to become more dependent on less-preferred plant species in cases where elevated CO2 results in reduced availability of leaves of a favoured plant species, and this greater dependency may eventually affect insect populations adversely.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, CHLOROPHYLL CONTENT, ECOSYSTEMS, ENRICHMENT, FOREST, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, RESPONSES

74

Arp, W.J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO2. *Plant, Cell and Environment 14(8):869-875.*

While photosynthesis of C3 plants is stimulated by an increase in the atmospheric CO2 concentration, photosynthetic capacity is often reduced after long-term exposure to elevated CO2. This reduction appears to be brought about by end product inhibition, resulting from an imbalance in the supply and demand of carbohydrates. A review of the literature revealed that the reduction of photosynthetic capacity in elevated CO2 was most pronounced when the increased supply of carbohydrates was combined with small sink size. The volume of pots in which plants were grown affected the sink size by restricting root growth. While plants grown in small pots had a reduced photosynthetic capacity, plants grown in the field showed no reduction or an increase in this capacity. Pot volume also determined the effect of elevated CO2 on the root/shoot ratio: the root/shoot ratio increased when root growth was not restricted and decreased in plants grown in small pots. The data presented in this paper suggest that plants growing in the field will maintain a high photosynthetic capacity as the atmospheric CO2 level continues to rise.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, CO2- ENRICHMENT, COTTON

PLANTS, LEAVES, LIQUIDAMBAR- STYRACIFLUA, LONG-TERM EXPOSURE, PINUS-TAEDA SEEDLINGS, PLANT GROWTH

75

Arp, W.J., and B.G. Drake. 1991. Increased photosynthetic capacity of scirpus-olneyi after 4 years of exposure to elevated co2. *Plant, Cell and Environment 14(9):1003-1006.*

While a short-term exposure to elevated atmospheric CO2 induces a large increase in photosynthesis in many plants, long-term growth in elevated CO2 often results in a smaller increase due to reduced photosynthetic capacity. In this study, it was shown that, for a wild C3 species growing in its natural environment and exposed to elevated CO2 for four growing seasons, the photosynthetic capacity has actually increased by 31%. An increase in photosynthetic capacity has been observed in other species growing in the field, which suggests that photosynthesis of certain field grown plants will continue to respond to elevated levels of atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2, C-3, CARBON DIOXIDE, ESTUARINE MARSH, FIELD, INSITU, LEAVES, PLANTS

76

Arp, W.J., B.G. Drake, W.T. Pockman, P.S. Curtis, and D.F. Whigham. 1993. Interactions between C-3 and C-4 salt-marsh plant-species during 4 years of exposure to elevated atmospheric co2. *Vegetatio 104:133-143.*

Elevated atmospheric CO2 is known to stimulate photosynthesis and growth of plants with the C3 pathway but less of plants with the C4 pathway. An increase in the CO2 concentration can therefore be expected to change the competitive interactions between C3 and C4 species. The effect of long term exposure to elevated CO2 (ambient CO2 concentration + 340 mumol CO2 mol-1) on a salt marsh vegetation with both C3 and C4 species was investigated. Elevated CO2 increased the biomass of the C3 sedge Scirpus olneyi growing in a pure stand, while the biomass of the C4 grass Spartina patens in a monospecific community was not affected. In the mixed C3/C4 community the C3 sedge showed a very large relative increase in biomass in elevated CO2 while the biomass of the C4 species declined. The C4 grass Spartina patens dominated the higher areas of the salt marsh, while the C3 sedge Scirpus olneyi was most abundant at the lower elevations, and the mixed community occupied intermediate elevations. Scirpus growth may have been restricted by drought and salt stress at the higher elevations, while Spartina growth at the lower elevations may be affected by the higher frequency of flooding. Elevated CO2 may affect the species distribution in the salt marsh if it allows Scirpus to grow at higher elevations where it in turn may affect the growth of Spartina.

KEYWORDS: COMMUNITIES, COMPETITION, ENRICHMENT, FIELD, GRASS, GROWTH, LIQUIDAMBAR- STYRACIFLUA, PERENNIALS, PINUS-TAEDA SEEDLINGS, STRESS

77

Arp, W.J., J.E.M. Van Mierlo, F. Berendse, and W. Snijders. 1998. Interactions between elevated CO2 concentration, nitrogen and water: effects on growth and water use of six perennial plant species. *Plant, Cell and Environment 21(1):1-11.*

Two experiments are described in which plants of six species mere grown for one full season in greenhouse compartments with 350 or 560 mu mol mol(-1) COL. In the first experiment two levels of nitrogen supply were applied to study the interaction between CO2 and nitrogen, In the second experiment two levels of mater supply were added to the experimental set-up to investigate the three-way interaction between CO2, nitrogen and water, Biomass and biomass distribution were determined at harvests, while water use and soil moisture were monitored throughout the experiments, In both experiments a positive effect of CO2 on growth was found at high nitrogen concentrations but not at low nitrogen concentrations, However, plants used much less water in the presence of low nitrogen concentrations, Drought stress increased the relative effect of elevated CO2 on growth, Available soil moisture was used more slowly at high CO2 during drought or at high nitrogen concentrations, while at low nitrogen concentrations decreased water use resulted in an increase in soil moisture, The response to the treatments was similar in all the species used, Although potentially faster growing species appeared to respond better to high CO2 when supplied with a high level of nitrogen, inherently slow-growing species were more successful at low nitrogen concentrations.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE, COTTON, DRY-MATTER, ENRICHMENT, HEATHLAND ECOSYSTEMS, NUTRITION, STRESS, YIELD

78

Ashenden, T.W., R. Baxter, and C.R. Rafarel. 1992. An inexpensive system for exposing plants in the field to elevated concentrations of co2. *Plant, Cell and Environment 15(3):365-372.*

An inexpensive, potentially mobile field exposure system is described which may be easily constructed by a small workshop. It may be operated as an open-top with a frustrum or covered with a polycarbonate 'lid'. The system is cost-effective for CO2 exposure work because the small size allows provision of CO2-enriched atmospheres over prolonged periods at relatively low cost. A preliminary assessment of the chambers has been made and concentrations can be maintained at +/- 6% for a target atmosphere of 680 cm3 m-3 CO2 under normal operating conditions. Other chamber environmental conditions are reported.

KEYWORDS: AIR-POLLUTION, CHAMBERS

79

Asner, G.P., T.R. Seastedt, and A.R. Townsend. 1997. The decoupling of terrestrial carbon and nitrogen cycles. *BioScience 47(4):226-234.*

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, CO2, FOREST ECOSYSTEMS, GLOBAL CHANGE, GRASSLAND, LAND-USE, LONG-TERM, NUTRIENT LIMITATION, SOILS

80

Atkin, O.K., M. Schortemeyer, N. McFarlane, and J.R. Evans. 1999. The response of fast- and slow-growing Acacia species to elevated atmospheric CO2: an analysis of the underlying components of relative growth rate. *Oecologia 120(4):544-554.*

In this study we assessed the impact of elevated CO2 with unlimited water and complete nutrient on the growth and nitrogen economy of ten woody Acacia species that differ in relative growth rate (RGR). Specifically. we asked whether fast- and slow-growing species systematically differ in their response to elevated CO2. Four slow-growing species from semi- arid environments (Acacia aneura, A. colei, A. coriacea and A. tetragonophylla) and six fast-growing species from mesic environments (Acacia dealbata, A. implexa, A. mearnsii, A. melanoxylon, A. irrorata and A. saligna) were grown in glasshouses with either ambient (similar to 350 ppm) or elevated (similar to 700 ppm) atmospheric CO2. All species reached greater final plant mass with the exception of A. aneura, and RGR, averaged across all species, increased by 10% over a 12-week period when plants were exposed to elevated

CO2. The stimulation of RGR was evident throughout the 12-week growth period. Elevated CO2 resulted in less foliage area per unit foliage dry mass, which was mainly the result of an increase in foliage thickness with a smaller contribution from greater dry matter content per unit fresh mass. The net assimilation rate (NAR, increase in plant mass per unit foliage area and time) of the plants grown at elevated CO2 was higher in all species (on average 30% higher than plants in ambient CO2) and was responsible for the increase in RGR. The higher NAR was associated with a substantial increase in foliar nitrogen productivity in all ten Acacia species. Plant nitrogen concentration was unaltered by growth at elevated CO2 for the slow-growing Acacia species, but declined by 10% for faster- growing species. The rate of nitrogen uptake per unit root mass was higher in seven of the species when grown under elevated CO2, and leaf area per unit root mass was reduced by elevated CO2 in seven of the species. The absolute increase in RGR due to growth under elevated CO2 was greater for fast- than for slow-growing Acacia species.

KEYWORDS: ALPINE, CARBON DIOXIDE, EFFICIENCY, FOREST, GRASSLAND, LEAF-AREA, NITROGEN ECONOMY, PLANTS, TREES

81

Atkinson, C.J., and J.M. Taylor. 1996. Effects of elevated CO2 on stem growth, vessel area and hydraulic conductivity of oak and cherry seedlings. *New Phytologist 133(4):617-626.*

Plants of Quercus robur L. and Prunus avium L. x P. pseudocerasus Lind, were grown in either ambient (350 vpm) or elevated (700 vpm) CO2. The intention was to examine the effects of elevated CO2 on the morphological and functional development of the stem. The relationships between stem longitudinal transport capacity and development were explored in several ways: stem hydraulic function was related to stem cross-sectional area, supplied leaf area and total stem vessel lumen area. The mean total vessel number and the total vessel lumen area per stem, for both species, was determined from basal sections of the xylem. In Prunus seedlings grown in different CO2 concentrations there was no significant change in the mean vessel size or number of vessels per stem. Quercus seedlings grown at elevated CO2 showed a significant increase in both vessel number and mean vessel size. When total stem vessel area was calculated it had increased twofold for Quercus plants grown at elevated CO2. Measured stem hydraulic conductivity was shown to increase linearly with supplied leaf area, except in Quercus seedlings grown at elevated CO2. Stem hydraulic conductivity for Quercus seedlings grown at elevated CO2 did not change with the increase in supplied leaf area. This absence of an increase in the stem hydraulic conductivity appeared to relate to changes in total stem vessel area. Despite total stem vessel area being greater at elevated CO2 than that at ambient, it similarly did not increase with supplied leaf area. The implications of this change in the relationship between leaf area and stem hydraulic conductivity are discussed with respect to the possible effects the change might have on the plant's water balance. The possible causes and significance of the changes in xylem anatomy are also considered in relation to direct effects caused by CO2 or indirect effects on changes in cambial maturity and tree growth.

KEYWORDS: ATMOSPHERIC CO2, CAVITATION, DIAMETER, EMBOLISM, TRANSPIRATION, TREES, WATER-STRESS, WOODY-PLANTS, XYLEM

82

Atkinson, C.J., J.M. Taylor, D. Wilkins, and R.T. Besford. 1997. Effects of elevated CO2 on chloroplast components, gas exchange and growth of oak and cherry. *Tree Physiology 17(5):319-325.*

Specific chloroplast proteins, gas exchange and dry matter production in oak (Quercus robur L.) seedlings and clonal cherry (Prunus avium L. x pseudocerasus Lind.) plants were measured during 19 months of growth in climate-controlled greenhouses at ambient (350 vpm) or elevated (700 vpm) CO2. In both species, the elevated CO2 treatment increased the PPFD saturated-rate of photosynthesis and dry matter production. After two months at elevated CO2, Prunus plants showed significant increases in leaf (55%) and stem (61%) dry mass but not in root dry mass. However, this initial stimulation was not sustained: treatment differences in net assimilation rate (A) and plant dry mass were less after 10 months of growth than after 2 months of growth, suggesting acclimation of A to elevated CO2 in Prunus. In contrast, after 10 months of growth at elevated CO2, leaf dry mass of Quercus increased (130%) along with shoot (356%) and root (219%) dry mass, and A was also twice that of plants grown and measured at ambient CO2. The amounts of Rubisco and the thylakoid-bound protein cytochrome f were higher in Quercus plants grown for 19 months in elevated CO2 than in control plants, whereas in Prunus there was less Rubisco in plants grown for 19 months in elevated CO2 than in control plants. Exposure to elevated CO2 for 10 months resulted in increased mean leaf area in both species and increased abaxial stomatal density in Quercus. There was no change in leaf epidermal cell size in either species in response to the elevated CO2 treatment. The lack of acclimation of photosynthesis in oak grown at elevated CO2 is discussed in relation to the production and allocation of dry matter. We propose that differences in carbohydrate utilization underlie the differing long-term CO2 responses of the two species.

KEYWORDS: ATMOSPHERIC CO2, BIOCHEMISTRY, CARBON DIOXIDE, LEAF DEVELOPMENT, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, PRUNUS-AVIUM, RESPONSES, TOMATO PLANTS, TREES

83

Atkinson, C.J., P.A. Wookey, and T.A. Mansfield. 1991. Atmospheric-pollution and the sensitivity of stomata on barley leaves to abscisic-acid and carbon-dioxide. *New Phytologist 117(4):535-541.*

Spring barley (Hordeum vulgare L. cv. Klaxon) plants were exposed to mixtures of SO2 + NO2 (at concentrations of 24-35 nl l-1 of each gas, depending upon fumigation system), or to charcoal-filtered, or unfiltered ambient air during the period in which the second, and subsequent, leaves were emerging. The ability of individual detached leaves to regulate water loss was then examined after terminating the pollutant treatment. Observations of diurnal changes in stomatal resistance of well- watered plants, using a viscous flow porometer, failed to indicate any major alterations which could be attributed to prior exposure to SO2 + NO2. By contrast, when an ABA solution (10(-1) mol m-3) was applied to detached leaves, the stomata of polluted plants were less responsive than plants previously exposed to control air. The dynamics of the observed responses strongly implicated impaired physiology of the guard cells rather than mechanical changes in the epidermis that might, for example, result from damage to the cuticle. Stomatal closure was considerably slower in polluted leaves compared with the controls. This decline in responsiveness to ABA was observed using leaves excised from well-watered plants and in the absence of any externally visible injury. The ability of stomata to respond to a range of CO2 concentrations from 195- 735-mu-mol mol-1 was also examined using individual leaves, attached to the plant, in an environmentally controlled cuvette. Here the stomata of leaves which had been fumigated with SO2 + NO2 behaved in a similar manner to the non-fumigated leaves, both showing closure in elevated CO2 concentrations.

KEYWORDS: CONDUCTANCE, FUMIGATION, NITROGEN-DIOXIDE, NO2, PLANTS, SO2, SULFUR-DIOXIDE, SYSTEM, WHEAT LEAVES

84

Austin, M.P. 1992. Modeling the environmental niche of plants - implications for plant community response to elevated CO2 levels. *Australian Journal of Botany 40(4-5):615-630.*

No simple natural gradients in CO2 concentration exist for testing predictions about changes in plant communities in response to elevated CO2. However indirect effects of CO2 via temperature increases can be tested by reference to natural analogues. Physiologists, vegetation modellers of climate change and community ecologists assume very different temperature responses for plants. Physiologists often assume a skewed non-monotonic curve with a tail towards low temperatures, forest modellers using FORET type models, a symmetric curve, and community ecologists a skewed response with a tail towards high temperatures. These assumptions are reviewed in relation to niche theory, and recent propositions concerning the continuum concept. Confusion exists between the different approaches over the shape of response curves to temperature. Distinctions need to be made between responses due to growth (physiological response), potential fitness (fundamental niche) and observed performance (realised niche). These types of response should be quantified and related to each other if process-models are to be tested for predictive success by reference to naturally occurring communities and temperature gradients. An example of a statistical method for quantifying the realised environmental niche respone of a species to temperature is provided. It is based on generalised linear modelling (GLM) of presence/absence data on Eucalyptus fastigata for 8377 sites in southern New South Wales, Australia. Seven environmental variables or factors are considered: mean annual temperature, mean annual rainfall, mean monthly solar radiation, topographic position, rainfall seasonality, lithology, and soil nutrient status. The temperature response is modelled with a beta-function, log y = a + alpha log (t - a) + delta log (b - t), where t is temperature and letters are parameters. The probability of occurrence is shown to be a skewed function of mean annual temperature. Any process-models of climate change for vegetation incorporating temperature changes due to elevated CO2 must be capable of generating such realised environmental niche responses for species.

KEYWORDS: DISTRIBUTIONS, ECOSYSTEMS, FIELD, FOREST, GRADIENTS, GROWTH, NORTH-AMERICA, SIMULATION, SPECIES RESPONSE, VEGETATION

85

Awmack, C.S., R. Harrington, and S.R. Leather. 1997. Host plant effects on the performance of the aphid Aulacorthum solani (Kalt.) (Homoptera : Aphididae) at ambient and elevated CO2. *Global Change Biology 3(6):545-549.*

In future elevated CO2 environments, chewing insects are likely to perform less well than at present because of the effects of increased carbon fixation on their host plants. When the aphid, Aulacorthum solani was reared on bean (Vicia faba) and tansy (Tanacetum vulgare) plants under ambient and elevated CO2, performance was enhanced on both hosts at elevated CO2. The nature of the response was different on each plant species suggesting that feeding strategy may influence an insect's response to elevated CO2. On bean, the daily rate of production of nymphs was increased by 16% but there was no difference in development time, whereas on tansy, development time was 10% shorter at elevated CO2 but the rate of production of nymphs was not affected. The same aphid clone therefore responded differently to elevated CO2 on different host plants. This increase in aphid performance could lead to larger populations of aphids in a future elevated CO2 environment.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, NOCTUIDAE, PHYTOCHEMISTRY, POPULATIONS, RESPONSES

86

Azconbieto, J., M.A. Gonzalezmeler, W. Doherty, and B.G. Drake. 1994. Acclimation of respiratory o-2 uptake in green tissues of field-grown native species after long-term exposure to elevated atmospheric co2. *Plant Physiology 106(3):1163-1168.*

C-3 and C-4 plants were grown in open-top chambers in the field at two CO2 concentrations, normal ambient (ambient) and normal ambient + 340 mu L L(-1) (elevated). Dark oxygen uptake was measured in leaves and stems using a liquid-phase Clark-type oxygen electrode. High CO2 treatment decreased dark oxygen uptake in stems of Scirpus olneyi (C-3) and leaves of Lindera benzoin (C-3) expressed on either a dry weight or area basis. Respiration of Sparfina patens (C-4) leaves was unaffected by CO2 treatment. Leaf dry weight per unit area was unchanged by CO2, but respiration per unit of carbon or per unit of nitrogen was decreased in the C-3 species grown at high CO2. The component of respiration in stems of S. olneyi and leaves of L. benzoin primarily affected by long-term exposure to the elevated CO2 treatment was the activity of the cytochrome pathway. Elevated CO2 had no effect on activity and capacity of the alternative pathway in S. olneyi. The cytochrome c oxidase activity, assayed in a cell-free extract, was strongly decreased by growth at high CO2 in stems of S. olneyi but it was unaffected in S. patens leaves. The activity of cytochrome c oxidase and complex III extracted from mature leaves of L. benzoin was also decreased after one growing season of plant exposure to elevated CO2 concentration. These results show that in some C-3 species respiration will be reduced when plants are grown in elevated atmospheric CO2. The possible physiological causes and implications of these effects are discussed.

KEYWORDS: CARBOHYDRATE STATUS, CARBON-DIOXIDE ENRICHMENT, DARK RESPIRATION, EFFLUX, INHIBITION, LEAF RESPIRATION, LEAVES, PHOTOSYNTHESIS, PLANTS, WORLD

87

Azevedo, R.A., R.M. Alas, R.J. Smith, and P.J. Lea. 1998. Response of antioxidant enzymes to transfer from elevated carbon dioxide to air and ozone fumigation, in the leaves and roots of wild-type and a catalase-deficient mutant of barley. *Physiologia Plantarum 104(2):280-292.*

A catalase-deficient mutant (RPr 794) and the wild-type (cv. Maris Mink) barley (Hordeum vulgare L.) counterpart. were grown for 3 weeks in high CO2 (0.7%) and then transferred to air and ozone (120 nl l(-1)) in the light and shade for a period of 3 days. Leaves and roots were analysed for catalase (CAT, EC 1.11.1.6), superoxide dismutase (SOD. EC 1.15.1.1) and glutathione reductase (GR, EC 1.6.4.2) activities. CAT activity in the leaves of the RPr 79/4 catalase-deficient mutant was around 5 10% of that determined in Maris Mink. but in the roots, both genotypes contained approximately the same levels of activity. CAT activity in Maris Mink increased in the leaves after transferring plants from 0.7% CO2 to air or ozone, reaching a maximum of 5-fold. after 4 days in shade and ozone. For the catalase-deficient mutant. only small increases in CAT activity were observed in light/air and light/ozone treatments. In the roots. CAT activity decreased consistently in both genotypes, after plants were transferred from 0.7% CO2. The total soluble SOD activity in the leaves and roots of both genotypes increased after plants were transferred from 0.7% CO2. The analysis of SOD isolated from leaves following non- denaturing PAGE, revealed the presence of up to eight SOD isoenzymes classified as Mn-SOD or Cu/Zn-SODs: Fr-SOD was not detected. Significant changes in Mn- and Cu/Zn-SOD isoenzymes were observed; however, they could not account for the increase in total SOD activity. Ill leaves. GR activity also increased in Maris Mink and RPr 79/4, following transfer from 0.7% CO2: however, no constant pattern could be established, while in roots, GR activity was reduced after 4 days of the treatments. The data suggest that elevated CO2 decreases oxidative stress in barley leaves and that soluble CAT and SOD activities increased rapidly after plants were

transferred from elevated CO2. irrespective of the treatment (light, shade, air or ozone).

KEYWORDS: ARABIDOPSIS-THALIANA, ASCORBATE PEROXIDASE, DIFFERENTIAL RESPONSE, GLUTAMINE-SYNTHETASE, GLUTATHIONE-REDUCTASE, HORDEUM VULGARE L, NICOTIANA-PLUMBAGINIFOLIA L, OXIDATIVE STRESS, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

88

Baattrup-Pedersen, A., and T.V. Madsen. 1999. Interdependence of CO2 and inorganic nitrogen on crassulacean acid metabolism and efficiency of nitrogen use by Littorella uniflora (L.) Aschers. *Plant, Cell and Environment 22(5):535-542.*

The hypothesis is tested that crassulacean acid metabolism (CAM) in isoetids is a mechanism which not only conserves inorganic carbon but also plays a role in nitrogen economy of the plants, This hypothesis was tested in an outdoor experiment, where Littorella uniflora (L,) Aschers, were grown at two CO2 and five inorganic nitrogen concentrations in a crossed factorial design. The growth of Littorella responded positively to enhanced nitrogen availability at high but not at low CO2 indicating that growth was limited by nitrogen at high CO2 only. For the nitrogen-limited plants, the capacity for CAM (CAM(cap)) increased with the degree of nitrogen limitation of growth and an inverse coupling between CAM and tissue-N was found. Although this might indicate a role of CAM in economizing on nitrogen in Littorella, the hypothesis was rejected for the following reasons: (1) although CAM(cap) was related to tissue-N no relationship between tissue-N and ambient CAM activity (CAM(ambient)) was found whereas a close relationship would be expected if CAM was regulated by nitrogen availability; (2) the photosynthetic nitrogen use efficiency for high CO2-grown plants declined with increased CAM(ambient) and with CAM(cap); and (3) growth per unit tissue-N per unit time declined with increased CAM(ambient) and CAM(cap).

KEYWORDS: ACCLIMATION, ACQUISITION, AQUATIC CAM PLANTS, CARBON ASSIMILATION, GROWTH, MACROPHYTES, PHOTOSYNTHETIC PERFORMANCE

89

Bacanamwo, M., and J.E. Harper. 1997. Response of a hypernodulating soybean mutant to increased photosynthate supply. *Plant Science 124(2):119-129.*

Growth chamber studies were conducted to determine if increased photoassimilate supply, through light enhancement and CO2 enrichment, could reverse the deleterious plant growth and enhance nodule function traits of NOD1-3, a hypernodulating mutant of Williams. Both light enhancement and CO2 enrichment increased nodule number, acetylene reduction activity plant(-1) (but not specific activity) and dry matter accumulation in all tissues in both genotypes. Total biomass and specific nitrogenase activity were always less in the mutant than in Williams 82, indicating that the inferiority of the mutant may not be reversed by enhanced photoassimilate supply. Under all growth conditions, the mutant allocated relatively more photosynthate to nodules and less photosynthate to roots, compared to the control. Despite this, the decreased growth of the mutant relative to the control was not solely attributable to excessive nodulation of the mutant, since decreased growth was observed even on uninoculated plants. It is suggested that light enhancement and CO2 enrichment may have stimulated nodulation through increased photosynthate supply, independent of the nodulation autoregulatory signal. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: ACETYLENE-REDUCTION ASSAY, CARBON DIOXIDE, CULTIVAR ENREI, CV BRAGG, GLYCINE-MAX, NITROGENASE ACTIVITY, NODULATION MUTANTS, ROOT NODULE ACTIVITY, SUPERNODULATING MUTANT, WILD-TYPE

90

Bachelet, D., D. Brown, M. Bohm, and P. Russell. 1992. Climate change in thailand and its potential impact on rice yield. *Climatic Change 21(4):347-366.*

In Thailand, the world's largest rice exporter, rice constitutes a major export on which the economy of the whole country depends. Climate change could affect rice growth and development and thus jeopardize Thailand's wealth. Current climatic conditions in Thailand are compared to predictions from four general circulation models (GCMs). Temperature predictions correlate well with the observed values. Predictions of monthly rainfall correlate poorly. Virtually all models agree that significant increases in temperature (from 1 to 7-degrees-C) will occur in the region including Thailand following a doubling in atmospheric carbon dioxide (CO2) concentration. The regional seasonality and extent of the rise in temperature varies with each model. Predictions of changes in rainfall vary widely between models. Global warming should in principle allow a northward expansion of rice-growing areas and a lengthening of the growing season now constrained by low temperatures. The expected increase in water-use efficiency due to enhanced CO2 might decrease the water deficit vulnerability of dryland rice areas and could make it possible to slightly expand them.

KEYWORDS: AMBIENT

91

Bachelet, D., and C.A. Gay. 1993. The impacts of climate change on rice yield - a comparison of 4 model performances. *Ecological Modelling 65(1-2):71-93.*

Increasing concentrations of carbon dioxide (CO2) and other greenhouse gases are expected to modify the climate of the earth in the next 50-100 years. Mechanisms of plant response to these changes need to be incorporated in models that predict crop yield estimates to obtain an understanding of the potential consequences of such changes. This is particularly important in Asia where demographic forecasts indicate that rice supplies worldwide will need to increase by 1.6% annually to the year 2000 to match population growth estimates. The objectives of this paper are (1) to review the major hypotheses and/or experimental results regarding rice sensitivity to climate change and (2) to evaluate the suitability of existing rice models for assessing the impact of global climate change on rice production. A review of four physiologically-based rice models (RICEMOD, CERES-Rice, MACROS, RICESYS) illustrates their potential to predict rice responses to elevated CO2 and increased temperature. RICEMOD does not respond to increases in CO2 nor to large increases in temperature. Both MACROS and CERES (wetland rice) responses to temperature and CO2 agree with recent experimental data. RICESYS is an ecosystem model which predicts herbivory and inter-species competition between rice and weeds but does not respond to CO2. Its response to increasing temperature also agrees with experimental data.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, CROP PLANTS, DRY-MATTER PRODUCTION, DYNAMICS, ECOSYSTEMS, PLANT GROWTH, RESPONSES, SIMULATION-MODEL, TEMPERATURE

92

Backhausen, J.E., and R. Scheibe. 1999. Adaptation of tobacco plants to elevated CO2: influence of leaf age on changes in physiology, redox states and NADP-malate dehydrogenase activity. *Journal of*

Experimental Botany 50(334):665-675.

Transgenic tobacco plants (Nicotiana tabacum L. cv. Xanthi) with altered chloroplast NADP-malate dehydrogenase (NADP-MDH) content were grown under ambient or under doubled atmospheric CO2 in order to analyse the effect of elevated CO2 on the redox state of the chloroplasts. Since large differences exist between the individual leaves of tobacco plants, gas exchange characteristics, enzyme capacities and metabolite contents were measured separately for each leaf of the plants, Large variations between leaves of different age were found in nearly every parameter analysed, and the differences between younger and older leaves were, in most cases, larger than the differences between comparable leaves at ambient or elevated CO2. For all parameters (chlorophyll fluorescence, P700 reduction, NADP-MDH activation) that are indicative for the redox situation in the electron transport chains and in the chloroplast stroma, more oxidized values were determined under elevated CO2. The increased redox state of ferredoxin, observed at ambient conditions in the NADP-MDH-under-expressing plants, disappeared under elevated CO2. It was concluded that the reduced rate of photorespiration under elevated CO2 decreases the amount of excess electrons. Interestingly, this lowered not only the activation state of NADP-MDH, but also the expression of the enzyme in the wild-type plants. The results are discussed with respect to a possible interaction between stromal reduction state and gene expression.

KEYWORDS: ACCLIMATION, CHLOROPHYLL FLUORESCENCE, DEVELOPMENTAL-CHANGES, EXPRESSION, ISOLATED SPINACH-CHLOROPLASTS, LEAVES, PHOTOSYNTHETIC ELECTRON-TRANSPORT, QUANTUM YIELD, SATURATING LIGHT, TRANSCRIPTION FACTOR

93

Badger, M. 1992. Manipulating agricultural plants for a future high CO2 environment. *Australian Journal of Botany 40(4-5):421-429.*

This paper discusses the potential ways in which C3 plant performance may benefit from a future high-CO2 environment. These include increases in the efficiencies for light, nitrogen and water utilisation, particularly at elevated temperatures, resulting from the improvement which will occur in the performance of the primary carboxylating enzyme, Rubisco. However, while growth experiments at elevated CO2 indicate that C3 plants show stimulation of dry matter accumulation, the potential gains are greatly ameliorated by a redistribution of plant resources. This primarily occurs via a reduction in the leaf area ratio which offsets increases in the net assimilation rate. In addition, there may be an overcommitment of nitrogen in key photosynthetic components such as Rubisco and the thylakoid electron transport system. It is concluded that plants may not be genetically adapted to optimise their growth and performance at elevated CO2 and that consideration should be given to exploring avenues for manipulating plants for more optimal responses. Targets for improvement of growth at elevated CO2 include (1) altering source-sink relations; (2) improving the redistribution of nitrogen between the photosynthetic machinery and the rest of the plant; and (3) changing the response of stomata to CO2 and humidity to increase water-use efficiency even further than is currently predicted.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE, DEPENDENCE, GROWTH, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TRANSPIRATION

94

Badiani, M., A. Dannibale, A.R. Paolacci, F. Miglietta, and A. Raschi. 1993. The antioxidant status of soybean (glycine-max) leaves grown under natural co2 enrichment in the field. *Australian Journal of Plant Physiology 20(3):275-284.*

The effects of progressively higher CO2 levels on the foliar antioxidant status were studied by growing soybean (Glycine max Merrill cv. Cresir) plants at decreasing distances from natural CO2 sources of geothermal origin in central Italy. When compared with neighbouring controls grown under normal CO2 concentration (C), soybean leaves grown at 2 x C, 7 x C and more than 20 x C showed a substantial reduction in the size of ascorbate pool and in the activity of Cu,Zn-superoxide dismutase; both the content of ascorbic acid and the activity of ascorbate peroxidase declined at 2 x C and 7 x C and recovered to the control values at 20 x C. The foliar titre of glutathione disulfide and the activities of glutathione disulfide reductase and Mn-superoxide dismutase progressively increased as CO2 concentration increased in ambient air. The results obtained suggest that the immanent risk of dioxygen toxicity associated with photosynthetic electron flow could be reduced in the presence of high CO2 levels. On the other hand, depending on both the CO2 exposure regimes and the cell compartment considered, high CO2 could promote oxidative processes which cause GSH oxidation and require an enhanced cellular ability to scavenge superoxide anion and hydrogen peroxide.

KEYWORDS: ACCUMULATION, EXCESS SULFUR, FLOW, PLANTS, RESPIRATION, TEMPERATURE

95

Badiani, M., A.R. Paolacci, A. Fusari, I. Bettarini, E. Brugnoli, M. Lauteri, F. Miglietta, and A. Raschi. 1998. Foliar antioxidant status of plants from naturally high-CO2 sites. *Physiologia Plantarum 104(4):765-771.*

We compared the foliar antioxidant status of native Agrostis stolonifera L. communities growing at two distinct CO2-enriched sites of geothermal origin (E) and at a control field location with normal CO2. Compared to the control, plants from both E- sites showed an increased size of the GSH pool, essentially due to enhanced GSSG levels, and a consequent decrease in the ratio between reduced and oxidised glutathione forms. Such differences were maintained and even enhanced in the vegetatively-propagated progenies of control and E-plants, grown under both greenhouse conditions and normal CO2 levels. The above results confirmed previous observations on native and crop plants exposed to elevated CO2 It is therefore suggested that changes in the glutathione redox balance might be of adaptive significance under conditions of permanent exposure to high CO2.

KEYWORDS: ACTIVE OXYGEN, DETOXIFICATION, DROUGHT STRESS, ELEVATED CO2, ENZYMES, EXCESS SULFUR, GLUTATHIONE, GLYCINE, LEAVES, PICEA-ABIES

96

Bailey, S., J. Rebbeck, and K.V. Loats. 1999. Interactive effects of elevated ozone plus carbon dioxide on duckweeds exposed in open-top chambers. *Ohio Journal of Science 99(2):19-25.*

The response of Lemna minor L. and Spirodela polyrhiza (L.) Schleiden to projected future ambient levels of O-3 and CO2 was studied under field conditions. The two duckweed species were treated with either charcoal-filtered air (CF), ambient O-3 (lXO(3)), tn ice ambient O-3 (2XO(3)), twice ambient CO2 plus twice ambient O-3 (2XCO(2)+2XO(3)), or chamberless open-air (OA). Two experiments were conducted. In Experiment I, L. minor was treated for 15 d with a cumulative O-3 exposure of 14.4 ppm.h. No O-3 effects were observed during Experiment I. Dry weight of individual fronds and photosynthesis per frond increased in L minor exposed to 2XCO(2)+2XO(3)(-) air. In Experiment II after 25 d of treatment (cumulative O-3 exposure of 16.2 ppm h), negative effects of 2XO(3) on the photosynthetic and growth rates of L. minor were observed. Dark respiration of L minor significantly increased in 2XO(3)-air compared with controls, but

declined significantly in 2XCO(2)+2XO(3)-air compared to those grown in 2XO(3)-air. Photosynthesis and drg weight per frond increased in 2XCO(2)+2XO(3)-air when compared with all other treatments. Measurement of A/C-i (assimilation versus intercellular CO2 concentration) curves in L. minor showed a significant reduction in carboxylation efficiency and maximum rates of photosynthesis in 2XCO(2)+2XO(3)-air compared with other treatments when expressed per weight. No differences in carboxylation efficiency were detected between treatments when expressed per frond. After 25 d of treatment, photosynthesis (per frond) and dry weight of S. polyrhiza were reduced in 2XO(3)-air, but final frond number was unaffected. Dark respiration of S. polyrhiza was unaffected in 2XO(3)(-) air, but when exposed to 2XCO(2)+2XO(3)-air, it declined significantly. Although S. polyrhiza photosynthesis per frond increased in 2XCO(2)+2XO(3)-air, dry weight was unaffected when compared with all other treatments. Only when comparisons were made between S. polyrhiza grown in 2XCO(2)+2XO(3)-air and 2XO(3)-air, were significant increases in dry weight observed. The addition of 2XCO(2) to 2XO(3)-air resulted in amelioration of negative O-3 effects for most responses for both duckweed species.

KEYWORDS: ASPEN CLONES, ATMOSPHERIC CO2, CO2 CONCENTRATION, FIELD, GROWTH, O-3, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC RESPONSES, PLANTS, SULFUR-DIOXIDE

97

Baille, M., R. RomeroAranda, and A. Baille. 1996. Gas-exchange responses of rose plants to CO2 enrichment and light. *Journal of Horticultural Science 71(6):945-956.*

This paper describes the response of gas exchange rates and water use efficiency of rose plants, by means of the characterization in situ and the analysis of the response of photosynthesis, transpiration and water use efficiency of whole plants to CO2 enrichment under the irradiance conditions prevailing in greenhouses of southern France. Net CO2 assimilation (A(n)) and transpiration (E) of whole rose plants (Rosa hybrida, cv. Sonia) were measured during winter and spring periods. The response of A(n) to light and CO2 were fitted to a double hyperbola function (r(2) = 0.84). Maximum net assimilation rate (A(nmax)), light and CO2 utilization efficiencies (alpha(1), alpha(c)) as well as light and CO2 compensation points (Gamma(1), Gamma(c)) were calculated for the whole plant and compared with leaf and canopy data in the literature. The whole-plant characteristics generally had values intermediate between those related to leaf and canopy. Light saturation at subambient air CO2 concentration (C-a) was reached for relatively low PFFD values (300 mu mol m(-2) s(- 1)), whereas at ambient and enriched C-a light saturation occurs for PPFD approximate to 1000 mu mol m(-2) s(-1). Doubling C-a from 350 to 700 mu mol mol(-1) increased A(nmax) and alpha(1) by respectively 40% and 30%, while reducing Gamma(1) by 27%. A threefold increase of C-a from 350 to 1050 mu mol mol(-1) induced a reduction of 20% of E. Instantaneous transpirational water use efficiency, WUE (=A(n)/E), is relatively insensitive to PPFD, although a slight decrease with PPFD is observed at high CO2 concentration, but shows marked variations with C-a and leaf to air vapour pressure deficit (D- 1). Increase of C-a from 350 to 1000 mu mol mol(-1) gave about 50% increase in WUE. Increase of D-1 from 0 to 2 kPa induced 30% decrease in WUE at ambient C-a and 50% decrease at 1000 mu mol mol(-1).

KEYWORDS: CARBON DIOXIDE, CROP, LEAF CONDUCTANCE, LEAVES, NET PHOTOSYNTHESIS, PRODUCTIVITY, SWEET-PEPPER, TOMATO, TRANSPIRATION, WATER-USE EFFICIENCY

98

Bainbridge, G., P. Madgwick, S. Parmar, R. Mitchell, M. Paul, J. Pitts, A.J. Keys, and M.A.J. Parry. 1995. Engineering rubisco to change its catalytic properties. *Journal of Experimental Botany 46:1269-1276.*

The initial steps of carbon assimilation and photorespiration are catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase (EC 4.1.1.39). Natural variation in the kinetic properties of the enzyme suggest that it is possible to alter the enzyme to favour the carboxylation activity relative to oxygenation, Mutagenesis in vitro of the gene encoding the large subunit of the enzyme from Anacystis nidulans has been used to modify catalytic properties. Residues at the C-terminal end of loop 6 of the beta/alpha barrel structure of the large subunit influence specificity towards the gaseous substrates, CO2 and O-2. None of the residues altered by mutagenesis appear to interact directly with the transition state analogue and their effect on the reaction of the enediolate intermediate with the gaseous substrates and stabilization of the resulting transition state intermediates by lysine 334 must be indirect. Interactions with other parts of the enzyme must also be important in determining substrate specificity, Backbone carbonyl groups close to lysine 334 interact with lysine 128; mutation of lysine 128 to residues of less positive polarity reduces enzyme activity and favours oxygenation relative to carboxylation, the likely effects on assimilation rates of altering the kinetic properties of Rubisco have been modelled. A leaf with cyanobacterial Rubisco may out-perform a higher plant Rubisco at elevated CO2 and cool temperatures.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE, ACTIVE-SITE, CO2/O2 SPECIFICITY, LARGE SUBUNIT, RHODOSPIRILLUM-RUBRUM, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SITE-DIRECTED MUTAGENESIS, SUBSTRATE-SPECIFICITY

99

Baker, J.T., S.L. Albrecht, D. Pan, L.H. Allen, N.B. Pickering, and K.J. Boote. 1994. Carbon-dioxide and temperature effects on rice (oryza-sativa L, CV ir-72). *Soil and Crop Science Society of Florida Proceedings 53:90-97.*

The current increase in atmospheric carbon dioxide concentration ([CO2]) along with predictions of possible future increases in global air temperatures have stimulated interest in the effects of [CO2] and temperature on the growth and yield of food crops. This study was conducted to determine the effects and possible interactions of elevated [CO2] and temperature on the development, growth and yield of rice (Oryza sativa L., cv. IR-72). Rice plants were grown season-long in outdoor, naturally sunlit, controlled-environment, plant growth chambers. Chamber air temperatures were controlled to follow a continuously and diurnally varying, near sine-wave control setpoint that operated between maximum (daytime) and minimum (nighttime) values. Day/night (maximum/minimum) air temperature treatments were: 32/23, 35/26, and 38/29-degrees-C. Dewpoint air temperatures were maintained at 18, 21, 24- degrees-C in the 32/23, 35/26, 38/29-degrees-C dry bulb air temperature treatment, respectively. Daytime [CO2] was controlled to 330 and 660 mumol CO2 mol-1 air in each of the air temperature treatments. The time interval between appearance of successive mainstrem leaves during reproductive development was reduced by increasing air temperature treatment (P less-than-or-equal-to 0.05) but was not affected by [CO2] enrichment. In this experiment [CO2] enrichment did not affect (P less-than-or-equal-to 0.10) grain yield, components of grain yield, final above ground biomass or harvest index. Increasing temperature during growth, particularly from the 35/26 to 38/29-degrees-C reduced grain yield, individual grain mass, and harvest index. The reduced grain yields with increasing temperature treatment suggest potential detrimental effects on rice production in some areas if air temperatures increase.

100

Baker, J.T., and L.H. Allen. 1993. Contrasting crop species responses to co2 and temperature - rice, soybean and citrus. *Vegetatio 104:239-260.*

The continuing increase in atmospheric carbon dioxide concentration ([CO2]) and projections of possible future increases in global air temperatures have stimulated interest in the effects of these climate variables on plants and, in particular, on agriculturally important food crops. Mounting evidence from many different experiments suggests that the magnitude and even direction of crop responses to [CO2] and temperature is almost certain to be species dependent and very likely, within a species, to be cultivar dependent. Over the last decade, [CO2] and temperature experiments have been conducted on several crop species in the outdoor, naturally- sunlit, environmentally controlled, plant growth chambers by USDA-ARS and the University of Florida, at Gainesville, Florida, USA. The objectives for this paper are to summarize some of the major findings of these experiments and further to compare and contrast species responses to [CO2] and temperature for three diverse crop species: rice (Oryza sativa, L.). soybean (Glycine max, L.) and citrus (various species). Citrus had the lowest growth and photosynthetic rates but under [CO2] enrichment displayed the greatest percentage increases over ambient [CO2] control treatments. In all three species the direct effect of [CO2] enrichment was always an increase in photosynthetic rate. In soybean, photosynthetic rate depended on current [CO2] regardless of the long-term [CO2] history of the crop. In rice, photosynthetic rate measured at a common [CO2], decreased with increasing long-term [CO2] growth treatment due to a corresponding decline in RuBP carboxylase content and activity. Rice specific respiration decreased from subambient to ambient and superambient [CO2] due to a decrease in plant tissue nitrogen content and a decline in specific maintenance respiration rate. In all three species, crop water use decreased with [CO2] enrichment but increased with increases in temperature. For both rice and soybean, [CO2] enrichment increased growth and grain yield. Rice grain yields declined by roughly 10% per each 1-degrees-C rise in day/night temperature above 28/21-degrees-C.

KEYWORDS: ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, DARK RESPIRATION, DEVELOPMENTAL STAGES, ELEVATED CO2, SHORT- TERM, SOUR ORANGE TREES, WATER-USE EFFICIENCY

101

Baker, J.T., and L.H. Allen. 1994. Assessment of the impact of rising carbon-dioxide and other potential climate changes on vegetation. *Environmental Pollution 83(1-2):223-235.*

The projected doubling of current levels of atmospheric carbon dioxide concentration ([CO2]) during the next century along with increases in other radiatively active gases have led to predictions of increases in global air temperature and shifts in precipitation patterns. Additionally, stratospheric ozone depletion may result in increased ultraviolet-B (UV-B) radiation incident at the Earth's surface in some areas. Since these changes in the Earth's atmosphere may have profound effects on vegetation, the objectives of this paper are to summarize some of the recent research on plant responses to [CO2], temperature and UV-B radiation. Elevated [CO2] increases photosynthesis and usually results in increased biomass, and seed yield. The magnitude of these increases and the specific photosynthetic response depends on the plant species, and are strongly influenced by other environmental factors including temperature, light level, and the availability of water and nutrients. While elevated [CO2] reduces transpiration and increases photosynthetic water-use efficiency, increasing air temperature can result in greater water use, accelerated plant developmental rate, and shortened growth duration. Experiments on UV-B radiation exposure have demonstrated a wide range of photobiological responses among plants with decreases in photosynthesis and plant growth among more sensitive species. Although a few studies have addressed the interactive effects of [CO2] and temperature on plants, information on the effects of UV-B radiation at elevated [CO2] is scarce. Since [CO2], temperature and UV-B radiation may increase concurrently, more research is needed to determine plant responses to the interactive effects of these environmental variables.

KEYWORDS: DIFFERENT CO2 ENVIRONMENTS, DRY-MATTER PRODUCTION, FIELD CONDITIONS, HIGH ATMOSPHERIC CO2, MILD WATER-STRESS, NET PHOTOSYNTHESIS, PHOTON FLUX-DENSITY, PLANT GROWTH, SOYBEAN CANOPY PHOTOSYNTHESIS, ULTRAVIOLET-B RADIATION

102

Baker, J.T., L.H. Allen, and K.J. Boote. 1990. Growth and yield responses of rice to carbon-dioxide concentration. *Journal of Agricultural Science 115:313-320.*

Rice plants (Oryza sativa L., cv. IR30) were grown in paddy culture in outdoor, naturally sunlit, controlled-environment, plant growth chambers at Gainesville, Florida, USA, in 1987. The rice plants were exposed throughout the season to subambient (160 and 250), ambient (330) or superambient (500, 660, 900 mu-mol CO2/mol air) CO2 concentrations. Total shoot biomass, root biomass, tillering, and final grain yield increased with increasing CO2 concentration, the greatest increase occurring between the 160 and 500 mu-mol CO2/mol air treatments. Early in the growing season, root:shoot biomass ratio increased with increasing CO2 concentration; although the ratio decreased during the growing season, net assimilation rate increased with increasing CO2 concentration and decreased during the growing season. Differences in biomass and lamina area among CO2 treatments were largely due to corresponding differences in tillering response. The number of panicles/plant was almost entirely responsible for differences in final grain yield among CO2 treatments. Doubling the CO2 concentration from 330 to 660 mu-mol CO2/mol air resulted in a 32% increase in grain yield. These results suggest that important changes in the growth and yield of rice may be expected in the future as the CO2 concentration of the earth's atmosphere continues to rise.

KEYWORDS: ATMOSPHERIC CO2, CENTURIES, CROP PLANTS, DRY-MATTER, ENRICHMENT, ICE CORE, LEAF-AREA, PLANT GROWTH, TEMPERATURE, WHEAT

103

Baker, J.T., L.H. Allen, and K.J. Boote. 1992. Response of rice to carbon-dioxide and temperature. *Agricultural and Forest Meteorology 60(3-4):153-166.*

The current increase in atmospheric carbon dioxide concentration ([CO2]) along with predictions of possible future increases in global air temperatures have stimulated interest in the effects of [CO2] and temperature on the growth and yield of food crops. This study was conducted to determine the effects and possible interactions of [CO2] and temperature on the growth and yield of rice (Oryza sativa L., cultivar IR-30). Rice plants were grown for a season in outdoor, naturally sunlit, controlled-environment, and plant growth chambers. Temperature treatments of 28/21/25, 34/27/31, and 40/33/37- degrees-C (daytime dry bulb air temperature/night-time dry bulb air temperature/paddy water temperature) were maintained in [CO2] treatments of 330 and 660-mu-mol CO2 mol-1 air. In the 40/33/37-degrees-C temperature treatment, plants in the 330-mu- mol mol-1 [CO2] treatment died during stem extension while the [CO2] enriched plants survived but produced sterile panicles. Plants in the 34/27/31-degrees-C temperature treatments accumulated biomass and leaf area at a faster rate early in the growing season than plants in the 28/21/25-degrees-C temperature treatments.

Tillering increased with increasing temperature treatment. Grain yield increases owing to [CO2] enrichment were small and non-significant. This lack of [CO2] response on grain yield was attributed to the generally lower levels of solar irradiance encountered during the late fall and winter when this experiment was conducted. Grain yields were affected much more strongly by temperature than [CO2] treatment. Grain yields declined by an average of approximately 7-8% per 1-degrees-C rise in temperature from the 28/21/25 to 34/27/31-degrees-C temperature treatment. The reduced grain yields with increasing temperature treatment suggests potential detrimental effects on rice production in some areas if air temperatures increase, especially under conditions of low solar irradiance.

KEYWORDS: AIR- TEMPERATURE, CLIMATE SENSITIVITY, CO2-ENRICHMENT, ENVIRONMENTS, ORYZA SATIVA L, PHOTOSYNTHESIS, PLANT GROWTH, TRANSPIRATION, WHEAT, YIELD

104

Baker, J.T., L.H. Allen, and K.J. Boote. 1992. Temperature effects on rice at elevated co2 concentration. *Journal of Experimental Botany 43(252):959-964.*

The continuing increase in atmospheric carbon dioxide concentration ([CO2]) and projections of possible future increases in global air temperatures have stimulated interest in the effects of these climate variables on agriculturally important food crops. This study was conducted to determine the effects of [CO2] and temperature on rice (Oryza sativa L., cv. IR-30). Rice plants were grown season-long in outdoor, naturally sunlit, controlled-environment, plant growth chambers in temperature regimes ranging from 25/18/21-degrees-C to 37/30/34-degrees-C (daytime dry bulb air temperature/night-time dry bulb air temperature/paddy water temperature) and [CO2] of 660-mu-mol CO2 mol-1 air. An ambient chamber was maintained at a [CO2] of 330-mu-mol mol-1 and temperature regime of 28/21/25- degrees-C. Carbon dioxide enrichment at 28/21/25-degrees-C increased both biomass accumulation and tillering and increased grain yield by 60%. In the 660-mu-mol mol-1 [CO2] treatment, grain yield decreased from 10.4 to 1.0 Mg ha-1 with increasing temperature from 28/21/25-degrees-C to the 37/30/34-degrees-C temperature treatment. Across this temperature range, the number of panicles plant-1 nearly doubled while the number of seeds panicle-1 declined sharply. These results indicate that while future increases in atmospheric [CO2] are likely to be beneficial to rice growth and yield, potentially large negative effects on rice yield are possible if air temperatures also rise.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, ENRICHMENT, GROWTH, ORYZA SATIVA L, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION, WHEAT, YIELD

105

Baker, J.T., L.H. Allen, K.J. Boote, and N.B. Pickering. 1997. Rice responses to drought under carbon dioxide enrichment .1. Growth and yield. *Global Change Biology 3(2):119-128.*

Projections of future climate change include a strong likelihood of a doubling of current atmospheric carbon dioxide concentration ([CO2]) and possible shifts in precipitation patterns. Drought stress is a major environmental limitation for crop growth and yield and is common in rainfed rice production systems. This study was conducted to determine the growth and grain yield responses of rice to drought stress under [CO2] enrichment. Rice (cv. IR-72) was grown to maturity in eight naturally sunlit, plant growth chambers in atmospheric carbon dioxide concentrations [CO2] of 350 and 700 mu mol CO2 mol(-1) air. In both [CO2], water management treatments included continuously hooded (CF) controls, flood water removed and drought stress imposed at panicle initiation (PI), anthesis (ANT), and both panicle initiation and anthesis (PI & ANT). The [CO2] enrichment increased growth, panicles plant(-1) and grain yield. Drought accelerated leaf senescence, reduced leaf area and above-ground biomass and delayed crop ontogeny. The [CO2] enrichment allowed 1-2 days more growth during drought stress cycles. Grain yields of the PI and PI & ANT droughts were similar to the CF control treatments while the ANT drought treatment sharply reduced growth, grain yield and individual grain mass. We conclude that in the absence of air temperature increases, future global increases in [CO2] should promote rice growth and yield while providing a modest reduction of near 10% in water use and so increase drought avoidance.

KEYWORDS: CO2- ENRICHMENT, CULTIVAR, INCREASE, NUTRITION, ORYZA SATIVA L, WHEAT

106

Baker, J.T., L.H. Allen, K.J. Boote, and N.B. Pickering. 1997. Rice responses to drought under carbon dioxide enrichment .2. Photosynthesis and evapotranspiration. *Global Change Biology 3(2):129-138.*

Future climate change is projected to include a strong likelihood of continued increases in atmospheric carbon dioxide concentration ([CO2]) and possible shifts in precipitation patterns. Due mainly to uncertainties in the timing and amounts of monsoonal rainfall, drought is common in rainfed rice production systems. The objectives of this study were to quantify the effects and possible interactions of [CO2] and drought stress on rice (Oryza sativa, L.) photosynthesis, evapotranspiration and water-use efficiency. Rice (cv. IR-72) was grown to maturity in eight naturally sunlit, plant growth chambers in atmospheric carbon dioxide concentrations [CO2] of 350 and 700 mu mol CO2 mol(-1) air. In both [CO2], water management treatments included continuously flooded controls, flood water removed and drought stress imposed at panicle initiation, anthesis, and both panicle initiation and anthesis. Potential acclimation of rice photosynthesis to long-term [CO2] growth treatments of 350 and 700 mu mol mol(-1) was tested by comparing canopy photosynthesis rates across short-term [CO2] ranging from 160 to 1000 mu mol mol(-1). These tests showed essentially no acclimation response with photosynthetic rate being a function of current short-term [CO2] rather than long- term [CO2] growth treatment. In both long-term [CO2] treatments, photosynthetic rate saturated with respect to [CO2] near 510 mu mol mol(-1). Carbon dioxide enrichment significantly increased both canopy net photosynthetic rate (21-27%) and water-use efficiency while reducing evapotranspiration by about 10%. This water saving under [CO2] enrichment allowed photosynthesis to continue for about one to two days longer during drought in the enriched compared with the ambient [CO2] control treatments.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBOXYLASE, DIFFERENT CO2 ENVIRONMENTS, DRY-MATTER PRODUCTION, ELEVATED CO2, PLANT GROWTH, SOYBEAN LEAVES, TEMPERATURE, TRANSPIRATION

107

Balaguer, L., J.D. Barnes, A. Panicucci, and A.M. Borland. 1995. Production and utilization of assimilates in wheat (triticum- aestivum L) leaves exposed to elevated o-3 and/or co2. *New Phytologist 129(4):557-568.*

This study examined the effects of elevated ozone (O-3) and/or carbon dioxide (CO2) on the diel allocation of photosynthetically fixed carbon in fully expanded leaves of young (growth stages 4-5) spring wheat (Triticum aestivum L. cv. Hanno). Plants were grown in controlled environment chambers and exposed to two O-3 regimes ['non-polluted' air (CF), < 5 nmol mol(-1); 'polluted' air, CF + 75 nmol mol(-1) 7 h d(-

1)] and two CO2 treatments ('ambient', 354 mu mol mol(-1); 'elevated', 700 mu mol mol(-1)) over a 30 d period. Neutral sugars (predominantly sucrose) were found to be the most abundant form of carbohydrate accumulated by leaves during the day, but significant quantities of starch and high degree of polymerization (d.p.) fructans were also present. Elevated concentrations of O-3 and/or CO2 were found to have marked effects on diel patterns of export, storage and respiration, whilst the proportions of fixed carbon allocated to each of these processes were broadly similar. O-3 depressed the rate of net CO2 assimilation (-20%) and reduced stomatal conductance (- 19%). This was reflected in a reduced amount of carbohydrate accumulated in, and exported by, source tissue during the day. Effects of O-3 on the rate of CO2 fixation were aggravated by an increased demand for carbon by dark respiratory processes. In contrast, doubling the atmospheric concentration of CO2 enhanced the rate of net CO2 assimilation (+ 47%) and reduced the proportion of fixed carbon retained in the leaf blade, increasing the rate of export. The favourable carbon balance of CO2 enriched leaves was further enhanced by a decrease in the cost of maintenance respiration, whilst simultaneous measurements of CO2 efflux and O-2 uptake at night suggested a shift in the substrates metabolized at high CO2. Effects of elevated CO2 and O-3 on the carbon balance of individual leaf blades over a single 24 h light/dark cycle were entirely consistent with the cumulative effects of the gases on plant growth over a 30 d period. O-3 reduced the rate of plant growth (-10%), but there were differential effects of O-3 on the growth of root and shoot which exacerbated the decrease in assimilate availability induced by O-3. In contrast the favourable effects of CO2 enrichment on the carbon balance of individual source leaves was reflected in the enhanced accumulation of dry matter in existing sinks, and the initiation of new sinks (i.e. increased tillering). In the combined treatment (elevated CO2 + O-3), O-3 counteracted the favourable effects of CO2 enrichment on the carbon balance of individual leaves, and the combined effects of the individual gases on the diel partitioning of photosynthetically fixed carbon in fully expanded leaf blades was reflected in a decreased rate of plant growth at elevated CO2, a situation further exacerbated by O-3-induced shifts in the relative partitioning of carbon between root and shoot. There was no evidence that CO2 enrichment afforded additional protection against O-3 damage: the extent of the O-3-induced reduction in photosynthesis, carbohydrate availability and growth observed at elevated CO2 was similar to that induced by O-3 in ambient air, despite additive effects of the gases on stomatal conductance that would reduce the effective dose of O-3 by approximate to 30%. The wider ecological significance of interactions between elevated CO2 and O-3 is discussed in the light of other recent findings.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, CLIMATE CHANGE, GAS-EXCHANGE, LEAF BLADES, MAINTENANCE RESPIRATION, OPEN-TOP CHAMBERS, OZONE, PICEA-ABIES L, SOURCE-SINK RELATIONS

108

Balaguer, L., E. Manrique, A. de los Rios, C. Ascaso, K. Palmqvist, M. Fordham, and J.D. Barnes. 1999. Long-term responses of the green-algal lichen Parmelia caperata to natural CO2 enrichment. *Oecologia 119(2):166-174.*

Acclimation to elevated CO2 was investigated in Parmelia caperata originating from the vicinity of a natural CO2 spring, where the average daytime CO2 concentration was 729 +/- 39 mu mol mol(-1) dry air. Thalli showed no evidence of a down- regulation in photosynthetic capacity following long-term exposure to CO2 enrichment in the field; carboxylation efficiency, total Ribulose bisphosphate carboxylase/oxygenase (Rubisco) content, apparent quantum yield of CO2 assimilation, and the light-saturated rate of CO2 assimilation (measured under ambient and saturating CO2 concentrations) were similar in thalli from the naturally CO2 enriched site and an adjacent control site where the average long-term CO2 concentration was about 355 mu mol mol(-1). Thalli from both CO2 environments exhibited low CO2 compensation points and early saturation of CO2 uptake kinetics in response to increasing external CO2 concentrations, suggesting the presence of an active carbon- concentrating mechanism. Consistent with the lack of significant effects on photosynthetic metabolism, no changes were found in the nitrogen content of thalli following prolonged exposure to elevated CO2. Detailed intrathalline analysis revealed a decreased investment of nitrogen in Rubisco in the pyrenoid of algae located in the elongation zone of thalli originating from elevated CO2, an effect associated with a reduction in the percentage of the cell volume occupied by lipid bodies and starch grains. Although these differences did not affect the photosynthetic capacity of thalli, there was evidence of enhanced limitations to CO2 assimilation in lichens originating from the CO2-enriched site. The light-saturated rate of CO2 assimilation measured at the average growth CO2 concentration was found to be significantly lower in thalli originating from a CO2-enriched atmosphere compared with that of thalli originating and measured at ambient CO2, At lower photosynthetic photon flux densities, the light compensation point of net CO2 assimilation was significantly higher in thalli originating from elevated CO2 and this effect was associated with higher usnic acid content.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, CHLOROPHYTA, ELEVATED CO2, EXCHANGE, GROWTH, PHOTOBIONTS, PHOTOSYNTHESIS, PLANTS, RISING ATMOSPHERIC CO2, WATER-CONTENT

109

Balaguer, L., F. Valladares, C. Ascaso, J.D. Barnes, A. DelosRios, E. Manrique, and E.C. Smith. 1996. Potential effects of rising tropospheric concentrations of CO2 and O-3 on green-algal lichens. *New Phytologist 132(4):641-652.*

Parmelia sulcata Taylor was used as a model to examine the effects of elevated CO2 and/or O-3 on green algal lichens. Thalli were exposed for 30 d in duplicate controlled- environment chambers to two atmospheric concentrations of CO2 ('ambient' [350 mu mol mol(-1)] and 'elevated' [700 mu mol mol(-1)] 24 h d(-1)) and two O-3 regimes ('non-polluted' air [CF, < 5 nmol mol(-1)] and 'polluted' air [15 nmol mol(-1) overnight rising to a midday maximum of 75 nmol mol(-1)]), in a factorial design. Elevated CO2 or elevated O-3 depressed the light saturated rate of CO2 assimilation (A(sat)) measured at ambient CO2 by 30%, and 18%, respectively. However, despite this effect ultrastructural studies revealed increased lipid storage in cells of the photobiont in response to CO2-enrichment. Simultaneous exposure to elevated O-3 reduced CO2-induced lipid accumulation and reduced A(sat) in an additive manner. Gold-antibody labelling revealed that the decline in photosynthetic capacity induced by elevated CO2 and/or O-3 was accompanied by a parallel decrease in the concentration of Rubisco in the algal pyrenoid (r = 0.93). Interestingly, differences in the amount of Rubisco protein were not correlated with changes in pyrenoid volume. Measurements of in vivo chlorophyll-fluorescence induction kinetics showed that the decline in A(sat) induced by elevated CO2 and/or O-3 was not associated with significant changes in the photochemical efficiency of photosystem (PS)II. Although the experimental conditions inevitably imposed some stress on the thalli, revealed a significant decline in the efficiency of PS II photochemistry, and enhanced starch accumulation in the photobiont over the fumigation period, the study shows that the green-algal lichen symbiosis might be influenced by future changes in atmospheric composition. Photosynthetic capacity, measured at ambient CO2, was found to be reduced after a controlled 30 d exposure to elevated CO2 and/or O-3 and this effect was associated with a parallel decline in the amount of Rubisco in the pyrenoid of algal chloroplasts.

KEYWORDS: BISPHOSPHATE CARBOXYLASE OXYGENASE, CARBON, CHLORELLA, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWTH, OZONE, PARMELIA-SULCATA,

PHOTOSYNTHESIS, ULTRASTRUCTURE

110

Baldocchi, D. 1994. A comparative-study of mass and energy-exchange rates over a closed C-3 (wheat) and an open C-4 (corn) crop .2. Co2 exchange and water-use efficiency. *Agricultural and Forest Meteorology 67(3-4):291-321.*

Major differences exist between the photosynthetic and transpiration rates Of C3 and C4 leaves as a result of biochemical and physiological factors. Whether or not differences between CO2 and water vapor exchange rates Of C3 and C4 species scale from leaf to field dimensions is poorly known. The aim of this work is to improve our understanding on how environmental, architectural and physiological variables affect the flux densities Of CO2 and water vapor over C3 and C4 crop stands during day and night periods. Experimental data were obtained over a closed wheat and an open com stand using the eddy correlation method. Interpretation of the field measurements is aided by the use of a canopy photosynthesis/evaporation model. The flux density of absorbed photosynthetically active radiation (Q(a)) had a disproportionate influence on CO2 flux densities measured over a closed C3 and an open C4 crop. Variations in Q(a) explained over 88% of the variance in daytime CO2 flux densities, F(c). At night, canopy radiative temperature was the main environmental factor controlling the respiratory CO2 efflux by the two crops. Leaf area index and growth stage were the plant variables that affected F(c) most. Incremental increases in leaf area index enhanced the com crop's ability to absorb incident solar radiation and enlarged the com's sink strength for CO2. Heading by the wheat caused rates of daytime CO2 gains to decrease and rates of night-time CO2 losses to increase. Water use efficiency of the wheat crop improved as the absolute humidity deficit of the atmosphere decreased. Water use efficiency of the com, on the other hand, was relatively insensitive to humidity deficits. With regard to canopy CO2 exchange and water use efficiency, differences in canopy structure between the wheat and com overwhelmed physiological differences. The closed C3 wheat crop assimilated CO2 at a higher rate than the sparse C4 com canopy, even though com uses a more efficient photosynthetic pathway. Consequently, water use efficiency of the com was not greater than values measured over the wheat, Instead, water use efficiencies of the two crops were similar. The com crop assimilated CO2 at a lower rate than wheat because the com's canopy quantum yield was lower and because its sparse canopy absorbed less photosynthetically active radiation than the closed wheat stand.

KEYWORDS: ASSIMILATION, CANOPY, CARBON DIOXIDE, FLUX MEASUREMENTS, LEAF-AREA INDEX, PHOTOSYNTHESIS, SOIL RESPIRATION, STOMATAL CONDUCTANCE, VAPOR, WINTER-WHEAT

111

Baldocchi, D.D., and P.C. Harley. 1995. Scaling carbon-dioxide and water-vapor exchange from leaf to canopy in a deciduous forest .2. Model testing and application. *Plant, Cell and Environment 18(10):1157-1173.*

The scaling of CO2 and water vapour transfer from leaf to canopy dimensions was achieved by integrating mechanistic models for physiological (photosynthesis, stomatal conductance and soil/root and bole respiration) and micrometeorological (radiative transfer, turbulent transfer and surface energy exchanges) processes, The main objectives of this paper are to describe a canopy photosynthesis and evaporation model for a temperate broadleaf forest and to test it against field measurements, The other goal of this paper is to use the validated model to address some contemporary ecological and physiological questions concerning the transfer of carbon and water between forest canopies and the atmosphere, In particular, we examine the role of simple versus complex radiative transfer models and the effect of environmental (solar radiation and CO2) and ecophysiological (photosynthetic capacity) variables on canopy-scale carbon and water vapour fluxes.

KEYWORDS: CLIMATE CHANGE, CO2 CONCENTRATIONS, ELEVATED CO2, PATTERNS, PHOTOSYNTHESIS, PLANT CANOPIES, SENSIBLE HEAT, STOMATAL CONDUCTANCE, TEMPERATURE, TRANSPIRATION

112

Ball, A.S. 1991. Degradation by Streptomyces viridosporus t7a of plant-material grown under elevated CO2 conditions. *Fems Microbiology Letters 84(2):139-142.*

The biodegradability of plant material derived from wheat grown under different concentrations of atmospheric CO2 was investigated using the lignocarbohydrate solubilising actinomycete, Streptomyces viridosporus. Growth of S. viridosporus and solubilisation of lignocarbohydrate were highest when wheat grown at ambient CO2 concentrations (350 ppm) was used as C-source. Growth of S. viridosporus and solubilisation were reduced when the plant material was derived from wheat grown at 645 PPM CO2. The results suggest that modifications in plant structure occur when wheat is grown under conditions of elevated atmospheric CO2 which make it more resistant to microbial digestion.

KEYWORDS: ENZYME, LIGNIN DEGRADATION, LIGNOCELLULOSE, POLYMERIC LIGNIN, STRAW

113

Ball, A.S. 1997. Microbial decomposition at elevated CO2 levels: effect of litter quality. *Global Change Biology 3(4):379-386.*

The decomposition of senesced plant litter represents an important intermediate step in the cycling of nutrients between above-and below-ground systems. The rate of decomposition of plant litter is sensitive to fluctuations in a number of parameters, including environmental conditions, and particularly to changes in the quality of the litter. Increased C:N ratios of litter are thought to be one possible consequence of growth of plants under elevated [CO2]. This response is likely to reduce the rate of decomposition of the litter. Evidence from the growth of plants in both pot and field studies suggests that growth of C3 plants in elevated atmospheric [CO2] (600-700 mu mol mol(-1)) may lead to a significant increase in either/both the C:N and the lignin: N ratios of litter. Short-term decomposition of lifter from plants showing this response in elevated [CO2] has confirmed that decomposition occurs at a significantly lower rate. The limited studies of both the response of C4 plants to elevated [CO2] and the subsequent degradability of the senescent litter suggest that no differences in litter quality or degradability occur. In terms of litter quality the response of plants therefore appears to be dependent upon photosynthetic type; the C:N and lignin:N ratios of litter from C3 plants exposed to elevated [CO2] are increased, leading to lower degradation rates, while the nutrient ratios and degradation rates of lifter from C4 plants grown in elevated [CO2] remain unchanged. To date, very few ecosystem studies of decomposition have been carried out. Further work is required at the ecosystem level to determine whether the effects observed in laboratory, pot and field studies are also observed in long-term, complex ecosystem studies. Clearly if these results are repeated at the ecosystem level then significant changes in the cycling of C and N in important terrestrial ecosystems may occur as a results of elevated [CO2].

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ECOSYSTEMS, HARDWOOD LEAF LITTER, LIGNIN CONTENT, MASS-LOSS, NITROGEN DYNAMICS, PLANT-MATERIAL, RESPONSES, SOIL

114

Ball, A.S., and B.G. Drake. 1997. Short-term decomposition of litter produced by plants grown in ambient and elevated atmospheric CO2 concentrations. *Global Change Biology 3(1):29-35.*

The effects of elevated atmospheric CO2 (ambient + 340 mu mol mol(-1)) on above-ground litter decomposition were investigated over a 6-week period using a field-based mesocosm system. Soil respiratory activity in mesocosms incubated in ambient and elevated atmospheric CO2 concentrations were not significantly different (t-test, P > 0.05) indicating that there were no direct effects of elevated atmospheric CO2 on litter decomposition. A study of the indirect effects of CO2 on soil respiration showed that soil mesocosms to which naturally senescent plant litter had been added (0.5% w/w) from the C-3 sedge Scirpus olneyi grown in elevated atmospheric CO2 was reduced by an average of 17% throughout the study when compared to soil mesocosms to which litter from Scirpus olneyi grown in ambient conditions had been added. In contrast, similar experiments using senescent material from the C-4 grass Spartina patens showed no difference in soil respiration rates between mesocosms to which litter from plants grown in elevated or ambient CO2 conditions had been added. Analysis of the C:N ratio and lignin content of the senescent material showed that, while the C:N ratio and lignin content of the Spartina patens litter did not vary with atmospheric CO2 conditions, the C:N ratio (but not the lignin content) of the litter from Scirpus olneyi was significantly greater (t-test; P < 0.05) when derived from plants grown under elevated CO2 (105:1 compared to 86:1 for litter derived from Scirpus olneyi grown under ambient conditions). The results suggest that the increased C:N ratio of the litter from the C-3 plant Scirpus olneyi grown under elevated CO2 led to the lower rates of biodegradation observed as reduced soil respiration in the mesocosms. Further longterm experiments are now required to determine the effects of elevated CO2 on C partitioning in terrestrial ecosystems.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, DYNAMICS, FORESTS, INSITU, LEAF LITTER, LEAVES, NITROGEN, RESPIRATION, SOIL

115

Ball, A.S., and B.G. Drake. 1998. Stimulation of soil respiration by carbon dioxide enrichment of marsh vegetation. *Soil Biology and Biochemistry 30(8-9):1203-1205.*

KEYWORDS: ELEVATED ATMOSPHERIC CO2, INSITU, NITROGEN, PLANTS

116

Ball, M.C., M.J. Cochrane, and H.M. Rawson. 1997. Growth and water use of the mangroves Rhizophora apiculata and R-stylosa in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO2. *Plant, Cell and Environment 20(9):1158-1166.*

Two mangrove species, Rhizophora apiculata and R. stylosa, mere grown for 14 weeks in a multifactorial combination of salinity (125 and 350 mol m(-3) NaCl), humidity (43 and 86% relative humidity at 30 degrees C) and atmospheric CO2 concentration (340 and 700 cm(3) m(-3)). Under ambient [CO2], growth responses to different combinations of salinity and humidity were consistent with interspecific differences in distribution along natural gradients of salinity and aridity in northern Australia. Elevated [CO2] had little effect on relative growth rate when it was limited by salinity but stimulated growth when limited by humidity. Both species benefited most from elevated [CO2] under relatively low salinity conditions in which growth was vigorous, but relative growth rate was enhanced more in the less salt-tolerant and more rapidly growing species, R. apiculata. Changes in both net assimilation rate and leaf area ratio contributed to changes in relative growth rates under elevated [CO2], with leaf area ratio increasing with decrease in humidity. Increase in water use efficiency under elevated [CO2] occurred with increase, decrease or no change in evaporation rates; water use characteristics which depended an both the species and the growth conditions. In summary, elevated [CO2] is unlikely to increase salt tolerance, but could alter competitive rankings of species along salinity x aridity gradients.

KEYWORDS: AUSTRALIA, AVICENNIA-MARINA, CARBON DIOXIDE, COTTON, ENRICHMENT, GAS-EXCHANGE, MANGLE L, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, RED MANGROVE

117

Ball, M.C., and R. Munns. 1992. Plant-responses to salinity under elevated atmospheric concentrations of CO2. *Australian Journal of Botany 40(4-5):515-525.*

This review explores effects of elevated CO2 concentrations on growth in relation to water use and salt balance of halophytic and non-halophytic species. Under saline conditions, the uptake and distribution of sodium and chloride must be regulated to protect sensitive metabolic sites from salt toxicity. Salt-tolerant species exclude most of the salt from the transpiration stream, but the salt flux from a highly saline soil is still considerable. To maintain internal ion concentrations within physiologically acceptable levels, the salt influx to leaves must match the capacities of leaves for salt storage and/or salt export by either retranslocation or secretion from glands. Hence the balance between carbon gain and the expenditure of water in association with salt uptake is critical to leaf longevity under saline conditions. Indeed, one of the striking features of halophytic vegetation, such as mangroves, is the maintenance of high water use efficiencies coupled with relatively low rates of water loss and growth. These low evaporation rates are further reduced under elevated CO2 conditions. This, with increased growth, leads to even higher water use efficiency. Leaves of plants grown under elevated CO2 conditions might be expected to contain lower salt concentrations than those grown under ambient CO2 if salt uptake is coupled with water uptake. However, salt concentrations in shoot tissues are similar in plants grown under ambient and elevated CO2 conditions despite major differences in water use efficiency. This phenomenon occurs in C3 halophytes and in both C3 and C4 non-halophytes. These results imply shoot/root communication in regulation of the salt balance to adjust to environmental factors affecting the availability of water and ions at the roots (salinity) and those affecting carbon gain in relation to water loss at the leaves (atmospheric concentrations of water vapour and carbon dioxide).

KEYWORDS: AUSTRALIAN MANGROVE FOREST, AVICENNIA-MARINA, BARLEY, CARBON DIOXIDE, DROUGHT, GAS-EXCHANGE, GROWTH, LIMITATIONS, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS

118

Bandara, D.C., H. Nobuyasu, K.G. Ofosu-Budu, T. Ando, and K. Fujita. 1998. Effect of CO2 enrichment on biomass production, photosynthesis, and sink activity in soybean cv. Bragg and its supernodulating mutant nts 1007. *Soil Science and Plant Nutrition 44(2):179-186.*

Soybean (Glycine max L. Merr.) cv. Bragg and its supernodulating mutant nts 1007 were grown in pots containing vermiculite with a N-free nutrient solution in order to examine the effect of elevated CO2 concentration (100+20 Pa CO2) on biomass production, photosynthesis, and biological nitrogen fixation. The whole plant weight increase in Bragg was higher than in the mutant at a high CO2 concentration.

Apparent photosynthetic activities of the upper leaves in both Bragg and the mutant increased up to 14 d after treatment initiation by the CO2 enrichment and thereafter decreased to some extent. Both leaf area and leaf thickness of Bragg increased more than in nts 1007. With the elevated CO2 concentration, biological nitrogen fixation (BNF) also responded in the same manner as biomass production in both Bragg and nts 1007. The increase of BNF in Bragg was largely due to an increase in nodule weight. Starch contents in the leaves of both Bragg and the mutant increased significantly by CO2 enrichment, with a higher increase in Bragg than in its mutant. Sugar content in leaf differed only slightly in both Bragg and the mutant. N content in leaf decreased in both Bragg and its mutant, with the decrease being more pronounced in Bragg. However, in other plant parts (roots, stem, and petiole + pods), N content increased in the mutant while in Bragg, it decreased in the pod. N accumulation rate was higher in Bragg than in the mutant and increased more in Bragg than in the mutant by CO2 enrichment. The ureide content in leaf decreased in Bragg but increased in the mutant by elevated CO2 concentration. In the nodules, ureide content increased in both Bragg and the mutant by CO2 enrichment. Based on these results, it is suggested that in terms of biomass production and photosynthetic rate, Bragg responded more to elevated CO2 concentration than its mutant nts 1007. The alleviation of the stunted vegetative growth of the mutant by CO2 enrichment was limited despite the significant increase in the photosynthetic activity, presumably due to the limitation of sink activity in the growing parts and not to insufficient supply of N through BNF.

KEYWORDS: CARBON, DINITROGEN FIXATION, GROWTH, L MERRILL MUTANTS, LEGUMES, NITRATE APPLICATION, NITROGEN, NTS1007, PLANTS, ROOTS

119

Barnes, J.D., J.H. Ollerenshaw, and C.P. Whitfield. 1995. Effects of elevated co2 and/or o-3 on growth, development and physiology of wheat (triticum-aestivum L). *Global Change Biology 1(2):129-142.*

Two cultivars of spring wheat (Triticum aestivum L. cvs. Alexandria and Hanno) and three cultivars of winter wheat (cvs. Riband, Mercia and Haven) were grown at two concentrations of CO2 [ambient (355 mu mol mol(-1)) and elevated (708 mu mol mol(-1))] under two O-3 regimes [clean air (< 5 nmol mol(-1) O- 3) and polluted air (15 nmol mol(-1) O-3 at night rising to a midday maximum of 75 nmol mol(-1))] in a phytotron at the University of Newcastle-upon-Tyne. Between the two-leaf stage and anthesis, measurements of leaf gas-exchange, non-structural carbohydrate content, visible O-3 damage, growth, dry matter partitioning, yield components and root development were made in order to examine responses to elevated CO2 and/or O-3. Growth at elevated CO2 resulted in a sustained increase in the rate of CO2 assimilation, but after roughly 6 weeks' exposure there was evidence of a slight decline in the photosynthetic rate (c.-15%) measured under growth conditions which was most pronounced in the winter cultivars. Enhanced rates of CO2 assimilation were accompanied by a decrease in stomatal conductance which improved the instantaneous water use efficiency of individual leaves. CO2 enrichment stimulated shoot and root growth to an equivalent extent, and increased tillering and yield components, however, non-structural carbohydrates still accumulated in source leaves. In contrast, long-term exposure to O-3 resulted in a decreased CO2 assimilation rate (c.-13%), partial stomatal closure, and the accumulation of fructan and starch in leaves in the light. These effects were manifested in decreased rates of shoot and root growth, with root growth more severely affected than shoot growth. In the combined treatment growth of O-3-treated plants was enhanced by elevated CO2, but there was little evidence that CO2 enrichment afforded additional protection against O-3 damage. The reduction in growth induced by O-3 at elevated CO2 was similar to that induced by O-3 at ambient CO2 despite additive effects of the individual gases on stomatal conductance that would be expected to reduce the O-3 flux by 20%, and also CO2-induced increases in the provision of substrates for detoxification and repair processes. These observations suggest that CO2 enrichment may render plants more susceptible to O-3 damage at the cellular level. Possible mechanisms are discussed.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CARBON-DIOXIDE, CARBOXYLASE-OXYGENASE, GAS-EXCHANGE, MODERN GREEK CULTIVARS, PICEA-ABIES L, PLANT GROWTH, SOURCE-SINK RELATIONS, SPRING WHEAT, WINTER-WHEAT

120

Barnes, J.D., and T. Pfirrmann. 1992. The influence of co2 and o-3, singly and in combination, on gas-exchange, growth and nutrient status of radish (raphanus- sativus L). *New Phytologist 121(3):403-412.*

Five days after emergence radish (Raphanus sativus L. cv. Cherry Belle) plants were transferred to a phytotron at the GSF Munchen, where they were exposed in four large controlled climate chambers to two at atmospheric concentrations of CO2 ('ambient', daily means of almost-equal-to 385-mu-mol mol-1; elevated, daily means of almost-equal-to 765-mu-mol mol-1) and two O3 regimes ('non-polluted' air, 24 h mean of 20 nmol mol-1; polluted air, 24 h mean of 73 nmol mol-1) Leaf gas-exchange measurements were made at intervals, and visible O3 damage, effects on growth, dry matter partitioning and mineral composition were assessed at a final whole-plant harvest after 27 d. In 'non-polluted air' CO2 enrichment resulted in a progressive stimulation in A(sat), whilst there was a decline in g(s) which decreased E (i.e. improved WUE(i)). The extra carbon fixed in elevated CO2 stimulated growth of the root (+ hypocotyl) by 43 %, but there was no significant effect on shoot growth or leaf area. Moreover, a decline in SLA and LAR in CO2-enriched plants suggested that less dry matter was invested in leaf area expansion. Tissue concentrations of N, S, P, Mg and Ca were lower (particularly in the root + hypocotyl) in elevated CO2, indicating that total uptake of these nutrients was not affected by CO2, and there was an increase in the C:N ratio in root (+ hypocotyl) tissue. In contrast, O3 depressed A(sat), (almost-equal-to 26 %) and induced slight stomatal closure, with the result that WUE(i) declined. All plants exposed to 'polluted' air developed typical visible symptoms of O3 injury, and effects on carbon assimilation were reflected in reduced growth, with shoot growth maintained at the expense of the root. In addition, O3 increased the P and K concentration in shoot and root (+hypocotyl) tissue, indicating enhanced uptake of these nutrients from the growth medium. However, there was no affect of O3 on tissue concentrations of N, S, Mg and Ca. Interactions between the gases were complex, and often subtle. In general, elevated CO2 counteracted (at least in part) the detrimental effects of phytotoxic concentrations of O3, whilst conversely, O3 reduced the impact of elevated CO2. Moreover, there were indications that cumulative changes in source:sink relations in O3-exposed plants may limit plant response to CO2-enrichment to an even greater extent in the long-term. The future ecological significance of interactions between CO2 and O3 are discussed.

KEYWORDS: ABIES L KARST, ACID MIST, AIR- POLLUTANTS, CARBON DIOXIDE, ENRICHMENT, OZONE ALTERS, PHOTOSYNTHESIS, PLANTS, USE EFFICIENCY, WHEAT

121

Barnes, J.D., T. Pfirrmann, K. Steiner, C. Lutz, U. Busch, H. Kuchenhoff, and H.D. Payer. 1995. Effects of elevated CO2, elevated O-3 and potassium deficiency on Norway spruce [Picea abies (L) Karst]: Seasonal changes in photosynthesis and non-structural carbohydrate content. *Plant, Cell and Environment 18(12):1345-1357.*

Two clones of 5-year-old Norway spruce [Picea abies (L.) Karst.] were exposed to two atmospheric concentrations of CO2 (350 and 750 mu mol mol(-1)) and O-3 (20 and 75 nmol mol(-1)) in a phytotron at the

GSF-Forschungszentrum (Munich) over the course of a single season (April to October), The phytotron was programmed to recreate an artificial climate similar to that at a high elevation site in the Inner Bavarian Forest, and trees were grown in Large containers of forest soil fertilized to achieve contrasting levels of potassium nutrition, designated well-fertilized or K-deficient. Measurements of the rate of net CO2 assimilation were made on individual needle year age classes over the course of the season, chlorophyll fluorescence kinetics were recorded after approximately 23 weeks, and seasonal changes in non-structural carbohydrate composition of the current year's foliage were monitored. Ozone was found to have contrasting effects on the rate of net CO2 assimilation in different needle age classes. After c. 5 months of fumigation, elevated O-3 increased (by 33%) the rate of photosynthesis in the current year's needles, However, O-3 depressed (by 30%) the photosynthetic rate of the previous year's needles throughout the period of exposure, Chlorophyll fluorescence measurements indicated that changes in photosystem II electron transport played no significant role in the effects of O-3 on photosynthesis, The reasons for the contrasting effects of O-3 on needles of different ages are discussed in the light of other recent findings, Although O-3 enhanced the rate at which CO2 was fixed in the current year's foliage, this was not reflected in increases in the non-structural carbohydrate ate content of the needles, The transfer of ambient CO2-grown trees to a CO2-enriched atmosphere resulted in marked stimulation in the photosynthetic rate of current and previous year's foliage, However, following expansion of the current year's growth, the photosynthetic rate of the previous year's foliage declined, The extent of photosynthetic adjustment in response to prolonged exposure to elevated CO2 depended upon the clone, providing evidence of intraspecific variation in the long-term response of photosynthesis to elevated CO2, The increase in photosynthesis induced by CO2 enrichment was associated with increased foliar concentrations of glucose, fructose and starch (but no change in sucrose) in the new growth, CO2 enrichment significantly enhanced the photosynthetic rate of K-deficient needles, but there was a strong CO2*soil interaction in the current year's needles, indicating that the long-term response of trees to a high CO2 environment may depend on soil fertility, Although the rate of photosynthesis and non- structural carbohydrate content of the new needles were increased in O-3-treated plants grown at higher levels of CO2, there was no evidence that elevated CO2 provided additional protection against O-3 damage, Simultaneous exposure to elevated O-3 modified the effects of elevated CO2 on needle photosynthesis and non-structural carbohydrate content, emphasizing the need to take into account not only soil nutrient status but also the impact of concurrent increases in photochemical oxidant pollution in any serious consideration of the effects of climate change on plant production.

KEYWORDS: ACID MIST, AIR- POLLUTANTS, ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NONSTOMATAL LIMITATION, OPEN-TOP CHAMBERS, STOMATAL CONDUCTANCE

122

Barr, A.G., K.M. King, G.W. Thurtell, and M.E.D. Graham. 1990. Humidity and soil-water influence the transpiration response of maize to CO2 enrichment. *Canadian Journal of Plant Science 70(4):941-948.*

123

Barrett, D.J., and R.M. Gifford. 1995. Acclimation of photosynthesis and growth by cotton to elevated CO2: Interactions with severe phosphate deficiency and restricted rooting volume. *Australian Journal of Plant Physiology 22(6):955-963.*

Acclimation of photosynthesis and growth at three CO2 concentrations (376, 652 and 935 mu mol mol(-1)) was examined in cotton grown under three growth-limiting phosphate (P) supplies (2.1, 6.1 and 18.2 mg P plant(-1)) and where biomass allocation between roots and shoots was altered by pots of three different sizes (0.32 X 10(-3), 0.72 X 10(-3) and 1.56 x 10(-3) m(3) pot(-1)). Phosphate supplies were chosen such that carbon gain at ambient CO2 increased linearly with P supply. Relative growth rates of these plants were 5-10-times less and photosynthetic rates 3-16-times less than for cotton supplied with abundant nutrients. Pot sizes were chosen so that root biomass and root:shoot ratios decreased with a decrease in rooting volume. Maximum carboxylation rates per unit leaf area (V-cmax) were lower in leaves grown at two elevated CO2 concentrations, compared with ambient CO2 concentrations, under all P and pot size treatments indicating that acclimation of photosynthesis had occurred. The degree of photosynthetic acclimation to elevated CO2 was not related to the degree by which whole plant carbon gain was stimulated by elevated CO2 concentration at the different P supplies, or to the degree by which allocation to root and shoots was altered by pot size. Thus there is no simple relationship between photosynthetic and growth acclimation by cotton to elevated CO2. At ambient CO2, the maximum carboxylation rate increased linearly with an increase in leaf P per unit area (mg P m(-2)), but rates were lower at elevated CO2 for a given P content m(-2). V-cmax also increased linearly with an increase in leaf P concentration (mg P g(-1) structural dry weight). However, values of V-cmax were similar for plants grown at ambient and elevated CO2, for a given P concentration. Acclimation of photosynthesis at elevated CO2 was associated with an increase in leaf starch determined 5 h into the light period. However, increased starch concentration with an increase in P supply was not associated with any decline in V-cmax.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO2, CARBON DIOXIDE, GLYCINE-MAX, LEAVES, LONG-TERM EXPOSURE, NITROGEN, PHOSPHORUS-NUTRITION, PLANTS, RESPONSES

124

Barrett, D.J., and R.M. Gifford. 1995. Photosynthetic acclimation to elevated CO2 in relation to biomass allocation in cotton. *Journal of Biogeography 22(2-3):331-339.*

Biomass allocation to leaf tissues and photosynthetic acclimation to CO2 by cotton were investigated in two experiments. Plants were grown at ambient and elevated CO2 concentrations with growth restricting phosphorus supplies in both experiments and in root restricting pot volumes in the first experiment. In both experiments, elevated CO2 concentrations decreased the maximum carboxylation rate (V- cmax) and the CO2 saturated rate of photosynthesis indicative of photosynthetic acclimation to elevated CO2 concentrations. In the first experiment, the percentage reduction in V-cmax under elevated CO2 concentration was least at a P supply of 2.1 mg P plant(-1), greatest at 6.1 mg P plant(-1), but then decreased at 18.2 mg P plant(-1). The greater acclimation at the middle P supply was associated with a higher ratio of leaf mass to plant mass (LMR) than in other treatments and the lesser acclimation at the highest P treatment coincided with a lower LMR. In the second experiment the reduction in V-cmax at elevated CO2 was less than in the first experiment but was also associated with a greater allocation of dry matter to leaf tissues during growth. In both experiments, V-cmax was not correlated to the relative degree of biomass enhancement at elevated CO2 nor with the degree of root growth restriction in small pots. These data support the hypothesis that acclimation of photosynthesis to elevated CO2 concentrations is mediated by shifts in allocation between leaves and the rest of the plant, induced by environmental conditions during growth, such that carbohydrate supply remains in balance with the utilization capacity of sink tissues.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, LIMITATIONS, PLANTS, SOURCE-SINK RELATIONS

125

Barrett, D.J., and R.M. Gifford. 1999. Increased C-gain by an endemic Australian pasture grass at elevated atmospheric CO2 concentration when supplied with non- labile inorganic phosphorus. *Australian Journal of Plant Physiology 26(5):443-451.*

Limited phosphorus (P) availability in Australia's highly weathered soils may constrain an increase in terrestrial net primary productivity (NPP) with the globally increasing atmospheric CO2 concentration. We examined whether an Australian temperate pasture grass (Danthonia richardsonii) grown in sand culture and supplied solely with virtually insoluble Al- and Fe-phosphate was able to increase C-gain when exposed to elevated (731 mu mol mol(-1)) compared with ambient (379 mu mol mol(-1)) CO2 concentrations. When supplied with 8 mg kg(-1) insoluble P concentration, total citrate efflux by root systems (mu mol h(-1)), plant P uptake, shoot photosynthesis rates and plant mass were all significantly greater at elevated than at ambient CO2 after a growth period of between 55 and 63 days. In this treatment, although the P concentration of the rooting medium limited growth at ambient CO2, elevated CO2 increased P-uptake from the non-labile source, increased photosynthesis rates per unit shoot soluble-P and increased plant mass. At P concentrations lower than 8 mg kg(-1), plant mass, specific citrate efflux and maximum leaf carboxylation rates were limited by the amount of P available in the rooting medium and no CO2 effect was observed. In all treatments, carbon supply did not appear to limit citrate efflux. Where an increase in P uptake at elevated CO2 was achieved, it was due to an increase in root mass (indicative of a potentially larger soil volume explored) rather than to increased specific rates of citrate efflux. Above 8 mg kg(-1), the supplied P concentration was sufficient that minimal rates of specific citrate efflux alone solubilised enough P for growth and a strong CO2 effect on plant mass, photosynthesis and P uptake was observed.

KEYWORDS: ACCLIMATION, GROWTH, LIMITATIONS, LUPINUS-ALBUS, ORGANIC-ACIDS, PHOSPHATE, PHOTOSYNTHESIS, PROTEOID ROOTS, ROOT EXUDATION, SOLUBILIZATION

126

Barrett, D.J., A.E. Richardson, and R.M. Gifford. 1998. Elevated atmospheric CO2 concentrations increase wheat root phosphatase activity when growth is limited by phosphorus. *Australian Journal of Plant Physiology 25(1):87-93.*

Wheat seedlings were grown in solution culture under adequate and limited phosphorus treatments at current ambient and elevated (approximately 2X ambient) CO2 concentrations. Acid phosphomonoesterase ('phosphatase') activity of root segments was measured using p-nitrophenyl phosphate as substrate. When plant growth was P-limited, elevated CO2 concentrations increased phosphatase activity more than at ambient CO2. This result (1) was evident when expressed on a unit root dry weight or root length basis, indicating that increased root enzyme activity was unlikely to be associated with CO2-induced changes in root morphology; (2) occurred when plants were grown aseptically, indicating that the increase in phosphatase activity originated from root cells rather than root-associated microorganisms; (3) was associated with shoot P concentrations below 0.18%; (4) occurred only when wheat roots were grown under P deficiency but not when a transient P deficiency was imposed; and (5) suggest that a previously reported increase in phosphatase activity at elevated CO2 by an Australian native pasture grass (Gifford, Lutze and Barrett 1996; Plant and Soil 187, 369-387) was also a root mediated response. The observed increase in phosphatase activity by plant roots at elevated CO2, if confirmed for a wide range of field pasture and crop species, is one factor which may increase mineralisation of soil organic P as the anthropogenic increase of atmospheric CO2 concentrations continues. But, whether a concomitant increase in plant uptake of P occurs will depend on the relative influence of root and microbial phosphatases, and soil geochemistry in determining the rate of mineralisation of soil organic P for any given soil.

KEYWORDS: ACCLIMATION, BIOMASS, CARBON DIOXIDE, DEFICIENCY, EFFICIENCY, ENRICHMENT, ORGANIC PHOSPHORUS, PHOTOSYNTHESIS, PLANT-ROOTS, SOIL

127

Bartak, M., I. Nijs, and I. Impens. 1996. The effect of long-term exposure of Lolium perenne L plants to elevated CO2 and/or elevated air temperature on quantum yield of photosystem 2 and net photosynthesis. *Photosynthetica 32(4):549-562.*

The effects of long-term exposure of Lolium perenne L. plants to CO2 concentration elevated to 700 mu mol (CO2) mol(-1) (EC) and air temperature elevated by 4 degrees C (ET) on the quantum yield of electron transport of photosystem 2, PS2 (phi(2)) and on the potential yield of photochemical reactions of PS2 (F- v/F-m) measured by the chlorophyll (Chl) fluorescence method, were studied. The plants were exposed for 6 months in opened field greenhouses to four treatments simulating global atmospheric changes: (1) ambient CO2 (AC) and ambient air temperature, AT (ACAT - control), (2) EC and AT (ECAT), (3) AC and ET (ACET), and (4) EC and ET (ECET). When the plants were exposed to stepwise increased irradiance, a decrease in phi(2) was found under both AC and EC measuring concentrations. At high irradiances a significantly higher yield of PS2 was detected when measured under EC compared to AC regardless of long-term CO2 and temperature treatment (i.e., positive short- term. effect of EC). The short-term effect of EC on phi(2) as related to net photosynthetic rate (P-N) Shift was detected from irradiance response curves. At high irradiances and AC, phi(2) was reduced in comparison to control for the plants of EC and ET treatments (i.e., negative long-term effect of treatment). The long-term effect of both EC and ET on the yield of PS2 was attributed to a down-regulation of P-N caused by the treatment. The phi(2) was related to the actual rate of photosynthesis and the relationship between phi(2) and phi(CO2) was linear over a wide range of irradiances. No effect of long- term treatments on the dark-adapted F-v/F-m ratio was found in plants cultivated under natural greenhouse irradiance.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DEPENDENCE, ELECTRON-TRANSPORT, FLOW, GROWTH, LEAVES, LIGHT, REDUCTION, RESPONSES, RISING CO2

128

Bartak, M., I. Nijs, and I. Impens. 1998. The susceptibility of PS II of Lolium perenne to a sudden fall in air temperature - response of plants grown in elevated CO2 and/or increased air temperature. *Environmental and Experimental Botany 39(1):85-95.*

The effect of a sudden fall in air temperature from 20 to 5 degrees C on fast kinetics of chlorophyll fluorescence, maximum yield of the photosystem II photochemical reactions (Fv/Fm), quantum yield of the photosystem II electron transport (Phi(II)) coefficients of photochemical (qP), non-photochemical quenching (qN) was studied in Lolium perenne using a modulated chlorophyll fluorescence technique. Before fluorescence measurement, the plants were cultivated in the treatments simulating the likely future climate characterized with elevated air temperature and CO2 concentration and combination of both. On fast kinetics curves the risetimes of the I and D points characterizing the redox state of Q(A) were affected by lowering the air temperature. At 5 degrees C both the I and D points were reached later than at 20 degrees C. Also the I to D risetime was prolonged at 5 degrees C and it was found significantly longer in plants cultivated in ambient + 4 degrees C temperature. While a significant difference was found in the area over the rising part of the fluorescence curve between 20 and 5 degrees C, no

difference was found in area over the relaxation curve part. Lowering of air temperature to 5 degrees C had no effect on Fv/Fm values in control plants and in the plants cultivated in elevated CO2 but brought significant decrease in plants cultivated in the ambient + 4 degrees C air temperature. Both Phi(II) and qP decreased with the temperature lowered to 5 degrees C while the values of qN increased. The changes in fluorescence parameters indicated altered functioning of PS II at low temperature. The changes in parameters are discussed as a consequense of decreased enzymatic activity, decreased turnover of plastoquinone pool and photoinhibition. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, CENTERS, CHLOROPHYLL FLUORESCENCE, LEAVES, PHOTOINHIBITION, PHOTOSYNTHESIS, PHOTOSYSTEM, QUANTUM YIELD, SENSITIVITY, VIOLAXANTHIN DEEPOXIDATION

129

Barton, C.V.M., and P.G. Jarvis. 1999. Growth response of branches of Picea sitchensis to four years exposure to elevated atmospheric carbon dioxide concentration. *New Phytologist 144(2):233-243.*

Branch bags were used to expose branches on mature Sitka spruce trees to either ambient [CO2] (A) or elevated [CO2] (E) for 4 yr. This paper reports the effects of this treatment on the growth, development and phenology of the branches, including shoot expansion, shoot numbers, needle dimensions, needle numbers and stomatal density. The effect of elevated [CO2] on the relationship between leaf area and sapwood area was investigated. Exposure to elevated [CO2] doubled photosynthetic rates in current-fear shoots and, despite some downregulation, 1-yr-old E shoots also had higher rates of photosynthesis than their A counterparts. Thus, the amount of assimilate fixed by E branches was substantially more than that fixed by A branches; hen-ever, this increase in the local production of assimilate did not lead to an increase in non-structural carbohydrate or stimulate growth or meristematic activity within the E branches. There was a very consistent relationship between leaf area and stem cross-sectional area that was not influenced by [CO2]. However, unbagged branches had thicker stems than bagged branches, resulting in a slightly lower ratio of leaf area to cross-sectional area. The implications of the results for the modelling of growth and allocation and the potential utility of the branch bag technique are discussed.

KEYWORDS: ALLOCATION, ASSIMILATION, CO2- ENRICHMENT, MORPHOLOGY, NUTRITION, PHOTOSYNTHETIC ACCLIMATION, PINE, RESISTANCE, STOMATAL CONDUCTANCE, TREES

130

Barton, C.V.M., H.S.J. Lee, and P.G. Jarvis. 1993. A branch bag and co2 control-system for long-term co2 enrichment of mature sitka spruce [picea-sitchensis (bong) carr]. *Plant, Cell and Environment 16(9):1139-1148.*

This paper describes the construction and performance of branch bags and a CO2 control system used to fumigate branches of mature Sitka spruce trees with air enriched in CO2 (700 mu mol mol(-1)). It contains some examples of results obtained using the system over the course of the first two growing seasons. The branch bags have run continuously for 2 years with very few problems. CO2 concentrations were within 20 mu mol mol(-1) of the target concentration for more than 90% of the time. Temperatures within the bags were slightly higher than ambient (1-2 degrees C) and this had some effect on phenology. Attenuation of quantum flux density (photosynthetically active radiation) was 10-15%. The branch bag system has enabled investigation into the effects of elevated CO2 on mature tissue without the problems and expense of fumigating whole trees. Growth in elevated CO2 resulted in an increase in starch and a decrease in soluble protein content of needles. Stomatal conductance was higher in elevated CO2 grown needles, and there was some evidence of an increase in photosynthetic capacity.

KEYWORDS: TREES

131

Basile, G., M. Arienzo, and A. Zena. 1993. Soil nutrient mobility in response to irrigation with carbon- dioxide enriched water. *Communications in Soil Science and Plant Analysis 24(11-12):1183-1195.*

In our experiments, carbonated water (CW) modified the equilibria in soil. Application of CW decreased the soil pH about 1.5 units one hour after irrigation ended. Minimal, though well defined, differences in soil pH were observed between the two carbonated treatments. The same relationship between the treatments was not found in pH levels of the leachate. This seems strictly related to the temporal and spatial changes in the carbon dioxide (CO2) acidifying effect caused by chemical and biological factors as water descended the soil column. The temporary reduction in soil pH in the CW treatment induced the highest nutrient mobility for most of the elements.

KEYWORDS: CO2

132

BassiriRad, H., K.L. Griffin, J.F. Reynolds, and B.R. Strain. 1997. Changes in root NH4+ and NO3- absorption rates of loblolly and ponderosa pine in response to CO2 enrichment. *Plant and Soil 190(1):1-9.*

Root growth and physiological uptake capacity for NH4+ and NO3- were examined for seedlings of loblolly and ponderosa pine grown for 160 days under two CO2 levels, ambient (35 Pa) and ambient plus 35 Pa (70 Pa). Fraction of biomass allocated to active fine roots as well as total N (NH4+ + NO3-) absorption per unit root dry mass were unaffected by CO2. On a whole-plant basis, elevated CO2 led to a significant increase in N acquisition in loblolly but not in ponderosa pine. However, even in loblolly pine where CO2 significantly increased plant N acquisition, the relative increase, in biomass far exceeded the gain in N, i.e. a 60% increase in total dry weight was accompanied by only a 30% increase in N gain in response to high CO2. We suggest that the commonly reported decline in tissue N concentration of these and other species at high CO2 is largely caused by inability of the root systems to sufficiently compensate for increased N demand. Elevated CO2 significantly altered root uptake capacity of the different N forms, i.e., high CO2 significantly increased NO3- absorption rates, but decreased NH4+ absorption rates in both species though the decrease in loblolly was insignificant. However, elevated CO2 increased root respiration rate in loblolly pine while significantly decreasing it in ponderosa pine. This indicates that CO2-induced changes in plant preference for inorganic N forms is not simply regulated by root energy status. If changes in plant preference for inorganic N forms represent typical responses to elevated CO2, the results could have important implications for N dynamics in managed and natural plant communities.

KEYWORDS: AMMONIUM, AVAILABILITY, BARLEY, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH, L SEEDLINGS, NITRATE ABSORPTION, NITROGEN CONCENTRATION, PLANT NUTRITION

133

Bassirirad, H., K.L. Griffin, B.R. Strain, and J.F. Reynolds. 1996. Effects of CO2 enrichment on growth and root (NH4+)-N-15 uptake rate of loblolly pine and ponderosa pine seedlings. *Tree Physiology 16(11-12):957-962.*

We examined changes in root growth and (NH4+)-N-15 uptake capacity of loblolly pine (Pinus taeda L.) and ponderosa pine (Pinus ponderosa Douglas. Ex Laws.) seedlings that were grown in pots in a phytotron at CO2 partial pressures of 35 or 70 Pa with NH4+ as the sole N source. Kinetics of N-15-labeled NH4+ uptake were determined in excised roots, whereas total NH4+ uptake and uptake rates were determined in intact root systems following a 48-h labeling of intact seedlings with N-15. In both species, the elevated CO2 treatment caused a significant downregulation of (NH4+)-N-15 uptake capacity in excised roots as a result of a severe inhibition of the maximum rate of root (NH4+)-N-15 uptake (V-max). Rates of (NH4+)-N-15 uptake in intact roots were, however, unaffected by CO2 treatment and were on average 4- to 10-fold less than the V-max in excised roots, suggesting that (NH4+)-N-15 absorption from the soil was not limited by the kinetics of root (NH4+)-N-15 uptake. Despite the lack of a CO2 effect on intact root absorption rates, (NH4+)-N-15 uptake on a per plant basis was enhanced at high CO2 concentrations in both species, with the relative increase being markedly higher in ponderosa pine than in loblolly pine. High CO2 concentration increased total (NH4+)-N-15 uptake and the fraction of total biomass allocated to fine roots (< 2 mm in diameter) to a similar relative extent. We suggest that the increased uptake on a per plant basis in response to CO2 enrichment is largely the result of a compensatory increase in root absorbing surfaces.

KEYWORDS: AMMONIUM, CARBON-DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO2, LIMITATION, NITROGEN, NUTRITION, PHOTOSYNTHESIS, PLANTS, RESPONSES

134

Bassirirad, H., J.F. Reynolds, R.A. Virginia, and M.H. Brunelle. 1997. Growth and root NO3- and PO43- uptake capacity of three desert species in response to atmospheric CO2 enrichment. *Australian Journal of Plant Physiology 24(3):353-358.*

In a phytotron experiment, we examined growth and rates of NO3- and PO43- uptake in seedlings of two desert C-3 shrubs (Larrea tridentata and Prosopis glandulosa) and a desert C-4 perennial grass (Bouteloua eriopoda) grown under CO2 partial pressures of 35 or 70 Pa. Plants were grown in soil but uptake studies were conducted on roots of intact seedlings placed in nutrient solutions containing both NO3- and PO43-. Elevated CO2 increased total biomass by 69 and 55% in Larrea and Prosopis seedlings and by 25% in Bouteloua. NO3- and PO43- uptake rates were more than doubled in Bouteloua at high compared to ambient CO2. In contrast, CO2 enrichment inhibited root NO3- uptake capacity in Larrea by about 55% without a significant effect on PO43- absorption rate; rates of NO3- and PO43- and uptake in Prosopis were insensitive to CO2 treatment. Elevated CO2 enhanced the proportion of biomass allocated to the fine roots in Bouteloua but markedly reduced this fraction in Larrea and Prosopis. Foliar N concentration of both shrubs decreased in response to elevated CO2, but was unaffected in Bouteloua. We suggest that compensatory changes in root size and activity are critical in determining interspecies variation in plant nutrient relations under high CO2.

KEYWORDS: CARBON DIOXIDE, COMPETITION, DRY-MATTER, ELEVATED CO2, MINERAL NUTRITION, NITROGEN, PHOSPHATE, PLANTS, RHIZOSPHERE, SEEDLINGS

135

Bassirirad, H., R.B. Thomas, J.F. Reynolds, and B.R. Strain. 1996. Differential responses of root uptake kinetics of NH4+ and NO3- to enriched atmospheric CO2 concentration in field-grown loblolly pine. *Plant, Cell and Environment 19(3):367-371.*

The nitrogen requirement of plants is predominantly supplied by NH4+ and/or NO3- from the soil solution, but the energetic cost of uptake and assimilation is generally higher for NO3- than for NH4+. We found that CO2 enrichment of the atmosphere enhanced the root uptake capacity for NO3-, but not for NH4+, in field-grown loblolly pine saplings. Increased preference for NO3- at the elevated CO2 concentration was accompanied by increased carbohydrate levels in roots. The results have important implications for the potential consequences of global climate change on plant- and ecosystem-level processes in many temperate forest ecosystems.

KEYWORDS: ABSORPTION, AMMONIUM, ASSIMILATION, BARLEY, FLUXES, FORESTS, PLANTS, RESPIRATION

136

Bassirirad, H., D.T. Tissue, J.F. Reynolds, and F.S. Chapin. 1996. Response of Eriophorum vaginatum to CO2 enrichment at different soil temperatures: Effects on growth, root respiration and PO43- uptake kinetics. *New Phytologist 133(3):423-430.*

In a phytotron experiment, we examined responses of a tussock sedge, Eriophorum vaginatum L., to changes in atmospheric CO2 concentration and soil temperature. We were particularly interested in phosphorus (P) acquisition and below ground plant characteristics that regulated its uptake in response to CO2 enrichment. Plants were grown at two CO2 partial pressures, 35 and 70 Pa, three soil temperature regimes, 5, 15 and 25 degrees C and a constant ambient air temperature of 15 degrees C. Elevated CO2 increased total plant biomass production, but decreased tissue P concentration. Although high CO2 enhanced root carbohydrate concentration, it inhibited root respiration with no significant effect on root PO43- absorption capacity or root:shoot ratio. Surprisingly, there were no significant interactions between CO2 and soil temperature. The inability of Eriophorum to exhibit root-level compensatory adjustments, e.g. increased root:shoot ratio or PO43- absorption capacity, was largely responsible for the observed decline in tissue P concentration under elevated CO2 conditions. This could ultimately limit longterm growth responses of Eriophorum to CO2 enrichment in the field where P availability is limiting. We found that uptake of PO43- in response to elevated CO2 was independent of changes in root respiration, but changes in root respiration could have important implications for ecosystem carbon budget under elevated CO2 levels. Our data indicated that although root respiration on a per unit biomass basis declined in response to CO2 enrichment, this effect was counterbalanced by increased root biomass, so that high CO2 stimulated root respiration on a whole-plant basis by 30%. This might help to explain why long-term exposure to high CO2 increases CO2 efflux from Eriophorum-dominated ecosystems.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO2, NITROGEN, NUTRIENT ACQUISITION, NUTRITION, PHOSPHATE ABSORPTION, PHOTOSYNTHESIS, PLANTS

137

Bassman, J.H., and J.C. Zwier. 1991. Gas-exchange characteristics of Populus trichocarpa, Populus deltoides and Populus trichocarpa X Populus deltoides clones. *Tree Physiology 8(2):145-159.*

Responses of net photosynthesis, dark respiration, photorespiration, transpiration, and stomatal conductance to irradiance, temperature, leaf-to-air vapor density difference (VDD), and plant water stress were examined in two Populus trichocarpa clones (one from a moist, coastal climate in western Washington and one from a dry, continental climate in eastern Washington), one P. deltoides clone, and two P. trichocarpa x P. deltoides clones. Light saturation of photosynthesis in greenhouse-grown trees occurred at about 800- mu-mol m-2 s-1 for P. deltoides, P. trichocarpa x P. deltoides, and the eastern Washington ecotype of P. trichocarpa, but at about 600-mu-mol m-2 s-1 for the western

Washington ecotype of P. trichocarpa. Average net photosynthesis (at saturating irradiance and the optimum temperature of 25-degrees-C) was 20.7, 18.8, 18.2 and 13.4-mu-mol CO2 m-2 s-1 for P. deltoides, P. trichocarpa x P. deltoides, and the eastern and western Washington clones of P. trichocarpa, respectively. In all clones, net photosynthesis decreased about 14% as VDD increased from 3 to 18 g H2O m-3. Stomatal conductance decreased sharply with decreasing xylem pressure potential (XPP) in all clones except the western Washington clone of P. trichocarpa. Stomata in this clone were insensitive to changes in XPP and did not control water loss. Complete stomatal closure (stomatal conductance < 0.05 cm s-1) occurred at about -2.0 MPa in the eastern Washington clone of P. trichocarpa and around -1.25 MPa in the P. deltoides and P. trichocarpa x P. deltoides clones. Transpiration rates were highest in the P. trichocarpa x P. deltoides clone and lowest in the western Washington clone of P. trichocarpa. The P. deltoides clone and eastern Washington clone of P. trichocarpa had the highest water use efficiency (WUE) and the western Washington clone of P. trichocarpa had the lowest WUE. The hybrids were intermediate. It was concluded that: (1) gas exchange characteristics of eastern and western Washington clones of P. trichocarpa reflected adaptation to their native environment; (2) crossing the western Washington clone of P. trichocarpa with the more drought resistant P. deltoides clone produced plants better adapted to the interior Pacific Northwest climate, although the stomatal response to soil water deficits in the hybrid was conservative compared with that of the eastern Washington clone of P. trichocarpa; and (3) introducing eastern Washington clones of black cottonwood into breeding programs is likely to yield lines with favorable growth characteristics combined with enhanced WUE and adaptation to soil water deficits.

138

Bassow, S.L., K.D.M. McConnaughay, and F.A. Bazzaz. 1994. The response of temperate tree seedlings grown in elevated co2 to extreme temperature events. *Ecological Applications 4(3):593-603.*

Mean global temperatures have been predicted to increase in the next century, if so the frequency of extreme temperature events may also increase. Extreme temperatures may damage plant tissue and consequently limit the survival of certain plant species in a region. Elevated concentrations of CO2 in the atmosphere alter plant allocation, physiology, and growth, and may accentuate or ameliorate the damage from extreme temperatures. In this paper we explore the interactive effects of atmospheric CO2 concentration, nutrient levels, and exposure to extreme temperatures on seedlings of three species of temperate deciduous trees. A1-d exposure to extreme heat (45-degrees-C) significantly decreased conductance the following day and decreased biomass as measured at both 35 and 105 d following the extreme temperature event, regardless of atmospheric CO2 concentration. The most shade-tolerant species, striped maple, was most severely impacted by the extreme heat event in both CO2 environments. Furthermore, striped maple seedlings grown in elevated CO2 concentrations had a significantly greater decrease in biomass due to the extreme heat event as compared with striped maple plants grown in ambient CO2 concentrations at 35 d after the heat event; however, al the end of the growing season at 105 d post treatment, this difference was not significant. A one-night exposure to low temperatures (4- degrees-C) did not affect biomass for any of these species. With an increase in global mean temperatures, the frequency of extreme temperature events, particularly hot weather events, may increase and may extend to shaded understory sites. If the frequency of extremely high temperatures increases, the role that temperature extremes may play in changing competitive interactions and thus affecting community composition may increase in importance, as these temperatures appear to severely alter plant survival and growth in some species.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE, ECOSYSTEMS, ENRICHMENT, FOLIAGE TEMPERATURE, HEAT-SHOCK PROTEINS, NIGHT TEMPERATURE, PLANTS, THERMOTOLERANCE, VARIABILITY

139

Batjes, N.H. 1998. Mitigation of atmospheric CO2 concentrations by increased carbon sequestration in the soil. *Biology and Fertility of Soils 27(3):230-235.*

The International Panel on Climate Change distinguished three main options for the mitigation of atmospheric CO2 concentrations by the agricultural sector: (1) reduction of agriculture-related emissions, (2) creation and strengthening of C sinks in the soil, and (3) production of biofuels to replace fossil fuels. Options for sustained sequestration of C in the soil through adapted management of land resources are reviewed in the context of the ongoing discussion on the need to reduce greenhouse gas concentrations in the atmosphere. Enhanced sequestration of atmospheric CO2 in the soil, ultimately as stable humus, may well prove a more lasting solution than (temporarily) sequestering CO2 in the standing biomass through reforestation and afforestation. Such actions will also help to reverse processes of land degradation, thus contributing to sustained food productivity and security for the people in the regions concerned.

KEYWORDS: C STORAGE, CYCLE, DECOMPOSITION, ELEVATED CO2, FERTILIZATION, MANAGEMENT, NITROGEN, ORGANIC-MATTER, TURNOVER, WORLD

140

Battaglia, M., and P.J. Sands. 1998. Process-based forest productivity models and their application in forest management. *Forest Ecology and Management 102(1):13-32.*

Few process-based forest productivity models have become incorporated into forest management systems. The prevalent perception is that process-based models are suited only for research applications and that management questions will be solved only by using descriptive empirical models. This is despite the fact that the latter can neither deal satisfactorily with changing environmental and management conditions nor answer all questions currently asked by managers. This paper develops the proposition that the end-use specifies the design and scale of forest simulation models, and that given the range of questions now asked in forest management a range of models is required. The spatial and temporal resolution, and the input and output data required to address typical forest management questions is examined. A survey of recent literature examines in which areas, and by whom, existing forest productivity models are being applied. It is concluded that many current management questions can be adequately answered using models in which a phenomenological approach is applied to predict annual forest growth at the stand-scale. Lumped-parameter process-based models and hybrid models provide the most immediate means through which our understanding of the biological processes underlying forest growth can be included in forest management systems. However, more detailed process-based models can Flay an important role in validating simpler models, in the development of generalizations applicable over long time scales and for testing hypotheses about the way trees function and respond to interacting stresses. Guidelines are also given on model structures appropriate for different classes of management questions. (C) 1998 Elsevier Science B.V.

KEYWORDS: DECISION-SUPPORT SYSTEMS, DOUGLAS-FIR, DRY-MATTER ACCUMULATION, ELEVATED CO2, GROWTH-MODELS, ORIENTED GROWTH, PINUS-RADIATA, SITE INDEX, SPRUCE, YIELD

141

Batts, G.R., R.H. Ellis, J.I.L. Morison, and P. Hadley. 1998. Canopy development and tillering of field-grown crops of two contrasting cultivars of winter wheat (Triticum aestivum) in response to CO2 and temperature. *Annals of Applied Biology 133(1):101-109.*

Elevated CO2 (691 cf. 371 mu mol CO2 mol(-1) air) and warmer temperatures (over the range 1.0 degrees C below to 1.6 degrees C above ambient) increased light interception by crops of two contrasting cultivars (Hereward and Soissons) of winter wheat (Triticum aestivum L.) during winter growth in the field. The fractional interception of light by the canopy increased more rapidly initially in Soissons than in Hereward, but Hereward showed a much greater response to CO2 (35% increase in Hereward but only 7% in Soissons) at 500 degrees Cd after sowing. By terminal spikelet formation, in contrast, fractional interception was greater in Hereward than in Soissons, while the effect of CO2 was the same in both cultivars (9%). Thus, although differences in the relative response of canopy development to CO2 were detected between cultivars initially, differences were negligible during later development. The greater interception of light by the canopy in elevated CO2, at any one temperature, resulted from increased tillering. The number of tillers plant(-1) at terminal spikelet was a linear function of main stem dry mass at this developmental stage but with a greater response in elevated CO2, viz 2.3 and 3.8 tillers g(-1) main stem dry mass at 371 and 691 mu mol CO2 mol(-1) air, respectively; these relations were unaffected by cultivar.

KEYWORDS: YIELD

142

Batts, G.R., R.H. Ellis, J.I.L. Morison, P.N. Nkemka, P.J. Gregory, and P. Hadley. 1998. Yield and partitioning in crops of contrasting cultivars of winter wheat in response to CO2 and temperature in field studies using temperature gradient tunnels. *Journal of Agricultural Science 130:17-27.*

Diverse cultivars of winter wheat (Triticum aestivum L.) were grown in the field in 1993/94 and 1994/95 at Reading UK in temperature gradient tunnels at normal atmospheric (c. 370) or elevated CO2 concentration (c. 700 mu mol CO2 mol(-1) air). In 1993/94, grain yield of cv. Avalon was insensitive to mean temperature (between 8.8 and 10.9 degrees C), while elevated CO2 increased yield by 1.3 t ha(-1) (12.6%). In all other cultivars, warming reduced grain yield and CO2 increased grain yield. In 1993/94, in cvs Galahad and Mercia the effects of CO2 and temperature on yield were additive. However, for cv. Hereward in both years and for cv. Soissons in 1994/95, there were negative interactions between the effects of CO2 and temperature on yield: the maximum benefit of doubling CO2 to grain yield, 4.5 and 2.7 t ha(-1) (65 and 29%) respectively, occurred at cooler temperatures; there was no benefit from doubling CO2 (i.e. 0%) once the temperature had increased above the seasonal mean by 2.2-2.6 degrees C in cv. Hereward and by 1.3 degrees C in cv. Soissons. The beneficial effect of doubling CO2 on grain yield in cvs Galahad, Hereward, Mercia and Soissons was negated by an increase in mean seasonal temperature of only 0.7-2.0 degrees C. Warming decreased root dry mass at anthesis in 1994/95 while it increased at elevated CO2 (49 and 186%, coolest and warmest regime, respectively). Carbon partitioned to roots declined progressively with warming, while at elevated CO2 there was an average of 56% increase in allocation to roots. The relative impacts of both CO2 and temperature were greater on root dry mass than on either grain yield or total above-ground biomass, while the effects on grain and biomass yield varied considerably between cultivars, suggesting that the impact of rising CO2 and temperature are likely to be dependent on cultivar.

KEYWORDS: CARBON DIOXIDE, DURATION, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, PRODUCTIVITY, ROOT-GROWTH, SYSTEM, TRITICUM-AESTIVUM CROPS

143

Batts, G.R., J.I.L. Morison, R.H. Ellis, P. Hadley, and T.R. Wheeler. 1997. Effects of CO2 and temperature on growth and yield of crops of winter wheat over four seasons. *European Journal of Agronomy 7(1-3):43-52.*

Crops of winter wheat (Triticum aestivum L. cv. Hereward) were grown in the field in four consecutive seasons from 1991/1992 to 1994/1995 at Reading, UK, within polyethylene-covered tunnels along which a temperature gradient was superimposed on the ambient temperature variation at normal atmospheric (ca. 370) or an increased [CO2] (ca. 700 mu mol CO2 mol(-1) air), producing many environments from one sowing date in each season at one location. Mean seasonal temperatures varied by up to 4 degrees C along the temperature gradient. Increased [CO2] had no effect on crop duration, or on the rate of reproductive development, which had the same temperature sensitivity across all years, A 2 degrees C warming, on the 4-year ambient mean temperature (10 degrees C), reduced crop duration by 42 days (from 254), and reduced the reproductive phase by 16 days (from 130). Crop biomass generally declined with increase in mean temperature, and was greater at increased [CO2], with the effect of increased [CO2] varying with temperature and between years (6-34% range in relative stimulation by increased [CO2]). Grain yield was substantially reduced by warmer temperatures, and increased by doubling [CO2], but the effect varied greatly between pears and with temperature (7-168% range). There were both positive and negative interactions of temperature and increased [CO2] on biomass and grain yield. In all 4 years, the increase in grain yield from doubling [CO2] was negated by an increase in mean seasonal temperature of only 1.0-2.0 degrees C, Year-to-year variation in the responses of biomass and grain yield to [CO2] and temperature resulted from differences in environmental conditions, influencing biomass partitioning and altering the role of different yield components. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, DURATION, ELEVATED CO2, FIELD, MODEL, PRODUCTIVITY, RESPONSES, TRITICUM-AESTIVUM CROPS, VARIABILITY

144

Batts, G.R., T.R. Wheeler, J.I.L. Morison, R.H. Ellis, and P. Hadley. 1996. Developmental and tillering responses of winter wheat (Triticum aestivum) crops to CO2 and temperature. *Journal of Agricultural Science 127:23-35.*

Winter wheat (Triticum aestivum L., cv. Hereward) was grown in the held within four double-walled polyethylene-covered tunnels along which near-linear temperature gradients were imposed at normal atmospheric or at an elevated CO2 concentration (c. 700 mu mol mol(-1) CO2) in 1991/92 and in a further experiment in 1992/93. Development was more rapid the warmer the temperature. In 1991/92 an increase in mean seasonal temperature of 3.5 degrees C reduced the duration from sowing to harvest maturity (the stage when grain moisture content reduced naturally to 15- 18%) by c. 38 days, and reduced the duration from the double ridge stage to harvest maturity by c. 34 days. A similar difference resulted from only 1.6 degrees C warming in 1992/93. Although the range of mean seasonal temperatures differed between years, the relation between temperature and rate of development from sowing to harvest maturity was common to both years (base temperature, -0.8 degrees C; thermal time 2410 degrees C d). Carbon dioxide concentration had no effect on this relation or on that between temperature and the rate of development from solving to the double ridge stage and from the double ridge stage to harvest maturity. Carbon dioxide enrichment increased tillering substantially in 1991/92; there were 200 more shoots m(-2) at terminal spikelet formation in crops grown at elevated compared to normal CO2 (additional shoots were principally coleoptile tillers and those developing after tiller 2) and this

difference was reduced to 100 shoots m(-2) approaching harvest maturity (additional shoots remaining were those developing after tiller 2). In contrast, no effect of CO2 enrichment on tillering was detected at any stage of development in 1992/93. The number of tillers per plant at terminal spikelet formation was a linear function of main stem dry weight at this developmental stage; this relationship was not affected by year or CO2. As CO2 enrichment increased main stem dry weight in the first year only, when main stem dry weights at normal CO2 were only one half of those values determined in the following year, it is concluded that any benefit of increase in CO2 concentration to tillering in winter wheat may be greatest in those crop production environments where main stem dry weights at terminal spikelet are least and vice versa.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, ENVIRONMENT, FIELD, GROWTH, IMPACT, INITIATION, LEAF APPEARANCE, SENSITIVITY, YIELD

145

Bawa, K.S., and S. Dayanandan. 1998. Global climate change and tropical forest genetic resources. *Climatic Change 39(2-3):473-485.*

Global climate change may have a serious impact on genetic resources in tropical forest trees. Genetic diversity plays a critical role in the survival of populations in rapidly changing environments. Furthermore, most tropical plant species are known to have unique ecological niches, and therefore changes in climate may directly affect the distribution of biomes, ecosystems, and constituent species. Climate change may also indirectly affect plant genetic resources through effects on phenology, breeding systems, and plant-pollinator and plant seed disperser interactions, and may reduce genetic diversity and reproductive output. As a consequence, population densities may be reduced leading to reduction in genetic diversity through genetic drift and inbreeding. Tropical forest plants may respond to climate change through phenotypic plasticity, adaptive evolution, migration to suitable site, or extinction. However, the potential to respond is limited by a rapid pace of change and the non-availability of alternate habitats due to past and present trends of deforestation. Thus climate change may result in extinction of many populations and species. Our ability to estimate the precise response of tropical forest ecosystems to climate change is limited by lack of long-term data on parameters that might be affected by climate change. Collection of correlative data from long-term monitoring of climate as well as population and community responses at selected sites offer the most cost-effective way to understand the effects of climate change on tropical tree populations. However, mitigation strategies need to be implemented immediately. Because many effects of climate change may be similar to the effects of habitat alteration and fragmentation, protected areas and buffer zones should be enlarged, with an emphasis on connectivity among conserved landscapes. Taxa that are likely to become extinct should be identified and protected through at situ conservation programs.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, DRY FOREST, ELEVATED CO2, INCOMPATIBILITY, PHENOLOGY, PLANT, RESPONSES, SYSTEMS, TREES

146

Baxter, R., T.W. Ashenden, and J.F. Farrar. 1997. Effect of elevated CO2 and nutrient status on growth, dry matter partitioning and nutrient content of Poa alpina var vivipara L. *Journal of Experimental Botany 48(312):1477-1486.*

Poa alpina var, vivipara L, was grown in an atmosphere containing either 340 or 680 mu mol CO2 mol(-1) within controlled environment chambers, The available nutrient regime was varied by altering the supply of nitrogen and phosphorus within a complete nutrient solution, At a high, but not low, N and P supply regime, elevated CO2 markedly increased growth, Differences between nutrient supply, but not atmospheric CO2 concentration, altered the allometric relations between root and shoot, Net photosynthesis of mature leaf blades and leaf N and P concentration were reduced in plants grown at the elevated CO, concentration, The question was asked: is it possible to ascribe all of these effects to elevated CO2 or are some due to nutrient deficiency caused by dilution with excess carbon? Several criteria, including the nutrient content of sink tissue, root:shoot allometry and the use of divalent cations to estimate integrated water flows are suggested in order to make this distinction, It is concluded that only at a low supply of N and P, and elevated CO2 concentration, was low leaf N concentration due to induced nutrient deficiency, The data are consistent with a model where the capacity of sinks to use photosynthetically assimilated carbon sets both the rate of import into those sinks (and thus rate of export from source leaves) and the rate of photosynthesis of source leaves themselves.

KEYWORDS: ALLOCATION, ANTISENSE RBCS, ATMOSPHERIC CARBON-DIOXIDE, NITROGEN, PHOSPHATE STATUS, PHOSPHORUS, PHOTOSYNTHESIS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOBACCO

147

Baxter, R., T.W. Ashenden, T.H. Sparks, and J.F. Farrar. 1994. Effects of elevated carbon-dioxide on 3 montane grass species .1. Growth and dry-matter partitioning. *Journal of Experimental Botany 45(272):305-315.*

Upland grasslands are a major component of natural vegetation within the UK. Such grasslands support slow growing relatively stable plant communities. The response of native montane grass species to elevated atmospheric carbon dioxide concentrations has received little attention to date. Of such studies, most have only focused on short-term (days to weeks) responses, often under favourable controlled environment conditions. In this study Agrostis capillaris L.(5), Festuca vivipara L. and Poa alpina L. were grown under semi-natural conditions in outdoor open-top chambers at either ambient (340 mu mol mol(- 1)) or elevated (680 mu mol mol(-1)) concentrations of atmospheric carbon dioxide (CO2) for periods from 79 to 189 d, with a nutrient availability similar to that of montane Agrostis-Fescue grassland in Snowdonia, N. Wales. Whole plant dry weight was increased for A. capillaris and P. alpina, but decreased for F. vivipara, at elevated CO2. Major components of relative growth rate (RGR) contributing to this change at elevated CO2 were transient changes in specific leaf area (SLA) and leaf area ratio (LAR). Despite changes in growth rate at 680 mu mol mol(-1) CO2, partitioning of dry weight between shoot and root in plants of A. capillaris and P. alpina was unaltered. There was a significant decrease in shoot relative to root growth at elevated CO2 in F. vivipara which also showed marked discoloration of the leaves and increased senescence of the foliage.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, COMMUNITIES, EXPOSURE, PHOTOSYNTHESIS, PLANTS, RESPIRATION, SENESCENCE, STRESS, TEMPERATURE

148

Baxter, R., S.A. Bell, T.H. Sparks, T.W. Ashenden, and J.F. Farrar. 1995. Effects of elevated co2 concentrations on 3 montane grass species .3. Source leaf metabolism and whole-plant carbon partitioning. *Journal of Experimental Botany 46(289):917-929.*

Agrostis capillaris L.(5), Festuca vivipara L. and Poa alpina L. were grown in outdoor open-top chambers at either ambient (340 +/- 3 mu mol mol(-1)) or elevated (680 +/- 4 mu mol mol(- 1)) concentrations of atmospheric carbon dioxide (GO,) for periods from 79-189 d. Photosynthetic capacity of source leaves of plants grown at both ambient and elevated CO2 concentrations was measured at saturating light and

5% CO2. Dark respiration of leaves was measured using a liquid phase oxygen electrode with the buffer solution in equilibrium with air (21% O-2, 0.034% CO2). Photosynthetic capacity of P. alpina was reduced by growth at 680 mu mol mol(-1) CO2 by 105 d, and that of F. vivipara was reduced at 65 d and 189 d after CO2 enrichment began, suggesting down-regulation or acclimation. Dark respiration of successive leaf blades of all three species was unaltered by growth at 680 relative to 340 mu mol mol(-1) CO2. In F. vivipara, leaf respiration rate was markedly lower at 189 d than at either 0 d or 65 d, irrespective of growth CO2 concentration. There was a significantly lower total non- structural carbohydrate (TNC) concentration in the leaf blades and leaf sheaths of A. capillaris grown at 680 mu mol mol(-1) CO2. TNC of roots of A. capillaris was unaltered by CO2 treatment. TNC concentration was increased in both leaves and sheaths of P. alpina and F. vivipara after 105 d and 65 d growth, respectively. A 4-fold increase in the water-soluble fraction (fructan) in P. alpina and in all carbohydrate fractions in F. vivipara accounted for the increased TNC content. In F. vivipara the relationship between leaf photosynthetic capacity and leaf carbohydrate concentration was such that there was a strong positive correlation between photosynthetic capacity and total leaf N concentration (expressed on a per unit structural dry weight basis), and total nitrogen concentration of successive mature leaves reduced with time, Multiple regression of leaf photosynthetic capacity upon leaf nitrogen and carbohydrate concentrations further confirmed that leaf photosynthetic capacity was mainly determined by leaf N concentration. In P. alpina, leaf photosynthetic capacity was mainly determined by leaf CHO concentration. Thus there is evidence for downregulation of photosynthetic capacity in P. alpina resulting from increased carbohydrate accumulation in source leaves. Leaf dark respiration and total N concentration were positively correlated in P. alpina and F. vivipara. Leaf dark respiration and soluble carbohydrate concentration of source leaves were positively correlated in A. capillaris. Changes in source leaf photosynthetic capacity and carbohydrate concentration of plants grown at ambient or elevated CO, are discussed in relation to plant growth, nutrient relations and availability of sinks for carbon.

KEYWORDS: ACCLIMATION, CALVIN CYCLE ENZYMES, CARBOHYDRATE CONTENT, COTTON PLANTS, DIOXIDE EFFLUX, GROWTH, HIGH ATMOSPHERIC CO2, PHOTOSYNTHETIC OXYGEN EVOLUTION, RESPIRATION, SPINACH LEAVES

149

Baxter, R., and J.F. Farrar. 1999. Export of carbon from leaf blades of Poa alpina L-at elevated CO2 and two nutrient regimes. *Journal of Experimental Botany 50(336):1215-1221.*

The hypothesis was tested that, in plants of the alpine! meadow grass (Poa alpina L,) exposed to elevated CO2, net photosynthesis and export from source leaves is; reduced as a result of feedback from sinks. Nutrient supply was used as one way of reducing photosynthesis and export. Single plants were grown in sand culture under specified controlled environmental conditions for a period of 50 d at two levels of nitrogen and phosphorus ('low': 0.2 mol m(-3) N, 0.04 mol m(-3) P;'high': 2.5 mol m(-3) N, 0.5 mol m(-3) P). Compartmentation within, and export of carbon from, individual youngest fully expanded leaves of acclimated plants was determined using C-14 feeding and efflux plus mass balance calculations of carbohydrate export. Independent of treatment, the bulk of soluble carbohydrate (65-75%) was present as fructan, with most of the remainder being sucrose. Depending on nutrient supply, CO2 could alter export from source leaves either by a reduction in the amount of sucrose present in a readily available pool for transport, or by altering the rate constant describing phloem loading.

KEYWORDS: ATMOSPHERIC CO2, BARLEY, DIOXIDE, EXCISED LEAVES, GROWTH, METABOLISM, PATTERNS, TEMPERATURE, TUSSOCK TUNDRA

150

Baxter, R., M. Gantley, T.W. Ashenden, and J.F. Farrar. 1994. Effects of elevated carbon-dioxide on 3 grass species from montane pasture .2. Nutrient-uptake, allocation and efficiency of use. *Journal of Experimental Botany 45(278):1267-1278.*

Agrostis capillaris L.(4), Festuca vivipara L. and Poa alpina L. were grown in outdoor open-top chambers at either ambient (340 mu mol mol(-1) or elevated (680 mu mol mol(-1)) CO2 for periods from 79 to 189 d. Under these conditions there is increased growth of A, capillaris and P. alpina, but reduced growth of F. vivipara. Nutrient use efficiency, nutrient productivity (total plant dry weight gain per unit of nutrient) and nutrient allocation of all three grass species were measured in an attempt to understand their individual growth responses further and to determine whether altered nutrient-use efficiencies and productivities enable plants exposed to an elevated atmospheric CO2 environment to overcome potential limitations to growth imposed by soil fertility. Total uptake of nutrients was, in general, greater in plants of A. capillaris and P. alpina (with the exception of N and K in the latter) when grown at 680 mu mol mol(-1) CO2. In F. vivipara, however, uptake was considerably reduced in plants grown at the higher CO2 concentration. Overall, a doubling of atmospheric CO2 concentration had little effect on the nutrient use efficiency or productivity of A, capillaris. Reductions in tissue nutrient content resulted from increased plant growth and not altered nutrient use efficiency. In P. alpina, potassium, magnesium and calcium productivities were significantly reduced and photosynthetic nitrogen and phosphorus use efficiencies were doubled at elevated CO2 with respect to plants grown at ambient CO2. F. vivipara grown for 189 d showed the most marked changes in nutrient use efficiency and nutrient productivity (on an extracted dry weight basis) when grown at elevated CO2. F. vivipara grown at elevated CO2, however, showed large increases in the ratio of nonstructural carbohydrate to nitrogen content of leaves and reproductive tissues, indicating a substantial imbalance between the production and utilization of assimilate.

KEYWORDS: ACQUISITION, ATMOSPHERIC CO2, AVAILABILITY, CHENOPODIUM-ALBUM L, CO2- ENRICHMENT, LEAF NITROGEN, NITROGEN CONCENTRATION, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, SOURCE-SINK RELATIONS

151

Bazzaz, F.A. 1998. Tropical forests in a future climate: Changes in biological diversity and impact on the global carbon cycle. *Climatic Change 39(2-3):317-336.*

Tropical forest ecosystems are large stores of carbon which supply millions of people with life support requirements. Currently tropical forests are undergoing massive deforestation. Here, I address the possible impact of global change conditions, including elevated CO2, temperature rise, and nitrogen deposition on forest structure and dynamics. Tropical forests may be particularly susceptible to climate change for the following reasons: (1) Phenological events (such as flowering and fruiting) are highly tuned to climatic conditions. Thus a small change in climate can have a major impact on the forest, its biological diversity and its role in the carbon cycle. (2) There are strong coevolutionary interactions, such as pollination seed dispersal, with a high degree of specialization, i.e., only certain animals can effect these activities for certain species. Global change can decouple these tight coevolutionary interactions. (3) Because of high species diversity per unit area, species of the tropical rain forest must have narrow niches. Thus changes in global climate can eliminate species and therefore reduce biological diversity. (4) Deforestation and other forms of disturbance may have significant feedback on hydrology both regionally and globally. The predicted decline in the rainfall in the Amazon Basin and the intensification of the Indian monsoon can have a large effect on water availability and floods which are already devastating low-lying areas. It is concluded that tropical forests may be very sensitive to

climate change. Under climatic change conditions their structure and function may greatly change, their integrity may be violated and their services to people may be greatly modified. Because they are large stores of great biological diversity, they require immediate study before it is too late. The study requires the collaboration of scientists with a wide range of backgrounds and experiences including biologists, climate modellers, atmospheric scientists, economists, human demographers and sociologists in order to carry out holistic and urgently needed work. Global climatic change brings a great challenge to science and to policy makers.

KEYWORDS: COOCCURRING BIRCH, DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH-RESPONSE, INSECT HERBIVORE INTERACTIONS, MODEL SYSTEMS, PLANTS, RESOURCE USE, TEMPERATURE, TREE SEEDLINGS

152

Bazzaz, F.A., D.D. Ackerly, F.I. Woodward, and L. Rochefort. 1992. Co2 enrichment and dependence of reproduction on density in an annual plant and a simulation of its population-dynamics. *Journal of Ecology 80(4):643-651.*

1. Populations of an annual plant, Abutilon theophrasti, were grown at four densities (100, 500, 1500 and 4000 m-2) and two CO2, concentrations (350 and 700 mul l-1) to examine the influence of CO2 environment on density-dependent patterns of demography and reproduction. Variables measured included survivorship, proportion of plants flowering and fruiting, number of fruiting individuals, number of seeds per individual, total seed production per population, mean seed mass, and germination of seeds produced in each environment. 2. All variables, except the number of fruiting individuals, declined with increasing density, and at the highest density no individuals set seed. The number of fruiting individuals was highest at a density of 500m-2. In the elevated CO2 environment, survivorship was significantly reduced but the proportion of plants flowering and fruiting and the number of fruiting individuals in each population all increased. Total population seed production was higher in the elevated CO2 environment at all densities, although the differences were not significant. Significant effects of CO2, concentration were observed only for population-level variables, but not for mean individual fecundity or seed size. Seed germination declined with increasing maternal density, and no germination was recorded for seeds produced at 1500 m-2 3. Simple models of population dynamics, utilizing difference equations, were constructed to examine potential population-level consequences of these density and CO2 effects. In the absence of a persistent seed pool, the simulated populations exhibited damped or stable oscillations under low germination values, but displayed non-cyclic ('chaotic') oscillations or went extinct for higher germination due to the complete failure of seed-set at high density. Because of its higher fecundity, the elevated- CO2 population generally exhibited greater oscillations, and the critical germination value at which the simulated populations went extinct was much lower for the elevated-CO2 than for the ambient-CO2 population.

KEYWORDS: ABUTILON-THEOPHRASTI, COMPETITION, CYCLES, ELEVATED CO2, GROWTH, NEIGHBORHOOD MODELS, SINGLE-SPECIES POPULATIONS

153

Bazzaz, F.A., J.S. Coleman, and S.R. Morse. 1990. Growth-responses of 7 major cooccurring tree species of the northeastern united-states to elevated CO2. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 20(9):1479-1484.*

154

Bazzaz, F.A., M. Jasienski, S.C. Thomas, and P. Wayne. 1995. Microevolutionary responses in experimental populations of plants to co2-enriched environments - parallel results from 2 model systems. *Proceedings of the National Academy of Sciences of the United States of America 92(18):8161-8165.*

Despite the critical role that terrestrial vegetation plays in the Earth's carbon cycle, very little is known about the potential evolutionary responses of plants to anthropogenically induced increases in concentrations of atmospheric CO2. We present experimental evidence that rising CO2 concentration may have a direct impact on the genetic composition and diversity of plant populations but is unlikely to result in selection favoring genotypes that exhibit increased productivity in a CO2-enriched atmosphere. Experimental populations of an annual plant (Abutilon theophrasti, velvetleaf) and a temperate forest tree (Betula alleghaniensis, yellow birch) displayed responses to increased CO2 that were both strongly density-dependent and genotype-specific. In competitive stands, a higher concentration of CO2 resulted in pronounced shifts in genetic composition, even though overall CO2-induced productivity enhancements were small, For the annual species, quantitative estimates of response to selection under competition were 3 times higher at the elevated CO2 level. However, genotypes that displayed the highest growth responses to CO2 when grown in the absence of competition did not have the highest fitness in competitive stands. We suggest that increased CO2 intensified interplant competition and that selection favored genotypes with a greater ability to compete for resources other than CO2. Thus, while increased CO2 may enhance rates of selection in populations of competing plants, it is unlikely to result in the evolution of increased CO2 responsiveness or to operate as an important feedback in the global carbon cycle, However, the increased intensity of selection and drift driven by rising CO2 levels may have an impact on the genetic diversity in plant populations.

KEYWORDS: AMBIENT, CO2- ENRICHMENT, COMPETITION, DENSITY, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSE, NITROGEN, SEEDLINGS, SELECTION

155

Bazzaz, F.A., and K.D.M. McConnaughay. 1992. Plant interactions in elevated CO2 environments. *Australian Journal of Botany 40(4-5):547-563.*

Increasing atmospheric carbon dioxide concentrations present a novel resource condition for plant communities. In order to understand and predict how plant community structure and function may be altered in a high CO2 world, we need to understand how interactions among neighbouring plants within a community will alter the growth and reproduction of component species. Because CO2 is readily diffusible, plants have little influence on the CO2 acquisition of their neighbours, except within particularly dense canopies. Thus, plants seldom compete directly for CO2. Rather, CO2 availability is likely to alter plant-plant interactions indirectly through its effects on plant growth and competition for other resources. As a consequence, competitive outcome under elevated CO2 atmospheres within even simple systems is not easy to predict. For example, under some conditions, C4 species in competitive assemblages have improved competitive ability relative to C3 competitors as a result of CO2 enrichment, contrary to expectations based on their photosynthetic pathways. It is now clear that individually grown plants can differ substantially from those within mono- or multispecific stands in response to CO2 enrichment. At present, our understanding of how stands of interacting plants modify the availability of CO2 and other resources is incomplete. We urgently need information about how elevated CO2 atmospheres influence stand formation and population dynamics, specifically with regard to the identities, numbers, sizes and reproductive fitnesses of individuals within single and multiple species stands, if we are to make multi-generational predictions concerning the fate of populations and communities in an elevated CO2

world.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, DECIDUOUS FOREST, ESTUARINE MARSH, OLD- FIELD PERENNIALS, QUERCUS-ALBA, SEEDLING GROWTH, SIZE HIERARCHIES, SOIL RESPIRATION, TUSSOCK TUNDRA

156

Bazzaz, F.A., and S.L. Miao. 1993. Successional status, seed size, and responses of tree seedlings to co2, light, and nutrients. *Ecology 74(1):104-112.*

We studied how an enriched CO2 atmosphere in a fully crossed design of light and nutrients, influenced 1 st-yr seedling growth in six New England deciduous forest tree species. The species, in the order of increasing shade tolerance, were gray birch (Betula populifolia), ash (Fraxinus americana L.), red maple (Acer rubrum L.), red oak (Quercus rubra L.), yellow birch (Betula alleghaniensis Britton), and striped maple (Acerpensylvanicum). Elevated CO2 environments significantly stimulated the seedling growth of all six species. Generally this was more pronounced in low light. The greatest stimulation was found under the condition of low light and high nutrients. However, individual species responded differently to elevated CO2 levels. Among the three early-successional species, gray birch, ash, and red maple, a significant increase in seedling growth under elevated CO2 conditions was found only with high nutrients. The three late-successional species grown under elevated CO2 conditions (red oak, yellow birch, and striped maple) showed a greater percentage increase in seedling growth in low light than in high light. Thus, for the early- successional species, the degree of enhancement of seedling growth by elevated CO2 levels was more sensitive to nutrient levels, while in the late-successional species the enhancement was more sensitive to the level of light. Moreover, species with large seeds (e.g., red oak) exhibited a greater response to elevated CO2 levels under low light than species with small seeds (e.g., gray birch). The results emphasize the importance of plant species as well as other environmental resources in modifying the response of plants to elevated CO2. Considering the light and nutrient environment observed in forest gaps of various sizes, the results of the present experiment suggest seedling regeneration in New England deciduous forests may be altered in a future high CO2 environment.

KEYWORDS: ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, NORTHEASTERN UNITED-STATES, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, PLANTS, TEMPERATURE

157

Bazzaz, F.A., S.L. Miao, and P.M. Wayne. 1993. Co2-induced growth enhancements of cooccurring tree species decline at different rates. *Oecologia 96(4):478-482.*

To elucidate how enriched CO2 atmospheres, soil fertility, and light availability interact to influence the long-term growth of tree seedlings, six co-occurring members of temperature forest communities including ash (Fraxinus americana L.), gray birch (Betula populifolia), red maple (Acer rubrum), yellow birch (Betula alleghaniensis), striped maple (Acer pensylvanicum), and red oak (Quercus rubra L.) were raised in a glasshouse for three years in a complete factorial design. After three years of growth, plants growing in elevated CO2 atmospheres were generally larger than those in ambient CO2 atmospheres, however, magnitudes of CO2-induced growth enhancements were contingent on the availability of nitrogen and light, as well as species identity. For all species, magnitudes of CO2-induced growth enhancements after one year of growth were greater than after three years of growth, though species' growth enhancements over the three years declined at different rates. These results suggest that CO2-induced enhancements in forest productivity may not be sustained for long periods of time. Additionally, species' differential growth responses to elevated CO2 may indirectly influence forest productivity via long-term species compositional changes in forests.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, COOCCURRING BIRCH, ELEVATED CO2, ENRICHMENT, PHOTOSYNTHETIC ACCLIMATION, RESPIRATION, RESPONSES, SEEDLINGS, SOURCE-SINK RELATIONS

158

Beaudry, R.M. 1999. Effect of O-2 and CO2 partial pressure on selected phenomena affecting fruit and vegetable quality. *Postharvest Biology and Technology 15(3):293-303.*

It is likely that from the time of the Roman Empire and perhaps before, people involved in the storage of plant material as food recognized that atmospheric modification can provide some benefit in improving storability. However, active, commercial modification of the atmosphere for the preservation of fresh fruit and vegetables dates to the early part of this century. Early successes with apple fruit has lead to the attempt to apply modified atmospheres to a wide range of commodities. Responses to atmospheric modification are found to vary dramatically among plant species, organ type and developmental stage and include both unwanted and beneficial physiological responses, Desirable responses include a reduction in respiration, a reduction in oxidative tissue damage or discoloration, a reduction in the rate of chlorophyll degradation and a reduction in ethylene sensitivity with the concomitant reduction in the rate of ripening and other ethylene-mediated phenomena. Undesirable responses have included the induction of fermentation, the development of disagreeable flavors? a reduction in aroma biosynthesis, the induction of tissue injury and an alteration in the makeup of microbial fauna. The physiological bases for some of these responses to elevated CO2 and reduced O-2 are discussed.

KEYWORDS: ATMOSPHERE, BIOSYNTHESIS, BLUEBERRY FRUIT, BROCCOLI, ENERGY-CHARGE, ETHYLENE, MAIZE ROOT-TIPS, OXYGEN PARTIAL PRESSURES, POSTHARVEST DECAY, VOLATILE COMPOUNDS

159

Becker, M., T.M. Nieminen, and F. Geremia. 1994. Short-term variations and long-term changes in oak productivity in northeastern france - the role of climate and atmospheric co2. *Annales Des Sciences Forestieres 51(5):477-492.*

A dendroecological study was carried out in 2 forests in northeastern France with the aim of identifying and quantifying possible long-term trends in the radial growth of sessile oak (Quercus petraea (Matt) Liebl) and pedunculate oak (Q robur L). A total of 150 sites were selected to represent the ecological diversity of these forests. An index Cd was used to correct annual ring width in order to compensate for the effect of different competition situations. The data were standardized with reference to the mean curve 'basal area increment vs cambial age'. The growth index curves revealed a strong increase in sessile oak growth (+ 64% during the period 1888 to 1987) as well as in that of peduncutate oak (+40%). The growth increase in the 'young' rings (<60 years) of sessile oak was + 87 %, and that of young rings of pedunculate oak was + 49%. The corresponding increase in the 'old' rings (>65 years) was + 48% and 15% respectively (not significant for the latter). It would thus appear that pedunculate oak has benefited to a lesser extent than sessile oak from the progressive changes in its environment. Years showing a strong growth decrease are more common for pedunculate oak than for sessile oak. These results are consistent with a recent hypothesis about a slow but general retreat of pedunculate oak, including severe episodic

declines, in favour of sessile oak in many regions of France. A model was created using a combination of meteorological data (monthly precipitation and temperature) starting in 1881, and increasing atmospheric CO, concentrations. The model explains 78.3% of the variance for sessile oak and 74.3% for pedunculate oak. This includes some monthly parameters of year y (year of ring formation), and also some parameters of the years y-1 to y-4 for sessile oak and y-1 to y-5 for pedunculate oak. The models satisfactorily reproduce the long-term trends and the interannual variation. The climatic variables alone (ie excluding the CO, concentration) were insufficient to explain the trends observed. The possible direct and indirect effects of increasing CO2 concentration on the growth of both species are discussed.

KEYWORDS: ABIES-ALBA MILL, CARBON DIOXIDE, FOREST, GROWTH, MOUNTAINS, PAST VITALITY, PINE, TREES, TRENDS, VEGETATION

160

Beckmann, K., C. Dzuibany, K. Biehler, H. Fock, R. Hell, A. Migge, and T.W. Becker. 1997. Photosynthesis and fluorescence quenching, and the mRNA levels of plastidic glutamine synthetase or of mitochondrial serine hydroxymethyltransferase (SHMT) in the leaves of the wild-type and of the SHMT-deficient stm mutant of Arabidopsis thaliana in relation to the rate of photorespiration. *Planta 202(3):379-386.*

The regulation by photorespiration of the transcript level corresponding to plastidic glutamine synthetase (GS-2) was investigated in the leaves of Arabidopsis thaliana (L.) Heynh. Photorespiration was suppressed by growing the plants in an atmosphere containing 300 Pa CO2. Suppression of photorespiration was demonstrated by the ability of the conditionally lethal serine hydroxymethyltransferase (SHMT)- deficient stm mutant of A. thaliana to grow normally under these conditions. In contrast to previous studies with bean or pea that were performed at very high CO2 partial pressure (2-4 kPa; Edwards and Coruzzi, 1989, Plant Cell 1: 241-248; Cock et al., 1991, Plant Mol Biol 17: 761-771), suppression of photorespiration during growth of A. thaliana in an atmosphere with 300 Pa CO2 had no effect on the leaf GS-2 transcript level. In the short term, neither suppression of photorespiration induced by the transfer of air-grown A. thaliana plants into a CO2-enriched atmosphere, nor an increase in the rate of photorespiration achieved by the transfer of high-CO2-grown A. thaliana plants into air resulted in a change in the GS-2 mRNA level. The absence of photorespiratory ammonium release in leaves of the stm mutant had no effect on the GS-2 transcript level. Overall, our data argue against a control by photorespiration of the A. thaliana leaf GS-2 mRNA pool. In contrast, regulation of the leaf SHMT mRNA level may involve a negative feedback effect of at least one metabolite derived from the glycine/serine conversion during photorespiration, as indicated by the overexpression of SHMT transcripts in the leaves of the stm mutant.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, EXCHANGE, EXPRESSION, GENES, LIGHT, SUNFLOWER LEAVES, TOBACCO

161

Beer, S., and E. Koch. 1996. Photosynthesis of marine macroalgae and seagrasses in globally changing CO2 environments. *Marine Ecology-Progress Series 141(1-3):199-204.*

Photosynthetic rates of many marine macroalgae are saturated by the present day inorganic carbon (Ci) composition of seawater, while those of seagrasses (or marine angiosperms) are CO2- limited. In this study we attempted to simulate the Ci conditions of near-shore seawater during the time that seagrasses colonised the sea (in the Cretaceous), and compare the photosynthetic performance of representatives of the 2 plant groups under those versus present day conditions. The results show that the seagrasses have an affinity for Ci at least as high as the algae under the low pH and high CO2/HCO3- concentration ratios simulating near-shore areas of the Cretaceous seas, indicating that their photosynthetic capacity then matched that of macroalgae. However, in the high pH and high CO2/HCO3- ratios of today, their affinity for Ci is lower than that of the macroalgae, and it is suggested that this deficiency renders them a lower ability for Ci utilisation. This situation may possibly be reversed again as global CO2 levels of the atmosphere and, consequently, of near-shore marine habitats increase in the future.

KEYWORDS: CELLS, ULVA SP

162

Beerling, D.J. 1994. Modeling palaeophotosynthesis - late cretaceous to present. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 346(1318):421-432.*

This paper presents an attempt to reconstruct potential changes in the photosynthetic rates of terrestrial C3 leaves over the past 120 Ma. The approach has been to couple palaeoatmospheric reconstructions of O-2, CO2 and temperature from geochemical modelling, and an independent estimate of ancient CO2 changes from fossil porphyrins, with a mechanistic biochemical model of C3 photosynthesis. The model accounts for the effect of each of these palaeoenvironmental changes, at the biochemical level, to predict leaf photosynthesis and has been parametrized for a typical gymnosperm and angiosperm. The results indicate clear potential for increased photosynthetic C3 fixation in the warm Cretaceous for both angiosperms and gymnosperms, despite the increased O-2 content of the atmosphere prevailing at the time. Photosynthetic rates are then predicted to progressively decline into the Tertiary, as a result of global cooling. The model simulations also point towards some leaf-level ecophysiological explanations for the rise in angiosperm dominance and the concomitant decline in gymnosperms from the late Cretaceous onwards, at mid-latitudes, which have not been considered previously. This work provides a basis for scaling up to the canopy level to predict the primary productivity of ancient ecosystems and their possible feedback on atmospheric composition and climate.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO2, HIGH-LATITUDES, PHANEROZOIC TIME, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, TERTIARY BOUNDARY

163

Beerling, D.J. 1994. Predicting leaf gas-exchange and delta-C-13 responses to the past 30000 years of global environmental-change. *New Phytologist 128(3):425-433.*

Theoretical developments in our understanding of leaf gas exchange processes and carbon isotope composition (delta(13)C) mean that it should now be possible to model their responses to global environmental change. Such a model would be of use for process-based interpretations of historical changes in leaf delta(13)C and for understanding the global stable carbon isotope balance. This paper describes the development and validation of a model towards this aim. The resulting model is used to simulate changes in leaf photosynthesis, stomatal conductance and delta(13)C of limber pine (Pinus flexilis) in response to the past 30000 y of global environmental change. The predictions of needle delta(13)C are in line with reported measurements of delta(13)C from fossilized Pinus flexilis needles preserved in packrat middens in western USA. Leaf gas exchange predictions show that the increased water use efficiency (WUE) of these trees growing in present-day environments, relative to the past, was brought about through an increase in photosynthetic rates and a decrease in stomatal conductance. This contrasts with the explanation of the recent (past 200 y) increase in the

WUE of temperate and Mediterranean ecosystems inferred from delta(13)C measurements which are predicted by the model to have arisen largely by a decrease in stomatal conductance in response to increases in the concentration of atmospheric CO2 since the pre-industrial era. The model as described offers the potential to contribute to our understanding of vegetation effects on the global carbon isotope balance during the glacial periods, and therefore to provide a further constraint on the carbon cycle models used to explain the low concentrations of atmospheric CO2 at these times.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, C-13/C-12 RATIO, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, EMPIRICAL-MODEL, ICE-CORE RECORD, LEAVES, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

164

Beerling, D.J. 1996. C-13 discrimination by fossil leaves during the late-glacial climate oscillation 12-10 ka BP: Measurements and physiological controls. *Oecologia 108(1):29-37.*

The late-glacial climatic oscillation, 12-10 ka BP, is characterised in ice core oxygen isotope profiles by a rapid and abrupt return to glacial climate. Recent work has shown that associated with this cooling was a drop in atmospheric CO2 concentration of ca. 50 ppm. In this paper, the impact of these environmental changes on C-13 discrimination is reported, based on measurements made on a continuous sequence of fossil Salix herbacea leaves from a single site. The plant responses were interpreted using an integrated model of stomatal conductance, CO2 assimilation and intercellular CO2 concentration, influenced by external environmental factors. According to the model, temperature exerts a marked influence on C-13 discrimination by leaves and the pattern of C-13 changes recorded by the fossil leaves is consistent with other palaeotemperature curves for 12-10 ka BP, particularly the deuterium isotope record from Alaskan Salix woods, which generally reflects ocean temperatures. The gas exchange model correctly accounts for these changes and so permits the reconstruction of ancient rates of leaf CO2 uptake and loss of water vapour in response to the abrupt late-glacial changes in global climate and CO2. The approach provides the required physiological underpinning for extracting quantitative estimates of past temperatures and for contributing an ecophysiological explanation for changes in C-13 discrimination in the fossil record.

KEYWORDS: ATMOSPHERIC CO2, C-13/C-12 RATIOS, C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, ELEVATED CO2, ENVIRONMENTAL-CHANGE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY, WESTERN NORWAY, YOUNGER DRYAS

165

Beerling, D.J. 1997. Carbon isotope discrimination and stomatal responses of mature Pinus sylvestris L trees exposed in situ for three years to elevated CO2 and temperature. *Acta Oecologica-International Journal of Ecology 18(6):697-712.*

The Climate Change Experiment (CLIMEX) is a unique large scale facility in which an entire undisturbed catchment of boreal vegetation has been exposed to elevated CO2 (560 ppm) and temperature (+3 degrees C summer, +5 degrees C winter) for the past three years with all the soil-plant-atmosphere linkages intact. Here, carbon isotope composition end stomatal density have been analysed from sequential year classes of needles of mature Scots pine trees (Pinus sylvestris L.) to investigate the response of time-integrated water-use efficiency (WUE) and stomatal density to CO2 enrichment and climate change. Cal bon isotope discrimination decreased and WUE increased in cohorts of needles developing under increased CO2 and temperature, compared to needles on the same trees developing in pretreatment years. Mid-season instantaneous gas exchange, measured on the same trees for the past four pears, indicated that these responses resulted from higher needle photosynthetic rates and reduced stomatal conductance. Needles of P. sylvestris developing under increased CO2 and temperature had consistently lower stomatal densities than their ambient grown counterparts on the same trees. The stomatal density of P. sylvestris needles was inversely correlated with delta(13)C- derived WUE, implying some effect of this morphological response on leaf gas exchange. Future atmospheric CO2 and temperature increases are therefore likely to improve the water economy of P. sylvestris, at least at the scale of individual needles, by affecting stomatal density and gas exchange processes.

KEYWORDS: 4-YEAR EXPOSURE, BOREAL VEGETATION, C-3 PLANTS, DENSITY, ENRICHMENT, GAS-EXCHANGE RESPONSES, LAST 3 CENTURIES, SCOTS PINE, WATER-USE EFFICIENCY, WHOLE-CATCHMENT

166

Beerling, D.J. 1997. Interpreting environmental and biological signals from the stable carbon isotope composition of fossilized organic and inorganic carbon. *Journal of the Geological Society 154:303-309.*

Stable carbon isotope studies on marine and terrestrial organic and inorganic carbon provide a means for detecting global climate change and for reconstructing past concentrations of atmospheric CO2. Comparison between the CO2 estimates reconstructed from carbon isotope studies for the past 150 Ma show good agreement with the predictions of a long-term carbon- cycle model based on mass-balance studies. Further, the CO2 estimates from these sources over the entire Phanerozoic show agreement with the fossil record of leaf stomatal density change-a feature inversely related to the concentration of atmospheric CO2. Isotopic studies on temporal sequences of fossilized terrestrial organic matter have contributed to palaeoecological studies on shifts in the dominance of plants with the C-4 photosynthetic pathway in ecosystems and historical changes in the metabolic processes of leaves of individual species. The long-term perspective offered by these studies provides critical information for assessing the responses of biological systems to future global environmental change.

KEYWORDS: ATMOSPHERIC CO2, C-4 PLANTS, CLIMATE CHANGE, DIOXIDE, ELEVATED CO2, ICE-CORE RECORD, LATE QUATERNARY, PERMIAN TRIASSIC BOUNDARY, STOMATAL DENSITY, WATER-USE EFFICIENCY

167

Beerling, D.J. 1998. The future as the key to the past for palaeobotany? *Trends in Ecology and Evolution 13(8):311-316.*

Continued increase in the concentration of atmospheric CO2 and its possible effects on global climate has generated intense research interest on the likely responses of terrestrial plants and vegetation. Results from this new research provide quantitative information on plant function and growth in an environment with a high CO2 concentration, but are also relevant to understanding plant growth in the distant past and to the techniques employed by palaeobotanists for reconstructing past climates from fossil plant remains. Experimental CO(2)enrichment of plants has demonstrated direct effects on leaf physiognomy, the tolerance of plants to low temperature and the relationship between tree rings, CO(2)and climate; it therefore signals the need for caution in interpreting palaeoclimates from fossils.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, CLIMATE, EARLY TERTIARY, ELEVATED CO2, ENRICHMENT, FOSSIL PLANTS, FROST HARDINESS, PHOTOSYNTHESIS, TEMPERATURE, TREE GROWTH

168

Beerling, D.J. 1999. Long-term responses of boreal vegetation to global change: an experimental and modelling investigation. *Global Change Biology 5(1):55-74.*

The response of boreal ecosystems to future global change is an uncertain but potentially critical component of the feedback between the terrestrial biosphere and the atmosphere. To reduce some of the uncertainties in predicting the responses of this key ecosystem, the climate change experiment (CLIMEX) exposed an entire undisturbed catchment of boreal vegetation to CO2 enrichment (560 ppmv) and climate change (+ 5 degrees C in winter, + 3 degrees C in summer) for three years (1994-96). This paper describes the leaf metabolic responses of the vegetation to the experimental treatment and model simulations of possible future changes in the hydrological and carbon balance of the site. Randomized intervention analysis of the leaf gas exchange measurements for the dominant species indicated Pinus sylvestris had significantly ($P < 0.01$) higher photosynthetic rates and Betula pubescens and Vaccinium myrtillus had significantly ($P < 0.01$) lower stomatal conductances after three years treatment compared to the controls. These responses led to sustained increases in leaf water-use efficiency of all species of trees and ground shrubs, as determined from carbon isotope analyses. Photosynthesis (A) vs. intercellular CO2 (c(i)) response curves (A/c(i) responses), RuBisCo analysis and leaf nitrogen data together suggested none of the species investigated exhibited down-regulation in photosynthetic capacity. At the whole ecosystem level, the improved water economy of the plants did not translate into increased catchment runoff. Modelling simulations for the site indicate this was most likely brought about by a compensatory increase in evapotranspiration. In terms of the carbon budget of the site, the ecosystem model indicates that increased CO2 and temperature would lead to boreal ecosystems of the type used in CLIMEX, and typical of much of southern Norway, acting as moderate net sinks for CO2.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, ECOSYSTEM EXPERIMENTS, ELEVATED CO2, FOREST ECOSYSTEMS, GAS-EXCHANGE RESPONSES, PHOTOSYNTHETIC RESPONSE, RISING ATMOSPHERIC CO2, SCOTS PINE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

169

Beerling, D.J., and W.G. Chaloner. 1993. Evolutionary responses of stomatal density to global co2 change. *Biological Journal of the Linnean Society 48(4):343-353.*

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, GROWTH, INCREASE, PLANTS, POPLAR CLONES, WATER-USE EFFICIENCY

170

Beerling, D.J., and W.G. Chaloner. 1993. The impact of atmospheric co2 and temperature-change on stomatal density - observations from quercus-robur lammas leaves. *Annals of Botany 71(3):231-235.*

KEYWORDS: CARBON ISOTOPES, CENTURIES, DIOXIDE, ELEVATED CO2, GROWTH, KRAKOW REGION, PLANTS, RECORD, RESPONSES

171

Beerling, D.J., and W.G. Chaloner. 1993. Stomatal density responses of egyptian olea-europaea L leaves to co2 change since 1327 bc. *Annals of Botany 71(5):431-435.*

KEYWORDS: ATMOSPHERIC CO2, CENTURIES, ENRICHMENT, RECORD, VOSTOK ICE-CORE

172

Beerling, D.J., W.G. Chaloner, B. Huntley, A. Pearson, and M.J. Tooley. 1991. Tracking stomatal densities through a glacial cycle - their significance for predicting the response of plants to changing atmospheric CO2 concentrations. *Global Ecology and Biogeography Letters 1(5):136-142.*

Continued increases in the global atmospheric CO2 concentration have been predicted from current and projected rates of fossil fuel burning. Understanding the response of stomatal density as an important ecophysiological parameter controlling the productivity of vegetation is essential if the role of plants in the global carbon budget are to be predicted. Experimental exposure of plants to elevated CO2 regimes in controlled environment chambers can only indicate immediate, phenotypic, short-term responses. The investigation of fossil leaves of extant species growing under the different atmospheric conditions of the last glacial and deglacial transition, when evidence from an Antarctic ice core (Barnola et al., 1987) indicates CO2 levels markedly different from pre-industrial levels, provides one means for eliciting long-term plant responses to changing CO2 regimes. We have prepared cuticles from Quaternary leaf fossils, from which stomatal density and index can be calculated. Our preliminary results give promise of extending the record of stomatal density response back at least 10,000 years.

KEYWORDS: ENRICHMENT, ICE, RECORD

173

Beerling, D.J., W.G. Chaloner, B. Huntley, J.A. Pearson, M.J. Tooley, and F.I. Woodward. 1992. Variations in the stomatal density of salix-herbacea L under the changing atmospheric co2 concentrations of late-glacial and postglacial time. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 336(1277):215-224.*

The rapidly rising CO2 concentration of the past 200 years has been shown to be accompanied by a fall in stomatal density in the leaves of temperate trees. The present study attempts to investigate the relationship of atmospheric CO2 change and stomatal density in the arctic-alpine shrub, Salix herbacea, over the longer time span of 11 500 years offered by fossil leaves from post-glacial deposits. Comparisons of fossil material from Scotland and Norway are made with leaves from living populations growing in Austria, Greenland and Scotland. The Austrian material, from an altitudinal gradient between 2000 and 2670 m above sea level, gives added comparison of contemporary differences of CO2 partial pressure with altitude. The results of our investigation indicate, rather surprisingly, that the rising CO2 concentration of the past 11 500 years has been accompanied by an increase in the stomatal density of S. herbacea in contrast to the shorter-term observations on the herbarium material of temperate trees. The most likely explanation appears to centre on the temperatures and water availability of the early post-glacial environment overriding the effect of the lower CO2 regime. However, the scale of the time interval involved may also be significant. Natural selection over the 11 500 year period concerned may have favoured a different response to what is, in effect, an acclimatory response observed in trees within the period of rapid CO2 rise of the past 200 years.

KEYWORDS: CARBON DIOXIDE, CLIMATE, ENRICHMENT, GRADIENT, GROWTH, LEAF ANATOMY, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, WATER-USE EFFICIENCY

174

Beerling, D.J., J. Heath, F.I. Woodward, and T.A. Mansfield. 1996.

Drought-CO2 interactions in trees: Observations and mechanisms. *New Phytologist 134(2):235-242.*

It is sometimes assumed that because increases in atmospheric CO2 concentration usually enhance water use efficiency per unit leaf area, there will be a tendency for plants to show greater drought tolerance as well as increased biomass in the future. A critical examination of the responses to elevated CO2 in three temperate tree species shows that this assumption might be incorrect in the case of two of them. Both beech (Fagus sylvatica L.) and birch (Betula pubescens Ehrh.) display minimal stomatal closing responses to elevated CO2, and in the case of F. sylvatica the stomatal control of transpiration per unit leaf area appears to be unable to compensate for the greater development of leaf area. By contrast, the stomata of oak (Quercus robur L.) close appreciably in elevated CO2, to an extent which might be sufficient to compensate for an increase in total leaf area. A simple model for the controls on water supply and consumption for the whole tree suggests that in F. sylvatica the potential height attainment for a given sapwood area might decrease as the atmospheric CO2 concentration rises. The conclusions drawn from experimental data and from modelling are supported by field observations made in the UK in 1995, when the three species responded very differently to severe drought. We suggest that the progressive increase in the concentration of atmospheric CO2 over the past 200 yr might have accentuated differences in drought sensitivity between these species.

KEYWORDS: ATMOSPHERIC CO2, BETULA-PENDULA ROTH, ELEVATED CARBON-DIOXIDE, FAGUS-SYLVATICA, GAS-EXCHANGE, GLOBAL ENVIRONMENTAL-CHANGE, GROWTH, PHOTOSYNTHESIS, PLANT-RESPONSES, TRANSPIRATION

175

Beerling, D.J., B. Huntley, and J.P. Bailey. 1995. Climate and the distribution of fallopia-japonica - use of an introduced species to test the predictive capacity of response surfaces. *Journal of Vegetation Science 6(2):269-282.*

The relationship between present climate and the distribution in Europe of the aggressively invasive exotic Fallopia japonica is described by fitting a response surface based on three bioclimatic variables: mean temperature of the coldest month, the annual temperature sum > 5 degrees C, and the ratio of actual to potential evapotranspiration. The close fit between the observed and simulated distributions suggests that the species' European distribution is climatically determined. The response surface also provides a simulation of the extent of the area of native distribution of F. japonica in Southeast Asia that is generally accurate, confirming the robustness of the static correlative model upon which it is based. Simulations of the potential distribution of F. japonica under two alternative 2 x CO2 climate change scenarios indicate the likelihood of considerable spread into higher latitudes and possible eventual exclusion of the species from central Europe. However, despite the robustness of the response surface with present-day climate, the reliability of these simulations as forecasts is likely to be limited because no account is taken of the direct effects of CO2 and their interaction with the species' physiological responses to climate. Similarly, no account is taken of the potential impact of interactions with 'new' species as ecosystems change in composition in response to climate change. Nevertheless, the simulations indicate both the possible magnitude of the impacts of forecast climate changes and the regions that may be susceptible to invasion by F. japonica.

176

Beerling, D.J., and C.K. Kelly. 1997. Stomatal density responses of temperate woodland plants over the past seven decades of CO2 increase: A comparison of Salisbury (1927) with contemporary data. *American Journal of Botany 84(11):1572-1583.*

We investigated the possible effect of recent (1927-1995) increases in the concentration of atmospheric CO2 on the stomatal densities of leaves of a wide range of tree, shrub, and herb species (N = 60) by making new measurements for comparison with corresponding data reported by E. J. Salisbury in 1917-a time when ice core studies indicate CO2 concentrations similar to 55 mu L/L lower than present. A detailed intraspecific study of the herb Mercurialis perenius showed plants of M. perennis in a Cambridgeshire woodland in 1994 had significantly lower stomatal densities, irrespective of leaf insertion point, compared with their 1927 counterparts. Comparisons made across species using evolutionary comparative methods (independent contrasts revealed a significant ($P < 0.01$) decrease in stomatal density over the past 70 yr. The results of both the inter-and intraspecific comparisons are consistent with the hypothesis that historical CO2 increases have influenced leaf morphology in a manner consistent with recent experiments and the palaeoecological record. Further analyses suggested that the strength of the stomatal density response was independent of life form but dependent on "exposure" and the initial leaf stomatal density. Consequently firmer predictions for future changes in stomatal density across all species, expected as a possible result of authropogenically related CO2 increases, may now be possible.

KEYWORDS: ATMOSPHERIC CO2, CENTURIES, DELTA C 13, ELEVATED CO2, ENRICHMENT, ENVIRONMENTAL-CHANGE, GAS-EXCHANGE, GROWTH, LEAF-AREA, TAXONOMIC RELATEDNESS

177

Beerling, D.J., J.C. McElwain, and C.P. Osborne. 1998. Stomatal responses of the 'living fossil' Ginkgo biloba L. to changes in atmospheric CO2 concentrations. *Journal of Experimental Botany 49(326):1603-1607.*

Leaf stomatal density and index of Ginkgo biloba L. were both significantly ($P < 0.05$) reduced after 3 years growth at elevated CO2 (560 ppm), with values comparable to those of cuticles prepared from Triassic and Jurassic fossil Ginkgo leaves thought to have developed in the high CO2 'greenhouse world' of the Mesozoic. A reciprocal transfer experiment indicated that reductions in stomatal density and index irreversibly reduced stomatal conductance, particularly at low leaf-to-air vapour pressure deficits and low internal leaf CO2 concentrations (C-i). These effects probably contributed to the high water-use efficiency of Ginkgo spp. in the Mesozoic relative to those of the present, as determined from carbon isotope measurements of extant and fossil cuticles.

KEYWORDS: CYCLE, DENSITY, ENVIRONMENTAL-CHANGE, LEAVES, RECORD

178

Beerling, D.J., and W.P. Quick. 1995. A new technique for estimating rates of carboxylation and electron-transport in leaves of C-3 plants for use in dynamic global vegetation models. *Global Change Biology 1(4):289-294.*

The possible responses of the terrestrial biosphere to future CO2 increases and associated climatic change are being investigated using dynamic global vegetation models (DGVMs) which include the Farquhar ef al. (1980) biochemical model of leaf assimilation as the primary means of carbon capture. This model requires representative values of the maximum rates of Rubisco activity, V-max, and electron transport, J(max), for different vegetation types when applied at the global scale. Here, we describe an approach for calculating these values based on measurements of the maximum rate of leaf photosynthesis (A(max)) and

C-13 discrimination. The approach is tested and validated by comparison with measurements of Rubisco activity assayed directly on wild-type and transgenic Nicotiana tabacum (tobacco) plants with altered Rubisco activity grown under ambient and elevated CO2 mole fractions with high and low N-supply. V-max and J(max) values are reported for 18 different vegetation types with global coverage. Both variables were linearly related reinforcing the idea of optimal allocation of resources to photosynthesis (light harvesting vs. Rubisco) at the global scale. The reported figures should be of value to the further development of vegetation and ecosystem models employing mechanistic DGVMs.

KEYWORDS: ANTISENSE GENE, CARBON ISOTOPE DISCRIMINATION, CLIMATE, CO2 CONCENTRATIONS, GROWTH, IMPACT, OXYGENASE, PHOTOSYNTHETIC RESPONSE, RBCS

179

Beerling, D.J., and F.I. Woodward. 1993. Ecophysiological responses of plants to global environmental- change since the last glacial maximum. *New Phytologist 125(3):641-648.*

Ecophysiological information on the responses of plants to past global environmental changes may be obtained from Quaternary fossil leaves by measurements of (i) stomatal density, (ii) stomatal dimensions and (iii) C-13 discrimination (DELTA C-13). The stomatal density and stomatal dimensions of leaves can be used to calculate stomatal conductance, while leaf DELTA C-13 values provide independent information on stomatal conductance and plant water use efficiency. In this paper, stomatal conductance is calculated for a sequence of radiocarbon dated fossil leaves of Salix herbacea L. which, together with herbarium and fresh material, represents a time-series spanning from the Last Glacial Maximum (LGM) (16 500 yr BP) to the present day. The calculated values were then tested against leaf DELTA C-13 values previously reported for the same material. Our calculations show that stomatal conductance is negatively correlated with increases in atmospheric CO2 concentration over the last 16 500 yr. This represents the first evidence of long-term response of stomatal conductance to increases in atmospheric CO2 concentration and confirms the response observed in experimental systems exposing plants to lower-than-present CO2 concentrations in controlled environments. The calculated decrease in conductance was positively correlated with leaf DELTA C-13 values, supporting this interpretation. The mean leaf DELTA C-13 value for the 18th and 19th centuries was significantly ($P < 0.05$) lower than the mean for the interval LGM-Holocene (10000 yr BP) implying an increase in plant water-use-efficiency over this time. These two lines of evidence, together with the stomatal density record from a glacial cycle, and experimental studies growing C3 plants in glacial-to-present CO2 concentrations, strongly imply that the water use efficiency of vegetation during the LGM was lower than at present and that it has increased since that time. Further evidence in support of this conclusion comes from the pattern of world vegetation types present during the LGM previously reconstructed using palaeoecological data. This evidence demonstrates that the distribution of vegetation types during the LGM was significantly different from that of the present day and showed a contraction in the area of rain forest and a major expansion of desert areas.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CARBON ISOTOPE DISCRIMINATION, CLIMATE CHANGE, FORESTS, RECORD, TEMPERATURES, TRANSPIRATION, VEGETATION, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

180

Beerling, D.J., and F.I. Woodward. 1994. The climate-change experiment (climex) - phenology and gas- exchange responses of boreal vegetation to global change. *Global Ecology and Biogeography Letters 4(1):17-26.*

Large-scale whole ecosystem experiments will become increasingly important for predicting and testing hypotheses of complex ecosystem responses to global change. The Climate Change Experiment (CLIMEX) uses a site with an entire undisturbed boreal-forested catchment enclosed within an existing very large scale (1200m2 ground area) greenhouse. In the forthcoming year temperature will be increased stepwise to +3-degrees-C in summer, +5-degrees-C in winter and the atmospheric CO2 concentration enriched to 560 ppm which together simulate future changes in global climate and atmospheric composition predicted by GCMs. Plants growing within this low nutrient ecosystem are strongly dependent upon mycorrhizal associations for nutrient uptake and rates of nutrient uptake. Therefore it will provide an important test of current ideas concerning how mycorrhizas might modify plant responses to global change. We describe predictions of community phenology and gas exchange at the CLIMEX site; in the latter case the effects of including and excluding rates of on nutrient supply are considered. The results are discussed with reference to the opportunities presented by CLIMEX to reveal important aspects of the physiological responses of boreal ecosystems to global change.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, BUDBURST, CARBON DIOXIDE, ELEVATED CO2, PLANT-RESPONSES, PRODUCTIVITY, TREES

181

Beerling, D.J., and F.I. Woodward. 1995. Leaf stable carbon-isotope composition records increased water- use efficiency of C-3 plants in response to atmospheric co2 enrichment. *Functional Ecology 9(3):394-401.*

1. A total of 17 temperate C-3 grass and herb species were grown for 5 weeks at three mole fraction treatments of atmospheric CO2 (350, 525 and 700 mu mol mol(-1)). Leaf stable carbon isotope compositions (delta(13)C) were determined to record long-term exchange responses together with instantaneous gas exchange measurements. The isotopic composition of the atmospheric CO2 (delta(13)C(a)) integrated over the course of the CO2 treatments was recorded biologically using the C-4 species Zea mays. 2. We found that increases in the mole fraction of atmospheric CO2 above current levels resulted in a sustained increase in instantaneous (photosynthesis, A/conductance, g(s)) leaf water-use efficiency (IWUE), as calculated from carbon isotope-derived p(i)/p(a) ratios. Grass species showed a marked decline in the magnitude of WUE increase as the CO2 mole fraction was increased from 525 to 700 mu mol mol(-1), a response which was absent in herb species. 3. Isotopic derivation of the ratio of intercellular CO2 mole fraction (p(i)) to that in the surrounding atmosphere (p(a)), considered as a set point of leaf metabolism, showed no significant ($P = 0.06$) changes in response to increases in the mole fraction of CO2, for herb and grass species. Measurements of p(i)/p(a) determined from measurements of leaf gas exchange differed significantly ($P<0.01$) from those derived from stable isotope ratios. These differences are attributed to contrasting stomatal behaviour between herb and grass species. 4. Leaf intercellular CO2 mole fraction and previously reported above- ground biomass responses to CO2 increases for the same species were positively correlated ($P < 0.05$). This suggests that as atmospheric CO2 levels continue to rise species showing sustained higher rates of leaf photosynthesis, may be translated into increased productivity depending on soil water and nutrient status.

KEYWORDS: DELTA C 13, DIOXIDE, DISCRIMINATION, LEAVES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, STOMATAL CONDUCTANCE

182

Beerling, D.J., and F.I. Woodward. 1995. Stomatal responses of variegated leaves to co2 enrichment. *Annals of Botany 75(5):507-511.*

The responses of stomatal density and stomatal index of five species of ornamental plants with variegated leaves grown at two mole fractions of atmospheric CO2 (350 and 700 mu mol mol(- 1)) were measured. The use of variegated leaves allowed any potential effects of mesophyll photosynthetic capacity to be uncoupled from the responses of stomatal density to changes in atmospheric CO2 concentration. There was a decrease in stomatal density and stomatal index with CO2 enrichment on both white (unpigmented) and green (pigmented) leaf areas. A similar response of stomatal density and index was also observed on areas of leaves with pigmentation other than green indicating that any differences in metabolic processes associated with coloured leaves are not influencing the responses of stomatal density to CO2 concentrations. Therefore the carboxylation capacity of mesophyll tissue has no direct influence on stomatal density and index responses as suggested previously (Friend and Woodward 1990 Advances in Ecological Research 20: 59-124), instead the responses were related to leaf structure. The stomatal characteristics (density and index) of homobaric variegated leaves showed a greater sensitivity to CO2 on green portions, whereas heterobaric leaves showed a greater sensitivity on white areas. These results provide evidence that leaf structure may play an important role in determining the magnitude of stomatal density and index responses to CO2 concentrations.

KEYWORDS: CHLOROPHYLL, LEAF

183

Beerling, D.J., and F.I. Woodward. 1996. In situ gas exchange responses of boreal vegetation to elevated CO2 and temperature: First season results. *Global Ecology and Biogeography Letters 5(3):117-127.*

The climate change experiment (CLIMEX) uses a large greenhouse to investigate the responses of an entire undisturbed boreal forested catchment to elevated CO2 (560 ppm) and temperature (+3 degrees C in summer and +5 degrees C in winter) treatments. In July and September of the first season of treatment the two dominant tree species, Pinus sylvestris and Betula pubescens, and the ground shrub Vaccinium myrtillus all showed an increase in leaf photosynthetic rates relative to the plants growing in the control section of the greenhouse and in an outside reference catchment. Stomatal density of needles of II sylvestris, and leaves of B. pubescens and V. myrtillus decreased under CO2 enrichment and temperature increases relative to the controls. Gas exchange and stable carbon isotope measurements will be made in future growing seasons to investigate whether acclimatory adjustments in plant metabolism occur-a critical issue affecting the carbon balance of these ecosystems.

KEYWORDS: CARBON DIOXIDE, NUTRITION, PHENOLOGY, PHOTOSYNTHESIS, STOMATAL DENSITY, WATER-USE

184

Beerling, D.J., and F.I. Woodward. 1996. Palaeo-ecophysiological perspectives on plant responses to global change. *Trends in Ecology and Evolution 11(1):20-23.*

Taxonomic classifications of plant species, based on morphological characteristics, provide a stable and robust approach for Inferring taxonomic and phylogenetic relationships between extant and extinct species. This implies that, although evolution is a continuous process for a species, there is no whole-scale change in those suites of morphological characteristics that define higher order (genus and greater) relationships. Recent research suggests that a higher order characteristic stomatal density - may reflect not only the atmospheric CO2 concentration during initial evolution, but may also strongly constrain the responses of higher order plant groups to future CO2-enrichment.

KEYWORDS: CO2, EVOLUTION, RECORD, VASCULAR PLANTS

185

Beerling, D.J., and F.I. Woodward. 1997. Changes in land plant function over the Phanerozoic: Reconstructions based on the fossil record. *Botanical Journal of the Linnean Society 124(2):137-153.*

Major fluctuations in the concentrations of atmospheric CO2 and O-2 are predicted by historical long-term carbon and oxygen cycle models of atmospheric evolution and will have impacted directly on past climates, plant function and evolutionary processes. Here, palaeobotanical evidence is presented from the stomatal density record of fossil leaves spanning the past 400 Myr supporting the predicted changes in atsmopheric CO2. Evidence from experiments on plants exposed to long-term high CO2 environments and the newly assembled fossil data indicate the potential for genetic modification of stomatal characters. The influence of tile changes in fossil stomatal characteristics and atmospheric composition on the rates of leaf gas exchange over the course of land plant evolution has been investigated through modelling. Three contrasting cras of plant water economies emerge in the Devonian (high), Carboniferous (low) and from the Upper Jurassic to the present-day (high but declining). These patterns of change result from structural changes of the leaves and the impact of atmospheric CO2 and O-2 concentrations on RuBisCO function and are consistent with the fossil evidence of sequential appearances of novel plant anatomical changes. The modelling approach is tested by comparing predicted leaf stable carbon isotope ratios with those measured on fossil plant and organic material. Viewed in a geological contest, current and future increases in the concentration of atmospheric CO2 might be considered as restoring-plant function to that more typically experienced by plants over the majority of their evolutionary history. (C) 1997 The Linnean Society of London.

KEYWORDS: C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, CO2- ENRICHMENT, EPIDERMAL STRUCTURE, LEAF, LEAVES, NORTH-AMERICA, PHOTOSYNTHESIS, RESPONSES, STOMATAL DENSITY

186

Beerling, D.J., F.I. Woodward, M. Lomas, and A.J. Jenkins. 1997. Testing the responses of a dynamic global vegetation model to environmental change: a comparison of observations and predictions. *Global Ecology and Biogeography Letters 6(6):439-450.*

Dynamic global vegetation - biogeochemistry models are required to predict the likely responses of the terrestrial biosphere to anticipated future global environmental change and for improved representation of an active vegetation surface within general circulation models of the Earth's global climate system. Testing the predictions of such models is essential to their development prior to use in a predictive capacity. The climate change experiment (CLIMEX) has exposed an entire catchment of boreal vegetation to elevated CO2 (560 ppmv) and temperature (+3 degrees C in summer, +5 degrees C in winter) for the past three years and has a considerable archive of pre-and posttreatment measurements of both CO2 and water vapour fluxes of the vegetation, catchment runoff and soil nutrient status. These data have been used to test the predictions of the University of Sheffield dynamic global vegetation model (SDGVM) for the same site using historical records of climate as input. Comparisons of observations and predictions at the scale of individual leaves and whole ecosystems are generally favourable, increasing our confidence in the application of the model to forecasting the responses of the terrestrial biosphere to various global change scenarios. The SDGVM has been used to predict the future responses of the ecosystem

at the site into the year 2003AD. The results indicate rather small changes in leaf area index and catchment runoff but quite large increases in net primary productivity. The model predictions are now open to testing further as the CO2 and temperature treatments continue in the CLIMEX greenhouse.

KEYWORDS: ATMOSPHERIC CO2, BOREAL VEGETATION, CARBON BALANCE, CLIMATE CHANGE, ELEVATED CO2, FOREST, GAS-EXCHANGE RESPONSES, SCALE, TEMPERATURE, WHOLE-CATCHMENT

187

Beeson, R.C., and M.E.D. Graham. 1991. CO2 enrichment of greenhouse roses affects neither rubisco nor carbonic-anhydrase activities. *Journal of the American Society for Horticultural Science 116(6):1040-1045.*

The effect of prolonged CO2 enrichment on the activities of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and carbonic anhydrase (CA) of greenhouse roses were studied. Plants of Rosa X hybrida 'Red Success' were grown for 2 years at ambient and 900-mu-l CO2/liter during winter and spring with 75-mu-mol.m-2.s-1 photosynthetically active radiation supplemental lighting for 2 years. Measurements of initial and Mg+2-Co2-activated activities of Rubisco and CA were made during shoot development and at different positions within the plant canopy. Generally, there were no significant differences measured in the enzyme activities between the two CO2 concentrations. The results suggest that the photosynthetic capacity did not change and that there were no characteristic adaptations to long-term growth (up to 20 weeks) at elevated C02 concentrations. The maintenance of Rubisco and CA activities with prolonged exposure to C02-enriched atmospheres is proposed as the reason for long-term yield increases in roses when grown in enriched environments.

KEYWORDS: ACCLIMATION, DIOXIDE, GROWTH, LEAVES, LONG-TERM, PHOTOSYNTHETIC REINVIGORATION, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SEEDLINGS, SHOOT DECAPITATION

188

Behboudian, M.H., and R. Lai. 1994. Carbon-dioxide enrichment in virosa tomato plant - responses to enrichment duration and to temperature. *Hortscience 29(12):1456-1459.*

Responses of the tomato (Lycopersicon esculentum Mill. cv. Virosa) plant to elevated CO2 concentrations applied throughout the photoperiod or part of it were studied under two temperature regimes. Plants were exposed to CO2 at 340 (control), 700, and 1000 mul-liter-1. The highest concentration was applied only at 22/16C (day/night) and 700 mul-liter-1 at 22/16C and 25/16C. Transpiration rates were lower and photosynthetic rates were higher under elevated CO2 than at the ambient level. Biomass production was higher only for plants grown at 700 mul-liter-1 and 25/16C. Concentrations of macronutrients were lower in plants exposed to 1000 mul CO2/liter than in the control plants. Intermittent CO2 was applied using two timing methods. In method 1, plants were exposed to 4- or 8-hour high-CO2 concentrations during their 12-hour photoperiod. In method 2, plants were exposed for 3.5 days of each week to 700 mul CO2/liter. Only two of the 8-hour exposures resulted in greater growth than the controls. The lack of higher growth for CO2-enriched plants at 22/16C was attributed to a higher dark respiration rate and to respiration rate and a lack of efficient transport of photosynthates out of leaves.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, GROWTH, PHOTOSYNTHETIC ACCLIMATION, STARCH, TRANSPIRATION, YIELD

189

Behboudian, M.H., and R. Lai. 1995. Partitioning of photoassimilates in virosa tomatoes under elevated co2 concentration. *Journal of Plant Physiology 147(1):43-47.*

The effect of CO2 enrichment on the distribution of assimilates in tomato plants, Lycopersicon esculentum Mill. cv. 'Virosa', was studied using C-14-label. Plants were defoliated except for leaves 8, 9, and 10 (numbered acropetally). Depending on the experiment, truss 1 or trusses 1 and 2 were maintained on the plant. Within a 24-h period, the labelled leaf (leaf 10) retained high levels of C-14 in both control and CO2-enriched plants. Truss 1 was the dominant sink for both CO2 treatments, drawing on a considerable supply of C-14 re-exported from leaf 8 and leaf 9. The stem and root were transitory sinks and had the capacity to re-export C-14 at different rates during the light and dark periods. Pattern of photoassimilate partitioning was not affected by CO2 treatment.

KEYWORDS: ENRICHMENT, LEAVES, PATTERNS, SOURCE-SINK RELATIONSHIPS, TRANSLOCATION

190

Behboudian, M.H., and C. Tod. 1995. Postharvest attributes of virosa tomato fruit produced in an enriched carbon-dioxide environment. *Hortscience 30(3):490-491.*

The effect of preharvest CO2 enrichment (1000 mu l . liter(-1)) on postharvest quality of tomato fruit (Lycopersicon esculentum Mill. 'Virosa') was studied with an emphasis on soluble sugars, ripening, and mineral composition. High-CO2 fruit had higher concentrations of sucrose, glucose, fructose, and total soluble solids than ambient-CO2 fruit. High-CO2 fruit also ripened more slowly and was characterized by lower respiration and ethylene production rates than ambient-CO2 fruit. Concentrations of N, P, and K were lower in the high-CO2 fruit than in the ambient- CO2 fruit, whereas those of S, Ca, and Mg were the same for both treatments. Preharvest CO2 enrichment of 'Virosa' tomato enhances fruit desirability in terms of slower postharvest ripening and higher concentrations of soluble sugars and total soluble solids.

KEYWORDS: CO2

191

Bellisario, L.M., J.L. Bubier, T.R. Moore, and J.P. Chanton. 1999. Controls on CH4 emissions from a northern peatland. *Global Biogeochemical Cycles 13(1):81-91.*

We examined the controls on summer CH4 emission from five sites in a peatland complex near Thompson, Manitoba, Canada, representing a minerotrophic gradient from bog to rich fen at wet sites, where the water table positions ranged from -10 to - 1 cm. Average CH4 flux, determined by static chambers on collars, ranged from 22 to 239 mg CH4-C m(-2) d(-1) and was related to peat temperature. There was an inverse relationship between water table position and CH4 flux: higher water tables led to smaller fluxes. The determination of anaerobic CH4 production and aerobic CH4 consumption potentials in laboratory incubations of peat samples was unable to explain much of the variation in CH4 flux. Average net ecosystem exchange of CO2 ranged from 1.4 to 2.5 g CO2-C m(-2) d(-1) and was strongly correlated with CH4 flux; CH4 emission averaged 4% of CO2 uptake. End-of-season sedge biomass was also strongly related to CH4 flux, indicating the important role that vascular plants play in regulating CH4 flux. Determination of isotopic signatures in peat pore water CH4 revealed average delta(13)C values of between -50 and -73 parts per thousand and delta D of between -368 and -388 parts per thousand. Sites with large CH4 emission rates also had high CO2 exchange rates and enriched delta(13)C CH4

signatures, suggesting the importance of the acetate fermentation pathway of methanogenesis. Comparison of delta D and delta(13)C signatures in pore water CH4 revealed a slope shallow enough to suggest that oxidation is not an important overall control on CH4 emissions at these sites, though it appeared to be important at one site. Analysis of C-14 in pore water CH4 showed that most of the CH4 was of recent origin with percent of modern carbon values of between 112 and 128%. The study has shown the importance of vascular plant activities in controlling CH4 emissions from these wetland sites through influences on the availability of fresh plant material for methanogenesis, rhizospheric oxidation, and plant transport of CH4.

KEYWORDS: ATMOSPHERE, CANADA, CARBON ISOTOPIC COMPOSITION, CO2 REDUCTION, DYNAMICS, HYDROGEN, METHANE-OXIDIZING BACTERIA, ONTARIO, WATER, WETLANDS

192

BenBrahim, M., D. Loustau, J.P. Gaudillere, and E. Saur. 1996. Effects of phosphate deficiency on photosynthesis and accumulation of starch and soluble sugars in 1-year-old seedlings of maritime pine (Pinus pinaster Ait). *Annales Des Sciences Forestieres 53(4):801-810.*

Maritime pine seedlings were grown in 4 L pots filled with coarse sand in a greenhouse. Seedlings were supplied with a nutrient solution with three different concentrations of phosphorus (0, 0.125 and 0.5 mM). After 1 year of growth, gas exchange measurements were performed on mature needles. From these measurements, the main parameters of CO2 assimilation (the carboxylation efficiency, the apparent quantum efficiency and the maximal rate of electron transport) were estimated using the biochemical model of photosynthesis as described by Farquhar et al (1980). Leaf nonstructural carbohydrates were also analyzed. Phosphorus deficiency decreased the phosphorus foliar concentration, but did not affect foliar nitrogen concentration. The maximal rate of photosynthesis, the carboxylation efficiency and the apparent quantum efficiency decreased in phosphorus deficient seedlings. However, the maximal rate of electron transport and stomatal conductance were not affected by phosphorus supply. Low phosphorus nutrition caused a dramatic increase in foliar starch level at the end of the photoperiod. These results indicate that inadequate phosphorus nutrition principally affected the dark reactions of photosynthesis, the apparent quantum efficiency and starch accumulation.

KEYWORDS: CARBON, ELECTRON-TRANSPORT, ELEVATED CO2, EUCALYPTUS- GRANDIS SEEDLINGS, GAS-EXCHANGE, GROWTH, MAIZE LEAVES, PHOSPHORUS-NUTRITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SITKA SPRUCE

193

Bender, J., U. Hertstein, and C.R. Black. 1999. Growth and yield responses of spring wheat to increasing carbon dioxide, ozone and physiological stresses: a statistical analysis 'ESPACE-wheat' results. *European Journal of Agronomy 10(3-4):185-195.*

One of the major goals of the European Stress Physiology and Climate Experiment (ESPACE-wheat) was to investigate the sensitivity of wheat growth and productivity to the combined effects of changes in CO2 concentration, ozone and other physiological stresses. Experiments were performed at different sites throughout Europe, over three consecutive growing-seasons using open-top chambers. This paper summarizes the main experimental findings of the effects of CO2 enrichment and other factors i.e. ozone (O-3), drought stress or nitrogen supply on the biomass and yield of spring wheat (Triticum aestivum cv. Minaret). Final harvest data from different sites and seasons were statistically analysed: (1) to identify main effects and interactions between experimentally controlled factors; and (2) to evaluate quantitative relationships between environmental variables and biological responses. Generally, 'Minaret' wheat did not respond significantly to O-3, suggesting that this cultivar is relatively tolerant to the O-3 levels applied. The main effect of CO2 was a significant enhancement of grain yield and above-ground biomass in almost all experiments. Significant interactions between CO2 and other factors were not common, although modifications in different N- and water supplies also led to significant effects on grain yield and biomass. In addition, climatic factors (in particular: mean air temperature and global radiation) were identified as important co-variables affecting grain yield or biomass, respectively. On average, the yield increase as a result of a doubling of [CO2] was 35% compared with that observed at ambient CO2 concentrations. However, linear regressions of grain yield or above-ground biomass for individual experiments revealed a large variability in the quantitative responses of 'Minaret' wheat to CO2 enrichment (yield increase ranging from 11 to 121%). Hence, CO2 responsiveness was shown to differ considerably when the same cultivar of wheat was grown at different European locations. Multiple regression analyses performed to evaluate the relative importance of the measured environmental parameters on grain yield indicated that although yield was significantly related to five independent variables (24 h mean CO2 concentration, 12 h mean O-3 concentration, temperature, radiation, and drought stress), a large proportion of the observed variability remained unexplained.

KEYWORDS: CO2- ENRICHMENT, CROP RESPONSES, IMPACTS, O-3, PLANT-RESPONSES, PROTECT, RADIATION, VEGETATION

194

Bender, J., U. Hertstein, A. Fangmeier, M. van Oijen, H.J. Weigel, and H.J. Jager. 1998. The impact of climate change on yield of wheat in Europe: Results of the European stress physiology and climate experiment (ESPACE-wheat). *Journal of Applied Botany-Angewandte Botanik 72(1-2):37-42.*

The European Stress Physiology and Climate Experiment (ESPACE-wheat) was funded by the EU from 1994-1997. Major goals of the project were 1) to investigate by means of experiments the sensitivity of wheat growth, development and productivity to the combined effects of changes in CO2 concentration, climatic variables and other physiological stresses, 2) to use experimental data for extension and improvement of process- based wheat growth simulation models, and 3) to apply models to assess the influences on crops of climatic change, CO2 concentration and additional stresses in Europe. Experimental studies were performed at different sites in Europe through three consecutive seasons by means of open-top chambers according to a common standard protocol, and two simulation models were used for the analysis: AFRCWHEAT2 and LINTULCC. This paper summarizes the main findings of the effects of CO2 enrichment and other factors such as ozone, drought stress or nitrogen supply on the yield response of spring wheat (Triticum aestivum cv. Minaret). A comparison of the measured data with the main outputs of the LINTULCC model simulations is are presented. Generally, Minaret wheat did not respond significantly to ozone. CO2 enrichment had a positive influence on grain yield in almost all experiments, however, significant interactions between CO2 and other factors were not common. The average measured yield increase due to CO2 doubling was 35 % compared to grain yield measured at ambient CO2 concentrations, although there was a great variability in yield responses between sites and years. LINTULCC predicted a 42 % yield increase, but a much smaller variation between individual experiments. Although the effects of CO2 and O-2 on crop growth and yield were acceptably simulated, observed process-rates often showed variation not related to light intensity, temperature, CO2 or O-2, ie, not related to the main driving variables of the models. This unexplained variability in the measured datasets suggested a role of factors which were not accounted for in the models.

KEYWORDS: CARBON DIOXIDE, CO2, FIELD, GROWTH, OZONE,

PLANT-RESPONSES, STIMULATION, TRITICUM-AESTIVUM L

195

Bernstson, G.M., K.D.M. McConnaughay, and F.A. Bazzaz. 1993. Elevated co2 alters deployment of roots in small growth containers. *Oecologia 94(4):558-564.*

Previously we examined how limited rooting space and nutrient supply influenced plant growth under elevated atmospheric CO2 concentrations (McConnaughay et al. 1993). We demonstrated that plant growth enhancement under elevated CO2 was influenced more by the concentration of nutrients added to growth containers than to either the total nutrient content per pot or amount or the dimensions of available rooting space. To gain insight into how elevated CO2 atmospheres affect how plants utilize available belowground space when rooting space and nutrient supply are limited we measured the deployment of roots within pots through time. Contrary to aboveground responses, patterns of below-ground deployment were most strongly influenced by elevated CO2 in pots of different volume and shape. Further, elevated CO2 conditions interacted differently with limited belowground space for the two species we studied, Abutilon theophrasti, a C3 dicot with a deep taproot, and Setaria faberii, a C4 monocot with a shallow fibrous root system. For Setaria, elevated CO2 increased the size of the largest region of low root density at the pot surface in larger rooting volumes independent of nutrient content, thereby decreasing their efficiency of deployment. For Abutilon, plants responded to elevated CO2 concentrations by equalizing the pattern of deployment in all the pots. Nutrient concentration, and not pot size or shape, greatly influenced the density of root growth. Root densities for Abutilon and Setaria were similar to those observed in field conditions, for annual dicots and monocots respectively, suggesting that studies using pots may successfully mimic natural conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, FIELD, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESTRICTION, SEEDLINGS, WATER RELATIONS, YIELD

196

Berntson, G.M., and F.A. Bazzaz. 1996. The allometry of root production and loss in seedlings of Acer rubrum (Aceraceae) and Betula papyrifera (Betulaceae): Implications for root dynamics in elevated CO2. *American Journal of Botany 83(5):608-616.*

Total root production (Sigma P), total root loss (Sigma L), net root production (NP), and biomass production were determined for seedlings of Betula papyrifera and Acer rubrum in ambient and elevated CO2 environments. Sigma P, Sigma L, and NP were calculated from sequential, independent observations of root length production through plexiglass windows. Elevated CO2 increased Sigma P, Sigma L, and NP in seedlings of Betula papyrifera but not Acer rubntm. Root production and loss were qualitatively similar to whole-plant growth responses to elevated CO2. Betula showed enhanced Sigma P. Sigma L, and biomass with elevated CO2 but Acer did not. However, the observed effects of CO2 on root production and loss did not alter the allometric relationship between root production and root loss for either Acer or Betula. Thus, in this experiment, elevated CO2 did not affect the relationship between root production and root loss. The results of this study have important implications for the potential effects of elevated CO2 on root dynamics. Elevated CO2 may lead to increases in root production and in root loss (turnover) where the changes in root turnover are largely a function of the magnitude of root production increases.

KEYWORDS: ATMOSPHERIC CO2, CARBON, COOCCURRING BIRCH, ECOSYSTEMS, FINE ROOTS, GROWTH-RESPONSE, LEAF LITTER, ORGANIC-MATTER, PLANTS, SYSTEM ARCHITECTURE

197

Berntson, G.M., and F.A. Bazzaz. 1996. Belowground positive and negative feedbacks on CO2 growth enhancement. *Plant and Soil 187(2):119-131.*

In this paper we present a conceptual model of integrated plant-soil interactions which illustrates the importance of identifying the primary belowground feedbacks, both positive and negative, which can simultaneously affect plant growth responses to elevated CO2. The primary negative feedbacks share the common feature of reducing the amount of nutrients available to plants. These negative feedbacks include increased litter C/N ratios, and therefore reduced mineralization rates, increased immobilization of available nutrients by a larger soil microbial pool, and increased storage of nutrients in plant biomass and detritus due to increases in net primary productivity (NPP). Most of the primary positive feedbacks share the common feature of being plant mediated feedbacks, the only exception being Zak et al.'s hypothesis that increased microbial biomass will be accompanied by increased mineralization rates. Plant nutrient uptake may be increased through alterations in root architecture, physiology, or mycorrhizal symbioses. Further, the increased C/N ratios of plant tissue mean that a given level of NPP can be achieved with a smaller supply of nitrogen. Identification of the net plant-soil feedbacks to enhanced productivity with elevated CO2 are a critical first step for any ecosystem. It is necessary, however, that we first identify how universally applicable the results are from one study or one ecosystem before ecosystem models incorporate this information. The effect of elevated CO2 on plant growth (including NPP, tissue quality, root architecture, mycorrhizal symbioses) can vary greatly for different species and environmental conditions. Therefore it is reasonable to expect that different ecosystems will show different patterns of interacting positive and negative feedbacks within the plant-soil system. This inter-ecosystem variability in the potential for long-term growth responses to rising CO2 levels implies that we need to parameterize mechanistic models of the impact of elevated CO2 on ecosystem productivity using a detailed understanding of each ecosystem of interest.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION, ELEVATED CO2, ENRICHMENT, FINE ROOTS, LONG-TERM RESPONSE, NITROGEN SATURATION, PLANT, SOIL SYSTEM, TEMPERATE FOREST ECOSYSTEMS

198

Berntson, G.M., and F.A. Bazzaz. 1997. Elevated CO2 and the magnitude and seasonal dynamics of root production and loss in Betula papyrifera. *Plant and Soil 190(2):211-216.*

The impact of elevated atmospheric CO2 on belowground plant growth is poorly understood relative to its effects on aboveground growth. We carried out a study of the seasonal dynamics of gross root production and death to determine how elevated CO2 affected the dynamics of net and gross root production through a full growing season. We quantified gross root production and root loss from sequential, in situ images of fine roots of Betula papyrifera in ambient (375 ppm.) and elevated (700 ppm) CO2 atmospheres from 2 weeks following germination through leaf senescence. We found that elevated CO2 led to increases in the magnitude of cumulative gross production (Sigma P) and cumulative gross loss (Sigma L) of roots. However, the effect of elevated CO2 on these processes was seasonally dependent. Elevated CO2 led to greater levels of enhancement in Sigma P early in the growing season, prior to maximum standing root length (NP). In contrast, elevated CO2 led to greater levels of enhancement in Sigma L in the last half of the growing season, after maximum NP had been reached. This difference in the timing of when elevated CO2 affects Sigma P and Sigma L led to a transitory, early enhancement in NP. By the end of the growing season, there was no significant effect of elevated CO2 on NP, and Sigma P was 87% greater than NP for ambient CO2 and 117% greater in elevated

CO2. We conclude that static assessments of belowground productivity may greatly underestimate gross fine root productivity and turnover and this bias can be exaggerated with elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, FINE ROOTS, LENGTH, NITROGEN, NORTHERN HARDWOOD FOREST, RESPONSES, TURNOVER

199

Berntson, G.M., and F.A. Bazzaz. 1997. Nitrogen cycling in microcosms of yellow birch exposed to elevated CO2: Simultaneous positive and negative below-ground feedbacks. *Global Change Biology 3(3):247-258.*

This study investigated simultaneous plant and soil feedbacks on growth enhancement with elevated [CO2] within microcosms of yellow birch (Betula alleghaniensis Britt.) in the second year of growth. Understanding the integrated responses of model ecosystems may provide key insight into the potential net nutrient feedbacks on [CO2] growth enhancements in temperate forests. We measured the net biomass production, C:N ratios, root architecture, and mycorrhizal responses of yellow birch, in situ rates gross nitrogen mineralization and the partitioning of available NH4+ between yellow birch and soil microbes. Elevated atmospheric [CO2] resulted in significant alterations in the cycling of N within the microcosms. Plant C/N ratios were significantly increased, gross mineralization and NH4+ consumption rates were decreased, and relative microbial uptake of NH4+ was increased, representing a suite of N cycling negative feedbacks on N availability. However, increased C/N ratios may also be a mechanism which allows plants to maintain higher growth with a constant or reduced N supply. Total plant N content was increased with elevated [CO2], suggesting that yellow birch had successfully increased their ability to acquire nutrients during the first year of growth. However, plant uptake rates of NH4+ had decreased in the second year. This discrepancy implies that, in this study, nitrogen uptake skewed a trend through ontogeny of decreasing enhancement under elevated [CO2]. The reduced N mineralization and relatively increased N immobilization are a potential feedback which may drive this ontogenetic trend. This study has demonstrated the importance of using an integrated approach to exploring potential nutrient-cycling feedbacks in elevated [CO2].

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION DYNAMICS, DIRECT EXTRACTION, FINE ROOTS, GROWTH ENHANCEMENT, HARDWOOD LEAF LITTER, LIGNIN CONTENT, MICROBIAL BIOMASS NITROGEN, POOL DILUTION, SOIL ORGANIC MATTER

200

Berntson, G.M., and F.A. Bazzaz. 1998. Regenerating temperate forest mesocosms in elevated CO2: belowground growth and nitrogen cycling. *Oecologia 113(1):115-125.*

The response of temperate forest ecosystems to elevated atmospheric CO2 concentrations is important because these ecosystems represent a significant component of the global carbon cycle. Two important but not well understood processes which elevated CO2 may substantially alter in these systems are regeneration and nitrogen cycling. If elevated CO2 leads to changes in species composition in regenerating forest communities then the structure and function of these ecosystems may be affected. In most temperate forests, nitrogen appears to be a limiting nutrient. If elevated CO2 leads to reductions in nitrogen cycling through increased sequestration of nitrogen in plant biomass or reductions in mineralization rates, long-term forest productivity may be constrained. To study these processes, we established mesocosms of regenerating forest communities in controlled environments maintained at either ambient (375 ppm) or elevated (700 ppm) CO2 concentrations. Mesocosms were constructed from intact monoliths of organic forest soil. We maintained these mesocosms for 2 years without any external inputs of nitrogen and allowed the plants naturally present as seeds and rhizomes to regenerate. We used N-15 pool dilution techniques to quantify nitrogen fluxes within the mesocosms at the end of the 2 years. Elevated atmospheric CO2 concentration significantly affected a number of plant and soil processes in the experimental regenerating forest mesocosms. These changes included increases in total plant biomass production, plant C/N ratios, ectomycorrhizal colonization of tree fine roots, changes in tree fine root architecture, and decreases in plant NH4+ uptake rates, gross NH4+ mineralization rates, and gross NH4+ consumption rates. In addition, there was a shift in the relative biomass contribution of the two dominant regenerating tree species; the proportion of total biomass contributed by white birch (Betula papyrifera) decreased and the proportion of total biomass contributed by yellow birch (B. alleghaniensis) increased. However, elevated CO2 had no significant effect on the total amount of nitrogen in plant and soil microbial biomass. In this study we observed a suite of effects due to elevated CO2, some of which could lead to increases in potential long term growth responses to elevated CO2, other to decreases. The reduced plant NH4+ uptake rates we observed are consistent with reduced NH4+ availability due to reduced gross mineralization rates. Reduced NH4+ mineralization rates are consistent with the increases in C/N ratios we observed for leaf and fine root material. Together, these data suggest the positive increases in plant root architectural parameters and mycorrhizal colonization may not be as important as the potential negative effects of reduced nitrogen availability through decreased decomposition rates in a future atmosphere with elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DIRECT EXTRACTION, LEAF LITTER, MICROBIAL BIOMASS NITROGEN, PLANT, POOL DILUTION, RESPONSES, SEEDLINGS, SOIL, TERRESTRIAL ECOSYSTEMS

201

Berntson, G.M., N. Rajakaruna, and F.A. Bazzaz. 1998. Growth and nitrogen uptake in an experimental community of annuals exposed to elevated atmospheric CO2. *Global Change Biology 4(6):607-626.*

Rising levels of atmospheric CO2 may alter patterns of plant biomass production. These changes will be dependent on the ability of plants to acquire sufficient nutrients to maintain enhanced growth. Species-specific differences in responsiveness to CO2 may lead to changes in plant community composition and biodiversity. Differences in species-level growth responses to CO2 may be, in a large part, driven by differences in the ability to acquire nutrients. To understand the mechanisms of how elevated CO2 leads to changes in community-level productivity, we need to study the growth responses and patterns of nutrient acquisition for each of the species that comprise the community. In this paper, we present a study of how elevated CO2 affects community-level and species-level patterns of nitrogen uptake and biomass production. As an experimental system we use experimental communities of 11 co- occurring annuals common to disturbed seasonal grasslands in south-western U.S.A. We established experimental communities with approximately even numbers of each species in three different atmospheric CO2 concentrations (375, 550, and 700 ppm). We maintained these communities for 1, 1.5, and 2 months at which times we applied a N-15 tracer ((NH4NO3)-N-15-N-15) to quantify the nitrogen uptake and then measured plant biomass, nitrogen content, and nitrogen uptake rates for the entire communities as well as for each species. Overall, community- level responses to elevated CO2 were consistent with the majority of other studies of individual- and multispecies assemblages, where elevated CO2 leads to enhanced biomass production early on, but this enhancement declines through time. In contrast, the responses of the individual species within the communities was highly variable, showing the full range of responses from positive to negative. Due to the large variation in size between the

different species, community- level responses were generally determined by the responses of only one or a few species. Thus, while several of the smaller species showed trends of increased biomass and nitrogen uptake in elevated CO2 at the end of the experiment, community-level patterns showed a decrease in these parameters due to the significant reduction in biomass and nitrogen content in the single largest species. The relationship between enhancement of nitrogen uptake and biomass production in elevated CO2 was highly significant for both 550 ppm and 700 ppm CO2. This relationship strongly suggests that the ability of plants to increase nitrogen uptake (through changes in physiology, morphology, architecture, or mycorrhizal symbionts) may be an important determinant of which species in a community will be able to respond to increased CO2 levels with increased biomass production. The fact that the most dominant species within the community showed reduced enhancement and the smaller species showed increased enhancement suggest that through time, elevated CO2 may lead to significant changes in community composition. At the community level, nitrogen uptake rates relative to plant nitrogen content were invariable between the three different CO2 levels at each hardest. This was in contrast to significant reductions in total plant nitrogen uptake and nitrogen uptake relative to total plant biomass. These patterns support the hypothesis that plant nitrogen uptake is largely regulated by physiological activity, assuming that physiological activity is controlled by nitrogen content and thus protein and enzyme content.

KEYWORDS: ARCHITECTURE, BIODIVERSITY, CARBON DIOXIDE, ECOSYSTEMS, ENRICHMENT, GAILLARDIA-PULCHELLA, LOBLOLLY-PINE, PHLOX, PLANTS, RESPONSES

202

Berntson, G.M., P.M. Wayne, and F.A. Bazzaz. 1997. Below-ground architectural and mycorrhizal responses to elevated CO2 in Betula alleghaniensis populations. *Functional Ecology 11(6):684-695.*

1. Replicate populations of crowded, regenerating stands of Betula alleghaniensis were grown in ambient and elevated (700 p.p.m.) atmospheric CO2 concentrations in monoliths of forest soil. Early in the second year the seedlings were harvested and detailed measurements of individual plant root architectural parameters and ectomycorrhizal colonization were made. 2. Comparing the average responses of individual plants within the populations, elevated CO2 had no significant effects on architectural parameters that improve a plant's ability to forage for and acquire soil resources. In contrast, the intensity and magnitude of mycorrhizal colonization, and whole plant C/N ratios were significantly enhanced with elevated CO2. 3. The allometric scaling relationship between total plant biomass and root biomass was not affected by CO2, suggesting that relative allocation between roots and shoots was not affected. However, the allometric scaling relationships between root architectural parameters and plant biomass, and between fine root biomass and woody root biomass were significantly altered by elevated CO2. For all of these relationships, elevated CO2 reduced the 'size bias' of architectural components in relation to plant size within the populations; in elevated CO2 root architectural size (e.g. root length) per unit biomass was more similar between the smallest and largest individuals within the population than was the case for ambient CO2. 4. Overall, the results of this study suggest that the average individual seedling biomass and architectural growth responses within populations of plants exposed to elevated atmospheric CO2 levels may be unresponsive, but that mycorrhizal responses and interactions among plants within populations may be altered significantly. These findings have important implications for how we make predictions about plant growth responses to elevated CO2 in natural ecosystems. Significant increases in mycorrhizal infection rates and architecture-biomass allometries suggest that below-ground competitive interactions within plant populations may be reduced in elevated CO2. Alterations in competitive interactions may lead to shifts in productivity and plant population structure.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMPETITION, ENRICHMENT, FOREST ECOSYSTEMS, GROWTH, PLANT-ROOT SYSTEMS, QUERCUS-ALBA, SEEDLINGS, SIZE HIERARCHIES, SOIL

203

Berntson, G.M., and F.I. Woodward. 1992. The root-system architecture and development of senecio- vulgaris in elevated co2 and drought. *Functional Ecology 6(3):324-333.*

1. The impact of elevated CO2 and drought on the architecture and development of root systems of Senecio vulgaris was examined and implications for water and nutrient uptake discussed. Plants were grown in miniature rhizotrons to non- destructively monitor the development of roots in situ at both an elevated (700-mu-mol mol-1) and ambient (350-mu-mol mol-1) atmospheric CO2 concentration and a high or a low supply of water. 2. CO2 and water had a significant impact on the way that S. vulgaris root systems filled the soil matrix. Elevated CO2 resulted in more branched, longer root systems that foraged through larger volumes of soil. Under elevated CO2 and a low water supply, root systems had branching and foraging patterns and root length similar to those grown under ambient CO2 with a high water supply. 3. Overall, water had a more pronounced impact on the growth rate of S. vulgaris roots than did CO2. The density of rooting remained unchanged across all treatments. Thus, under elevated CO2 the intensity of foraging S. vulgaris root systems might be unchanged while the extent of foraging by these root systems, as indicated by the horizontal spread of roots, may be increased.

204

Berry, S.C., G.T. Varney, and L.B. Flanagan. 1997. Leaf delta C-13 in Pinus resinosa trees and understory plants: Variation associated with light and CO2 gradients. *Oecologia 109(4):499-506.*

Our objective was to evaluate the relative importance of gradients in light intensity and the isotopic composition of atmospheric CO2 for variation in leaf carbon isotope ratios within a Pinus resinosa forest. In addition, we measured photosynthetic gas exchange and leaf carbon isotope ratios on four understory species (Dryopteris carthusiana, Epipactus helleborine, Hieracium floribundum, Rhamnus frangula), in order to estimate the consequence of the variation in the understory light microclimate for carbon gain in these plants. During midday, CO2 concentration was relatively constant at vertical positions ranging from 15 m to 3 m above ground. Only at positions below 3 m was CO2 concentration significantly elevated above that measured at 15 m. Based on the strong linear relationship between chan in CO2 concentration and delta(13)C values for air samples collected during a diurnal cycle, we calculated the expected vertical profile for the carbon isotope ratio of atmospheric CO2 within the forest. These calculations indicated that leaves at 3 m height and above were exposed to CO2 of approximately the same isotopic composition during daylight periods. There was no significant difference between the daily mean delta(13)C values at 15 m (- 7.77 parts per thousand) and 3 m (-7.89 parts per thousand), but atmospheric CO2 was significantly depleted in C-13 closer to the ground surface, with daily average delta(13)C values of -8.85 parts per thousand at 5 cm above ground. The light intensity gradient in the forest was substantial, with average photosynthetically active radiation (PAR) on the forest floor approximately 6% of that received at the top of the canopy. In contrast, there were only minor changes in air temperature, and so it is likely that the leaf-air vapour pressure difference was relatively constant from the top of the canopy to the forest floor. For red pine and elm tree samples, there was a significant correlation between leaf delta(13)C value and the height at which the leaf sample was collected. Leaf tissue sampled near the forest floor, on average, had lower delta(13)C values than samples collected near the top of the canopy. We suggest that the average light intensity gradient through the

canopy was the major factor influencing vertical changes in tree leaf delta(13)C values. In addition, there was a wide range of variation (greater than 4 parts per thousand) among the four understory plant species for average leaf delta(13)C values. Measurements of leaf gas exchange, under natural light conditions and with supplemental light, were used to estimate the influence of the light microclimate on the observed variation in leaf carbon isotope ratios in the understory plants. Our data suggest that one species, Epipactus helleborine, gained a substantial fraction of carbon during sunflecks.

KEYWORDS: AMAZONIAN RAIN FORESTS, ATMOSPHERIC CO2, C 13/C 12, CANOPIES, CARBON ISOTOPE DISCRIMINATION, LEAVES, PHOTOSYNTHESIS, STRATIFICATION, SUNFLECKS, VALUES

205

Berryman, C.A., D. Eamus, and G.A. Duff. 1993. The influence of co2 enrichment on growth, nutrient content and biomass allocation of maranthes-corymbosa. *Australian Journal of Botany 41(2):195-209.*

Seedlings of Maranthes corymbosa Blume, an evergreen tree of tropical Australia and Indonesia were grown for 32 weeks under conditions of ambient and elevated (700 mumol CO2 mol-1) CO2 in tropical northern Australia. Seedlings were exposed to ambient temperature, vapour pressure deficit and photon flux density fluctuations. Rates of germination and percentage germination were not affected by elevated CO2.Total plant biomass, height growth, total plant leaf area, numbers of leaves and branches and specific leaf weight were significantly increased by elevated CO2. Root:shoot ratio and foliar P, K, Mg, Mn and Ca levels were unaffected but foliar nitrogen levels were decreased by elevated CO2, Nutrient-use-efficiency was unaffected for phosphorus, magnesium, manganese, calcium and potassium but nitrogen-use-efficiency increased in response to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE ENRICHMENT, CARBOXYLASE, ECOLOGY, ELEVATED CO2, FOREST, LIRIODENDRON-TULIPIFERA L, NITROGEN, PHOTOSYNTHESIS, SEEDLING GROWTH

206

Berryman, C.A., D. Eamus, and G.A. Duff. 1994. Stomatal responses to a range of variables in 2 tropical tree species grown with co2, enrichment. *Journal of Experimental Botany 45(274):539-546.*

Seedlings of Maranthes corymbosa (Blume) and Eucalyptus tetrodonta (F. Muell) were grown with or without CO2 enrichment (700 mu mol CO2 mol(-1)). The response of stomatal conductance (g(s)) to leaf drying, exogenous abscisic acid and calcium ions was investigated in M. corymbosa. Reciprocal transfer experiments were also conducted whereby plants were grown in one treatment and then transferred to the other before g(s) was measured. Stomatal conductance in M. corymbosa was more sensitive (a greater percentage decline in g(s) per unit percentage decline in leaf fresh weight) to leaf water status under conditions of CO2 enrichment compared to ambient conditions. However, the rate of reduction of g(s) in response to exogenous abscisic acid was not influenced by CO2 treatment. In contrast, the rate of reduction of g(s) in response to exogenous CaCl2 was decreased under conditions of CO2 enrichment. Reciprocal transfer experiments showed that exposure to CO2 enrichment results in a short-term, reversible decline in g(s) as a result of decreased stomatal aperture and a long-term, irreversible decline in g(s) as a result of a decreased stomatal density. Seedlings of E. tetrodonta were used to investigate the response of g(s) to light flux density, leaf-to-air vapour pressure difference (LAVPD), leaf internal CO2 concentration (C-i) and temperature. Reciprocal transfer experiments were also conducted. CO2 enrichment did not influence the pattern or sensitivity of response of g(s) to LAVPD and C-i in E. tetrodonta. In contrast, the slope of the response of g(s) to temperature decreased for trees grown under elevated [CO2](a) conditions and the equilibrium g(s) attained at saturating light was also decreased for plants grown under elevated [CO2](a) conditions.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO2, BEHAVIOR, CALCIUM, HUMIDITY, LEAVES, PRESSURE, SOLANUM-MELONGENA, WATER-STRESS

207

Bertani, A., I. Brambilla, S. Mapelli, and R. Reggiani. 1997. Elongation growth in the absence of oxygen: The rice coleoptile. *Russian Journal of Plant Physiology 44(4):543-547.*

Rice, one of the few plant species adapted to growth in wetland conditions, is able to germinate in waterlogged soils promoting only the growth of a white coleoptile in order to reach the surface of the water, contact the atmosphere, and transfer oxygen to the seed, allowing subsequent growth of the radicle and leaf. In the anoxic cells of rice coleoptiles, an efficient alcoholic fermentation allows an elevated energy charge to be maintained. Significant RNA and protein syntheses including phosphorylation and glycosylation occur too. The cytoplasmic pH is maintained at a level far from acidosis. The anoxic growth of rice coleoptiles, essentially an elongation growth, is sustained by a high turgor pressure, with free amino acids and potassium as main components. Among the metabolic processes involved in the regulation of the elongation of rice coleoptiles, a crucial role is played by amino acid metabolism and the accumulation of putrescine, which is able to stimulate plasmalemma ATPase activity. Anaerobic elongation is also stimulated in the presence of 20% CO2 in the growth medium, inhibited by light and abscisic acid, unaffected by ethylene, and slightly promoted by auxin. The role of both metabolites and hormones along with environmental factors in maintaining cellular homeostasis and coleoptile elongation are reconsidered and discussed in Light of new data.

KEYWORDS: ACCUMULATION, ANAEROBIOSIS, ANOXIA, GERMINATION, METABOLIC-RATE, ORYZA SATIVA L, PH, POLYAMINES, PROTEIN-SYNTHESIS, SEEDLINGS

208

Bertin, N., and C. Gary. 1993. Evaluation of tomgro, a dynamic-model of growth and development of tomato (lycopersicon-esculentum mill) at various levels of assimilate supply-and-demand. *Agronomie 13(5):395-405.*

TOMGRO, a tomato growth and development model, has been examined under different levels of assimilate source and sink activities, induced by CO2 enrichment and truss thinning. The main purpose was the evaluation of the assumptions on dry matter partitioning and fruit setting. The photosynthesis submodel has been calibrated to fit the daily dry matter production. The main input parameters to the development and growth submodels have been experimentally measured. The calibrated model provides good simulations of the leaf area expansion, but it takes no account of the variations in the assimilates stored in leaf blades. Total fruit growth is well simulated in spite of a small underestimation for of development and simulations of source/sink balance leads to good simulations of the number of set fruits. This result confirms the hypothesis that fruit set depends on the ratio between assimilate source and sink activities. This calibration with a beef tomato cultivar proves the robustness of the model and permits some improvements to be suggested. The surplus assimilates should be stored in a pool, which could exert a buffer effect during low supply periods. Sink strength of reproductive and vegetative parts should be measured for different cultivars, and under various climatic conditions. Finally, whether the functions of assimilate distribution and fruit set are still valid under very low supply conditions or whether some organs have

priority over the others remains to be determined.

209

Bertin, N., and C. Gary. 1998. Short and long term fluctuations of the leaf mass per area of tomato plants - Implications for growth models. *Annals of Botany 82(1):71-81.*

The leaf mass per unit leaf area (LMA) is a key variable in many growth models, since it is often used to predict leaf area expansion from leaf dry weight increase, or vice versa. Influences of source-sink balance on leaf area, leaf dry weight, LMA, and leaf content in non-structural carbohydrates were investigated in glasshouse tomato crops. The source-sink balance was manipulated by artificial shading, CO2 enrichment or fruit removal using different tomato cultivars. Leaf area was hardly affected by competition for assimilates except under extreme conditions. Iri contrast, leaf dry weight, and consequently LMA, underwent large and rapid fluctuations in response to any factor that changed source and sink activities. A 60% reduction of photosynthetically active radiation involved a 24% decrease in LMA after 10 d. Carbon dioxide enrichment and fruit removal induced about a 45% and 15% increase in LMA, respectively, on plants with two fruiting trusses, but hardly affected LMA of producing plants. No significant cultivar effect could be identified. Changes in starch and soluble sugar content in leaves accounted for only 29% of diurnal variations in LMA, suggesting regular fluctuations of other components. We propose that structural LMA varies between a maximum and a minimum value according to the ratio of assimilate supply and demand during leaf development. Leaf area is independent of the supply of assimilates when the minimum structural LMA is realised. When the maximum structural LMA is attained, a storage pool of assimilates may accumulate in leaves during periods of high supply and low demand. We present a model including these hypotheses, which predicts structural and non- structural LMA variations of plants with different source-sink ratios. (C) 1998 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROP, LEAVES, PHOTOSYNTHESIS, SOURCE-SINK RELATIONSHIPS

210

Bertin, N., and E. Heuvelink. 1993. Dry-matter production in a tomato crop - comparison of 2 simulation-models. *Journal of Horticultural Science 68(6):995-1011.*

TOMSIM(1.0) and TOMGRO(1.0) are two dynamic models for tomato growth and development. Their submodels for dry matter production are compared and discussed. In TOMSIM(1.0), dry matter production is simulated by a modified version of SUCROS87 (Spitters et al., 1989). Single leaf photosynthesis rates are calculated separately for shaded and sunlit leaf area at different depths in the canopy, according to the direct and diffuse components of light; daily crop gross assimilation rate (A) is computed by integration of these rates over the different depths and over the day. In TOMSIM(1.0) leaf photochemical efficiency (epsilon) and potential leaf gross photosynthesis rate at saturating light level (P(g,max)) both depend on temperature and CO2 level. In TOMGRO(1.0) crop gross photosynthesis rate is calculated by the equation of Acock et al. (1978); epsilon is a constant and P(g,max) is a linear function of CO2. In both models leaf photosynthesis characteristics are assumed to be identical in the whole canopy. Maintenance respiration (R(m)) and conversion efficiency (C(f)) are taken into account in the same way, except that root maintenance respiration is neglected in TOMGRO(1.0). For both models a sensitivity analysis was performed on the input variables (light intensity, temperature, CO2 and leaf area index (LAI)) and on some of the model parameters. Under most conditions considered, simulated A was found to be 5-30% higher in TOMSIM(1.0) than in TOMGRO(1.0). At temperatures above 18-degrees-C R(m) was also higher in TOMSIM(1.0), and C(f) was 4% higher in TOMGRO(1.0). The two models were very sensitive to changes in epsilon and to a lesser extent to changes in the light extinction coefficient, whereas the scattering coefficient of leaves had hardly any effect on the simulated A. TOMGRO(1.0) appeared to be rather sensitive to the CO2 use efficiency, whereas at ambient CO2 level mesophyll resistance was quite important in TOMSIM(1.0). Four sets of experimental data (differences in cultivar, CO2 enrichment and planting date) from Wageningen (The Netherlands) and Montfavet (southern France) were used to validate the models. Average 24 h temperature and average daily CO2 concentration values were used as input to the models. For the Wageningen experiments, hourly PAR values were calculated from the daily global radiation sum by TOMSIM(1.0) and used as input in both models. For the Montfavet experiment, average hourly PAR measurements were used. Also measured LAI, dry matter distribution and organ dry weights (for calculation of R(m)) were input to the simulation. In the Wageningen experiments, total dry matter production was simulated reasonably well by both models, whereas in the Montfavet experiment an under- estimation of about 35% occurred. TOMGRO(1.0) and TOMSIM(1.0) simulated almost identical curves in all four experiments. Strong and weak points of both models are discussed.

KEYWORDS: CANOPY, CO2, GAS-EXCHANGE, GROWTH, LEAVES, LIGHT, PHOTOSYNTHESIS, YIELD

211

Bertoni, G.P., and W.M. Becker. 1996. Expression of the cucumber hydroxypyruvate reductase gene is down-regulated by elevated CO2. *Plant Physiology 112(2):599-605.*

We examined the effects of CO2 concentration on the white- light-stimulated expression of the cucumber (Cucumis sativus L.) Hpr gene. Hpr encodes hydroxypyruvate reductase, an enzyme important in the photorespiratory glycolate pathway, which plays an integral role in carbon allocation in C-3 plants. Because CO2 is an end product of this pathway and because increased CO2 concentrations lessen the need for photorespiration, we tested whether exposure of plants to elevated CO2 would affect white-light-stimulated Hpr gene expression. Exposure of dark-adapted cucumber seedlings to elevated CO2 (2 to 3 times ambient) during a 4-h white-light irradiation significantly inhibited the accumulation of Hpr mRNA. Increasing the CO2 concentration during irradiation to 6 or 9 times ambient did not further inhibit Hpr mRNA accumulation. The depressing effect of high CO2 on Hpr mRNA accumulation was seen in both high and low light, but was more pronounced in higher light. These results suggest that maximum sensitivity to CO2 occurs in conditions near those normally encountered by the plant (high light, CO2 concentration near ambient) and support a model in which white-light-regulated Hpr expression is modulated in part by environmental CO2 concentration.

KEYWORDS: COTYLEDONS, PHOTORESPIRATION, PLANT, SEQUENCE

212

Besford, R.T. 1993. Photosynthetic acclimation in tomato plants grown in high co2. *Vegetatio 104:441-448.*

The effects of prolonged CO2 enrichment of tomato plants on photosynthetic performance and Calvin cycle enzymes, including the amount and activity of ribulose-1,5-bisphosphate carboxylase (RuBPco), were determined. Also the light-saturated rate of photosynthesis (P(max)) of the 5th leaf throughout leaf development was predicted based on the amount and kinetics of RuBPco. With short-term CO2 enrichment, i.e. only during the photosynthesis measurements, P(max) of the young leaves did not increase while the leaves reaching full

expansion more than doubled their net rate of CO2 fixation. However, with longer- term CO2 enrichment, i.e. growing the crop in high CO2, the plants did not maintain this photosynthetic gain. Compared with leaves of plants grown in normal ambient CO2 the high CO2-grown leaves, when almost fully expanded, contained only about half as much RuBPco protein and P(max) in 300 and 1000 vpm CO2 was similarly reduced. The loss of RuBPco protein may be a factor associated with the accelerated fall in P(max) since P(max) was close to that predicted from the amount and kinetics of RuBPco assuming RuBP saturation. Acclimation to high CO2 is fundamentally different from acclimation to high light. In contrast to acclimation to high light, acclimation to high CO2 does not usually involve an increase in photosynthetic machinery so the synthesis and maintenance costs (as indicated by the dark respiration rate) are generally lower.

KEYWORDS: ACTIVATION, CALVIN CYCLE ENZYMES, ENRICHMENT, HIGH ATMOSPHERIC CO2, LEAVES, NITROGEN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RICE, WHEAT

213

Betsche, T. 1994. Atmospheric co2 enrichment - kinetics of chlorophyll a fluorescence and photosynthetic co2 uptake in individual, attached cotton leaves. *Environmental and Experimental Botany 34(1):75-86.*

Chl fluorescence and gas exchange of attached cotton leaves (Gossypium hirsutum L.) were measured in ambient air and in a highly CO2-enriched atmosphere (4000 mu l l(-1) CO2; photosynthetic saturation). In the shore term (hours to one day), net CO2 uptake approximately doubled in all leaves examined. Photochemical (q(P)) and nonphotochemical (q(NP)) quenching of chlorophyll fluorescence, and calculated linear photosynthetic electron Row, did not change significantly when CO2 rose from 250 to 4000 mu l l(-1) CO2. These results show that high CO2 concentration did not inhibit photosynthesis in any leaf. In contrast, the long-term response of leaves to atmospheric CO2-enrichment was variable, Some leaves sustained the initial high level of photosynthetic stimulation for more than a week while in others photosynthetic CO2-uptake declined more or less. These leaves turned yellowish-green although chlorophyll content declined little. Variance in the degree of leaf yellowing was also encountered in experiments with clover when sets of plants were CO2-enriched. Gas exchange and chi fluorescence results suggest that yellowing of cotton leaves in high CO2 was not equivalent to 'natural' senescence although some chlorophyll fluorescence parameters changed similarly. During extended high CO2 treatment the level of q(NP) increased notably in the yellowing leaves. The high levels of q(NP) and relaxation kinetics of chi fluorescence quenching recorded upon darkening demonstrate that thylakoid energization increased during the decline of photosynthetic CO2 uptake in high CO2. This shows that the photosynthetic decline was not caused by decreasing thylakoid energization because of physical damage by oversized starch grains. Calculated photosynthetic electron flow declined little suggesting that CO2 at ribulosebisphosphate carboxylase-oxygenase fell and thus photorespiration rose. With regard to growth limitation in high CO2 concentration, these results support the concept that high CO2 concentration tends to induce low inorganic phosphate concentrations (Morin et al. Plant Physiol. 99, 89-95, 1992; Duchein et al. J. Exp. Bet. 44, 17-22, 1993) which can limit chloroplast ATP synthase and thus increase thylakoid energization. It is proposed that the different responses of individual leaves to atmospheric CO2 enrichment reflects variety among leaves in the phosphate status or in the capacity for Pi-recycling (assimilate utilization).

KEYWORDS: CARBON DIOXIDE, CROP RESPONSES, DROUGHT STRESS, ELECTRON-TRANSPORT, ELEVATED CO2, GROWTH, INORGANIC- PHOSPHATE, PHASEOLUS-VULGARIS L, PLANT NUTRITION, STARCH

214

Bettarini, I., G. Calderoni, F. Miglietta, A. Raschi, and J. Ehleringer. 1995. Isotopic carbon discrimination and leaf nitrogen-content of erica-arborea L along a co2 concentration gradient in a co2 spring in italy. *Tree Physiology 15(5):327-332.*

We studied a Mediterranean species (Erica arborea L.) growing in a CO2 spring in Italy that was naturally exposed for generations to a gradient of atmospheric CO2 concentrations. The CO2 concentration gradient to which different individual plants were exposed was determined by an indirect method based on radioisotope analysis. The stable carbon isotope ratio of sampled leaves was determined by mass spectrometry, and isotopic discrimination was then calculated. Leaf nitrogen, specific leaf area, total soil nitrogen, soil organic matter content and soil pH were also measured. In one group of plants, grown on a homogeneous soil and exposed to moderate CO2 enrichment, isotopic discrimination was significantly reduced in response to increasing CO2 concentrations, whereas the intercellular CO2 concentration and leaf nitrogen content were almost unaffected. In a second group of plants, grown along a gradient of CO2 concentration and soil nitrogen content, leaf nitrogen content was reduced when nitrogen availability was limiting. However, when soil nitrogen was available in excess, even very high CO2 concentrations did not result in increased discrimination or reduced leaf nitrogen content in the long term. The results are discussed with respect to current theories about the long-term CO2 response of plants based on several years of experimentation with elevated atmospheric CO2 concentrations under controlled conditions.

KEYWORDS: ELEVATED CO2, ENVIRONMENT, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, STOMATAL DENSITY

215

Bettarini, I., F.P. Vaccari, and F. Miglietta. 1998. Elevated CO2 concentrations and stomatal density: observations from 17 plant species growing in a CO2 spring in central Italy. *Global Change Biology 4(1):17-22.*

Stomatal density (SD) and stomatal conductance (g(s)) can be affected by an increase of atmospheric CO2 concentration. This study was conducted on 17 species growing in a naturally enriched CO2 spring and belonging to three plant communities. Stomatal conductance, stomatal density and stomatal index (SI) of plants from the spring, which were assumed to have been exposed for generations to elevated [CO2], and of plants of the same species collected in a nearby control site, were compared. Stomatal conductance was significantly lower in most of the species collected in the CO2 spring and this indicated that CO2 effects on g, are not of a transitory nature but persist in the long term and through plant generations. Such a decrease was, however, not associated with changes in the anatomy of leaves: SD was unaffected in the majority of species (the decrease was only significant in three out of the 17 species examined), and also SI values did not vary between the two sites with the exception of two species that showed increased SI in plants grown in the CO2-enriched area. These results did not support the hypothesis that long-term exposure to elevated [CO2] may cause adaptive modification in stomatal number and in their distribution.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CONDUCTANCE, EXPOSURE, GAS-EXCHANGE, GRASSLAND, INCREASE, LEAVES, RESPONSES, TREES

216

Betts, R.A., P.M. Cox, S.E. Lee, and F.I. Woodward. 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. *Nature 387(6635):796-799.*

Anthropogenic increases in the atmospheric concentration of carbon

dioxide and other greenhouse gases are predicted to cause a warming of the global climate by modifying radiative forcing(1). Carbon dioxide concentration increases may make a further contribution to warming by inducing a physiological response of the global vegetation-a reduced stomatal conductance, which suppresses transpiration(2). Moreover, a CO2-enriched atmosphere and the corresponding change in climate may also alter the density of vegetation cover, thus modifying the physical characteristics of the land surface to provide yet another climate feedback(3-6). But such feedbacks from changes in vegetation structure have not yet been incorporated into general circulation model predictions of future climate change. Here we use a general circulation model iteratively coupled to an equilibrium vegetation model to quantify the effects of both physiological and structural vegetation feedbacks on a doubled- CO2 climate. On a global scale, changes in vegetation structure are found to partially offset physiological vegetation-climate feedbacks in the long term, but overall vegetation feedbacks provide significant regional-scale effects.

KEYWORDS: CANOPY, EUROPE, FOREST, IMPACT, LAND, MODEL, SENSITIVITY

217

Bezemer, T.M., and T.H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO2: quantitative analyses and guild effects. *Oikos 82(2):212-222.*

Interactions between insect herbivores and plants grown under conditions of ambient and elevated CO2 were investigated by analysing data on 43 herbivores, representing 61 plant- herbivore interactions. Changes in herbivore performance in enhanced CO2 environments were correlated with changes in the quality of the host plants, measured as nitrogen content, water content, carbohydrate content and secondary plant compounds. The data were analysed to determine whether CO2 mediated effects on insect performance differed between feeding guilds (leaf-chewers, leaf miners, phloem-feeders (root and shoot), xylem-feeders, whole-cell-feeders and seed-eaters) or instar stage. Host-plant quality changed in elevated CO2; leaf nitrogen content decreased, on average, by 15% while carbohydrates increased by 47% and secondary plant compounds (phenolics) by 31%. Water content did not change. Of the variables measured, changes in nitrogen and carbohydrate levels only were found to be correlated with changes in food consumption. No differences were found in CO2-mediated herbivore responses on woody plant compared with non-woody plants. Insects from different feeding guilds respond to CO2 mediated changes in host-plant quality in various ways. Leaf- chewers generally seem able to compensate for the decreased nitrogen levels in the plant tissues by increasing their food consumption (by 30%) and with no adverse effects on pupal weights. Leaf-miners only slightly increase their food consumption. The negative effect on pupal weight suggests that their population dynamics may change over several generations. Limited data on seed-eaters suggest that enhanced CO2 conditions have no effect on these insects. Phloem-feeders and whole-cell-feeders are the only insects to show a positive CO2 response. Population sizes generally increased in elevated CO2 and development lime of phloem-feeders was reduced by 17%. Early instar larvae are restricted more by CO2 enhancement than late instars. Although changes in food consumption are similar, changes in development times are much more pronounced in young instars (18% vs 6%).

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CLIMATE CHANGE, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, NOCTUIDAE, NUTRIENT BALANCE, PAPER BIRCH, PERFORMANCE, RESPONSES

218

Bezemer, T.M., T.H. Jones, and K.J. Knight. 1998. Long-term effects of elevated CO2 and temperature on populations of the peach potato aphid Myzus persicae and its parasitoid Aphidius matricariae. *Oecologia 116(1-2):128-135.*

Model terrestrial ecosystems were set-up in the Ecotron controlled environment facility. The effects of elevated CO2 (ambient + 200 mu mol/mol) and temperature (ambient + 2.0 degrees C) on plant chemistry, the abundance of the peach potato aphid Myzus persicae, and on the performance of one of its parasitoids Aphidius matricariae, were studied. Total above-ground plant biomass at the end of the experiment was not affected by elevated atmospheric CO2, nor were foliar nitrogen and carbon concentrations. Elevated temperature decreased final plant biomass while leaf nitrogen concentrations increased. Aphid abundance was enhanced by both the CO2 and temperature treatment. Parasitism rates remained unchanged in elevated CO2, but showed an increasing trend in conditions of elevated temperature. Our results suggest that M. persicae, an important pest of many crops, might increase its abundance under conditions of climate change.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, DECOMPOSITION, DYNAMICS, ECOSYSTEMS, HERBIVORY, HOMOPTERA, INSECT PERFORMANCE, PHYTOCHEMISTRY, RESPONSES

219

Bezemer, T.M., K.J. Knight, J.E. Newington, and T.H. Jones. 1999. How general are aphid responses to elevated atmospheric CO2? *Annals of the Entomological Society of America 92(5):724-730.*

We studied the impact of elevated CO2 on 2 aphid pest species, Myzus persicae and Brevicoryne brassicae (Homoptera: Aphididae), on a series of host plants in 3 independent studies each differing in experimental complexity. Measurements on individual aphids showed that host plant and aphid species significantly influenced the response to elevated CO2. These differences occurred not only in the level of responsiveness but also directionally. B. brassicae reared on Brassica oleracea produced significantly less offspring at elevated CO2, whereas the opposite was found for M. persicae on the same host. No response was found for M. persicae on Senecio vulgaris. When populations of B. brassicae and M. persicae were followed for a longer period, no differences were observed in population sizes, Comparisons between different experimental systems show that long-term population responses to elevated CO2 can not be reliably predicted from detailed measurements on individual aphids. The consequences of these findings for climate change research are discussed.

KEYWORDS: BREVICORYNE-BRASSICAE, CARBON DIOXIDE, CLIMATE CHANGE, DECIDUOUS TREES, HERBIVORE INTERACTIONS, INSECT PERFORMANCE, MYZUS-PERSICAE, PLANT, POPULATION-DYNAMICS, TERRESTRIAL ECOSYSTEMS

220

Bezemer, T.M., L.J. Thompson, and T.H. Jones. 1998. Poa annua shows inter-generational differences in response to elevated CO2. *Global Change Biology 4(6):687-691.*

Inter-generational effects on the growth of Poa annua (L.) in ambient and elevated atmospheric CO2 conditions (350 and 550 mu l l(-1), respectively) were studied in two different experiments. Both experiments showed similar results. In a greenhouse experiment growth, measured as the numbers of tillers produced per week, was compared for plants grown from first and second generation seeds. Second generation seeds were obtained from plants grown for one whole generation in either ambient or elevated atmospheric CO2 ('ambient' and 'elevated' seeds, respectively). First generation plants and second generation 'ambient' plants did not respond to elevated CO2. Second generation 'elevated' plants produced significantly more tillers in elevated CO2. In

the second experiment model terrestrial ecosystems growing in the Ecotron and which included Poa annua were used. Above-ground biomass after one and two generations of growth were compared. At the end of Generation 1 no difference was found in biomass production while at the end of Generation 2 biomass increased in elevated CO2 by 50%. The implications for climate change research are discussed.

KEYWORDS: ECOTRON, ENVIRONMENTS, FACILITY, GROWTH, PLANTS, POPULATION

221

Bhattacharya, N.C., D.R. Hileman, P.P. Ghosh, R.L. Musser, S. Bhattacharya, and P.K. Biswas. 1990. Interaction of enriched CO2 and water-stress on the physiology of and biomass production in sweet-potato grown in open-top chambers. *Plant, Cell and Environment 13(9):933-940.*

The objective of this study was to investigate the effects of water stress in sweet potato (Ipomoea batatas L. [Lam] 'Georgia Jet') on biomass production and plant-water relationships in an enriched CO2 atmosphere. Plants were grown in pots containing sandy loam soil (Typic Paleudult) at two concentrations of elevated CO2 and two water regimes in open-top field chambers. During the first 12 d of water stress, leaf xylem potentials were higher in plants grown in a CO2 concentration of 438 and 666-mu-mol mol-1 than in plants grown at 364-mu-mol mol-1. The 364-mu-mol mol-1 CO2 grown plants had to be rewatered 2d earlier than the high CO2-grown plants in response to water stress. For plants grown under water stress, the yield of storage roots and root:shoot ratio were greater at high CO2 than at 364-mu-mol mol-1; the increase, however, was not linear with increasing CO2 concentrations. In well-watered plants, biomass production and storage root yield increased at elevated CO2, and these were greater as compared to water-stressed plants grown at the same CO2 concentration.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, FIELD, PHOTOSYNTHESIS, SOYBEANS, YIELD

222

Bhattacharya, N.C., J.W. Radin, B.A. Kimball, J.R. Mauney, G.R. Hendrey, J. Nagy, K.F. Lewin, and D.C. Ponce. 1994. Leaf water relations of cotton in a free-air co2-enriched environment. *Agricultural and Forest Meteorology 70(1-4):171-182.*

As part of an intensive study of crop response to CO2 enrichment in a free-air CO2 enrichment (FACE) experiment in the field, we determined aspects of the water relations of a cotton crop on selected dates in 1991. The atmosphere was enriched from 370 mumol CO2 mol-1 (control) to about 550 mumol mol-1 in free air during daylight hours. Under full irrigation, CO2 enrichment decreased stomatal conductance and single-leaf transpiration only toward the end of the season, and these changes led to increased leaf water potentials only at that time of year. Under water-stressed (deficit irrigation) conditions, CO2 enrichment decreased conductance throughout the season but there was no corresponding consistent effect on leaf water potentials. As with the fully irrigated controls, CO2 enrichment increased leaf water potentials only at the end of the season. CO2 enrichment increased season-long biomass accumulation 39% under full irrigation and 34% under deficit irrigation. These results are consistent with previous studies of cotton in open-top chambers that found only small effects of CO2 enrichment on internal water relations of cotton, and no water stress-induced increase in crop responsiveness to elevated CO2.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHMENT, CONDUCTANCE, GROWTH, PHOSPHORUS, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STRESS, YIELD

223

Bialczyk, J., Z. Lechowski, and A. Libik. 1998. Modification of tannin concentration by abiotic factors in Lycopersicon esculentum Mill. seedlings. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection 105(3):264-273.*

Results of the study on the effect of some abiotic factors on the modification of Leaf tannin concentration of greenhouse tomato seedlings are discussed in the work. The total content of soluble and insoluble tannins was calculated as tannic acid equivalent x g(-1) dry matter. The cultivars of tomato were characterized by the differentiated tannin content in leaves, stems; and roots, the proportion being 1 : 1/2 and 1/3, respectively. Two of the investigated cultivars were characterized by extreme values of che natural tannin content (cv. 'Baron' with the greatest content and cv. 'Perkoz' with the smallest one), the differences between them reaching about 240 %. A partial defoliation-or mechanical wounding of leaf blades increased the content of tannins in these organs, In relation to the effect of the partial defoliation (about 50 % of leaves being cut oft), the content of tannins was higher in the case of pricking the leaves with needles. Depending on the number of pricks per cm(2) of the leaf blade (8, 20 or; 40), associated with a different degree of its wounding (1 %, 2.5 %, and 5 %, respectively), a maximum increase in tannin content was 180 % with 20 pricks x cm(-2) as compared with the control. The intensity of photosynthetically active radiation (PAR) significantly affected the kinetics of tannin synthesis. In the case of a 90 % reduction of daily PAR intensity, the content of tannins was reduced by about 50 % after a 2-week experiment with the two cultivars. Changes in CO2 concentration in the environment of seedlings differently modified the level of leaf tannins. With CO2 concentration reduced to 170 mu mol x mol(-1) air, the content of tannins decreased to about 76 % of the value evidenced in atmospheric air. CO, elevated to 680 mu mol x mol(-1) air induced an increase in leaf tannins to about 112- 121 % in, relation to the control. The enrichment of soil solution with phosphorus or nitrogen compounds had different and opposing effects on tannin content. With phosphorus enrichment of the substrate, the content of tannins in leaves increased to about 120 % in relation to the control. The elevated nitrogen concentration reduced the content of tannins by about 30 % after a 2-week experiment. The results concerning the effect of abiotic factors on the tannin level in the leaves of greenhouse tomato seedlings could lead to the development of control measures based-on the activation of the natural defense system of planes against herbivores.

KEYWORDS: CARBON NUTRIENT BALANCE, CO2, PATHWAY, PHYTOCHEMISTRY, POLYPHENOL OXIDASE, RESPONSES

224

Bialczyk, J., Z. Lechowski, and A. Libik. 1999. The protective action of tannins against glasshouse whitefly in tomato seedlings. *Journal of Agricultural Science 133:197-201.*

The synthesis and accumulation of tannins on tomato seedlings are regulated by environmental factors. The variation in the content of tannins was sufficiently important to bring about the occurrence of significant differences in the numbers of glasshouse whitefly on the seedlings. During a 2-week experiment, the treatments included mechanical wounding (20 prickings per cm(2)), spraying with kinetin solutions of 10(-4) mol/dm(3), plant growth regulators, and the atmosphere enrichment to 680 mu mol CO2/mol air, the content of tannins being increased by c. 40, 70, 10-45 and 25 % above the values obtained in the control. These results were correlated with a decrease in the numbers of insects occurring on the seedlings by c. 35, 45, 8-29 and 18 %, respectively. Contrary to the above results the spraying with solutions of abscisic acid, gibberellic acid, and the incubation of plants in an atmosphere containing 170 mu mol CO2/mol air, reduced the content of tannins by c. 69, 22 and 25 %, respectively. This was reflected in the respective increases by c. 70, 40 and 35% in the numbers

of insects occurring on the seedlings. The obtained results suggest that tannins seem to have a dosage-dependent effect on glasshouse whitefly. Decreasing the host plant quality by increasing tannin content may act as an important selective agent limiting the losses brought about by glasshouse whitefly in tomato cultivation.

KEYWORDS: CHEMICAL DEFENSE, CO2, GROWTH, METABOLISM, NUTRIENT, PLANT POLYPHENOLS, RESPONSES, TREE

225

Billes, G., H. Rouhier, and P. Bottner. 1993. Modifications of the carbon and nitrogen allocations in the plant (triticum-aestivum L) soil system in response to increased atmospheric co2 concentration. *Plant and Soil 157(2):215-225.*

The aim of this work was to examine the response of wheat plants to a doubling of the atmospheric CO2 concentration on: (1) carbon and nitrogen partitioning in the plant, (2) carbon release by the roots; and (3) the subsequent N uptake by the plants. The experiment was performed in controlled laboratory conditions by exposing fast-growing spring wheat plants, during 28 days, to a (CO2)-C-14 concentration of 350 or 700 muL L-1 at two levels of soil nitrogen fertilization. Doubling CO2 availability increased total plant production by 34% for both N treatment. In the N-fertilized soil, the CO2 enrichment resulted in an increase in dry mass production of 41% in the shoots and 23% in the roots; without N fertilization this figure was 33% and 37%, respectively. In the N-fertilized soil, the CO2 increase enhanced the total N uptake by 14% and lowered the N concentration in the shoots by 23%. The N concentration in the roots was unchanged. In the N-fertilized soil, doubling CO2 availability increased N uptake by 32% but did not change the N concentrations, in either shoots or roots. The CO2 enrichment increased total root-derived carbon by 12% with N fertilization, and by 24% without N fertilization. Between 85 and 90% of the total root derived-C-14 came from respiration, leaving only 10 to 15% in the soil as organic C-14. However, when total root-derived C-14 was expressed as a function of root dry weight, these differences were only slightly significant. Thus, it appears that the enhanced carbon release from the living roots in response to increased atmospheric CO2, is not due to a modification of the activity of the roots, but is a result of the increased size of the root system. The increase of root dry mass also resulted in a stimulation of the soil N mineralization related to the doubling atmospheric CO2 concentration. The discussion is focused on the interactions between the carbon and nitrogen allocation, especially to the root system, and the implications for the acquisition of nutrients by plants in response to CO2 increase.

KEYWORDS: DIOXIDE, DRY-MATTER, ELEVATED CO2, ENRICHMENT, GROWTH, METABOLISM, MICROBIAL BIOMASS, MINERAL NUTRITION, RESPIRATION, ROOT-DERIVED MATERIAL

226

Bindi, M., L. Fibbi, B. Gozzini, S. Orlandini, and F. Miglietta. 1996. Modelling the impact of future climate scenarios on yield and yield variability of grapevine. *Climate Research 7(3):213-224.*

A mechanistic growth model was used to evaluate the mean yield and yield variability of grapevine Vitis vinifera L. under current and future climates. The model used was previously validated using field experiment data. The effect of elevated CO2 on grapevine growth was also considered. Adaptation of 2 varieties (Sangiovese and Cabernet Sauvignon) to scenarios of increased CO2 and climate change, and potential changes in agricultural risk (i.e. inter-seasonal variability), were examined. Before testing the effect of climate scenarios, we analysed the sensitivity of modelled grapevine yield to arbitrary changes in the 3 driving variables (temperature, solar radiation and CO2). The results showed the model to be more sensitive to changes in CO2 concentration and temperature than to changes in radiation. Analyses made using transient GCM (general circulation model) scenarios (UKTR and GFDL) showed different changes in mean fruit dry matter for the different scenarios, whereas mean total dry matter, and fruit and total dry matter variability, were predicted to increase under almost all the scenarios. Predictions based on equilibrium scenarios (UKLO and UKHI) gave similar results. For Sangiovese, variety adaptation analysis suggested a better adaptation in terms of mean production, but a worse adaptation in terms of yield variability.

KEYWORDS: CO2, RADIATION, TEMPERATURE

227

Biondi, F., and J.E. Fessenden. 1999. Response of lodgepole pine growth to CO2 degassing at Mammoth Mountain, California. *Ecology 80(7):2420-2426.*

We conducted dendroclimatic and stable isotope analyses of lodgepole pines (Pinus contorta) located in high-mortality sites at Mammoth Mountain (California, USA) to test for tree responses to magmatic degassing. Existing climatic and tree- ring data from nearby Yellowstone National Park were used for comparison. Sampled trees were scarcely sensitive to climate, and their growth showed an overall decline during the 20th century. Past growth rates of currently dead and stressed pines plummeted after 1990, when degassing of magmatic CO2 was first reported in the area. No consistent or strong correlation was found with monthly and seasonal climatic parameters. Stable carbon isotopes were measured on holocellulose extracted from annual rings of a dead pine, a stressed pine, and a live pine. The delta(13)C signature of the dead and stressed pines showed enrichment in heavy carbon beginning in 1990, which could be related to stomatal closure following impairment of root systems by high levels of magmatic CO2 in the soil.

KEYWORDS: CARBON, EMISSION, ISOTOPE, LONG VALLEY CALDERA, RATIOS, RINGS, UNREST

228

Bishop, D.L., and B.G. Bugbee. 1998. Photosynthetic capacity and dry mass partitioning in dwarf and semi-dwarf wheat (Triticum aestivum L.). *Journal of Plant Physiology 153(5-6):558-565.*

Efficient use of space and high yields are critical for long- term food production aboard the International Space Station. The selection of a full dwarf wheat (less than 30 cm tall) with high photosynthetic and yield potential is a necessary prerequisite for growing wheat in the controlled, volume- limited environments available aboard long-term spaceflight missions. This study evaluated the photosynthetic capacity and carbon partitioning of a full-dwarf wheat cultivar, Super Dwarf, which is routinely used in spaceflight studies aboard U.S. space shuttle and NASA/Mir missions and made comparisons with other dwarf and semidwarf wheat cultivars utilized in other ground-based studies in plant space biology. Photosynthetic capacity of the flag leaf in two dwarf (Super Dwarf, BB-19), and three semi-dwarf (Veery-10, Yecora Rojo, IBWSN 199) wheat cultivars (Triticum aestivum L.) was assessed by measuring: net maximum photosynthet ic rate, RuBP carboxylation efficiency, chlorophyll concentration and flag leaf area. Dry mass partitioning of carbohydrates to the leaves, sheaths, stems and ear was also assessed. Plants were grown under controlled environmental conditions in three replicate studies: slightly enriched CO2 (370 mu mol mol(-1)), high photosynthetic photon flux (1000 mu mol m(-2) s(-1); 58 mol m(-2) d(-1)) for a 16 h photoperiod, 22/15 degrees C day/night temperatures, ample nutrients and water provided by one-half strength Hoagland's nutrient solution (Hoagland and Amen, 1950). Photosynthetic capacity of the flag leaf was determined at anthesis using net CO2 exchange rate versus internal CO2 concentration curves

measured under saturating light (2000 mu mol m(-2) s(-1)) and CO2 (1000 mu mol mol(-1)). Dwarf wheat cultivars had greater photosynthetic capacities than the taller semi-dwarfs, they averaged 20 % higher maximum net photosynthetic rates compared to the taller semi-dwarfs, but these higher rates occurred only at anthesis, had slightly greater carboxylation efficiencies and significantly increased chlorophyll concentrations per unit leaf area. The reduced- height wheat had significantly less dry mass fraction in the stem but greater dry mass partitioned to the ear than the taller semi-dwarfs (Yecora rojo, IBWSN-199). Studies with detached heads confirm that the head is a significant sink in the shorter wheat cultivars.

KEYWORDS: BIOCHEMISTRY, CANOPY, FLAG LEAF, GAS-EXCHANGE, HEIGHT, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SPRING WHEAT, SUCROSE METABOLISM, WINTER-WHEAT

229

Biswas, P.K., D.R. Hileman, P.P. Ghosh, N.C. Bhattacharya, and J.N. McCrimmon. 1996. Growth and yield responses of field-grown sweetpotato to elevated carbon dioxide. *Crop Science 36(5):1234-1239.*

Root crops are important in developing countries, where food supplies are frequently marginal. Increases in atmospheric CO2 usually lead to increases in plant growth and yield, but little is known about the response of root crops to CO2 enrichment under field conditions, This experiment was conducted to investigate the effects of CO2 enrichment on growth and yield of field-grown sweetpotato [Ipomoea batatas (L.) Lam.]. Plants were grown in open-top chambers in the field at four CO2 levels ranging from 354 (ambient) to 665 mu mol mol(-1) in two growing seasons, Shoot growth was not affected significantly by elevated CO2. Yield of storage roots increased 46 and 75% at the highest CO2 level in the 2 yr, The yield enhancement occurred through increases in the number of storage roots in the first year and through increases in both the number and size of the storage roots in the second year, Storage- root/shoot ratios increased 44% and leaf nitrogen concentrations decreased by 24% at the highest CO2 level, A comparison of plants grown in the open field to plants grown in open-top chambers at ambient CO2 concentrations indicated that open-top chambers reduced shoot growth in the first year and storage-root yield in both years, These results are consistent with the majority of CO2-enrichment studies done on pot-grown sweetpotato.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, COTTON, ENVIRONMENT, IRRIGATION, NITROGEN, OPEN-TOP CHAMBERS, PHYSIOLOGY, PLANT-RESPONSES, SWEET-POTATO, WATER-STRESS

230

Bjorn, L.O., T.V. Callaghan, I. Johnsen, J.A. Lee, Y. Manetas, N.D. Paul, M. Sonesson, A.R. Wellburn, D. Coops, H.S. HeideJorgensen, C. Gehrke, D. GwynnJones, U. Johanson, A. Kyparissis, E. Levizou, D. Nikolopoulos, Y. Petropoulou, and M. Stephanou. 1997. The effects of UV-B radiation on European heathland species. *Plant Ecology 128(1-2):252-264.*

The effects of enhanced UV-B radiation on three examples of European shrub-dominated vegetation were studied in situ. The experiments were in High Arctic Greenland, northern Sweden and Greece, and at all sites investigated the interaction of enhanced UV-B radiation (simulating a 15% reduction in the ozone layer) with artificially increased precipitation, The Swedish experiment also involved a study of the interaction between enhanced UV-B radiation and elevated CO2 (600 ppm). These field studies were supported by an outdoor controlled environment study in the United Kingdom involving modulated enhancement of UV-B radiation in combination with elevated CO2 (700 ppm). Effects of the treatments on plant growth, morphology, phenology and physiology were measured. The effects observed were species specific, and included both positive and negative responses to the treatments. In general the negative responses to UV-B treatments of up to three growing seasons were small, but included reductions in shoot growth and premature leaf senescence. Positive responses included a marked increase in flowering in some species and a stimulation of some photosynthetic processes. UV-B treatment enhanced the drought tolerance of Pinus pinea and Pinus halepensis by increasing leaf cuticle thickness. In general, there were few interactions between the elevated CO2 and enhanced UV-B treatments. There was evidence to suggest that although the negative responses to the treatments were small, damage may be increasing with time in some long-lived woody perennials. There was also evidence in the third year of treatments for effects of UV-B on insect herbivory in Vaccinium species. The experiments point to the necessity for long-term field investigations to predict the likely ecological consequences of increasing UV-B radiation.

KEYWORDS: ACTION SPECTRA, DROUGHT, FIELD CONDITIONS, GROWTH, LEAVES, PHOTOSYNTHESIS, SOLAR ULTRAVIOLET-RADIATION, STOMATAL CLOSURE, SURFACE, TERRESTRIAL PLANTS

231

Bladier, C., and P. Chagvardieff. 1993. Growth and photosynthesis of photoautotrophic callus derived from protoplasts of solanum-tuberosum L. *Plant Cell Reports 12(6):307-311.*

We describe a photoautotrophic culture procedure of potato (cvs Kennebec, Haig, DTO-33) callus derived from mesophyll protoplasts. The protoplast culture was initiated at very low concentration of glucose (down to 0.25 g l-1). Callus was subcultured under CO2 enriched air and glucose was suppressed by the successive dilutions with glucose free media. Regeneration was successfully obtained under photoautotrophic conditions. The characterization of oxygen exchange and of some enzymes and metabolites of carbon assimilation indicated that chlorophyllous callus, grown on carbohydrate free medium, developed the photosynthetic pathway typical of C3 plants. By comparing the fresh weight of callus cultivated in the light or in non-photosynthetic conditions (in darkness or in the light +3-(3,4-Dichlorophenyl)-1,1-dimethylurea) we concluded that growth depended to about 70 to 88 % on photosynthesis.

KEYWORDS: CELL-SUSPENSION CULTURES, CO2, LIGHT, METABOLISM, MUTANTS, NICOTIANA-PLUMBAGINIFOLIA, OXYGEN- EXCHANGE, PLANTS, RESPIRATION, SUCROSE

232

Blobner, M., R. Bogdanski, E. Kochs, J. Henke, A. Findeis, and S. Jelen-Esselborn. 1998. Effects of intraabdominally insufflated carbon dioxide and elevated intraabdominal pressure on splanchnic circulation - An experimental study in pigs. *Anesthesiology 89(2):475-482.*

Background Intraabdominally insufflated carbon dioxide (CO2) during laparoscopy may have a specific effect on splanchnic circulation that may be unrelated to the effects of increased intraabdominal pressure alone. Therefore, the influences of insufflation with CO2 versus air on splanchnic circulation were compared. Methods: Pigs were chronically instrumented for continuous recording of mesenteric artery, portal venous, inferior vena cava, and pulmonary arterial blood flow and portal venous pressure. After induction of anesthesia, CO2 or air was insufflated in 14 and 10 pigs, respectively. with the pigs in the supine position, intraabdominal pressure was increased in steps of 4 mmHg up to 24 mmHg by graded gas insufflation, Results: During air insufflation, mesenteric artery vascular resistance was unchanged, whereas mesenteric arterial blood flow decreased with increasing intraabdominal

pressure. Shortly after CO2 insufflation to an intraabdominal pressure of 4 mmHg, mean arterial pressure, mesenteric arterial blood flow, and mesenteric arterial vascular resistance were increased by 21%, 12% and 9%, respectively. Subsequently, with the onset of CO2 resorption in the third minute, mean arterial pressure declined to baseline values and mesenteric arterial vascular resistance declined to 85% of baseline values, whereas mesenteric arterial blood flow continued to increase to a maximum of 24% higher than baseline values. At steady-state conditions during CO2 insufflation, mesenteric arterial blood flow was increased up to an intraabdominal pressure less than or equal to 16 mmHg but decreased at higher intraabdominal pressures. Conclusions: in contrast to air insufflation, intraabdominal insufflation of CO2 resulted in a moderate splanchnic hyperemia at an intraabdominal pressure less than or equal to 12 mmHg. At higher intraabdominal pressure values, pressure-induced changes became more important than the type of gas used.

KEYWORDS: BLOOD-FLOW, DOGS, HALOTHANE ANESTHESIA, INTRA-ABDOMINAL PRESSURE, LAPAROSCOPIC CHOLECYSTECTOMY, PNEUMOPERITONEUM, RESPONSES, TENSION, VASOPRESSIN RELEASE

233

Blum, H., G. Hendrey, and J. Nosberger. 1997. Effects of elevated CO2, N fertilization, and cutting regime on the production and quality of Lolium perenne L. shoot necromass. *Acta Oecologica-International Journal of Ecology 18(3):291-295.*

In the Swiss grassland FACE experiment, we measured the effect of elevated CO2 on the shoot necromass production and quality of Lolium perenne in 1995. Dead stubble of reproductive tillers and dead leaf sheaths were the main components of necromass. Elevated CO2 did not significantly change the amount and the nitrogen concentration of necromass. Significantly more necromass was produced and the N concentration was lower in the low N supply treatments. Total necromass amounted to 250-500 g m(-2). Necromass N content was in the order of 5-6 g m(-2) This underscores the importance of the carbon and nitrogen fluxes included in necromass and their importance for soil biology and fertility.

234

Blumenthal, C., H.M. Rawson, E. McKenzie, P.W. Gras, E.W.R. Barlow, and C.W. Wrigley. 1996. Changes in wheat grain quality due to doubling the level of atmospheric CO2. *Cereal Chemistry 73(6):762-766.*

Elevated levels of atmospheric CO2 have been shown to increase grain yield and reduce grain nitrogen concentration. The object of this study was to determine whether elevated CO2 levels would modify other aspects of grain quality relevant to processing, particularly protein and starch quality. Wheat of two genotypes (Hartog and Late Hartog) was grown in the field in controlled-atmosphere tunnels at either the ambient level of CO2 (350 mu l/L) or an elevated level (700 mu l/L). This elevated level of CO2 produced significant increases in grain yield, but decreases in 1,000-kernel weight. Grain grown in the elevated CO2 atmosphere produced poorer dough and decreased loaf volume, farinograph development time, and dough extensibility. These changes were largely attributable to the lower protein content of the grain grown at elevated CO2. There did not appear to be major changes in protein composition or in the functional properties of the protein. Grain produced at elevated CO2 yielded starch with a significantly higher proportion of large (A-type) starch granules but no overall change in amylose-to-amylopectin ratio. These studies indicate that elevated levels of CO2 may result in decreased quality of bread wheats largely due to lowered protein content.

KEYWORDS: CARBON DIOXIDE, CLIMATE, GENOTYPES, GROWTH, NITROGEN APPLICATION, NUTRITION, SPRING WHEAT, TEMPERATURE, YIELD

235

Boerner, R.E.J., and J. Rebbeck. 1995. Decomposition and nitrogen release from leaves of 3 hardwood species grown under elevated o-3 and/or co2. *Plant and Soil 170(1):149-157.*

Elevated concentrations of O-3 and CO2 have both been shown to affect structure, nutrient status, and deposition of secondary metabolites in leaves of forest trees. While such studies have produced robust models of the effects of such air pollutants on tree ecophysiology and growth, few have considered the potential for broader, ecosystem-level effects after these chemically and structurally altered leaves fall as leaf litter and decay. To determine the effects of elevated O-3 and/or CO2 on the subsequent decomposition and nutrient release from the leaves grown in such altered atmospheres, we grew seedlings of three widespread North American forest trees, black cherry (Prunus serotina) (BC), sugar maple (Acer saccharum) (SM), and yellow-poplar (Liriodendron tulipifera) (YP) for two growing seasons in charcoal-filtered air (CF-air=approximately 25% ambient O-3), ambient O-3 (1X) or twice-ambient O-3 (2X) in outdoor open-top chambers. We then assayed the loss of mass and N from the litter derived from those seedlings through one year litterbag incubations in the forest floor of a neighboring forest stand. Mass loss followed linear functions and was not affected by the O-3 regime in which the leaves were grown. Instantaneous decay rates (i.e. k values) averaged SM:-0.707 y(-1), BC:-0.613 y(-1), and YP:-0.859 y(-1). N loss from ambient (1X) O-3-grown SM leaves was significantly greater than from CF-air leaves; N loss from BC leaves did not differ among treatments. Significantly less N was released from CF-air-grown YP leaves than from 1X or 2X O-3-treated leaves. YP leaves from plants grown in pots at 2X O-3 and 350 ppm supplemental CO2 in indoor pollutant fumigation chambers (CSTRs or Continuously Stirred Tank Reactors) loss 40% as much mass and 27% as much N over one year as did leaves from YP grown in CF-air or 2X O-3. Thus, for leaves from plants grown in pots in controlled environment fumigation chambers, the concentrations of both O-3 and CO2 can affect N release from litter incubated in the field whereas mass loss rate was affected only by CO2. Because both mass loss and N release from leaves grown at elevated CO2 were reduced significantly (at least for yellow-poplar), forests exposed to elevated CO2 may have significantly reduced N turnover rates, thereby resulting in increased N limitation of tree growth, especially in forests which are already N-limited.

KEYWORDS: ACIDIC RAIN, ATMOSPHERIC CO2, CARBON DIOXIDE, OZONE, PHOTOSYNTHESIS, QUALITY, RESPONSES, SEEDLINGS, SULFUR-DIOXIDE, TREE

236

Boese, S.R., and D.W. Wolfe. 1995. Elevated-temperatures limit sink development and photosynthetic benefit from elevated co2. *Plant Physiology 108(2):26.*

237

Boese, S.R., D.W. Wolfe, and J.J. Melkonian. 1997. Elevated CO2 mitigates chilling-induced water stress and photosynthetic reduction during chilling. *Plant, Cell and Environment 20(5):625-632.*

Bean, cucumber and corn plants were grown in controlled- environment chambers at 25/18 degrees C day/night temperature and either ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 concentration, and at 20-30 d after emergence they were exposed to a 24 h chilling treatment (6.5 +/- 1.5 degrees C) at their growth CO2

concentration. Whole-plant transpiration rates (per unit leaf area basis) during the first 3 h of chilling were about 26, 28 and 13% lower at elevated than at ambient CO2 for bean, cucumber and corn, respectively. The decline in leaf water potential (Psi(L)) and visible wilting of bean and cucumber during chilling were significantly less at elevated than at ambient CO2. Corn Psi(L) was not significantly affected by chilling, and corn did not exhibit any other symptoms of chilling-induced water stress. Leaf osmotic potentials (measured before chilling only) of bean and cucumber were more negative at elevated than at ambient CO2, and the corresponding calculated leaf turgor potentials were significantly higher at elevated than at ambient CO2. Leaf relative water content (RWC) during chilling at ambient CO2 fell to 62 and 48% for bean and cucumber, respectively, RWC during chilling at elevated CO2 was never below 79% for bean or 63% for cucumber. Corn RWC was not measured, After 24 h of chilling at ambient CO2, net photosynthetic rate (PN) reductions were 83, 89 and 24% for bean, cucumber and corn, respectively. P-N reductions during chilling were less at elevated CO2: 53, 40 and 4% for bean, cucumber and corn, respectively. At ambient CO2, none of the species fully recovered to pre-chilling P-N, but at elevated CO2 both bean and corn recovered fully. The average percentage leaf area with visible leaf damage due to chilling was 20.6 and 9.6% at ambient and elevated CO2, respectively, for bean, and 32.4 and 23.6% at ambient and elevated CO2, respectively, for cucumber. Corn showed no significant permanent leaf damage from chilling at either CO2 concentration. These results indicate that cucumber was most sensitive to chilling as imposed in this study, followed by bean and corn. The results support the hypothesis that, at least in young plants under controlled- environment conditions, elevated CO2 improves plant water relations during chilling and can mitigate photosynthetic depression and chilling damage. The implications for long-term growth and reproductive success in managed and natural ecosystems will require testing of this hypothesis under field conditions.

KEYWORDS: ABSCISIC- ACID, LEAF GAS- EXCHANGE, LIGHT, LOW-TEMPERATURE, PHASEOLUS-VULGARIS L, PHOTOINHIBITION, PISUM SATIVUM L, SENSITIVE PLANTS, STOMATAL BEHAVIOR, ZEA-MAYS

238

Boetsch, J., J. Chin, M. Ling, and J. Croxdale. 1996. Elevated carbon dioxide affects the patterning of subsidiary cells in Tradescantia stomatal complexes. *Journal of Experimental Botany 47(300):925-931.*

The influence of elevated CO2 concentration (670 ppm) on the structure, distribution, and patterning of stomata in Tradescantia leaves was studied by making comparisons with plants grown at ambient CO2. Extra subsidiary cells, beyond the normal complement of four per stoma, were associated with nearly half the stomatal complexes on leaves grown in elevated CO2. The extra cells shared characteristics, such as pigmentation and expansion, with the typical subsidiary cells, The position and shape of the extra subsidiary cells in face view differed in the green and purple varieties of Tradescantia. Substomatal cavities of complexes with extra subsidiary cells appeared larger than those found in control leaves, Stomatal frequency expressed on the basis of leaf area did not differ from the control. Stomatal frequency based on cell counts (stomatal index) was greater in leaves grown in CO,enriched air when all subsidiary cells were counted as part of the stomatal complex. This difference was eliminated when subsidiary cells were included in the count of epidermal cells, thereby evaluating the frequency of guard cell pairs, The extra subsidiary cells were, therefore, recruited from the epidermal cell population during development, Stomatal frequency in plants grown at elevated temperature (29 degrees C) was not significantly different from that of the control (24 degrees C). The linear aggregations of stomata were similar in plants grown in ambient and elevated CO2. Since enriched CO2 had no effect on the structure or patterning of guard cells, but resulted in the formation of additional subsidiary cells, it is likely that separate and independent events pattern the two cell types. Plants grown at enriched CO2 levels had significantly greater internode lengths, but leaf area and the time interval between the appearance of successive leaves were similar to that of control plants. Porometric measurements revealed that stomatal conductance of plants grown under elevated CO2 was lower than that of control leaves and those grown at elevated temperature, Tradescantia was capable of regulating stomatal conductance in response to elevated CO2 without changing the relative number of stomata present on the leaf.

KEYWORDS: ARABIDOPSIS, CO2- ENRICHMENT, DIFFERENTIATION, LEAF DEVELOPMENT, MORPHOLOGY, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS

239

Bolin, B. 1999. Effect on the biosphere of elevated atmospheric CO2 (pg 1851). *Science 286(5440):684.*

240

Bolin, B., J. Canadell, B. Moore, I. Noble, and W. Steffen. 1999. Effect on the biosphere of elevated atmospheric CO2. *Science 285(5435):1851-1852.*

241

Bolker, B.M., S.W. Pacala, F.A. Bazzaz, C.D. Canham, and S.A. Levin. 1995. Species-diversity and ecosystem response to carbon-dioxide fertilization - conclusions from a temperate forest model. *Global Change Biology 1(5):373-381.*

This paper explores how the response of a temperate forest ecosystem to climate change might depend on species diversity and community change. In particular, we look at the dynamics of a model of temperate forest growth under doubled CO2. We combine a detailed, field-calibrated model of forest dynamics (Pacala et al. 1993) with greenhouse data on the range of seedling biomass growth response to doubled CO2 concentrations (Bazzaz et al. 1990; Bazzaz & Miao 1993). Because total ecosystem response to climate change depends delicately on many environmental variables other than CO2, we isolate the effects of community change by comparing runs of the regular model, allowing dynamic community change, with runs of a reduced model that holds species composition static by using a single tree species with average parameters. Simulations that allowed community change instead of holding species composition constant showed a roughly 30% additional increase in total basal area over time scales of 50-150 years. Although the model omits many possible feedbacks and mechanisms associated with climate change, it suggests the large potential effects that species differences and feedbacks can have in ecosystem models and reinforces the possible importance of diversity to ecosystem function (Naeem et al. 1994; Tilman & Downing 1994) over time scales within the planning horizon for global change policy.

KEYWORDS: ATMOSPHERIC CO2, CANOPY, CO2-INDUCED CLIMATE CHANGE, ENRICHMENT, GROWTH, LIGHT, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, STORAGE, TERRESTRIAL ECOSYSTEMS

242

Bonghi, C., A. Ramina, B. Ruperti, R. Vidrih, and P. Tonutti. 1999. Peach fruit ripening and quality in relation to picking time, and hypoxic and high CO2 short-term postharvest treatments. *Postharvest Biology and Technology 16(3):213-222.*

Peach fruits (Prunus persica L. Batsch, cv Springcrest) were harvested at two ripening stages (flesh firmness of 60 N, first harvest, and 45 N, second harvest) and maintained at 20 degrees C in air (control) or for 24 and 48 h in streams of ultra low(<l%) oxygen (ULO) or high (30%) CO2 concentration and then transferred to air for up to 8 days. The decline in flesh firmness was strongly reduced by ULO and CO2 treatments in fruits of both harvests, although the effect was stronger in fruits picked earlier in which ethylene biosynthesis remained at the basal level. In fruits of the second harvest, endo beta- 1,4-glucanase (EGase) activity was lower in ULO- and CO2- treated fruits than in control fruits at the end of the 24 h treatment and the following two days in air. Acetaldehyde (AA) gradually accumulated in control fruit and the highest concentrations were detected during late ripening. Both treatments induced a strong accumulation of AA but, with the exception of the 24 and 48 h CO2 treatments performed on fruits of the second harvest, a decrease in AA content was observed when the fruits were transferred to air. A slight increase in ethanol (EtOH) was found throughout the ripening process in control fruits; ULO and CO2 strongly stimulated EtOH production. When fruits were transferred to air, EtOH concentration declined rapidly. Alcohol dehydrogenase (ADH) activity significantly increased in control fruit only in the late stages of ripening. Greater ADH activity was found throughout the experimental period in fruits of the first harvest treated for 24 h in ULO and CO2, whereas, at day 8, control and treated fruits of the second harvest showed similar ADH activity values. Hypoxic and, to a lesser extent, CO2- enriched atmospheres stimulated Adh gene expression.

KEYWORDS: ETHYLENE, EXPRESSION, LOW-OXYGEN ATMOSPHERES, NECTARINES, RESPONSES, STORAGE

243

Booker, F.L. 1997. Effects of elevated CO2 and nitrogen on proanthocyanidins in cotton. *Plant Physiology 114(3):489.*

244

Booker, F.L., C.D. Reid, S. BrunschonHarti, E.L. Fiscus, and J.E. Miller. 1997. Photosynthesis and photorespiration in soybean [Glycine max (L.) Merr.] chronically exposed to elevated carbon dioxide and ozone. *Journal of Experimental Botany 48(315):1843-1852.*

The effects of elevated carbon dioxide (CO2) and ozone (O-3) on soybean [Glycine max (L.) Merr.] photosynthesis and photorespiration-related parameters were determined periodically during the growing season by measurements of gas exchange, photorespiratory enzyme activities and amino acid levels, Plants were treated in open-top field chambers from emergence to harvest maturity with seasonal mean concentrations of either 364 or 726 mu mol mol(-1) CO2 in combination with either 19 or 13 nmol mol(-1) O-3 (12 h daily averages). On average at growth CO2 concentrations, net photosynthesis (A) increased 56% and photorespiration decreased 36% in terminal mainstem leaves with CO2-enrichment. Net photosynthesis and photorespiration were suppressed 30% and 41%, respectively, by elevated O-3 during late reproductive growth in the ambient CO2 treatment, but not in the elevated CO2 treatment. The ratio of photorespiration to A at growth CO2 was decreased 61% by elevated CO2. There was no statistically significant effect of elevated O-3 in the ratio of photorespiration to A. Activities of glycolate oxidase, hydroxypyruvate reductase and catalase were decreased 10-25% by elevated CO2, and by 46-66% by elevated O-3 at late reproductive growth. The treatments had no significant effect on total amino acid or glycine levels, although serine concentration was lower in the elevated CO2 and O-3 treatments at several sampling dates. The inhibitory effects of elevated O-3 on photorespiration-related parameters were generally commensurate with the O-3-induced decline in A. The results suggest that elevated CO2 could promote productivity both through increased photoassimilation and suppressed photorespiration.

KEYWORDS: ARABIDOPSIS-THALIANA, ATMOSPHERIC CO2, CARBOXYLASE ACTIVITY, GAS-EXCHANGE, L LEAVES, PHASEOLUS-VULGARIS L, PLANT-RESPONSES, SPRING WHEAT, SUPEROXIDE-DISMUTASE, ULTRAVIOLET-B

245

Boone, R.D., K.J. Nadelhoffer, J.D. Canary, and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature 396(6711):570-572.*

The temperature sensitivity of soil respiration will largely determine the effects of a warmer world on net carbon flux from soils to the atmosphere. CO2 flux from soils to the atmosphere is estimated to be 50-70 petagrams of carbon per year and makes up 20-38% of annual inputs of carbon (in the form of CO2) to the atmosphere from terrestrial and marine sources(1,2). Here we show that, for a mixed temperate forest, respiration by roots plus oxidation of rhizosphere carbon, which together produce a large portion of total effluxed soil CO2, is more temperature-sensitive than the respiration of bulk soil. We determine that the Q(10) value (the coefficient for the exponential relationship between soil respiration and temperature, multiplied by ten) is 4.6 for autotrophic root respiration plus rhizosphere decomposition, 2.5 for respiration by soil lacking roots and 3.5 for respiration by bulk soil. If plants in a higher-CO2 atmosphere increase their allocation of photosynthate to roots(3-6), these findings suggest that soil respiration should be more sensitive to elevated temperatures, thus limiting carbon sequestration by soils.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO2, EXCHANGE, FLUXES, FOREST, LITTER, VEGETATION

246

Boote, K.J., and N.B. Pickering. 1994. Modeling photosynthesis of row crop canopies. *Hortscience 29(12):1423-1434.*

KEYWORDS: CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, CO2/O2 SPECIFICITY, DIRECT COMPONENT, ELEVATED CO2, GLOBAL RADIATION, LEAF NITROGEN, NET PHOTOSYNTHESIS, SOYBEAN CANOPIES, USE EFFICIENCY

247

Borkhsenious, O.N., C.B. Mason, and J.V. Moroney. 1998. The intracellular localization of ribulose-1,5-bisphosphate carboxylase/oxygenase in Chlamydomonas reinhardtii. *Plant Physiology 116(4):1585-1591.*

The pyrenoid is a proteinaceous structure round in the chloroplast of most unicellular algae. Various studies indicate that ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) is present in the pyrenoid, although the fraction of Rubisco localized there remains controversial. Estimates of the amount of Rubisco in the pyrenoid of Chlamydomonas reinhardtii range from 5% to nearly 100%. Using immunolocalization, the amount of Rubisco localized to the pyrenoid or to the chloroplast stroma was estimated for C. reinhardtii cells grown under different conditions. It was observed that the amount of Rubisco in the pyrenoid varied with growth condition; about 40% was in the pyrenoid when the cells were grown under elevated CO2 and about 90% with ambient CO2. In addition, it is likely that pyrenoidal Rubisco is active in CO2 fixation because in vitro activity measurements showed that most of the Rubisco must be active to account for CO2-fixation rates observed in whole cells. These results are consistent with the idea that the pyrenoid is the site of CO2 fixation in C. reinhardtii and other unicellular algae containing CO2-concentrating mechanisms.

KEYWORDS: CARBONIC-ANHYDRASE, CHLOROPLAST, MECHANISM, OXYGENASE, PHOTOSYNTHESIS

248

Borodin, V.B. 1995. Photosynthetic o-2 exchange in chlorella cells adapted to low co2 concentration under blue or red-light. *Russian Journal of Plant Physiology 42(1):31-36.*

The effect of light quality on the adaptation to low atmospheric CO2 concentration was studied on the cells of unicellular green al,oa Chlorella pyrenoidosa 82T grown under 2% CO2 concentration and white light. The adaptation of Chlorella cells was more successful under blue than under red light. Thus, the air-adapted cells under blue light showed a higher affinity for CO2, a higher quantum efficiency of apparent photosynthesis at CO2 limitation, and acceleration of O-2 evolution at light saturation, as compared to the red- light-adapted cells. In air-adapted cells, the photosynthetic rates at low CO2 concentration were enhanced with increased intensities of both blue and red light, but the differences between the two treatments were retained. It was inferred that Chlorella cell adaptation depended on both light intensity and its spectral composition. The light intensity exerts its action via photosynthetic apparatus while spectral composition of light exerts its effect via a system of photoreception, which absorbs blue light. This additional blue light absorption is considered favorable for Chlorella cell adaptation to low CO2 concentration.

KEYWORDS: ACETABULARIA- MEDITERRANEA, CARBONIC-ANHYDRASE, CHLAMYDOMONAS-REINHARDTII, INDUCTION, PROTEIN

249

Bosac, C., S.D.L. Gardner, G. Taylor, and D. Wilkins. 1995. Elevated co2 and hybrid poplar - a detailed investigation of root and shoot growth and physiology of populus-euramericana, primo. *Forest Ecology and Management 74(1-3):103-116.*

Exposure of the hybrid poplar clone 'Primo' (Populus deltoides X Populus nigra) to 580 mu l 1(-1) carbon dioxide for just 68 days significantly (P less than or equal to 0.05) increased stem height by 13% compared with trees grown in ambient CO2 concentrations. The stem diameter was significantly (P less than or equal to 0.05) increased and both total biomass and woody stem biomass also showed higher values (38% and 31% increases respectively) in elevated CO2. Trees in elevated CO2 had more leaves and a greater total leaf area, whilst the specific leaf area was decreased in elevated CO2 on four out of five occasions and was significantly (P less than or equal to 0.05) lower after 68 days, an effect indicating that leaves were thicker and/or heavier. Rates of photosynthesis (A) measured after 49 and 67 days of exposure revealed that trees in the elevated CO2 treatment had lower values of A when measured at either 350 or 580 mu l 1(-1) CO2. Sequential harvests at intervals during the study in which the root and shoot components were analysed separately allowed the construction of root:shoot ratios and allometric coefficients; there was no significant effect on the allometric coefficient and the root:shoot ratio was significantly increased on only one occasion. However, measurements of the 'apparent' root length suggested that root lengths were greater in the CO2 treatment. There was a significant increase in the number of fine root tips visible down the surface of specially designed rooting tubes (P less than or equal to 0.05), indicating more fine roots or an increase in fine root branching. The growth rates of individual fine or large roots over 24 h were unaffected, again suggesting that increases in biomass may be due to more root segments rather than longer individual roots. Root water relations were also examined and showed a tendency towards solute accumulation and increases in turgor pressure (P) and effective tugor (P-e) at times when root growth was stimulated, although these were not consistent. Cell wall plasticity of the tips of large roots was significantly (P less than or equal to 0.01) reduced in elevated CO2, possibly indicating a greater tendency to divert resources to the formation of root branches. The results of the study are discussed in the light of the possible consequences of changes in poplar growth and physiology for forestry practice in an increased CO2 environment.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CELL-WALLS, CLONES, CONDUCTANCE, DROUGHT, ENRICHMENT, LEAF GROWTH, PHOTOSYNTHESIS, SOURCE-SINK RELATIONS

250

Bottomley, P.A., H.H. Rogers, and S.A. Prior. 1993. Nmr imaging of root water distribution in intact vicia-faba L plants in elevated atmospheric co2. *Plant, Cell and Environment 16(3):335-338.*

The effect of elevated atmospheric CO2 on water distribution in the intact roots of Vicia faba L. bean seedlings grown in natural soil was studied noninvasively with proton (H-1) nuclear magnetic resonance (NMR) imaging. Exposure of 24-d-old plants to atmospheric Co2-enriched air at 650 cm3 m-3 produced significant increases in water imaged in upper roots, hypogeal cotyledons and lower stems in response to a short-term drying- stress cycle. Above ground, drying produced negligible stem shrinkage and stomatal resistance was unchanged. In contrast, the same drying cycle caused significant depletion of water imaged in the same upper root structures in control plants subject to ambient CO2 (350 m3 m-3), and stem shrinkage and increased stomatal resistance. The results suggest that inhibition of transpiration caused by elevated CO2 does not necessarily result in attenuation of water transport from lower root structures. Inhibition of water loss from upper roots and lower stem in elevated CO2 environments may be a mitigating factor in assessing deleterious effects of greenhouse changes on crops during periods of dry climate.

KEYWORDS: CARBON DIOXIDE, INSITU, MAGNETIC-RESONANCE MICROSCOPY, TRANSPORT

251

Bouma, T.J., K.L. Nielsen, D.M. Eissenstat, and J.P. Lynch. 1997. Estimating respiration of roots in soil: Interactions with soil CO2, soil temperature and soil water content. *Plant and Soil 195(2):221-232.*

Little information is available on the variability of the dynamics of the actual and observed root respiration rate in relation to abiotic factors. In this study, we describe I) interactions between soil CO2 concentration, temperature, soil water content and root respiration, and II) the effect of short-term fluctuations of these three environmental factors on the relation between actual and observed root respiration rates. We designed an automated, open gas-exchange system that allows continuous measurements on 12 chambers with intact roots in soil. By using three distinct chamber designs with each a different path for the air flow, we were able to measure root respiration over a 50-fold range of soil CO2 concentrations (400 to 25000 ppm) and to separate the effect of irrigation on observed vs. actual root respiration rate. All respiration measurements were made on one-year-old citrus seedlings in sterilized sandy soil with minimal organic material. Root respiration was strongly affected by diurnal fluctuations in temperature (Q(10) = 2), which agrees well with the literature. In contrast to earlier findings for Douglas-fir (Qi et al., 1994), root respiration rates of citrus were not affected by soil CO2 concentrations (400 to 25000 ppm CO2; pH around 6). Soil CO2 was strongly affected by soil water content but not by respiration measurements, unless the air flow for root respiration measurements was directed through the soil. The latter method of measuring root respiration reduced soil CO2 concentration to that of incoming air. Irrigation caused a temporary reduction in CO2 diffusion, decreasing the observed respiration rates obtained by techniques that depended on diffusion. This

apparent drop in respiration rate did not occur if the air flow was directed through the soil. Our dynamic data are used to indicate the optimal method of measuring root respiration in soil, in relation to the objectives and limitations of the experimental conditions.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, FIELD, GROWTH, PLANTS, RESPONSES, SEEDLINGS, SOUR ORANGE TREES

252

Bowden, R.D., K.M. Newkirk, and G.M. Rullo. 1998. Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions. *Soil Biology and Biochemistry 30(12):1591-1597.*

Carbon dioxide and methane are important greenhouse gases whose exchange rates between soils and the atmosphere are controlled strongly by soil temperature and moisture. We made a laboratory investigation to quantify the relative importance of soil moisture and temperature on fluxes of CO2 and CH4 between forest soils and the atmosphere. Forest floor and mineral soil material were collected from a mixed hardwood forest at the Harvard Forest. Long-Term Ecological Research Site (MA) and were incubated in the laboratory under a range of moisture (air-dry to nearly saturated) and temperature conditions (5-25 degrees C). Carbon dioxide emissions increased exponentially with increasing temperature in forest floor material, with emissions reduced at the lowest and highest soil moisture contents. The forest floor Q(10) of 2.03 (from 15-25 degrees C) suggests that CO2 emissions were controlled primarily by soil biological activity. Forest floor CO2 emissions were predicted with a multiple polynomial regression model (r(2) = 0.88) of temperature and moisture, but the fit predicting mineral soil respiration was weaker (r(2) = 0.59). Methane uptake was controlled strongly by soil moisture, with reduced fluxes under conditions of very low or very high soil moisture contents. A multiple polynomial model accurately described CH4 uptake by mineral soil material (r(2) = 0.81), but only weakly (r(2) = 0.45) predicted uptake by forest floor material. The mineral soil Q(10) of 1.11 for CH4 uptake indicates that methane uptake is controlled primarily by physical processes. Our work suggests that inclusion of both moisture and temperature can improve predictions of soil CO2 and CH4 exchanges between soils and the atmosphere. Additionally, global change models need to consider interactions of temperature and moisture in evaluating effects of global climate change on trace gas fluxes. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC METHANE, CONSUMPTION, DYNAMICS, ECOSYSTEMS, NITROGEN, OXIDATION, RESPIRATION, RESPONSES, WATER

253

Bowes, G. 1991. Growth at elevated CO2 - photosynthetic responses mediated through rubisco. *Plant, Cell and Environment 14(8):795-806.*

The global uptake of CO2 in photosynthesis is about 120 gigatons (Gt) of carbon per year. Virtually all passes through one enzyme, ribulose bisphosphate carboxylase/oxygenase (rubisco). which initiates both the photosynthetic carbon reduction, and photorespiratory carbon oxidation, cycles. Both CO2 and O2 are substrates; CO2 also activates the enzyme. In C3 plants, rubisco has a low catalytic activity, operates below its K(m) (CO2), and is inhibited by O2. Consequently, increases in the CO2/O2 ratio stimulate C3 photosynthesis and inhibit photorespiration. CO2 enrichment usually enhances the productivity of C3 plants, but the effect is marginal in C4 species. It also causes acclimation in various ways: anatomically. morphologically, physiologically or biochemically. So, CO2 exerts secondary effects in growth regulation, probably at the molecular level, that are not predictable from its primary biochemical role in carboxylation. After an initial increase with CO2 enrichment, net photosynthesis often declines. This is a common acclimation phenomenon, less so in field studies, that is ultimately mediated by a decline in rubisco activity, though the RuBP/P(i)-regeneration capacities of the plant may play a role. The decline is due to decreased rubisco protein, activation state, and/or specific activity, and it maintains the rubisco fixation and RuBP/P(i)-regeneration capacities in balance. Carbohydrate accumulation is sometimes associated with reduced net photosynthesis, possibly causing feedback inhibition of the RuBP/P(i)-regeneration capacities, or chloroplast disruption. As exemplified by field-grown soybeans and salt marsh species, a reduction in net photosynthesis and rubisco activity is not inevitable under CO2 enrichment. Strong sinks or rapid translocation may avoid such acclimation responses. Over geological time, aquatic autotrophs and terrestrial C4 and CAM plants have genetically adapted to a decline in the external CO2/O2 ratio, by the development of mechanisms to concentrate CO2 internally; thus circumventing O2 inhibition of rubisco. Here rubisco affinity for CO2 is less, but its catalytic activity is greater, a situation compatible with a high-CO2 internal environment. In aquatic autotrophs, the CO2 concentrating mechanisms acclimate to the external CO2, being suppressed at high-CO2. It is unclear, whether a doubling in atmospheric CO2 will be sufficient to cause a de-adaptive trend in the rubisco kinetics of future C3 plants, producing higher catalytic activities.

KEYWORDS: 1,5-DIPHOSPHATE CARBOXYLASE, CARBON-DIOXIDE CONCENTRATIONS, CO2-ENRICHED ATMOSPHERE, ECHINOCHLOA CRUS GALLI, HIGH ATMOSPHERIC CO2, KINETIC-PROPERTIES, LONG-TERM EXPOSURE, MONOECIOUS CUCUMBERS, PHOSPHOENOLPYRUVATE CARBOXYLASE, RIBULOSE BISPHOSPHATE CARBOXYLASE

254

Bowes, G. 1993. Facing the inevitable - plants and increasing atmospheric co(2). *Annual Review of Plant Physiology and Plant Molecular Biology 44:309-332.*

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CO2-ENRICHMENT, ELEVATED CO2, INORGANIC CARBON, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SHORT- TERM, SOURCE-SINK RELATIONS, SOYBEAN LEAVES

255

Bowes, G., J.C.V. Vu, M.W. Hussain, A.H. Pennanen, and L.H. Allen. 1996. An overview of how rubisco and carbohydrate metabolism may be regulated at elevated atmospheric [CO2] and temperature. *Agricultural and Food Science in Finland 5(3):261-270.*

Although atmospheric CO2 concentration ([CO2]) has been up to 16-fold higher than at present, the past several million years have seen atypically low values. Thus, modern-day plants are adapted to cope with a low [CO2]/[O-2] ratio. The present [CO2] does nor saturate C-3 photosynthesis, so its doubling produces an "efficiency effect", but it is not always fully realized. Acclimation to high [CO2] during growth can down-regulate photosynthesis, presumably to optimize carbon acquisition and utilization. A primary factor in acclimation is a reduction in rubisco. Two crops, rice and soybean, were used to study this phenomenon. Rice photosynthesis and growth peaked at 500 mu mol mol(-1), whereas soybean responded up to 990 mu mol mol(-1) Rubisco concentration declined under CO2-enrichment and increasing temperatures, more so in rice than soybean. The rubisco k(cat) Of rice was unaffected by growth [CO2] or temperature, but that from soybean was increased by both. In rice the capacity to handle carbohydrate, as measured by sucrose phosphate synthase activity was up-regulated by CO2- enrichment, but not by temperature. Leaf carbohydrates were increased by [CO2], but decreased by higher temperatures, starch more

so than sucrose. Even though C-3 species differ in response to [CO2] and temperature, CO2-enrichment can moderate adverse effects of temperature extremes.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE, EXPRESSION, GROWTH, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, RICE, SOURCE-SINK RELATIONS

256

Bowler, J.M., and M.C. Press. 1993. Growth-responses of 2 contrasting upland grass species to elevated co2 and nitrogen concentration. *New Phytologist 124(3):515-522.*

Growth parameters of Agrostis capillaris L. and Nardus stricta L. were measured in relation to ambient and elevated concentrations of CO2 (340 and 550 mul CO2 l-1, respectively) and at low and high concentrations of nitrogen (0.8 and 3 mm NH4NO3, respectively). After 60 d of growth A. capillaris had attained approx. four times the total dry weight of N. stricta in all treatments, which was attributed to the greater leaf area ratio of the former. A. capillaris grown at the low nitrogen concentration attained 30% of the total dry weight of plants grown at high nitrogen. Over the 60 d period, destructive harvests (seven in total) showed the growth of N. stricta to be less sensitive than that of A. capillaris to the concentration of nitrogen, but in both species growth analysis showed the lower total dry weight at low nitrogen to be attributable to lower unit leaf rate. There was a differential response of both species to elevated concentrations of CO2 which was nitrogen dependent. A. capillaris grown at elevated CO2 attained a greater total dry weight than at ambient CO2 and this response was proportionately greater at low nitrogen (78% increase) than at high nitrogen (58% increase). In contrast, in N. stricta there was no effect of CO2 concentration on the total dry weight at low nitrogen whilst at high nitrogen plants grown at elevated CO2 had a greater total dry weight after 48 d of growth. Calculation of the allometric coefficient (K) relating root growth to shoot growth indicated that the effect of the lower nitrogen concentration was to increase partitioning to the roots while the higher CO2 concentration did not alter partitioning.

KEYWORDS: AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, IRRADIANCE, MINERAL NUTRITION, PHOTOSYNTHESIS, PLANTS, SEEDLINGS, SOURCE-SINK RELATIONS, TEMPERATURE, WHEAT

257

Bowler, J.M., and M.C. Press. 1996. Effects of elevated CO2, nitrogen form and concentration on growth and photosynthesis of a fast- and slow-growing grass. *New Phytologist 132(3):391-401.*

Growth and photosynthesis of Agrostis capillaris L. and Nardus stricta L. were measured for plants grown under ambient and elevated concentrations of CO2 (340 and 550 mu l CO2 l(-1) respectively) and a range of nitrogen concentrations (0.01, 0.1, 1 and 5 mg N l(-1)) supplied as either ammonium sulphate or sodium nitrate. After 42 d of growth for A. capillaris and 49 d of growth for N. stricta, the higher nitrogen concentrations resulted in stimulation of growth. The form of nitrogen did not affect the total dry weight attained by A. capillaris. However, ammonium-grown N. stricta attained a greater total dry weight than did nitrate-grown plants. Nitrogen form influenced leaf area ratio, which was greater in nitrate-grown A. capillaris and in ammonium-grown N. stricta. At the two lowest nitrogen concentrations there was no effect of elevated CO2 on total dry weight in either species, whilst at the two highest nitrogen concentrations positive growth responses to elevated CO2 were observed. Photosynthetic capacity and carboxylation efficiency were lower in plants grown in elevated CO2 at the two lowest nitrogen concentrations, and were associated with greater leaf soluble carbohydrate content and lower foliar nitrogen concentrations. By contrast, the CO2 treatment did not affect these parameters at the two highest nitrogen concentrations employed.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXPOSURE, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, LEAVES, NUTRITION, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

258

Brailsford, R.W., L.A.C.J. Voesenek, C.W.P.M. Blom, A.R. Smith, M.A. Hall, and M.B. Jackson. 1993. Enhanced ethylene production by primary roots of zea-mays L in response to sub-ambient partial pressures of oxygen. *Plant, Cell and Environment 16(9):1071-1080.*

Ethylene production by primary roots of 72-h-old intact seedlings of Zea mays L. cv. LG11 was studied under ambient and sub-ambient oxygen partial pressures (pO(2)) using a gas how- through system linked to a photoacoustic laser detector. Despite precautions to minimize physical perturbation to seedlings while setting-up, ethylene production in air was faster during the first 6h than later, in association with a small temporary swelling of the roots. When roots were switched from air (20.8kPa O-2) to 3 or 5kPa O-2 after 6h, ethylene production increased within 2-3h. When, the roots were returned to air 16h later, ethylene production decreased within 2-3h. The presence of 1OkPa CO2 did not interfere with the effect of 3kPa O-2. Transferring roots from air to 12.5kPa did not change ethylene production, while a reduction to 1kPa O-2 induced a small increase. The extra ethylene formed in 3 and 5kPa O-2 was associated with plagiotropism, swelling, root hair production, and after 72h, increased amounts of intercellular space (aerenchyma) in the root cortex. Root extension was also slowed down, but the pattern of response to oxygen shortage did not always match that of ethylene production. On return to air, subsequent growth patterns became normal within a few hours. In the complete absence of oxygen, no ethylene production was detected, even when anaerobic roots were returned to air after 16h.

KEYWORDS: ANOXIA, BIOSYNTHESIS, DEEP-WATER RICE, FORMING ENZYME, GROWTH, PLANTS, STIMULATION, SUBMERGENCE

259

Brakke, M., and L.H. Allen. 1995. Gas-exchange of citrus seedlings at different temperatures, vapor-pressure deficits, and soil-water contents. *Journal of the American Society for Horticultural Science 120(3):497-504.*

Midday reductions of stomatal conductance and carbon dioxide assimilation rates (A(CO2)) in Citrus are typically attributed to large leaf-to-air vapor-pressure differences or high atmospheric vapor-pressure deficits (VPD). This study investigated air temperature (T-a) and available soil water (ASW) level as corollary factors of atmospheric VPD that influence midday reduction of net gas exchange in citrus leaves. The influence of elevated atmospheric CO2 under conditions that inhibit net canopy A(CO2) was also investigated. Net canopy A(CO2) and evapotranspiration rates of Carrizo citrange [Poncirus trifoliata Raf x Citrus sinensis (L.) Osbeck] and Swingle citrumelo (P. trifoliata Raf x C. paradisii Macf.) seedlings grown in outdoor controlled- environment growth chambers were measured under two levels of T-a with concomitant changes in VPD and two levels of atmospheric CO2 concentration, which were changed in steps over time. Cyclical depletion of ASW was allowed to occur at each set of T-a/VPD and CO2 combinations. Highest net canopy A(CO2) rates at ambient CO2 concentration (330 mu mol . mol(-1)) were obtained at the low T-a/VPD level (29C/2.4 kPa) and ASW >50%. Diurnal canopy CO2 uptake rates decreased at the high T-a/VPD level (37C/3.6 kPa), and midday depression of canopy A(CO2) was observed at ASW levels <50%. Net canopy A(CO2) decreased at higher levels of ASW under the high T-

a/VPD treatment than at the low T-a/VPD treatment. At the elevated CO2 concentration (840 mu mol . mol(-1)) net canopy CO2 uptake rates were double those that occurred at ambient CO2 levels and they did not exhibit midday reduction. Our data indicate that, when soil water is not readily available, citrus seedlings are more sensitive to high levels of T-a and VPD which results in reduction of CO2 uptake. The inhibitory effects of elevated VPD and reduced ASW on citrus net A(CO2) were lessened at the elevated atmospheric CO2 level.

KEYWORDS: CARBON DIOXIDE, GROWTH, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION, TREES, VALENCIA ORANGE

260

Brandrud, T.E., and J.G.M. Roelofs. 1995. Enhanced growth of the macrophyte Juncus bulbosus in S Norwegian limed lakes. A regional survey. *Water, Air, and Soil Pollution 85(2):913-918.*

The effects of liming on the aquatic macrophyte vegetation have been investigated in S and SW Norway. In the western part of the study area, Juncus bulbosus was considerably more frequent in the limed than in the unlimed lakes, whilst in the eastern part there were no such differences, and the J. bulbosus populations were generally not so vital. In some southwestern areas a luxuriant and massiv nuisance growth of Juncus bulbosus in the depth zone 0-4 m was recorded. The most vital plants produced up to 1 m long annual shoots, and developed extensive, dense and vital surface mats in shallow areas (depth zone 0-3 m) after 4-5 years. The original isoetid vegetation had disappeared in the areas of dense J. bulbosus populations, and this development seems to be more or less irreversible. The massive J. bulbosus expansion is seen mainly in directly limed lakes with a sometimes visible layer of calcium carbonate on the sediment surface, but enhanced growth has been observed also in lakes downstream liming. The massive expansion is believed to be due to an increase of CO2 and ammonium in the sediment pore water, combined with a mild climate with a very high precipitation. In many areas the liming has led to an increase in species diversity, and a (re-)establishment of some acid-intolerant species such as Myriophyllum alterniflorum and Potamogeton spp.

KEYWORDS: ACIDIFICATION

261

Bransby, D.I., S.B. McLaughlin, and D.J. Parrish. 1998. A review of carbon and nitrogen balances in switchgrass grown for energy. *Biomass & Bioenergy 14(4):379-384.*

Increased atmospheric CO2, caused partly by burning fossil fuels, is assumed to elevate the risk of global warming, while nitrate contamination of surface runoff and groundwater from fertilizer and agricultural wastes constitutes a serious environmental hazard on a regional scale. Switchgrass (Panicum virgatum L.) grown as an energy crop could reduce atmospheric CO2 accumulation by replacing fossil fuels and sequestering C. It could also improve soil productivity by C sequestration, and reduce NO3-1 contamination of water by absorbing N lost from fertilizer and agricultural waste if planted in filter strips on adjacent land. The objective of this study was to assess potential impacts of switchgrass on C and N balances by reviewing and synthesizing information from current literature, unpublished data and on-going research. Replacing fossil fuels with switchgrass, or any other biomass, will have a much greater effect on atmospheric CO2 than C sequestration. This is because replacing fossil fuels provides a cumulative effect, while C sequestration offers only a one-time benefit. Furthermore, switchgrass will provide net gains in C sequestration only if it replaces annual row crops, but not if it replaces grazed pasture. Nitrogen recovery by switchgrass in an Alabama study was 65.6%, which compares favorably with the 50% recovery frequently quoted as the norm for wheal (Triticum aestivum L.) and corn (Zea mays L).

262

Brearley, J., M.A. Venis, and M.R. Blatt. 1997. The effect of elevated CO2 concentrations on K+ and anion channels of Vicia faba L. guard cells. *Planta 203(2):145-154.*

The effects of elevated CO2 concentrations on stomatal movement, anion-and K+-channel activities were examined in guard cells from epidermal strips of Vicia faba. Membrane voltage was measured using intracellular, double-barrelled microelectrodes and ion-channel currents were recorded under voltage clamp during exposure to media equilibrated with ambient (350 mu l . l(-1)), 1000 mu l . l(-1) and 10 000 mu l . l(-1) CO2 in 20% O-2 and 80% N-2. The addition of 1000 mu l . l(-1) CO2 to the bathing solution caused stomata to close with a halftime of approx. 40 min, and with 10 000 mu l . l(-1) CO2 closure occurred with a similar time course. Under voltage clamp, exposure to 1000 mu l . l(-1) and 10 000 mu l . l(-1) CO2 resulted in a rapid increase (mean, 1.5 +/- 0.2-fold, n = 8; range 1.3- to 2.5-fold) in the magnitude of current carried by outward-rectifying K+ channels (I-K,I-out). The effect of CO2 on I-K,I-out was essentially complete within 30 s and was independent of clamp voltage, but was associated with 25-40% (mean, 30 +/- 4%) decrease in the halftime for current activation. Exposure to CO2 also resulted in a four-fold increase in background current near the free-running membrane voltage, recorded as the instantaneous current at the start of depolarising and hyperpolarising voltage steps, and a decrease in the magnitude of current carried by inward-rectifying K+ channels (I-K,I-in). The effect of CO2 on I-K,I-in was generally slower than on I-K,I-out; it was allied with a transient acceleration of its activation kinetics during the first 60-120 s of treatment; and it was associated with a negative shift in the voltage-sensitivity of gating over a period of 3-5 min. Measurements carried out to isolate the background currents attributable to anion channels (I-Cl), using tetraethylammonium chloride and CsCl, showed that CO2 also stimulated I-CL and dramatically altered its relaxation kinetics. Within the timeframe of CO2 action at the membrane, no significant effect was observed on cytosolic pH, measured using the fluorescent dye 2',7'-bis-(2-carboxyethyl)-5,6-carboxyflourescein (BCECF) and ratio fluorescence microphotometry. These results are broadly consistent with the pattern of guard-cell response to abscisic acid, and indicate that guard cells control both anion and K+ channels to achieve net solute loss in CO2. By contrast with the effects of abscisic acid, however, the data indicate that CO2 action is not mediated through changes in cytosolic pH and thereby implicate new and, as yet, unidentified pathway(s) for channel regulation in the guard cells.

KEYWORDS: ABSCISIC- ACID, CYTOSOLIC-FREE CALCIUM, ELECTRICAL CHARACTERISTICS, FUSICOCCIN ACTION, PLASMA-MEMBRANE, PROTEIN PHOSPHATASE, SIGNAL-TRANSDUCTION, STOMATAL CLOSURE, TRANSPORT, VOLTAGE

263

Bremer, D.J., J.M. Ham, and C.E. Owensby. 1996. Effect of elevated atmospheric carbon dioxide and open-top chambers on transpiration in a tallgrass prairie. *Journal of Environmental Quality 25(4):691-701.*

Increasing concentrations of atmospheric carbon dioxide (CO2) may influence plant-water relations in natural and agricultural ecosystems. A tallgrass prairie near Manhattan, KS, was exposed to elevated atmospheric CO2 using open-top chambers (OTCs). Heat balance sap Bow gauges were used to measure transpiration in ironweed [Vernonia baldwini var. interior (Small) Schub.], a C-3 forb, and on individual grass culms of big bluestem (Andropogon gerardii Vitman) and indiangrass [Sorghastrum nutans (L.) Nash], both C-4 grasses, in each

of three treatments: (i) CE (chamber enriched, 2x ambient CO2); (ii) CA (chamber ambient, no CO2 enrichment); and (iii) NC (no chamber, no CO2 enrichment). Sap Bow data were coupled with measurements of stomatal conductance, plant/canopy resistance, and whole- chamber evapotranspiration (ET) to determine the effect of elevated CO2 on water use at different scales. Because of frequent rainfall during the study, all data were collected under well-watered conditions, Comparisons of CE and CA showed that sap Bow was reduced by 33% in ironweed, 18% in big bluestem, and 22% in indiangrass under CO2 enrichment. Whole- chamber ET was reduced by 23 to 27% under CO2 enrichment. Comparisons of CA and NC showed that the environmental effect of the OTCs caused a 21 to 24% reduction in transpiration, Stomatal conductance decreased from 7.9 to 3.6 mm s(-1) in big bluestem and from 5.3 to 3.2 mm s(-1) in indiangrass under CO2 enrichment. Soil water was consistently highest under elevated CO2, reflecting the large reductions in transpiration, During sap flow measurements, whole-plant stomatal resistance to water vapor Bur in big bluestem increased from 103 to 194 s m(-1) under elevated CO2.

KEYWORDS: CO2, FLOW, PHOTOSYNTHESIS, RESPONSES, WATER RELATIONS

264

Bremer, D.J., J.M. Ham, C.E. Owensby, and A.K. Knapp. 1998. Responses of soil respiration to clipping and grazing in a tallgrass prairie. *Journal of Environmental Quality 27(6):1539-1548.*

Soil-surface CO2 flux (F-s) is an important component in prairie C budgets. Although grazing Is common in grasslands, its effects on F-s have not been well documented. Three clipping treatments: (i) early-season clipping (EC); (ii) full- season clipping (FC); and (iii) no clipping (NC); which represented two grazing strategies and a control, were applied to plots in a tallgrass prairie in northeastern Kansas, USA. Measurements of F-s were made with a portable gas-exchange system at weekly to monthly intervals for 1 yr. Concurrent measurements of soil temperature and volumetric soil water content at 0.1 m were obtained with dual-probe heat-rapacity sensors. Measurements of F-s also were obtained in grazed pastures. F-s ranged annually from 8.8 x 10(-3) mg m(-2) s(-1) during the winter to 0.51 mg m(-2) s(-1) during the summer, following the patterns of soil temperature and canopy growth and phenology. Clipping typically reduced F-s 21 to 49% by the second day after clipping despite higher soil temperatures in clipped plots. Cumulative annual F-s were 4.94 4.04, and 4.11 kg m(-2) yr(-1) in NC, EC, and FC treatments, respectively; thus, clipping reduced annual F-s by 17.5%. Differences in F-s between EC and FC were minimal, suggesting that different grazing strategies had little additional impact on annual F-s. Daily F-s in grazed pastures was 20 to 37% less than F-s in ungrazed pastures. Results suggest that grazing moderates F-s during the growing season by reducing canopy photosynthesis and slowing translocation of carbon to the rhizosphere.

KEYWORDS: ANDROPOGON-GERARDII, ATMOSPHERIC CO2, CARBON, ELEVATED CO2, EXCHANGE, FLUXES, PANICUM-VIRGATUM, PLANT, ROOT RESPIRATION, TEMPERATE GRASSLAND

265

Briones, G.L., P. Varoquaux, Y. Chambroy, J. Bouquant, G. Bureau, and B. Pascat. 1992. Storage of common mushroom under controlled atmospheres. *International Journal of Food Science and Technology 27(5):493-505.*

The effect of controlled atmosphere (CA) on the shelf-life of the common mushroom (Agaricus bisporus) was assessed using six parameters correlated with its commerical qualities. Low CO2 concentrations (up to 2.5%) reduced brown discolouration compared to the control in air. Higher CO2 concentrations enhanced both internal and external browning. Low O2 concentrations reduced growth of micro-organisms, including pseudomonads. Respiration rate, when the mushrooms are placed again in normal air, is proportional to CO2 concentration during storage suggesting that CO2 exhibits a phytotoxic effect on mushrooms. A lower mannitol content was noted in mushrooms stored under CA than those stored in air (control). Mushrooms stored in a 5% CO2 atmosphere for 7 days did not break their veil but their texture was very soft and spongy. Texture losses decreased when CO2 concentrations increased.

KEYWORDS: AGARICUS-BISPORUS

266

Brioua, A.H., and C.T. Wheeler. 1994. Growth and nitrogen-fixation in alnus-glutinosa (L) gaertn under carbon-dioxide enrichment of the root atmosphere. *Plant and Soil 162(2):183-191.*

The effects of aeration of the N-free rooting medium with elevated CO2 on (a) acetylene reduction by perlite-grown plants and (b) N-2-fixation and long-term growth of nutrient solution- grown plants were determined for nodulated Alnus glutinosa (L.) Gaertn. In the former experiments, roots of intact plants were incubated in acetylene in air in darkened glass jars for 3 hr, followed by a further 3 hr incubation period in air enriched with CO2 (0-5%). During incubation, the CO2 content of the jars increased by 0.17% per hour due to respiration of the root system, so that the CO2 content at 3 hr was 0.5%. Additional enrichment of the rooting medium gas-phase with CO2 equivalent to 1.1% and 1.75% CO2 of the gas volume significantly increased nitrogenase activity (ethylene production) by 55% and 50% respectively, while enrichment with greater than 2.5% CO2 decreased activity. In contrast, ethylene production by control plants, where CO2 was not added to the assay jars, decreased by 8% over the assay period. In long-term growth experiments, nodulated roots of intact Alnus glutinosa plants were sealed into jars containing N-free nutrient solution (pH 6.3) and aerated with air, or air containing elevated levels of CO2 (1.5% and 5%). Comparison of the appearance of CO2-treated with air treated plants suggested that 1.5% CO2 stimulated plant growth. However, at harvest after 5 or 6 weeks variability between plants masked the significance of differences in plant dry weight. A significant increase of 33% in total nitrogen of plants aerated with 1.5% CO2, compared with air-treated plants, was demonstrated, broadly in line with the short-term increase in acetylene reducing activity observed following incubations with similar CO2 concentrations. Shoot dry weight was not affected significantly by long-term exposure to 5% CO2, the main effect on growth being a 20% reduction in dry weight of the root system, possibly through inhibition of root system respiration. However, in contrast to the inhibitory effects of high CO2 on acetylene reduction there was no significant effect on the amounts of N-2 fixed.

KEYWORDS: ACETYLENE-REDUCTION, CO2- ENRICHMENT, METABOLISM, N2 FIXATION, NODULATION, NODULE DEVELOPMENT, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHYSIOLOGY, PISUM-SATIVUM, RESPIRATION

267

Britz, S.J., D.T. Krizek, D.R. Lee, W.G. Harris, W.E. Hungerford, and W.A. Bailey. 1993. Soybean growth under microwave-powered lamps, high-irradiance- discharge lamps, or solar-radiation at ambient or elevated co2. *Plant Physiology 102(1):141.*

268

Brklacich, M., P. Curran, and D. Brunt. 1996. The application of agricultural land rating and crop models to CO2 and climate change

issues in Northern regions: The Mackenzie Basin case study. *Agricultural and Food Science in Finland 5(3):351-365.*

The Mackenzie Basin in northwestern Canada covers approximately 1.8 million km(2) and extends from 52 degrees N to 70 degrees N. Much of the Basin is currently too cool and remote from markets to support a viable agricultural sector, but the southern portion of the Basin has the physical potential to support commercial agriculture. This case study employed agricultural land rating and crop models to estimate the degree to which a CO2-induced global warming might alter the physical potential for commercial agriculture throughout the Basin. The two climate change scenarios considered in this analysis would relax the current constraints imposed by a short and cool frost-free season, but without adaptive measures, drier conditions and accelerated crop development rates were estimated to offset potential gains stemming from elevated CO2 levels and warmer temperatures. In addition to striving for a better understanding of the extent to which physical constraints on agriculture might be modified by climate change, there is a need to expand the research context and to consider the capacity of agriculture to adapt to altered climates.

KEYWORDS: CANADA

269

Broadmeadow, M.S.J., J. Heath, and T.J. Randle. 1999. Environmental limitations to O-3 uptake - Some key results from young trees growing at elevated CO2 concentrations. *Water, Air, and Soil Pollution 116(1-2):299-310.*

Elevated carbon dioxide concentrations and limited water supply have been shown to reduce the impact of ozone pollution on the growth and physiology of Quercus petraea in a long-term factorial experiment. These responses can be explained by observed reductions in stomatal conductance, and thus potential ozone exposure of 28% and 40% for CO2 and drought treatments respectively. However, parameterisation of a stomatal conductance model for Quercus robur and Fagus sylvatica grown under ambient and elevated CO2 concentrations in a separate experiment has demonstrated that elevated CO2 also reduces the responsiveness of stomata to both saturation deficit (LAVPD) and soil moisture deficit (psi) in beech, and to a lesser extent, in oak. Season-long model simulations of ozone fluxes suggest that LAVPD and psi conductance parameters derived at ambient CO2 concentrations will lead to these fluxes being underestimated by 24% and 2% for beech and oak respectively at 615 ppm CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FOREST TREES, GAS-EXCHANGE, OZONE UPTAKE, PLANTS, SENSITIVITY, SITCHENSIS BONG CARR, STOMATAL RESPONSE

270

Brooks, G.L., and J.B. Whittaker. 1998. Responses of multiple generations of Gastrophysa viridula, feeding on Rumex obtusifolius, to elevated CO2. *Global Change Biology 4(1):63-75.*

Rumex obtusifolius plants and three generations of the tri- voltine leaf beetle Gastrophysa viridula were simultaneously exposed to elevated CO2 (600 ppm) to determine its effect on plant quality and insect performance. This exposure resulted in a reduction in leaf nitrogen, an increase in the C/N ratio and lower concentrations of oxalate in the leaves than in ambient air (350 ppm). Despite these changes in food quality, the effect of elevated CO2 on larvae of Gastrophysa viridula over three generations was minimal. However, the effect of CO2 did differ slightly between the generations of the insect. For the first generation, the results obtained were different from many of the published results in that elevated CO2 had no measurable effects on performance, except that third instar larvae showed compensatory feeding. Food quality, including leaf nitrogen content, declined over time in material grown in both ambient and elevated CO2. The results obtained for the second generation were similar to the first except that first instar larvae showed reduced relative growth rate in elevated CO2. Development time from hatching to pupation decreased over each generation, probably as a result of increasing temperatures. Measurements of adult performance showed that fecundity at the end of the second generation was reduced relative to the first, in line with the reduction in food quality. In addition at the end of the second generation, but not at the end of the first generation, adult females in elevated CO2 laid 30% fewer eggs per day and the eggs laid were 15% lighter than those in ambient conditions. These lighter eggs, coupled with no effect of elevated CO2 on growth during the third generation, meant that the larvae were consistently smaller in elevated CO2 during this generation. These results offer further insights into the effect that elevated CO2 will have on insect herbivores and provide a more detailed basis for population predictions.

KEYWORDS: CARBON DIOXIDE, DIETARY NITROGEN, GAS-EXCHANGE, GROWTH, JUNONIA-COENIA, LARVAE, LEPIDOPTERA, MANDUCA-SEXTA CATERPILLARS, NUTRITIONAL ECOLOGY, PERFORMANCE

271

Brooks, G.L., and J.B. Whittaker. 1999. Responses of three generations of a xylem-feeding insect, Neophilaenus lineatus (Homoptera), to elevated CO2. *Global Change Biology 5(4):395-401.*

A population of the xylem-feeding spittlebug, Neophilaenus lineatus, on blocks of natural vegetation transferred to large hemispherical chambers was studied over two generations with continuous exposure to elevated CO2 (600 ppm). The third generation was transferred from the blocks to potted Juncus squarrosus to enable measurements of fecundity. The principal food plant throughout was Juncus squarrosus. Survival of the nymphs was reduced by more than 20% in elevated CO2 relative to ambient (350 ppm) in both years of the main experiment. Elevated CO2 also delayed development by one or more nymphal instars in each year. Fecundity was not significantly affected. The C/N ratio of whole Juncus leaves was increased in elevated CO2 and the transpiration rates of the plants were reduced. These changes may have been responsible for the effect of elevated CO2 on spittlebug performance. However, other factors such as plant architecture and microclimate may also be important.

KEYWORDS: CICADELLIDAE, FLUID, GROWTH, HOMALODISCA-COAGULATA, LEAFHOPPER, PERFORMANCE, PREFERENCE, RUMEX, SAP, SPITTLEBUG

272

Brooks, J.R., L.B. Flanagan, N. Buchmann, and J.R. Ehleringer. 1997. Carbon isotope composition of boreal plants: Functional grouping of life forms. *Oecologia 110(3):301-311.*

We tested the hypothesis that life forms (trees, shrubs, forbs, and mosses; deciduous or evergreen) can be used to group plants with similar physiological characteristics. Carbon isotope ratios (delta(13)C) and carbon isotope discrimination (Delta) were used as functional characteristics because delta(13)C and Delta integrate information about CO2 and water fluxes, and so are useful in global change and scaling studies. We examined delta(13)C values of the dominant species in three boreal forest ecosystems: wet Picea mariana stands, mesic Populus tremuloides stands, and dry Pinus banksiana stands. Life form groups explained a significant fraction of the variation in leaf carbon isotope composition; seven life-form categories explained 50% of the variation in delta(13)C and 42% of the variation in Delta and 52% of the variance

not due to intraspecific genetic differences (n=335). The life forms were ranked in the following order based on their values: evergreen trees<deciduous trees=evergreen and deciduous shrubs=evergreen forbs<deciduous forbs=mosses. This ranking of the life forms differed between deciduous (Populus) and evergreen (Pinus and Picea) ecosystems. Furthermore, life forms in the Populus ecosystem had higher discrimination values than life forms in the dry Pinus ecosystem; the Picea ecosystem had intermediate Delta values. These correlations between Delta and life form were related to differences in plant stature and leaf longevity. Shorter plants had lower Delta values than taller plants, resulting from reduced light intensity at lower levels in the forest. After height differences were accounted for, deciduous leaves had higher discrimination values than evergreen leaves, indicating that deciduous leaves maintained higher ratios of intracellular to ambient CO2 (c(i)/c(a)) than did evergreen leaves in a similar environment within these boreal ecosystems. We found the same pattern of carbon isotope discrimination in a year with above-average precipitation as in a year with below-average precipitation, indicating that environmental fluctuations did not affect the ranking of life forms. Furthermore, plants from sites near the northern and southern boundaries of the boreal forest had similar patterns of discrimination. We concluded that life forms are robust indicators of functional groups that are related to carbon and water fluxes within boreal ecosystems.

KEYWORDS: C-13, COMMUNITIES, CONSEQUENCES, DISCRIMINATION, FOREST, MODEL, PHOTOSYNTHESIS, TEMPERATURE, TRANSPIRATION, WATER-USE EFFICIENCY

273

Brooks, J.R., L.B. Flanagan, G.T. Varney, and J.R. Ehleringer. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO2 within boreal forest canopies. *Tree Physiology 17(1):1-12.*

We compared vertical gradients in leaf gas exchange, CO2 concentrations, and refixation of respired CO2 in stands of Populus tremuloides Michx., Pinus banksiana Lamb. and Picea mariana (Mill.) B.S.P. at the northern and southern boundaries of the central Canadian boreal forest. Midsummer gas exchange rates in Populus tremuloides were over twice those of the two conifer species, and Pinus banksiana rates were greater than Picea mariana rates. Gas exchange differences among the species were attributed to variation in leaf nitrogen concentration. Despite these differences, ratios of intercellular CO2 to ambient CO2 (c(i)/c(a)) were similar among species, indicating a common balance between photosynthesis and stomatal conductance in boreal trees. At night, CO2 concentrations were high and vertically stratified within the canopy, with maximum concentrations near the soil surface. Daytime CO2 gradients were reduced and concentrations throughout the canopy were similar to the CO2 concentration in the well-mixed atmosphere above the canopy space. Photosynthesis had a diurnal pattern opposite to the CO2 profile, with the highest rates of photosynthesis occurring when CO2 concentrations and gradients were lowest. After accounting for this diurnal interaction, we determined that photosynthesizing leaves in the understory experienced greater daily CO2 concentrations than leaves at the top of the canopy. These elevated CO2 concentrations were the result of plant and soil respiration. We estimated that understory leaves in the Picea mariana and Pinus banksiana stands gained approximately 5 to 6% of their carbon from respired CO2.

KEYWORDS: ATMOSPHERE, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, PLANTS, RATIOS, SEEDLINGS, SPATIAL VARIATION, STOMATAL CONDUCTANCE, TEMPERATURE, USE EFFICIENCY

274

Brooks, P.D., D.H. Campbell, K.A. Tonnessen, and K. Heuer. 1999. Natural variability in N export from headwater catchments: snow cover controls on ecosystem N retention. *Hydrological Processes 13(14-15):2191-2201.*

The causes of natural variability in catchment scale N export need to be understood and quantified before the effects of increased N deposition in high elevation catchments can be evaluated. This study evaluates controls on the size of the leachable soil N pool concurrent with the spring hydrologic flush that is primarily responsible for the transport of N to surface water. In high elevation catchments in the western United States, sources of N during this snowmelt flush include both atmospheric N deposition stored in the snowpack until melt and mobile soil N pools, and sinks are dominated by biogeochemical processes that occur in soil under snow cover. Because soil processes may serve either as a source or sink for N, controls on the amount of inorganic N leached from soil during the snowmelt period were evaluated in the major landscape types in four catchments in Colorado. Measurements of leached N were inversely related to measurements of over-winter CO2 flux at all sites, indicating that N was immobilized in soil heterotrophic biomass. Because over-winter soil heterotrophic activity is controlled primarily by the depth and timing of snow accumulation, the importance of these plot scale measurements to catchment scale N export were evaluated using a long-term record of winter precipitation, N deposition, and N export from Loch Vale in Rocky Mountain National Park. This data set identified a strong, linear relationship (r(2) = 0.68) between catchment scale N retention and winter snow cover, consistent with subnivean, soil based controls on the mobile N pool identified at the plot scale. These results indicate that the winter snow pack is the major control both on hydrologic N export and on soil source/sink relationships for N concurrent with this transport mechanism. The effect of winter snow cover on the fate of both atmospheric and soil N needs to be considered when evaluating potential the effects of increased N deposition on either terrestrial or aquatic ecosystems in seasonally snow-covered watersheds. In these systems, changes in surface water chemistry are likely to occur in high deposition, snow-covered sites during low snow years before terrestrial vegetation is affected.

KEYWORDS: ALPINE TUNDRA, CO2, COLORADO, FLUX, FOREST, FRONT RANGE, INORGANIC NITROGEN, NITROGEN MINERALIZATION, NIWOT RIDGE, SATURATION

275

Brown, K.R. 1991. Carbon-dioxide enrichment accelerates the decline in nutrient status and relative growth-rate of Populus tremuloides Michx seedlings. *Tree Physiology 8(2):161-173.*

Changes in growth dynamics and mineral nutrient concentrations were measured in Populus tremuloides Michx., trembling aspen, grown for 100 days following germination in atmospheres containing 350 or 750-mu-l l-1 CO2. Seedlings were fertilized with nitrogen (N) at concentrations of 15.5 mM (high-N), 1.55 mM (medium-N), or 0.155 mM (low-N). Initially, relative growth rates were enhanced by CO2 enrichment in each N regime, but the effects did not persist. In plants grown in high-N or medium-N, foliar concentrations of Ca and Mg decreased in response to CO2 enrichment. During the 100-day study, whole-plant concentrations of N and P decreased in all treatments. The decreases in mineral nutrient concentrations over time were accelerated in CO2-enriched plants and accompanied the disappearance of the CO2-induced growth enhancement. It is concluded that the depression of relative growth rates often associated with long-term CO2 enrichment of plants may result from decreases in plant nutrient status.

276

Brown, R.A., and N.J. Rosenberg. 1999. Climate change impacts on

the potential productivity of corn and winter wheat in their primary United States growing regions. *Climatic Change 41(1):73-107.*

We calculate the impacts of climate effects inferred from three atmospheric general circulation models (GCMs) at three levels of climate change severity associated with change in global mean temperature (GMT) of 1.0, 2.5 and 5.0 degrees C and three levels of atmospheric CO2 concentration ([CO2]) - 365 (no CO2 fertilization effect), 560 and 750 ppm - on the potential production of dryland winter wheat (Triticum aestivum L.) and corn (Zea mays L.) for the primary (current) U.S. growing regions of each crop. This analysis is a subset of the Global Change Assessment Model (GCAM) which has the goal of integrating the linkages and feedbacks among human activities and resulting greenhouse gas emissions, changes in atmospheric composition and resulting climate change, and impacts on terrestrial systems. A set of representative farms was designed for each of the primary production regions studied and the Erosion Productivity Impact Calculator (EPIC) was used to simulate crop response to climate change. The GCMs applied were the Goddard Institute of Space Studies (GISS), the United Kingdom Meteorological Transient (UKTR) and the Australian Bureau of Meteorological Research Center (BMRC), each regionalized by means of a scenario generator (SCENGEN). The GISS scenarios have the least impact on corn and wheat production, reducing national potential production for corn by 6% and wheat by 7% at a GMT of 2.5 degrees C and no CO2 fertilization effect, the UKTR scenario had the most severe impact on wheat, reducing production by 18% under the same conditions; BMRC had the greatest negative impact on corn, reducing produc tion by 20%. A GMT increase of 1.0 degrees marginally decreased corn and wheat production. Increasing GMT had a detrimental impact on both corn and wheat production, with wheat production suffering the greatest losses. Decreases for wheat production at GMT 5.0 and [CO2] = 365 ppm range from 36% for the GISS to 76% for the UKTR scenario. Increases in atmospheric [CO2] had a positive impact on both corn and wheat production. AT GMT 1.0, an increase in [CO2] to 560 ppm resulted in a net increase in corn and wheat production above baseline levels (from 18 to 29% for wheat and 2 to 5% for corn). Increases in [CO2] help to offset yield reductions at higher GMT levels; in most cases, however, these increases are not sufficient to return crop production to baseline levels.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2, EPIC MODEL, EROSION, METHODOLOGY, RESPONSES, SENSITIVITY, SIMULATION, VARIABILITY, YIELD

277

Brown, S., C.A.S. Hall, W. Knabe, J. Raich, M.C. Trexler, and P. Woomer. 1993. Tropical forests - their past, present, and potential future- role in the terrestrial carbon budget. *Water, Air, and Soil Pollution 70(1-4):71-94.*

In this paper we review results of research to summarize the state-of-knowledge of the past, present, and potential future roles of tropical forests in the global C cycle. In the pre- industrial period (ca. 1850), the flux from changes in tropical land use amounted to a small C source of about 0.06 Pg yr-1. By 1990, the C source had increased to 1.7 +/- 0.5 Pg yr-1. The C pools in forest vegetation and soils in 1990 was estimated to be 159 Pg and 216 Pg, respectively. No concrete evidence is available for predicting how tropical forest ecosystems am likely to respond to CO2 enrichment and/or climate change. However, C sources from continuing deforestation are likely to overwhelm any change in C fluxes unless land management efforts become more aggressive. Future changes in land use under a "business as usual" scenario could release 41-77 Pg C over the next 60 yr. Carbon fluxes from losses in tropical forests may be lessened by aggressively pursued agricultural and forestry measures. These measures could reduce the magnitude of the tropical C source by 50 Pg by the year 2050. Policies to mitigate C losses must be multiple and concurrent, including reform of forestry, land tenure, arid agricultural policies, forest protection, promotion of on-farm forestry, and establishment of plantations on non-forested lands. Policies should support improved agricultural productivity, especially replacing non-traditional slash-and-burn agriculture with more sustainable and approaches.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CYCLE, DIOXIDE, LAND-USE CHANGE, MODEL, NET, ORGANIC-MATTER, PRIMARY PRODUCTIVITY, SINKS

278

Bryant, J., G. Taylor, and M. Frehner. 1998. Photosynthetic acclimation to elevated CO2 is modified by source : sink balance in three component species of chalk grassland swards grown in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment 21(2):159-168.*

Artificial chalk grassland swards were exposed to either ambient air or air enriched to 600 mu mol mol(-1) CO2, using free-air CO2 enrichment technology, and subjected to an 8 week simulated grazing regime. After 14 months of treatment, ribulose-1,5-bisphosphate carboxylase (Rubisco) activity (V- c,V-max) and electron transport mediated ribulose-1,5- bisphosphate (RuBP) regeneration capacity (J(max)), estimated from leaf gas exchange, were significantly lower in fully expanded leaves of Anthyllis vulneraria L. (a legume) and Sanguisorba minor Scop, grown in elevated CO2. After a change in source:sink balance brought about by defoliation, photosynthetic capacity was fully restored in A. vulneraria and S. minor, but acclimation continued in the grass Bromopsis erecta (Hudson) Fourr. Changes in net photosynthesis (P-n) with growth at elevated CO2 ranged from a 1.6% reduction in precut leaves of A. vulneraria to a 47.1% stimulation in postcut leaves of S. minor. Stomatal acclimation was observed in leaves of A. vulneraria (reduced stomatal density) and B. erecta (reduced stomatal conductance). The results are discussed in terms of whole-plant resource-use optimization and chalk grassland community competitive interactions at elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BIOCHEMISTRY, C-3, GAS-EXCHANGE, LEAVES, METABOLISM, PLANT GROWTH, STOMATAL DENSITY

279

Bucher, J.B., D.P. Tarjan, R.T.W. Siegwolf, M. Saurer, H. Blum, and G.R. Hendrey. 1998. Growth of a deciduous tree seedling community in response to elevated CO2 and nutrient supply. *Chemosphere 36(4-5):777-782.*

In a FACE experiment, one year old alder, ash, beech, and oak seedlings were planted together in tubs containing calcareous sandy alluvial soil with or without a slow release NPK- fertilizer, and exposed to ambient and elevated CO2 concentrations (360 and 600 mu l mol(-1)) for 20 weeks. In addition to the fertilizer, all tubs received N-15-ammonium nitrate as a marker. Elevated CO2 significantly increased biomass production in alder, but had no effect on oak and ash. In beech, due to disease and mortality in all treatments, any possible effects were obscured. The addition of fertilizer had no effect on biomass production in alder, but increased production in oak and ash significantly. In oak a treatment synergism may be present. The non-appearance of a synergistic CO2 and fertilizer effect in alder may be explained by a fertilizer induced reduction of the N-fixing root-nodule biomass concurrent with a switch of the N-assimilation from atmospheric N to soil N supply, as the delta(15)N measurements in the leaves of alder as opposed to oak indicate. Although elevated CO2 resulted in a significant biomass increase in alder, it did not lead to an appreciable increase in the proportional presence of the species as measured on total plant biomass in the tub. Increasing the nutrient supply in the soil, however,

did lead to appreciable gains in the proportional presence of oak and ash.

KEYWORDS: ATMOSPHERE, ECOSYSTEMS, ENRICHMENT

280

Buchi, R., M. Bachmann, and F. Keller. 1998. Carbohydrate metabolism in source leaves of sweet basil (Ocimum basilicum L.), a starch-storing and stachyose-translocating labiate. *Journal of Plant Physiology 153(3-4):308-315.*

Sweet basil (Ocimum basilicum L.) is an annual aromatic herb that grows in temperate to tropical regions. During ontogeny, the predominant non-structural carbohydrate of mature leaves of plants older than 2 months after sowing was starch (up to 66 mg.g fresh weight(-1)), followed by the raffinose family oligosaccharides (RFO) and galactinol (metabolic RFO precursor) (both up to 1.0 mg.g fresh weight(-1)). Sucrose was only a minor component (up to 0.5 mg.g fresh weight(-1)). All of these carbohydrates displayed distinct diurnal patterns with an increase during the day and a decrease during the night. Starch concentrations showed the most pronounced diurnal change, with an almost tenfold increase during the day. A treatment combining leaf excision, continuous illumination, and high CO2 levels was aimed at elevating the leaf carbohydrate status and resulted in an increase of the concentrations of starch and soluble carbohydrates (mainly glucose and fructose) of 60- and 12-fold, respectively. We conclude that sweet basil leaves use starch as their main storage carbohydrate, and nor RFO or sucrose. Phloem exudates were collected by the classical EDTA- method and analyzed by HPLC. More than 85 % of the translocated sugars were RFO (mainly stachyose) and only 5 % sucrose. To study the tissue compartmentation of stachyose synthesis in source leaves, leaf pieces and mesophyll protoplasts isolated from them were compared. Stachyose and its anabolic enzyme, stachyose synthase, were totally absent from mesophyll protoplasts. Likewise, isolated mesophyll protoplasts were not capable of photosynthesizing [C-14]stachyose from (CO2)-C-14, even after GO min, whereas osmotically stressed leaf pieces were. These results are in support of the current polymer tray model of symplastic phloem loading of stachyose, which states that stachyose is synthesized in the intermediary cells of minor vein phloem.

KEYWORDS: ACCUMULATION, AJUGA- REPTANS L, CELL, COMPARTMENTATION, CUCUMIS-MELO L, DIURNAL PATTERN, MESOPHYLL, MINOR-VEIN ANATOMY, PROTOPLASTS, RAFFINOSE FAMILY OLIGOSACCHARIDES

281

Buchmann, N., J.R. Brooks, K.D. Rapp, and J.R. Ehleringer. 1996. Carbon isotope composition of C-4 grasses is influenced by light and water supply. *Plant, Cell and Environment 19(4):392-402.*

The carbon isotope composition of C-4 grasses has the potential to be used as an indicator of changes in the isotopic composition and concentration of atmospheric CO2, especially for climate reconstruction. The usefulness of C-4 grasses far this purpose hinges on the assumption that their photosynthetic discrimination against C-13 remains constant in a wide range of environmental conditions. We tested this assumption by examining the effects of light and water stress on the carbon isotope composition of C-4 grasses using different biochemical subtypes (NADP-ME, NAD-ME, PCK) in glasshouse experiments. We grew 14 different C-4 grass species in four treatments: sun- watered, sun-drought, shade-watered and shade-drought. Carbon isotope discrimination (Delta) rarely remained constant. In general, Delta values were lowest in sun-watered grasses, greater for sun-drought plants and even higher for plants of the shade-watered treatment. The highest Delta values were generally found in the most stressed grasses, the shade-drought plants. Grasses of the NADP-ME subtype were the least influenced by a change in environmental variables, followed by PCK and NAD-ME subtypes. Water availability affected the carbon isotope discrimination less than light limitation in PCK and NAB-ME subtypes, but similarly in NADP-ME subtypes. In another experiment, we studied the effect of increasing light levels (150 to 1500 mu mol photons m(-2) s(-1)) on the Delta values of 18 well-watered C-4 grass species. Carbon isotope discrimination remained constant until photon flux density (PFD) was less than 700 mu mol photons m(-2) s(-1). Below this light level, Delta values increased with decreasing irradiance for all biochemical subtypes. The change in Delta was less pronounced in NADP-ME and PCK than in NAD-ME grasses. Grasses grown in the field and in the glasshouse showed a similar pattern. Thus, caution should be exercised when using C-4 plants under varying environmental conditions to monitor the concentration or carbon isotopic composition of atmospheric CO2 in field/glasshouse studies or climate reconstruction.

KEYWORDS: ATMOSPHERIC CO2, C-4 PLANTS, CO2 ASSIMILATION, DISCRIMINATION, IRRADIANCE, LEAF CONDUCTANCE, LEAVES, NUTRITION, PARTIAL-PRESSURE, PHOTOSYNTHESIS

282

Buddendorfjoosten, J.M.C., and E.J. Woltering. 1994. Components of the gaseous environment and their effects on plant-growth and development in-vitro. *Plant Growth Regulation 15(1):1-16.*

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, CONTROLLED INVITRO ENVIRONMENT, DENOVO SHOOT REGENERATION, ETHYLENE INHIBITORS, PHOTOSYNTHETIC CHARACTERISTICS, STAGE-II MICROPROPAGATION, STRAWBERRY PLANTLETS, TISSUE-CULTURE, VOLATILE EMISSIONS

283

Bugbee, B., B. Spanarkel, S. Johnson, O. Monje, and G. Koerner. 1994. Co2 crop growth enhancement and toxicity in wheat and rice. *Life Sciences and Space Research XXV (3) 14(11):257-267.*

The effects of elevated CO2 on plant growth are reviewed and the implications for crop yields in regenerative systems are discussed. There is considerable theoretical and experimental evidence indicating that the beneficial effects of CO2 are saturated at about 0.12% CO2 in air. However, CO2 can easily rise above 1% of the total gas in a closed system, and we have thus studied continuous exposure to CO2 levels as high as 2%. Elevating CO2 from 340 to 1200 mu mol mol(-1) can increase the seed yield of wheat and rice by 30 to 40%; unfortunately, further CO2 elevation to 2500 mu mol mol(-1) (0.25%) has consistently reduced yield by 25% compared to plants grown at 1200 mu mol mol(-1); fortunately, there was only an additional 10% decrease in yield as the CO2 level was further elevated to 2% (20,000 mu mol mol(-1)). Yield increases in both rice and wheat were primarily the result of increased number of heads per m(2), with minor effects on seed number per head and seed size. Yield increases were greatest in the highest photosynthetic photon flux. We used photosynthetic gas exchange to analyze CO2 effects on radiation interception, canopy quantum yield, and canopy carbon use efficiency. We were suprised to find that radiation interception during early growth was not improved by elevated CO2. As expected, CO2 increased quantum yield, but there was also a small increase in carbon use efficiency. Super-optimal CO2 levels did not reduce vegetative growth, but decreased seed set and thus yield. The reduced seed set is not visually apparent until final yield is measured. The physiological mechanism underlying CO2 toxicity is not yet known, but elevated CO2 levels (0.1 to 1% CO2) increase ethylene synthesis in some plants and ethylene is a potent inhibitor of seed set in wheat.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-4 PLANTS, ELEVATED CO2, ETHYLENE RELEASE, LONG-TERM

EXPOSURE, PHOTOSYNTHETIC INHIBITION, QUANTUM YIELD, SOURCE-SINK RELATIONS, WATER-STRESS

284

Bugmann, H. 1997. Sensitivity of forests in the European Alps to future climatic change. *Climate Research 8(1):35-44.*

Model-based assessments of the impacts of climatic change on forests are confronted with 2 fundamental problems: first, there is a considerable uncertainty in the predictions of future climate; second, the forest models contain simplified parameterizations of ecological processes. In this paper, the sensitivity of forest models to different steady-state climate scenarios, to different process formulations and to different assumptions on the transient behaviour of climate is studied. The effects of 3 scenarios of climatic change and the behaviour of 5 forest gap models of the FORECE/FORCLIM family are compared at sites along an elevational gradient in the European Alps. A wide variety of species compositions may be obtained al a given site depending on the scenario of future climate. At some sites all future forests differ radically from today's forest, suggesting that these current forests are highly sensitive to climatic change. At some sites, the results of the 5 forest models differ strongly with respect to species composition and carbon storage when subjected to the same climate scenario, showing that the models need to be improved in order to arrive at reliable and robust parameterizations of abiotic and biotic influences in forest models. When comparing the effects of step, Linear, and sigmoid changes of the mean climatic parameters over 100 yr, it becomes evident that the type of change modelled is not crucial because the climatic change proceeds fast compared to the successional dynamics. It is concluded that simulations of the possible effects of climatic change on forests should be considered as sensitivity tests, not as predictions. Given the current uncertainties in atmospheric sciences (climate predictions) and in ecology (modelling of long-term forest dynamics), the most promising research strategy is to compare the effects of several climate scenarios and the projections of several forest models to arrive at slate-of-the-art ecological impact assessments.

KEYWORDS: CO2, MATTER, MODEL

285

Bukhov, N.G., N. Boucher, and R. Carpentier. 1997. Aftereffect of short-term heat shock on photosynthetic reactions in barley leaves. *Russian Journal of Plant Physiology 44(4):526-532.*

Effects of preheating 8- to 10-day-old barley (Hordeum vulgare L.) leaves at 40-46 degrees C on oxygen evolution, chlorophyll fluorescence, and photoacoustic signals were examined. Preheating of leaves at 40 degrees C led to a threefold decrease in the initial slope of the light-response curve of photosynthesis and a marked enhancement of the nonphotochemical quenching of chlorophyll fluorescence, which indicates a drastic increase in the nonradiative dissipation of absorbed light quanta. The maximum photosynthetic activity attained at saturating light and elevated CO2 concentration was suppressed by this heat treatment by no more than 30%. The photochemical activity of PS LT reaction centers in dark-adapted leaves also decreased to the same extent after the heat treatment. In preheated leaves, strong light pulses increased the photobaric component of the photoacoustic signal (measured at 35 Hz) instead of suppressing the signal. The magnitude of the rise- phase of the photoacoustic signal increased with the preheating temperature. An enhancement of the photoacoustic signal induced by strong light pulses was also observed in leaves in which the normal photosynthetic process was disturbed by feeding them methylviologen. It is concluded that the short-term heating of leaves impairs photochemical conversion of light quanta in reaction centers of PS II due to an increase in the magnitude of the proton gradient across the thylakoid membrane. This indicates that dark reactions of photosynthesis in preheated leaves cannot efficiently use the ATP and reduced NADP formed in the course of photosynthetic electron transport.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, INDUCTION, OXYGEN EVOLUTION, PHOTOINHIBITION, PHOTOSYSTEM-I, RESOLUTION, SPINACH LEAVES, STIMULATION, TEMPERATURE

286

Bunce, J.A. 1992. Light, temperature and nutrients as factors in photosynthetic adjustment to an elevated concentration of carbon-dioxide. *Physiologia Plantarum 86(1):173-179.*

The short-term stimulation of the net rate of carbon dioxide exchange of leaves by elevated concentrations of CO2 usually observed in C3 plants sometimes does not persist. Experiments were conducted to test whether the patterns of response to the environment during growth were consistent with the hypotheses that photosynthetic adjustment to elevated CO2 concentration is due to (1) feedback inhibition or (2) nutrient stress. Soybean [Glycine max (L.) Merr. cv. Williams] and sugar beet (Beta vulgaris L. cv. Mono Hye-4) were grown from seed at 350 and 700 mul l-1 CO2, at 20 and 25-degrees-C, at a photon flux density of 0.5 and 1.0 mmol m-2 s-1 and with three nutrient regimes until the third trifoliolate leaf of soybean or the sixth leaf of sugar beet had finished expanding. Net rates Of CO2 exchange of the most recently expanded leaves were then measured at both 350 and 700 mul l-1 CO2. Plants grown at the elevated CO2 concentration had net rates of leaf CO2 exchange which were reduced by 33% in sugar beet and 23% in soybean when measured at 350 mul l-1 CO2 and when averaged over all treatments. Negative photosynthetic adjustment to elevated CO2 concentration was not greater at 20 than at 25-degrees-C, was not greater at a photon flux density of 1.0 than at 0.5 mmol M- 2 s-1 and was not greater with limiting nutrients. Furthermore, in soybean, negative photosynthetic adjustment could be induced by a single night at elevated CO2 concentration, with net rates of CO2 exchange the next day equal to those of leaves of plants grown from seed at the elevated concentration Of CO2. These patterns do not support either the feedback-inhibition or the nutrient-stress hypothesis of photosynthetic adjustment to elevated concentrations of CO2.

KEYWORDS: CO2, COTTON, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, LONG-TERM EXPOSURE, PLANTS, RESPONSES

287

Bunce, J.A. 1992. Stomatal conductance, photosynthesis and respiration of temperate deciduous tree seedlings grown outdoors at an elevated concentration of carbon-dioxide. *Plant, Cell and Environment 15(5):541-549.*

Seedlings of temperate deciduous tree species were grown outdoors at ambient and at an elevated concentration of carbon dioxide to examine how aspects of their gas exchange would be altered by growth at elevated carbon dioxide concentration. Leaf conductances to water vapour and net carbon dioxide exchange rates were determined periodically near midday. Whole- plant carbon dioxide efflux rates in darkness were also determined. The stomatal conductance of leaves of plants grown and measured at 700 cm3 m-3 carbon dioxide did not differ from that of plants grown and measured at 350 cm3 m-3 in Malus domestica, Quercus prinus and Quercus robur at any measurement time. In Acer saccharinum, lower conductances occurred for plants grown and measured at elevated carbon dioxide concentration only at measurement temperatures above 33- degrees-C. Photosynthetic adjustment to elevated carbon dioxide concentration was evident only in Q. robur. All species examined had lower rates of dark respiration per unit of mass when grown and measured at elevated carbon dioxide concentration.

KEYWORDS: CO2 CONCENTRATION, FORESTS, RESPONSES

288

Bunce, J.A. 1993. Effects of doubled atmospheric carbon-dioxide concentration on the responses of assimilation and conductance to humidity. *Plant, Cell and Environment 16(2):189-197.*

Experiments were performed to determine if growth at elevated partial pressure of CO2 altered the sensitivity of leaf water vapour conductance and rate of CO2 assimilation to the leaf-to- air difference in the partial pressure of water vapour (DELTAw). Comparisons were made between plants grown and measured at 350 and 700 muPa Pa-1 partial pressures of CO2 for amaranth, soybean and sunflower grown in controlled environment chambers, soybean grown outdoors in pots, and orchard grass grown in field plots. In amaranth, soybean and orchard grass, both the absolute and the relative sensitivity of conductance to DELTAw at the leaf surface were less in plants grown and measured at the elevated CO2. In sunflower, there was no change in the sensitivity of conductance to DELTAw for the two CO2 partial pressures. Tests in soybeans and amaranth showed that the change in sensitivity resulted from elevated CO2 during the measurement of the DELTAw response. Assimilation rate of CO2 was not altered by DELTAw in amaranth, which has C4 metabolism. In sunflower, the assimilation rate of plants grown and measured at elevated CO2 was insensitive to DELTAw, consistent with the response of assimilation rate to intercellular CO2 partial pressure in the prevailing range. In soybean, the sensitivity of assimilation rate to DELTAw was not different between CO2 treatments, in contrast to what would be expected from the response of assimilation rate to intercellular CO2 partial pressure.

KEYWORDS: ARBUTUS-UNEDO, EFFICIENCY, LEAVES, MIDDAY DEPRESSION, NET CO2 UPTAKE, PHOTOSYNTHETIC CAPACITY, SUNFLOWER, TRANSPIRATION, VAPOR-PRESSURE DEFICIT, WATER-STRESS

289

Bunce, J.A. 1993. Growth, survival competition, and canopy carbon-dioxide and water-vapor exchange of 1st year alfalfa at an elevated co2 concentration. *Photosynthetica 29(4):557-565.*

Alfalfa was grown in field plots at the current CO2 concentration (350 mumol mol-1 = c350) and at 350 mumol mol-1 above the current concentration (= c700). Alfalfa and weed growth, and canopy water vapor (E) and carbon dioxide exchange (F) were determined for the first year. Alfalfa yield summed for the three harvests.in the first year was greater for the c700 treatment in two of the years studied, but significantly less in a third year. Weed growth was unaffected. Survival of alfalfa plants was greater at c700 for years in which there was substantial mortality, even when yield was not increased by the c700 treatment. In spite of a persistent reduction in leaf conductance to water vapor (g(l)), total canopy conductance (g(c)) to water vapor did not differ between CO2 treatments when averaged over years, because of compensating changes in canopy leaf area. CO2 efflux (F) at night per unit of ground area was consistently less in the c700 treatment even when daytime CO2 uptake was higher. Hence the periodic harvesting of alfalfa crops does not necessarily allow elevated CO2 to cause persistent growth stimulation nor reduced water use.

KEYWORDS: ENRICHMENT, PHOTOSYNTHESIS, PLANTS, RESPIRATION, RESPONSES, TEMPERATURE, WHEAT, YIELD

290

Bunce, J.A. 1995. The effect of carbon-dioxide concentration on respiration of growing and mature soybean leaves. *Plant, Cell and Environment 18(5):575-581.*

Soybean plants were grown continuously at 350 and 700cm(3)m(-3) CO2 at constant temperature, Respiration rates of third trifoliolate leaves were measured at the growth CO2 concentration for the whole dark period from 5d before through to 5d after full area expansion, The short-term response of respiration rate to the measurement CO2 concentration was also determined at each age, Respiration rates per unit of dry mass declined with age and were significantly less at a given age or RGR in leaves grown and measured at the elevated CO2. The difference in respiration rate was largest in mature leaves and resulted from the different measurement CO2 concentrations, The respiratory costs of the tissue synthesis, estimated from the elemental composition of the tissue, did not differ substantially between CO2 treatments, The response of respiration rate to carbon dioxide concentration was not strongly affected by the form of nitrogen supplied. Maintenance respiration calculated by subtracting growth respiration from total respiration was negative in rapidly growing leaves for both CO2 treatments, This indicates that CO2 efflux in the dark does not accurately reflect the average 24h rate of energy expenditure on growth and maintenance for soybean leaves.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, EFFLUX, ELEVATED CO2, GROWTH, INHIBITION, MAINTENANCE, PLANT RESPIRATION, TERM

291

Bunce, J.A. 1995. Effects of elevated carbon-dioxide concentration in the dark on the growth of soybean seedlings. *Annals of Botany 75(4):365-368.*

Previous work has shown that elevated carbon dioxide (CO2) concentrations in the dark reversibly reduce the rate of CO2 efflux from soybeans. Experiments were performed exposing soybean plants continually to concentrations of 350 or 700 cm(3) m(-3) for 24 h d(-1), or to 350 during the day and 700 cm(3) m(-3) at night, in order to determine the importance of the reduced rate of dark CO2 efflux for plant growth. High CO2 applied only at night conserved carbon and increased dry mass during initial growth compared with the constant 350 cm(3) m-3 treatment. Long-term net assimilation rate was increased by high CO2 in the dark, without any increase in daytime leaf photosynthesis. However, leaf area ratio was reduced by the dark CO2 treatment to values equal to those of plants continually exposed to the higher concentration. From days 14- 21, leaf area was less for the elevated night-time CO2 treatment than for either the constant 350 or 700 cm(3) m(-3) treatments. For the day 7-21-period, relative growth rate was significantly reduced by the high night CO2 treatment compared with the 350 cm(3) m(-3) continuous treatment. The results indicate that some functionally significant component of respiration was reduced by the elevated CO2 concentration in the dark.

KEYWORDS: RESPIRATION, TEMPERATURE

292

Bunce, J.A. 1995. Long-term growth of alfalfa and orchard grass plots at elevated carbon dioxide. *Journal of Biogeography 22(2-3):341-348.*

Alfalfa (Medicago sativa L.) and orchard grass (Dactylis glomerata L.) plots were exposed to ambient or ambient plus 350 cm(3) m(-3) carbon dioxide concentrations at Beltsville, Maryland, U.S.A. Replicate plots were established in different years and fertilized annually. We report here data for the second and third years after establishment. There has been no increase in the yearly production of either species at the elevated carbon dioxide concentration after the first season. In orchard grass, reduced growth at the high carbon dioxide concentration in the spring offset growth stimulation in the summer. Weed growth was consistently increased by carbon dioxide enrichment, but weed species composition was unaffected. Leaf photosynthetic capacity was reduced by the high carbon dioxide concentration in both crop species, as was leaf nitrogen

content. Canopy carbon dioxide uptake was slightly higher in the elevated carbon dioxide treatments, consistent with the increased weed growth. In alfalfa, elevated carbon dioxide significantly reduced canopy carbon dioxide efflux at night for the same daytime uptake rate and temperature. The growth conversion efficiency estimated from elemental composition of the tissue was not substantially altered by carbon dioxide treatment in either crop species, indicating little effect of carbon dioxide treatment on the respiratory cost of tissue synthesis. Canopy conductance to water vapour averaged 23% less at high than at low carbon dioxide in the orchard grass plots, and 14% less in the alfalfa plots. This was consistent with the smaller short-term response of conductance to carbon dioxide concentration in the alfalfa plots. It is concluded that a warm climate and fertile soil does not guarantee a persistent response of production to elevated carbon dioxide concentration in these herbaceous perennial species.

KEYWORDS: ATMOSPHERIC CO2, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSPIRATION, TREES

293

Bunce, J.A. 1996. Growth at elevated carbon dioxide concentration reduces hydraulic conductance in alfalfa and soybean. *Global Change Biology 2(2):155-158.*

Hydraulic conductances of alfalfa and soybean plants grown in controlled environment chambers at the current ambient carbon dioxide concentration and at twice the current ambient concentration were determined from measurements of transpiration rate and leaf and stem water potentials in the growth conditions. Growth at elevated carbon dioxide concentration reduced both transpiration rate and hydraulic conductance from the soil to the leaf in both species. Hydraulic conductance from the soil to the base of the stem was also lower at elevated carbon dioxide in soybean, but not alfalfa. These measurements identified the stem to leaf hydraulic pathway as a major target of the carbon dioxide effect in both species. The conductance of excised stem segments was much less in plants grown at elevated carbon dioxide in soybeans.

KEYWORDS: ATMOSPHERIC CO2, WATER RELATIONS

294

Bunce, J.A. 1997. Variation in growth stimulation by elevated carbon dioxide in seedlings of some C-3 crop and weed species. *Global Change Biology 3(1):61-66.*

Seven C-3 crop and three C-3 weed species were grown from seed at 360 and at 700 cm(3) m(-3) carbon dioxide concentrations in a controlled environment chamber to compare dry mass, relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and photosynthetic acclimation at ambient and elevated carbon dioxide. The dry mass at the final harvest at elevated carbon dioxide relative to that at ambient carbon dioxide was highly correlated with the RGR at the lower carbon dioxide concentration. This relationship could be quite common, because it does not require that species differ in the response of RGR or photosynthesis to elevated carbon dioxide, and holds even when species differ moderately in these responses. RGR was also measured for a limited period at the end of the experiment to determine relationships with leaf gas exchange measured at this time. Relative increases in RGR at elevated carbon dioxide at this time were more highly correlated with the relative increase in NAR at elevated carbon dioxide than with the response of LAR. The amount of acclimation of photosynthesis was a good predictor of the relative increase in NAR at elevated carbon dioxide, and the longterm increase in photosynthesis in the growth environment. No differences between crops and weeds or between cool and warm climate species were found in the responses of growth or photosynthetic acclimation to elevated carbon dioxide.

KEYWORDS: CO2- ENRICHMENT

295

Bunce, J.A. 1998. Effects of environment during growth on the sensitivity of leaf conductance to changes in humidity. *Global Change Biology 4(3):269-274.*

Soybeans (Glycine max) and grain amaranth (Amaranthus hypochondriacus) were grown at a range of temperatures, carbon dioxide concentrations and light conditions in controlled environment chambers, and the response of leaf conductance to water vapour to changes in humidity was then measured under a standard set of conditions. The sensitivity of conductance was analysed in terms of (i) the absolute sensitivity of conductance to changes in leaf to air water vapour pressure difference (LAVPD), (ii) the sensitivity of conductance relative to the absolute value of conductance, and (iii) the slope of the relationship between conductance and an index incorporating assimilation rate, carbon dioxide concentration and relative humidity. The sensitivity of conductance varied substantially with growth conditions for all three analyses in both species. The growth temperature of 25 degrees C increased the sensitivity of conductance by all three measures compared with growth at 20 or 30 degrees C in amaranth, with little difference between 25 and 30 degrees C in soybean. Growth at elevated carbon dioxide decreased sensitivity in amaranth by all three measures, and decreased the absolute but not the relative sensitivity in soybean. Growth at reduced photon flux density and growth at high stand density reduced sensitivity in amaranth by all three measures. In soybean, growth at high stand density reduced sensitivity by all three measures, but growth at low photon flux density increased the relative sensitivity. The sensitivity of leaf conductance to changes in humidity varied by a factor of two or more with growth environment by all measures of sensitivity in both the C3 and the C4 species.

KEYWORDS: C-3, CARBON DIOXIDE, CO2, MODEL, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION

296

Bunce, J.A. 1998. The temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide in wheat and barley. *Journal of Experimental Botany 49(326):1555-1561.*

The temperature dependencies of the solubility of carbon dioxide and oxygen in water and the temperature dependency of the kinetic characteristics of the ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco) enzyme result in the short-term stimulation of photosynthesis with a doubling of carbon dioxide from 350 to 700 mu mol mol(-1) usually decreasing from about 90% at 30 degrees C to about 25% at 10 degrees C at high photon flux. In field-grown wheat and barley, the expected values at 30 degrees C were observed, but also values as high as 60% at 10 degrees C. The much larger than expected stimulation at cool temperatures in these species also occurred in plants grown at 15 degrees C, but not at 23 degrees C in controlled environment chambers. Gas exchange analysis indicated that an unusually high diffusive limitation was not an explanation for the large response. Assessment of the apparent in vivo specificity of Rubisco by determining the carbon dioxide concentration at which carboxylation equalled carbon dioxide release from oxygenation, indicated that growth at row temperatures altered the apparent enzyme specificity in these species compared to these species grown at the warmer temperature. Inserting the observed specificities into a biochemical model of photosynthesis indicated that altered Rubisco specificity was consistent with the observed rates of assimilation. Whether altered apparent Rubisco specificity is caused by altered stoichiometry of photorespiration or an actual change in enzyme specificity, the results indicate that the temperature dependence of the stimulation of photosynthesis by elevated carbon dioxide may vary greatly with species and with prior exposure to low temperatures.

KEYWORDS: ASSIMILATION, CO2/O2 SPECIFICITY, EXCHANGE, LIGHT, PLANTS, RESPIRATION, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

297

Bunce, J.A., K.B. Wilson, and T.N. Carlson. 1997. The effect of doubled CO2 on water use by alfalfa and orchard grass: Simulating evapotranspiration using canopy conductance measurements. *Global Change Biology 3(1):81-87.*

Alfalfa and orchard grass crops were grown at ambient and twice ambient carbon dioxide concentrations in field plots for several years in Beltsville, MD, using semiopen chambers. Canopy conductances throughout many days were determined from water vapour exchange measurements, and indicated significant reductions in canopy conductance to water vapour at elevated carbon dioxide in both species. However, recognizing that the artificial ventilation in the chambers made direct comparisons of evapotranspiration rates questionable, we used a soil- vegetation-atmosphere model to determine what field-scale evapotranspiration rates would have been with natural ventilation. Unlike the 'omega' approach, the model used allowed feedbacks between the canopy and the atmosphere, such that, for example, canopy conductance responses affected profiles of temperature and water vapour. Simulations indicated that although canopy conductances were lower at elevated carbon dioxide by as much as 20% in alfalfa and 60% in orchard grass, evapotranspiration rates never differed by more than 3% in alfalfa or 8% in orchard grass. Daily totals of evapotranspiration were only 1-2% lower at elevated carbon dioxide in alfalfa, and 2-5% lower in orchard grass. The results are partly explained by the fact that aerodynamic conductances to water vapour were generally smaller than the stomatal conductance, and also by canopy-atmosphere feedback processes which largely compensated for the lower conductance at elevated carbon dioxide by increasing the gradient for evaporation.

KEYWORDS: ASSIMILATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, LEAF, RESPONSES, STOMATAL CONDUCTANCE, TRANSPIRATION

298

Bunce, J.A., and L.H. Ziska. 1996. Responses of respiration to increases in carbon dioxide concentration and temperature in three soybean cultivars. *Annals of Botany 77(5):507-514.*

The purpose of this experiment was to determine how respiration of soybeans may respond to potential increases in atmospheric carbon dioxide concentration and growth temperature. Three cultivars of soybeans (Glycine max L. Merr.), from maturity groups 00, IV, and VIII, were grown at 370, 555 and 740 cm(3) m(-3) carbon dioxide concentrations at 20/15, 25/20, and 31/26 degrees C day/night temperatures. Rates of carbon dioxide efflux in the dark were measured for whole plants several times during exponential growth. These measurements were made at the night temperature and the carbon dioxide concentra:ion at which the plants were grown. For the lowest and highest temperature treatments, the short term response of respiration rate to measurement at the three growth carbon dioxide concentrations was also determined. Elemental analysis of the tissue was used to estimate the growth conversion efficiency. This was combined with the observed relative growth rates to estimate growth respiration. Maintenance respiration was estimated as the difference between growth respiration and total respiration. Respiration rates were generally sensitive to short term changes in the measurement carbon dioxide concentration for plants grown at the lowest, but not the highest carbon dioxide concentration. At all temperatures, growth at elevated carbon dioxide concentrations decreased total respiration measured at the growth concentration, with no significant differences among cultivars. Total respiration increased very little with increasing growth temperature, despite an increase in relative growth rate. Growth respiration was not affected by carbon dioxide treatment at any temperature, but increased with temperature because of the increase in relative growth rare. Values calculated for maintenance respiration decreased with increasing carbon dioxide concentration and also decreased with increasing temperature. Calculated values of maintenance respiration were sometimes zero or negative at the warmer temperatures. This suggests that respiration rates measured in the dark may not have reflected average 24-h rates of energy use. The results indicate that increasing astmospheric carbon dioxide concentration may reduce respiration in soybeans, and respiration may be insensitive to climate warming. (C) 1996 Annals of Botany Company

KEYWORDS: EFFLUX, ELEVATED CO2, ENRICHMENT, GROWTH, INHIBITION, LEAVES, MAINTENANCE REQUIREMENTS, PHOTOSYNTHESIS, PLANT RESPIRATION, WHITE CLOVER

299

Bunce, J.A., and L.H. Ziska. 1998. Decreased hydraulic conductance in plants at elevated carbon dioxide. *Plant, Cell and Environment 21(1):121-126.*

Previous work indicated that long-term exposure to elevated carbon dioxide levels can reduce hydraulic conductance in some species, but the basis of the response was not determined, In this study, hydraulic conductance was measured at concentrations of both 350 and 700 cm(3) m(-3) carbon dioxide for plants grown at both concentrations, to determine the reversibility of the response, In Zea mays and Amaranthus hypochondriacus, exposure to the higher carbon dioxide concentration for several hours reduced whole-plant transpiration rate by 22-40%, without any consistent change in leaf water potential, indicating reversible reductions in hydraulic conductance at elevated carbon dioxide levels, Hydraulic conductance in these species grown at both carbon dioxide concentrations responded similarly to measurement concentration of carbon dioxide, indicating that the response was reversible, In Glycine max, which in earlier work had shown a long-term decrease in hydraulic conductance at elevated carbon dioxide levels, and in Abutilon theophrasti, no short- term changes in hydraulic conductance with measurement concentration of carbon dioxide were found, despite lower transpiration rates at elevated carbon dioxide, In G. max and Medicago sativa, growth at high dew-point temperature reduced transpiration rate and decreased hydraulic conductance, The results indicate that both reversible and irreversible decreases in hydraulic conductance can occur at elevated carbon dioxide concentrations, and that both could be responses to reduced transpiration rate, rather than to carbon dioxide concentration itself.

KEYWORDS: ATMOSPHERIC CO2, CONDUCTIVITY, COTTON PLANTS, ENRICHMENT, GRASSLAND, GROWTH, RESISTANCE, STRESS, WATER TRANSPORT, YIELD

300

Burton, A.J., G.P. Zogg, K.S. Pregitzer, and D.R. Zak. 1997. Effect of measurement CO2 concentration on sugar maple root respiration. *Tree Physiology 17(7):421-427.*

Accurate estimates of root respiration are crucial to predicting belowground C cycling in forest ecosystems. Inhibition of respiration has been reported as a short-term response of plant tissue to elevated measurement [CO2]. We sought to determine if measurement [CO2] affected root respiration in samples from mature sugar maple (Acer saccharum Marsh.) forests and to assess possible errors associated with root respiration measurements made at [CO2]s lower than that typical of the soil atmosphere. Root respiration was measured as both CO2 production and O-2 consumption on excised fine roots (less than or equal to 1.0 mm) at [CO2]s ranging from 350 to > 20,000 mu l l(-1).

Root respiration was significantly affected by the [CO2] at which measurements were made for both CO2 production and O-2 consumption. Root respiration was most sensitive to [CO2] near and below normal soil concentrations (< 1500 mu l l(-1)). Respiration rates changed little at [CO2]s above 3000 mu l l(-1) and were essentially constant above 6000 mu l l(-1) CO2. These findings call into question estimates of root respiration made at or near atmospheric [CO2], suggesting that they overestimate actual rates in the soil. Our results indicate that sugar maple root respiration at atmospheric [CO2] (350 mu l l(-1)) is about 139% of that at soil [CO2]. Although the causal mechanism remains unknown, the increase in root respiration at low measurement [CO2] is significant and should be accounted for when estimating or modeling root respiration. Until the direct effect of [CO2] on root respiration is fully understood, we recommend making measurements at a [CO2] representative of, or higher than, soil [CO2]. In all cases, the [CO2] at which measurements are made and the [CO2] typical of the soil atmosphere should be reported.

KEYWORDS: CARBON-DIOXIDE CONCENTRATIONS, ENRICHMENT, FOREST ECOSYSTEMS, HIGHER-PLANTS, INTRACELLULAR PH, MAINTENANCE RESPIRATION, PINE PLANTATIONS, SHORT- TERM, SOIL O2, TEMPERATURE

301

Burton, P.J., and S.G. Cumming. 1995. Potential effects of climatic-change on some western canadian forests, based on phenological enhancements to a patch model of forest succession. *Water, Air, and Soil Pollution 82(1-2):401-414.*

We enhanced the forest patch model, Zelig, to explore the implications of 2xCO(2) climate change scenarios on several forest regions in British Columbia and Alberta, Canada. In addition to the processes and phenomena commonly represented in individual-based models of forest stand dynamics, we added some species-specific phenology and sire-specific frost events. The consideration of bud-break heat sum requirements, growing season limits, and chilling requirements for the induction of dormancy and cold hardiness slightly improved the ability of Zelig to predict the present composition of B.C. forests. Simulations of the predicted effects of future climatic regimes (based on the averaged predictions of four general circulation models) include some major shifts in equilibrial, forest composition and productivity. Lowland temperate coastal forests are predicted to be severely stressed because indigenous species will no longer have their winter chilling requirements met. High-elevation coastal forests are expected to increase in productivity, while interior subalpine forests are expected to remain stable in productivity but will gradually be replaced by species currently characteristic of lower elevations. Dry, interior low-elevation forests in southern B.C. are likely to persist relatively unchanged, while wet interior forests are expected to support dramatic increases in yield, primarily by western hemlock. Northern interior sub-boreal forests are likewise expected to increase in productivity through enhanced growth of lodgepole pine. Conversely, the precipitous collapse of spruce stands in the true boreal forests of northeastern B.C. is expected to be associated with reduced productivity as they are replaced by pine species. Boreal-Cordilleran and Moist Boreal Mixedwood forests in Alberta are less likely to undergo compositional change, while becoming somewhat more productive. We believe these model enhancements to be a significant improvement over existing formulations, but the resulting predictions must still be viewed with caution. Model limitations include: (1) the current inability of climate models to predict future variation in monthly temperature and precipitation; (2) sparse information on the phenological behaviour of several important tree species; and (3) a poor understanding of the degree to which growth is constrained by different suboptimal climatic events.

KEYWORDS: BUDBURST, CARBON, CO2, FREEZING RESISTANCE, GLOBAL CLIMATE, SCALE, SENSITIVITY, TREES

302

Buse, A., and J.E.G. Good. 1996. Synchronization of larval emergence in winter moth (Operophtera brumata L) and budburst in pedunculate oak (Quercus robur L) under simulated climate change. *Ecological Entomology 21(4):335-343.*

1. The hypothesis that a 3 degrees C elevation in temperature and doubled CO2 concentration would have no effect on the synchronization of winter moth egg hatch with budburst in oak was tested by comparing the separate and interactive effects of ambient and elevated (+ 3 degrees C) temperature and ambient and elevated (doubled to 340 p.p.m.) CO2 in eight experimental Solardomes. In addition, an outdoor control was compared with the ambient temperature/CO2 treatment combination. 2. Elevated temperature accelerated darkening (preceding egg hatch by about 5-10 days) and hatching of eggs developing off the trees; elevated CO2 had no effect. The same effects were observed in eggs developing on the trees. 3. Within treatments, date of egg hatch was the same on trees with early or late budburst. 4. Egg darkening and budburst were closely synchronized at both ambient and elevated temperatures. 5. Both eggs and trees required fewer cumulative heat units (day degrees > 4 degrees C), for hatching and budburst, respectively, at ambient than elevated temperatures. The requirements in the outdoor control treatment were similar to those in the ambient Solardome treatment. 6. Egg hatch between 10 and 25 degrees C, on a temperature gradient in the laboratory, required a constant number of heat units; fewer were required below 10 degrees C. 7. Elevated temperatures, in the Solardomes and the field, delayed adult emergence from the pupae. 8. The results suggest that a general increase in temperature with climatic change would not affect the closeness of the synchronization between egg hatch of winter moth and budburst of oak.

KEYWORDS: BRITAIN, GEOMETRIDAE, LEPIDOPTERA, OUTBREAKS, SCOTLAND, SITKA SPRUCE, TEMPERATURE, TREES

303

Buse, A., J.E.G. Good, S. Dury, and C.M. Perrins. 1998. Effects of elevated temperature and carbon dioxide on the nutritional quality of leaves of oak (Quercus robur L.) as food for the Winter Moth (Operophtera brumata L.). *Functional Ecology 12(5):742-749.*

1. Pedunculate Oak trees were grown in ambient and elevated temperatures and CO2. Leaves were fed to Winter Moth caterpillars reared either in constant conditions or with the trees (caged or on-tree). 2. Caterpillars in constant conditions ate the same mass and produced the same mass of faeces whether fed elevated or ambient temperature leaves. However, less was assimilated from elevated leaves, resulting in lighter pupae and fewer, lighter eggs. 3. Caterpillars in constant conditions ate more and produced more faeces when fed elevated CO2 leaves than when fed ambient CO2 leaves, but the mass assimilated and pupal mass were unchanged. 4. Caged caterpillars reared with the trees from which they were fed had constant pupal mass in all treatments, but pupated earlier at elevated temperature. Pupal mass was also unaffected when caterpillars fed on the trees. 5. Nitrogen was reduced in both elevated temperature and elevated CO2 leaves. Increased fibre in the former prevented increased consumption and resulted in reduced pupal mass and fecundity. Reduced fibre in the latter allowed increased consumption, resulting in pupae of normal mass. 6. Despite the clear effect of nutrient quality, experiments rearing caterpillars and trees together suggest that anticipated climatic change will have no nutritional effect on Winter Moth development.

KEYWORDS: ATMOSPHERIC CO2, DECIDUOUS TREES, FEEDING RESPONSE, GROWTH, HERBIVORE INTERACTIONS, HOST PLANTS, INSECT PERFORMANCE, LYMANTRIA-DISPAR, NITROGEN, PLANT-RESPONSES

304

Bytnerowicz, A. 1996. Physiological aspects of air pollution stress in forests. *Phyton-Annales Rei Botanicae 36(3):15-22.*

Air pollutants, such as ozone, sulfur dioxide, nitrogen compounds and others, affect health of forests in Europe and North America. Gaseous air pollutants enter plants mainly through stomata, although transcuticular transport can also be important for some pollutants. Toxic effects of pollutants depend on their effective dose that is proportional to pollutant ambient concentration and plant stomatal conductance. Mechanisms of air pollution toxicity are very complex and depend on various physiological and biochemical properties of plants. These mechanisms (including formation of free radicals) are still poorly understood. In addition, physiological responses of forest plants to air pollution stress can be modified by various biotic (e.g., insects, pathogens, mycorrhizae associations, genetic variation) and abiotic (e.g., increasing CO2 concentrations, ultraviolet-B radiation, nitrogen deposition, nutrient deficiencies, drought) factors. An example of air pollution effects on forest trees may be responses of ponderosa pine seedlings to elevated concentrations of ozone in the Sierra Nevada. Various physiological changes caused by ozone (e.g., lowered net photosynthesis, altered carbon allocation, deterioration of photosynthetic pigments, etc.) have led to the reduced growth and biomass of the seedlings.

KEYWORDS: ATMOSPHERIC OZONE, B RADIATION, NITROGEN, PINE, SULFUR, VEGETATION

305

Cairney, J.W.G., and A.A. Meharg. 1999. Influences of anthropogenic pollution on mycorrhizal fungal communities. *Environmental Pollution 106(2):169-182.*

Mycorrhizal fungi form complex communities in the root systems of most plant species and are thought to be important in terrestrial ecosystem sustainability. We have reviewed the literature relating to the influence of the major forms of anthropogenic pollution on the structure and dynamics of mycorrhizal fungal communities. All forms of pollution have been reported to alter the structure of below-ground communities of mycorrhizal fungi to some degree, although the extent to which such changes will be sustained in the longer term is at present not clear. The major limitation to predicting the consequences of pollution-mediated changes in mycorrhizal fungal communities to terrestrial habitats is our limited understanding of the functional significance of mycorrhizal fungal diversity. While this is identified as a priority area for future research, it is suggested that, in the absence of such data, an understanding of pollution-mediated changes in mycorrhizal mycelial systems in soil may provide useful indicators for sustainability of mycorrhizal systems.

KEYWORDS: ABIES L KARST, ELEVATED ATMOSPHERIC CO2, LANDFILL SITE RESTORATION, LOBLOLLY-PINE SEEDLINGS, NORWAY SPRUCE, RED SPRUCE SEEDLINGS, SCOTS PINE, SIMULATED ACID-RAIN, TAEDA L SEEDLINGS, VESICULAR-ARBUSCULAR MYCORRHIZAE

306

Callaway, R.M., E.H. Delucia, E.M. Thomas, and W.H. Schlesinger. 1994. Compensatory responses of co2 exchange and biomass allocation and their effects on the relative growth-rate of ponderosa pine in different co2 and temperature regimes. *Oecologia 98(2):159-166.*

Increases in the concentration of atmospheric carbon dioxide may have a fertilizing effect on plant growth by increasing photosynthetic rates and therefore may offset potential growth decreases caused by the stress associated with higher temperatures and lower precipitation. However, plant growth is determined both by rates of net photosynthesis and by proportional allocation of fixed carbon to autotrophic tissue and heterotrophic tissue. Although CO2 fertilization may enhance growth by increasing leaf-level assimilation rates, reallocation of biomass from leaves to stems and roots in response to higher concentrations of CO2 and higher temperatures may reduce whole-plant assimilation and offset photosynthetic gains. We measured growth parameters, photosynthesis, respiration, and biomass allocation of Pinus ponderosa seedlings grown for 2 months in 2 x 2 factorial treatments of 350 or 650mu bar CO2 and 10/25-degrees-C or 15/30-degrees-C night/day temperatures. After 1 month in treatment conditions, total seedling biomass was higher in elevated CO2, and temperature significantly enhanced the positive CO2 effect. However, after 2 months the effect of CO2 on total biomass decreased and relative growth rates did not differ among CO2 and temperature treatments over the 2-month growth period even though photosynthetic rates increased almost-equal-to 7% in high CO2 treatments and decreased almost- equal-to 10% in high temperature treatments. Additionally, CO2 enhancement decreased root respiration and high temperatures increased shoot respiration. Based on CO2 exchange rates, CO2 fertilization should have increased relative growth rates (RGR) and high temperatures should have decreased RGR. Higher photosynthetic rates caused by CO2 fertilization appear to have been mitigated during the second month of exposure to treatment conditions by a almost-equal-to 3% decrease in allocation of biomass to leaves and a almost-equal-to 9% increase in root:shoot ratio. It was not clear why diminished photosynthetic rates and increased respiration rates at high temperatures did not result in lower RGR. Significant diametrical and potentially compensatory responses of CO2 exchange and biomass allocation and the lack of differences in RGR of ponderosa pine after 2 months of exposure of high CO2 indicate that the effects of CO2 fertilization and temperature on whole-plant growth are determined by complex shifts in biomass allocation and gas exchange that may, for some species, maintain constant growth rates as climate and atmospheric CO2 concentrations change. These complex responses must be considered together to predict plant growth reactions to global atmospheric change, and the potential of forest ecosystems to sequester larger amounts of carbon in the future.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GREAT-BASIN, LEAF-AREA, RESPIRATION, SEEDLINGS, SOIL, VEGETATION, WATER-USE EFFICIENCY, WOODY-PLANTS

307

Campbell, B.D., W.A. Laing, D.H. Greer, J.R. Crush, H. Clark, D.Y. Williamson, and M.D.J. Given. 1995. Variation in grassland populations and species and the implications for community responses to elevated CO2. *Journal of Biogeography 22(2-3):315-322.*

Variation in plant characteristics and potential responses to CO2 was measured in controlled environments for a set of different forage plant species and populations. The response of the plants to elevated CO2 was strongly determined by temperature. The greatest responses to elevated CO2 were observed at warm temperatures in C3 species with high potential growth rates at these temperatures. This suggests that the community composition could change most rapidly in response to CO2 in warm seasons, with the greatest positive responses to CO2 occurring in warm-season active species. This prediction was tested in a microcosm experiment. The prediction was confirmed under well-watered conditions but water stress resulted in an ingress of C4 species with low potential responses to CO2. The results suggest that variation between populations and species must be considered when predicting grassland community responses to CO2, and that it is inappropriate to ignore compositional changes in communities when modelling CO2 effects on pasture production. Given the importance of temperature in determining CO2 responsiveness, phenology may prove to be a useful attribute in plant functional type analyses of community responses to CO2.

KEYWORDS: ENRICHMENT

308

Campbell, B.D., D.M.S. Smith, and G.M. McKeon. 1997. Elevated CO2 and water supply interactions in grasslands: A pastures and rangelands management perspective. *Global Change Biology 3(3):177-187.*

Water is a key variable driving the composition and productivity of pastures and rangelands, and many of the ecosystems in these grasslands are highly sensitive to changes in water supply. The possibility that elevated CO2 concentrations may alter plant water relations is therefore particularly relevant to pastures and rangelands, and may have important consequences for grassland ecosystem function, water use, carbon storage and nutrient cycling. The planning of effective research to better understand these changes requires attention to both: (i) gaps in knowledge about CO2 and water interactions, and (ii) knowledge of how precisely the effects of CO2 must be understood in relation to other factors, in order to predict changes in grassland structure and production. A recent microcosm experiment illustrates that non-linear effects of CO2 and water stress could perturb primary production by triggering changes in grassland community composition. The magnitudes of the effects of CO2 on key grassland ecosystems remain to be precisely determined through ecosystem-level experiments. A simplified simulation of the impact of different levels of productivity change in a water- limited Australian rangeland system was conducted by varying effects of CO2 on radiation and water use efficiency. The results indicate that direct effects of CO2 may be moderated at the enterprise scale by accompanying changes in adaptive management by farmers. We conclude that future research should aim to construct quantitative relationships and identify thresholds of response for different grassland systems. The sensitivity of these systems to management (such as grazing pressure) should also be considered when developing integrated predictions of future effects of CO2 on water supply to grassland ecosystems.

KEYWORDS: DESERT ECOSYSTEMS, TALLGRASS PRAIRIE, UNITED-STATES

309

Campbell, W.J. 1997. Intraspecific variation of rubisco and rubisco activase protein levels in tomato leaves grown at elevated CO2 concentration. *Plant Physiology 114(3):1056.*

310

Canadell, J.G., L.F. Pitelka, and J.S.I. Ingram. 1996. The effects of elevated [CO2] on plant-soil carbon below- ground: A summary and synthesis. *Plant and Soil 187(2):391-400.*

We undertake a synthesis of the most relevant results from the presentations at the meeting "Plant-Soil Carbon Below-Ground: The Effects of Elevated CO2" (Oxford-UK, September 1995), many of which are published in this Special Issue. Below-ground responses to elevated [CO2] are important because the capacity of soils for long-term carbon sequestration. We draw the following conclusions: (i) several ecosystems exposed to elevated [CO2] showed sustained increased CO2 uptake at the plot level for many years. A few systems, however, showed complete down-regulation of net CO2 uptake after several years of elevated [CO2] exposure; (ii) under elevated [CO2], a greater proportion of fixed carbon is generally allocated below-ground, potentially increasing the capacity of below- ground sinks; and (iii) some of the increased capacity of these sinks may lead to increased long-term soil carbon sequestration, although strong evidence is still lacking. We highlight the need for more soil studies to be undertaken within ongoing ecosystem-level experiments, and suggest that while some key experiments already established should be maintained to allow long term effects and feedbacks to lake place, more research effort should be directed to mechanisms of soil organic matter stabilization.

KEYWORDS: DIOXIDE, ECOSYSTEMS, GAS-EXCHANGE, GRASSLAND, INCREASING ATMOSPHERIC CO2, NITROGEN, ORGANIC-MATTER, PHOTOSYNTHESIS, RESPONSES, TURNOVER

311

Cannell, M.G.R., and J.H.M. Thornley. 1998. N-poor ecosystems may respond more to elevated [CO2] than N- rich ones in the long term. A model analysis of grassland. *Global Change Biology 4(4):431-442.*

The Hurley Pasture Model was used to examine the short and long-term responses of grazed grasslands in the British uplands to a step increase from 350 to 700 mu mol mol(-1) CO2 concentration ([CO2]) with inputs of 5 or 100 kg N ha(-1) y(- 1). In N-rich grassland, [CO2] doubling quickly increased net primary productivity (NPP), total carbon (C-sys) and plant biomass by about 30%. By contrast, the N-poor grassland underwent a prolonged 'transient', when there was little response, but eventually NPP, C-sys and plant biomass more than doubled. The 'transient' was due to N immobilization and severe depletion of the soil mineral N pool. The large long-term response was due to slow N accumulation, as a result of decreased leaching, decreased gaseous N losses and increased N- 2-fixation, which amplified the CO2 response much more in the N-poor than in the N-rich grassland. It was concluded that (i) ecosystems use extra carbon fixed at high [CO2] to acquire and retain nutrients, supporting the contention of Gifford et al. (1996), (ii) in the long term, and perhaps on the real timescale of increasing [CO2], the response (in NPP, C-sys and plant biomass) of nutrient-poor ecosystems may be proportionately greater than that of nutrient-rich ones, (iii) short-term experiments on nutrient-poor ecosystems may observe only the transient responses, (iv) the speed of ecosystem responses may be limited by the rate of nutrient accumulation rather than by internal rate constants, and (v) ecosystem models must represent processes affecting nutrient acquisition and retention to be able to simulate likely real-world CO2 responses.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ENRICHMENT, FOREST ECOSYSTEMS, GAS-EXCHANGE, GLOBAL CARBON-CYCLE, GROWTH-RESPONSES, PLANT-RESPONSES, ROOT-GROWTH, TERRESTRIAL ECOSYSTEMS

312

Cannell, M.G.R., and J.H.M. Thornley. 1998. Temperature and CO2 responses of leaf and canopy photosynthesis: A clarification using the non-rectangular hyperbola model of photosynthesis. *Annals of Botany 82(6):883-892.*

The responses of C-3 leaf and canopy gross photosynthesis to increasing temperature and CO2 can be readily understood in terms of the temperature and CO2 dependencies of quantum yield (phi(i)) and light-saturated photosynthesis (A(sat)) the two principal parameters in the non-rectangular hyperbola model of photosynthesis. Here, we define these dependencies within the mid-range for C-3 herbaceous plants, based on a review of the literature. Then, using illustrative parameter values, we deduce leaf and canopy photosynthesis responses to temperature and CO, in different environmental conditions (including shifts in the temperature optimum) from the assumed sensitivities of phi(i) and A(sat) to temperature and CO2. We show that: (1) elevated CO2 increases photosynthesis more at warm than at cool temperatures because of the large combined CO2-responses of both phi(i) and A(sat) at high temperatures; (2) elevated CO2 may substantially raise the temperature optimum of photosynthesis at warm temperatures, but not at the cool temperatures which prevail for much of the time at temperate

and high latitudes; (3) large upward shifts in the temperature optimum of canopy gross photosynthesis occur at high irradiances, following the response of A(sat), and are probably important for global carbon fixation; (4) canopy gross photosynthesis shows smaller CO2-temperature interactions than leaf photosynthesis, because leaves in canopies receive lower average irradiances and sep more strongly follow the dependencies of phi(i); and (5) at very low irradiances, the temperature optimum of photosynthesis is low and is raised very little by increasing CO2 .(C) 1998 Annals of Botany Company.

KEYWORDS: C-4 PLANTS, CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, CHLOROPHYLL FLUORESCENCE, CLIMATE CHANGE, DEPENDENCE, EUCALYPTUS-PAUCIFLORA, LIGHT, QUANTUM YIELDS, VASCULAR PLANTS

313

Cannon, R.J.C. 1998. The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology 4(7):785-796.*

Recent estimates for global warming predict increases in global mean surface air temperatures (relative to 1990) of between 1 and 3.5 degrees C, by 2100. The impact of such changes on agricultural systems in mid- to high-latitude regions are predicted to be less severe than in low-latitude regions, and possibly even beneficial, although the influence of pests and diseases is rarely taken into account. Most studies have concluded that insect pests will generally become more abundant as temperatures increase, through a number of inter-related processes, including range extensions and phenological changes, as well as increased rates of population development, growth, migration and overwintering. A gradual, continuing rise in atmospheric CO2 will affect pest species directly (i.e. the CO2 fertilization effect) and indirectly (via interactions with other environmental variables). However, individual species responses to elevated CO2 vary: consumption rates of insect herbivores generally increase, but this does not necessarily compensate fully for reduced leaf nitrogen. The consequent effects on performance are strongly mediated via the host species. Some recent experiments under elevated CO2 have suggested that aphids may become more serious pests, although other studies have discerned no significant effects on sap- feeding homopterans. However, few, if any of these experiments have fully considered the effects on pest population dynamics. Climate change is also considered from the perspective of changes in the distribution and abundance of species and communities. Marked changes in the distribution of well- documented species - including Odonata, Orthoptera and Lepidoptera - in northwestern Europe, in response to unusually hot summers, provide useful indications of the potential effects of climate change. Migrant pests are expected to respond more quickly to climate change than plants, and may be able to colonize newly available crops/habitats. Range expansions, and the removal of edge effects, could result in the increased abundance of species presently near the northern limits of their ranges in the UK. However, barriers to range expansions, or shifts, may include biotic (competition, predation, parasitism and disease), as well as abiotic, factors. Climatic phenomena, ecosystem processes and human activities are interactive and interdependent, making long-term predictions extremely tenuous. Nevertheless, it appears prudent to prepare for the possibility of increases in the diversity and abundance of pest species in the UK, in the context of climate change.

KEYWORDS: BRITISH BUTTERFLY FAUNA, CARBON-DIOXIDE ATMOSPHERES, DECIDUOUS TREES, ELEVATED CO2, ENRICHED CO2 ATMOSPHERES, GLOBAL CHANGE, HERBIVORE INTERACTIONS, JUNONIA-COENIA, LARVAL EMERGENCE, POPULATION-DYNAMICS

314

Cantin, D., M.F. Tremblay, M.J. Lechowicz, and C. Potvin. 1997. Effects of CO2 enrichment, elevated temperature, and nitrogen availability on the growth and gas exchange of different families of jack pine seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 27(4):510-520.*

Many economically important tree species respond positively to an elevated CO2 environment. However, the variability and stability in growth responses among genotypes grown in a global change environment are generally not documented. The present study investigated the differences, at the seedling stage, among 15 maternal families of jack pine (Pinus banksiana Lamb.) in response to an elevated CO2-temperature environment (CO2T) (700 mu L CO2.L-1 with temperatures 4 degrees C higher than in the ambient CO2T environment), with different nitrogen concentrations. While the elevated CO2T did not significantly alter the overall height growth of seedlings, it significantly increased their total biomass, with needle and root biomass being most responsive. Growth in the elevated CO2T resulted in a 24% reduction in the leaf weight ratio as more biomass was allocated to roots. Significant genotypic differences were observed for height, biomass, and water-use efficiency. Generally, most families kept their rank relative to other families, from the ambient to the elevated CO2T. Also, rank correlations between height of families grown in elevated CO2T and height of families at 10 years of age in the field were significant. This result, combined with the stability we observed in family response from the ambient to the elevated CO2T, suggested that jack pine families currently chosen for their fast-growing capacity will probably remain as such in a global change environment, at least during the seedling establishment stage.

KEYWORDS: AGE-AGE CORRELATIONS, ATMOSPHERIC CO2, BLACK SPRUCE SEEDLINGS, CLIMATE CHANGE, EARLY SELECTION, PATTERNS, PHENOTYPIC PLASTICITY, PICEA MARIANA, RESPONSES, X ENVIRONMENT INTERACTIONS

315

Cao, M.K., and F.I. Woodward. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology 4(2):185-198.*

Evaluating the role of terrestrial ecosystems in the global carbon cycle requires a detailed understanding of carbon exchange between vegetation, soil, and the atmosphere. Global climatic change may modify the net carbon balance of terrestrial ecosystems, causing feedbacks on atmospheric CO2 and climate. We describe a model for investigating terrestrial carbon exchange and its response to climatic variation based on the processes of plant photosynthesis, carbon allocation, litter production, and soil organic carbon decomposition. The model is used to produce geographical patterns of net primary production (NPP), carbon stocks in vegetation and soils, and the seasonal variations in net ecosystem production (NEP) under both contemporary and future climates. For contemporary climate, the estimated global NPP is 57.0 Gt C y(-1), carbon stocks in vegetation and soils are 640 Gt C and 1358 Gt C, respectively, and NEP varies from -0.5 Gt C in October to 1.6 Gt C in July. For a doubled atmospheric CO2 concentration and the corresponding climate, we predict that global NPP will rise to 69.6 Gt C y(-1), carbon stocks in vegetation and soils will increase by, respectively, 133 Gt C and 160 Gt C, and the seasonal amplitude of NEP will increase by 76%. A doubling of atmospheric CO2 without climate change may enhance NPP by 25% and result in a substantial increase in carbon stocks in vegetation and soils. Climate change without CO2 elevation will reduce the global NPP and soil carbon stocks, but leads to an increase in vegetation carbon because of a forest extension and NPP enhancement in the north. By combining the effects of CO2 doubling, climate change, and the consequent redistribution of vegetation, we predict a strong enhancement in NPP and carbon stocks of terrestrial ecosystems. This study simulates the possible variation in the carbon

exchange at equilibrium state. We anticipate to investigate the dynamic responses in the carbon exchange to atmospheric CO2 elevation and climate change in the past and future.

KEYWORDS: ATMOSPHERIC CO2, DECOMPOSITION, DYNAMICS, FOREST ECOSYSTEMS, GLOBAL-MODEL, PHOTOSYNTHESIS, PLANT, SIMULATION, SINK, SOIL

316

Cao, W.X., and T.W. Tibbitts. 1997. Starch concentration and impact on specific leaf weight and element concentrations in potato leaves under varied carbon dioxide and temperature. *Journal of Plant Nutrition 20(7-8):871-881.*

Foliar concentrations of starch and major elements, nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), along with specific leaf weight (SLW) were determined in the potato (Solanum tuberosum L.) cvs 'Denali', 'Norland', and 'Russet Burbank' grown for 35 days under CO2 concentrations of 500, 1,000, 1,500 and 2,000 mu mol . mol(-1) at both 16 degrees C and 20 degrees C air temperature. The starch concentration, pooled from the three cultivars, increased with increasing CO, concentration at both 16 degrees C and 20 degrees C and was consistently higher at 16 degrees C than at 20 degrees C. The SLW (g . m(-2)) was positively related to the foliar starch concentration on the basis of leaf area or dry weight. The concentrations of N, P, Ca, and Mg in leaves were negatively related to starch concentration under approximate to 14% starch on a dry weight basis. Above 14% starch, there was no significant relationship between element and starch concentrations. Similar patterns were seen when the SLW and element concentrations were expressed on a starch-free basis. In contrast, the leaf concentration of K was not closely related to the starch concentration because the K concentration was similar at varied CO2 levels. The results of this study indicate that the changes in SLW and concentrations of N, P, Ca, and Mg in potato leaves only partially resulted from the changed starch concentration.

KEYWORDS: CO2- ENRICHMENT, GROWTH, LIFE SUPPORT SYSTEMS, NITROGEN, PHOTOPERIODS, RESPONSES, WHEAT

317

Cao, W., T.W. Tibbitts, and R.M. Wheeler. 1994. Carbon-dioxide interactions with irradiance and temperature in potatoes. *Life Sciences and Space Research XXV (3) 14(11):243-250.*

Separate controlled environment studies were conducted to determine the interaction of CO2 with irradiance and interaction of CO2 with temperature on growth of three potato cultivars. In the first study, an elevated CO2 concentration of 1000 mu mol mol(-1) and an ambient CO2 of 350 mu mol mol(-1) were maintained at the photosynthetic photon fluxes (PPF) of 17 and 34 mol m(-2) d(-1) with 12 h photoperiod, and at the PPF of 34 and 68 mol m(-2) d(-1) with 24 h photoperiod (400 and 800 mu mol m(-2) s(-1) PPF at each photoperiod). Tuber and total dry weights of 90-day old potatoes were significantly increased with CO2 enrichment, but the CO2 stimulation was less with higher PPF and longer photoperiod. Shoot dry weight was affected more by photoperiod than by PPF and CO2 concentrations. The elevated CO2 concentration increased leaf CO2 assimilation rates and decreased stomatal conductance with 12 h photoperiod, but had only a marginal effect with 24 h photoperiod. In the second study, four CO2 concentrations of 500, 1000, 1500 and 2000 mu mol mol(-1) were combined with two air temperature regimes of 16 and 20 degrees C under a 12 h photoperiod. At harvest, 35 days after transplanting, tuber and total dry weights of potatoes reached a maximum with 1000 mu mol mol(-1) CO2 at 16 degrees C, but continued to increase up to 2000 mu mol mol(-1) CO2 at 20 degrees C. Plant growth was greater at 20 degrees C than at 16 degrees C under all CO2 concentrations. At 16 degrees C specific leaf weight increased substantially with increasing CO2 concentrations as compared to 500 mu mol mol(-1) CO2, but increased only slightly at 20 degrees C. This suggests a carbohydrate build-up in the leaves at 16 degrees C temperature that reduces plant response to increased CO2 concentrations. The data in the two studies indicate that a PPF of 34 mol m(-2) d(-1), 20 degrees C temperature, and 1000-2000 mu mol mol(-1) CO2 produces optimal tuber yield in potatoes.

KEYWORDS: 24-H, CO2- ENRICHMENT, GROWTH, LIFE SUPPORT SYSTEMS, PHOTOPERIODS, PHOTOSYNTHESIS, PLANTS, RESPONSES, SOLANUM-TUBEROSUM, SPACE

318

Caporn, S.J.M., A.L. Brooks, M.C. Press, and J.A. Lee. 1999. Effects of long-term exposure to elevated CO2 and increased nutrient supply on bracken (Pteridium aquilinum). *Functional Ecology 13:107-115.*

1. Bracken (Pteridium aquilinum) is an important fern with a global distribution. Little is known of the response of this species to elevated CO2. We investigated the effects of high CO2 (570 compared with 370 mu mol mol(-1)) with and without an increased nutrient supply (a combined N, P, K application) on the growth and physiology of bracken, growing in containers in controlled-environment glasshouses, over two full growing seasons. Results of growth and physiology determinations are reported for the second season. 2. Elevated CO2 had little impact on the growth or allocation of dry mass in bracken. No significant changes were detected in dry mass of the total plant or any of the organs: rhizomes, roots and fronds. In contrast to the small effects of high CO2 the high nutrient treatment caused a three-fold stimulation of total plant dry mass and an increase in the allocation of dry mass to above ground when compared with low nutrient controls. 3. Net photosynthetic rates in saturating light were increased by both high CO2 and nutrient treatments, particularly in spring months (May and June). Growth in elevated CO2 did not cause a down- regulation in light-saturated rates of photosynthesis. The increased carbon gain in the high CO2 treatments was accompanied, in the low-nutrient plants, by higher concentrations of carbohydrates. However, in high-nutrient plants the CO2 treatment did not cause an accumulation of carbohydrates. The absence of a growth response to elevated CO2 in bracken despite significant increases in photosynthesis requires further investigation.

KEYWORDS: ENGLAND, GROWTH, MANAGEMENT, NITROGEN, PHOTOSYNTHESIS

319

Caporn, S.J.M., D.W. Hand, T.A. Mansfield, and A.R. Wellburn. 1994. Canopy photosynthesis of co2-enriched lettuce (lactuca-sativa L) - response to short-term changes in co2, temperature and oxides of nitrogen. *New Phytologist 126(1):45-52.*

The canopy net photosynthesis (P-n) of lettuce (Lactuca sativa L. cv. 'Ambassador') was analyzed under controlled conditions simulating the winter glasshouse atmosphere. Prior to measurements the plants were grown in CO2- enriched air of 1000 mu mol mol(-1), at a photosynthetic photon flux density (PPFD) of 280 mu mol m(2) s(-1) (400-700 nm) and a day/night air temperature of 16/13 degrees C. Short-term changes in CO2 concentration significantly changed the initial gradient of the photosynthetic response to incident PPFD. Maximum photosynthetic efficiency of the crop increased from 0.041 mol CO2 mol photons(-1) (equivalent to 8.2 mu g CO2 J(-1) and 9.4% on an energy basis) at 350 mu mol mol(-1) to 0.055 mol CO2 photons(-1) (10.9 mu g CO2 J(-1) and 12.7% on an energy basis) at 1000 mu mol mol(-1). Transfer from low to high CO2 also lowered the light compensation point, but did not affect dark respiration. The large response of P-n to transient changes in CO2 indicated that the lettuce canopy did not acclimate to growth in

1000 mu mol CO2 mol(-1), in contrast with the effect of growth in high CO2 on P-n in single mature leaves reported earlier. A reduction in air temperature from 16 to 6 degrees C at a concentration of 1000 mu mol CO2 mol(-1) halved the rate of dark respiration and reduced the light compensation point, but had no direct effect on the maximum efficiency with which the crop utilized light. Subsequently, at low light (below 200 mu mol m(-2) s(-1)) P-n was greater at 6 than 16 degrees C. Between a PPFD of 250 and 300 mu mol m(-2) s(-1) canopy P-n was similar at all temperatures. Addition of 2.0 mu mol mol(-1) nitric oxide to an atmosphere of 1000 mu mol CO2 mol(-1) caused a rapid and reversible reduction of canopy P-n which was greater at the lowest temperatures. The average inhibition was 6.6% at 16 degrees C and 28.8% at 6 degrees C; this was not explained by differences in the rate of pollutant uptake, which was less in the cooler conditions. The results are discussed in relation to development of optimal growing conditions for production of glasshouse lettuce at low light and low temperature during winter in the UK.

KEYWORDS: CONTROLLED-ENVIRONMENT CHAMBER, DIOXIDE, ENRICHMENT, GROWTH, INHIBITION, INTEGRATED ANALYSIS, LEAF PHOTOSYNTHESIS, LIGHT INTERCEPTION, PLANTS, WINTER LETTUCE

320

Caporn, S.J.M., T.A. Mansfield, and D.W. Hand. 1991. Low temperature-enhanced inhibition of photosynthesis by oxides of nitrogen in lettuce (Lactuca sativa L). *New Phytologist 118(2):309-313.*

The response of photosynthetic gas exchange to oxides of nitrogen (NO(x)) was studied in leaves of lettuce (Lactuca sativa L.) at different temperatures. Exposure to high concentrations (e.g. 1.3-mu-mol NO(x) mol-1), similar to those often found in commercial glasshouses, caused a rapid inhibition of the net assimilation of CO2. This appeared to be by a direct effect on photosynthesis rather than by a change in the stomatal conductance. In ambient CO2 (345-mu-mol mol-1), the percentage inhibition at 10 and 5-degrees-C was approximately 3 x and 5 x, respectively, that measured at 20- degrees-C. This effect of temperature also occurred when measured in CO2 enriched air (1050-mu-mol mol-1), which would normally accompany NO(x) in a glasshouse. The extent of photosynthetic inhibition caused by NO(x) was, however, always less in high than in low CO2. The results suggest that when burning fuel to raise the CO2 concentration and heat the glasshouse air, growers should avoid generating high concentrations of NO(x) in conditions of low temperature.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NO2, PLANTS, SO2, SULFUR-DIOXIDE, TOMATO

321

Cardon, Z.G. 1996. Influence of rhizodeposition under elevated CO2 on plant nutrition and soil organic matter. *Plant and Soil 187(2):277-288.*

Atmospheric CO2 concentrations can influence ecosystem carbon storage through net primary production (NPP), soil carbon storage, or both. In assessing the potential for carbon storage in terrestrial ecosystems under elevated CO2, both NPP and processing of soil organic matter (SOM), as well as the multiple links between them, must be examined. Within this context, both the quantity and quality of carbon flux from roots to soil are important, since roots produce specialized compounds that enhance nutrient acquisition (affecting NPP), and since the flux of organic compounds from roots to soil fuels soil microbial activity (affecting processing of SOM). From the perspective of root physiology, a technique is described which uses genetically engineered bacteria to detect the distribution and amount of flux of particular compounds from single roots to non-sterile soils. Other experiments from several labs are noted which explore effects of elevated CO2 on root acid phosphatase, phosphomonoesterase, and citrate production, all associated with phosphorus nutrition. From a soil perspective, effects of elevated CO2 on the processing of SOM developed under a C4 grassland but planted with C3 California grassland species were examined under low (unamended) and high (amended with 20 g m(-2) NPK) nutrients; measurements of soil atmosphere delta(13)C combined with soil respiration rates show that during vegetative growth in February, elevated CO2 decreased respiration of carbon from C4 SOM in high nutrient soils but not in unamended soils. This emphasis on the impacts of carbon loss from roots on both NPP and SOM processing will be essential to understanding terrestrial ecosystem carbon storage under changing atmospheric CO2 concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, RESPONSES, RHIZOSPHERE, ROOTS, TALLGRASS PRAIRIE

322

Cardon, Z.G., J.A. Berry, and I.E. Woodrow. 1995. Fluctuating [CO2] drives species-specific changes in water use efficiency. *Journal of Biogeography 22(2-3):203-208.*

We have investigated the effects of fluctuating carbon dioxide (CO2) concentration on water use efficiency of Zea mays L. and Phaseolus vulgaris L. We found that species-specific kinetics of stomatal movements combine with photosynthetic characteristics to influence shea-term water use efficiency strongly under fluctuating environmental conditions. Specifically, under oscillating [CO2], average transpiration in Z. mays was driven higher than that observed at steady-state at the median CO2 concentration, while average photosynthesis remained fairly constant. Consequently, water use efficiency was lower during the fluctuations in [CO2] than it was at the steady, median [CO2]. Under similar oscillations in [CO2], stomatal conductance and transpiration of P. vulgaris were driven lower than observed at steady-state at the median [CO2]. A concomitant slight restriction of photosynthesis balanced this decrease in transpiration, and in this case water use efficiency under fluctuating [CO2] remained practically constant in P. vulgaris. The frequency of oscillations in [CO2] interacted with asymmetries in stomatal opening and closing kinetics in both Z. mays and P. vulgaris to determine the extent to which average transpiration (and water use efficiency in Z. mays) departed during fluctuations from the steady-state condition at the median CO2 level.

KEYWORDS: LIGHT, RESPONSES

323

Cardon, Z.G., and R.B. Jckson. 1995. Root acid-phosphatase-activity in bromus-hordeaceus and avena- barbata remains unchanged under elevated [co2]. *Plant Physiology 108(2):148.*

324

Carey, E.V., R.M. Callaway, and E.H. DeLucia. 1997. Stem respiration of ponderosa pines grown in contrasting climates: Implications for global climate change. *Oecologia 111(1):19-25.*

We examined the effects of climate and allocation patterns on stem respiration in ponderosa pine (Pinus ponderosa) growing on identical substrate in the cool, moist Sierra Nevada mountains and the warm, dry, Great Basin Desert. These environments are representative of current climatic conditions and those predicted to accompany a doubling of atmospheric CO2, respectively, throughout the range of many western

north American conifers. A previous study found that trees growing in the desert allocate proportionally more biomass to sapwood and less to leaf area than montane trees. We tested the hypothesis that respiration rates of sapwood are lower in desert trees than in montane trees due to reduced stem maintenance respiration (physiological acclimation) or reduced construction cost of stem tissue (structural acclimation). Maintenance respiration per unit sapwood Volume at 15 degrees C did not differ between populations (desert: 6.39 +/- 1.14 SE mu mol m(- 3) s(-1), montane: 6.54 +/- 1.13 SE mu mol m(-3) s(-1), P = 0.71) and declined with increasing stem diameter (P = 0.001). The temperature coefficient of respiration (Q(10)) varied seasonally within both environments (P = 0.05). Construction cost of stem sapwood was the same in both environments (desert: 1.46 +/- 0.009 SE g glucose g(-1) sapwood, montane: 1.48 +/- 0.009 SE glucose g(-1) sapwood, P = 0.14). Annual construction respiration calculated from construction cost, percent carbon and relative growth rate was greater in montane populations due to higher growth rates. These data provide no evidence of respiratory acclimation by desert trees. Estimated yearly stem maintenance respiration was greater in large desert trees than in large montane trees because of higher temperatures in the desert and because of increased allocation of biomass to sapwood. By analogy, these data suggest that under predicted increases in temperature and aridity, potential increases in aboveground carbon gain due to enhanced photosynthetic rates may be partially offset by increases in maintenance respiration in large trees growing in CO2-enriched atmospheres.

KEYWORDS: ABOVEGROUND PARTS, ACCLIMATION, ALLOCATION, CARBON, CO2, HINOKI FOREST TREE, MAINTENANCE RESPIRATION, PINUS-TAEDA, SCOTS PINE, TEMPERATURE

325

Carey, E.V., E.H. DeLucia, and J.T. Ball. 1996. Stem maintenance and construction respiration in Pinus ponderosa grown in different concentrations of atmospheric CO2. *Tree Physiology 16(1-2):125-130.*

To determine whether long-term growth in enriched CO2 atmospheres changes the woody tissue respiration component of aboveground carbon budgets, we measured woody tissue respiration of stems of 3-year-old ponderosa pine (Pinus ponderosa Laws.) grown in ambient (350 ppm) or twice ambient (700 ppm) atmospheric CO2 concentrations in open-top field chambers located in Placerville, CA. Total respiration rate was measured by gas exchange, and construction respiration was calculated from the construction cost, percent carbon of stem samples and relative growth rate. Maintenance respiration was determined as the difference between total and construction respiration. The Q(10) of respiration was greater in stems grown in elevated CO2 than in stems grown in ambient CO2 (2.20 versus 1.67). As a result, mean daily respiration per unit volume of wood modeled for the month of September was greater in trees growing in elevated CO2 than in ambient CO2 (46.75 versus 40.45 mol m(-3) day(-1)). These effects of atmospheric CO? concentration were not the result of differences in relative growth rate. Calorimetric analyses of woody tissue construction cost indicated no difference between treatments; however, trees in the elevated CO2 treatment showed a 1% lower carbon concentration than trees in the ambient CO2 treatment. Estimates of construction respiration did not differ between treatments, confirming that the treatment differences in mean daily respiration rate were attributable to the maintenance component. Under future predicted atmospheric conditions, changes in the maintenance respiration of woody tissue may lead to an increase in the respiration component of whole-plant carbon budgets of ponderosa pine. Our results suggest that potential increases in the maintenance component of stem respiration should be considered when modeling the response of forest stand growth to enriched CO2 atmospheres.

KEYWORDS: COST, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FIELD, FOREST TREE, LEAVES, PLANT RESPIRATION, SEEDLINGS, TEMPERATURE

326

Carlsson, A.S., G. Wallin, and A.S. Sandelius. 1996. Species- and age-dependent sensitivity to ozone in young plants of pea, wheat and spinach: Effects on acyl lipid and pigment content and metabolism. *Physiologia Plantarum 98(2):271-280.*

Acyl lipids and pigments were analyzed in young plants of garden pea, spring wheat and spinach exposed to <5 or 65 nl l(- 1) ozone 12 h per day for 6 days. In one set of experiments, the plants were exposed to (CO2)-C-14 for 2 h 3 days prior to ozone exposure. The plants responded differently to the moderately enhanced level of ozone used Spinach was not at all sensitive while in both pea and wheat, leaves of different ages differed in ozone sensitivity. In pea, ozone sensitivity increased with leaf age. In the second and third oldest leaves, the amounts of galactolipids per leaf area and the proportions of 18:3 of the total lipid extract and of phosphatidylglycerol decreased. In the second oldest leaf, ozone also caused a decreased proportion of 18:3 of monogalactosyldiacylglycerol. In the fourth oldest leaf, Lipid composition and galactolipid unsaturation was unaffected, but ozone caused decreased leaf expansion resulting in increased acyl lipid content per leaf area. In both the first and second leaves of wheat, ozone fumigation caused a marked decrease in the content of monogalactosyldiacylglycerol and in the first leaf, the contents of phosphatidylcholine and phosphatidylethanolamine increased. The proportion of 18:3 in phosphatidylcholine was larger in ozone-fumigated than in control plants, while the reverse applied for phosphatidylglycerol. In the oldest sampled leaves of pea and wheat, ozone caused an increase in the radioactivity associated with beta-carotene, indicating increased turnover. Thus, while spinach was unaffected, in both pea and wheat ozone caused a decrease in the proportion of chloroplast membrane lipids to non-chloroplast membrane lipids in older leaves while younger leaves were less sensitive.

KEYWORDS: LEAVES, MODERATELY ENHANCED LEVELS, PISUM-SATIVUM, POLAR LIPIDS, PROTECTION, TRITICUM-AESTIVUM

327

Carlsson, B.A., and T.V. Callaghan. 1994. Impact of climate-change factors on the clonal sedge carer bigelowii - implications for population-growth and vegetative spread. *Ecography 17(4):321-330.*

Hypothesized life-cycle responses to climate change for the arctic, clonal perennial Carer bigelowii are constructed using a range of earlier observations and experiments together with new information from monitoring and an environmental perturbation study. These data suggest, that under current climate change scenarios, increases in CO2, temperature and nutrient availability would promote growth in a qualitatively similar way. The evidence suggests that both tiller size and daughter tiller production will increase, and be shifted towards production of phalanx tillers which have a greater propensity for flowering. Furthermore, age at tillering as well as tiller life span may decrease, whereas survival of younger age classes might be higher. Mathematical models using experimental data incorporating these hypotheses were used to a) integrate the various responses and to calculate the order of magnitude of changes in population growth rate (lambda), and b) to explore the implications of responses in individual demographic parameters for population growth rate. The models suggest that population growth rate following climate change might increase significantly, but not unrealistically so, with the younger, larger, guerilla tillers being the most important tiller categories contributing to lambda. The rate of vegetative spread is calculated to more than double, while cyclical trends in flowering and population growth are predicted to decrease substantially.

KEYWORDS: CARBON DIOXIDE, DWARF-SHRUB, DYNAMICS, ELEVATED CO2, ENVIRONMENTAL-CHANGE, ERIOPHORUM VAGINATUM, PLANTS, RESPONSES, SIZE, TUSSOCK TUNDRA

328

Carmi, A. 1993. Effects of shading and co2 enrichment on photosynthesis and yield of winter grown tomatoes in subtropical regions. *Photosynthetica 28(3):455-463.*

The effects of exposing winter-grown tomato (Lycopersicon esculentum L.) to various sunlight irradiances and CO2 concentrations, on dark respiration (R(D)), night respiration (R(N)), net photosynthetic-rate (P(N)), dry matter production (DMP), yield earliness and yield amount were studied. Plants were grown in greenhouses under controlled temperatures and exposed to: full (FS) or half (HS) sunlight irradiance in combinafion with atmospheric (A) or enriched (E) concentrations of 300-330 or 1400-1500 g(CO2) m-3, respectively. The P(N) of intact leaves at noontime reached 10.7, 15.2, 5.9 and 9.6 mumol(CO2) m-2 s-1 in treatments of FSA, FSE, HSA and HSE, respectively. The irradiances on the upper leaf surface during the P(N) measurements ranged between 160-190 and 450-550 mumol m-2 s-1 in the HS and FS treatments, respectively. R(D) of leaves which were kept in darkness following the P(N) measurement arrived at efflux of 2.6, 2.5, 1.4 and 1.4 mumol(CO2) m-2 s-1 While their R(N) (between 20:00 and 24:00) reached values of 0.9, 1.3, 0.8 and 0.8 mumol(CO2) m-2 s-1 in treatments of FSA, FSE, HSA and HSE, respectively. Elevating the CO2 concentration from 300 to 1500 g m-3 increased P(N) by 16, 28, 30 and 46% under an irradiance of 160 mumol m-2 s-1, and 19, 34, 59 and 44% under irradiance of 320 mumol m-2 s-1 in the FSA, FSE, HSA and HSE treatments, respectively. Increasing the measurement irradiance from 160 to 320 mumol m-2 s-1 enhanced P(N) by 69, 78, 23 and 49% in an atmosphere of 300 g m-3 CO2, and by 73, 84, 49 and 47% in an atmosphere of 1500 g m-3 CO2, in the FSA, FSE, HSA and HSE treatments, respectively. DMP was strongly influenced by the different environmental conditions and the total dry matter accumulation in the shoot per plant during 145 d reached 580, 347, 398 and 235 g in the FSA, FSE, HSA and 14SE treatments, respectively. CO2 enrichment promoted early yield under both full and partial sunlight irradiance. The HSE treatment led to earlier yield harvesting than the FSA and HSA treatments. The yield of the seven first trusses reached 6.8, 4.6, 5.7 and 3.2 kg per plant in the FSA, FSE, HSA and HSE treatments, respectively. Some increase in fruit fresh matter and diameter of fruits was detected in the CO2-enriched treatments as compared to the non-enriched ones. Thus the combination of moderate shading and CO2 enrichment might provide a more productive option for winter-grown tomatoes in regions of subtropical climate, even in the winter, than the conventional management of aerated greenhouses without CO2 enrichment which are exposed to full sunlight.

329

Carpenter, S.R., S.G. Fisher, N.B. Grimm, and J.F. Kitchell. 1992. Global change and fresh-water ecosystems. *Annual Review of Ecology and Systematics 23:119-139.*

KEYWORDS: AQUATIC SYSTEMS, CADDISFLY POPULATION, CO2-INDUCED CLIMATIC-CHANGE, DESERT STREAM, GRADIENT HEADWATER STREAMS, GREAT- LAKES BASIN, ORGANIC-CARBON, POTENTIAL CHANGES, THERMAL HABITAT, WATER-RESOURCES

330

Carter, E.B., M.K. Theodorou, and P. Morris. 1997. Responses of Lotus corniculatus to environmental change .1. Effects of elevated CO2, temperature and drought on growth and plant development. *New Phytologist 136(2):245-253.*

Five clonal plants of three genotypes of Lotus corniculatus were grown in each of eight controlled environments under combinations of two temperature regimes (18/10 degrees C and 25/15 degrees C), two CO2 concentrations (ambient and 700 ppmv) and two water applications (ad libitum or 60% droughted). Plants were harvested at full flower and measurements made of plant growth and development. Of the three environmental variables studied, higher growth temperatures resulted in the largest number of significant changes to the measured variables. Reproductive capacity, growth rate, shoot biomass, water use efficiency and chlorophyll content were all enhanced by raising the growth temperature from 18 to 25 degrees C. Doubling the CO2 concentration enhanced the growth rate, shoot biomass and water use efficiency and ameliorated some of the effects of drought, including reproductive capacity, and biomass production, but reduced flowering lime, specific leaf area, and chlorophyll content of both droughted and undroughted plants. Drought alone reduced reproductive capacity, growth rate and above ground biomass but significantly increased root biomass in all environments. The agronomic effects resulting from a combined increase in growth temperature, doubled CO2 concentration and mild drought in this experiment were a shorter vegetative period and an increase in biomass, but a fall in reproductive capacity.

KEYWORDS: CARBON DIOXIDE, EFFICIENCY, ENRICHMENT, INCREASING CO2, N2 FIXATION, PHOTOSYNTHESIS, RESPIRATION, WATER-STRESS, WHITE CLOVER, YIELD

331

Carter, E.B., M.K. Theodorou, and P. Morris. 1999. Responses of Lotus corniculatus to environmental change. 2. Effect of elevated CO2, temperature and drought on tissue digestion in relation to condensed tannin and carbohydrate accumulation. *Journal of the Science of Food and Agriculture 79(11):1431-1440.*

Clonal plants of three genotypes of Lotus corniculatus (cv Lee) were grown in eight controlled environments under combinations of two temperature regimes, two CO2 concentrations and two watering regimes. Condensed tannins (proanthocyanidins), in- vitro digestibility, initial rates of gas evolution las an indicator of the initial rates of fermentation of the substrate), volatile fatty acid evolution, and non-structural carbohydrate (NSC) levels were determined in leaves, stems and roots at full flowering. Under control conditions (average midsummer conditions in the United Kingdom) the total condensed tannin content of leaves varied six-fold between genotypes but condensed tannin contents in stems and roots were similar. Condensed tannin levels were significantly increased in leaves and stems of all three genotypes by doubling the CO2 concentration while raising the temperature towards the optimum for growth significantly reduced condensed tannin levels. Drought stress significantly reduced condensed tannin levels in leaves and, particularly, in roots. Nutritive value was inversely related to condensed tannin levels in leaves and a negative relationship was observed between condensed tannin concentrations of more than 25-30 g kg(-1) dry matter and the initial rates of gas evolution when subjected to in-vitro fermentation with rumen micro-organisms. In leaves, digestibility was significantly increased by drought and by increasing temperature but reduced by high CO2. In stems, digestibility was significantly increased by drought, but not significantly affected by increasing temperature, or by high CO2 alone. In roots, digestibility was significantly increased by drought, and decreased by increasing temperature or CO2. Increasing the growth temperature towards optimum growth reduced the content of NSC in all tissues with the greatest changes occurring in root tissue. Doubling the CO2 concentration increased NSC levels in leaves and stems with starch content more than doubled under high CO2 while, in roots, increased levels were only observed in combination with drought stress. There was a linear correlation between condensed tannin concentration and total

NSC that was positive for leaves, neutral for stems and negative for roots. The relationship between carbohydrate levels and rates of gas production was negative for leaves and positive for stem and roots. (C) 1999 Society of Chemical Industry.

KEYWORDS: DIGESTIBILITY, GAS-PRODUCTION, GROWTH, ISOSYNTHETIC STRAINS, METABOLISM, PEDUNCULATUS, PROANTHOCYANIDINS, PROTEIN, RUMEN, SHEEP

332

Carter, G.A., J. Rebbeck, and K.E. Percy. 1995. Leaf optical-properties in liriodendron-tulipifera and pinus- strobus as influenced by increased atmospheric ozone and carbon-dioxide. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(3):407-412.*

Seedlings of Liriodendron tulipifera L. and Pinus strobus L. were grown in open-top chambers in the field to determine leaf optical responses to increased ozone (O-3) or O-3 and carbon dioxide (CO2). In both species, seedlings were exposed to charcoal-filtered air, air with 1.3 times ambient O-3 concentrations (1.3X), or air with 1.3 times ambient O-3 and 700 mu L . L(-1) CO2 (1.3X + CO2). Exposure to 1.3X increased reflectance in the 633-697 nm range in L. tulipifera. Also, 1.3X decreased transmittance within the 400-420 nm range, increased transmittance at 686-691 nm, and decreased absorptance at 655-695 nm. With 700 mu L . L(-1) CO2, O-3 did not affect reflectance in L. tulipifera, but decreased transmittance and increased absorptance within the 400-421 nm range and increased transmittance and decreased absorptance in the 694-697 nm range. Under 1.3X, reflectance in P. strobus was not affected. However, 1.3X + CO2 increased pine reflectance in the 538-647, 650, and 691-716 nm ranges. Transmittances and absorptances were not determined for P. strobus. Reflectance in both species, and transmittance and absorptance in L. tulipifera, were most sensitive to O-3 near 695 nm. Reflectance at 695 nm, but particularly the ratio of reflectance at 695 nm to reflectance at 760 nm, was related closely to ozone-induced decreases in leaf chlorophyll contents, particularly chlorophyll a (r(2) = 0.82).

KEYWORDS: CHLOROPHYLL CONTENT, ELEVATED CO2, INJURY, LEAVES, NITROGEN, RED EDGE, RESPONSES, SLASH PINE, SPECTRAL REFLECTANCE

333

Case, A.L., P.S. Curtis, and A.A. Snow. 1998. Heritable variation in stomatal responses to elevated CO2 in wild radish, Raphanus raphanistrum (Brassicaceae). *American Journal of Botany 85(2):253-258.*

Rising atmospheric carbon dioxide may affect plant populations in the short term through effects on photosynthesis and carbon allocation, and over the long term as an agent of natural selection. To test for heritable effects of elevated CO2 on stomatal responses and plant fecundity in Raphanus raphanistrum, we grew plants from 12 paternal families in outdoor open-top chambers at ambient (35 Pa) or elevated (67 Pa) CO2. Contrary to results from a previous study of this species, total flower and fruit production were marginally lower under elevated CO2. Across families, stomatal index and guard cell length showed little response to CO2 enrichment, but these characters varied significantly among paternal families in both the direction and magnitude of their response to changing CO2. Although these family-by-CO2, interactions suggest that natural selection might affect stomatal characters when ambient CO2 levels increase, we found no significant correlation between either character and flower or fruit production. Therefore, our data suggest that while heritable variation for stomatal index and guard cell length exists in this population, selection due to increasing CO2 is not likely to act on these traits because they had no detectable effect on lifetime fecundity.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DENSITY, ENRICHMENT, EVOLUTION, GAS-EXCHANGE, GROWTH, LEAVES, PERFORMANCE, PLANTS

334

Casella, E., and J.F. Soussana. 1997. Long-term effects of CO2 enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany 48(311):1309-1321.*

Perennial ryegrass swards were grown in large containers on a soil, at two N fertilizer supplies and were exposed during two years in highly ventilated plastic tunnels to elevated (700 mu l l(-1) [CO2]) or ambient atmospheric CO2 concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO2. The irrigation was adjusted to obtain a soil water deficit during summer. The daily net C assimilation was increased in elevated CO2 by 29 and 36% at the low and high N supplies, respectively, Canopies grown in elevated CO2 for 14 to 27 months photosynthetized significantly less rapidly, in both elevated and normal CO2 concentrations, than their counterparts developed in ambient CO2, but the magnitude of this effect was small (-8% to -13%). Elevated CO2 resulted in a large increase in the fructan concentration in the pseudostems and laminae (+46% and +189%, respectively). In elevated CO2, the hexose and sucrose pool increased by 28% in the laminae, whereas it did not vary significantly in the pseudo-stems, A 3 degrees C temperature increase in elevated CO2 did not affect significantly the average WSC concentrations in the pseudostems and laminae, The elevated CO2 effects on the net C assimilation and on the nocturnal shoot respiration were greater in summer than in spring. On average, a 35% increase in the below-ground respiration was measured in elevated CO2. At the high N supply, a 3 degrees C increase in air temperature led to a decline in the below-ground respiration due to a low soil moisture, The below-ground carbon storage was increased by 32% and 96% in elevated CO2 at the low and high N supplies, respectively, with no significant increased temperature effect. The role for the below-ground carbon storage of CO2-induced changes in the root fraction of the grass and of temperature- induced changes in the moisture content of the soil are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERE, DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NET PHOTOSYNTHESIS, NITROGEN, PLANT-RESPONSES, SOIL CARBON

335

Casella, E., J.F. Soussana, and P. Loiseau. 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward .1. Productivity and water use. *Plant and Soil 182(1):83-99.*

Perennial ryegrass swards were grown in large containers on a soil, at two N fertilizer supplies, and were exposed over two years in highly ventilated plastic tunnels to elevated (700 mu L L(-1) [CO2]) or ambient atmospheric CO2 concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO2. These swards were either fully irrigated (kept at field capacity) in each climatic condition (W+), or received the same amount of water in the three climate treatments (W-). In the latter case, the irrigation was adjusted to obtain a soil water deficit during summer and drainage in winter. Using a lysimeter approach, the evapotranspiration, the soil water balance, the productivity (dry-matter yield) and the water use efficiency of the grass swards were measured. During both years, elevated CO2 increased the annual above-ground drymatter yield of the W-swards, by 19% at N- and by 14% at N+. Elevated CO2 modified yield to a variable extent during the growing season: a small, and sometime not significant effect (+6%, on average) was obtained in spring and in autumn, while the summer growth response was stronger (+48%, on average). In elevated CO2, the

temperature increase effect on the annual above-ground dry-matter yield was not significant, due to a gain in dry-matter yield in spring and in autumn which was compensated for by a lower summer productivity. Elevated CO2 slightly reduced the evapotranspiration during the growing season and increased drainage by 9% during winter. A supplemental 3 degrees C in elevated CO2 reduced the drainage by 29-34%, whereas the evapotranspiration was increased by 8 and 63% during the growing season and in winter, respectively. During the growing season, the soil moisture content at W- and at the high N supply declined gradually in the control climate, down to 20- 30% of the water holding capacity at the last cut (September) before rewatering. This decline was partly alleviated under elevated CO2 in 1993, but not in 1994, and was enhanced at +3 degrees C in elevated CO2. The water use efficiency of the grass sward increased in elevated CO2, on average, by 17 to 30% with no significant interaction with N supply or with the soil water deficit. The temperature increase effect on the annual mean of the water use efficiency was not significant. Highly significant multiple regression models show that elevated CO2 effect on the dry-matter yield increased with air temperatures above 14.5 degrees C and was promoted by a larger soil moisture in elevated compared to ambient CO2. The rate of change in relative dry-matter yield at +3 degrees C in elevated CO2 became negative for air temperatures above 18.5 degrees C and was reduced by a lower soil moisture at the increased air temperature. Therefore, the altered climatic conditions acted both directly on the productivity and on the water use of the grass swards and, indirectly, through changes in the soil moisture content.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP YIELD, EFFICIENCY, ELEVATED CO2, GROWTH, LEAF-AREA, LIMITED CONDITIONS, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS

336

Cater, M., P. Simoncic, and F. Batic. 1999. Pre-dawn water potential and nutritional status of pedunculate oak (Quercus robur L.) in the north-east of Slovenia. *Phyton-Annales Rei Botanicae 39(4):13-21.*

In the 1997 growth period monthly measurements of pre-dawn water potential, electrical resistance of the cambial zone, groundwater level and quality together with annual dynamics of macronutrive elements in leaves and heavy metals (Zn, Ph, Cd) were performed. Two plots having different groundwater tables and crown defoliation were studied in the pedunculate oak forest complex (Querco Roboris-Carpinetum M. Wraber) in the north-east of Slovenia. Results showed lower (more negative) values of pre-dawn water potential and higher values of cambial electrical resistance on the plot with greater crown defoliation, which also had a lower groundwater table. Groundwater seems to be the key factor in the process of oak decline.

KEYWORDS: DECLINE, DROUGHT, ELEVATED CO2, EMBOLISM, FIR, GROWTH, PHOTOSYNTHESIS, SEEDLINGS, STANDS, STRESS

337

Catovsky, S., and F.A. Bazzaz. 1999. Elevated CO2 influences the responses of two birch species to soil moisture: implications for forest community structure. *Global Change Biology 5(5):507-518.*

Increased levels of atmospheric CO2 may alter the structure and composition of plant communities by affecting how species respond to their physical and biological environment. We investigated how elevated CO2 influenced the response of paper birch (Betula papyrifera Marsh.) and yellow birch (Betula alleghaniensis Britt.) seedlings to variation in soil moisture. Seedlings were grown for four months on a soil moisture gradient, individually and in mixed species stands, in controlled environment facilities at ambient (375 mu L L-1) and elevated (700 mu L L-1) atmospheric CO2. For both individually and competitively grown paper birch seedlings, there was a greater CO2 growth enhancement for seedlings watered less frequently than for well-watered seedlings. This differential change in CO2 responsiveness across the moisture gradient reduced the difference in seedling growth between high and low water levels and effectively broadened the regeneration niche of paper birch. In contrast, for yellow birch seedlings, elevated CO2 only produced a significant growth enhancement at the wet end of the soil moisture gradient, and increased the size difference between seedlings at the two ends of the gradient. Gas exchange measurements showed that paper birch seedlings were more sensitive than yellow birch seedlings to declines in soil moisture, and that elevated CO2 reduced this sensitivity. Additionally, elevated CO2 improved survival of yellow birch seedlings growing in competition with paper birch in dry stands. Thus, elevated CO2 may influence regeneration patterns of paper birch and yellow birch on sites of differing soil moisture. In the future, as atmospheric CO2 levels rise, growth of paper birch seedlings and survival of yellow birch seedlings may be enhanced on xeric sites, while yellow birch may show improved growth on mesic sites.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CONTRASTING SHADE TOLERANCE, COOCCURRING BIRCH, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PINUS-TAEDA SEEDLINGS, TERRESTRIAL ECOSYSTEMS, WATER-STRESS

338

Catsky, J., J. Pospisilova, J. Solarova, H. Synkova, and N. Wilhelmova. 1995. Limitations on photosynthesis under environment-simulating culture in-vitro. *Biologia Plantarum 37(1):35-48.*

Limitations on photosynthesis, characterized by leaf CO2 exchange, chlorophyll fluorescence, and thylakoid structure, were studied under environmental conditions simulating culture in vitro. These were simulated by growing Phaseolus vulgaris plants in nutrient solution under high relative humidity of air (> 90%), and CO2 concentrations (c(a)) that decreased with the development of photosynthetic activities during plant ontogeny (1200 to 300 mg m-3). The ontogeny of such model plants was more rapid, primary leaves reached photosynthetic maturity 2 to 3 d earlier and their life span was 7 to 14 d shorter than in control plants. Their photosynthetic activity in situ was limited, after reaching "photosynthetic maturity", similarly to plants grown in vitro. When measured under optimal conditions, however, 50 to 70% higher net photosynthetic rate (P(N)) were found in leaves of different ages as compared with plants grown under c(a) of 700 mg m-3 and a lower air humidity (30 - 35%). This increase in P(N) was associated with a high conductance for CO2 transfer by adaxial and abaxial epidermes. In model plants, the dark respiration rate (R(D)) was almost twice that in the control, while the photorespiration rates were similar to controls; CO2 compensation concentration was about 50% of that in controls. The ratios P(N)/R(D) were similar in control and in model plants. Chlorophyll a+b content in leaves of the model plants was lower than that in the control plants. Grana extent increased with plant age in the model plants while it decreased in the control ones. In both the stomal and granal membranes of the chloroplasts in model plants, a marked accumulation of carotenoids occurred independent of age. The ratio of variable to maximal fluorescence, F(v)/F(m), did not differ in the model and the control plants. In the control plants, photochemical quenching (qp) slightly increased with plant age and was not affected by CO2 concentration present during measurement. In the model plants, qp increased with elevated CO2 concentration in young plants and decreased in saturating CO2 concentrations in older plants. Nonphotochemical quenching (q(NP)) was lower in the model plants and increased under CO2 saturating conditions. Vitality index, Rfd, was markedly lower in the model plants than in the control ones and a decline was found in saturating CO2 concentration.

339

Caulfield, F., and J.A. Bunce. 1994. Elevated atmospheric carbon-dioxide concentration affects interactions between spodoptera-exigua (lepidoptera, noctuidae) larvae and 2 host-plant species outdoors. *Environmental Entomology 23(4):999-1005.*

Beet armyworm, Spodoptera exigua (Hubner), larvae were placed on sugarbeet (Beta vulgaris L.) and pigweed (Amaranthus hybridus L.) plants in outdoor chambers in which the plants were growing at either the ambient (almost-equal-to 350 mul liter-1) or ambient plus 350 mul liter-1 (almost-equal-to 700 mul liter-1) carbon dioxide concentration. A series of experiments was performed to determine if larvae reduced plant growth differently at the two carbon dioxide concentrations in either species and if the insect growth or survival differed with carbon dioxide concentration. Leaf nitrogen, water, starch, and soluble carbohydrate contents were measured to assess carbon dioxide concentration effects on leaf quality. Insect feeding significantly reduced plant growth in sugarbeet plants at 350 mul liter-1 but not at 700 mul liter-1 nor in pigweed at either carbon dioxide concentration. Larval survival was greater on sugarbeet plants at the elevated carbon dioxide concentration. Increased survival occurred only if the insects were at the elevated carbon dioxide concentration and consumed leaf material grown at the elevated concentration. Leaf quality was only marginally affected by growth at elevated carbon dioxide concentration in these experiments. The results indicate that in designing experiments to predict effects of elevated atmospheric carbon dioxide concentrations on plant- insect interactions, both plants and insects should be exposed to the experimental carbon dioxide concentrations, as well as to as realistic environmental conditions as possible.

KEYWORDS: COTTON, ENRICHED CO2 ATMOSPHERES, GROWTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEAVES, PERIODS, PHOTOSYNTHESIS, RESPONSES, STARCH

340

Cavender-Bares, J.M., P.B. Voss, and F.A. Bazzaz. 1998. Consequences of incongruency in diurnally varying resources for seedlings of Rumex crispus (Polygonaceae). *American Journal of Botany 85(9):1216-1223.*

The incongruency of diurnally varying resources essential to plants may detrimentally affect plants early in their development as indicated by reduced water use efficiency and carbon gain. Typical diurnal patterns of light and CO2 availability in a midsized temperate herbaceous or forest gap were simulated in specially designed growth chambers. A sinusoidally varying CO2 treatment (400 ppm minimum, 800 ppm maximum) approximated the diurnal cycle of CO2 at the soil surface, while a steady-state CO2 treatment (600 ppm) with the same average CO2 concentration provided a control. Crossed with these two CO2 treatments were two light regimes, one with 3 h of high light (850 mu mol.m(-2).s(-1)) in the morning (west side of a gap), and the other with 3 h of high light in the afternoon (east side). All treatments received baseline low light (55 mu mol.m(-2).s(-1)) for 14 h during the day. Rumex crispus was selected as a model species because of its rosette leaves, which grow close to the ground where diurnal CO2 variation is greatest. The relative timing of diurnal variations in light and CO2 significantly affected seedling water use efficiency, carbon gain, and morphology. Total biomass, photosynthetic rates, daily integrated carbon, water use efficiency, and leaf area were enhanced by morning exposure to high light. Seedlings that were exposed to peak values of light and CO2 incongruently, i.e., those plants receiving intense afternoon light with diurnally varying CO2, were detrimentally affected relative to control plants receiving intense afternoon light with steady-state CO2. The results of this experiment indicate that the incongruent availability of required resources-such as light and CO2-can detrimentally affect performance relative to when resources are congruent. These contrasting resource regimes can occur on the east and west side of gaps.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, FOREST, GAS-EXCHANGE, GROWTH, LIGHT, PLANTS, RESPONSES, WATER RELATIONS

341

Cebrian, J. 1999. Patterns in the fate of production in plant communities. *The American Naturalist 154(4):449-468.*

I examine, through an extensive compilation of published reports, the nature and variability of carbon flow (i.e., primary production, herbivory, detrital production, decomposition, export, and biomass and detrital storage) in a range of aquatic and terrestrial plant communities. Communities composed of more nutritional plants (i.e., higher nutrient concentrations) lose higher percentages of production to herbivores, channel lower percentages as detritus, experience faster decomposition rates, and, as a result, store smaller carbon pools. These results suggest plant palatability as a main limiting factor of consumer metabolical and feeding rates across communities. Hence, across communities, plant nutritional qualify may be regarded as a descriptor of the importance of herbivore control on plant biomass ("top-down" control), the rapidity of nutrient and energy recycling, and the magnitude of carbon storage. These results contribute to an understanding of how much and why the trophic routes of carbon flow, and their ecological implications, vary across plant communities. They also offer a basis to predict the effects of widespread enhancement of plant nutritional quality due to large-scale anthropogenic eutrophication on carbon balances in ecosystems.

KEYWORDS: CARBON BALANCE, ECOSYSTEMS, ELEVATED CO2, FRESH-WATER, GROWTH RATE, HERBIVORY, MARINE WATERS, NITROGEN, NUTRIENT LIMITATION, ORGANIC-MATTER

342

Centritto, M., and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (Picea sitchensis). II. Photosynthetic capacity and nitrogen use efficiency. *Tree Physiology 19(12):807-814.*

Four clones of Sitka spruce (Picea sitchensis (Bong.) Carr.) from two provenances, at 53.2 degrees N (Skidegate a and Skidegate b) and at 41.3 degrees N (North Bend a and North Bend b, were grown for three growing seasons in ambient (similar to 350 mu mol mol(-1)) and elevated (similar to 700 mu mol mol(- 1)) CO2 concentrations. The clones were grown in stress-free conditions (adequate nutrition and water) to assess the effect of elevated [CO2] on tree physiology. Growth in elevated [CO2] significantly increased instantaneous photosynthetic rates of the clonal Sitka spruce saplings by about 62%. Downward acclimation of photosynthesis (A) was found in all four clones grown in elevated [CO2]. Rubisco activity and total chlorophyll concentration were also significantly reduced in elevated [CO2]. Provenance did not influence photosynthetic capacity. Best-fit estimates of J(max) (maximum rate of electron transport), V-cmax (RuBP-saturated rate of Rubisco) and A(max) (maximum rate of assimilation) were derived from responses of A to intercellular [CO2] by using the model of Farquharetal.(1980). At any leaf N concentration, the photosynthetic parameters were reduced by growth in elevated [CO2]. However, the ratio between J(max) and V-cmax was unaffected by CO2 growth concentration, indicating a tight coordination in the allocation of N between thylakoid and soluble proteins. In elevated [CO2] the more southerly clones had a higher initial N use efficiency (more carbon assimilated per unit of leaf N) than the more northerly clones, so that they had more N available for those processes or organs that were most limiting to growth at a particular time. This may explain the initial higher growth stimulation by elevated [CO2] in the North Bend clones

than in the Skidegate clones.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, GAS-EXCHANGE, GENE-EXPRESSION, LOBLOLLY-PINE TREES, NUTRITION, PLANTS, SEEDLINGS, TEMPERATURE

343

Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Increased growth in elevated [CO2]: an early, short-term response? *Global Change Biology 5(6):623-633.*

Saplings of four clones of Sitka spruce and cherry were grown for three and two growing seasons, respectively, in open top chambers at two CO2 concentrations (approximate to 350 and approximate to 700 mu mol mol(-1)) to determine whether the increase in total biomass brought about by enhanced [CO2] is a result of a transient or persistent effect in nonlimiting conditions. Classical growth analysis was applied to both species and mean current relative growth rate of total dry mass (R-T) and leaf dry mass (R-L), and period relative growth rate of total dry mass (R-T(t)) and leaf dry mass (R-L(t)) were calculated. Sitka spruce saplings and cherry seedlings showed a positive growth response to elevated [CO2], and at the end of the experiments both species were approximate to 40% larger in elevated [CO2] than in ambient [CO2]. As a result, the period mean R-T(t) and R-L(t) were significantly higher in elevated [CO2]. The differences in plant dry mass at the end of the experiments were a consequence of the more rapid growth in the early phase of exposure to elevated [CO2]. After this initial phase mean R-T and R-L were similar or even lower in elevated [CO2] than in ambient [CO2]. NAR of both species was much higher in elevated [CO2], whereas both LAR, SLA, and LMR showed the opposite trend. The higher LAR and SLA of plants in ambient [CO2] contributed to a compensation by which they maintained R- T Similar to that of elevated [CO2] saplings despite lower NAR and photosynthetic rate. However, when the same size the trees were similar amongst the [CO2] treatments, indicating that one of the main effect of elevated [CO2] on tree growth is to speed-up early development in all aspects.

KEYWORDS: ACCLIMATION, AMBIENT, ATMOSPHERIC CO2, BETULA-PENDULA ROTH, BIOMASS ALLOCATION, CARBON, PHOTOSYNTHESIS, PLANTAGO-MAJOR, PONDEROSA PINE, RESPIRATION

344

Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Interactive effects of elevated [CO2] and drought on cherry (Prunus avium) seedlings - I. Growth, whole-plant water use efficiency and water loss. *New Phytologist 141(1):129-140.*

Seeds of cherry (Prunus avium) were germinated and grown for two growing seasons in ambient (similar to 350 mu mol mol(-1)) or elevated (ambient + similar to 350 mu mol mol(-1)) CO2 mole fractions in six open-top chambers. The seedlings were fertilized once a week, following Ingestad principles in order to supply mineral nutrients at free-access rates. In the first growing season gradual drought was imposed on rapidly growing cherry seedlings by withholding water for a 6-wk drying cycle. In the second growing season, the rapid onset of drought was imposed at the height of the growing season on the seedlings which had already experienced drought in the first growing season. Elevated [CO2] significantly increased total dry-mass production in both water regimes, but did not ameliorate the growth response to drought of the cherry seedlings subjected to two sequential drying cycles. Water loss did not differ in either well watered or droughted seedlings between elevated and ambient [CO2]; consequently whole-plant water-use efficiency (the ratio of total dry mass produced to total water consumption) was significantly increased. Similar patterns of carbon allocation between shoot and root were found in elevated and ambient [CO2] when the seedlings were the same size. Thus, elevated [CO2] did not improve drought tolerance, but it accelerated ontogenetic development irrespective of water status.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-WEIGHT, ENRICHMENT, GAS-EXCHANGE, LEAF-AREA, NUTRIENT AVAILABILITY, RESPONSES, SITCHENSIS BONG CARR, STRESS, WHEAT

345

Centritto, M., H.S.J. Lee, and P.G. Jarvis. 1999. Long-term effects of elevated carbon dioxide concentration and provenance on four clones of Sitka spruce (Picea sitchensis). I. Plant growth, allocation and ontogeny. *Tree Physiology 19(12):799-806.*

Four clones of Sitka spruce (Picea sitchensis (Bong.) Carr.) from two provenances, at 53.2 degrees N (Skidegate a and Skidegate b) and at 41.3 degrees N (North Bend a and North Bend b), were grown near Edinburgh (55.5 degrees N), U.K., for three growing seasons in ambient (similar to 350 mu mol mol(-1)) and elevated (similar to 700 mu mol mol(-1)) CO2 concentrations under conditions of non-limiting water and nutrient supply. Bud phenology was not affected by elevated [CO2] in the second growing season, but in the third year, the duration of shoot extension growth in three of the four clones (North Bend clones and Skidegate a) was significantly shortened, because of the suppression of lammas growth. Saplings in elevated [CO2] had significantly greater dry masses of all components than saplings in ambient [CO2]. However, comparison of relative component dry masses between plants of similar size showed no effect of [CO2] treatment on plant allometric relationships. This finding, and the observed suppression of lammas growth by high [CO2] during the third growing season suggests that the main effect of increasing [CO2] is to accelerate sapling development. Clonal provenance did not affect dry mass production in ambient [CO2]. However in elevated [CO2] the more southerly clones significantly out-performed the more northerly clones when grown at a latitude close to the latitudinal provenance of the Skidegate clones. As atmospheric carbon dioxide concentration rises, such changes in the relative performance of genotypes may be exploited for economic gain through appropriate selection of provenances for forest plantings.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, BONG CARR, ENRICHMENT, FROST HARDINESS, INCREASE, NUTRITION, PHOTOSYNTHESIS, PHYSIOLOGY, SEEDLINGS

346

Centritto, M., F. Magnani, H.S.J. Lee, and P.G. Jarvis. 1999. Interactive effects of elevated [CO2] and drought on cherry (Prunus avium) seedlings - II. Photosynthetic capacity and water relations. *New Phytologist 141(1):141-153.*

Cherry seedlings (Prunus avium) were grown from seed for two growing seasons in three ambient [CO2] (similar to 350 mu mol mol(-1)) and three elevated [CO2] (ambient + similar to 350 mu mol mol(-1)) open-top chambers, and in three outside blocks. A drying cycle was imposed in both the growing seasons to half the seedlings: days 69-115 in the first growing season, and in the second growing season days 212-251 on the same seedlings which had already experienced drought. Stomatal conductance was significantly reduced in elevated [CO2]-grown, unstressed seedlings in both the first and second growing seasons, but was not caused by a decrease in stomatal density. Droughted seedlings showed little or no reduction in stomatal conductance in response to elevated [CO,]. However, stomatal conductance was highly correlated with soil water status. Photosynthetic rate increased significantly in response to elevated [CO2] in both water regimes, leading to improvement in instantaneous transpiration efficiency over the whole duration of the experiment, bur there was no relationship between instantaneous transpiration efficiency and long-term water use

efficiency. The A(max) was strongly reduced in the second growing season, but unaffected by [CO2] treatment. Although photosynthetic rate was not down-regulated, Rubisco activity was decreased by elevated [CO2], possibly because of the increased leaf carbon:nitrogen ratio which had occurred by the ends of the two growing seasons. Elevated [CO2] did not improve plant water relations (for example, bulk leaf - water potential, osmotic potentials at full and zero turgor, relative water content at zero turgor, bulk modulus of elasticity of the cell) and thus did not increase water-stress tolerance of cherry seedlings.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, STOMATAL CONTROL, TRANSPIRATION, TREES

347

Ceulemans, R., I.A. Janssens, and M.E. Jach. 1999. Effects of CO2 enrichment on trees and forests: Lessons to be learned in view of future ecosystem studies. *Annals of Botany 84(5):577-590.*

Because of their prominent role in global bioproductivity and because of their complex structure and function, forests and tree species deserve particular attention in studies on the likely impact of elevated atmospheric CO2 on terrestrial vegetation. Besides a synoptic review of some of the most prominent above-ground response processes, particular attention is given to below-ground responses of trees to elevated atmospheric CO2, while some feedback processes and interactions with Various biotic and abiotic factors are also briefly summarized. At the leaf level there is little evidence of the long-term loss of sensitivity to CO2 that was suggested by earlier experiments with tree seedlings in pots. Future studies on photosynthesis measurements will probably not alter our conclusions about acclimation, but should focus more on respiration under elevated CO2, which is still poorly understood. At the tree level, the increase in growth observed in elevated CO2 results from an increase in both leaf area and leaf photosynthetic rate (per unit leaf area). Tree growth enhancement is generally larger at high rates of nutrient supply; when nutrient supply rates do not meet growth rates, tree nutrient status declines and nutrients become limiting. In many studies at the canopy level, a shift in whole-tree carbon allocation pattern towards below-ground parts has been associated with increased atmospheric CO2 concentrations. At the ecosystem level, a larger amount of carbon being allocated below-ground could show up by either (1) more root growth and turnover, (2) enhanced activity of root-associated microorganisms, (3) larger microbial biomass pools and enhanced microbial activity, or (4) increased losses of soil carbon through soil respiration. Fine root production is generally enhanced, but it is not clear whether this response would persist in a forest. As elevated CO2 stimulates biomass production, litterfall and rhizodeposition also increase. This increased delivery of labile organic matter to the soil could influence soil microbial communities and subsequent decomposition rates, nutrient availability and carbon storage in soil. There are, however, contradictory hypothesis about the direction in which nutrient availability will be affected. Knowledge of the response of these and other ecophysiological processes to elevated CO2 is the key to understanding the functioning of the whole forest ecosystem. Our current knowledge is sufficiently large with regard to how the carbon uptake process and individual tree growth respond under atmospheric changes, but more emphasis should be put in future experiments on the interactions between various processes, such as the carbon and nitrogen cycles, and on below-ground responses. (C) 1999 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO2, LEAF GAS- EXCHANGE, LONG-TERM CO2, MYCORRHIZAL COLONIZATION, OPEN-TOP CHAMBERS, PHOTOSYNTHETIC ACCLIMATION, PINE PINUS-PONDEROSA, SCOTS PINE, SOIL ORGANIC MATTER

348

Ceulemans, R., X.N. Jiang, and B.Y. Shao. 1995. Effects of elevated atmospheric CO2 on growth, biomass production and nitrogen allocation of two Populus clones. *Journal of Biogeography 22(2-3):261-268.*

Two hybrid poplar (Populus) clones (i.e. fast growing clone Beaupre and slower growing clone Robusta) were grown from cuttings at close spacings in four open top chambers (OTCs) on the Campus of the University of Antwerpen, Belgium. The four OTCs represented two atmospheric CO2 treatments, i.e. ambient and elevated (= ambient + 350 mu mol mol(-1)). Treatments lasted for a full growing season (April-November 1993) and results of the first growing season are being reported. In both clones the elevated CO2 treatment resulted in a significant increase in plant height and in biomass production, both of stems and branches. Plants of both clones produced significantly more, but shorter, side branches under the elevated CO2 treatment. In terms of biomass accumulation the slower growing clone Robusta benefited relatively more (+ 37%) from the elevated CO2 concentrations than the fast growing clone Beaupre (+ 24%). In terms of leaf weight ratio, the slower growing clone became relatively more efficient under elevated CO2 than the fast growing clone. The elevated atmospheric CO2 treatment significantly increased the total leaf area per plant and leaf area index per OTC; maximum LAI increased by 18% in clone Beaupre and by only 8% in the slower growing clone Robusta. In the fast growing elope the increase in leaf area index was entirely caused by an increase in individual leaf area, while in the slower growing clone also a 5% higher leaf production was observed under the elevated CO2. The total length of the growing season was on average reduced by the elevated CO2 treatment; in the slower growing clone mainly by an advancement of bud set and in the faster growing clone by a slight delay of bud break in early spring. In both clones elevated CO2 decreased nitrogen concentration and increased C/N ratio in all plant organs, but no data for the below-ground compartment were available. Therefore, although similar trends in the responses to elevated atmospheric CO2 were observed in both clones, the relative efficiency of these responses differed between the fast and the slower growing poplar clones, suggesting interactions between growth rate, growth strategy and response to elevated atmospheric CO2.

KEYWORDS: ENRICHMENT, POPLAR CLONES, SEEDLINGS, SOIL, TEMPERATURE

349

Ceulemans, R., X.N. Jiang, and B.Y. Shao. 1995. Growth and physiology of one-year-old poplar (populus) under elevated atmospheric co2 levels. *Annals of Botany 75(6):609-617.*

The effects of elevated atmospheric CO2 concentrations on the ecophysiological responses (gas exchange, chlorophyll a fluorescence, Rubisco activity, leaf area development) as well as on the growth and biomass production of two poplar clones (i.e. Populus trichocarpa x P. deltoides clone Beaupre and P. x euramericana clone Robusta) were examined under open top chamber conditions. The elevated CO2 treatment (ambient + 350 mu mol mol-1) stimulated above-ground biomass of clones Robusta and Beaupre after the first growing season by 55 and 38 %, respectively. This increased biomass production under elevated CO2 was associated with a significant increase in plant height, the latter being the result of enhanced internode elongation rather than an increased production of leaves or internodes. Both an increased leaf area index (LAI) and a stimulated net photosynthesis per unit leaf contributed to a significantly higher stem biomass per unit leaf area, and thus to the increased above-ground biomass production under the elevated CO2 concentrations in both clones. The larger LAI was caused by a larger individual leaf size and leaf growth rate; the number of leaves was not altered by the elevated CO2 treatment. The higher net leaf photosynthesis was the result of an increase in the photochemical (maximal chlorophyll fluorescence Fm and photochemical efficiency

Fv/Fm) as well as in the biochemical (increased Rubisco activity) process capacities. No significant differences were found in dark respiration rate, neither between clones nor between treatments, but specific leaf area significantly decreased under elevated CO2 conditions. (C) 1995 Annals of Botany Company

KEYWORDS: BRANCH BAG, CARBON DIOXIDE, CLONES, ENRICHMENT, GAS-EXCHANGE, LEAF-AREA, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, RESPONSES, WATER-STRESS

350

Ceulemans, R., and M. Mousseau. 1994. Tansley review no-71 - effects of elevated atmospheric co2 on woody-plants. *New Phytologist 127(3):425-446.*

Because of their prominent role in the global carbon balance and their possible carbon sequestration, trees are very important organisms in relation to global climatic changes. Knowledge of these processes is the key to understanding the functioning of the whole forest ecosystem which can be modelled and predicted based on the physiological process information. This paper reviews the major methods and techniques used to examine the likely effects of elevated CO2 on woody plants, as well as the major physiological responses of trees to elevated CO2. The available exposure techniques and approaches are described. An overview table with all relevant literature data over the period 1989-93 summarizes the percent changes in biomass, root/shoot ratio, photosynthesis, leaf area and water use efficiency under elevated CO2. Interaction between growth, photosynthesis and nutrition is discussed with a special emphasis on downward regulation of photosynthesis. The stimulation or reduction found in the respiratory processes of woody plants are reviewed, as well as the effect of elevated CO2 on stomatal density, conductance and water use efficiency. Changes in plant quality and their consequences are examined. Changes in underground processes under elevated CO2 are especially emphasized and related to the functioning of the ecosystem. Some directions for future research are put forward.

KEYWORDS: BETULA-PENDULA ROTH, BLACK SPRUCE SEEDLINGS, CARBON-DIOXIDE ENRICHMENT, CASTANEA-SATIVA MILL, INSECT HERBIVORE INTERACTIONS, LIRIODENDRON-TULIPIFERA L, LOBLOLLY-PINE SEEDLINGS, SITCHENSIS BONG CARR, SOUR ORANGE TREES, SOURCE-SINK RELATIONS

351

Ceulemans, R., and M. Mousseau. 1995. Effects of elevated atmospheric co2 on woody-plants (vol 12m, pg 425, 1995). *New Phytologist 129(3):535.*

352

Ceulemans, R., B.Y. Shao, X.N. Jiang, and J. Kalina. 1996. First- and second-year aboveground growth and productivity of two Populus hybrids grown at ambient and elevated CO2. *Tree Physiology 16(1-2):61-68.*

Two hybrid poplar (Populus) clones (the fast-growing clone Beaupre (P trichocarpa Torr. and Gray x P. deltoides Bartr. ex Marsh.) and the slow-growing clone Robusta (P deltoides Bartr. ex Marsh. x P. nigra L.)) were grown from hardwood cuttings for one or two growing seasons (1993-1994) in either ambient or elevated (= ambient + 350 mu mol mol(-1)) CO2 in open-top chambers at the University of Antwerpen. Both clones responded positively to the elevated CO2 treatment with increased stem volume and aboveground biomass production; however, the clones exhibited different response strategies to the elevated CO2 treatment, and the responses varied with cutting age and duration of exposure. Clone Beaupre responded to the elevated CO2 treatment with increases in leaf area and leaf area index during both the first and second growing seasons, but little increase in height growth. Clone Robusta exhibited increased height growth, leaf biomass and total leaf nitrogen content in response to elevated CO2, but no increase in leaf area index. The elevated CO2 treatment increased the total number of branches and total branch biomass in both clones during both growing seasons. At the end of the first growing season, woody stem biomass of the fast- and slow-growing clones was increased by 38 and 55%, respectively. At the end of the second growing season, stem volume was increased by 43% in clone Beaupre and by 58% in clone Robusta. The increase in stem volume was a result of the stimulation of both height and diameter growth in the slow-growing clone, whereas only height growth was stimulated in the fast-growing clone. In the fall of the first growing season, the average date of bud set in clone Robusta was advanced by 4 days in the elevated CO2 treatment; there were no other significant effects of the elevated CO2 treatment on bud set. The elevated CO2 treatment enhanced leaf C/N ratios in both clones in both years.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CASTANEA-SATIVA MILL, CLONES, ENRICHMENT, GAS-EXCHANGE, PLANTS, RESPONSES, SEEDLINGS, TREES

353

Ceulemans, R., G. Taylor, C. Bosac, D. Wilkins, and R.T. Besford. 1997. Photosynthetic acclimation to elevated CO2 in poplar grown in glasshouse cabinets or in open top chambers depends on duration of exposure. *Journal of Experimental Botany 48(314):1681-1689.*

The effects of elevated CO2 were studied on the photosynthetic gas exchange behaviour and leaf physiology of two contrasting poplar (Populus) hybrids grown and treated in open top chambers (OTCs in Antwerp, Belgium) and in closed glasshouse cabinets (GHCs in Sussex, UK). The CO2 concentrations used in the OTCs were ambient and ambient +350 mu mol mol(-1), while in the GHCs they were c, 360 mu mol mol(-1) versus 719 mu mol mol(-1). Measurements of photosynthetic gas exchange were made for euramerican and interamerican poplar hybrids in combination with measurements of dark respiration rate and Rubisco activity. Significant differences in the leaf anatomy and structure (leaf mass per area and chlorophyll content) were observed between the leaves grown in the OTCs and those grown in the GHCs. Elevated CO2 stimulated net photosynthesis in the poplar hybrids after 1 month in the GHCs and after 4 months in the OTCs, and there was no evidence of downward acclimation (or downregulation) of photosynthesis when the plants in the two treatments were measured in their growth CO2 concentration. There was also no evidence of downregulation of Rubisco activity and there were even examples of increases in Rubisco activity. Rubisco exerted a strong control over the light- saturated rate of photosynthesis, which was demonstrated by the close agreement between observed net photosynthetic rates and those that were predicted from Rubisco activities and Michaelis-Menten kinetics. After 17 months in elevated CO2 in the OTCs there was a significant loss of Rubisco activity for one of the hybrid clones, i.e. Beaupre, but not for clone Robusta, The effect of the CO2 measurement concentration (i.e. the short-term treatment effect) on net photosynthesis was always larger than the effect of the growth concentration in both the OTCs or GHCs (i.e. the long-term growth CO2 effect), with one exception, For the interamerican hybrid Beaupre dark respiration rates in the OTCs were not significantly affected by the elevated CO2 concentrations. The results suggest that for rapidly growing tree species, such as poplars, there is little evidence for downward acclimation of photosynthesis when plants are exposed to elevated CO2 for up to 4 months; longer term exposure reveals loss of Rubisco activity.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-

EXCHANGE, HYBRID POPLAR, LEAF DEVELOPMENT, LONG-TERM ELEVATION, POPULUS- EURAMERICANA, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE, TOMATO

354

Ceulemans, R., L. Vanpraet, and X.N. Jiang. 1995. Effects of co2 enrichment, leaf position and clone on stomatal index and epidermal-cell density in poplar (populus). *New Phytologist 131(1):99-107.*

The effects of CO2 enrichment and leaf position on stomatal characteristics (stomatal density, stomatal index and stomatal pore length) and epidermal cell density were examined for two different Populus clones, Beaupre and Robusta, grown from cuttings in open-top chambers under ambient and elevated atmospheric CO2 conditions. Both clones had amphistomatous leaves, and stomatal density was significantly larger on the abaxial leaf surface than on the adaxial. Significant interactions between CO2 enrichment, leaf position and clone were observed for most stomatal and epidermal characteristics. A significant reduction of the number of stomata mm(-2) under elevated CO2 was observed in expanding leaves near the upper portion of the plant for both leaf surface sides and in both clones. For the abaxial leaf side only, this reduction under elevated CO2 was accompanied by a similar reduction of the stomatal index in both clones. In mature leaves on the middle and lower portion of the plants, there was no significant effect of the CO2 treatment on stomatal density. In young, expanding leaves near the upper part of the plant there were significant interactions between the CO2 treatment and leaf surface side for epidermal cell density. The latter increased under elevated CO2 at the abaxial leaf surface, but decreased at the adaxial surface on the upper part of the plant. Total epidermal cell numbers of mature, fully expanded leaves increased under elevated CO2 in both clones. The observation that interactions with leaf age and/or leaf position significantly confound the CO2 treatment effect on stomatal and epidermal cell densities, might contribute to the elucidation of the problem of the phenomenon of stomatal density reduction under elevated atmospheric CO2.

KEYWORDS: ANATOMY, ATMOSPHERIC CO2, GROWTH, INCREASE, NUMBERS, OAK LEAVES, TEMPERATURE

355

Chabot, S., R. Belrhlid, R. Chenevert, and Y. Piche. 1992. Hyphal growth promotion invitro of the va mycorrhizal fungus, gigaspora-margarita becker and hall, by the activity of structurally specific flavonoid compounds under co2-enriched conditions. *New Phytologist 122(3):461-467.*

Plant phenolic compounds are known to be inducers of virulence genes in plant-pathogen interactions such as those involving Agrobacterium, and flavonoids are known to be inducers or inhibitors of Nod genes in Rhizobium-legume symbiosis. More recent studies suggest that some of these compounds act as molecular signals in the development of vesicular-arbuscular mycorrhizas (VAM). The present study has shown that hyphal growth of the VAM fungus, Gigaspora margarita Becker & Hall, is affected by both stimulatory and inhibitory flavonoids, when applied at 10 muM together with an optimal carbon dioxide enrichment. Stimulatory compounds were all flavonols (kaempferol, quercetin and morin) and possessed at least one hydroxyl group on the B ring. Conversely, two isoflavones (biochanin A, and genistein), a single flavanone (hesperetin) and two compounds without any hydroxyl group on the B ring, galangin (flavonol) and chrysin (flavone), were all inhibitors of hyphal growth.

KEYWORDS: AGROBACTERIUM-TUMEFACIENS, DNA TRANSFORMED ROOTS, EXPRESSION, HOST, IDENTIFICATION, MELILOTI NODULATION GENES, PHENOLIC-COMPOUNDS, RHIZOBIUM, SIGNAL COMPOUNDS, SPORE GERMINATION

356

Chagvardieff, P., T. Daletto, and M. Andre. 1994. Specific effects of irradiance and co2 concentration doublings on productivity and mineral-content in lettuce. *Life Sciences and Space Research XXV (3) 14(11):269-275.*

Experiments in growth chambers with controlled atmosphere were performed to compare the effects on the productivity of two treatments stimulating photosynthesis : the doubling of CO2 concentration, the doubling of irradiance; the combining of both was also tested. A large effect of light was noticed : (i) the accumulation of carbon was, contrarily to CO2 effect, amplified within time, and led to the most important dry matter production. (ii) the specific leaf weight was about two-fold increased. (iii) the nitrate content was 2-3 fold less. A significant positive effect of CO2 was detected on the fresh biomass production and the iron content of lettuce. A synergy was observed on dry matter production by the interaction of the two factors.

KEYWORDS: CARBOHYDRATE, ENRICHMENT, GROWTH, HIGH-PRESSURE SODIUM, LAMPS, LIGHT, PHOTOSYNTHESIS

357

Chagvardieff, P., B. Dimon, A. Souleimanov, D. Massimino, S. Le Bras, M. Pean, and D. Louche-Teissandier. UNKNOWN YEAR. Effects of modified atmosphere on crop productivity and mineral content. *Life Sciences: Life Support Systems Studies-I :1971-1974.*

Wheat, potato, pea and tomato crops were cultivated from seeding to harvest in a controlled and confined growth chamber at elevated CO2 concentration (3700 mu L.L-1) to examine the effects on biomass production and edible part yields. Different responses to high CO2 were recorded, ranging from a decline in productivity for wheat, to slight stimulation for potatoes, moderate increase for tomatoes, and very large enhancement for pea. Mineral content in wheat and pea seeds was not greatly modified by the elevated CO2. Short-term experiments (17 d) were conducted on potato at high (3700 mu L.L-1) and very high (20,000 mu L.L-1) CO2 concentration and/or low O-2 partial pressure (similar to 20,600 mu L.L-1 or 2 kPa). Low O-2 was more effective than high CO2 in total biomass accumulation, but development was affected: Low O-2 inhibited tuberization, while high CO2 significantly increased production of tubers. (C) 1997 COSPAR. Published by Elsevier Science Ltd.

KEYWORDS: INCOMPLETE, CARBON DIOXIDE, CO2 CONCENTRATION, GROWTH, IRRADIANCE, POTATO, TEMPERATURE, WHEAT

358

Chalabi, Z., and J.E. Fernandez. 1992. Spatiotemporal responses of a glasshouse to gaseous enrichment. *Journal of Agricultural Engineering Research 51(2):139-151.*

KEYWORDS: SUMMER CO2 ENRICHMENT, SYSTEMS, YIELD

359

Chalabi, Z.S., and J.E. Fernandez. 1994. Estimation of net photosynthesis of a greenhouse canopy using a mass-balance method and mechanistic models. *Agricultural and Forest Meteorology 71(1-2):165-182.*

Two mechanistic models for estimating net photosynthesis of a greenhouse canopy are evaluated against measurements using mass balance of CO2 fluxes. The discrepancies observed between the mechanistic models and the CO2 mass balance measurement method are

attributed to the underestimation of leakage rate, the error in estimating radiation transmission in direct light conditions, and the spatial inhomogeneity of the CO2 concentration inside the glasshouse.

KEYWORDS: CO2- ENRICHMENT, CROP, OPTIMIZATION, STRATEGY, VENTILATION

360

Chan, Y.S.G., M.H. Wong, and B.A. Whitton. 1998. Effects of landfill gas on growth and nitrogen fixation of two leguminous trees (Acacia confusa, Leucaena leucocephala). *Water, Air, and Soil Pollution 107(1-4):409-421.*

A study was made on the effects of landfill gas on ARA (acetylene reducing activity) of nodules of two woody legumes (Acacia confusa and Leucaena leucocephala) widespread on landfill sites in Hong Kong. The effects of the three main components of landfill gas, O2, CO2 and CH4, were first measured separately over a I-hr period. Maximum ARA was found at 20% O2 (close to atmospheric partial pressure) and ARA decreased as the O2 decreased in the range of 16-1%. Acacia confusa nodular ARA was significantly inhibited at 30-50% CO2, but not Leucaena leucocephala nodular ARA. CH4 had no significant effect on ARA of either species. As the landfill gas concentrations in the landfill topsoil were mostly > 10% O2 and < 10% CO2, root nodules should fix N2 effectively over these ranges of gases. A four-week test was conducted to assess the long-term influence of landfill gas on seedlings of the two legumes. Landfill gas and elevated CO2 both suppressed their growth and their nodular ARA. Even under the influence of the gases, however, seedlings with nodules formed a higher biomass than seedlings lacking nodules. The growth of the two legumes under actual landfill conditions was investigated by transplanting non-inoculated and pre-inoculated seedlings to two landfill sites in Hong Kong: Junk Bay and Shuen Wan Landfill. After six months, most of the non-inoculated seedlings became infected: Acacia confusa 63 and 70%, Leucaena leucocephala 17 and 89%, respectively, at the test sites. The results indicate that there were free rhizobia at these landfill sites to infect the legumes and they had formed effective nodules to fix N2 under landfill conditions.

KEYWORDS: CARBON DIOXIDE, NODULES, PLANTS

361

Chapin, F.S., E. Rincon, and P. Huante. 1993. Environmental responses of plants and ecosystems as predictors of the impact of global change. *Journal of Biosciences 18(4):515-524.*

An understanding of plant responses to fluctuations in environment is critical to predictions of plant and ecosystem responses to climate change. In the northern hemisphere, the northern limits of distribution of major biomes are probably determined by the tolerance of their dominant physiognomic types (e.g., deciduous hardwood trees) to minimum winter temperatures and can thus be predicted from long-term patterns of temperature fluctuations. At a more detailed level, the responses of functional groups of plants to altered climate can be predicted from their known responses to fluctuations in soil resources (nutrients and water) and the expected effect of climatic change on these soil resources. Laboratory and field experiments demonstrate the feasibility of this approach.

KEYWORDS: CO2-INDUCED CLIMATE CHANGE, CONTRASTED ECOLOGY, ENRICHMENT, FOREST, GROWTH, MEXICO, NORTH-AMERICA, PLASTICITY, ROOT-SYSTEM, SEEDLINGS

362

Chaves, M.M., and J.S. Pereira. 1992. Water-stress, co2 and climate change. *Journal of Experimental Botany 43(253):1131-1139.*

Climatic change may bring about increased aridity to large areas of Europe. Higher temperatures, larger water deficits and high light stress are likely to occur in conjunction with elevated atmospheric CO2. This raises the question whether a high CO2 concentration in the atmosphere can compensate for the decrease in carbon gain in water-stressed plants. The processes which determine dry matter production and the ways they are affected by soil water deficits are discussed. It is now well established that in most species and under most circumstances stomata are the main limiting factor to carbon uptake under water deficit, the photosynthetic machinery being highly resistant to dehydration. However, when other stresses are superimposed, a decline in photosynthetic capacity may be observed. In the short term, under drought conditions, the increase in CO2 in the atmosphere may diminish the importance of stomatal limitation for carbon assimilation, inhibit photorespiration, stimulate carbon partitioning to soluble sugars and increase water-use efficiency. Some recent evidence seems to indicate that under conditions of high irradiance, plants growing at elevated CO2 may develop protection towards photoinhibition, which might otherwise result in significant losses in plant production under stress conditions. In the longer term though, a negative acclimation of photosynthesis appears to occur in many species, an explanation for which still needs to be clearly identified. Similarly, the effects of extended exposure to elevated CO2 under arid conditions are not known. Plant production is more closely related to the integral of photosynthesis over time and total foliage area than to the instantaneous rates of the photosynthetic process. Water deficits result in a decrease in foliage area biomass and, therefore, in productivity. On the other hand, the increase in air temperature may result in more respiratory losses. However, experimental as well as simulatory evidence suggests that doubling CO2 concentration in the air may improve carbon assimilation and compensate partially for the negative effects of water stress even if we assume a down-regulation of the photosynthetic process as a result of acclimation to elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DROUGHT STRESS, DRY-WEIGHT, ELEVATED CO2, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC INHIBITION, RIBULOSE BISPHOSPHATE CARBOXYLASE, STOMATAL DENSITY, SUCROSE PHOSPHATE SYNTHASE

363

Chaves, M.M., J.S. Pereira, S. Cerasoli, J. CliftonBrown, F. Miglietta, and A. Raschi. 1995. Leaf metabolism during summer drought in Quercus ilex trees with lifetime exposure to elevated CO2. *Journal of Biogeography 22(2-3):255-259.*

A marginal improvement in the response of Quercus ilex adult trees to drought appears to occur under a long-term natural CO2 enrichment. This is expressed, for example, by the absence of midday stomatal closure in trees growing under elevated CO2. Some protection against high irradiance and high temperature seems also to occur at the photochemical level, presumably as a result of more carbon available to the consumption of excess light energy. This would allow a better performance of the plants grown under elevated CO2 during the warmer hours of the day and therefore playing an important adaptation role under drought conditions. A marginal increase in the concentration of soluble sugars and starch was observed in the leaves of trees growing at elevated CO2 as compared with plants at ambient CO2, mainly during the midday hours. We may speculate that this will be advantageous both in terms of carbohydrate reserves for growth (e.g. more roots) and osmotic adjustment.

KEYWORDS: FIELD, LEAVES, QUANTUM YIELD

364

Chemeris, Y.K., L.V. Shenderova, and P.S. Venediktov. 1996. Chloroplast respiration in Chlorella pyrenoidosa CALU-175: Effects of nitrogen deficiency, exogenous glucose, and elevated temperature. *Russian Journal of Plant Physiology 43(4):474-479.*

The rate of chloroplast respiration in Chlorella was studied with respect to some changes in the physiological state induced by nitrogen deficiency, heterotrophic growth, and incubation at supraoptimal temperature. Iodoacetamide (an inhibitor of glycolysis), salicylhydroxamate (an inhibitor of nonmitochondrial respiration), and 2-deoxy-D-glucose (a nonmetabolizable analogue of glucose), inhibited the respiration of chloroplasts. Treatments that inactivate photosystem II (PS II), i.e., the addition of glucose, nitrogen deprivation, or dark incubation at elevated temperatures (39-43 degrees C), drastically (8-10 times) increased the rate of chloroplast respiration. In the absence of CO2, no enhancement of chloroplast respiration was recorded in nitrogen-starved cells. Cycloheximide, an inhibitor of cytoplasmic protein synthesis, and 2-deoxy-D-glucose prevented the increase in the chloroplast respiration rate caused by the addition of glucose or incubation at elevated temperatures. It is suggested that the inhibition of PS II, previously described in Chlorella incubated for a long time at supraoptimal temperature, is associated with the enhancement of chloroplast respiration.

KEYWORDS: CELLS, CHLAMYDOMONAS-REINHARDTII, CHLORORESPIRATION, TRANSPORT

365

Chemeris, Y.K., P.S. Venediktov, and A.B. Rubin. 1996. Role of chloroplast respiration in the inactivation of photosystem II in Chlorella. *Russian Journal of Plant Physiology 43(6):716-723.*

Nitrogen deficiency, dark incubation on glucose, and dark incubation at an elevated temperature (41 degrees C) were previously shown to inactivate photosystem II (PS LI) in Chlorella pyrenoidosa Chick, strain CALU-175. These treatments also increased chloroplast respiration by 7-11 times, At the same time, any attempt to inhibit the accumulation of substrates for chloroplast respiration (CO2 deprivation during nitrogen starvation, inhibition of glucose metabolism by a nonmetabolizable analog of glucose, 2-deoxy-D-glucose, or inhibition of protein synthesis by cycloheximide during dark incubation on glucose or by heat shock) prevented the stimulation of chloroplast respiration and PS II inactivation, Inhibition of the oxygen-dependent oxidation of the plastoquinone pool under anaerobic conditions or in the presence of salicylhydroxamate, an inhibitor of chloroplast oxidases, markedly increased the extent and rate of PS II inactivation in cells subjected to heat shock. The dependencies of chloroplast respiration and the PS II inactivation rate on the hear-shock temperature exactly matched one another. Diuron, an inhibitor of photosynthetic electron transport between the primary and secondary quinone electron accepters, did not affect the rate of chloroplast respiration, but prevented PS II inactivation. We propose that the inactivation of PS II caused by these treatments is due to the loss of the primary quinone electron acceptor as a consequence of its two-electron reduction from the plastoquinone reduced by the electron flow from the substrates of chloroplast respiration.

KEYWORDS: CHLAMYDOMONAS-REINHARDTII, CHLORORESPIRATION

366

Chen, C.L., C.C. Li, and J.M. Sung. 1994. Carbohydrate-metabolism enzymes in co2-enriched developing rice grains of cultivars varying in grain-size. *Physiologia Plantarum 90(1):79-85.*

The increased supply of photosynthate from maternal tissue is known to promote grain growth in several crop species. However, the effect of increasing photosynthate supply on grain growth receives little attention in rice. This study was aimed at evaluating the effect of increasing photosynthate supply through CO2 enrichment (650 mul l-1) on grain growth in three rice cultivars differing in grain size. CO2 enrichment was applied to the pot-grown plants between anthesis and final harvest. The results indicated that high CO2 treatment enhanced the CO2 exchange rate of leaf tissue, and subsequently increased the sucrose level of peduncle exudate, but it did not promote starch accumulation in the developing grains. This phenomenon was linked to the poor CO2 responses for the grain activities of sucrose synthase, UDP-glucose pyrophosphorylase, ADP-glucose pyrophosphorylase, and starch synthases involved in the converison of sucrose to starch. Significant cultivar differences also existed for the activities of sucrose to starch conversion enzymes with larger grain size cultivars tending to have higher enzymes activities (expressed on a grain basis), resulting in a greater carbohydrate accumulation.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, CO2, GROWTH, MAIZE, ORYZA-SATIVA, STARCH, SUCROSE SYNTHASE, ULTRAVIOLET-B RADIATION, WHEAT

367

Chen, C.T., and T.L. Setter. 1997. Potato response to elevated CO2 and temperature. *Plant Physiology 114(3):490.*

368

Chen, D.X., and M.B. Coughenour. 1996. A mechanistic model for submerged aquatic macrophyte photosynthesis: Hydrilla in ambient and elevated CO2. *Ecological Modelling 89(1-3):133-146.*

There are significant knowledge gaps about the responses of submerged aquatic macrophytes to CO2 enrichment and global warming. A mechanistic steady-state photosynthesis model for submerged aquatic macrophytes was developed to provide an analysis tool to investigate the responses of plant photosynthesis to CO2, temperature and light. The model was based upon a general simplified scheme for inorganic carbon assimilation of submerged aquatic macrophytes which integrated the knowledge about aquatic plant photosynthesis from previous research, mainly on Hydrilla. The model includes: (1) diffusion and/or active transfer of inorganic carbon (CO2 and/or HCO3-) in the bathing medium into the leaf mesophyll and cytosol; (2) diffusion and/or 'pumping' of CO2 through the PEPcase-related C-4 pathway into the chloroplast; (3) inter-conversions between CO2 and HCO3- inside cells; (4) photosynthetic carbon reduction cycle (PCR) in the chloroplast. In the model, the PCR processes in the chloroplast were described using the widely accepted C-3 photosynthesis model. The activity of the C-4 cycle was related to environmental CO2 'stress'. In this way, the model can simulate the shift between C-3-like and C-4-like photosynthesis under different environmental conditions. The model was validated using gas exchange data from Hydrilla plants grown in ambient and elevated CO2. The model predicted quite well photosynthetic responses to incident PAR, temperature and ambient CO2 for both ambient and elevated atmospheric CO2 treatments. Model predictions agreed well with measured Hydrilla gas exchange data. The simulated and measured CO compensation points of Hydrilla leaf photosynthesis were about 100 ppm. The light compensation point of photosynthesis was about 25 mu mol m(-2)s(-1) (PAR), and photosynthesis rate was saturated at about 100 mu mol m(-2)s(-1) (PAR). Higher pH slightly increased photosynthesis rates at ambient CO2 (similar to 350 ppm). There was no significant acclimation of Hydrilla photosynthesis to elevated CO2 within the experimental period. Simulated CO2 compensation point decreased with increasing activity of C-4-cycle processes.

KEYWORDS: ASSIMILATION, CARBOXYLASE, FIXATION, LEAVES,

OXYGEN, PLANTS, RESPIRATION, TEMPERATURE-DEPENDENCE

369

Chen, D.X., M.B. Coughenour, D. Eberts, and J.S. Thullen. 1994. Interactive effects of co2 enrichment and temperature on the growth of dioecious hydrilla-verticillata. *Environmental and Experimental Botany 34(4):345-353.*

Experiments of plant growth responses to different CO2 concentrations and temperatures were conducted in growth chambers to explore the interactive effects of atmospheric CO2 enrichment and temperature on the growth and dry matter allocation of dioecious Hydrilla [Hydrilla verticillata (L.f.) Royle]. Hydrilla plants were exposed to two atmospheric CO2 concentrations (350 and 700 ppm) and three temperatures (15, 25 and 32 degrees C) under a 12-hr photoperiod for about 2 months. The plant growth analysis showed that elevated CO2 appeared to enhance the growth of Hydrilla, and that the percentage of the enhancement is strongly temperature-dependent. Maximum biomass production was achieved at 700 ppm CO2 and 32 degrees C. At 15 degrees C, the total dry matter production was increased about 27% by doubling CO2, due to a 26% enhancement of leaf biomass, a 34% enhancement of stem biomass and 16% enhancement of root biomass. At 25 degrees C, the dry matter production was increased about 46% by doubling CO2, due to a 29% enhancement of leaf biomass, a 27% enhancement of stem biomass and 40% enhancement of root biomass. At 32 degrees C, however, the percentage of the enhancement of total dry matter production by doubling CO2 was only about 7%. The dry matter allocation among different plant parts was influenced by temperature but not by elevated CO2 concentration.

KEYWORDS: AQUATIC MACROPHYTES, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, ENVIRONMENT, PHOTOSYNTHETIC RESPONSE, YIELD

370

Chen, D.X., M.B. Coughenour, A.K. Knapp, and C.E. Owensby. 1994. Mathematical simulation of C4 grass photosynthesis in ambient and elevated co2. *Ecological Modelling 73(1-2):63-80.*

A mechanistic leaf photosynthesis model was developed for C4 grasses based on a general simplified scheme of C4 plant carbon metabolism. In the model, the PEPcase-dependent C4-cycle was described in terms of CO2 concentration in the mesophyll space using Michaelis-Menten kinetics, and the activity of PEPcase was related to the incident PAR to take account of the influence of light on the activty of C4-cycle processes. The CO2 refixation by Rubisco in the bundle sheath was described using a widely accepted C3 photosynthesis model. The model assumes a steady state balance among CO2 diffusion from surrounding atmosphere into the mesophyll space, CO2 transport into the bundle sheath by the C4-cycle, CO2 refixation by the C3-cycle in the bundle sheath, and CO2 leakage from the bundle sheath. The response to temperature of photosynthesis was incorporated via the temperature dependence of model parameters. The photosynthesis model was coupled with a stomatal conductance model in order to predict leaf photosynthesis rates at different atmospheric conditions. The empirical model of Ball et al. (1987) was adopted and slightly modified to describe responses in stomatal conductance. The coupled model was parameterized for the C4 grass Andropogon gerardii grown in both ambient (350 ppm) and elevated (700 PPM) CO2 atmospheres. The key parameters of the model were estimated by fitting the model to the measured data using non-linear regression. The model was validated by comparison the predicted photosynthetic response to PAR in both CO2-pretreatments with the measured data from an independent gas exchange experiment. The predicted photosynthesis and stomatal conductance matched the measured data quite well for both atmospheric CO2-pretreatments. At 25-degrees-C, the estimated maximum carboxylation rate of Rubisco V(cm,25), potential electron transport rate J(m,25) and quantum efficiency alpha were increased by CO2 enrichment. The maximum PEPcase activity V(pm,25) was lower in elevated CO2. The model predicted that the light-saturated leaf photosynthesis will increase by about 10% with the rising of atmospheric CO2 from 350 to 700 ppm at 30-degrees-C, and that the optimal temperature of photosynthesis will shift from 37 to 38.5-degrees-C. The estimated slope of the stomatal conductance model was increased by atmospheric CO2 enrichment. Stomatal conductance was significantly reduced by increasing atmospheric CO2 concentration.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE OXYGENASE, BUNDLE SHEATH-CELLS, C-4, INORGANIC CARBON, LEAVES, MECHANISM, MODEL, PLANTS, TALLGRASS PRAIRIE, TEMPERATURE-DEPENDENCE

371

Chen, D.X., H.W. Hunt, and J.A. Morgan. 1996. Responses of a C-3 and C-4 perennial grass to CO2 enrichment and climate change: Comparison between model predictions and experimental data. *Ecological Modelling 87(1-3):11-27.*

Ecological responses to CO2 enrichment and climate change are expressed at several interacting levels: photosynthesis and stomatal movement at the leaf level, energy and gas exchanges at the canopy level, photosynthate allocation and plant growth at the plant level, and water budget and nitrogen cycling at the ecosystem level. Predictions of these ecosystem responses require coupling of ecophysiological and ecosystem processes. Version GEM2 of the grassland ecosystem model linked biochemical, ecophysiological and ecosystem processes in a hierarchical approach. The model included biochemical level mechanisms of C-3 and C-4 photosynthetic pathways to represent direct effects of CO2 on plant growth, mechanistically simulated biophysical processes which control interactions between the ecosystem and the atmosphere, and linked with detailed biogeochemical process submodels. The model was tested using two-year full factorial (CO2, temperature and precipitation) growth chamber data for the grasses Pascopyrum smithii (C-3) and Bouteloua gracilis (C-4). The C-3-C-4 photosynthesis submodels fitted the measured photosynthesis data from both the C-3 and the C-4 species subjected to different CO2, temperature and precipitation conditions. The whole GEM2 model accurately fitted plant biomass dynamics and plant N content data over a wide range of temperature, precipitation and atmospheric CO2 concentration. Both data and simulation results showed that elevated CO2 enhanced plant biomass production in both P. smithii (C-3) and B. gracilis (C- 4). The enhancement of shoot production by elevated CO2 varied with temperature and precipitation. Doubling CO2 increased modeled annual net primary production (NPP) of P. smithii by 36% and 43% under normal and elevated temperature regimes, respectively, and increased NPP of B. gracilis by 29% and 24%. Doubling CO2 decreased modeled net N mineralization rate (Nmin) of soil associated with P. smithii by 3% and 2% at normal and high temperatures, respectively. Nmin of B. gracilsi soil decreased with doubled CO2 by 5% and 6% at normal and high temperatures. NPP increased with precipitation. The average NPP and Nmin of P. smithii across the treatments was greater than that of B. gracilis. In the C-3 species the response of NPP to increased temperatures was negative under dry conditions with ambient CO2, but was positive under wet conditions or doubled CO2. The responses of NPP to elevated CO2 in the C-4 species were positive under all temperature and precipitation treatments. Nmin increased with precipitation in both the C-3 and C-4 species. Elevated CO2 decreased Nmin in the C-4 system. The effects of elevated CO2 on Nmin in the C-3 system varied with precipitation and temperature. Elevated temperature decreased Nmin under dry conditions, but increased it under wet conditions. Thus, there are strong interactions among the effects of CO2 enrichment, precipitation, temperature and species on NPP and Nmin. Interactions between ecophysiological processes and ecosystem

processes were strong. GEM2 coupled these processes, and was able to represent the interactions and feedbacks that mediate ecological responses to CO2 enrichment and climate change. More information about the feedbacks between water and N cycling is required to further validate the model. More experimental and modeling efforts are needed to address the possible effects of CO2 enrichment and climate change on the competitive balance between different species in a plant community and the feedbacks to ecosystem function.

KEYWORDS: AMBIENT, CARBON, ELEVATED ATMOSPHERIC CO2, GROWTH, LEAVES, PLANTS, RISING CO2, SIMULATION-MODEL, TEMPERATURE-DEPENDENCE, WATER-USE

372

Chen, J.L., and J.F. Reynolds. 1997. GePSi: A generic plant simulator based on object-oriented principles. *Ecological Modelling 94(1):53-66.*

The Generic Plant Simulator (GePSi) is a physiologically-based model that combines modules for canopy, root environment, water relations, and potential growth to generate whole-plant carbon, nitrogen, and water balances. The version presented here is coded in the object-oriented programming (OOP) language, C++, to enhance the implementation of modularity. In the aboveground aerial environment, the Weather module defines the weather conditions above a canopy, and MicroWeather defines the vertical profiles of micro-meteorological variables in a canopy. The belowground soil environment contains the SoilProperty modules, which define vertical profiles of physical and chemical variables in a soil column. The 'part-of' hierarchy in GePSi follows the structure of a real plant: the Plant module calls canopy and root system modules; the Canopy module, in turn, calls leaf, stem and fruit modules, and the RootSystem module calls coarse and fine root modules, etc. Our long-term goal is for GePSi to serve as a template for building a plant growth simulator by simply selecting appropriate modules for the question being asked. We are building a suite of plant modules (and their interfaces) based on general principles that are fundamentally similar for different kinds of plants. This includes photosynthesis, growth, nutrient and carbon allocation, water uptake, etc. These modules can be parameterized for specific species, related groups of species, life-forms, or broader groups depending on how variable the processes are across the groupings and the amount of unexplained variability that is acceptable for the question being investigated. Our modular-based approach has numerous advantages, including improving the understanding of the model, reducing duplication of effort, and facilitating the adaptation of the model for different sites and ecosystems. (C) 1997 Elsevier Science B.V.

KEYWORDS: DESIGN, ECOLOGICAL MODEL, GROWTH, SYSTEMS

373

Chen, K., G.Q. Ha, N. Keutgen, M.J.J. Janssens, and F. Lenz. 1999. Effects of NaCl salinity and CO2 enrichment on pepino (Solanum muricatum Ait.) - I. Growth and yield. *Scientia Horticulturae 81(1):25-41.*

One-month old, rooted, semi-hardwood cutting plants of pepino cv. Xotus in sand-potted culture were treated with 200 mi Hoagland nutrient solution with or without additional 25 mM NaCl twice a week for 2 months, and exposed to 350 +/- 10, 700 +/- 10 or 1050 +/- 10 ppm CO2 in controlled environment chambers during the last month of the experiment. NaCl salinity in the rhizosphere reduced growth of all the organs, but raised stem dry weight ratio and root dry weight ratio. In contrast, atmospheric CO2 enrichment increased plant and fruit growth. Leaf dry weight ratio and fruit dry weight ratio rose, but stem dry weight ratio and root dry weight Patio decreased at high CO2 levels. Daily expansion rate of leaf area, growth rate of side-shoot length, rate of plant dry mass production, and increased rate of fresh fruit weight decreased due to NaCl stress, but increased with CO2 enrichment. Side-shoot diameter rose, whereas specific leaf area, leaf area ratio, and side- shoot dry weight ratio declined under both NaCl-stressed and CO2-enriched conditions. In comparison with the 350 ppm CO2 treatment without NaCl salinity in the rhizosphere, net assimilation rate and relative growth rate of plants were reduced by 8-13% and 16-32% due to NaCl salinity, and enhanced by 22-23% and 42-64% at 700 ppm CO2, and by 36-44% and 64-101% at 1050 pm CO2, respectively. The simultaneous treatments of NaCl salinity and high CO2 resulted in indefinite effects on vegetative and reproductive growth as well as on dry mass production of different plant organs. Nevertheless, the negative impacts of NaCl stress on plant growth and fruit yield diminished at high CO2 levels. Atmospheric CO2 enrichment increased the tolerance of pepino to NaCl salinity in the root medium. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CELLS, ECOSYSTEMS, FRUIT, PHOTOSYNTHESIS, PLANTS, RESPONSES

374

Chen, K., G.Q. Hu, N. Keutgen, M. Blanke, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. II. Leaf photosynthetic function. *Journal of Applied Botany-Angewandte Botanik 71(5-6):173-178.*

Two-week-old strawberry (Fragaria x ananassa Duch, cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 days. An elevated CO2 concentration up to 750 ppm reduced total chlorophyll, chlorophyll a and chlorophyll b contents as well as the a/b ratio. Long-term CO2 enrichment induced leaf senescence and decreased photosynthetic efficiency as well as photochemical conversion efficiency of PS II. Intercellular CO2 concentration significantly increased with CO2 enrichment. Stomatal conductance, transpiration rate, and net photosynthesis rate of young leaves increased with raising CO2 concentrations. However, CO2 levels above 600 ppm markedly reduced net photosynthetic rate of adult and old leaves. High CO2 concentrations up to 900 ppm did not significantly affect dark respiration rate of the leaves. Photosynthetic water-use efficiency was highest in old leaves and lowest in young ones. Increased CO2 concentrations up to 600-750 ppm improved leaf photosynthetic capacity by increasing photosynthetic water-use efficiency.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, PLANTS, RESPONSES, WATER-USE

375

Chen, K., G.Q. Hu, N. Keutgen, M.J.J. Janssens, and F. Lenz. 1999. Effects of NaCl salinity and CO2 enrichment on pepino (Solanum muricatum Ait.) - II. Leaf photosynthetic properties and gas exchange. *Scientia Horticulturae 81(1):43-56.*

One-month old, rooted semi-hardwood cutting plants of pepino cv. Xotus in sand-potted culture were treated with 200 ml Hoagland nutrient solution with or without additional 25 mM NaCl twice a week for 2 months, and exposed to 350 +/- 10, 700 +/- 10 or 1050 +/- 10 ppm CO2 in controlled environment chambers during the last month of the experiment. Both NaCl salinity in the rhizosphere and atmospheric CO2 enrichment reduced the leaf content of total chlorophyll, chlorophyll a and chlorophyll b, as well as stomatal conductance and transpiration rate, but raised intercellular CO2 concentration and C2H4 emission of leaves. Minimal fluorescence yield, maximal fluorescence yield, variable fluorescence yield of dark-adapted leaves, optimal quantum yield and effective quantum yield of PS II, photochemical quenching coefficient, net photosynthetic rate, leaf water-potential, and photosynthetic water-

use efficiency decreased under NaCl stress, but rose with an increase of the atmospheric CO2 concentration. In addition, the non-photochemical quenching coefficient and the dark respiration rate of leaves increased due to NaCl salinity and decreased at high CO2 conditions. On average, net photosynthetic rate and photosynthetic water-use efficiency of leaves decreased by 26-35% and 19-29% due to the presence of NaCl stress in the root medium, but increased by 75-98% and 85-123% at 700 ppm CO2, and by 72-91% and 124-147% at 1050 ppm CO2 in comparison with 350 ppm CO2 treatments. Under NaCl stress, high CO2 improved photosynthetic water-use efficiency of leaves. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, GROWTH, RESPIRATION, RESPONSES, STRAWBERRY, STRESS

376

Chen, K., G.Q. Hu, N. Keutgen, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. I. Plant Growth analysis. *Journal of Applied Botany-Angewandte Botanik 71(5-6):168-172.*

Two-week-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 days, Elevated CO2 promoted plant growth as indicated by a higher number of leaves, runners and daughter plants, larger leaf area index and dry mass per unit leaf area, increased total length of runners, plant height, canopy diameter, and enhanced daily growth of leaf area, runner and plant biomass. In contrast, specific leaf area and leaf area ratio of the plants decreased with increasing CO2 concentration, whereas neither average leaf area nor average runner length was significantly affected by CO2 enrichment. When compared with the 300 ppm CO2 treatment, 600 and 900 ppm CO2-treated plants led to a daily increment of 1.6 and 1.9 total leaf area, 1.1 and 1.8 total runner length, and 2.5 and 3.9 plant biomass, respectively, Increased CO2 concentration from 300 to 600 and 750 ppm markedly accelerated both relative growth rate and net assimilation rate of the plants. Leaf weight ratio and root weight ratio were significantly higher, while stem weight ratio was significantly lower above 600 ppm CO2 as a result of proportionally more biomass allocated to leaves and roots than to stems. Apart from an enhancement of plant growth, the long-term CO2 enrichment boosted vegetative propagation of strawberry plants as well. From an economical point of view, however, it is more efficient to use elevated CO2 concentrations of up to 600-750 ppm rather than 900 ppm for greenhouse cultivation of strawberry.

KEYWORDS: SCIENCE

377

Chen, K., G.Q. Hu, N. Keutgen, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. III. Dry matter production and water consumption. *Journal of Applied Botany-Angewandte Botanik 71(5-6):179-182.*

Two-week-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 days. Elevated CO2 concentrations enhanced dry matter production, the root/shoot ratio and total water consumption of the plants. High CO2 promoted total dry matter increment and total leaf area increment of the plants, and improved dry matter- production efficiency and plant water-use efficiency. Water- consumption rate of plants and water-uptake efficiency of roots, however, declined at CO2-enriched conditions. In comparison with the 300 ppm CO2 treatment, 600 and 900 ppm CO2-grown plants increased dry matter-production efficiency by 37 % and 67 %, water-use efficiency by 137 % and 272 %, while reduced water-consumption rate by 39 % and 55 %, and water- uptake efficiency of roots by 53 % and 76 %, respectively. Increasing CO2 concentrations from 300 to 900 ppm enabled strawberry plants to produce dry matter more efficiently and to use soil water more economically because it reduced the impact of water stress on plant productivity.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, PLANTS, RESPONSES, ROOTS

378

Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. IV. Carbohydrate production and accumulation. *Journal of Applied Botany-Angewandte Botanik 71(5-6):183-188.*

Two-week-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 days. Increasing CO2 concentration from 300 to 900 ppm promoted carbohydrate production of the plants, and subsequently increased carbohydrate accumulation in the plant organs, especially starch in leaves. Relative distribution of non-structural carbohydrates decreased in leaves and stems at 750 and 900 ppm CO2, increased in roots from 300 to 750 ppm CO2. Elevating CO2 concentration from 300 to 750 ppm reduced the proportions of glucose, fructose, and sucrose, but raised the proportion of starch in non-structural carbohydrates of the plants, as well as increased starch/sucrose ratio in leaves, stems, and whole plants. CO2 enrichment up to 900 ppm improved carbohydrate-production efficiency of the plants. This effect was particularly pronounced for starch. In comparison with 300 ppm CO2-grown plants, those treated by 600 and 900 ppm CO2 raised starch-, glucose-, fructose-, sucrose-, and non- structural carbohydrate-production efficiency by 2.6 and 16.1 fold, 1.6 and 2.1 fold, 0.6 and 1.0 fold, 0.8 and 1.6 fold, and 1.2 and 3.5 fold, respectively.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, ROOTS

379

Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. V. Macronutrient uptake and utilization. *Journal of Applied Botany-Angewandte Botanik 71(5-6):189-194.*

Two-week-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 days. Raising CO2 concentration from 300 to 900 ppm promoted macronutrient accumulation in all organs of the plants, particularly in roots. It, however, reduced contents of macronutrients in most organs of the plants, especially in leaves, because of the dilution effect of larger amounts of carbohydrate accumulation in the plant organs. When compared with the 300 ppm CO2 treatment, 600 and 900 ppm CO2 increased accumulation of N by 93 % and 87 %, P by 113 % and 122 %, K by 98 % and 92 %, Ca by 212 % and 244 %, and Mg by 177 % and 200 %, respectively CO2 enrichment decreased the proportions of N and K, increased those of Ca and Mg, but did not affect the proportion of P in the plants. Increasing CO2 levels depressed macronutrient-uptake efficiency of the plant roots, but promoted macronutrient-use efficiency of the plants. In comparison with the 300 ppm CO2-treated plants, those treated with 600 and 900 ppm CO2 showed lower N-, P-, K-, Ca, and Mg- uptake efficiency of the roots and higher N-, P-, K-, Ca-, and Mg-use effficiency of the plants.

KEYWORDS: ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, GROWTH, NITROGEN, PHOSPHORUS, RESPONSES, STRESS, TREES

380

Chen, K., G.Q. Hu, and F. Lenz. 1997. Effects of CO2 concentration on strawberry. VI. Fruit yield and quality. *Journal of Applied Botany-*

Angewandte Botanik 71(5-6):195-200.

Two-week-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants were acclimatized to 300, 450, 600, 750 or 900 ppm CO2 in controlled environment chambers for 50 and 60 days during vegetative growth in late autumn of 1995 and reproductive growth in early spring of 1996. High CO2 promoted branch-crown and pedicel development as well as flower-bud differentiation. It also induced a second bloom. Flowering and fruit ripening started earlier and lasted for a longer period under high rather than low CO2 concentrations. CO2 enrichment shortened the periods of anthesis and single fruit growth but prolonged the periods of flowering and fruit harvest. Elevated CO2 concentrations enhanced fruit productivity as indicated by increases in pedicel number per plant, fruit setting per pedicel, fruit size, and dry matter content of the fruits. In comparison with the 300 ppm CO2 treatment, 450, 600, 750, and 900 ppm CO2 increased average fruit yield per plant by 0.7, 2.7, 3.6, and 4.1 fold, daily growth per fresh fruit by 0.4, 1.0, 1.1, and 1.3 fold, and growth rate of fruit biomass per plant by 1.0, 3.9, 5.5, and 6.9 fold, respectively. High CO2 tended to improve fruit quality as well. Raising CO2 concentrations accelerated dry matter increment and total sugar accumulation in the fruits, especially for sucrose, and decreased titratable acid content, resulting in a higher sugar/acid ratio of the fruits. Contents of starch and minerals in the fruits slightly decreased when CO2 rose.

KEYWORDS: ENRICHMENT

381

Chen, K., and F. Lenz. 1997. Responses of strawberry to doubled CO2 concentration and phosphorus deficiency .1. Distribution of dry matter, macronutrients, and carbohydrates. *Gartenbauwissenschaft 62(1):30-37.*

One-year-old strawberry (Fragaria x ananassa Duch. cv. 'Elsanta') plants grown in controlled environmental chambers were supplied with a modified P-sufficient (0.5 mmol P l(-1)) or P-deficient (0.05 mmol P l(-1)) Hoagland nutrient solution and acclimatized by an ambient CO2 (340 +/- 20 ppm) or doubled CO2 (680 +/- 20 ppm) concentration for one month. Doubled CO2 concentration promoted plant vegetative growth and dry matter assimilation, especially in leaf area enlargement, leaf dry weight, and runner extending growth. The plant responses to doubled CO2 concentration were more pronounced under P- sufficient than P-deficient conditions. P deficiency not only moderated the above plant responses to CO2 enrichment, but also accelerated premature leaf senescence and aggravated P- deficient symptoms at doubled CO2 concentration. The mean increment in total dry matter of the plants in virtue of doubled CO2 concentration and P-sufficiency were 25-63 % and 123-191 %, respectively. Doubled CO2 concentration reduced N level in the plant organs, particularly in both new and old leaves and runners, while increased the contents of starch, glucose, fructose, sucrose, and total non-structural carbohydrates in most organs; but not particularly affected contents of P, K, Ca, and Mg. P deficiency decreased contents of N, P, K, Mg, and soluble carbohydrates, while increased root : shoot ratio and starch level in roots, stems, runners, and leaves whether at the ambient CO2 or at doubled CO2 condition. Neither doubled CO2 nor P deficiency definitely altered Ca content in the plant organs.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH, INCREASES, PLANTS, YIELD

382

Chen, S.G., I. Impens, and R. Ceulemans. 1997. Modelling the effects of elevated atmospheric CO2 on crown development, light interception and photosynthesis of poplar in open top chambers. *Global Change Biology 3(2):97-106.*

An open-top chamber experiment was carried out to examine the likely effects of elevated atmospheric [CO2] on architectural as well as on physiological characteristics of two poplar clones (Populus trichocarpa x P. deltoides clone Beaupre and P. deltoides x P. nigra clone Robusta). Crown architectural parameters required as input parameters for a three-dimensional (3D) model of poplar structure, such as branching frequency and position, branch angle, internode length and its distribution pattern, leaf size and orientation, were measured following growth in ambient and elevated [CO2] (ambient + 350 mu mol mol(-1)) treated open-top chambers. Based on this information, the light interception and photosynthesis of poplar canopies in different [CO2] treatments were simulated using the 3D poplar tree model and a 3D radiative transfer model at various stages of the growing season. The first year experiments and modelling results showed that the [CO2] enrichment had effects on light intercepting canopy structure as well as on leaf photosynthesis properties. The elevated [CO2] treatment resulted in an increase of leaf area, canopy photosynthetic rate and above- ground biomass production of the two poplar clones studied. However, the structural components responded less than the process components to the [CO2] enrichment. Among the structural components, the increase of LAI contributed the most to the canopy light interception and canopy photosynthesis; the change of other structural aspects as a whole caused by the [CO2] enrichment had little effect on daily canopy light interception and photosynthesis.

KEYWORDS: CANOPY STRUCTURE, CARBON DIOXIDE, FORESTS, GROWTH, PLANTS, POPULUS, SYSTEM

383

Chen, S.G., I. Impens, and R. Ceulemans. 1997. Modelling the effects of elevated atmospheric CO2 on crown development, light interception and photosynthesis of poplar in open top chambers (vol 3, pg 97, 1997). *Global Change Biology 3(6):550.*

384

Chen, X.M., G.B. Begonia, D.M. Alm, and J.D. Hesketh. 1993. Responses of soybean leaf photosynthesis to co2 and drought. *Photosynthetica 29(3):447-454.*

Soybean [Glycine max (L.) Merr. cv. Jack] was grown in the field in rain-protected plots to study effects of drought and atmospheric CO2 enrichment. on leaf gas exchange. Midday depressions in leaf photosynthetic CO2 exchange rates (P(N)) were found in drought-stressed plants and the diurnal changes were mostly stomatal-regulated, although accumulated drought stress eventually resulted in some non-stomatal limitations. However, seasonal changes in P(N) were mostly limited by non- stomatal factors. Water use efficiency was always higher for drought stressed plants and depended on the severity of stress and associated stomatal or nonstomatal limitations. At enriched atmospheric CO2 levels, stomatal limitations to P(N) under drought stress were less important than at ambient atmospheric CO2 levels. Morning and afternoon leaf starch levels were enhanced in both irrigated and nonirrigated plants in enriched CO2. Afternoon starch levels were higher in stressed leaves than in non-stressed leaves at normal CO2 levels.

KEYWORDS: AIR, EXPOSURE, RATES, STRESS, WATER DEFICIT

385

Chen, X.M., G.B. Begonia, and J.D. Hesketh. 1995. Soybean stomatal acclimation to long-term exposure to co2- enriched atmospheres. *Photosynthetica 31(1):51-57.*

Soybean [Glycine max (L.) cv. Jack] grown in open top chambers under controlled laboratory and field conditions was used to study the

acclimation of leaf gas exchange processes to CO2 enrichment. Air inside the open top chambers was maintained at either 700-800 or 350-400 mu mol(CO2) mol(-1)(air). Leaf gas exchange rates were measured for some plants switched between treatments. When measured in the CO2-enriched atmosphere, stomatal conductances (g(s)) were higher in leaves grown in CO2-enriched atmospheres than in those grown under ambient conditions, and the lower g(s) values for plants in the CO2-enriched atmospheres were limiting to leaf net photosynthetic CO2 exchange rates (P-N). P-N of enriched leaves was higher than those of the ambient controls when measured at elevated CO2 levels in both controlled environment and field studies, while it was depressed in enriched leaves when measured under ambient CO2 conditions, and this drop in P-N did not recover until 6-15 d after plants were placed back in ambient conditions.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, PHOTOSYNTHETIC INHIBITION

386

Chenevard, D., C. Jayallemand, M. Gendraud, and J.S. Frossard. 1995. The effect of sucrose on the development of hybrid walnut microcuttings (juglans-nigra X juglans-regia) - consequences on their survival during acclimatization. *Annales Des Sciences Forestieres 52(2):147-156.*

We studied the effect of sucrose concentration in the root- development medium on the formation of adventitious roots and survival of microcuttings during acclimatization in 2 interspecific hybrid walnut (Juglans nigra n degrees 23 x J regia) clones. Sucrose increased the rooting percentage (fig 1), the number of adventitious roots (fig 2A) and the dry- matter content (table I) per rooted shoot. These effects were due to the energy properties of sucrose rather than to its osmotic function. High sucrose concentrations in the root- development medium (> 20 g.l(-1)) resulted in a high soluble carbohydrate content in the plantlets (fig 3), mainly located in roots and callus. The 2-clones showed different capacities in rooting and growth. Survival of microcuttings during acclimatization was not directly influenced by the sucrose concentration (fig 5) but was correlated with the number of adventitious roots (fig 6A) as well as with the number of leaves (fig 6B) present at the time of transfer to the growth chamber for each individual plant.

KEYWORDS: ACCUMULATION, CO2- ENRICHMENT, CULTURE, GROWTH, INVITRO, PLANTS, PROPAGATION, SHOOT, TEMPERATURE

387

Cheng, S.H., B.D. Moore, and J.R. Seemann. 1998. Effects of short- and long-term elevated CO2 on the expression of ribulose-1,5-bisphosphate carboxylase/oxygenase genes and carbohydrate accumulation in leaves of Arabidopsis thaliana (L) Heynh. *Plant Physiology 116(2):715-723.*

To investigate the proposed molecular characteristics of sugar- mediated repression of photosynthetic genes during plant acclimation to elevated CO2, we examined the relationship between the accumulation and metabolism of,nonstructural carbohydrates and changes in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) gene expression in leaves of Arabidopsis thaliana exposed to elevated CO2. Long-term growth of Arabidopsis at high CO2 (1000 mu L L-1) resulted in a 2-fold increase in nonstructural carbohydrates, a large decrease in the expression of Rubisco protein and in the transcript of rbcL, the gene encoding the large subunit of Rubisco (approximately 35-40%), and an even greater decline in mRNA of rbcS, the gene encoding the small subunit (approximately 60%). This differential response of protein and mRNAs suggests that transcriptional/posttranscriptional processes and protein turnover may determine the final amount of leaf Rubisco protein at high CO2. Analysis of mRNA levels of individual rbcS genes indicated that reduction in total rbcS transcripts was caused by decreased expression of all four rbcS genes. Short-term transfer of Arabidopsis plants grown at ambient CO2 to high CO2 resulted in a decrease in total rbcS mRNA by d 6, whereas Rubisco content and rbcL mRNA decreased by d 9. Transfer to high CO2 reduced the maximum expression level of the primary rbcS genes (1A and, particularly, 3B) by limiting their normal pattern of accumulation through the night period. The decreased nighttime levels of rbcS mRNA were associated with a nocturnal increase in leaf hexoses. We suggest that prolonged nighttime hexose metabolism resulting from exposure to elevated CO2 affects rbcS transcript accumulation and, ultimately, the level of Rubisco protein.

KEYWORDS: CARBON METABOLISM, LEAF DEVELOPMENT, MESSENGER-RNA, METABOLIC REPRESSION, PHOTOSYNTHESIS, RBCS GENES, SMALL-SUBUNIT, TOMATO PLANTS, TRANSGENIC TOBACCO PLANTS, YEAST- DERIVED INVERTASE

388

Cheng, W.X. 1999. Rhizosphere feedbacks in elevated CO2. *Tree Physiology 19(4-5):313-320.*

Understanding rhizosphere processes in relation to increasing atmospheric CO2 concentrations is important for predicting the response of forest ecosystems to environmental changes, because rhizosphere processes are intimately linked with nutrient cycling and soil organic matter decomposition, both of which feedback to tree growth and soil carbon storage. Plants grown in elevated CO2 substantially increase C input to the rhizosphere. Although it is known that elevated CO2 enhances rhizosphere respiration more than it enhances root biomass, the fate and function of this extra carbon input to the rhizosphere in response to elevated CO2 are not clear. Depending on specific plant and soil conditions, the increased carbon input to the rhizosphere can result in an increase, a decrease, or no effect on soil organic matter decomposition and nutrient mineralization. Three mechanisms may account for these inconsistent results: (1) the "preferential substrate utilization" hypothesis; (2) the "priming effect" hypothesis; and (3) the "competition" hypothesis, i.e., competition for mineral nutrients between plants and soil microorganisms. A microbial growth model is developed that quantitatively links the increased rhizosphere input in response to elevated CO2 with soil organic matter decomposition. The model incorporates the three proposed mechanisms, and simulates the complexity of the rhizosphere processes. The model also illustrates mechanistically the interactions among nitrogen availability, substrate quality, and microbial dynamics when the system is exposed to elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, LONG-TERM, MICROBIAL BIOMASS, MYCORRHIZAL COLONIZATION, NITROGENASE ACTIVITY, PINE SEEDLINGS, PISUM-SATIVUM, QUERCUS-ALBA, SOIL ORGANIC MATTER

389

Cheng, W.X., and D.W. Johnson. 1998. Elevated CO2, rhizosphere processes, and soil organic matter decomposition. *Plant and Soil 202(2):167-174.*

The rhizosphere is one of the key fine-scale components of C cycles. This study was undertaken to improve understanding of the potential effects of atmospheric CO2 increase on rhizosphere processes. Using C isotope techniques, we found that elevated atmospheric CO2 significantly increased wheat plant growth, dry mass accumulation, rhizosphere respiration, and soluble C concentrations in the rhizosphere. When plants were grown under elevated CO2 concentration, soluble C concentration in the rhizosphere increased by approximately 60%. The degree of elevated CO2 enhancement on rhizosphere respiration was

much higher than on root biomass. Averaged between the two nitrogen treatments and compared with the ambient CO2 treatment, wheat rhizosphere respiration rate increased 60% and root biomass only increased 26% under the elevated CO2 treatment. These results indicated that elevated atmospheric CO2 in a wheat-soil system significantly increased substrate input to the rhizosphere due to both increased root growth and increased root activities per unit of roots. Nitrogen treatments changed the effect of elevated CO2 on soil organic matter decomposition. Elevated CO2 increased soil organic matter decomposition (22%) in the nitrogen-added treatment but decreased soil organic matter decomposition (18%) without nitrogen addition. Soil nitrogen status was therefore found to be important in determining the directions of the effect of elevated CO2 on soil organic matter decomposition.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GLOBAL CHANGE, GROWTH, NITROGENASE ACTIVITY, PINE SEEDLINGS, PISUM-SATIVUM, RESPONSES, SYSTEM

390

Chernikova, T., J.M. Robinson, E.H. Lee, and C.L. Mulchi. 1997. Evaluation of ozone tolerance mechanisms in soybean cultivars exposed to ambient and elevated CO2. *Plant Physiology 114(3):201.*

391

Chmora, S.N., and A.T. Mokronosov. 1994. The global increase of co2 in the atmosphere - adaptive strategies in plants. *Russian Journal of Plant Physiology 41(5):677-685.*

The effects of short- and long-term exposure to increased CO2 concentrations on the life activity and productivity of plants are discussed. Two strategies of plant adaptation to an increasing CO2 concentration are outlined that reflect the diversity of adaptive plant responses at the ecological and physiological levels: physiological adaptation that occurs at all organization levels from molecular to cenotic and changes in areas of species that lead to changes in ecosystem composition occurring in correspondence to the biochemical diversity of photosynthetic pathways.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, WHEAT, YIELD

392

Chomba, B.M., R.D. Guy, and H.G. Weger. 1993. Carbohydrate reserve accumulation and depletion in engelmann spruce (picea-engelmannii parry) - effects of cold-storage and prestorage co2 enrichment. *Tree Physiology 13(4):351-364.*

The effects of pre-storage CO2 enrichment on growth, non- structural carbohydrates and post-storage root growth potential of Engelmann spruce (Picea engelmannii Parry) seedlings were studied. Seedlings were grown from seed for 202 days in growth chambers with ambient (340 mu l l(-1)) or CO(2)ched (1000 mu l l(-1)) air. Some seedlings were transferred between CO2 treatments at 60 and 120 days. Photoperiod was reduced at 100 days to induce bud set and temperature was reduced at 180 days to promote frost hardiness development for storage at -5 degrees C for 2 or 4 months. Stored seedlings were planted in a growth chamber after thawing for one week at +5 degrees C. At 80, 120, 140 and 202 days, and at each planting time after storage, seedlings were harvested for growth measurements and analysis of starch and soluble sugar concentrations. Planted seedlings were assessed for bud break every two days and new roots > 5 mm long were counted after four weeks. Carbon dioxide enrichment increased root collar diameter and almost doubled seedling biomass, with the most obvious effects occurring after bud set. Stem height was affected only slightly and shoot/root ratios were not affected at all. Carbon dioxide enrichment increased the rate of reserve carbohydrate accumulation, but did not influence the final concentration attained before storage (accounting for 32% of seedling dry weight). Needles were the major storage organ for soluble sugars, whereas roots were the major storage organ for starch. Soluble sugars were not strongly affected by two or four months of storage, but starch was reduced by more than 50% in all plant parts. None of the CO2 treatments had an impact on bud break or root growth potential.

393

Christ, R.A., and C. Korner. 1995. Responses of shoot and root gas-exchange, leaf blade expansion and biomass production to pulses of elevated co2 in hydroponic wheat. *Journal of Experimental Botany 46(292):1661-1667.*

Short-term effects of elevated CO2 during the early life phase of plants may have long lasting consequences for growth and biomass in later periods. We exposed hydroponically grown wheat seedlings to 5 d pulses of elevated CO2 while leaf expansion growth as well as shoot and root gas exchange were measured simultaneously and continuously. Shoot photosynthesis, night- time shoot respiration and below-ground respiration (largely by roots) roughly doubled when atmospheric CO2 concentration was doubled. An interruption of CO2 enrichment caused CO2 assimilation and respiration to return to control levels, However, while the response of photosynthesis was immediate, that of respiration showed a hysteresis of about 3 d. Since shoot biomass increased at elevated CO2 (with no change in allocation pattern) equal fluxes per shoot or root system after a return to control CO2 concentrations indicate substantial downward adjustment of the capacity for CO2 fixation and release in high-CO2 grown plants. Leaf expansion growth was completely unaffected by CO2 enrichment, whereas tiller initiation was significantly increased (doubled in 18 d). We conclude that leaf growth in these wheat plants was already carbon-saturated at ambient CO2 concentration at optimum mineral nutrient supply. The stimulation of growth of whole plants was exclusively due to enhanced tillering during this very early part of the life of these wheat plants.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, EXTENSION, FIELD, GROWTH, LEAVES, PLANTS, RESPIRATION, TEMPERATURE, WINTER-WHEAT, YIELD

394

Christensen, T.R., S. Jonasson, T.V. Callaghan, and M. Havstrom. 1999. On the potential CO2 release from tundra soils in a changing climate. *Applied Soil Ecology 11(2-3):127-134.*

About 30% of the carbon in terrestrial ecosystems is stored in northern wetlands and boreal forest regions. Prevailing cold and wet soil conditions have largely been responsible for this carbon accumulation. It has been suggested that a warmer and drier climate in these regions might increase the decomposition rate and, hence, release more CO2 to the atmosphere than at present. This study reports on the spatial variability and temperature dependence of the potential carbon release after incubating highly organic soils from the European Arctic and Siberia at different temperatures. We found that the decay potential, measured as CO2 production in laboratory experiments, differed strongly within and among sites, particularly at higher soil temperatures. Furthermore, both the decay potential and its temperature response decreased significantly with depth in the soil, presumably because the older soils at deeper layers contained higher proportions of recalcitrant carbon than the younger soil organic matter at the surface. These results have implications for global models of potential feedbacks on climate

change inferred from changes in the carbon balance of northern wetlands and tundra. Firstly, because the decay potential of the organic matter varies locally as well as regionally, predictions of how the tundra carbon balance may change will be unreliable if these are based on measurements at a few sites only. Secondly, any increase in CO2 production may be transitional as both the carbon flux and its temperature sensitivity decrease when the most easily degradable organic material near the soil surface has decomposed. Consequently, it is crucial to account for transient responses and regional differences in the models of potential feedbacks on climate change from changed carbon cycling in northern terrestrial ecosystems. (C) 1999 Elsevier Science B.V.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, FLUX, SINK

395

Christensen, T.R., S. Jonasson, T.V. Callaghan, M. Havstrom, and F.R. Livens. 1999. Carbon cycling and methane exchange in Eurasian tundra ecosystems. *Ambio 28(3):239-244.*

This paper provides an overview of data and results obtained through a number of studies of actual and potential trace gas exchanges in northern Eurasia, made possible through the Swedish-Russian Tundra Ecology - 94 expedition. It was found that: i) long-term accumulation rates of carbon in organic tundra soils, i.e. net uptake of atmospheric CO2, correlated with simple climatic parameters, such as mean July temperature and annual precipitation; ii) the release of carbon through ecosystem respiration is also strongly controlled by climate. Increased temperature and decrease of water-logging enhanced the CO2 flux. However, the release of organic soil carbon as CO2 is also constrained by other factors such as poor decomposability of the stored organic compounds; and iii) methane emissions from typical tundra habitats in northern Eurasia were found to be slightly lower than from seemingly similar habitats in North America. This difference can probably be attributed to lower temperatures along the Russian arctic coast than at North American sites in general.

KEYWORDS: DIOXIDE, EMISSION

396

Chu, C.C., J.S. Coleman, and H.A. Mooney. 1992. Controls of biomass partitioning between roots and shoots - atmospheric co2 enrichment and the acquisition and allocation of carbon and nitrogen in wild radish. *Oecologia 89(4):580-587.*

The effects of CO2 enrichment on plant growth, carbon and nitrogen acquisition and resource allocation were investigated in order to examine several hypotheses about the mechanisms that govern dry matter partitioning between shoots and roots. Wild radish plants (Raphanus sativus x raphanistrum) were grown for 25 d under three different atmospheric CO2 concentrations (200 ppm, 330 ppm and 600 ppm) with a stable hydroponic 150-mu- mol l-1 nitrate supply. Radish biomass accumulation, photosynthetic rate, water use efficiency, nitrogen per unit leaf area, and starch and soluble sugar levels in leaves increased with increasing atmospheric CO2 concentration, whereas specific leaf area and nitrogen concentration of leaves significantly decreased. Despite substantial changes in radish growth, resource acquisition and resource partitioning, the rate at which leaves accumulated starch over the course of the light period and the partitioning of biomass between roots and shoots were not affected by CO2 treatment. This phenomenon was consistent with the hypothesis that root/shoot partitioning is related to the daily rate of starch accumulation by leaves during the photoperiod, but is inconsistent with hypotheses suggesting that root/shoot partitioning is controlled by some aspect of plant C/N balance.

KEYWORDS: CARROT, COMPETITION, DIOXIDE, ELEVATED CO2, MODEL, NITRATE, PLANT GROWTH, PROGRAM, RESPONSES, TOMATO

397

Chu, C.C., C.B. Field, and H.A. Mooney. 1996. Effects of CO2 and nutrient enrichment on tissue quality of two California annuals. *Oecologia 107(4):433-440.*

The effects of CO2 enrichment and soil nutrient status on tissue quality were investigated and related to the potential effect on growth and decomposition. Two California annuals, Avena fatua and Plantago erecta, were grown at ambient and ambient plus 35 Pa atmospheric CO2 in nutrient unamended and amended serpentine soil. Elevated CO2 led to significantly increased Avena shoot nitrogen concentrations in the nutrient amended treatment. It also led to decreased lignin concentrations in Avena roots in both nutrient treatments, and in Plantago shoots and roots with nutrient addition. Concentrations of total nonstructural carbohydrate (TNC) and carbon did not change with elevated CO2 in either species. As a consequence of increased biomass accumulation, increased CO2 led to larger total pools of TNC, lignin, total carbon, and total nitrogen in Avena with nutrient additions. Doubling CO2 had no significant effect on Plantago. Given the limited changes in the compounds related to decomposibility and plant growth, effects of increased atmospheric CO2 mediated through tissue composition on Avena and Plantago are likely to be minor and depend on site fertility. This study suggests that other factors such as litter moisture, whether or not litter is on the ground, and biomass allocation among roots and shoots, are likely to be more important in this California grassland ecosystem. CO2 could influence those directly as well as indirectly.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, LIGNIN CONTROL, LITTER DECOMPOSITION, LONG-TERM DECOMPOSITION, NITROGEN, PLANTS, RESPONSES, SCOTS PINE FOREST

398

Ciais, P., P. Friedlingstein, D.S. Schimel, and P.P. Tans. 1999. A global calculation of the delta C-13 of soil respired carbon: Implications for the biospheric uptake of anthropogenic CO2. *Global Biogeochemical Cycles 13(2):519-530.*

The continuing emissions of fossil CO2 depleted in C-13 have been causing a gradual decrease in atmospheric delta(13)C by roughly 1.4 parts per thousand since preindustrial times. The progressive penetration of this perturbation into the land biota causes the soil organic matter to be enriched in 13C with respect to recently formed plant material. This effect which we call the "biotic isotope disequilibrium" is important when it comes to deducing the terrestrial carbon fluxes by using delta(13)C in atmospheric CO2. We have estimated the geographical distribution of the isotopic disequilibrium, which is primarily influenced by the turnover of carbon in the various ecosystems, from the output of two biospheric models, (SLAVE and CENTURY). The disequilibrium is estimated to shift up the delta(13)C of atmospheric CO2 by the same amount as a net sink of 0.6 Gt C yr(-1) in the land biota. This "fake" terrestrial sink due to the isotopic disequilibrium is distributed mainly in northern midlatitudes (0.2 Gt C yr(-1)) and tropical forests (0.3 Gt C yr(-1)).

KEYWORDS: ATMOSPHERIC CO2, ISOTOPE, SIMULATION, TURNOVER, WORLDWIDE

399

Cipollini, M.L., B.G. Drake, and D. Whigham. 1993. Effects of

elevated co2 on growth and carbon/nutrient balance in the deciduous woody shrub lindera benzoin (L.) blume (lauraceae). *Oecologia 96(3):339-346.*

We examined the effects of elevated CO2 on growth and carbon/nutrient balance in a natural population of the deciduous temperate zone shrub Lindera benzoin. Our data concern whole plant, leaf, and stem growth for the first two seasons of a long-term field experiment in which CO2 levels were manipulated in situ. In addition to growth parameters, we evaluated changes in leaf and stem chemistry, including total nitrogen, nonstructural carbohydrates, and total phenolics. Over the course of this study, L. benzoin appeared to respond to elevated CO2 primarily by physiological and biochemical changes, with only a slight enhancement in aboveground growth (ramet height). Positive effects on aboveground growth were primarily evident in young (nonreproductive) ramets. Our results suggest that nitrogen limitation may have constrained plants to allocate carbohydrates produced in response to elevated CO2 primarily to storage and belowground growth, and perhaps to increased secondary chemical production, rather than to increased stem and leaf growth. We discuss our results in terms of changes in carbon/nutrient balance induced by elevated CO2, and provide predictions for future changes in this system based upon constraints imposed by intrinsic and extrinsic factors and their potential effects on the reallocation of stored reserves.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, FOREST, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, TREES

400

Clark, D.G., J.W. Kelly, and N.C. Rajapakse. 1993. Production and postharvest characteristics of rosa-hybrida L meijikatar grown in pots under carbon-dioxide enrichment. *Journal of the American Society for Horticultural Science 118(5):613-617.*

The effects of carbon dioxide enrichment on growth, photosynthesis, and postharvest characteristics of 'Meijikatar' potted roses were determined. Plants were grown in 350, 700, or 1050 mul CO2/liter until they reached 50% flower bud coloration and then were placed into dark storage for 5 days at 4 or 16C. Plants grown in 700 or 1050 mul CO2/liter reached the harvest stage earlier and were taller at harvest than plants produced in 350 mul CO2/liter, but there were no differences in the number of flowers and flower buds per plant among CO2 treatments. Plants grown in early spring were taller and had more flowers and flower buds than plants grown in late winter. Shoot and root growth of plants grown in 700 or 1050 mul CO2/liter were higher than in plants produced in 350 mul CO2/liter, with plants grown in early spring showing greater increases than plants grown in late winter. Immediately after storage, plants grown in 350 mul CO2/liter and stored at 4C had the fewest etiolated shoots, while plants grown in 1050 mul CO2/liter and stored at 16C had the most. Five days after removal from storage, chlorophyll concentration of upper and lower leaves had been reduced by almost-equal-to 50% from the day of harvest. Carbon dioxide enrichment had no effect on postharvest leaf chlorosis, but plants grown in early spring and stored at 16C had the most leaf chlorosis while plants grown in late winter and stored at 4C had the least leaf chlorosis.

KEYWORDS: CO2- ENRICHMENT, ENVIRONMENT, LIGHT, MORIFOLIUM RAMAT, N,N-DIMETHYLFORMAMIDE, PLANTS, RESPONSES

401

Clark, H., P.C.D. Newton, and D.J. Barker. 1999. Physiological and morphological responses to elevated CO2 and a soil moisture deficit of temperate pasture species growing in an established plant community. *Journal of Experimental Botany 50(331):233-242.*

Periods of limited soil water availability are a feature of many temperate pasture systems and these have the potential to modify pasture plant and community responses to elevated atmospheric CO2. Using large pasture turves, previously exposed to elevated CO2 concentrations of 350 or 700 mu mol mol(-1) for 324 d under well-watered conditions, the morphological and physiological responses of pasture species growing at these CO2 concentrations were compared when subjected to a soil moisture deficit-and to recovery from the deficit-with those that continued to be well watered. Net leaf photosynthesis of Trifolium repens (C-3 legume), Plantago lanceolata (C-3) and Paspalum dilatatum (C-4) was increased by exposure to elevated CO2, but there was no consistent effect of CO2 on stomatal conductance. At low soil moistures, net photosynthesis declined and stomatal conductance increased in these three species. There was a strong CO2 x water interaction in respect of net photosynthesis; in Trifolium repens, for example, elevated CO2 increased net photosynthesis by approximately 50% under well- watered conditions and this increased to over 300% when soil moisture levels reached their minimum values. Similar values were recorded for both Paspalum dilatatum and Plantago lanceolata. Potential water use efficiency (net photosynthesis/stomatal conductance) was increased by both exposure to elevated CO2 and drought. Leaf water status was measured in three species: Trifolium repens, Paspalum dilatatum and Holcus lanatus (C-3). Total leaf water potential (psi(t)) and osmotic potential (psi(pi)) were decreased by drought, but CO2 concentration had no consistent effect. psi(t) and psi(pi) were highest in the C-4 species Paspalum dilatatum and lowest in the legume Trifolium repens. In the wet turves, rates of leaf extension of the C-3 grasses Holcus lanatus and Lolium perenne at elevated CO2 were frequently higher than those at ambient CO2, but there was no effect of CO2 concentration on the rate recorded in the C-4 grass Paspalum dilatatum or the rate of leaf appearance in the legume Trifolium repens. Drought reduced leaf extension rate irrespective of CO2 in all species, but in Holcus lanatus the reduction was less severe at elevated CO2. Immediately after the dry turves were rewatered the leaf extension rates on tillers of Holcus lanatus and Lolium perenne were higher than on tillers in the wet turves, but only at ambient CO2. Consequently, despite the greater leaf extension rate during the soil moisture deficit at elevated CO2, because of the overcompensation after rewatering at ambient CO2, total leaf extension over both the drying and rewetting period did not differ between CO2 concentrations for these C-3 grass species. Further investigation of this difference in response between CO2 treatments is warranted given the frequent drying and wetting cycles experienced by many temperate grasslands.

KEYWORDS: BIOMASS PRODUCTION, C-4 GRASS, CARBON-DIOXIDE CONCENTRATIONS, GAS-EXCHANGE, LOLIUM-PERENNE, SIMULATED SEASONAL-CHANGES, STOMATAL RESPONSES, TRIFOLIUM- REPENS, WATER-USE, WHITE CLOVER

402

Clark, H., P.C.D. Newton, C.C. Bell, and E.M. Glasgow. 1995. The influence of elevated co2 and simulated seasonal-changes in temperature on tissue turnover in pasture turves dominated by perennial ryegrass (lolium-perenne) and white clover (trifolium-repens). *Journal of Applied Ecology 32(1):128-136.*

1. Tissue turnover, leaf morphology and population dynamics of perennial ryegrass and white clover were studied in pasture turves grown at ambient (350 mu molmol(-1)) or double ambient (700 mu molmol(-1)) CO2 concentrations for 217 days in controlled environment rooms. The turves were subjected sequentially to three day/night temperature regimes; 10/4 degrees C, 16/10 degrees C and 22/16 degrees C and harvested at 3-week intervals. The photoperiod was 12 hours for all of the temperature treatments with a mean photon flux density of 480 mu E m(-2) s(-1). 2. Ryegrass leaf extension and leaf death rates did not differ between CO2 treatments and there was no effect of CO2 on rates of leaf appearance in white clover. Weight per unit length of ryegrass

laminae was unaffected by elevated CO but lamina weight per unit area, lamina area and petiole weight per unit length in white clover showed a small positive response, especially at the two higher temperatures. Rates of growth and senescence per ryegrass tiller were therefore similar between CO2 treatments, but rates of growth per white clover growing point were increased by 4, 23 and 13% at 10/4 degrees C, 16/10 degrees C and 22/16 degrees C, respectively, at elevated CO2. Responses to CO2 could not be attributed to any consistent change in morphological characteristics in either species and exposure to elevated concentrations of CO2 did not appear to change the relationship between growth and senescence per meristem. 3. Total grass tiller populations were similar at both CO2 concentrations, but ryegrass tiller densities more than halved in both CO2 treatments as the temperature was increased. The fall was most severe at 700 mu mol mol(-1) and at the end of the experiment ryegrass tiller densities in this treatment were only 47% of those found at 350 mu molmol(-1). There was no consistent effect of CO2 concentration on clover growing point numbers and they increased from 800 m(-2) to over 3000 m(-2) in both treatments with maximum densities occurring at 22/16 degrees C. 4. The results imply that, in plant communities dominated by ryegrass and white clover, exposure to elevated CO2 concentrations will alter the species composition in favour of white clover. Responses in above-ground dry matter yield to elevated CO2 will be a balance between the positive response shown by white clover and the negative response of perennial ryegrass. Temperature will have a major influence on the magnitude of this response since both the response of white clover to CO2 and the ratio of white clover growing points to ryegrass tillers are temperature-dependent.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, COMMUNITIES, DEATH, LEAF, PHOTOSYNTHESIS, REPRODUCTIVE GROWTH, SENESCENCE, SWARDS, TILLER

403

Clark, H., P.C.D. Newton, C.C. Bell, and E.M. Glasgow. 1997. Dry matter yield, leaf growth and population dynamics in Lolium perenne Trifolium repens-dominated pasture turves exposed to two levels of elevated CO2. *Journal of Applied Ecology 34(2):304-316.*

1. Dry matter yield, leaf growth and population dynamics of turves taken from an old Lolium perenne/Trifolium repens- dominated pasture were studied in controlled environment rooms at CO2 concentrations of 350 mu mol mol(-1), 525 mu mol mol(-1) and 700 mu mol mol(-1). Starting with September data the turves were subjected sequentially to the mean monthly temperature and photoperiod taken from long-term climatic data for the area of New Zealand where the pasture was located. Each temperature and photoperiod regime was applied for 21 days to provide 12 different simulated 'months' of environmental conditions. The experiment ran for 14 simulated months, with September and October conditions being repeated at the end of the first simulated 'year'. Mean photon flux density throughout was 500 mu E m(-2) s(-1). 2. The total quantity of herbage harvested was increased by 7% and 14% at 525 mu mol mol(-1) and 700 mu mol mol(-1) CO2, respectively. The increase in the amount of T. repens harvested by the end of the experiment was 63% at 525 mu mol mol(-1) CO2 and 48% at 700 mu mol mol(-1) CO2. In contrast, neither the yield of C3 grasses nor the yield of the only C4 grass present, Paspalum dilatatum, was significantly affected by CO2 concentration. The implications of this increase in the proportion of T. repens in temperate pastures at elevated CO2 is discussed briefly. 3. With the exception of a small increase in the specific leaf area of T. repens, detailed measurements of leaf growth on marked tillers (L. perenne and P. dilatatum) and growing points (T. repens) showed no consistent effects of exposure to elevated CO2 concentrations. 4. Differences in yield between CO2 concentrations were mainly attributable to changes in the number and balance of population units. By the middle of the 'winter' conditions T. repens growing point densities at 700 mu mol mol(-1) CO2 were more than double those found at 350 mu mol mol(-1) but total grass tiller densities were unchanged. Growing point densities were also more than doubled at 525 mu mol mol(-1) CO2 compared with 350 mu mol mol(-1) but grass tiller densities were reduced significantly below those recorded in the other two treatments. The relationship between the stability of herbage production and population densities is discussed and the potential interaction between population density, elevated CO2 and grazing considered. 5. Although exposure to elevated levels of CO2 did result in large changes in population numbers, this did not happen immediately and so the yield response of this particular community to CO2 varied with time. The average yield increases recorded here at elevated CO2 may therefore tend to underestimate those likely to be shown by communities that, at the population level, have become fully adapted to growth in a CO2-enriched atmosphere.

KEYWORDS: BIOMASS PRODUCTION, CARBON DIOXIDE, ENRICHMENT, INCREASING CO2, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, SIMULATED SEASONAL-CHANGES, TEMPERATURE, WHITE CLOVER

404

Claussen, M., and M. Esch. 1994. Biomes computed from simulated climatologies. *Climate Dynamics 9(4-5):235-243.*

The biome model of Prentice et al. (1992a) is used to predict global patterns of potential natural plant formations, or biomes, from climatologies simulated by ECHAM, a model used for climate simulations at the Max-Planck-Institut fur Meteorologie, This study is undertaken in order to show the advantage of this biome model in diagnosing the performance of a climate model and assessing effects of past and future climate changes predicted by a climate model. Good overall agreement is found between global patterns of biomes computed from observed and simulated data of present climate. But there are also major discrepancies indicated by a difference in biomes in Australia, in the Kalahari Desert, and in the Middle West of North America, These discrepancies can be traced back to failures in simulated rainfall as well as summer or winter temperatures. Global patterns of biomes computed from an ice age simulation reveal that North America, Europe, and Siberia should have been covered largely by tundra and taiga, whereas only small differences are seen for the tropical rain forests. A potential northeast shift of biomes is expected from a simulation with enhanced CO2 concentration according to the IPCC Scenario A. Little change is seen in the tropical rain forest and the Sahara. Since the biome model used is not capable of predicting changes in vegetation pat terns due to a rapid climate change, the latter simulation has to be taken as a prediction of changes in conditions favourable for the existence of certain biomes, not as a prediction of a future distribution of biomes.

KEYWORDS: ATMOSPHERE, MODEL

405

Clifford, S.C., C.R. Black, J.A. Roberts, I.M. Stronach, P.R. Singletonjones, A.D. Mohamed, and S.N. Azamali. 1995. The effect of elevated atmospheric co2 and drought on stomatal frequency in groundnut (arachis-hypogaea (L)). *Journal of Experimental Botany 46(288):847-852.*

The effects of elevated atmospheric CO2, alone or in combination with water stress, on stomatal frequency in groundnut (Arachis hypogaea (L.) cv. Kadiri-3) were investigated. CO2 exerted significant effects on stomatal frequency only in irrigated plants. The effects of drought on leaf development outweighed the smaller effects of CO2 concentration, although reductions in stomatal frequency induced by elevated atmospheric CO2 were still observed. When stands of groundnut were grown under irrigated conditions with unrestricted root systems, an increase in atmospheric CO2 from 375 to 700 ppmv decreased stomatal

frequency on both leaf surfaces by up to 16%; in droughted plants, stomatal frequency was reduced by 8% on the adaxial leaf surface only, Elevated atmospheric CO2 promoted larger reductions in leaf conductance than the changes in stomatal frequency, indicating partial stomatal closure. As a result, the groundnut stands grown at elevated CO2 utilized the available soil moisture more slowly than those grown under ambient CO2, thereby extending the growing period. Despite the large variations in cell frequencies induced by drought, there was no treatment effect on either stomatal index or the adaxial/abaxial stomatal frequency ratio. The data suggest that the effects of future increases in atmospheric CO2 concentration on stomatal frequency in groundnut are likely to be small, especially under conditions of water stress, but that the combination of associated reductions in leaf conductance and enhanced assimilation at elevated CO2 will be important in semi-arid regions.

KEYWORDS: DENSITY, ENRICHMENT, INCREASE, RESPONSES

406

Clifford, S.C., I.M. Stronach, A.D. Mohamed, S.N. Azamali, and N.M.J. Crout. 1993. The effects of elevated atmospheric carbon-dioxide and water- stress on light interception, dry-matter production and yield in stands of groundnut (arachis-hypogaea L). *Journal of Experimental Botany 44(269):1763-1770.*

Stands of groundnut (Arachis hypogaea L.), a C-3 legume, were grown in controlled-environment glasshouses at 28 degrees C (15 degrees C) under two levels of atmospheric CO2 (350 ppmv or 700 ppmv) and two levels of soil moisture (irrigated weekly or no water from 35 d after sowing). Elevated CO2 increased the maximum rate of net photosynthesis by up to 40%, with an increase in conversion coefficient for intercepted radiation of 30% (from 1.66 to 2.16 g MJ(-1)) in well-irrigated conditions, and 94% (from 0.64 to 1.24 g MJ(-1)) on a drying soil profile. In plants well supplied with water, elevated CO2 increased dry matter accumulation by 16% (from 13.79 to 16.03 t ha(-1)) and pod yield by 25% (from 2.7 to 3.4 t ha(-1)). However, the harvest index (total pod dry weight/above-ground dry weight) was unaffected by CO2 treatment. The beneficial effects of elevated CO2 were enhanced under severe water stress, dry matter production increased by 112% (from 4.13 to 8.87 t ha(- 1)) and a pod yield of 1.34 t ha(-1) was obtained in elevated CO2, whereas comparable plots at 350 ppmv CO2 only yielded 0.22 t ha(-1). There was a corresponding decrease in harvest index from 0.15 to 0.05. Following the withholding of irrigation, plants growing on a stored soil water profile in elevated CO2 could maintain significantly less negative leaf water potentials (P<0.01) for the remainder of the season than comparable plants grown in ambient CO2, allowing prolonged plant activity during drought. In plants which were well supplied with water, allocation of dry matter between leaves, stems, roots, and pods was similar in both CO2 treatments. On a drying soil profile, allocation in plants grown in 350 ppmv CO2 changed in favour of root development far earlier in the season than plants grown at 700 ppmv CO2, indicating that severe water stress was reached earlier at 350 ppmv CO2. The primary effects of elevated CO2 on growth and yield of groundnut stands were mediated by an increase in the conversion coefficient for intercepted radiation and the prolonged maintenance of higher leaf water potentials during increasing drought stress.

KEYWORDS: CO2- ENRICHMENT, ECOSYSTEMS, FIELD, GROWTH, RESPONSES

407

Clinton, B.D., and J.M. Vose. 1999. Fine root respiration in mature eastern white pine (Pinus strobus) in situ: the importance of CO2 in controlled environments. *Tree Physiology 19(7):475-479.*

We measured seasonal fine root respiration rate in situ while controlling chamber temperature and [CO2]. Atmospheric [CO2] ([CO2](a)) and measured soil [CO2] ([CO2](s)) were alternately delivered to a cuvette containing intact fine roots of eastern white pine (Pinus strobus L.). Respiration rates were consistently higher in [CO2](a) than in [CO2](s) and were almost three times higher during midsummer. Respiration rates were immediately reversed after returning to the alternate [CO2] (i.e., [CO2](a) --> [CO2](s) --> [CO2](a), and vice versa) suggesting a direct effect of elevated [CO2] on apparent respiration. Soil-[CO2]-based respiration rates decreased with increasing [CO2] on a dry mass and tissue [N] basis. We conclude that estimates of soil CO2 flux and soil carbon budgets may be improved by more completely accounting for the rhizosphere microclimate (i.e., soil temperature and [CO2](s)) during measurement of fine root respiration.

KEYWORDS: CLIMATE, EXCHANGE, FOREST, SEEDLINGS, SOIL CARBON-DIOXIDE, TEMPERATURE, WORLD

408

Colelli, G., F.G. Mitchell, and A.A. Kader. 1991. Extension of postharvest life of mission figs by CO2-enriched atmospheres. *Hortscience 26(9):1193-1195.*

Good quality of fresh 'Mission' figs (Ficus carica L.) was maintained for up to 4 weeks when kept at 0, 2.2, or 5C in atmospheres enriched with 15% or 20% CO2. The visible benefits of exposure to high CO2 levels were reduction of decay incidence and maintenance of bright external appearance. Ethylene production was lower, and fruit softening (as measured with a deformation tester) was slower in the high-CO2-stored figs than in those kept in air. Ethanol content of the CO2-treated fruit increased slightly during the first 3 weeks and moderately during the 4th week, while acetaldehyde concentration increased during the first week, then decreased. The results may be applicable to the transport and storage of fresh 'Mission' figs, as high CO2 extended their postharvest life, especially near 0C.

409

Coleman, J.S., and F.A. Bazzaz. 1992. Effects of co2 and temperature on growth and resource use of cooccurring C3 and C4 annuals. *Ecology 73(4):1244-1259.*

We examined how CO2 concentrations and temperature interacted to affect growth, resource acquisition, and resource allocation of two annual plants that were supplied with a single pulse of nutrients. Physiological and growth measurements were made on individuals of Abutilon theophrasti (C3) and Amaranthus retroflexus (C4) grown in environments with atmospheric CO2 levels of 400 or 700-muL/L and with light/dark temperatures of 28-degrees/22-degrees or 38-degrees/31-degrees-C. Elevated CO2 and temperature treatments had significant independent and interactive effects on plant growth, resource allocation, and resource acquisition (i.e., photosynthesis and nitrogen uptake), and the strength and direction of these effects were often dependent on plant species. For example, final biomass of Amaranthus was enhanced by elevated CO2 at 28-degrees but was depressed at 38-degrees. For Abutilon, elevated CO2 increased initial plant relative growth rates at 28-degrees but not at 38-degrees, and had no significant effects on final biomass at either temperature. These results are interpreted in light of the interactive effects of CO2 and temperature on the rates of net leaf area production and loss, and on net whole- plant nitrogen retention. At 28-degrees-C, elevated CO2 stimulated the initial production of leaf area in both species, which led to an initial stimulation of biomass accumulation at the higher CO2 level. However, in elevated CO2 at 28-degrees, the rate of net leaf area loss for Abutilon increased while that of Amaranthus decreased. Furthermore, high CO2 apparently enhanced the ability of Amaranthus to retain nitrogen at this temperature, which may have helped to enhance photosynthesis, whereas nitrogen retention was

unaffected in Abutilon. Thus, at 28-degrees, final biomass of Abutilon was not stimulated in a high CO2 environment whereas the final biomass of Amaranthus was. At 38-degrees, Abutilon had slightly reduced peak leaf areas under elevated CO2 in comparison to ambient CO2 grown plants, but increased rates of photosynthesis per unit leaf area early in the experiment apparently compensated for reduced leaf area. For Amaranthus at 38-degrees, peak leaf area production was not affected by CO2 treatment, but the rate of net leaf area loss hastened under elevated CO2 conditions and was accompanied by substantial reductions of whole-plant nitrogen content and leaf photosynthesis. This may have led to the reduced biomass accumulation of high CO2 grown plants that we observed during the last 30 d of growth. Plants of both species grown in elevated CO2 exhibited reduced tissue-specific rates of nitrogen absorption, increased plant photosynthetic rate per unit of conductance, and increased initial allocation of biomass to roots, irrespective of temperature. Plants of both species grown under an elevated temperature regime had substantially decreased reproductive allocation, increased allocation to stem biomass, and increased plant water flux at both CO2 treatments. The age of plants also affected our interpretations of plant responses to CO2 and temperature treatments. For example, significant effects of CO2 treatment on the growth of Abutilon were evident early, prior to the initiation of flowering, when nitrogen availability would have been highest and pot space would not have been limited. Nevertheless, the opposite was true for Amaranthus, in which significant effects of CO2 treatment on plant growth were not detectable until the final 30 d of the experiment. Elevated CO2 interacted with temperature to affect plant productivity in different ways than would have been predicted from plant responses to elevated CO2 alone. Furthermore, a majority of the interactive effects of CO2 concentration and temperature on plant growth could be interpreted in light of their effects on the rates of net leaf area production and loss, nitrogen retention, and, to a lesser degree, photosynthesis and resource partitioning.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, C-4 PLANTS, CHENOPODIUM-ALBUM L, ELEVATED CO2, ENRICHMENT, LEAF NITROGEN, NITROGEN-USE EFFICIENCY, OLD-FIELD ANNUALS, PHOTOSYNTHETIC RESPONSE

410

Coleman, J.S., K.D.M. McConnaughay, and F.A. Bazzaz. 1993. Elevated co2 and plant nitrogen-use - is reduced tissue nitrogen concentration size-dependent. *Oecologia 93(2):195-200.*

Plants often respond to elevated atmospheric CO2 levels with reduced tissue nitrogen concentrations relative to ambient CO2- grown plants when comparisons are made at a common time. Another common response to enriched CO2 atmospheres is an acceleration in plant growth rates. Because plant nitrogen concentrations are often highest in seedlings and subsequently decrease during growth, comparisons between ambient and elevated CO2-grown plants made at a common time may not demonstrate CO2-induced reductions in plant nitrogen concentration per se. Rather, this comparison may be highlighting differences in nitrogen concentration between bigger, more developed plants and smaller, less developed plants. In this study, we directly examined whether elevated CO2 environments reduce plant nitrogen concentrations independent of changes in plant growth rates. We grew two annual plant species, Abutilon theophrasti (C3 photosynthetic pathway) and Amaranthus retroflexus (C, photosynthetic pathway), from seed in glass-sided growth chambers with atmospheric CO2 levels of 350 mumol . mol-1 or 700 mumol . mol- 1 and with high or low fertilizer applications. Individual plants were harvested every 2 days starting 3 days after germination to determine plant biomass and nitrogen concentration. We found: 1. High CO2-grown plants had reduced nitrogen concentrations and increased biomass relative to ambient CO2-grown plants when compared at a common time; 2. Tissue nitrogen concentrations did not vary as a function of CO2 level when plants were compared at a common size; and 3. The rate of biomass accumulation per rate of increase in plant nitrogen was unaffected by CO2 availability, but was altered by nutrient availability. These results indicate that a CO2- induced reduction in plant nitrogen concentration may not be due to physiological changes in plant nitrogen use efficiency, but is probably a size-dependent phenomenon resulting from accelerated plant growth.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, ENRICHMENT, GROWTH, INCREASE, INSECT HERBIVORE, LEAF LITTER, NUTRITION, ROOT, SHOOT RATIO

411

Coleman, J.S., L. Rochefort, F.A. Bazzaz, and F.I. Woodward. 1991. Atmospheric CO2, plant nitrogen status and the susceptibility of plants to an acute increase in temperature. *Plant, Cell and Environment 14(7):667-674.*

Elevated levels of CO2 in the atmosphere are expected to affect plant performance and may alter global temperature patterns. Changes in mean air temperatures that might be induced by rising levels of CO2 and other greenhouse gases could also be accompanied by increased variability in daily temperatures such that acute increases in air temperature may be more likely than at present. Consequently, we investigated whether plants grown in a CO2 enriched atmosphere would be differently affected by a heat shock than plants grown at ambient CO2 levels. Plants of a C3 annual (Abutilon theophrasti), a C3 annual crop (Sinapis alba) and a C4 annual (Amaranthus retroflexus) were grown from seed in growth chambers under either 400 or 700 cm3 m-3 CO2, and were fertilized with either a high or low nutrient regime. Young seedlings of S. alba, as well as plants of all species in either the vegetative or reproductive phase of growth were exposed to a 4-h heat shock in which the temperature was raised an additional 14-23-degrees-C (depending on plant age). Total biomass and reproductive biomass were examined to determine the effect of CO2, nutrient and heat shock treatments on plant performance. Heat shock, CO2, and nutrient treatments, all had some significant effects on plant performance, but plants from both CO2 treatments responded similarly to heat shocks. We also found, as expected, that plants grown under high CO2 had dramatically decreased tissue N concentrations relative to plants grown under ambient conditions. We predicted that high- CO2-grown plants would be more susceptible to a heat shock than ambient-CO2-grown plants, because the reduced N concentrations of high-CO2 grown plants could result in the reduced synthesis of heat shock proteins and reduced thermotolerance. Although we did not examine heat shock proteins, our results showed little relationship between plant nitrogen status and the ability of a plant to tolerate an acute increase in temperature.

KEYWORDS: C-3, ELEVATED CO2, ENRICHMENT, GROWTH, HEAT-SHOCK PROTEINS, INSECT HERBIVORE, RESPONSES, THERMOTOLERANCE

412

Coleman, W.K., and J. McInerney. 1997. Enhanced dormancy release and emergence from potato tubers after exposure to a controlled atmosphere. *American Potato Journal 74(3):173-182.*

The North American potato industry requires an effective and environmentally-appropriate, dormancy-release methodology. The present study examined dormancy release and subsequent sprout emergence based on a modified, controlled-atmosphere (CA) approach using such environmentally-compatible gases as nitrogen, carbon dioxide and oxygen with or without trace amounts of ethylene (50 ppm). This paper is the first published report of a semi-automated, controlled-atmosphere system for dormancy release of potato tubers. The system allows computer- controlled gas application and analysis for up to four gas mixtures simultaneously. Low oxygen concentrations (<10%) for 10

days in the presence of 10 to 60% carbon dioxide or a high carbon dioxide (60%)/oxygen (40%) treatment caused tuber break- down regardless of cultivar. The most effective mixtures for enhanced dormancy release and sprout emergence were 20% CO2/40% O-2 or 60% CO2/18-20% O-2 and their effects were further enhanced by 50 ppm C2H4 (ethylene). In the presence of 50 ppm C2H4, the 20% CO2/40% O-2 mixture was comparable to bromoethane in effectiveness. Temperature and light exposure affected subsequent Russet Burbank tuber responses to CO2/O-2/C2H4 gas mixtures.

413

Coley, P.D. 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Climatic Change 39(2-3):455-472.*

The interactions between plants and herbivores are key determinants of community structure world wide. Their role is particularly important in lowland tropical rain forests where rates of herbivory are higher, plants are better defended chemically and physically, and herbivores have specialized diets. In contrast to the temperate zone, most of the herbivory in the tropics occurs on ephemeral young leaves (>70%), which requires herbivores to have finely tuned host-finding abilities. As a consequence of these tight ecological and evolutionary linkages, the interplay between plants and herbivores in the tropics may be more susceptible to perturbations of climate change. Increases in global temperature, atmospheric CO2, and the length of the dry season are all likely to have ramifications for plant/herbivore interactions in the tropics. Here I extrapolate from our current and incomplete understanding of the mechanisms regulating plant/herbivore interactions and present a scenario for possible trends under a changing climate. Although elevated CO2 tends to enhance plant growth rates, the larger effects of increased drought stress will probably result in lower growth. In atmospheres experimentally enriched in CO2, the nutritional quality of leaves declines substantially due to a dilution of nitrogen by 10-30%. This response is buffered in plant species associated with nitrogen fixers. Elevated CO2 should also cause a slight decrease in nitrogen-based defenses(e.g., alkaloids) and a slight increase in carbon-based defenses (e.g., tannins). The most dramatic and robust predicted effect of climate change is on rates of herbivory. Lower foliar nitrogen due to CO2 fertilization of plants causes an increase in consumption per herbivore by as much as 40% and unusually severe drought appears to cause herbivore populations to explode. In areas where elevated CO2 is combined with drying, rates of herbivory may rise 2-4 fold. The frequency of insect outbreaks is also expected to increase. Higher herbivory should further reduce plant growth rates, perhaps favoring plant species that are well-defended or fix nitrogen. The predicted increase in the number of herbivores is primarily due to relaxed pressure from predators and parasitoids. Elevated temperatures may increase herbivore developmental times, affording them partial escape from discovery by natural enemies, and drought appears to decimate parasitoid populations. The expected decline in parasitoid numbers may be due to direct effects of dry season drought or to the relative scarcity of herbivores during that period. As a consequence, the relative abundance of species will change, and overall biodiversity should decline.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ELEVATED ATMOSPHERIC CO2, INSECT HERBIVORE INTERACTIONS, LEAF PRODUCTION, LONG-TERM EXPOSURE, MULTIPLE ALLELOCHEMICALS, PAPER BIRCH, PERFORMANCE, PLANT, UNDERSTORY COMMUNITY

414

Colinvaux, P.A. 1998. A new vicariance model for Amazonian endemics. *Global Ecology and Biogeography Letters 7(2):95-96.*

It is unlikely that ice age climates of the Amazon were sufficiently arid to fragment the forest as required by the Haffer refugial hypothesis. However, glacial Amazon climates were colder and had reduced CO2 concentrations that would have had their strongest effects on the biota in the elevated areas stipulated to have been refugia. If local endemicity of butterflies or birds records Pleistocene speciation, this is because glacial climates provided cool, CO2 starved islands in a sea of continuous forest.

KEYWORDS: TEMPERATURE DEPRESSION

415

Combe, L., J.M. Bertolini, and P. Quetin. 1993. Effects of carbon-dioxide and light on photosynthesis of primrose (primula-obconica hance). *Canadian Journal of Plant Science 73(4):1149-1161.*

Net CO2 exchange rates were measured on a 1 m2 crop of Primula obconica placed in a closed loop growing chamber as a function of irradiation and CO2 concentration. Greenhouse cultivation with CO2 enrichment (700 ppm) or without (350 ppm) had only very little effect on dry weight or on flowering rate and did not modify photosynthetic capacity of primrose. Productivity differences between horticultural techniques, such as supplemental lighting and/or CO, enrichment, can be partly explained by study of photosynthesis curves: light increase is more efficient than carbon dioxide increase, the latter giving the best results with young primroses under strong irradiation.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ELEVATED CO2, ENRICHMENT, ENVIRONMENTS, GAS-EXCHANGE, GROWTH, HIGH ATMOSPHERIC CO2, TEMPERATURE, YIELD

416

Comins, H.N. 1994. Equilibrium-analysis of integrated plant-soil models for prediction of the nutrient limited growth-response to co2 enrichment. *Journal of Theoretical Biology 171(4):369-385.*

Although higher ambient CO, concentration is known to promote increased plant productivity under optimal growing conditions, it is not obvious if there will be a sustained growth response in natural and plantation ecosystems, where other resources, such as nutrients, may become limiting. Comins and McMurtrie (1993, Ecol. Applic. 3, 666-681) have constructed the G'DAY (Generic Decomposition A nd Field) integrated plant-soil model to investigate this CO2-nutrient interaction, and have described an analytic method for predicting the long-term response of their model to a step change in CO2 concentration, using the analytic "two timing" approximation. This analysis gives insights into the interactions of the numerous parameters in a comprehensive plant-soil model, and may be generalizable to other such models. The current paper explores the accuracy of the approximation, and discusses various generalizations of the basic model to which the analytic model can still be applied. The very long-term CO2 response of G'DAY was predicted by considering the dynamics of the passive soil organic matter pool in the "two timing" approximation. It was found that the two-timing approximation underestimates the 50-100 year CO2 response in systems that lose a very small proportion of nitrogen per recycling cycle. The other areas considered here are as follows. (i) More complex relationships between N:C ratios and carbon allocation fractions for plant organs, including variable heartwood N:C ratio (which has been identified as an important determinant of long-term CO2 response). Typical results are presented for a range of sensitivities of heartwood N:C ratio to changes in foliar N:C ratio. (ii) Variants of the CENTURY soil model were examined, having variable N:C ratios in the soil organic matter pools and/or carbon flux partition fractions influenced by N:C ratios. (iii) Results are presented for a preliminary analysis of variable nitrogen fixation.

KEYWORDS: CLIMATE, DECOMPOSITION, ECOSYSTEMS, FORESTS, GRASSLANDS

417

Comins, H.N., and R.E. McMurtrie. 1993. Long-term response of nutrient-limited forests to co2 enrichment - equilibrium behavior of plant-soil models. *Ecological Applications 3(4):666-681.*

Established process-based models of forest biomass production in relation to atmospheric CO2 concentration (McMurtrie 1991) and soil carbon/nutrient dynamics (Parton et al. 1987) are integrated to derive the "Generic Decomposition and Yield" model (G'DAY). The model is used to describe how photosynthesis and nutritional factors interact to determine the productivity of forests growing under nitrogen-limited conditions. A simulated instantaneous doubling of atmospheric CO2 concentration leads to a growth response that is initially large (27% above productivity at current CO2) but declines to <10% elevation within 5 yr. The decline occurs because increases in photosynthetic carbon gain at elevated CO2 are not matched by increases in nutrient supply. Lower foliar N concentrations at elevated CO2 have two countervailing effects on forest production: decreased rates of N cycling between vegetation and soils (with negative consequences for productivity), and reduced rates of N loss through gaseous emission, fire, and leaching. Theoretical analysis reveals that there is an enduring response to CO2 enrichment, but that the magnitude of the long-term equilibrium response is extremely sensitive to the assumed rate of gaseous emission resulting from mineralization of nitrogen. Theory developed to analyze G'DAY is applicable to other published production-decomposition models describing the partitioning of soil carbon among compartments with widely differing decay-time constants.

KEYWORDS: CLIMATE, COMMUNITIES, DYNAMICS, ELEVATED ATMOSPHERIC CO2, ESTUARINE MARSH, GRASSLANDS, GROWTH, PRODUCTIVITY, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

418

Conroy, J.P. 1992. Influence of elevated atmospheric CO2 concentrations on plant nutrition. *Australian Journal of Botany 40(4-5):445-456.*

The rising levels of atmospheric CO2 are likely to increase biomass production of C3 species in both natural and managed ecosystems because photosynthetic rates will be higher. The greatest absolute increase in productivity will occur when nitrogen and phosphorus availability in the soil is high. Low nitrogen does not preclude a growth response to high CO2, whereas some C3 species fail to respond to high CO2 when phosphorus is low, possibly because insufficient phosphorus is available to maintain maximum photosynthetic activity at high CO2. C3 plants response to high CO2 because the flux of carbon through the photoreductive cycle is increased and photorespiration is suppressed. This change in metabolism appears to alter the foliar nutrient concentration required to promote maximum productivity (critical concentration). Higher phosphorus concentrations are needed at elevated CO2, whereas the nitrogen requirement is reduced by CO2 enrichment. Since critical concentrations are used to evaluate nutrient status of crop and forest species and to manage fertiliser programs, they will need reassessing as the atmospheric CO2 concentration rises. Another consequence of the altered nutrient requirement at high CO2 is that the nitrogen concentrations of foliage, roots and grain are consistently lower in plants grown at elevated CO2, irrespective of availability of nitrogen in the soil. In natural ecosystems, the lower nitrogen to carbon ratio of the litter may alter rates of nutrient cycling. For farmers, the rising CO2 concentrations could cause reductions in grain nitrogen, and therefore protein content. This could have important implications for baking quality of hard wheats as well as affecting the nutrient value of grain such as rice.

KEYWORDS: C-3, CARBON DIOXIDE, ENRICHMENT, GROWTH, NITROGEN CONCENTRATIONS, PHOTOSYNTHESIS, RADIATA D-DON, STRESS, WATER-USE, WHEAT

419

Conroy, J.P. 1993. Influence of elevated atmospheric co2 concentrations on plant nutrition (vol 40, pg 445, 1992). *Australian Journal of Botany 41(1):143.*

420

Conroy, J., and P. Hocking. 1993. Nitrogen nutrition of C-3 plants at elevated atmospheric co2 concentrations. *Physiologia Plantarum 89(3):570-576.*

The atmospheric CO2 concentration has risen from the preindustrial level of approximately 290 mu 1 1(-1) to more than 350 mu 1 1(-1) in 1993. The current rate of rise is such that concentrations of 420 mu 1 1(-1) are expected in the next 20 years. For C-3 plants, higher CO2 levels favour the photosynthetic carbon reduction cycle over the photorespiratory cycle, resulting in higher rates of carbohydrate production and plant productivity. The change in balance between the two photosynthetic cycles appears to alter nitrogen and carbon metabolism in the leaf, possibly causing decreases in nitrogen concentrations in the leaf. This may result from increases in the concentration of storage carbohydrates of high molecular weight (soluble or insoluble) and/or changes in distribution of protein or other nitrogen containing compounds. Uptake of nitrogen may also be reduced at high CO2 due to lower transpiration rates. Decreases in foliar nitrogen levels have important implications for production of crops such as wheat, because fertilizer management is often based on leaf chemical analysis, using standards estimated when the CO2 levels were considerably lower. These standards will need to be re- evaluated as the CO2 concentration continues to rise. Lower levels of leaf nitrogen will also have implications for the quality of wheat grain produced, because it is likely that less nitrogen would be retranslocated during grain filling.

KEYWORDS: ACCLIMATION, CARBOHYDRATE, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, MINERAL NUTRITION, NITRATE, PHOTOSYNTHESIS, WHEAT

421

Conroy, J.P., P.J. Milham, and E.W.R. Barlow. 1992. Effect of nitrogen and phosphorus availability on the growth- response of eucalyptus-grandis to high co2. *Plant, Cell and Environment 15(7):843-847.*

The response of Eucalyptus grandis seedlings to elevated atmospheric CO2 concentrations was examined by growing seedlings at either 340 or 660-mu-mol CO2 mol-1 for 6 weeks. Graded increments of phosphorus and nitrogen fertilizers were added to a soil deficient in these nutrients to establish if the growth response to increasing nutrient availability was affected by CO2 concentration. At 660-mu-mol CO2 mol-1, seedling dry weight was up to five times greater than at 340- mu-mol CO2 mol-1. The absolute response was largest when both nitrogen and phosphorus availability was high but the relative increase in dry weight was greatest at low phosphorus availability. At 340-mu-mol CO2 mol-1 and high nitrogen availability, growth was stimulated by addition of phosphorus up to 76 mg kg-1 soil. Further additions of phosphorus had little effect. However, at 660-mu-mol CO2 mol-1, growth only began to plateau at a phosphorus addition rate of 920 mg kg-1 soil. At 340-mu-mol CO2 mol-1 and high phosphorus availability, increasing nitrogen from 40 to 160 mg kg-1 soil had little effect on plant growth. At high CO2, growth

reached a maximum at between 80 and 160 mg nitrogen kg-1 soil. Total uptake of phosphorus was greater at high CO2 concentration at all fertilizer addition rates, but nitrogen uptake was either lower or unchanged at high CO2 concentration except at the highest nitrogen fertilizer rate. The shoot to root ratio was increased by CO2 enrichment, primarily because the specific leaf weight was greater. The nitrogen and phosphorus concentration in the foliage was lower at elevated CO2 concentration partly because of the higher specific leaf weight. These results indicate that critical foliar concentrations currently used to define nutritional status and fertilizer management may need to be reassessed as the atmospheric CO2 concentration rises.

KEYWORDS: CARBON DIOXIDE, DEFICIENCY, ENRICHMENT, METABOLISM, PLANTS, RADIATA D-DON, SEEDLINGS, STRESS, WHEAT

422

Conroy, J.P., P.J. Milham, D.I. Bevege, and E.W.R. Barlow. 1990. Influence of phosphorus deficiency on the growth-response of 4 families of Pinus radiata seedlings to CO2-enriched atmospheres. *Forest Ecology and Management 30(1-4):175-188.*

423

Conroy, J.P., P.J. Milham, M. Mazur, and E.W.R. Barlow. 1990. Growth, dry-weight partitioning and wood properties of Pinus radiata d don after 2 years of CO2 enrichment. *Plant, Cell and Environment 13(4):329-337.*

424

Conroy, J.P., P.J. Milham, M.L. Reed, and E.W. Barlow. 1990. Increases in phosphorus requirements for CO2-enriched pine species. *Plant Physiology 92(4):977-982.*

425

Conroy, J.P., S. Seneweera, A.S. Basra, G. Rogers, and B. Nissenwooller. 1994. Influence of rising atmospheric co2 concentrations and temperature on growth, yield and grain quality of cereal crops. *Australian Journal of Plant Physiology 21(6):741-758.*

A possible scenario for the end of the 21st century is that the atmospheric CO2 concentration will be in the range of 510-760 mu L L(-1) and that the mean global temperature will be 1.5-4.5 degrees C higher. Further, there may be greater incidences of extreme climatic events, which together with the CO2 and temperature changes will influence development, growth and grain yield of cereals such as rice and wheat. For these C-3, plants, the driving force for the growth response to elevated CO2 is higher leaf CO2 assimilation rates (4). However, the response of A to CO2 depends on temperature with maximum absolute increases occuring at temperatures which do not cause flower abortion, while negligible increases are observed at low temperatures. At high temperatures, where A is reduced because of partial inactivation of photosynthetic enzymes, the increase in A due to CO2 enrichment is still observed. Other factors, such as changes in shoot water relations or hormone concentrations, may influence growth at elevated CO2 concentrations. Wheat and rice development is accelerated by high temperature and consequently grain yield is reduced because there is less time for radiation to be intercepted during the vegetative phase. Although high CO2 also accelerates development in rice and, to a lesser extent in wheat, the extra carbohydrate produced by increases in A results in at least a 40% increase in grain yield at temperatures which do not cause flower abortion. This is due mainly to increased tiller numbers rather than increases in the number or weight of individual grains. However, the yield enhancement due to high CO2 will not necessarily compensate for decreases in yield caused by accelerated development at high temperatures. As predicted by the response of A to high CO2, the relative increase in yield, due to rising CO2 concentrations, is smaller at lower temperatures. Elevated atmospheric CO2 may improve the tolerance of plants to heat-induced drought stress by facilitating the maintenance of cell volume and photosynthetic function in the leaves. Increased carbohydrate storage in the stems may also be an advantage during grain filling if the flag leaves senesce prematurely. However, it is unlikely that the effect of very high temperatures on newer abortion will be ameliorated by high CO2. For bread making, the quality of flour produced from grain developed at high temperatures is poorer. High CO2 may also have an effect through a reduction in the protein content of wheat grain. For rice, the amylose content of the grain, a major determinant of cooking quality is increased under elevated CO2.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, NITROGEN, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANT GROWTH, RICE, WATER RELATIONS, WHEAT PLANTS

426

Constable, J.V.H., A.B. Guenther, D.S. Schimel, and R.K. Monson. 1999. Modelling changes in VOC emission in response to climate change in the continental United States. *Global Change Biology 5(7):791-806.*

The alteration of climate is driven not only by anthropogenic activities, but also by biosphere processes that change in conjunction with climate. Emission of volatile organic compounds (VOCs) from vegetation may be particularly sensitive to changes in climate and may play an important role in climate forcing through their influence on the atmospheric oxidative balance, greenhouse gas concentration, and the formation of aerosols. Using the VEMAP vegetation database and associated vegetation responses to climate change, this study examined the independent and combined effects of simulated changes in temperature, CO2 concentration, and vegetation distribution on annual emissions of isoprene, monoterpenes, and other reactive VOCs (ORVOCs) from potential vegetation of the continental United States. Temperature effects were modelled according to the direct influence of temperature on enzymatic isoprene production and the vapour pressure of monoterpenes and ORVOCs. The effect of elevated CO2 concentration was modelled according to increases in foliar biomass per unit of emitting surface area. The effects of vegetation distribution reflects simulated changes in species spatial distribution and areal coverage by 21 different vegetation classes. Simulated climate warming associated with a doubled atmospheric CO2 concentration enhanced total modelled VOC emission by 81.8% (isoprene + 82.1%, monoterpenes + 81.6%, ORVOC + 81.1%), whereas a simulated doubled CO2 alone enhanced total modelled VOC emission by only + 11.8% (isoprene + 13.7%, monoterpenes + 4.1%, ORVOC + 11.7%). A simulated redistribution of vegetation in response to altered temperatures and precipitation patterns caused total modelled VOC emission to decline by 10.4% (isoprene - 11.7%, monoterpenes -18.6%, ORVOC 0.0%) driven by a decline in area covered by vegetation classes emitting VOCs at high rates. Thus, the positive effect of leaf-level adjustments to elevated CO2 (i.e. increases in foliar biomass) is balanced by the negative effect of ecosystem-level adjustments to climate (i.e. decreases in areal coverage of species emitting VOC at high rates).

KEYWORDS: AEROSOL FORMATION, ALPHA- PINENE, BETA-PINENE, BIOGENIC EMISSIONS, CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH, ISOPRENE, ORGANIC-COMPOUND EMISSIONS

427

Constable, J.V.H., M.E. Litvak, J.P. Greenberg, and R.K. Monson. 1999. Monoterpene emission from coniferous trees in response to elevated CO2 concentration and climate warming. *Global Change Biology 5(3):255-267.*

It was hypothesized that high CO2 availability would increase monoterpene emission to the atmosphere. This hypothesis was based on resource allocation theory which predicts increased production of plant secondary compounds when carbon is in excess of that required for growth. Monoterpene emission rates were measured from needles of (a) Ponderosa pine grown at different CO2 concentrations and soil nitrogen levels, and (b) Douglas fir grown at different CO2 concentrations. Ponderosa pine grown at 700 mu mol mol(-1) CO2 exhibited increased photosynthetic rates and needle starch to nitrogen (N) ratios when compared to trees grown at 350 mu mol mol(-1) CO2. Nitrogen availability had no consistent effect on photosynthesis. Douglas fir grown at 550 mu mol mol(-1) CO2 exhibited increased photosynthetic rates as compared to growth at 350 mu mol mol(-1) CO2 in old, but not young needles, and there was no influence on the starch/N ratio. In neither species was there a significant effect of elevated growth CO2 on needle monoterpene concentration or emission rate. The influence of climate warming and leaf area index LAD on monoterpene emission were also investigated. Douglas fir grown at elevated CO2 plus a 4 degrees C increase in growth temperature exhibited no change in needle monoterpene concentration, despite a predicted 50% increase in emission rate. At elevated CO2 concentration the LAI increased in Ponderosa pine, but not Douglas fir. The combination of increased LAI and climate warming are predicted to cause an 80% increase in monoterpene emissions from Ponderosa pine forests and a 50% increase in emissions from Douglas fir forests. This study demonstrates that although growth at elevated CO2 may not affect the rate of monoterpene emission per unit biomass, the effect of elevated CO2 on LAI, and the effect of climate warming on monoterpene biosynthesis and volatilization, could increase canopy monoterpene emission rate.

KEYWORDS: ATMOSPHERIC CHEMISTRY, CARBON, GROWTH, ISOPRENE, NITROGEN, PONDEROSA PINE, RATE VARIABILITY, SEEDLINGS

428

Constable, J.V.H., G.E. Taylor, J.A. Laurence, and J.A. Weber. 1996. Climatic change effects on the physiology and growth of Pinus ponderosa: Expectations from simulation modeling. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(8):1315-1325.*

The TREGRO model was used to simulate the growth response of mature Piizus ponderosa Dougl. ex Laws. to the interacting effects of changes in CO2 (+200 mu L/L), temperature (+4 degrees C), and O-3 (0.5x, 1x, and 2x ambient). Relative to simulated growth under the base-line climate in Corvallis, Oregon, elevated CO2 and temperature individually increased total-tree biomass gain by 29% and 13%, respectively, but when combined increased biomass gain by 49%. Ozone at all exposures reduced total-tree biomass gain by 1%, 19%, and 39%, respectively, as compared with simulated base-line conditions. Elevated CO2 increased photosynthesis and reduced stomatal conductance and partially offset growth reductions due to 2 x O-3. Elevated temperature, however, increased both photosynthesis and stomatal conductance and was less effective at mitigating growth reductions due to 2x O-3. Growth at 2x O-3 in elevated CO2 and temperature conditions had little effect on total-tree growth, but decreased fine-root growth by 61%. The simulated changes in stomatal conductance and fine-root biomass are expected to interact with the availability of soil resources to affect tree growth and possibly alter the distribution of Pinus ponderosa.

KEYWORDS: COMPENSATORY RESPONSES, DROUGHT, ELEVATED CO2, GAS-EXCHANGE, NET PHOTOSYNTHESIS, OZONE EXPOSURE, PHOTOSYNTHETIC CAPACITY, STOMATAL CONDUCTANCE, STRESSES, USE EFFICIENCY

429

Conway, T.J., L.P. Steele, and P.C. Novelli. 1993. Correlations among atmospheric co2, ch4 and co in the arctic, march 1989. *Atmospheric Environment Part A-General Topics 27(17-18):2881-2894.*

During six aircraft flights conducted as part of the third Arctic Gas and Aerosol Sampling Program (AGASP III, March 1989), 189 air samples were collected throughout the Arctic troposphere and lower stratosphere for analysis of CO2, CH4 and CO. The mixing ratios of the three gases varied significantly both horizontally and vertically. Elevated concentrations were found in layers with high anthropogenic aerosol concentrations (Arctic Haze), The mixing ratios of CO2, CH4 and CO were highly correlated on all flights. A linear regression of CH4 vs CO2 for pooled data from all flights yielded a correlation coefficient (r(2)) of 0.88 and a slope of 13.5 ppb CH4/ppm CO2 (n = 186). For CO vs CO2 a pooled linear regression gave r(2) = 0.91 and a slope of 15.8 ppb CO/ppm CO2 (n = 182). Carbon dioxide, CH4 and CO also exhibited mean vertical gradients with slopes of 0.37, -4.4 and -4.2 ppb km(-1), respectively. Since the carbon dioxide variations observed in the Arctic atmosphere during winter are due primarily to variations in the emissions and transport of anthropogenic CO2 from Europe and Asia, the strong correlations that we have found suggest that a similar interpretation applies to CH4 and CO. Using reliable estimates of CO2 emissions for the source regions and the measured CH4/CO2 and CO/CO2 ratios, we estimate a regional European CH4 source of 47+/-6 Tg CH4 yr(-1) that may be associated with fossil fuel combustion. A similar calculation for CO results in an estimated regional CO source of 82+/- 2Tg CO yr(-1).

KEYWORDS: AEROSOL, AGASP, AIR-POLLUTION, ALASKA, APRIL, ARCTIC HAZE, BARROW, CARBON DIOXIDE, METHANE, VARIABILITY

430

Cook, A.C., D.T. Tissue, S.W. Roberts, and W.C. Oechel. 1998. Effects of long-term elevated [CO2] from natural CO2 springs on Nardus stricta: Photosynthesis, biochemistry, growth and phenology. *Plant, Cell and Environment 21(4):417-425.*

Plants of Nardus stricta growing near a cold, naturally emitting CO2 spring in Iceland were used to investigate the long-term (> 100 years) effects of elevated [CO2] on photosynthesis, biochemistry, growth and phenology in a northern grassland ecosystem. Comparisons were made between plants growing in an atmosphere naturally enriched with CO2 (approximate to 790 mu mol mol(-1)) near the CO2 spring and plants of the same species growing in adjacent areas exposed to ambient CO2 concentrations (approximate to 360 mu mol mol(-1)). Nardus stricta growing near the spring exhibited earlier senescence and reductions in photosynthetic capacity (approximate to 25%), Rubisco content (approximate to 26%), Rubisco activity (approximate to 40%), Rubisco activation state (approximate to 23%), chlorophyll content (approximate to 33%) and leaf area index (approximate to 22%) compared,vith plants growing away from the spring. The potential positive effects of elevated [CO2] on grassland ecosystems in Iceland are likely to be reduced by strong down-regulation in the photosynthetic apparatus of the abundant N, stricta species.

KEYWORDS: ACCLIMATION, ALASKAN TUSSOCK TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, CARBOXYLASE ACTIVITY, ENRICHMENT, ERIOPHORUM VAGINATUM, PLANTS, RESPONSES, RUBISCO, SEEDLINGS

431

Corey, K.A., M.E. Bates, and S.L. Adams. UNKNOWN YEAR. Carbon-dioxide exchange of lettuce plants under hypobaric conditions. *Physical, Chemical, Biochemical and Biological Techniques and Processes :301-308.*

Growth of plants in a Controlled Ecological Life Support System (CELSS) may involve the use of hypobaric pressures enabling lower mass requirements for atmospheres and possible enhancement of crop productivity, A controlled environment plant growth chamber with hypobaric capability designed and built at Ames Research Center was used to determine if reduced pressures influence the rates of photosynthesis (Ps) and dark respiration (DR) of hydroponically grown lettuce plants, The chamber, referred to as a plant volatiles chamber (PVC), has a growing area of about 0.2 m(2), a total gas volume of about 0.7 m(3), and a leak rate at 50 kPa of < 0.1%/day. When the pressure in the chamber was reduced from ambient to 51 kPa, the rate of net Ps increased by 25% and the rate of DR decreased by 40%, The rate of Ps increased linearly with decreasing pressure, There was a greater effect of reduced pressure at 41 Pa CO2 than at 81 Pa CO2. This is consistent with reports showing greater inhibition of photorespiration (Pr) in reduced O-2 at low CO2 concentrations. When the partial pressure of O-2 was held constant but the total pressure was varied between 51 and 101 kPa, the rate of CO2 uptake was nearly constant, suggesting that low pressure enhancement of Ps may be mainly attributable to lowered partial pressure of O-2 and the accompanying reduction in Pr, The effects of lowered partial pressure of O-2 on Ps and DR could result in substantial increases in the rates of biomass production, enabling rapid throughput of crops or allowing flexibility in the use of mass and energy resources for a CELSS.

KEYWORDS: INCOMPLETE, ENVIRONMENTS, PRODUCTIVITY, WHEAT

432

Corlett, R.T., and J.V. LaFrankie. 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change 39(2-3):439-453.*

Changes in plant phenology will be one of the earliest responses to rapid global climate change and could potentially have serious consequences both for plants and for animals that depend on periodically available plant resources. Phenological patterns are most diverse and least understood in the tropics. In those parts of tropical Asia where low temperature or drought impose a seasonal rest period, regular annual cycles of growth and reproduction predominate at the individual, population, and community level. In aseasonal areas, individuals and populations show a range of sub- to supra- annual periodicities, with an overall supra-annual reproductive periodicity at the community level. There is no evidence for photoperiod control of phenology in the Asian tropics, and seasonal changes in temperature are a likely factor only near the northern margins. An opportunistic response to water availability is the simplest explanation for most observed patterns where water is seasonally limiting, while the great diversity of phenological patterns in the aseasonal tropics suggests an equal diversity of controls. The robustness of current phenological patterns to high interannual and spatial variability suggests that most plant species will not be seriously affected by the phenological consequences alone of climate change. However, some individual plant species may suffer, and the consequences of changes in plant phenology for flower- and fruit-dependent animals in fragmented forests could be serious.

KEYWORDS: ASEASONAL TROPICS, CONSEQUENCES, COSTA-RICA, DRY FOREST, ELEVATED CO2, MOIST FOREST, PATTERNS, RAIN-FOREST, REPRODUCTIVE PHENOLOGY, TREES

433

Cornelissen, J.H.C., A.L. Carnelli, and T.V. Callaghan. 1999. Generalities in the growth, allocation and leaf quality responses to elevated CO2 in eight woody species. *New Phytologist 141(3):401-409.*

This paper reports general patterns of relative growth rate and related traits in response to elevated atmospheric CO2 in eight woody species ranging widely in life form, leaf habit, taxonomy and ecology. Young plants of these species, all of comparable ontogenetic phases, R-ere grown simultaneously in large containers with favourable nutrient and water availability in transparent outdoor chambers at 350 and 700 mu l l(-1) CO2 for one growing season. We found the following consistent responses. (1) All species grew faster at elevated CO2, whereas the following leaf and allocation traits were consistently lower in CO2-enriched environments: specific leaf area (quotient of leaf area and leaf weight), leaf area ratio (quotient of total leaf area and plant weight), weight-based foliar N concentration and, to a smaller extent, leaf weight fraction (quotient of leaf weight and plant weight). (2) There was important interspecific variation in the magnitude of the response of relative growth rate to CO2. Specific leaf area at ambient CO2 explained 88% of the variation in relative growth rate response to CO2 among the eight species. At ambient CO2, relative growth rate itself, was significantly correlated with the relative growth rate response to CO2 only if the leafless species Ulex gallii was excluded from analysis. (3) The four deciduous species had a significantly stronger relative growth rate response to CO2 than the four evergreens. This corresponded with their generally higher specific leaf area. (4) Specific leaf area and leaf habit might be useful for scaling up exercises, as easy-to-measure substitutes for growth responses of (woody) vegetation to elevated CO2. However, the usefulness of such traits in this contest needs to be tested in realistic, longer-term manipulative experiments in real ecosystems.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CHEMICAL-COMPOSITION, ECOSYSTEMS, MODEL, NITROGEN, PLANT-RESPONSES, SEEDLINGS, TREE, WIDE-RANGE

434

Corrigan, V.K., and A. Carpenter. 1993. Effects of treatment with elevated carbon-dioxide levels on the sensory quality of asparagus. *New Zealand Journal of Crop and Horticultural Science 21(4):349-357.*

Asparagus spears (Asparagus officinalis L. cv. Limbras 10) were stored for 3-5 days in atmospheres containing between 40 and 90% carbon dioxide (CO2) to evaluate the effect of insecticidal CO2 atmospheres on sensory quality based on sensory panel ratings of characteristic asparagus flavour, off-flavours, flavour acceptability, and overall acceptability. Sensory quality of spears after 4 days storage in 60% CO2 was similar to air-stored spears but 5 days storage caused deterioration in the CO2-stored spears relative to the air-stored spears. Using higher CO2 levels than this for shorter storage times resulted in spears with CO2 injury and poor sensory quality. Spear quality deteriorated with shelf period but previous CO2 treatment did not affect the rate of deterioration. Storing spears at 5-degrees-C in 60% CO2 or 0-degrees-C in air gave consistently higher (lower for off-flavours) sensory quality ratings for all characteristics assessed than vice versa. Thick spears had more flavour and were more acceptable than thin spears. Thick spears had more flavour than thin spears when stored in CO2, but thin spears had more flavour when stored in air than in CO2. In 60% CO2, spears stored dry had a more acceptable flavour and were more acceptable overall (where panellists considered aspects such as flavour, texture, and off-flavours in the overall rating) than those stored with their butts in water. Spears stored in air with their butts in water had a more acceptable flavour and were more acceptable overall, spears stored with their butts in water had less characteristic asparagus flavour than those stored dry. High levels of CO2 could be used as a disinfestation treatment of fresh asparagus spears without significant effect on spear quality (compared to spears stored in air under similar conditions)

providing levels >60% CO2 are not used, and storage time in the atmosphere is kept to 4 days or less.

KEYWORDS: CONTROLLED-ATMOSPHERE STORAGE, HARVEST, SPEARS

435

Cotrufo, M.E., and P. Ineson. 1995. Effects of enhanced atmospheric co2 and nutrient supply on the quality and subsequent decomposition of fine roots of betula- pendula roth and picea-sitchensis (bong) carr. *Plant and Soil 170(2):267-277.*

Fine root litter derived from birch (Betula pendula Roth.) and Sitka spruce (Picea sitchensis (Bong.) Carr.) plants grown under two CO2 atmospheric concentrations (350 ppm and 600 ppm) and two nutrient regimes was used for decomposition studies in laboratory microcosms. Although there were interactions between litter type, CO2/fertiliser treatments and decomposition rates, in general, an increase in the C/N ratio of the root tissue was observed for roots of both species grown under elevated CO2 in unfertilized soil. Both weight loss and respiration of decomposing birch roots were significantly reduced in materials derived from enriched CO2, whilst the decomposition of spruce roots showed no such effect. A parallel experiment was performed using Betula pendula root litter grown under different N regimes, in order to test the relationship between C/N ratio of litter and root decomposition rate. A highly significant ($p < 0.001$) negative correlation between C/N ratio and root litter respiration was found, with an r(2) = 0.97. The results suggest that the increased C/N ratio of plant tissues induced by elevated CO2 can result in a reduction of decomposition rate, with a resulting increase in forest soil C stores.

KEYWORDS: ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FERTILIZATION, FOREST, GROWTH, NITROGEN, ORGANIC-MATTER, PINE, RESPONSES

436

Cotrufo, M.F., M.J.I. Briones, and P. Ineson. 1998. Elevated CO2 affects field decomposition rate and palatability of tree leaf litter: Importance of changes in substrate quality. *Soil Biology and Biochemistry 30(12):1565-1571.*

Field decomposition rates of ash (Fraxinus excelsior L.) and sycamore (Acer pseudoplatanus L.) leaf litters were measured for litters grown at ambient and elevated concentration of atmospheric CO2 inside solar domes. Litter raised at 600 mu l l(-1) CO2 retained significantly more mass at the end of the first year of field decomposition than material raised at 350 mu l l(-1). This reduction in decomposition could be related to changes in tissue quality resulting from growing the plants at higher CO2 concentrations, with C-to-N ratios and lignin contents being significantly increased. The elevated CO2 treatment also affected the rate of consumption of ash leaf litter by Oniscus asellus L. (Isopoda: Oniscoidea), with significantly less (-16%) material being consumed for litter derived from the high CO2 regime. Our results indicate that changes in litter quality, which we may expect under elevated CO2, may affect litter palatability for soil fauna.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GRASS, GROWTH, NITROGEN, ONISCUS-ASELLUS, PLANTS, RESPONSES, SOIL BIOTA

437

Cotrufo, M.F., and A. Gorissen. 1997. Elevated CO2 enhances below-ground C allocation in three perennial grass species at different levels of N availability. *New Phytologist 137(3):421-431.*

Three perennial grass species, Lolium perenne L., Agrostis capillaris L. and Festuca ovina L., were homogeneously labelled in phytotrons with (CO2)-C-14 at two CO2 concentrations (350 and 700 mu l l(-1)). Plants were grown under two nitrogen regimes: one with a minor addition of 8 kg N ha(-1), the other with an addition of 278 kg N ha2(-1). Carbon allocation over the different compartments of the plant/soil systems was measured: shoots, roots, rhizosphere soil (soil solution, microbial biomass and soil residue), and bulk soil. Elevated CO2 increased total net C-14 recovery in all species by 14%, and significantly enhanced the below-ground C-14 allocation by 26%, this enhancement was 24%, 39% and 21%, for root, rhizosphere soil and bulk soil, respectively. Within the rhizosphere soil, the C-14 amounts in the soil solution (+ 69 %) and soil residue (+ 49 %) increased significantly. Total microbial biomass-C in the rhizosphere soil was also increased (15%) by the elevated CO2 treatment, but only in proportion to the increased root mass. No interactions were observed between the elevated CO2 and N treatments. The N treatment increased total net C-14 recovery by more than 300% and C-14 was preferentially allocated to the shoots, leading to a significant increase in shoot-to-root ratio. However, N fertilization also increased(+ 111 %)the absolute amount of C- 14 in soil. The three species behaved differently, but no interactions were observed between CO2 treatment and plant species. These results show that elevated CO2 induces an increased C input into soil for all three grass species at both N levels. However, the highest absolute amounts were found in the soils of the fastest growing species and at the highest N level.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS CARBON, CARBON DIOXIDE, CO2- ENRICHMENT, DECOMPOSITION, GROWTH, NITROGEN, RESPONSES, ROOT, SOIL SYSTEM

438

Cotrufo, M.F., and P. Ineson. 1996. Elevated CO2 reduces field decomposition rates of Betula pendula (Roth) leaf litter. *Oecologia 106(4):525-530.*

The effect of elevated atmospheric CO2 and nutrient supply on elemental composition and decomposition rates of tree leaf litter was studied using litters derived from birch (Betula pendula Roth.) plants grown under two levels of atmospheric CO2 (ambient and ambient+250 ppm) and two nutrient regimes in solar domes. CO2 and nutrient treatments affected the chemical composition of leaves, both independently and interactively. The elevated CO2 and unfertilized soil regime significantly enhanced lignin/N and C/N ratios of birch leaves. Decomposition was studied using field litter-bags, and marked differences were observed in the decomposition rates of litters derived from the two treatments, with the highest weight remaining being associated with litter derived from the enhanced CO2 and unfertilized regime. Highly significant correlations were shown between birch litter decomposition rates and lignin/N and C/N ratios. It can be concluded, from this study, that at levels of atmospheric CO2 predicted for the middle of the next century a deterioration of litter quality will result in decreased decomposition rates, leading to reduction of nutrient mineralization and increased C storage in forest ecosystems. However, such conclusions are difficult to generalize, since tree responses to elevated CO2 depend on soil nutritional status.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON DIOXIDE, CASTANEA-SATIVA MILL, ENRICHMENT, LIGNIN CONTROL, NITROGEN, PLANTS, QUALITY, SEEDLINGS

439

Cotrufo, M.F., P. Ineson, and A.P. Rowland. 1994. Decomposition of tree leaf litters grown under elevated co2 - effect of litter quality. *Plant and Soil 163(1):121-130.*

Ash (Fraxinus excelsior L.), birch (Betula pubescens Ehrh.), sycamore

(Acer pseudoplatanus L.) and Sitka spruce (Picea sitchensis (Bong.) Carr.) leaf litters were monitored for decomposition rates and nutrient release in a laboratory microcosm experiment. Litters were derived from solar domes where plants had been exposed to two different CO2 regimes: ambient (350 mu L L(-1) CO2) and enriched (600 mu L L(-1) CO2). Elevated CO2 significantly affected some of the major litter quality parameters, with lower N, higher lignin concentrations and higher ratios of C/N and lignin/N for litters derived from enriched CO2. Respiration rates of the deciduous species were significantly decreased for litters grown under elevated CO2, and reductions in mass loss at the end of the experiment were generally observed in litters derived from the 600 ppm CO2 treatment. Nutrient mineralization, dissolved organic carbon, and pH in microcosm leachates did not differ significantly between the two CO2 treatments for any of the species studied. Litter quality parameters were examined for correlations with cumulative respiration and decomposition rates: N concentration, C/N and lignin/N ratios showed the highest correlations, with differences between litter types. The results indicate that higher C storage will occur in soil as a consequence of litter quality changes resulting from higher atmospheric concentrations of CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, LIGNIN CONTROL, NITROGEN, NUTRIENT-UPTAKE, ORGANIC-MATTER, RESPONSES, SEEDLINGS, SUBSTRATE QUALITY

440

Cotrufo, M.F., P. Ineson, and A. Scott. 1998. Elevated CO2 reduces the nitrogen concentration of plant tissues. *Global Change Biology 4(1):43-54.*

We summarize the impacts of elevated CO2 on the N concentration of plant tissues and present data to support the hypothesis that reductions in the quality of plant tissue commonly occur when plants are grown under elevated CO2. Synthesis of existing data showed an average 14% reduction of N concentrations in plant tissue generated under elevated CO2 regimes. However, elevated CO2 appeared to have different effects on the N concentrations of different plant types, as the reported reductions in N have been larger in C3 plants than in C4 plants and N-2-fixers. Under elevated CO2 plants changed their allocation of N between above-and below-ground components: root N concentrations were reduced by an average of 9% compared to a 14% average reduction for above-ground tissues. Although the concentration of CO2 treatments represented a significant source of variance for plant N concentration, no consistent trends were observed between them.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CARBON-DIOXIDE, BETULA-PENDULA ROTH, CLOVER TRIFOLIUM-REPENS, INSECT PERFORMANCE, LEAF GAS- EXCHANGE, LIRIODENDRON-TULIPIFERA L, LITTER DECOMPOSITION, MINERAL NUTRITION, NUTRIENT STATUS

441

Cotrufo, M.F., A. Raschi, M. Lanini, and P. Ineson. 1999. Decomposition and nutrient dynamics of Quercus pubescens leaf litter in a naturally enriched CO2 Mediterranean ecosystem. *Functional Ecology 13(3):343-351.*

1. The chemical composition (i.e. N, P, C, lignin and polyphenol concentrations) of Quercus pubescens leaf litter derived from a natural CO2 spring in Tuscany (Italy) was analysed and compared to litter from a nearby reference site. Litter was incubated for 25 months at both the natural CO2 spring and the reference site, and monitored for decomposition rates, nutrient and lignin concentrations. 2. Long-term exposure to elevated CO2 concentrations from the natural spring was associated with a change in the chemical composition of the Oak leaf litter, with decreases in P and polyphenol concentrations and increases in lignin. No differences in N concentrations were observed between the enriched CO2 litter from the natural spring and the reference litter. 3. Decomposition was reduced in the CO2 spring, with the lower P concentration of the native litter, combined with the lack of soil fauna observed at that site, being the factors most probably responsible for the measured decreases in mass loss. However, litter from the CO2 spring and reference litter decomposed at the reference site showed similar rates of decomposition. 4. All litter showed similar N concentrations during decomposition, with N being mineralized throughout the incubation period from both litter regardless of the site of incubation. In contrast, P dynamics differed between litter, with P being immobilized in the litter derived from the spring, and mineralized from the reference litter. When the litter from the spring was incubated at the reference site, there was a trend for net P uptake from the surrounding environment. The chemical composition of decomposing litter from the spring appeared to match that of the reference litter after 3 months of incubation at the reference site. 5. The results from the CO2 spring suggest that litter decomposition may be retarded under elevated levels of atmospheric CO2. However, results from field surveys around CO2 vents should be viewed with caution because differences may relate to factors other than the known differences in CO2 concentrations.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, LIGNIN CONTROL, NITROGEN, QUALITY, RATES, RELEASE, SCOTS PINE FOREST, SOIL CARBON, TALLGRASS PRAIRIE

442

Coughenour, M.B., and D.X. Chen. 1997. Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models. *Ecological Applications 7(3):802-827.*

Models of photosynthesis, plant growth, and biophysical processes were linked with models that simulate water, nutrient, and carbon flows through plant-soil ecosystems. The linked ecosystem model was applied to examine ecosystem-level responses to CO2, temperature, precipitation, and global- warming scenarios in grasslands of Colorado and Kansas, USA, and Kenya. The model predicted that increased temperatures would decrease primary production at current CO2 levels, but decreases were reversed by doubling atmospheric CO2 concentration. Greater increases in daily minimum temperatures than daily maximum temperatures mitigated reductions in photosynthesis and water-use efficiency (WUE) later in the day, more than offseting increases in nighttime respiration rates under warmer temperatures. A temperature increase of 5 degrees C reduced organic carbon in grassland soils by 20-30%, through effects on plant growth and decomposition, but the doubled CO2 negated soil carbon losses by increasing plant growth. Under higher precipitation and doubled CO2, soil carbon stocks increased, or decreased little, in response to warmer temperatures. Doubling CO2 increased net primary production (NPP) by 31-45% in a simulated Colorado C-4 grassland, by 20- 70% in a Colorado C-3 grassland, by 23-31% in a Kansas C-4 grassland, and by 23-35% in a Kenya C-4 grassland at ambient precipitation levels. Growth was shifted belowground, thus weakening aboveground responses. Higher temperatures strengthened the positive NPP responses to CO2. Larger positive responses to elevated CO2 were modeled under drier conditions, and smaller responses were modeled under wetter conditions. NPP increases under elevated CO2 were mostly caused by increased plant WUE at all sites, which was brought about by partial stomatal closure. Decreased N concentrations in plant litter under elevated CO2 slowed N mineralization, but greater plant production and thus greater litter inputs into the soil under elevated CO2 offset the negative effects of lower litter quality. Decreases in plant N concentration under elevated CO2 also reduced plant N requirements. At current atmospheric CO2 (350 mu mol/mol), a general circulation model (GCM) climate- change scenario decreased NPP and soil organic matter (SOM) in Colorado but not in Kansas or Kenya. A second GCM climate- change scenario either

affected NPP and SOM little, or increased NPP and SOM at current CO2. NPP and SOM responses in the simulated grasslands were very sensitive to precipitation, which GCMs predict with relatively low confidence. Doubled CO2 partially or completely offset decreases in NPP and SOM under climate-change scenarios.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO2 CONCENTRATIONS, LEAF GAS- EXCHANGE, MIXED-LAYER MODEL, RISING CO2, STOMATAL CONDUCTANCE, TALLGRASS PRAIRIE, WATER-USE

443

Cournac, L., B. Dimon, P. Carrier, A. Lohou, and P. Chagvardieff. 1991. Growth and photosynthetic characteristics of Solanum tuberosum plantlets cultivated invitro in different conditions of aeration, sucrose supply, and CO2 enrichment. *Plant Physiology 97(1):112-117.*

Growth characteristics, oxygen exchange, and carbohydrate and chlorophyll contents were determined 30 days after subculturing of single node-derived plantlets of Solanum tuberosum cv Haig cultivated in vitro. Cultivation conditions were: (a) photomixotrophy in closed vessel, (b) photomixotrophy in closed vessel on medium supplemented with silver thiosulfate, (c) photomixotrophy in aerated vessel, (d) photoautotrophy in air, (e) photoautotrophy in CO2-enriched air. In photomixotrophic conditions, aeration of the vessel enhanced sucrose utilization and had a positive effect on plantlet growth. In photoautotrophic conditions, growth of the plantlets was slow in air and was strongly enhanced by CO2 enrichment of the atmosphere. Starch to sucrose ratios were higher in plants grown photoautotrophically than in plants grown with sucrose in the medium. Oxygen exchange characteristics on a chlorophyll basis were similar between the plantlets when measured under moderate light, and resembled those of greenhouse plant leaves. In high light, however, plantlets grown photoautotrophically in a CO2-enriched atmosphere had higher oxygen exchange rates. We concluded from these results that potato plantlets in vitro in conditions (c), (d), and (e) developed C3-plant photosynthetic characteristics, which were in photoautotrophically grown plantlets comparable to those of field-grown plants.

KEYWORDS: CARBON DIOXIDE, CULTURE, ETHYLENE, EXCHANGE, LEAVES, LIGHT, O2, POTATO, RESPIRATION, SPECIFICITY

444

Cournac, L., B. Dimon, and G. Peltier. 1993. Evidence for o-18 labeling of photorespiratory co2 in photoautotrophic cell-cultures of higher-plants illuminated in the presence of o-18(2). *Planta 190(3):407-414.*

The O-18-enrichment of CO2 produced in the light or during the post-illumination burst was measured by mass spectrometry when a photoautotrophic cell suspension of Euphorbia characias L. was placed in photorespiratory conditions in the presence of molecular O-18(2). The only O-18-labeled species produced was (COO)-O-18-O-16; no (COO)-O-18-O-16 could be detected. Production of (COO)-O-18-O-16 ceased after addition of two inhibitors of the photosynthetic carbon-oxidation cycle, aminooxyacetate or aminoacetonitrile, and was inhibited by high levels of CO2. The average enrichment during the post- illumination burst was estimated to be 46+/-15% of the enrichment of the O2 present during the preceding light period. Addition of exogenous carbonic anhydrase, by catalyzing the exchange between CO2 and H2O, drastically diminished the O-18- enrichment of the produced CO2. The very low carbonio-anhydrase level of the photoautotrophic cell suspension probably explains why the O-18 labeling of photorespiratory CO2 Could be observed for the first time. These data allow the establishment of a direct link between O2 consumption and CO2 production in the light, and the conclusion that CO2 produced in the light results, at least partially, from the mitochondrial decarboxylation of the glycine pool synthesized through the photosynthetic carbon-oxidation cycle. Analysis of the (COO)-O- 18-O-16 and CO2 kinetics provides a direct and reliable way to assess in vivo the real contribution of photorespiratory metabolism to CO2 production in the light.

KEYWORDS: INHIBITION, LEAVES, LIGHT, MASS-SPECTROMETRIC DETERMINATION, O2, OXYGEN- EXCHANGE, PHOSPHOGLYCOLATE, PHOTORESPIRATION, PHOTOSYNTHESIS, WHEAT

445

Couteaux, M.M., C. Kurz, P. Bottner, and A. Raschi. 1999. Influence of increased atmospheric CO2 concentration on quality of plant material and litter decomposition. *Tree Physiology 19(4-5):301-311.*

Nitrogen (N) and lignin concentrations in plant tissues and litter of plants grown in greenhouses or open-top chambers in elevated atmospheric CO2 concentration were compared with those of plants grown in ambient air in shortterm studies. We also compared the N concentration of plant material of Quercus ilex L. and Q. pubescens Willd. growing in the vicinity of natural CO2-springs with that of the same species growing at a control site. In the short-term studies, elevated CO2 caused significant decreases in tissue N concentration and the extent of the decrease varied with species. Nitrogen amendment of the soil lessened the CO2-enrichment effect. Lignin concentration was modified by elevated CO2 and the effect was species specific, but no general positive or negative trend was evident. A comparison of trees growing under natural conditions near a natural CO2-spring and at a control site revealed no site differences in N concentration of the plant material. A comparison of published results on decomposition rates of litter produced in elevated atmospheric CO2 and in ambient air indicated that CO2 enrichment can cause both enhancements and decreases of carbon mineralization. We conclude that (1) long- term responses to elevated CO2 could differ from the results obtained from short-term studies and that (2) biodiversity could be an important factor altering the sign of the feedback on atmospheric CO2 concentration. We also discuss the implications of our finding of a long-term, inhibitory effect of the initial N concentration of litter on the decomposition rate of litter and its consequence on ecosystem feedback.

KEYWORDS: BETULA-PENDULA ROTH, CARBON DIOXIDE, ELEVATED CO2, LEAF LITTER, LIGNIN CONTROL, NITROGEN, ORGANIC-MATTER, RATES, SOIL CARBON, TERM DECOMPOSITION

446

Couteaux, M.M., L.J. Monrozier, and P. Bottner. 1996. Increased atmospheric CO2: Chemical changes in decomposing sweet chestnut (Castanea sativa) leaf litter incubated in microcosms under increasing food web complexity. *Oikos 76(3):553-563.*

Increased concentrations of atmospheric CO2 induced a lower nitrogen concentration in sweet chestnut litter. The C:N ratio was about 35 at a 350 mu l 1(-1) CO2 concentration and about 70 at 700 mu l 1(-1). The CO2 enrichment increased the proportion of hemicelluloses and cellulose and decreased the proportion of lignin. Both litters were decomposed in microcosms with animal food webs of different complexities. The chemical composition of the decomposed litter (nitrogen, water-soluble compounds, cellulose. hemicelluloses and lignin) was related to the initial composition and to the mass loss. Rates of hemicelluloses and lignin decomposition and nitrogen dynamics were the most affected by the change in litter quality due to atmospheric CO2 enrichment. In N-rich litter, hemicelluloses were almost completely decomposed and lignin remained intact without effect of animal grazing.

In N-poor litter derived From CO2-enriched atmosphere, increased complexity of invertebrates food webs significantly enhanced decomposition of all the chemical components. By adding different groups of animals, some limiting factors were overcome and new substrates were liberated for microbial decomposition. It was hypothesized that the decomposition process was controlled by the interaction between lignin and nitrogen.

KEYWORDS: DYNAMICS, ELEVATED CO2, FOREST, LIGNIN CONTROL, LONG-TERM DECOMPOSITION, MASS-LOSS, NITROGEN, PINE NEEDLE LITTER, SOIL, SUBSTRATE QUALITY

447

Couteaux, M.M., M. Mousseau, M.L. Celerier, and P. Bottner. 1991. Increased atmospheric CO2 and litter quality - decomposition of sweet chestnut leaf litter with animal food webs of different complexities. *Oikos 61(1):54-64.*

Two-year-old chestnut trees were grown for two yr under ambient (350 ppm) and enriched (700 ppm) CO2 concentrations, in two naturally lit growth chambers. The doubling of CO2 resulted in a dilution of the nitrogen concentration in the leaf litter, with C:N ratios of 40 and 75 for the ambient and enriched CO2 concentrations, respectively. The litter was sterilized and inoculated with microflora and animal groups of increasing complexity (microflora + Protozoa; + nematodes; + Collembola; + Isopoda) and incubated over 24 wk. Every two wk, the CO2 release was measured and the litter was leached with demineralized H2O. The following analyses were performed on the leachates: pH, total nitrogen, dissolved and particulate carbon, inorganic nitrogen (NH4+ and NO3-), phosphate, and biological counts (Protozoa, nematodes and Rotifera). The initial decomposition stages (the first 12 wk) were dominated by the litter quality factor: CO2 release and nitrogen losses in leachates were higher and carbon losses lower in water leaching from the litter with low C:N ratio. Towards the late stages, when carbon mineralization decreased in the control litter, the animal effect emerged in litter with a high C:N ratio. Two groups appeared: (1) In the microflora + Protozoa units, carbon mineralization was reduced by 60% compared with the control litter. (2) In the diversified food web combinations, it became progressively higher with increasing complexity of the animal community and was enhanced by 30% compared with the control litter. This unexpected fundamental difference was explained by a change in the composition and activity of the microflora. Litter bleaching, respiration, C and N leaching and acidification rose with increasing animal complexity of the systems. Biological and chemical reasons explaining the invasion by white-rot fungi and its activity only in the material with a high C:N ratio are discussed. During the 24 wk. nitrogen and phosphorus mineralization was very low, indicating a high incorporation of the nutrient in the soil biomass.

KEYWORDS: BREAKDOWN, CARBON, CASTANEA-SATIVA MILL, DECIDUOUS WOODLAND SOILS, FAUNA, LIGNIN CONTROL, MINERALIZATION, NITROGEN, RAW HUMUS, WEIGHT-LOSS

448

Coviella, C.E., and J.T. Trumble. 1999. Effects of elevated atmospheric carbon dioxide on insect-plant interactions. *Conservation Biology 13(4):700-712.*

In the enriched carbon dioxide atmosphere expected in the next century, many, species of herbivorous insects will confront less nutritious host plants that will induce both lengthened larval developmental times and greater mortality The limited data currently available suggest that the effect of increased atmospheric CO2 on herbivory will be nor only highly species- specific brit also specific to each insect-plant system. Several scenarios can be predicted however. (1) local extinctions will occur; (2) the endangered species status as well as the pest status of some insect species will change; (3) geographic distributions for some insect species will shift with host-plant ranges; and (4) changes in the population dynamics of affected insect species will influence their interactions with other insects and plants. For insect conservation purposes, it is critical to begin long-term studies on the effects of enhanced CO2 levels on insect populations. An analysis of the available literature indicates that many orders containing insect species important for ecosystem conservation, and even those important as agricultural or medical pests, have not been examined. Without a major increase in research on this topic, we will be unprepared for the species changes that will occur, we will lose the opportunity to document just how some insects adapt to elevated CO2 levels, and we will lack the information necessary for effective conservation efforts.

KEYWORDS: CACTOBLASTIS-CACTORUM, CLIMATE CHANGE, CORN-ROOTWORM COLEOPTERA, ENRICHED CO2 ATMOSPHERES, GYPSY-MOTH, HERBIVORE INTERACTIONS, LOBLOLLY-PINE, SECONDARY METABOLITES, SOUR ORANGE TREES, SPODOPTERA-EXIGUA

449

Cowling, S.A. 1999. Simulated effects of low atmospheric CO2 on structure and composition of North American vegetation at the Last Glacial Maximum. *Global Ecology and Biogeography 8(2):81-93.*

1. Physiological experiments have indicated that the lower CO2 levels of the last glaciation (200 mu mol mol(-1)) probably reduced plant water-use efficiency (WUE) and that they combined with increased aridity and colder temperatures to alter vegetation structure and composition at the Last Glacial Maximum (LGM). 2. The effects of low CO2 on vegetation structure were investigated using BIOME3 simulations of leaf area index (LAI), and a two-by-two factorial experimental design (modern/LGM CO2, modern/ LGM climate). 3. Using BIOME3, and a combination bf lowered CO2 and simulated LGM climate (from the NCAR-CCM1 model), results in the introduction of additional xeric vegetation types between open woodland and closed-canopy forest along a latitudinal gradient in eastern North America. 4. The simulated LAI of LGM vegetation was 25- 60% lower in many regions of central and eastern United States relative to modern climate, indicating that glacial vegetation was much more open than today. 5. Comparison of factorial simulations show that low atmospheric CO2 has the potential to alter vegetation structure (LAI) to a greater extent than LGM climate. 6. If the magnitude of LAI reductions simulated for glacial North America were global, then low atmospheric CO2 may have promoted atmospheric warming and increased aridity, through alteration of rates of water and heat exchange with the atmosphere.

KEYWORDS: C-4 ANNUALS, CARBON ISOTOPE DISCRIMINATION, CLIMATE CHANGE, ELEVATED CO2, FOREST ECOSYSTEMS, GENERAL-CIRCULATION MODEL, ICE CORE, LEAF-AREA INDEX, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

450

Cowling, S.A., and R.F. Sage. 1998. Interactive effects of low atmospheric CO2 and elevated temperature on growth, photosynthesis and respiration in Phaseolus vulgaris. *Plant, Cell and Environment 21(4):427-435.*

For most of the past 250 000 years, atmospheric CO, has been 30-50% lower than the current level of 360 mu mol CO2 mol-l air. Although the effects of CO2 on plant performance are well recognized, the effects of low CO2 in combination with abiotic stress remain poorly understood. In this study, a growth chamber experiment using a two-by-two factorial design of CO2 (380 mu mol mol(-1), 200 mu mol mol(-1)) and temperature (25/20 degrees C day/night, 36/29 degrees C) was conducted to evaluate the interactive effects of CO2 and temperature

variation on growth, tissue chemistry and leaf gas exchange of Phaseolus vulgaris. Relative to plants grown at 380 pmol mol(-1) and 25/20 degrees C, whole plant biomass was 36% less at 380 mu mol mol(-1) x 36/29 degrees C, and 37% less at 200 mu mol mol(-1) x 25/20 degrees C, Most significantly, growth at 200 mu mol mol(- 1) x 36/29 degrees C resulted in 77% less biomass relative to plants grown at 380 pmol mol(-1) x 25/20 degrees C, The net CO2 assimilation rate of leaves grown in 200 mu mol mol(-1) x 25/20 degrees C was 40% lower than in leaves from 380 pmol mol(-1) x 25/20 degrees C, but similar to leaves in 200 mu mol mol(-1) x 36/29 degrees C. The leaves produced in low CO2 and high temperature respired at a rate that was double that of leaves from the 380 mu mol mol(-1) x 25/20 degrees C treatment. Despite this, there was little evidence that leaves at low CO2 and high temperature were carbohydrate deficient, because soluble sugars, starch and total non-structural carbohydrates of leaves from the 200 mu mol mol(-1) x 36/29 degrees C treatment were not significantly different in leaves from the 380 mu mol mol(-1) x 25/20 degrees C treatment. Similarly, there was no significant difference in percentage root carbon, leaf chlorophyll and leaf/root nitrogen between the low CO2 x high temperature treatment and ambient CO2 controls. Decreased plant growth was correlated with neither leaf gas exchange nor tissue chemistry. Rather, leaf and root growth were the most affected responses, declining in equivalent proportions as total biomass production. Because of this close association, the mechanisms controlling leaf and root growth appear to have the greatest control over the response to heat stress and CO2 reduction in P. vulgaris.

KEYWORDS: ACCLIMATION, ALLOCATION, BIOCHEMISTRY, C-4 ANNUALS, CARBON DIOXIDE, GAS-EXCHANGE, LEAF RESPIRATION, LEAVES, PLANTS, SENESCENCE

451

Cowling, S.A., and M.T. Sykes. 1999. Physiological significance of low atmospheric CO2 for plant- climate interactions. *Quaternary Research 52(2):237-242.*

Methods of palaeoclimate reconstruction from pollen are built upon the assumption that plant-climate interactions remain the same through time or that these interactions are independent of changes in atmospheric CO2. The latter may be problematic because air trapped in polar ice caps indicates that atmospheric CO2 has fluctuated significantly over at least the past 400,000 yr, and likely the last 1.6 million yr, Three other points indicate potential biases for vegetation-based climate proxies. First, C-3-plant physiological research shows that the processes that determine growth optima in plants (photosynthesis, mitochondrial respiration, photorespiration) are all highly CO2-dependent, and thus were likely affected by the lower CO2 levels of the last glacial maximum. Second, the ratio of carbon assimilation per unit transpiration (called water-use efficiency) is sensitive to changes in atmospheric CO2 through effects on stomatal conductance and may have altered C-3-plant responses to drought, Third, leaf gas- exchange experiments indicate that the response of plants to carbon-depleting environmental stresses are strengthened under low CO2 relative to today. This paper reviews the scope of research addressing the consequences of low atmospheric CO2 for plant and ecosystem processes and highlights why consideration of the physiological effects of low atmospheric CO2 on plant function is recommended for any future refinements to pollen- based palaeoclimatic reconstructions. (C) 1999 University of Washington.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, DIOXIDE STARVATION, ECOSYSTEMS, ELEVATED CO2, LAST GLACIAL MAXIMUM, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, POLLEN, VEGETATION, WATER-USE EFFICIENCY

452

Cox, P.M., R.A. Betts, C.B. Bunton, R.L.H. Essery, P.R. Rowntree, and J. Smith. 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Climate Dynamics 15(3):183-203.*

Recent improvements to the Hadley Centre climate model include the introduction of a new land surface scheme called "MOSES" (Met Office Surface Exchange Scheme). MOSES is built on the previous scheme, but incorporates in addition an interactive plant photosynthesis and conductance module, and a new soil thermodynamics scheme which simulates the freezing and melting of soil water, and takes account of the dependence of soil thermal characteristics on the frozen and unfrozen components. The impact of these new features is demonstrated by comparing 1 x CO2 and 2 x CO2 climate simulations carried out using the old (UKMO) and new (MOSES) land surface schemes. MOSES is found to improve the simulation of current climate. Soil water freezing tends to warm the high-latitude land in the northern Hemisphere during autumn and winter, whilst the increased soil water availability in MOSES alleviates a spurious summer drying in the mid-latitudes. The interactive canopy conductance responds directly to CO2, suppressing transpiration as the concentration increases and producing a significant enhancement of the warming due to the radiative effects of CO2 alone.

KEYWORDS: GENERAL-CIRCULATION MODELS, INCREASED CO2, PARAMETRIZATION, PHOTOSYNTHESIS, PROJECT, SCALE, SCHEMES, SOILS, STOMATAL CONDUCTANCE, TRANSPIRATION

453

Craig, S.G., and K.J. Holmen. 1995. Uncertainties in future co2 projections. *Global Biogeochemical Cycles 9(1):139-152.*

The perceived budget imbalance in the global carbon cycle has been suggested to result from, among other processes, CO2 fertilization of the terrestrial biosphere and/or enhanced regrowth of previously felled temperate forest. These two processes are incorporated into a box diffusion model of the ocean-atmosphere system coupled to a five-box terrestrial biosphere. The extent to which historical fossil fuel and land use change emission data can be reconciled with the observed atmospheric CO2 concentration record is examined. Furthermore, the sensitivity of future CO2 projections to the nature of the budget imbalance is investigated. It is found that the CO2 record can accommodate a carbon budget balanced by CO2 fertilization but that the balance with forest regrowth is more difficult. Future CO2 projections are found to be sensitive to how the carbon budget is balanced, even relative to uncertainties in future emissions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CYCLE, DIFFUSION-MODEL, EMISSIONS, FORESTS, FOSSIL-FUELS, PAST 2 CENTURIES, SINKS, STORAGE

454

Cramer, M.D., Z.F. Gao, and S.H. Lips. 1999. The influence of dissolved inorganic carbon in the rhizosphere on carbon and nitrogen metabolism in salinity-treated tomato plants. *New Phytologist 142(3):441-450.*

The influence of variation in the concentration of dissolved inorganic carbon (DIC) in the form of CO2 and HCO3- in the root media on the C and N metabolism of Lycopersicon esculentum cv. F144 was investigated under both saline and non-saline conditions. Tomato seedlings were grown in hydroponic culture (pH 6.5) with or without NaCl, and the root solution was aerated with either ambient CO2 (360 mol mol(-1)) or CO2- enriched air (5000 mu mol mol(-1)). Nitrate uptake and root tissue NO3- concentrations were increased slightly by elevated rhizosphere DIC concentrations in both control and salinity-treated plants. This is associated with 46% higher nitrate reductase activity in the roots of control plants supplied with elevated DIC than in

those supplied with ambient DIG. The activity of phosphoenolpyruvate carboxylase (PEPc) in vitro in control and salinity-treated plants was unaffected by the supply of elevated rhizosphere DIC concentrations. However, PEPc activity in vitro was considerably higher than the rates of PEPc activity in vivo reported previously, indicating that PEPc activity was not in itself a limitation on the provision of anaplerotic C. Therefore elevated DIC concentration in the rhizosphere stimulated the uptake of NO3- and provided alternative C skeletons for the assimilation of the NH4+ resulting from NO3- reduction into amino acids within the roots. Salinity stimulated root glutamine synthetase (GS) activity up to double that in control plants. Furthermore, elevated DIC caused an increase in leaf and root GS activity of control plants while inhibiting GS activity in the roots of salinity-treated plants. Glutamine:2-oxoglutarate aminotransferase (GOGAT) activity of salinity-treated plants was doubled by elevated rhizosphere DIC concentrations. These changes in GS and GOGAT activity must reflect changes in amino acid synthesis. Under saline conditions the xylem transport of NO3- is partly blocked and a larger root assimilation develops, requiring not only the transamination of 2-oxoglutarate to glutamate but also that of oxaloacetate to aspartate and the transamidation of aspartate to asparagine.

KEYWORDS: AMMONIUM NUTRITION, ANHYDRASE ACTIVITY, ASSIMILATION, BARLEY, CO2, FIXATION, NITRATE REDUCTASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, ROOTS, SEEDLINGS

455

Cramer, M.D., and S.H. Lips. 1995. Enriched rhizosphere co2 concentrations can ameliorate the influence of salinity on hydroponically grown tomato plants. *Physiologia Plantarum 94(3):425-432.*

Our previous work indicated that salinity caused a shift in the predominant site of nitrate reduction and assimilation from the shoot to the root in tomato plants. In the present work we tested whether an enhanced supply of dissolved inorganic carbon (DIC, CO2 + HCO3-) to the root solution could increase anaplerotic provision of carbon compounds for the increased nitrogen assimilation in the root of salinity-stressed Lycopersicon esculentum (L.) Mill. cv. F144. The seedlings were grown in hydroponic culture with 0 or 100 mM NaCl and aeration of the root solution with either ambient or CO2-enriched air (5 000 mu mol mol(-1)). The salinity-treated plants accumulated more dry weight and higher total N when the roots were supplied with CO2-enriched aeration than when aerated with ambient air. Plants grown with salinity and enriched DIC also had higher rates of NO3- uptake and translocated more NO3- and reduced N in the xylem sap than did equivalent plants grown with ambient DIC. Incorporation of DIC was measured by supplying a 1-h pulse of (HCO3-)-C-14 to the roots followed by extraction with 80% ethanol. Enriched DIC increased root incorporation of DIC 10- fold in both salinized and non-salinized plants. In salinity-stressed plants, the products of dissolved inorganic C-14 were preferentially diverted into amino acid synthesis to a greater extent than in non-salinized plants in which label was accumulated in organic acids. It was concluded that enriched DIC can increase the supply of N and anaplerotic carbon for amino acid synthesis in roots of salinized plants. Thus enriched DIC could relieve the limitation of carbon supply for ammonium assimilation and thus ameliorate the influence of salinity on NO3- uptake and assimilation as well as on plant growth.

KEYWORDS: AMMONIUM, INORGANIC CARBON, METABOLISM, NITRATE ASSIMILATION, NITROGEN, NUTRITION, REDUCTION, ROOTS, SEEDLINGS, SHOOT

456

Cramer, M.D., and S.H. Lips. 1995. The influence of enriched root-zone CO2 concentrations on growth, nitrogen metabolism and root HCO3- incorporation in salinity stressed Lycopersicon esculentum. *Acta Phytopathologica Et Entomologica Hungarica 30(1-2):105-118.*

Tomato plants grown with salinity reduce/assimilate a larger proportion of NO3- taken up in the roots than do non-salinized plants. We investigated whether enriched CO2 in the root solution could increase anaplerotic provision of carbon for root nitrogen assimilation in salinity stressed plants. Tomato seedlings were grown in hydroponic culture with and without 100 mM NaCl and with aeration of the root solution with either ambient or CO2 enriched air (5000 mu mol mol(-1)). The salinity treated plants accumulated more dry weight and higher total N when the roots were supplied with CO2 enriched aeration than when aerated with ambient air. Concentrations of K+ in the leaves and roots were higher in plants treated with enriched CO2. Enriched root-zone CO2 increased root incorporation of dissolved inorganic carbon (DIC). In salinity stressed plants the products of (DIC)-C-14 were diverted into amino acid synthesis to a greater extent than in non-salinized plants. It was concluded that enriched root-zone DIC could provide an increased anaplerotic source of carbon for amino acid synthesis in roots, partially ameliorating the influence of salinity on plant growth.

KEYWORDS: AMMONIUM, CARBON DIOXIDE, LEAF RESPIRATION, NITRATE ASSIMILATION, NUTRITION, PLANTS, REDUCTION, RESPONSES, SHOOT

457

Cramer, M.D., and M.B. Richards. 1999. The effect of rhizosphere dissolved inorganic carbon on gas exchange characteristics and growth rates of tomato seedlings. *Journal of Experimental Botany 50(330):79-87.*

The possibility that an enhanced supply of dissolved inorganic carbon (DIC = CO2 + HCO3-) to the root solution could increase the growth of Lycopersicon esculentum (L,) Mill. cv, F144 was investigated under both saline and non-saline root medium conditions, Tomato seedlings were grown in hydroponic culture with and without NaCl and the root solution was aerated with CO2 concentrations in the range between 0 and 5000 mu mol mol(- 1). The biomass of both control and salinity-stressed plants grown at high temperatures (daily maximum of 37 degrees C) and an irradiance of 1500 mu mol m(-2) s(-1) was increased by up to 200% by enriched rhizosphere DIG. The growth rates of plants grown with irradiances of less than 1000 mu mol m(-2) s(-1) were increased by elevated rhizosphere DIC concentrations only when grown at high shoot temperatures (35 degrees C) or with salinity (28 degrees C), At high light intensities, the photosynthetic rate, the CO2 and light-saturated photosynthetic rate (J(max)) and the stomatal conductance of plants grown at high light intensity were lower in plants supplied with enriched compared to ambient DIG. This was interpreted as 'down-regulation' of the photosynthetic system in plants supplied with elevated DIG. Labelled organic carbon in the xylem sap derived from root (DIC)-C-14 incorporation was found to be sufficient to deliver carbon to the shoot at rates equivalent to 1% and 10% of the photosynthetic rate of the plants supplied with ambient- and enriched-DIC, respectively. It was concluded that organic carbon derived from DIC incorporation and translocated in the xylem from the root to the shoot may provide a source of carbon for the shoots, especially under conditions where low stomatal conductance may be advantageous, such as salinity stress, high shoot temperatures and high light intensities.

KEYWORDS: AMMONIUM NUTRITION, ASSIMILATION, BARLEY, CO2, METABOLISM, NITRATE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PLANTS, ROOTS, SALINITY

458

Cramer, M.D., N.A. Savidov, and S.H. Lips. 1996. The influence of enriched rhizosphere CO2 on N uptake and metabolism in wild-type and NR-deficient barley plants. *Physiologia Plantarum 97(1):47-54.*

Positive influences of high concentrations of dissolved inorganic carbon (DIC) in the growth medium of salinity- stressed plants are associated with carbon assimilation through phosphoenolpyruvate carboxylase (PEPc) activity in roots; and also in salinity-stressed tomato plants, enriched CO2 in the rhizosphere increases NO(3)(-)uptake. In the present study, wild-type and nitrate reductase-deficient plants of barley (Hordeum vulgare L. cv. Steptoe) were used to determine whether the influence of enriched CO2 on NO(3)(-)uptake and metabolism is dependent on the activity of nitrate reductase (NR) in the plant. Plants grown in NH4+ and aerated with ambient air, were transferred to either NO3- or NH4+ solutions and aerated with air containing between 0 and 6500 mu mol mol(-1) CO2. Nitrogen uptake acid tissue concentrations of NO3- and NH4+ were measured as well as activities of NR and PEPc. The uptake of NO3- by the wild-type was increased by increasing CO2. This was associated with increased in vitro NR activity, but increased uptake of NO3- was found also in the NR-deficient genotype when exposed to high CO2 concentrations; so that the influence of CO2 on NO3- uptake was independent of the reduction of NO3- and assimilation into amino acids. The increase in uptake of NO; in wild-type plants with enriched CO2 was the same at pH 7 as at pH 5, indicating that the relative abundance of HCO3- or CO2 in the medium did not influence NO3- uptake. Uptake of NH4+ was decreased by enriched CO2 in a pH (5 or 7) independent fashion. Thus NO3- and NH4+ uptakes are influenced by the CO2 component of DIC independently of anaplerotic carbon provision for amino acid synthesis, and CO2 may directly affect the uptake of NO3- and NH4+ in ways unrelated to the NR activity in the tissue.

KEYWORDS: AMMONIUM NUTRITION, INORGANIC CARBON, MAIZE ROOTS, NH4, NITRATE ASSIMILATION, NO3, PHOSPHOENOLPYRUVATE CARBOXYLASE, SHOOT

459

Crick, S.G., and R. McConchie. 1999. Ethanol vapour reduces leaf blackening in cut flower Protea 'Pink Ice' stems. *Postharvest Biology and Technology 17(3):227-231.*

The effect of ethanol vapour on postharvest leaf blackening of Protea susannae X compacta 'Pink Ice' stems stored in plastic bags under darkness at 20 degrees C (+/- 1 degrees C) was assessed over a 19 day period. Application of ethanol vapour to the stems significantly reduced leaf blackening. Stems exposed to 5.6 g ethanol kg(-1) stem weight, had the least amount of leaf blackening with less than 20% of leaves blackened by day 14. In contrast, the control stems had 50% of leaves blackened by day 9, and 100% by day 15. The highest ethanol treatment at 11.2 g ethanol kg(-1) stem weight caused substantial blackening within the first 24 h of the treatment being applied. Ethanol vapour concentrations in the bag head space decreased rapidly in comparison with the bags with no stems, suggesting that ethanol was rapidly taken up by the stems. Only the highest ethanol treatment had detectable levels of ethanol in the bags after 17 days, and ethanol vapour had no effect on CO2 concentration in the bag head space. Carbon dioxide concentrations ranged between 1.0 and 2.5%. The rate of leaf blackening on the bagged stems without ethanol was significantly less than on stems not in bags, suggesting that elevated CO2 levels may have contributed to reduced blackening.

KEYWORDS: FRUIT, NERIIFOLIA R

460

Crookshanks, M., G. Taylor, and M. Broadmeadow. 1998. Elevated CO2 and tree root growth: contrasting responses in Fraxinus excelsior, Quercus petraea and Pinus sylvestris. *New Phytologist 138(2):241-250.*

Root growth and respiration in elevated CO2 (700 mu mol mol(- 1)) was studied in three tree species, Fraxinus excelsior L., Quercus petraea. L. and Pinus sylvestris L. grown in open-top chambers (OTCs) during a long-term exposure (20 months), during which root systems were allowed to develop without restriction imposed by pots. Root growth, measured as root length using root in-growth bags was increased significantly in trees exposed to elevated CO2, although the magnitude of the response differed considerably between species and with time of sampling, the greatest effect observed after 6 months in ash (ratio of elevated:ambient, e:a; 3.40) and the smallest effect observed in oak (e:a; 1.95). This was accompanied by changes in specific root length, with a significant decrease in all species after 6 months, suggesting that root diameter or root density were increased in elevated CO2. Increases in root length might have resulted from an acceleration in root cell expansion, since epidermal cell size was significantly increased in the zone of elongation in ash root tips ($P < 0.05$). Contrasting effects of elevated CO2 were observed for root carbohydrates, with significant increases in soluble sugars for all species ($P < 0.05$), but both increases and decreases in starch content were observed, depending on species, and producing a significant interaction between species and CO2 ($P < 0.001$). Exposure to elevated CO2 increased the total root d. wt for whole trees of all three species after 8 months of exposure, although the magnitude of this effect, in contrast to the root in-growth study, was greatest in Scots pine and smallest in ash. No significant effect of elevated CO2 was observed on the root:shoot ratio. Further detailed analysis of whole root systems after 20 months confirmed that species differences in root responses to elevated CO2 were apparent, with increased coarse and fine root production in elevated CO2 for Scots pine and ash respectively. Lateral root number was increased in elevated CO2 for all species, as was mean root diameter. Root respiration rates were significantly reduced in elevated CO2 for all three species. These results provide firm evidence that exposure of trees to future CO2 concentrations will have large effects on root system development, growth, carbohydrate status and respiration. The magnitude and direction of such effects will differ, depending on species. The consequences of such responses for the three species studied are discussed.

KEYWORDS: ARCHITECTURE, ATMOSPHERIC CARBON-DIOXIDE, EFFICIENCY, ENRICHMENT, HYBRID POPLAR, PLANT, RESPIRATION, SOIL, TEMPERATURE, WATER-USE

461

Crookshanks, M., G. Taylor, and L. Dolan. 1998. A model system to study the effects of elevated CO2 on the developmental physiology of roots: the use of Arabidopsis thaliana. *Journal of Experimental Botany 49(320):593-597.*

Three developmental changes were observed in the roots of Arabidopsis thaliana (Columbia) when shoots were exposed to elevated CO2, (i) The allometric coefficient, k, was enhanced significantly ($P<0.001$), (ii) primary root length and root extension rate were enhanced ($P<0.001$), Accelerated cortical cell expansion contributed to this effect and was associated with increased cell wall extensibility, measured as % plasticity. (iii) Lateral root formation and extension were also increased in elevated CO2 ($P<0.05$). These results illustrate that root growth and structure was altered following exposure to elevated CO2, The changes observed suggest that Arabidopsis provides a useful model which should, in future, be amenable to study using appropriate mutants allowing the genetic basis of the responses to be identified.

KEYWORDS: CELLULAR MECHANISMS, ENRICHMENT, EXPANSION, GROWTH, MUTANTS, RESPONSES

462

Crosson, P.R., and N.J. Rosenberg. 1993. An overview of the mink study. *Climatic Change 24(1-2):159-173.*

Highlights of the previous papers in this series are reviewed. Methodology developed for the MINK study has improved the ability of impacts analysis to deal with questions of (1) spatial and temporal variability in climate change; (2) CO2- enrichment effects; (3) the reactions of complex enterprises (farms and forests) to climate change and their ability to adjust and adapt; and (4) integrated effects on current and, more particularly, on future regional economies. The methodology also provides for systematic study of adjustment and adaptation opportunities and of the inter-industry linkages that determine what the overall impacts on the regional economy might be. The analysis shows that with a 1930s 'dust bowl' climate the region-wide economic impacts would be small, after adjustments in affected sectors. In this final paper we consider whether synergistic effects among sectoral impacts and more severe climate change scenarios might alter this conclusion. The MINK analysis, as is, leads to the conclusion that a strong research capacity will be required to ensure that technologies facilitating adaptation to climate change will be available when needed. The capacity to deal with climate change also requires an open economy allowing for free trade and movement of people and for institutions that protect unpriced environmental values. More severe climate scenarios and negative synergisms can only strengthen these conclusions.

463

Crowley, T.J., and S.K. Baum. 1997. Effect of vegetation on an ice-age climate model simulation. *Journal of Geophysical Research-Atmospheres 102(D14):16463-16480.*

A growing number of studies suggest that vegetation changes can significantly influence regional climate variations. Herein we utilize a climate model (GENESIS) with a land surface vegetation package to evaluate the potential role of the very large vegetation changes that occurred during the last glacial maximum (LGM), In particular, we focus on the potential response to a significant reduction in the area of tropical rainforest. Simulations employed a global vegetation reconstruction for the LGM and Climate/Long-Range Investigation, Mapping and Prediction (CLIMAP) sea surface temperature (SST) estimates. Results indicate that expansion of dryland vegetation causes a 15-30% additional LGM cooling for Australia (0.4 degrees C) and Africa (0.9 degrees C), respectively, Turnover from conifer to tundra also causes cooling of 2 degrees-4 degrees C or mon in western Europe and Siberia. However, for the largest rainforest area (Amazon Basin), inclusion of realistic vegetation increased modeled temperatures 2 degrees-4 degrees C and decreased precipitation by 10-35%. These latter results are similar to those obtained with sensitivity experiments of the effects of future Amazon deforestation, Initial assessment of the potential effect of decreased stomatal resistance due to lower ice age CO2 levels indicates little significant response to this effect. Comparison of model-predicted low-elevation LGM temperature Changes with estimates from proxy data indicate that inclusion of realistic vegetation estimates for the LGM results in slightly more than 50% agreement between models and data for low-elevation sites in low-mid latitudes. Data at variance with model predictions would appear to be explainable by considering additional changes in vegetation, ice age dust, or a 1 degrees- 2 degrees C cooling below CLIMAP values. This conclusion is at Variance with a 3 degrees-4 degrees C tropical cooling suggested by some studies for explaining estimated land temperature changes during the LGM. In some western European sites model temperatures are colder than proxy data by 2 degrees-8 degrees C. This model-data discrepancy may be explained by less sea ice in the subpolar North Atlantic than stipulated by CLIMAP, a conclusion consistent with new marine data from that region.

KEYWORDS: BOUNDARY-CONDITIONS, EURASIAN SNOW COVER, GENERAL-CIRCULATION MODELS, GLOBAL CLIMATE, LAST GLACIAL MAXIMUM, LATE QUATERNARY, SEA-SURFACE TEMPERATURE, STOMATAL-RESISTANCE, TERRESTRIAL CARBON STORAGE, TRANSFER SCHEME LSX

464

Crush, J.R. 1993. Hydrogen evolution from root-nodules of trifolium-repens and medicago-sativa plants grown under elevated atmospheric co2. *New Zealand Journal of Agricultural Research 36(2):177-183.*

Nitrogenase activity and hydrogen (H-2) evolution from nodules of Trifolium repens L. and Medicago sativa L. were measured on plants grown under 700 or 350 mul/l atmospheric CO2 and day/night temperatures of 18/13-degrees-C or 28/23-degrees-C. Assays were done after 39, 47, and 54 days' exposure to the treatments. In Trifolium, nitrogenase activity/plant was stimulated by elevated CO2 and higher temperatures but in Medicago only temperature had an effect. Hydrogen emission/plant was greater in Trifolium plants grown at 700 mul/l CO2 than in plants at 350 mul/l CO2, but in Medicago, H-2 emission rates did not respond to elevated CO2. Elevated CO2 reduced nodule relative efficiency (RE) in 39-day-old Trifolium plants growing at 18/13-degrees-C, but not under other conditions. It is concluded that predicted future CO2 concentration will lead to a greater contribution from legume nitrogen (N) fixation to global H-2 sources. The magnitude of the increase will be influenced by the legume species involved and temperature.

KEYWORDS: ECONOMY, EFFICIENCY, LEGUME, MOLECULAR-HYDROGEN, NITROGEN-FIXATION, REDUCTION, RHIZOBIA, WHITE CLOVER

465

Crush, J.R. 1994. Elevated atmospheric co2 concentration and rhizosphere nitrogen-fixation in 4 forage plants. *New Zealand Journal of Agricultural Research 37(4):455-463.*

Lolium x boucheanum (2n and 4n), Plantago lanceolata, and Pennisetum clandestinum were grown in pots of soil in growth rooms with factorial combinations of 350 or 700 mul/l atmospheric CO2 and day/night temperatures of 28/23-degrees-C or 18/13-degrees-C. Both cultivars of Lolium and P. lanceolata grew faster with elevated CO2 but P. clandestinum was unaffected. Rhizosphere nitrogenase activity, assessed by acetylene reduction, was reduced by the 700 mul/l CO2 treatment in the tetraploid Lolium but otherwise did not vary significantly with CO2 level.

KEYWORDS: ACETYLENE-REDUCTION ASSAY, ASSOCIATION, CARBON, CEREALS, GRASSES, GRASSLAND, GROWTH, ROOTS, SPECIFICITY, TRIFOLIUM- REPENS

466

Cruz, C., S.H. Lips, and M.A. Martinsloucao. 1993. The effect of nitrogen-source on photosynthesis of carob at high co2 concentrations. *Physiologia Plantarum 89(3):552-556.*

Carob seedlings (Ceratonia siliqua L. cv. Mulata), fed with nitrate or ammonium, were grown in growth chambers containing two levels of CO2 (360 or 800 mu 1 1(-1)), three root temperatures (15, 20 or 25 degrees C), and the same shoot temperature (20/24 degrees C, night/day temperature). The response of the plants to CO2 enrichment was affected by environmental factors such as the type of inorganic nitrogen in the medium and root temperature. Increasing root temperature enhanced photosynthesis rate more in the presence of nitrate than in the presence of ammonium. Differences in photosynthetic products were also observed between nitrate- and ammonium-fed carob seedlings. Nitrate-grown plants showed an enhanced content of sucrose, while ammonium led to enhanced storage of starch. Increase in root temperature caused an increase in dry mass of the plants of similar proportions in both nitrogen sources. The enhancement of the rates of photosynthesis by CO2 enrichment was proportionally much larger than the resulting increases

in dry mass production when nitrate was the nitrogen source. Ammonium was the preferred nitrogen source for carob at both ambient and high CO, concentrations. The level of photosynthesis of a plant is limited not only by atmospheric CO2 concentration but also by the nutritional and environmental conditions of the root.

KEYWORDS: AMMONIUM, CELLS, LEAVES, PLANTS

467

Cruz, C., S.H. Lips, and M.A. Martins-Loucao. 1997. Changes in the morphology of roots and leaves of carob seedlings induced by nitrogen source and atmospheric carbon dioxide. *Annals of Botany 80(6):817-823.*

Carob seedlings were grown hydroponically for 9 weeks under 360 and 800 mu l l(-1) CO2. One of two nitrogen sources, nitrate or ammonium, was added to the nutrient medium at concentrations of 3 mol m(-3). Root systems of the developing plants supplied with nitrate compared to those supplied with ammonium were characterized by: (a) more biomass on the lower part of the root; (b) fewer lateral roots of first and second order; (c) longer roots; (d) higher specific root length; (e) a smaller root diameter. The morphology of the root systems of nitrate- fed plants changed in the presence of elevated carbon dioxide concentrations, resembling, more closely, that of ammonium-fed plants. Total leaf area was higher in ammonium-than in nitrate- fed plants. Nitrate-fed plants had greater total leaf area in the presence of high carbon dioxide than in normal CO2, due to an increase in epidermal cell size that led to development of larger leaflets with lower stomatal frequency. The observed changes in the morphology of roots and shoots agreed with the results observed for total biomass production. Nitrate-fed plants increased their biomass production by 100% in the presence of elevated CO2 compared to 15% in ammonium-fed plants, indicating that the response of carob to high CO2 concentrations is very dependent on the nitrogen source. Under elevated CO2, nitrate grown plants had a larger content of sucrose in both roots and shoots, while no significant difference was observed in the content of sucrose in ammonium- grown plants, whether in ambient or enriched carbon dioxide. Hence, the differences in soluble carbohydrate contents can, at least partly, account for differences in root and shoot morphology. (C) 1997 Annals of Botany Company.

KEYWORDS: AMMONIUM ASSIMILATION, CELLULAR MECHANISMS, CERATONIA-SILIQUA, CO2- ENRICHMENT, ELEVATED CO2, GROWTH, NITRATE, PHOTOSYNTHESIS, PLANTS, RESPONSES

468

Csintalan, Z., Z. Tuba, H.K. Lichtenthaler, and J. Grace. 1996. Reconstitution of photosynthesis upon rehydration in the desiccated leaves of the poikilochlorophyllous shrub Xerophyta scabrida at elevated CO2. *Journal of Plant Physiology 148(3-4):345-350.*

We report the resynthesis of the photosynthetic apparatus and the restoration of its function in the monocotyledonous C-3 shrub Xerophyta scabrida (Pax) Th. Dur. et Schinz (Velloziaceae) following a period of 5 years in the air-dried state. Detached leaves were rehydrated at present (350 mu mol mol(-1)) and at elevated CO2 (700 mu mol mol(-1)). Elevated CO2 concentration had no effect on the rate of rehydration, nor on the de novo resynthesis pattern of the chlorophylls and carotenoids or the development of photochemical activity in the reviving desiccated leaves. The time required to fully reconstitute the photosynthetic apparatus and its function in the air-dried achlorophyllous leaves on rehydration did not differ at the two CO2 concentrations. However, respiratory activity during rehydration was more intensive and of longer duration at high CO2 and net CO2 assimilation first became apparent 12 h later than in the leaves rehydrated at present CO2. After reconstitution of the photosynthetic apparatus, the net CO2 assimilation rate was higher in the high CO2 leaves, however it rapidly declined to a value lower than that in the present CO2 plants due to acclimation. This acclimation to elevated CO2 occurred only after complete reconstitution of the photosynthetic apparatus. The downward acclimation of photosynthesis was accompanied by a decrease in content of photosynthetic pigments (chlorophyll a + b and carotenoids x + c) and stomatal conductance. The initial slope of the A/c(i) curve for the high CO2 leaves was much lower and net CO2 assimilation rates were lower at all c(i)'s than in the present CO2 plants. The rate of respiration also decreased and the C- balance of the high CO2 leaves therefore remained similar to that of leaves in present CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CAPACITY, EXPOSURE, PLANTS, RESPIRATION

469

Cui, M., P.M. Miller, and P.S. Nobel. 1993. Co2 exchange and growth of the crassulacean acid metabolism plant opuntia-ficus-indica under elevated co2 in open-top chambers. *Plant Physiology 103(2):519-524.*

CO2 uptake, water vapor conductance, and biomass production of Opuntia ficus-indica, a Crassulacean acid metabolism species, were studied at CO2 concentrations of 370, 520, and 720 muL L-1 in open-top chambers during a 23-week period. Nine weeks after planting, daily net CO2 uptake for basal cladodes at 520 and 720 muL L-1 Of CO2 was 76 and 98% higher, respectively, than at 370 muL L-1. Eight weeks after daughter cladodes emerged, their daily net CO2 uptake was 35 and 49% higher at 520 and 720 muL L-1 of CO2, respectively, than at 370 muL L-1. Daily water-use efficiency was 88% higher under elevated CO2 for basal cladodes and 57% higher for daughter cladodes. The daily net CO2 uptake capacity for basal cladodes increased for 4 weeks after planting and then remained fairly constant, whereas for daughter cladodes, it increased with cladode age, became maximal at 8 to 14 weeks, and then declined. The percentage enhancement in daily net CO2 uptake caused by elevated CO2 was greatest initially for basal cladodes and at 8 to 14 weeks for daughter cladodes. The chlorophyll content per unit fresh weight of chlorenchyma for daughter cladodes at 8 weeks was 19 and 62% lower in 520 and 720 muL L-1 Of CO2, respectively, compared with 370 muL L-1. Despite the reduced chlorophyll content, plant biomass production during 23 weeks in 520 and 720 muL L-1 of CO2 was 21 and 55% higher, respectively, than at 370 muL L-1. The root dry weight nearly tripled as the CO2 concentration was doubled, causing the root/shoot ratio to increase with CO2 concentration. During the 23-week period, elevated CO2 significantly increased CO2 uptake and biomass production of O. ficus-indica.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, PHOTOSYNTHESIS, PRODUCTIVITY, RESPIRATION, RESPONSES, TEMPERATURE, WATER-USE, YIELD

470

Cui, M., and P.S. Nobel. 1994. Gas-exchange and growth-responses to elevated co2 and light levels in the cam species opuntia-ficus-indica. *Plant, Cell and Environment 17(8):935-944.*

Gas exchange and dry-weight production in Opuntia ficus-indica, a CAM species cultivated worldwide for its fruit and cladodes, were studied in 370 and 750 mu mol mol(-1) CO2 at three photosynthetic photon flux densities (PPFD: 5, 13 and 20 mol m(-2) d(-1)). Elevated CO2 and PPFD enhanced the growth of basal cladodes and roots during the 12-week study. A rise in the PPFD increased the growth of daughter cladodes; elevated CO2 enhanced the growth of first-daughter cladodes but decreased the growth of the second-daughter cladodes produced on them. CO2 enrichment enhanced daily net CO2 uptake during the initial 8 weeks after planting for both basal and first- daughter cladodes. Water

vapour conductance was 9 to 15% lower in 750 than in 370 mu mol mol(-1) CO2. Cladode chlorophyll content was lower in elevated CO2 and at higher PPFD. Soluble sugar and starch contents increased with time and were higher in elevated CO2 and at higher PPFD. The total plant nitrogen content was lower in elevated CO2. The effect of elevated CO2 on net CO2 uptake disappeared at 12 weeks after planting, possibly due to acclimation or feedback inhibition, which in turn could reflect decreases in the sink strength of roots. Despite this decreased effect on net CO2 uptake, the total plant dry weight at 12 weeks averaged 32% higher in 750 than in 370 mu mol mol(-1) CO2. Averaged for the two CO2 treatments, the total plant dry weight increased by 66% from low to medium PPFD and by 37% from medium to high PPFD.

KEYWORDS: AGAVE-VILMORINIANA, CARBON DIOXIDE, CO2-ENRICHMENT, CRASSULACEAN ACID METABOLISM, PHOTOSYNTHESIS, PHYSIOLOGY, PLANT GROWTH, PRODUCTIVITY, SHORT- TERM, WATER-USE EFFICIENCY

471

Cure, J.D., T.W. Rufty, and D.W. Israel. 1989. Alterations in soybean leaf development and photosynthesis in a CO2-enriched atmosphere. *Botanical Gazette 150(4):337-345.*

472

Cure, J.D., T.W. Rufty, and D.W. Israel. 1991. Assimilate relations in source and sink leaves during acclimation to a co2-enriched atmosphere. *Physiologia Plantarum 83(4):687-695.*

Evidence from previous studies suggested that adjustments in assimilate formation and partitioning in leaves might occur over time when plants are exposed to enriched atmospheric CO2. We examined assimilate relations of source (primary unifoliolate) and developing sink (second mainstem trifoliolate) leaves of soybean [Glycine max (L.) Merr. cv. Lee] plants for 12 days after transfer from a control (350-mu-l l-1) to a high (700-mu-l l-1) CO2 environment. Similar responses were evident in the two leaf types. Net CO2 exchange rate (CER) immediately increased and remained elevated in high CO2. Initially, the additional assimilate at high CO2 levels in the light and was utilized in the subsequent dark period. After approximately 7 days, assimilate export in the light began to increase and by 12 days reached rates 3 to 5 times that of the control. In the developing sink leaf, high rates of export in the light occurred as the leaf approached full expansion. The results indicate that a specific acclimation process occurs in source leaves which increases the capacity for assimilate export in the light phase of the diurnal cycle as plants adjust to enriched CO2 and a more rapid growth rate.

KEYWORDS: CO2- ENRICHMENT, ELEVATED CARBON-DIOXIDE, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANTS, SEED YIELD, STARCH FORMATION, TRANSLOCATION, WATER-STRESS

473

Curtis, P.S. 1996. A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant, Cell and Environment 19(2):127-137.*

The response of trees to rising atmospheric CO2 concentration ([CO2]) is of concern to forest ecologists and global carbon modellers and is the focus of an increasing body of research work, I review studies published up to May 1994, and several unpublished works, which reported at least one of the following: net CO2 assimilation (A), stomatal conductance (g(s)), leaf dark respiration (R(d)), leaf nitrogen or specific leaf area (SLA) in woody plants grown at <400 mu mol mol(-1) CO2 or at 600-800 mu mol mol(-1) CO2, The resulting data from 41 species were categorized according to growth conditions (unstressed versus stressed), length of CO2 exposure, pot size and exposure facility [growth chamber (GC), greenhouse (GH), or open-top chamber (OTC)] and interpreted using meta-analytic methods, Overall, A showed a large and signifcant increase at elevated [CO2] but length of CO2 exposure and the exposure facility were important modifiers of this response, Plants exposed for <50 d had a significantly greater response, and those from GCs had a significantly lower response than plants from longer exposures or from OTC studies, Negative acclimation of A was significant and general among stressed plants, but in unstressed plants was influenced by length of CO2 exposure, the exposure facility and/or pot size, Growth at elevated [CO2] resulted in moderate reductions in g(s) in unstressed plants, but there was no significant effect of CO2 on g(s) in stressed plants, Leaf dark respiration (mass or area basis) was reduced strongly by growth at high [CO2], while leaf N was reduced only when expressed on a mass basis, This review is the first meta- analysis of elevated CO2 studies and provides statistical confirmation of several general responses of trees to elevated [CO2]. It also highlights important areas of continued uncertainty in our understanding of these responses.

KEYWORDS: ATMOSPHERIC CO2, CLUTCH-SIZE, CO2 CONCENTRATION, DARK RESPIRATION, LIRIODENDRON-TULIPIFERA L, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, SEEDLINGS, STOMATAL CONDUCTANCE, WATER-USE

474

Curtis, P.S., L.M. Balduman, B.G. Drake, and D.F. Whigham. 1990. Elevated atmospheric CO2 effects on belowground processes in C3 and C4 estuarine marsh communities. *Ecology 71(5):2001-2006.*

475

Curtis, P.S., A.A. Snow, and A.S. Miller. 1994. Genotype-specific effects of elevated co2 on fecundity in wild radish (raphanus-raphanistrum). *Oecologia 97(1):100-105.*

Rising atmospheric CO2 may lead to natural selection for genotypes that exhibit greater fitness under these conditions. The potential for such evolutionary change will depend on the extent of within-population genetic variation in CO2 responses of wild species. We tested for heritable variation in CO2- dependent life history responses in a weedy, cosmopolitan annual, Raphanus raphanistrum. Progeny from five paternal families were grown at ambient and twice ambient CO2 using outdoor open-top chambers (160 plants per CO2 treatment). Elevated CO2 stimulated net assimilation rates, especially in plants that had begun flowering. Across paternal families, elevated CO2 led to significant increases in flower and seed production (by 22% and 13% respectively), but no effect was seen on time to bolting, leaf area at bolting, fruit set, or number of seeds per fruit. Paternal families differed in their response to the CO2 treatment: in three families there were no significant CO2 effects, while in one family lifetime fecundity increased by > 50%. These genotype-specific effects altered fitness rankings among the five paternal families. Although we did not detect a significant genotype X CO2 interaction, our results provide evidence for heritable responses to elevated CO2. In a subset of plants, we found that the magnitude of CO2 effects on fecundity was also influenced by soil fertility.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, INTRASPECIFIC VARIATION, L BRASSICACEAE, LIFE-HISTORY, SATIVUS L, SEED-WEIGHT VARIATION, SIZE VARIATION

476

Curtis, P.S., and J.A. Teeri. 1992. Seasonal responses of leaf gas-

exchange to elevated carbon- dioxide in populus-grandidentata. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22(9):1320-1325.*

Rising atmospheric carbon dioxide concentrations may have important consequences for forest ecosystems. We studied above- and below-ground growth and leaf gas exchange responses of Populus grandidentata Michx. to elevated CO2 under natural forest conditions over the course of a growing season. Recently emerged P. grandidentata seedlings were grown in native, nutrient-poor soils at ambient and twice ambient (707 mubar (1 bar = 100 kPa)) CO2 partial pressure for 70 days in open-top chambers in northern lower Michigan. Total leaf area and shoot and root dry weight all increased in high CO2 grown plants. Photosynthetic light and CO2 response characteristics were measured 28, 45, and 68 days after exposure to elevated CO2. In ambient grown plants, light saturated assimilation rates increased from day 28 to day 45 and then declined at day 68 (15 September). This late-season decline, typical of senescing Populus leaves, was due both to a decrease in the initial slope of the net CO2 assimilation versus intercellular CO2 Partial pressure relationship and to decreased CO2 saturated assimilation rates. Specific leaf nitrogen (mg N . (cm2 leaf area)-1) did not change during this period, although leaf carbon content and leaf weight (mg . cm-2) both increased. In ambient grown plants stomatal conductance also declined at day 68. In contrast, plants grown at elevated CO2 showed no late- season decline in photosynthetic capacity or changes in leaf weight, suggesting a delay in senescence with long-term exposure to high CO2. High CO2 grown plants also maintained photosynthetic sensitivity to increasing C(i) throughout the exposure period, while ambient CO2 grown plants were insensitive to C(i) above 400 mubar on day 68. These results indicate the potential for direct CO2 fertilization of P. grandidentata in the field and provide evidence for a new mechanism by which elevated atmospheric CO2 could influence seasonal carbon gain.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2 ENRICHMENT, GROWTH-RESPONSES, IRRADIANCE, LEAVES, LIQUIDAMBAR-STYRACIFLUA, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, PINUS-TAEDA SEEDLINGS, VEGETATION

477

Curtis, P.S., C.S. Vogel, K.S. Pregitzer, D.R. Zak, and J.A. Teeri. 1995. Interacting effects of soil fertility and atmospheric co2 on leaf-area growth and carbon gain physiology in populus X euramericana (dode) guinier. *New Phytologist 129(2):253-263.*

Two important processes which may limit productivity gains in forest ecosystems with rising atmospheric CO2 are reduction in photosynthetic capacity following prolonged exposure to high CO2 and diminution of positive growth responses when soil nutrients, particularly N, are limiting. To examine the interacting effects of soil fertility and CO2 enrichment on photosynthesis and growth in trees we grew hybrid poplar (Populus x euramericana) for 158 d in the field at ambient and twice ambient CO2 and in soil with low or high N availability. We measured the timing and rate of canopy development, the seasonal dynamics of leaf level photosynthetic capacity, respiration, and N and carbohydrate concentration, and final above- and belowground dry weight. Single leaf net CO2 assimilation (A) increased at elevated CO2 over the majority of the growing season in both fertility treatments. At high fertility, the maximum size of individual leaves, total leaf number, and seasonal leaf area duration (LAD) also increased at elevated CO2, leading to a 49% increase in total dry weight. In contrast, at low fertility leaf area growth was unaffected by CO2 treatment. Total dry weight nonetheless increased 25% due to CO2 effects on A. Photosynthetic capacity (A at constant internal p(CO2), (C-i)) was reduced in high CO2 plants after 100 d growth at low fertility and 135 d growth at high fertility. Analysis of A responses to changing C-i indicated that this negative adjustment of photosynthesis was due to a reduction in the maximum rate of CO2 fixation by Rubisco. Maximum rate of electron transport and phosphate regeneration capacity were either unaffected or declined at elevated CO2. Carbon dioxide effects on leaf respiration were most pronounced at high fertility, with increased respiration mid-season and no change (area basis) or reduced (mass basis) respiration late- season in elevated compared to ambient CO2 plants. This temporal variation correlated with changes in leaf N concentration and leaf mass per area. Our results demonstrate the importance of considering both structural and physiological pathways of net C gain in predicting tree responses to rising CO2 under conditions of suboptimal soil fertility.

KEYWORDS: DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO2, ENRICHMENT, FEEDBACK, GAS-EXCHANGE, NITROGEN, PHOTOSYNTHESIS, PLANTS, SHORT- TERM

478

Curtis, P.S., and X.Z. Wang. 1998. A meta-analysis of elevated CO2 effects on woody plant mass, form, and physiology. *Oecologia 113(3):299-313.*

Quantitative integration of the literature on the effect of elevated CO2 on woody plants is important to aid our understanding of forest health in coming decades and to better predict terrestrial feedbacks on the global carbon cycle. We used meta-analytic methods to summarize and interpret more than 500 reports of effects of elevated CO2 on woody plant biomass accumulation and partitioning, gas exchange, and leaf nitrogen and starch content. The CO2 effect size metric we used was the log-transformed ratio of elevated compared to ambient response means weighted by the inverse of the variance of the log ratio. Variation in effect size among studies was partitioned according to the presence of interacting stress factors, length of CO2 exposure, functional group status, pot size, and type of CO2 exposure facility. Both total biomass (WT) and net CO2 assimilation (A) increased significantly at about twice ambient CO2, regardless of growth conditions. Low soil nutrient availability reduced the CO2 stimulation of WT by half, from + 31 % under optimal conditions to + 16 %, while low light increased the response to + 52 %. We found no significant shifts in biomass allocation under high CO2. Interacting stress factors had no effect on the magnitude of responses of A to CO2, although plants grown in growth chambers had significantly lower responses (+ 19 %) than those grown in greenhouses or in open-top chambers (+ 54 %). We found no consistent evidence for photosynthetic acclimation to CO2 enrichment except in trees grown in pots < 0.51 (- 36 %) and no significant CO2 effect on stomatal conductance. Both leaf dark respiration and leaf nitrogen were significantly reduced under elevated CO2 (- 18 % and - 16 % respectively, data expressed on a leaf mass basis), while leaf starch content increased significantly except in low nutrient grown gymnosperms. Our results provide robust, statistically defensible estimates of elevated CO2 effect sizes against which new results may be compared or for use in forest and climate model parameterization.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BETULA-PENDULA ROTH, CASTANEA-SATIVA MILL, LEAF GAS-EXCHANGE, LOBLOLLY-PINE SEEDLINGS, NET PRIMARY PRODUCTION, PICEA-ABIES L, QUERCUS-ALBA, RELATIVE GROWTH-RATE, STOMATAL CONDUCTANCE

479

Curtis, P.S., D.R. Zak, K.S. Pregitzer, and J.A. Teeri. 1994. Aboveground and belowground response of populus grandidentata to elevated atmospheric co2 and soil n-availability. *Plant and Soil 165(1):45-51.*

Soil N availability may play an important role in regulating the long-term responses of plants to rising atmospheric CO2 partial pressure. To further examine the linkage between above- and belowground C and N cycles at elevated CO2, we grew clonally propagated cuttings of Populus

grandidentata in the field at ambient and twice ambient CO2 in open bottom root boxes filled with organic matter poor native soil. Nitrogen was added to all root boxes at a rate equivalent to net N mineralization in local dry oak forests. Nitrogen added during August was enriched with N-25 to trace the flux of N within the plant-soil system. Above- and belowground growth, CO2 assimilation, and leaf N content were measured non- destructively over 142 d. After final destructive harvest, roots, stems, and leaves were analyzed for total N and N-15. There was no CO2 treatment effect on leaf area, root length, or net assimilation prior to the completion of N addition. Following the N addition, leaf N content increased in both CO2 treatments, but net assimilation showed a sustained increase only in elevated CO2 grown plants. Root relative extension rate was greater at elevated CO2, both before and after the N addition. Although final root biomass was greater at elevated CO2, there was no CO2 effect on plant N uptake or allocation. While low soil N availability severely inhibited CO2 responses, high CO2 grown plants were more responsive to N. This differential behavior must be considered in light of the temporal and spatial heterogeneity of soil resources, particularly N which often limits plant growth in temperate forests.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, QUERCUS-ALBA, SEEDLING GROWTH, TREES

480

Cushman, J.C., and H.J. Bohnert. 1997. Molecular genetics of Crassulacean acid metabolism. *Plant Physiology 113(3):667-676.*

Most higher plants assimilate atmospheric CO2 through the C-3 pathway of photosynthesis using ributose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). However, when CO2 availability is reduced by environmental stress conditions, the incomplete discrimination of CO2 over O-2 by Rubisco leads to increased photorespiration, a process that reduces the efficiency of C-3 photosynthesis. To overcome the wasteful process of photorespiration, approximately 10% of higher plant species have evolved two alternate strategies for photosynthetic CO2 assimilation, C-3 photosynthesis and Crassulacean acid metabolism. Both of these biochemical pathways employ a "CO2 pump" to elevate intracellular CO2 concentrations in the vicinity of Rubisco, suppressing photorespiration and therefore improving the competitiveness of these plants under conditions of high light intensity, high temperature, or low water availability. This CO2 pump consists of a primary carboxylating enzyme, phosphoenolpyruvate carboxylase. In C-4 plants, this CO2-concentrating mechanism is achieved by the coordination of two carboxylating reactions that are spatially separated into mesophyll and bundle-sheath cell types (for review, see R.T. Furbank, W.C. Taylor [1995] Plant Cell 7:797-802; M.S.B. Ku, Y. Kano-Murakami, M. Matsuoka [1996] Plant Physiol 111:949-957). In contrast, Crassulacean acid metabolism plants perform both carboxylation reactions within one cell type, but the two reactions are separated in time. Both pathways involve cell- specific changes in the expression of many genes that are not present in C-3 plants.

KEYWORDS: ABSCISIC- ACID, C-3 PHOTOSYNTHESIS, CAM, COMMON ICE PLANT, DIFFERENTIAL EXPRESSION, INDUCTION, MESEMBRYANTHEMUM-CRYSTALLINUM L, NADP-MALIC ENZYME, PHOSPHOENOLPYRUVATE CARBOXYLASE, SALT STRESS

481

Dacey, J.W.H., B.G. Drake, and M.J. Klug. 1994. Stimulation of methane emission by carbon-dioxide enrichment of marsh vegetation. *Nature 370(6484):47-49.*

THERE is substantial evidence that many plants respond to increased concentrations of atmospheric carbon dioxide by increasing their productivity(1-4) This observation has led to the suggestion that, by taking up CO2, the terrestrial biosphere might mitigate the potential greenhouse warming associated with anthropogenic CO2 emissions(5). Whiting and Chanton(6) have found, however, that for wetlands of varying productivity around the world, higher net primary production is associated with higher emissions of methane-another important greenhouse gas. Here we present measurements of methane emissions from a marsh that has been exposed to twice the present ambient concentration of atmospheric CO2. We find that over a one-week period, the CO2-enriched sites had significantly higher emissions of methane than the control sites. Our results suggest that future increases in atmospheric CO2 concentration may lead to significant increases in methane emissions from wetlands.

KEYWORDS: COMMUNITIES, ELEVATED CO2, ESTUARINE MARSH, FIELD, GROWTH, PLANTS, PRODUCTIVITY, RESPONSES, RICE PADDIES, WETLANDS

482

Dahlman, R.C. 1993. Co2 and plants - revisited. *Vegetatio 104:339-355.*

The decade-long USA research program on the direct effects of CO2 enrichment on vegetation has achieved important milestones and has produced a number of interesting and exciting findings. Research beginning in 1980 focused on field experiments to determine whether phenomena observed in the laboratory indeed occurred in natural environments. The answer is yes. Data obtained from numerous field studies show mixed response of crop and native species to CO2 enrichment however. Nearly all experiments demonstrate that plants exhibit positive gain when grown at elevated CO2; although the magnitude varies greatly. Most crop responses range from 30 to 50 % increase in yield. Results from long-term experiments with woody species and ecosystems are even more variable. Huge growth responses (100 to nearly 300 % increase relative to controls) are reported from several tree experiments and the salt-marsh ecosystem experiment. Other results from experiments with woody species and the tundra ecosystem suggest little no effect of CO2 on physiology, growth or productivity. Numerous studies of the physiology of the CO2 effect are continuing in attempts to understand controlling mechanisms and to explain the variable growth responses. Particular emphasis needs to be given to physiological measures of interactions involving the CO2 effect and other environmental influences, and to the wide-ranging observations of photosynthesis acclimation to CO2. Prospects for future research are identified.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED LEVELS, ENRICHMENT, GROWTH, INHIBITION, PHOTOSYNTHESIS, SEEDLINGS, SHORT- TERM, TEMPERATURE

483

Dale, H., and M.C. Press. 1998. Elevated atmospheric CO2 influences the interaction between the parasitic angiosperm Orobanche minor and its host Trifolium repens. *New Phytologist 140(1):65-73.*

The influence of the root holoparasitic angiosperm Orobanche minor Sm. on the biomass, photosynthesis, carbohydrate and nitrogen content of Trifolium repens L. was determined for plants grown at two CO2 concentrations (350 and 550 mu mol mol(-1)). Infected plants accumulated less biomass than their uninfected counterparts, although early in the association there was a transient stimulation of growth. Infection also influenced biomass allocation both between tissues (infected plants had lower root:shoot ratios) and within tissues: infected roots were considerably thicker before the point of parasite attachment and thinner below. Higher concentrations of starch were also found in roots above the point of attachment, particularly for plants grown in

elevated CO2. Elevated CO2 stimulated the growth of T. repens only during the early stages of development. There was a significant interaction between infection and CO2 on growth, with infected plants showing a greater response, such that elevated CO2 partly alleviated the effects of the parasite on host growth. Elevated CO2 did not affect total O. minor biomass per host, the number of individual parasites supported by each host, or their time of attachment to the host root system. Photosynthesis was stimulated by elevated CO2 but was unaffected by O. minor. There was no evidence of down-regulation of photosynthesis in T. repens grown at elevated CO2 in either infected or uninfected plants. The data are discussed with regard to the influence of elevated CO2 on other parasitic angiosperm-host associations and factors which control plant responses to elevated CO2.

KEYWORDS: CARBON DIOXIDE, GROWTH, METABOLISM, N2 FIXATION, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, SORGHUM, STRIGA-HERMONTHICA, TEMPERATURE, WHITE CLOVER

484

Dalen, L.S., O. Johnsen, and G. Ogner. 1997. Frost hardiness development in young Picea abies seedlings under simulated autumn conditions in a phytotron - effects of elevated CO2, nitrogen and provenance. *Plant Physiology 114(3):576.*

485

Damesin, C., C. Galera, S. Rambal, and R. Joffre. 1996. Effects of elevated carbon dioxide on leaf gas exchange and growth of cork-oak (Quercus suber L) seedlings. *Annales Des Sciences Forestieres 53(2-3):461-467.*

Leaf gas exchange and growth were determined on cork-oak (Quercus suber L) seedlings which were grown from acorns for periods of up to 4 months in greenhouses at ambient (350 mu mol mol(-1)) and at elevated (700 mu mol mol(-1)) concentrations of carbon dioxide. In well-watered conditions, daily maximum photosynthesis (15 mu mol m(-2) s(-1)) and stomatal conductance (440 mmol m(-2) s(-1)) of plants grown and measured at 700 mu mol mol(-1) CO2 did not differ from those of plants grown and measured at 350 mu mol mol(-1). In conditions of moderate drought, net CO2 assimilation was at least twice as great in elevated CO2, but stomatal conductance was unchanged. Elevated CO2 affected total biomass production, the average increase being 76 and 97% at 3 and 4 months, respectively. Shoot biomass, root biomass, stem height and total leaf area were increased by elevated CO2. Root and stem ramification were also enhanced by elevated CO2, but no change in root/shoot ratio was observed.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CO2 CONCENTRATION, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, RESPONSES, STOMATAL CONDUCTANCE, TREES, WATER

486

Daniel, E. 1997. The temperature dependence of photoinhibition in leaves of Phaseolus vulgaris (L) - Influence of CO2 and O-2 concentrations. *Plant Science 124(1):1-8.*

The interactive effect of temperature and CO2 concentration on the susceptibility to photoinhibition was assessed using chlorophyll a fluorescence to estimate the reduction of the quantum yield of PSII photochemistry (F-w/F-m) after high-light exposure. Leaves exposed to high photon flux density always exhibit a decrease in F-w/F-m, resulting from both a decrease in the rate constant for photochemistry and an increase in the rate constant for non photochemical dissipation of excess excitation energy. At a-given CO2 concentration, there was almost no difference in the degree of photoinhibition between leaves exposed to high light in 10 or 210 mmol O-2/mol. But photoinhibition was more pronounced at 10 mmol O-2/mol and 0 mu mol CO2/mol than at 210 mmol O-2/mol and 50 pmol CO2/mol, i.e. when both photorespiration and CO2 refixation are suppressed. Despite this photoprotective role of photorespiration, photoinhibition was enhanced by decreasing CO2 concentration in bean leaves, especially at elevated (30-35 degrees C)temperatures. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CHLOROPLAST PROTEIN, DROUGHT, LIGHT, PHOTOCHEMICAL EFFICIENCY, PHOTORESPIRATION, PHOTOSYNTHETIC ELECTRON FLOW, PHOTOSYSTEM, WATER-STRESS

487

Darrah, P.R. 1996. Rhizodeposition under ambient and elevated CO2 levels. *Plant and Soil 187(2):265-275.*

As global CO2 levels rise, can soils store more carbon and so buffer atmospheric CO2 levels? Answering this question requires a knowledge of the rates of C inputs to soil and of CO2 outputs via decomposition. Below-ground inputs from roots are a major component of the C flow into soils but are still poorly understood. In this article, new techniques for measuring rhizodeposition are reviewed and discussed and the need for cross-comparisons between methods is identified. One component of rhizodeposition, root exudation, is examined in more detail and evidence is presented which suggests that current estimates of exudate flow into soils are incorrect. A mechanistic mathematical model is used to explore how exudate hows might change under elevated CO2.

KEYWORDS: AMINO-ACIDS, ARBUSCULAR MYCORRHIZAL FUNGUS, BRASSICA-NAPUS L, CARBON FLUXES, CITRIC-ACID, CUCUMIS-SATIVUS L, PSEUDOMONAS- FLUORESCENS, SOIL-ROOT INTERFACE, WHEAT RHIZOSPHERE, ZEA MAYS L

488

Darrigo, R.D., and G.C. Jacoby. 1993. Tree growth-climate relationships at the northern boreal forest tree line of north-america - evaluation of potential response to increasing carbon-dioxide. *Global Biogeochemical Cycles 7(3):525-535.*

Tree growth at the northern limit of the range of boreal forests is primarily limited by temperature-related factors. Thus the position of this range limit, and the growth rates of trees along the northern forest border, may undergo significant change if predictions of enhanced greenhouse warming at northern latitudes are realized. In this paper we evaluate tree ring width and maximum latewood density chronologies of white spruce for three temperature-sensitive tree line sites in northern North America: in the Brooks Range, Alaska, the Franklin Mountains, Northwest Territories, and Churchill, Manitoba. The ring width data, which more strongly integrate low-frequency temperature trends than the density series, show overall enhanced growth and inferred warming during the period of anthropogenic increase in greenhouse gases. The recent growth at these sites equals or exceeds that which has occurred during earlier centuries of more clearly natural climate variability. When the ring width and density variations are estimated using temperature and precipitation data in principal components regession analysis, no substantial residual trends are detected which might require CO2 or other nutrient fertilization as an additional explanation for recent growth changes.

KEYWORDS: ATMOSPHERIC CO2, CANADA, CHRONOLOGY, CIRCULATION, DENSITY, ENHANCEMENT, RING DATA, TEMPERATURE, TRENDS, WIDTH

489

Davey, P.A., A.J. Parsons, L. Atkinson, K. Wadge, and S.P. Long. 1999. Does photosynthetic acclimation to elevated CO2 increase photosynthetic nitrogen-use efficiency? A study of three native UK grassland species in open-top chambers. *Functional Ecology 13:21-28.*

1, The photosynthetic response to elevated CO2 and nutrient stress was investigated in Agrostis capillaris, Lolium perenne and Trifolium repens grown in an open-top chamber facility for 2 years under two nutrient regimes. Acclimation was evaluated by measuring the response of light-saturated photosynthesis to changes in the substomatal CO2 concentration. 2. Growth at elevated CO2 resulted in reductions in apparent Rubisco activity in vivo in all three species, which were associated with reductions of total leaf nitrogen content on a unit area basis for A. capillaris and L. perenne. Despite this acclimation, photosynthesis was significantly higher at elevated CO2 for T. repens and A. capillaris, the latter exhibiting the greatest increase of carbon uptake at the lowest nutrient supply. 3. The photosynthetic nitrogen-use efficiency (the rate of carbon assimilation per unit leaf nitrogen) increased at elevated CO2, Mot purely owing to higher values of photosynthesis at elevated CO2, but also as a result of lower leaf nitrogen contents. 4. Contrary to most previous studies, this investigation indicates that elevated CO2 can stimulate photosynthesis under a severely limited nutrient supply. Changes in photosynthetic nitrogen-use efficiency may be a critical determinant of competition within low nutrient ecosystems and low input agricultural systems.

KEYWORDS: C-3 PLANTS, CAPACITY, COTTON, GAS-EXCHANGE, GROWTH, LEAVES, NUTRIENT STATUS, NUTRITION, RISING ATMOSPHERIC CO2, SEEDLINGS

490

Davies, S.J., and L. Unam. 1999. Smoke-haze from the 1997 Indonesian forest fires: effects on pollution levels, local climate, atmospheric CO2 concentrations, and tree photosynthesis. *Forest Ecology and Management 124(2-3):137-144.*

Atmospheric composition, local climate and sapling gas exchange were monitored to assess the short-term effects of smoke-haze from the 1997 Indonesian forest fires. Atmospheric concentrations of particulate matter, SO2, CO, CH4 and CO2, and relative humidity were elevated, and photosynthetically active radiation and ambient temperature were reduced by the smoke- haze. Despite elevated CO2 levels, photosynthesis in three tree species was reduced by the smoke-haze, both indirectly through reduced PAR levels, and directly through elevated aerosol and atmospheric pollutant levels. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ASIA, BIOMASS, CARBON DIOXIDE, DEFORESTATION, ELEVATED CO2, EMISSIONS, GROWTH, LAND-USE CHANGE, LATIN-AMERICA, PLANTS

491

Day, F.P., E.P. Weber, C.R. Hinkle, and B.G. Drake. 1996. Effects of elevated atmospheric CO2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. *Global Change Biology 2(2):143-148.*

Atmospheric CO2 concentration is rising and it has been suggested that a portion of the additional carbon is being sequestered in terrestrial vegetation and much of that in below-ground structures. The objective of the present study was to quantify the effects of elevated atmospheric CO2 on fine root length and distribution with depth with minirhizotrons in an open-top chamber experiment in an oak-palmetto scrub ecosystem at Kennedy Space Centre, Florida, USA. Observations were made five times over a period of one and a half years in three ambient chambers (350 p.p.m. CO2), three CO2 enriched chambers (700 p.p.m. CO2), and three unchambered plots. Greater root length densities were produced in the elevated CO2 chambers (14.2 mm cm(-2)) compared to the ambient chambers (8.7 mm cm(-2)). More roots may presumably lead to more efficient acquisition of resources. Fine root abundance varied significantly with soil depth, and there appeared to be enhanced proliferation of fine roots near the surface (0-12 cm) and at greater depth (49-61 cm) in the elevated CO2 chambers. The vertical root distribution pattern may be a response to availability of nutrients and water. More studies are needed to determine if increased root length under CO2 enriched conditions actually results in greater sequestering of carbon below ground.

KEYWORDS: CARBON, CLIMATE CHANGE, GROWTH, HETEROGENEITY, MICROSITES, RESPONSES

492

Dayan, E., H. Vankeulen, J.W. Jones, I. Zipori, D. Shmuel, and H. Challa. 1993. Development, calibration and validation of a greenhouse tomato growth-model .1. Description of the model. *Agricultural Systems 43(2):145-163.*

A dynamic crop growth model. TOMGRO, for an indeterminate tomato variety is presented. The model describes the phenological development and increase in dry weight of various organs (roots, stem nodes, leaves and fruits) from planting till maturity under variable environmental conditions. Phenological development is governed by genetic plant properties and environmental conditions (e.g. air temperature and CO2 level) and expressed in a plastochron index, i.e. the current stem node number. Total dry matter accumulation is based on a quantitative description of the carbon balance, including gross CO2 assimilation, maintenance respiration and growth respiration. Partitioning of dry matter increase over the various organs is governed by their relative sink strengh, defined on the basis of a genetically determined 'potential' growth rate, achieved under non-limiting carbohydrate supply. The model is both schematic and modular in set-up. This means it can be adapted easily and most of its subroutines can be replaced easily by others if better descriptions become available. It can also be combined with a more comprehensive model describing greenhouse climate and appears robust for use in procedures of economic optimization of climate conditions in greenhouses or for management purposes.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, FRUIT- GROWTH, IMPORT, LEAF, LYCOPERSICON-ESCULENTUM MILL, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, TRANSLOCATION

493

Daymond, A.J., T.R. Wheeler, P. Hadley, R.H. Ellis, and J.I.L. Morison. 1997. The growth, development and yield of onion (Allium cepa L) in response to temperature and CO2. *Journal of Horticultural Science 72(1):135-145.*

Stands of two cultivars (cv. Hysam and Site) of onion (Allium cepa L.) were grown in the held within polyethylene-covered tunnels along which a temperature adient was imposed. Pairs of tunnels were maintained at either 374 or 532 mu mol mol(-1) CO2. The rates of progress from transplanting to bulbing, and from bulbing to harvest maturity, were positive linear functions of mean temperature for each cultivar. At a given temperature, the time of bulbing was earlier, but the duration of bulb growth longer, at elevated compared with normal CO2. Canopy architecture was not affected by CO2, temperature or cultivar; an estimate of 0.25 for the canopy light extinction coefficient was common to all treatment combinations. Radiation use efficiency was greater at elevated compared with normal CO2 in the period up to bulbing, but was the same at both CO2 concentrations during subsequent bulb growth. Total crop dry weight at bulbing was increased by 32-44% due to

elevated CO2. Bulb yields at harvest maturity declined with progressively warmer temperatures and to a greater extent in cv. Site than cv. Hysam. Enrichment with CO2 increased bulb yields by 29-37% and by 35-51% in cvs Hysam and Site, respectively. From comparison of the temperature rise needed to offset entirely the yield increases of each cultivar due to elevated CO2, it is concluded that current estimates of climate change should be beneficial for bulb onion production, particularly for long- season cultivars.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FIELD, LEAF-AREA, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY

494

De Angelis, P., and G.E. Scarascia-Mugnozza. 1998. Long-term CO2-enrichment in a Mediterranean natural forest: An application of large open top chambers. *Chemosphere 36(4-5):763-770.*

It is crucial to be able to anticipate the possible effects of environmental changes on the Mediterranean woodland communities given their essential role on protecting lands that are under a strong pressure by man and climate. Predictions of the effects of increasing CO2 concentration on plants have been inferred by short- and long-term studies, conducted at different scales and by different technologies. Open Top Chambers (OTCs) are experimental facilities that have been widely used to expose field grown plants to different pollutant gases, and more recently to elevated [CO2]. In this paper, we present the natural site and the experimental system (six large OTCs enclosing clumps of natural vegetation) that we have been utilizing for 3 years, to assess the impact of elevated [CO2] on a Mediterranean natural forest community. The results show that large OTCs can be usefully used to simulate CO2 doubling even under the harsh environmental conditions of the mediterranean region. (C) 1998 Elsevier Science Ltd.

KEYWORDS: BALANCE, CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ELEVATED CO2, EXCHANGE, RESPONSES

495

Debevec, E.M., and S.F. Maclean. 1993. Design of greenhouses for the manipulation of temperature in tundra plant-communities. *Arctic and Alpine Research 25(1):56-62.*

Passive greenhouses can be used to elevate the temperature of natural communities, but they also introduce other effects. We tested the effects of potential greenhouse materials-clear polyethylene plastic film, polyester fabric, and rigid fiberglass panels-on light transmission, photosynthesis of Salix planifolia, elevation of air and soil temperature, and thaw depth. Plastic had the greatest light transmittance and caused the least depression of photosynthesis (- 5%). Greenhouses covered with plastic elevated daily maximum and daily mean air temperatures by an average of 7.8 and 2.0- degrees-C and depressed daily minimum temperature by 1.1- degrees-C compared with the control. Plastic is impervious to gases and may alter CO2 concentration and humidity within greenhouses. Fiberglass had lower transmittance, especially of short wavelength radiation. Fabric had the lowest light transmission and reduced photosynthesis by 10%, but it has the advantage of permeability to CO2 and water vapor. Greenhouses covered with fabric, alone, produced only a small effect (daily mean temperature elevated 0.4-degrees-C above controls). A mixed greenhouse design (plastic and fabric) raised daily mean temperatures by 0.9-degrees-C and may minimize adverse effects on gas diffusion. Because of the effect of the materials on amount and spectral distribution of radiation and on photosynthesis, the appropriate treatment control for any greenhouse design is an open plot shaded with the same material. Soil temperature at 10 cm depth was elevated in all greenhouses, but no effect on depth of thaw was detected.

KEYWORDS: CARBON NUTRIENT BALANCE

496

Debruin, H.A.R., and C.M.J. Jacobs. 1993. Impact of co2 enrichment on the regional evapotranspiration of agroecosystems, a theoretical and numerical modeling study. *Vegetatio 104:307-318.*

This paper gives a brief overview of factors determining evapotranspiration of vegetated surfaces. It indicates which of these factors are sensitive to CO2 enrichment. A qualitative analysis is presented of the impact of large scale climate changes. Data in literature indicate that the surface resistance of vegetated areas may change within the range -25 % and +50 % if the atmospheric CO2-concentration doubles. The impact of such changes on regional scale transpiration is evaluated using a numerical model in which the interaction between the evapotranspiration and the Planetary Boundary Layer is accounted for. It is concluded that the impact of CO2 enrichment on the transpiration at the regional scale is relatively small for aerodynamically smooth surfaces (between +7 % and -11 %). For aerodynamically rough surfaces the effects are somewhat larger (between +15 % and -21 %).

KEYWORDS: ATMOSPHERIC BOUNDARY-LAYER, CANOPY RESISTANCE, CARBON DIOXIDE, CONDUCTANCE, EVAPORATION, FOREST, SCALE, SENSITIVITY, STOMATAL CONTROL, TRANSPIRATION

497

Deepak, S.S., and M. Agrawal. 1999. Growth and yield responses of wheat plants to elevated levels of CO2 and SO2, singly and in combination. *Environmental Pollution 104(3):411-419.*

Wheat plants (Triticum aestivum L. cv. Malviya 234) were exposed to 600 ppm of carbon dioxide (CO2) and 0.06 ppm sulphur dioxide (SO2), singly and in combination for 8 h daily (8 a.m. to 4 p.m.) from germination to maturity in open top chambers (OTCs) in field conditions to investigate their individual as well as interactive influence on plant growth and yield. Exposure of plants to 0.06 ppm SO2 significantly reduced plant height, leaf area, biomass and yield. Elevated CO2, on the other hand, stimulated the growth and yield of plants. Combination of CO2 and SO2 showed a similar response pattern as that of CO2 alone. Pattern of biomass allocation also varied in response to different treatments. RGR was significantly increased due to CO2 and CO2 + SO2 treatments, whereas the same reduced due to SO2 exposure. Root/shoot ratio decreased significantly due to CO2 and CO2 + SO2 treatment at 45 days age. CO2 modified the responses of plants to SO2. Combined exposure of SO2 and CO2 stimulated the growth as well as the yield maximally. This suggests that the CO2 enrichment has not only reduced the adverse effect of low level of SO2, but at the same time the extra carbon provided by CO2 enrichment took the advantage of air borne sulphur as nutrient and showed maximum increment in growth and yield. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, FUMIGATION, LEAVES, PHOTOSYNTHESIS, RESPIRATION, STOMATAL CONDUCTANCE, SULFUR-DIOXIDE, TEMPERATURE, WINTER-WHEAT

498

Dehaan, B.J., M. Jonas, O. Klepper, J. Krabec, M.S. Krol, and K. Olendrzynski. 1994. An atmosphere-ocean model for integrated assessment of global change. *Water, Air, and Soil Pollution 76(1-2):283-318.*

This paper describes the atmosphere-ocean system of the integrated model IMAGE 2.0. The system consists of four linked models, for

atmospheric composition, atmospheric climate, ocean climate and for ocean biosphere and chemistry. The first model is globally averaged, the latter are zonally averaged with additional resolution in the vertical. The models reflect a compromise between describing the physical, chemical and biological processes and moderate computational requirements. The system is validated with direct observations for current conditions (climate, chemistry) and is consistent with results from General Circulation Model experiments. The system is used in the integrated setting of the IMAGE 2.0 model to give transient climate projections. Global surface temperature is simulated to increase by 2.5 K over the next century for socio- economic scenarios with continuing economic and population growth. In a scenario study with reduced ocean circulation, the climate system and the global C cycle are found to be appreciably sensitive to such changes.

KEYWORDS: ANTHROPOGENIC CO2, BALANCE, BUDGET, CARBON DIOXIDE, CLIMATE, SEA

499

Delatorre, A., B. Delgado, and C. Lara. 1991. Nitrate-dependent O2 evolution in intact leaves. *Plant Physiology 96(3):898-901.*

Evolution Of O2 by illuminated intact detached leaves from barley (Hordeum vulgare L. cv Athos) and pea (Pisum sativum L. cv Lincoln) in a CO2-saturating atmosphere was enhanced when KNO3 (1-2.5 millimolar) had been previously supplied through the transpiration stream. The extra O2 evolution observed after feeding KNO3 increased with the light intensity, being maximal at near saturating photon flux densities and resulting in no changes in the initial slope of the O2 versus light-intensity curve. No stimulation Of O2 evolution was otherwise observed after feeding KCl or NH4Cl. The data indicate that nitrate assimilation uses photosynthetically generated reductant and stimulates the rate of noncyclic electron flow by acting as a second electron-accepting assimilatory process in addition to CO2 fixation.

KEYWORDS: ANACYSTIS-NIDULANS, ASSIMILATION, CHLOROPLASTS, OXYGEN, REDUCTION, TRANSLOCATOR

500

de la Vina, G., F. Pliego-Alfaro, S.P. Driscoll, V.J. Mitchell, M.A. Parry, and D.W. Lawlor. 1999. Effects of CO2 and sugars on photosynthesis and composition of avocado leaves grown in vitro. *Plant Physiology and Biochemistry 37(7-8):587-595.*

The effects of micropropagation conditions on avocado (Persea americana Mill.) have been measured in leaves and plants cultured in vitro. The consequences of the type and concentration of sugar in the medium and of carbon dioxide concentration in the atmosphere on the rates of photosynthesis and amounts of ribulose 1,5-biphosphate carboxylase-oxygenase (EC 4.1.1.39; Rubisco) and total soluble protein (TSP) were measured. At the highest sucrose supply (87.6 mM), Rubisco content was substantially decreased in leaves, and even more when elevated CO2 (1 000 mu mol mol(-1)) was supplied. Maximum photosynthetic rate (P-max) was significantly decreased when plants developed in high sucrose and elevated CO2. However, Rubisco concentration was significantly greater when glucose was supplied at the same molar concentration or when the concentration of sucrose was small (14.6 mM), and no differences were observed due to the CO2 concentration in the air in these treatments. The ratio of Rubisco to total soluble protein (Rubisco/TSP) was dramatically decreased in plants grown in the highest concentration of sucrose and with elevated CO2. Leaf area and ratio of leaf fresh weight/(stem + root) fresh weight, were greater in plants grown with CO2, enriched air. However, upon transplanting, survival was poorer in plants grown on low sucrose/high CO2 compared to those grown on high sucrose/high CO2. (C) Elsevier, Paris.

KEYWORDS: (CO2) C 14, ACCLIMATIZATION, EXPRESSION, FIXATION, INHIBITION, INVITRO, MECHANISM, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SINK REGULATION

501

Delesalle, V.A., and S. Blum. 1994. Variation in germination and survival among families of sagittaria-latifolia in response to salinity and temperature. *International Journal of Plant Science 155(2):187-195.*

We studied seed germination and seedling growth in eight maternal families of Sagittaria latifolia (Alismataceae), a freshwater perennial, in response to salinity (four levels) and temperature effects (two levels) in the greenhouse. Salinity decreased germination, delayed emergence, and decreased survival and growth rates. The negative effects of salinity on germination were greater at the high-temperature regime, but the effects on growth were greater at the low-temperature regime. Some seeds were capable of germinating and surviving (with minimal growth) even in 0.8% NaCl solution. Families also differed in their response to salinity but not to temperature. In particular, high salinities had little effect on the germination of some families. Growth rate always decreased with increasing salinity, but again the magnitude of the effect differed among maternal families. Our data show that S. latifolia can germinate but cannot grow well under low-salinity conditions; thus, S. latifolia might be minimally affected by short-term salt intrusions. In order to understand how plant populations respond to disturbances, such as increased salinity or increased temperature, we need to consider the source, either environmental or genetic, of maternal effects.

KEYWORDS: ECOPHYSIOLOGY, ELEVATED CO2, EVOLUTIONARY CONSEQUENCES, GROWTH, HORDEUM-JUBATUM, INBREEDING DEPRESSION, INTRASPECIFIC VARIATION, PLANTS, SEED-GERMINATION, SIZE

502

Delgado, E., R.A.C. Mitchell, M.A.J. Parry, S.P. Driscoll, V.J. Mitchell, and D.W. Lawlor. 1994. Interacting effects of co2 concentration, temperature and nitrogen supply on the photosynthesis and composition of winter-wheat leaves. *Plant, Cell and Environment 17(11):1205-1213.*

Winter wheat (Triticum aestivum L., cv. Mercia) was grown at two different atmospheric CO, concentrations (350 and 700 mu mol mol(-1)) two temperatures [ambient temperature (i.e. tracking the open air) and ambient +4 degrees C] and two rates of nitrogen supply (equivalent to 489 kg ha(-1) and 87 kg ha(- 1)). Leaves grown at 700 mu mol mol(-1) CO2 had slightly greater photosynthetic capacity (10% mean increase over the experiment) than those grown at ambient CO2 concentration, but there were no differences in carboxylation efficiency or apparent quantum yield. The amounts of chlorophyll, soluble protein and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) per unit leaf area did not change with long-term exposure to elevated CO2 concentration. Thus winter wheat, grown under simulated field conditions, for which total biomass was large compared to normal field production, did not experience loss of components of the photosynthetic system or loss of photosynthetic competence with elevated CO2 concentration. However, nitrogen supply and temperature had large effects on photosynthetic characteristics but did not interact with elevated CO2 concentration. Nitrogen deficiency resulted in decreases in the contents of protein, including Rubisco, and chlorophyll, and decreased photosynthetic capacity and carboxylation efficiency. An increase in temperature also reduced these components and shortened the effective life of the leaves, reducing the duration of high photosynthetic capacity.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE

CONCENTRATION, CARBOXYLASE-OXYGENASE, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, PLANTS, PROTEIN, RESPONSES, RUBISCO

503

Delmas, R.J. 1998. Ice-core records of global climate and environment changes. *Proceedings of the Indian Academy of Sciences-Earth and Planetary Sciences 107(4):307-319.*

Precipitation accumulating on the Greenland and Antarctic ice sheets records several key parameters (temperature, accumulation, composition of atmospheric gases and aerosols) of primary interest for documenting the past global environment over recent climatic cycles and the chemistry of the preindustrial, atmosphere. Several deep ice cores from Antarctica and Greenland have been studied over the last fifteen years. In both hemispheres, temperature records (based on stable isotope measurements in water) show the succession of glacial and interglacial periods. However, detailed features of the climatic stages are not identical in Antarctica and in Greenland. A tight link between global climate and greenhouse gas concentrations was discovered, CO2 and CH4 concentrations being lower in glacial conditions by about 80 and 0.3 ppmv, respectively, with respect to their pre-industrial levels of 280 and 0.65 ppmv. Coldest stages are also characterized by higher sea-salt and crustal aerosol concentrations. In Greenland, contrary to Antarctica, ice-age ice is alkaline. Gas-derived aerosol (in particular, sulfate) concentrations are generally higher for glacial periods, but not similar in both the hemispheres. Marine and continental biomass-related species are significant in Antarctica and Greenland ice, respectively. Finally, the growing impact of anthropogenic activities on the atmospheric composition is well recorded in both polar regions for long-lived compounds (in particular greenhouse gases), but mostly in Greenland for short-lived pollutants.

KEYWORDS: ANTARCTIC ICE, ATMOSPHERIC METHANE, CENTRAL GREENLAND ICE, CYCLE, DUST, GLACIAL PERIOD, HYDROGEN- PEROXIDE, NITRATE CONCENTRATIONS, SUMMIT, VOSTOK

504

Delucia, E.H., R.M. Callaway, and W.H. Schlesinger. 1994. Offsetting changes in biomass allocation and photosynthesis in ponderosa pine (pinus-ponderosa) in response to climate-change. *Tree Physiology 14(7-9):669-677.*

We examined the effect of climate on aboveground biomass allocation of ponderosa pine (Pinus ponderosa) by measuring trees in disjunct forest stands growing on the same substrate at high-elevation montane sites and low-elevation desert sites. Climatic differences between the sites were comparable to the difference between present and future climates of interior North America that is expected to result from a doubling of atmospheric CO2 concentration. Relative to the montane populations, the desert populations allocated a greater proportion of biomass to sapwood (functional xylem) at the expense of foliage. The leaf/sapwood area ratio and percent of aboveground biomass in sapwood for trees of the same height were 0.201 m2 cm-2 and 58% for montane trees and 0.104 m2 cm-2 and 71% for desert trees. In a phytotron experiment, increases in net photosynthesis and net assimilation rate for seedlings grown under future conditions of high CO2 and temperature were offset by a decrease in leaf area ratio. As was observed for large trees at different elevations, increased temperatures caused an increase in biomass allocation to stem in the phytotron seedlings. Thus, CO2- and temperature-driven shifts in biomass allocation negated the effect on growth of the CO2- driven increase in carbon assimilation rate. Our data from the controlled growth chamber and field experiments suggest that future climate conditions, including elevated atmospheric CO2, may not stimulate growth and productivity of ponderosa pine.

505

Delucia, E.H., R.M. Callaway, E.M. Thomas, and W.H. Schlesinger. 1997. Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO2 and temperature. *Annals of Botany 79(2):111-120.*

To test the hypothesis that elevated atmospheric CO2 and elevated temperature, simulating current and predicted future growing season conditions, act antagonistically on phosphorus acquisition of ponderosa pine, seedlings were grown in controlled-environment chambers in a two temperature (25/10 degrees C and 30/15 degrees C)xtwo CO2 (350 and 700 mu l(-1)) experimental design. Mycorrhizal seedlings were watered daily with a nutrient solution with P added in organic form as inositol hexaphosphate (64ppm P). Thus seedlings were challenged to use active forms of P acquisition. Elevated CO2 increased the relative growth rate by approx. 5% which resulted in an approx. 33% increase in biomass after 4 months. There was no main effect of temperature on growth. Increased growth under elevated CO2 and temperature was supported by increases in specific absorption rate and the specific utilization rate of P. The contribution of mycorrhizae to P uptake may have been greater under simulated future conditions, as elevated CO2 increased the number of mycorrhizal roots. There was no main effect of temperature on root phosphatase activity, but elevated CO2 caused a decrease in activity. The inverse pattern of root phosphatase activity and mycorrhizal infection across treatments suggests a physiological coordination between these avenues of P acquisition. The concentration of oxalate in the soil increased under elevated CO2 and decreased under elevated temperature. This small molecular weight acid solubilizes inorganic P making it available for uptake. Increased mycorrhizal infection and exudation of oxalate increased P uptake in ponderosa pine seedlings under elevated CO2, and there was no net negative effect of increased temperature. The increased carbon status of pine under elevated CO2 may facilitate uptake of limiting P in native ecosystems. (C) 1997 Annals of Botany Company.

KEYWORDS: CALCIUM-OXALATE, CARBON DIOXIDE, COMPENSATORY RESPONSES, ELEVATED ATMOSPHERIC CO2, NUTRIENT, PHOSPHATASE-ACTIVITY, PLANTS, RHIZOSPHERE, SOILS, TAEDA L SEEDLINGS

506

DeLucia, E.H., J.G. Hamilton, S.L. Naidu, R.B. Thomas, J.A. Andrews, A. Finzi, M. Lavine, R. Matamala, J.E. Mohan, G.R. Hendrey, and W.H. Schlesinger. 1999. Net primary production of a forest ecosystem with experimental CO2 enrichment. *Science 284(5417):1177-1179.*

The concentration of atmospheric carbon dioxide was increased by 200 microliters per Liter in a forest plantation, where competition between organisms, resource Limitations, and environmental stresses may modulate biotic responses. After 2 years the growth rate of the dominant pine trees increased by about 26 percent relative to trees under ambient conditions. Carbon dioxide enrichment also increased Litterfall and fine-root increment. These changes increased the total net primary production by 25 percent. Such an increase in forest net primary production globally would fix about 50 percent of the anthropogenic carbon dioxide projected to be released into the atmosphere in the year 2050. The response of this young, rapidly growing forest to carbon dioxide may represent the upper Limit for forest carbon sequestration.

KEYWORDS: BIOMASS, CLIMATE, ELEVATED CO2, GROWTH TRENDS, LOBLOLLY-PINE, RESPONSES, RISING ATMOSPHERIC CO2, SODA-LIME, TREE GROWTH, UNITED-STATES

507

DeLucia, E.H., and W.H. Schlesinger. 1999. Effect on the biosphere of elevated atmospheric CO2 - Response. *Science 285(5435):1852.*

508

De Luis, I., J.J. Irigoyen, and M. Sanchez-Diaz. 1999. Elevated CO2 enhances plant growth in droughted N-2-fixing alfalfa without improving water status. *Physiologia Plantarum 107(1):84-89.*

The long-term interaction between elevated CO2 and soil mater deficit was analysed in N-2-fixing alfalfa plants in order to assess the possible drought tolerance effect of CO2. Elevated CO2 could delay the onset of drought stress by decreasing transpiration rates, but this effect was avoided by subjecting plants to the same soil water content. Nodulated alfalfa plants subjected to ambient (400 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 were either men watered or partially watered by restricting water to obtain 30% of the water content at field capacity (approximately 0.55 g water cm(-3)). The negative effects of sop water deficit on plant growth were counterbalanced by elevated CO2. In droughted plants, elevated CO2 stimulated carbon fixation and, as a result, biomass production was even greater than in well-watered plants grown in ambient CO2. Below-ground production was preferentially stimulated by elevated CO2 in droughted plants, increasing nodule biomass production and the availability of photosynthates to the nodules. As a result, total nitrogen content in droughted plants was higher than in well-watered plants grown in ambient CO2. The beneficial effect of elevated CO2 was not correlated with a better plant water status. It is concluded that elevated CO2 enhances growth of droughted plants by stimulating carbon fixation, preferentially increasing the availability of photosynthates to below-ground production (roots and nodules) without improving water status. This means that elevated CO2 enhances the ability to produce more biomass in N-2-fixing alfalfa under given soil water stress, improving drought tolerance.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, N2 FIXATION, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, SOIL, STARCH, TEMPERATURE

509

Demmers-Derks, H., R.A.C. Mitchell, V.J. Mitchell, and D.W. Lawlor. 1998. Response of sugar beet (Beta vulgaris L.) yield and biochemical composition to elevated CO2 and temperature at two nitrogen applications. *Plant, Cell and Environment 21(8):829-836.*

Effects on sugar beet (Beta vulgaris L.) of current and elevated CO2 and temperature alone and in combination and their interactions with abundant and deficient nitrogen supply (HN and LN, respectively) have been studied in three experiments in 1993, 1994 and 1995. Averaged over all experiments, elevated CO2 (600 mu mol mol(-1) in 1993 and 700 mu mol mol-l in 1994 and 1995) increased total dry mass at final harvest by 21% (95% confidence interval (CI) = 21, 22) and 11% (CI = 6, 15) and root dry mass by 26% (CI = 19, 32) and 12% (CI = 6, 18) for HN and LN plants, respectively. Warmer temperature decreased total dry mass by 11% (CI = - 15, - 7) and 9% (CI = - 15, - 5) and root dry mass by 7% (CI = - 12, - 2) and 7% (CI = - 10, 0) for HN and LN plants, respectively. There was no significant interaction between temperature and CO2 on total or root dry mass. Neither elevated CO2 nor temperature significantly affected sucrose concentration per unit root dry mass. Concentrations of glycinebetaine and of amino acids, measured as alpha-amino-N, decreased in elevated CO2 in both N applications; glycinebetaine by 13% (CI = - 21, - 5) and 16% (CI = - 24, - 8) and alpha-amino-N by 24% (CI = - 36, - 11) and 16% (CI = - 26, - 5) for HN and LN, respectively. Warmer temperature increased alpha-amino-N, by 76% (CI = 50, 107) for HN and 21% (CI = 7, 36) for LN plants, but not glycinebetaine.

KEYWORDS: CARBON DIOXIDE, CROPS, FIELD, GROWTH, PLANT, PRODUCTIVITY, SOURCE-SINK RELATIONS, WINTER-WHEAT

510

DeMothes, M.A.G. 1996. Effects of enhanced CO2 concentration on wheat photosynthesis and long- and short-term stomatal behaviour. *Photosynthetica 32(2):193-202.*

Wheat (Triticum aestivum L.) plants were cultivated in a growth chamber at normal (35 Pa = c(35)) and increased (70 Pa = c(70)) CO2 partial pressure. Environmental conditions other than CO2 concentration were similar for the c(35) and the c(70) plants. For the c(35) and the c(70) plants stomatal density was similar. When both variants were measured at growth conditions, the net photosynthetic rate (P-N) Of c(70) plants was 44 % higher and stomatal conductance to water vapour pressure (g(s)) was 22 % lower than those of the c(35) plants, while the relation between internal partial pressure of CO2 (pci) and external partial pressure (pea) was similar for both variants. Plants were also submitted to a sequence of increments in CO2 concentration (from 10 Pa up to saturating CO2 concentration) at saturating photosynthetically active radiation (PAR). Following 1.5 h at saturating CO2 concentration and PAR, CO2 concentration was decreased stepwise. Both variants showed hysteresis in the response of P-N, transpiration rate (E), g(s) and water use efficiency (WUE) to pci. While CO2 concentration was incremented, P-N and g(s) were linearly related indicating that mesophyll activity and g(s) were correlated. At saturating CO2 concentration and PAR, end product feedback inhibition on photosynthesis disrupted this correlation for both variants. Plants were also submitted to a sequence of increments in PAR (from 40 mu mol m(-2), s(-1) up to saturating PAR) at saturating CO2 concentration. Following 1.5 h at saturating CO2 concentration and PAR, PAR was decreased stepwise. While both variants showed hysteresis in the response of P-N, E and g(s), the c(35) plants showed also hysteresis in the response of pci/pca and WUE to PAR. Stomatal conductance and activity of mesophyll remained co-ordinated during the whole experiment for the c(70) plants, while for the c(35) plants the correlation between g(s) and mesophyll activity present during step-up PAR response was disrupted at saturating CO2 concentration and PAR.

KEYWORDS: FIELD, LEAF, WATER-USE EFFICIENCY

511

DeMothes, M.A.G., M. Baumgarten, and D. Knoppik. 1996. Hysteresis in the response of photosynthesis to CO2 and saccharide pools of wheat leaves grown at normal and enhanced CO2. *Photosynthetica 32(2):181-191.*

Wheat plants were cultivated in a growth chamber at 35 Pa (c(35) variant) and 70 Pa CO2 partial pressure (c(70) variant) during the whole vegetation period. The response of net photosynthetic rate (P-N) Of the nag leaf of both variants to successive increases in CO2 partial pressure (step-up curve) showed hysteresis when the direction of the sequence was reversed (step-down curve) after 1.5 h at saturating CO2 partial pressure and photosynthetically active radiation (PAR). Saccharose, glucose and fructose accumulated during the measurement of a step-up CO2 curve for the c(35) and c(70) plants as the export rate was not able to keep pace with the rate of saccharide synthesis. Remaining 1.5 h at saturating CO2 partial pressure and PAR, the saccharose pool increased further for both variants while glucose and fructose decreased reaching the values at growth conditions. The electron transport rate decreased after 1.5 h at saturating CO2 partial pressure and PAR for the two variants due to end product feedback. Glucose and fructose contents fell 50 % below the initial contents when partial pressure of CO2 was lowered stepwise. The c(35) plants showed a double fold increase in the content of saccharose at the end point of the hysteresis curve. Contents

of saccharose for the c(70) variant in contrast were similar to the initial values.

KEYWORDS: ACCLIMATION, ASSIMILATION, CARBON DIOXIDE, ELECTRON-TRANSPORT, ELEVATED CO2, ENRICHMENT, PHASEOLUS-VULGARIS L, RESPIRATION, TEMPERATURE

512

Demothes, M.A.G., and D. Knoppik. 1994. Effects of long-term enhanced co2 partial-pressure on gas- exchange parameters and saccharide pools of wheat leaves. *Photosynthetica 30(3):435-445.*

Wheat plants were cultivated in a growth chamber at normal (35 Pa, c35 plants) and enhanced (70 Pa, c70 plants) CO2 partial pressure. In C35 plants the net photosynthetic rate (P(N)) of flag leaves and the concentrations of saccharides such as sucrose, glucose, fructose and starch were increased. The c70 plants possessed higher chlorophyll (Chl) a and Chl b contents. The CO2 response of P(N) at saturating photosynthetically active radiation (PAR) was very similar for both variants. At the highest CO2 concentration saccharides accumulated in both variants as a consequence of decreased export rate. The response of P(N) to PAR at saturating CO2 concentrations was similar in the two variants. On the other hand, the response of water vapour pressure conductance (gH2O) to PAR in c35 plants followed a hyperbolic response to PAR, while in the c70 plants it was linearly related to PAR up to the mean PAR used for growth. In this variant gH2O seemed to change parallelly to changes in the mesophyll demand for CO2 caused by PAR.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, TEMPERATURE, YIELD

513

Denelzen, M.G.J., and J. Rotmans. 1993. Modeling climate related feedback processes. *Journal of Environmental Science and Health Part A- Environmental Science and Engineering & Toxic and Hazardous Substance Control 28(9):2095-2151.*

Feedback mechanisms play a crucial role in the climate system, amplifying or dampening the climate response to enhanced concentrations of greenhouse gases from anthropogenic perturbations. Many of these feedbacks are known, but most of them only potentially. This article evaluates the role of a number of these feedback processes within the climate system. In order to assess their impact, the feedbacks which at present can be quantified reasonably are built into the Integrated Model to Assess the Greenhouse Effect (IMAGE). Unlike previous studies, this study describes the scenario- and time-dependent role of biogeochemical feedbacks. A number of simulation experiments are performed with IMAGE to project climate changes. Besides estimates of their absolute importance, the relative importance of individual biogeochemical feedbacks is considered by calculating the gain for each feedback process. This study focuses on feedback processes in the carbon cycle and the methane (semi-) cycle. Modeled feedbacks are then used to balance the past and present carbon budget. This results in substantially lower projections for atmospheric carbon dioxide than the Intergovernmental Panel on Climate Change (IPCC) estimates. The difference is approximately 18% from the 1990 level for the IPCC "Business-as-Usual" scenario. Furthermore, the IPCC's "best guess" value of the CO2 concentration in the year 2100 falls outside the uncertainty range estimated with our balanced modeling approach. For the IPCC "Business-as- Usual" scenario, the calculated total gain of the feedbacks within the carbon cycle appears to be negative, a result of the dominant role of the fertilization feedback. This study also shows that if temperature feedbacks on methane emissions from wetlands, rice paddies, and hydrates do materialize, methane concentrations might be increased by 30% by 2100. The total effect of the methane feedbacks and the carbon dioxide feedbacks modeled can be expressed in the carbon dioxide- equivalent concentrations. Our simulated CO2-equivalent concentrations are lower than the IPCC estimates.

KEYWORDS: ATMOSPHERIC CO2, ECOSYSTEMS, GLOBAL CLIMATE, GREENHOUSE, ICE CORE, INCREASE, METHANE EMISSIONS, PAST 2 CENTURIES, SENSITIVITY, SIMULATION

514

Deng, R., and D.J. Donnelly. 1993. In-vitro hardening of red raspberry by co2 enrichment and reduced medium sucrose concentration. *Hortscience 28(10):1048-1051.*

Micropropagated 'Festival' red raspberry (Rubus idaeus L.) shoots were rooted in specially constructed plexiglass chambers in ambient (340 +/- 20 ppm) or enriched (1500 +/- 50 ppm) CO2 conditions on a medium containing 0, 10, 20, or 30 g sucrose/liter. Plantlet growth and leaf (CO2)-C-14 fixation rates were evaluated before and 4 weeks after ex vitro transplantation. In vitro CO2 enrichment promoted in vitro hardening; it increased root count and length, plantlet fresh weight, and photosynthetic capacity but did not affect other variables such as plantlet height, dry weight, or leaf count and area. No residual effects of in vitro CO2 enrichment were observed on 4-week-old transplants. Sucrose in the medium promoted plantlet growth but depressed photosynthesis and reduced in vitro hardening. Photoautotrophic plantlets were obtained on sucrose-free rooting medium under ambient and enriched CO2 conditions and they performed better ex vitro than mixotrophic plantlets grown with sucrose. Root hairs were more abundant and longer on root tips of photoautotrophic plantlets than on mixotrophic plantlets. The maximum CO2 uptake rate of plantlet leaves was 52% that of greenhouse control plant leaves. This did not change in the persistent leaves up to 4 weeks after ex vitro transplantation. The photosynthetic ability of persistent and new leaves of 4-week-old ex vitro transplants related neither to in vitro CO2 nor medium sucrose concentration. Consecutive new leaves of transplants took up more CO2 than persistent leaves. The third new leaf of transplants had photosynthetic rates up to 90% that of greenhouse control plant leaves. These results indicate that in vitro CO2 enrichment was beneficial to in vitro hardening and that sucrose may be reduced substantially or eliminated from red raspberry rooting medium when CO2 enrichment is used.

KEYWORDS: ACCLIMATIZATION, CULTURE, EXVITRO, FIXATION, GROWTH, LEAF ANATOMY, LEAVES, SOIL, STRAWBERRY PLANTLETS

515

Deng, R., and D.J. Donnelly. 1993. In-vitro hardening of red raspberry through co2 enrichment and relative-humidity reduction on sugar-free medium. *Canadian Journal of Plant Science 73(4):1105-1113.*

Micropropagated shoots of red raspberry (Rubus idaeus L. 'Comet') were rooted on modified Murashige-Skoog medium lacking sucrose, in specially 'constructed plexiglass chambers, under ambient (340 +/- 20 ppm) or enriched (1500 +/- 50 PPM) CO2 and ambient (ca. 100 %) or reduced (90 +/- 5 %) relative humidity. Cultured plantlets were evaluated for their survival, rooting and relative vigor, leaf and root number, stem and root length, total leaf area, total fresh and dry weight, gas exchange rate, and stomatal features, prior to transplantation to soil and at intervals for 6 wk ex vitro. In vitro CO2 enrichment promoted plantlet growth, rooting and both the survival and early growth of transplants. CO2 enrichment increased stomatal aperture of plantlet leaves but did not apparently increase water stress at transplantation. Reduced in vitro RH did not affect plantlet growth but decreased stomatal apertures and stomatal index on leaves of cultured plantlets and promoted both the survival and early growth of transplants. In vitro CO2

and RH levels did not affect the photosynthetic rate of either plantlets or transplants. Only the stomata on leaves of plantlets from the ambient CO2 and reduced RH treatment were functional. Normal stomatal function was not observed in persistent leaves of transplants from the other treatments, even 2 wk after transplantation. In vitro CO2 enrichment acted synergistically with RH reduction in improving growth of plantlets both in vitro and ex vitro. Hardened red raspberry plantlets obtained through CO2 enrichment and RH reduction survived direct transfer to ambient greenhouse conditions without the necessity for specialized ex vitro acclimatization treatment.

KEYWORDS: ANATOMY, CULTURE, GROWTH, LEAVES, LIGHT, PLANTLETS INVITRO, SOIL, STRAWBERRY

516

Deng, X., and F.I. Woodward. 1998. The growth and yield responses of Fragaria ananassa to elevated CO2 and N supply. *Annals of Botany 81(1):67-71.*

Strawberry plants (Fragaria ananassa Duchesne var. Elsanta) were grown in pots at two concentrations of carbon dioxide (partial pressures of 39 and 56 Pa) and with three rates of nitrogen supply (0.04, 0.4 and 4 mM as nutrient solution) to study their individual and interactive effects on plant growth and fruit yield. Nitrogen deficiency reduced total dry biomass and relative growth rate (RGR), mainly through reductions in leaf area ratio (LAR) and plant N concentration (PNC), although both the net assimilation rare (NAR) and root weight ratio (RWR) increased. Elevated CO2 increased the N productivity (NP) but reduced the LAR. High CO2 increased the fruit yield by 42% at high N supply and by 17% at low N supply. The CO2 yield enhancement occurred through an increase in the flower and fruit number of individual plants. This resulted in an increase in the fruit weight ratio (FWR) of plants at high CO2. Nitrogen deficiency reduced the fruit yield by about 50% through decreases in fruit size, fruit set and the number of fruits. However, N deficiency increased the proportion of total plant dry biomass allocated to fruits. There were no significant interactions between CO2 and N supply on yield. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, GRASSES, NITROGEN, NUTRITION, WHEAT

517

denHertog, J., I. Stulen, F. Fonseca, and P. Delea. 1996. Modulation of carbon and nitrogen allocation in Urtica dioica and Plantago major by elevated CO2: Impact of accumulation of nonstructural carbohydrates and ontogenetic drift. *Physiologia Plantarum 98(1):77-88.*

Doubling the atmospheric CO2 concentration from 350 to 700 mu l l(-1) increased the relative growth rate (RGR) of hydroponically grown Urtica dioica L. and Plantago major ssp. pleiosperma Pilger only for the first 10-14 days. Previous experiments with P. major led to the conclusion that RGR did not respond in proportion to the rate of photosynthesis. The present paper is focussed on the analysis of the impact of changes in leaf morphology, dry matter partitioning, dry matter chemical composition and ontogenetic drift on this discrepancy. Soon after the start of the treatment, carbohydrate concentrations were higher at elevated CO2; a reaction that was largely due to starch accumulation. An increase in the percentage of leaf dry matter and decreases in the specific leaf area (SLA) and the shoot nitrogen concentration were correlated with an increase in the total nonstructural carbohydrate concentration (TNC). A combination of accumulation of soluble sugars and starch and ontogenetic drift explains the decrease in SLA at the elevated CO2 level. A similar ontogenetic effect of elevated CO2 was observed on the specific root length (SRL). Other variables such as shoot nitrogen concentration and percentage leaf dry matter were not affected by correction of data for TNC levels. The net diurnal fluctuation of the carbohydrate pool in P. major was equal for both CO2 concentrations, indicating that the growth response to elevated CO2 may be ruled by variables other than photosynthesis, as for instance sink strength. Elevated CO2 did not greatly influence the partitioning of nitrogen between soluble and insoluble, reduced N and nitrate, nor the allocation of dry matter between leaf, stem and root. The finding that the root to shoot ratio (R/S) was not affected by elevated CO2 implies that, in order to maintain a balanced activity between roots and shoot, no shift in partitioning of dry matter upon doubling of the atmospheric CO2 concentration is required. Our data on R/S are in good agreement with the response of R/S to high CO2 predicted by models based on such a theorem.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, DIOXIDE ENRICHMENT, LEAF-AREA, NITRATE, PHOTOSYNTHESIS, PRODUCTIVITY, RELATIVE GROWTH-RATE, ROOT, SHOOT RATIO

518

Denhertog, J., I. Stulen, and H. Lambers. 1993. Assimilation, respiration and allocation of carbon in plantago major as affected by atmospheric co2 levels - a case-study. *Vegetatio 104:369-378.*

The response of Plantago major ssp. pleiosperma plants, grown on nutrient solution in a climate chamber, to a doubling of the ambient atmospheric CO2 concentration was investigated. Total dry matter production was increased by 30 % after 3 weeks of exposure, due to a transient stimulation of the relative growth rate (RGR) during the first 10 days. Thereafter RGR returned to the level of control plants. Photosynthesis, expressed per unit leaf area, was stimulated during the first two weeks of the experiment, thereafter it dropped and nearly reached the level of the control plants. Root respiration was not affected by increased atmospheric CO2 levels, whereas shoot, dark respiration was stimulated throughout the experimental period. Dry matter allocation over leaves stems and roots was not affected by the CO2 level. SLA was reduced by 10%, which can partly be explained by an increased dry matter content of the leaves. Both in the early and later stages of the experiment, shoot respiration accounted for a larger part of the carbon budget in plants grown at elevated atmospheric CO2. Shifts in the total carbon budget were mainly due to the effects on shoot respiration. Leaf growth accounted for nearly 50 % of the C budget at all stages of the experiment and in both treatments.

KEYWORDS: DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, RELATIVE GROWTH-RATE

519

den Hertog, J., I. Stulen, F. Posthumus, and H. Poorter. 1998. Interactive effects of growth-limiting N supply and elevated atmospheric CO2 concentration on growth and carbon balance of Plantago major. *Physiologia Plantarum 103(4):451-460.*

To assess the interactions between concentration of atmospheric CO2 and N supply, the response of Plantago major ssp. pleiosperma Pilger to a doubling of the ambient CO2 concentration of 350 mu l l(-1) was investigated in a range of exponential rates of N addition. The relative growth rate (RGR) as a function of the internal plant nitrogen concentration (Ni), was increased by elevated CO2 at optimal and intermediate N-i. The rate of photosynthesis, expressed per unit leaf area and plotted Versus N-i, was increased by 20-30% at elevated CO2 for N-i above 30 mg N g(-1) dry weight. However, the rate of photosynthesis, expressed on a leaf dry matter basis and plotted versus N-i, was not affected by the CO2 concentration. The allocation of dry matter between shoot and root was not affected by the CO2 concentration at any of the N addition rates. This is in good agreement with theoretical models, based on a balance between the rate of photosynthesis of the shoot and

the acquisition of N by the roots. The concentration of total nonstructural carbohydrates (TNC) was increased at elevated CO2 and at N limitation, resulting in a shift in the partitioning of photosynthates from structural to nonstructural and, in terms of carbon balance, unproductive dry matter. The increase in concentration of TNC led to a decrease in both specific leaf area (SLA) and Ni at all levels of nutrient supply, and was the cause of the increased rate of photosynthesis per unit leaf area. Correction of the relationship between RGR and Ni for the accumulation of TNC made the effect of elevated CO2 on the relationship between RGR and Ni disappear. We conclude that the shift in the relationship between RGR and Ni was due to the accumulation of TNC and not due to differences in physiological variables such as photosynthesis and shoot and root respiration, changes in leaf morphology or allocation of dry matter.

KEYWORDS: BETULA-PENDULA ROTH, DRY-MATTER, ENRICHMENT, LEAF-AREA, MINERAL NUTRITION, NITROGEN CONCENTRATION, NUTRIENT AVAILABILITY, PHOTON FLUX-DENSITY, PHOTOSYNTHETIC ACCLIMATION, SHOOT RATIO

520

Denmead, O.T., F.X. Dunin, S.C. Wong, and E.A.N. Greenwood. 1993. Measuring water-use efficiency of eucalypt trees with chambers and micrometeorological techniques. *Journal of Hydrology 150(2-4):649-664.*

Enclosure appears to be the only feasible way to examine the gas exchange of small groups of trees or to answer questions about the effects of increased atmospheric CO2 on the assimilation, evaporation and water use efficiency of forests. To be effective, enclosures must necessarily change the microclimate, but few studies have been made of the consequences. In this paper, the assimilation, evaporation and water use efficiency of a community of Eucalyptus trees inside a ventilated chamber are compared with the same attributes for the surrounding forest. Assimilation and evaporation for the chamber were measured by the depletion in CO2 and the enrichment in water vapour of air passing through the chamber. For the forest, assimilation and evaporation were determined by micrometeorological techniques based on the energy balance, and for CO2, additional chamber measurements of the soil efflux. Water use efficiencies were calculated as the ratio of mol CO2 assimilated to mol water evaporated. There are some important microclimatic differences between chamber and forest: net radiation is reduced by about 30% in the chamber, the vapour pressure deficit of the chamber air is lower, and the light climate there tends to be diffuse rather than direct. Despite these differences, evaporation rates for both chamber and forest were generally similar, perhaps due to compensating effects in the chamber from higher boundary layer conductances (because of greater ventilation rates) and higher stomatal conductances (because of increased humidity). However, assimilation rates and water use efficiencies were markedly different for the two communities in clear sky conditions, with higher values of both being recorded in the chamber for most of the daylight hours. Only on cloudy days, when the light climate was diffuse in both chamber and forest, were similar assimilation rates and water use efficiencies observed. This behaviour seems to be attributable in part to the light climate in the chamber being predominantly diffuse and that in the forest predominantly direct. Diffuse light enhances the photosynthesis of lower leaves in the canopy. This contention is supported by model calculations of canopy assimilation under diffuse and direct radiation which produced qualitatively the same light response functions as observed for chamber and forest. The study suggests that the use of chambers for exploring questions of forest productivity and water use efficiency must be circumspect. The act of enclosure, by itself, can change the daily water use efficiency of the tree community by as much as 50%.

KEYWORDS: FOREST, PHOTOSYNTHESIS, TRANSPIRATION, VENTILATED CHAMBER

521

Desjardins, Y., A. Gosselin, and M. Lamarre. 1990. Growth of transplants and invitro-cultured clones of asparagus in response to CO2 enrichment and supplemental lighting. *Journal of the American Society for Horticultural Science 115(3):364-368.*

522

Devakumar, A.S., M.S.S. Shayee, M. Udayakumar, and T.G. Prasad. 1998. Effect of elevated CO2 concentration on seedling growth rate and photosynthesis in Hevea brasiliensis. *Journal of Biosciences 23(1):33-36.*

To study the effect of elevated CO2 concentration on plant growth and photosynthesis, two clones of Hevea brasiliensis were grown in polybags and exposed to elevated concentration (700+/-25 ppm) for 60 days. There was higher biomass accumulation, leaf area and better growth when compared to ambient air grown plants. From A/Ci curves it is clear that photosynthetic rates increases with increase in CO2 concentrations. After 60 days of exposure to higher CO2 concentration, a decrease in the carbon assimilation rate was noticed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FIELD, TEMPERATURE, YIELD

523

Devakumar, A.S., M. Udayakumar, and T.G. Prasad. 1996. A simple technique to expose tree seedlings to elevated CO2 for increased initial growth rates. *Current Science 71(6):469-472.*

Initial growth rates of most tree species that are used in afforestation programmes are very low. Therefore, polybag planted seedlings have to be maintained in the nurseries for a long period of time. Growing plants in an elevated CO2 atmosphere increases the growth rates as well as biomass production in many annual crop and tree species. Higher temperature and relative humidity in association with elevated CO2 concentration helps to boost the biomass and leaf area production. We demonstrate here an easy and cost-effective method for obtaining elevated CO2 concentrations for better growth of tree seedlings in the nursery.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, PLANTS, RESPIRATION, TEMPERATURE

524

de Wild, H.P.J., E.J. Woltering, and H.W. Peppelenbos. 1999. Carbon dioxide and 1-MCP inhibit ethylene production and respiration of pear fruit by different mechanisms. *Journal of Experimental Botany 50(335):837-844.*

Ethylene production in relation to O-2 partial pressure of whole pear fruit stored at 2 degrees C could be described by a Michaelis-Menten equation. This was indicated by the use of a gas exchange model. The maximum ethylene production rate was strongly inhibited while the K-mO2 value (1.25 kPa) was not affected by elevated CO2. Ethylene production was also inhibited by 1-MCP, an inhibitor of ethylene perception. The reduction in ethylene production by CO2 was similar for 1-MCP treated and untreated pears. Elevated CO2, therefore, must have had an influence on ethylene production other than through ethylene perception. A possible site of inhibition by CO2 is the conversion of ACC to ethylene. The O-2 uptake rate in relation to O-2 partial pressure of whole pear fruit could be described by a Michaelis-Menten equation. The O-2 uptake rate was inhibited by elevated CO2 at a level similar to the inhibition of ethylene production. Again the K-mO2 value (0.68 kPa)

was not affected by CO2. Using 1-MCP treatments it was shown that there was no direct effect of inhibited ethylene production on O-2 uptake rate.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACC OXIDASE, APPLES, ATMOSPHERES, AVOCADO FRUIT, BIOSYNTHESIS, ELEVATED CO2 CONCENTRATIONS, INTRACELLULAR PH, TISSUE, VEGETABLES

525

Deyton, D.E., C.E. Sams, and J.C. Cummins. 1992. Application of dormant oil to peach-trees modifies bud twig internal atmosphere. *Hortscience 27(12):1304-1305.*

Treatments of single applications of 0%, 3%, 6%, 9%, or 12% dormant oil were sprayed on peach (Prunus persica L. Batsch) trees on 6 Feb. 1990. A repeat application of 6% oil plus 6% oil applied 6 days later was also made. Internal CO2 concentrations of oil-treated buds and twigs were higher than the control the day after treatment and continued to be higher for 6 days. The second application of 10% oil prolonged the elevated CO2 concentration. Applications of 9% or 12% oil delayed flower bud development and bloom. The repeated application of 6% oil delayed bud development and bloom more than a single application of 6% oil. Damage to fruit buds increased as oil concentration increased, but repeated application of 6% oil resulted in less damage than a single application of 12% oil.

526

Dhakhwa, G.B., and C.L. Campbell. 1998. Potential effects of differential day-night warming in global climate change on crop production. *Climatic Change 40(3-4):647-667.*

Recent studies on the nature of global warming indicate the likelihood of an asymmetric change in temperature, where night- time minimum temperature increases more rapidly than the daytime maximum temperature. We used a physically based scenario of asymmetric warming combined with climate change scenarios from General Circulation Models (GCMs) outputs and the EPIC (Erosion Productivity Impact Calculator) plant process model to examine the effects of asymmetric temperature change on crop productivity. Our results indicated that the potential effects of global change on crop productivity may be less severe with asymmetric day-night warming than with equal day- night warming.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2 CONCENTRATIONS, EPIC MODEL, GROWTH, MAXIMUM, MINIMUM TEMPERATURE, SENSITIVITY, SOUR ORANGE TREES, VARIABILITY, YIELD

527

Dhakhwa, G.B., C.L. Campbell, S.K. LeDuc, and E.J. Cooter. 1997. Maize growth: assessing the effects of global warming and CO2 fertilization with crop models. *Agricultural and Forest Meteorology 87(4):253-272.*

Projected future climate change scenarios derived from two General Circulation Models (GCMs): Geophysical Fluid Dynamics Laboratory (GFDL) and United Kingdom Meteorological Office (UKMO), and two crop models: Crop Estimation through Resources and Environmental Synthesis (CERES), and Erosion/Productivity Impact Calculator (EPIC), were considered to assess the climate change impact on the yield and biomass of maize. Climate change scenarios included changes in temperature, precipitation and solar radiation from two GCMs interpolated to 1 degrees x1 degrees grid cells in the central Piedmont in North Carolina. Changes in mean monthly temperature and precipitation from the GCMs were used to adjust observed daily climate records from 1949-1988. There is convincing evidence that future temperature linked to global warming might be characterized by asymmetric change between daily daytime maxima and daily nighttime minima. Two hypotheses regarding how GCM temperature would alter observational record were examined. The first hypothesis assumed that daytime and nighttime warming occurs symmetrically, i.e., maximum and minimum temperatures are raised equally. The second hypothesis assumed that nighttime minima change is three times greater than daytime maxima change and the change in mean diurnal temperature range is approximately equal to the change in daily mean temperature. For the equal day-night warming scenario, when only the effects of climate change (i.e., changes in temperature, precipitation and solar radiation) were considered, simulations with CERES and EPIC indicated substantial losses in maize grain yield and total above ground biomass with both the GCM scenarios. For the asymmetric warming, the reduction in biomass and yield due to climate change was less than that obtained with symmetric warming. Simulated maize yield and biomass with CERES and EPIC increased when only effects due to CO2-fertilization were considered. The inclusion of CO2 fertilization effects with those due to climate change resulted in higher biomass and yield compared to values obtained with effects of climate change alone. When CERES was used with the GFDL scenario, and the effects of CO2 fertilization and the climate change were combined, no difference in simulated yield was found between the two hypotheses; only an 8% difference in aboveground biomass was found when the UKMO scenario was used. When EPIC was used, the differential day-night warming hypothesis resulted in 9-13% less reduction in biomass and yield than did the use of the equal day-night warming hypothesis. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, EPIC MODEL, PRODUCTIVITY, RESPONSES, TEMPERATURE, UNITED-STATES, WATER-USE, YIELD

528

Dhillion, S.S., J. Roy, and M. Abrams. 1996. Assessing the impact of elevated CO2 on soil microbial activity in a Mediterranean model ecosystem. *Plant and Soil 187(2):333-342.*

The fate, as well as the consequence for plant nutrition, of the additional carbon entering soil under elevated CO2 is largely determined by the activity of soil microorganisms. However, most elevated CO2 studies have documented changes (generally increases) in microbial biomass and total infection by symbiotic organisms, which is only a first step in the understanding of the modification of soil processes. Using a Mediterranean model ecosystem, we complemented these variables by analyzing changes in enzymatic activities, hyphal lengths, and bacterial substrate assimilation, to tentatively identify the specific components affected under elevated CO2 and those which suggest changes in soil organic matter pools. We also investigated changes in the functional structures of arbuscular mycorrhizas. Most of the microbial variables assessed showed significant and substantial increase under elevated CO? of the same order or less than those observed for root mass and length. The increase in dehydrogenase activity indicates that the larger biomass of microbes was accompanied by an increase in their activity. The increase in hyphal length (predominantly of saprophytic fungi), and xylanase, cellulase and phosphatase activities, suggests an overall stimulation of organic matter decomposition. The higher number of substrates utilized by microorganisms from the soil under elevated CO2 was significant for the amine/amide group. Total arbuscular and vesicular mycorrhizal infection of roots was higher under elevated CO2, but the proportion of functional structures was not modified. These insights into the CO2-induced changes in soil biological activity point towards potential areas of investigation complementary to a direct

analysis of the soil organic matter pools.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOCIDAL TREATMENTS, BIOMASS, COMMUNITIES, ENRICHMENT, MYCORRHIZAL COLONIZATION, RESPIRATION, RESPONSES, RHIZOSPHERE, ROOTS

529
Diaz, S. 1995. Elevated CO2 responsiveness, interactions at the community level and plant functional types. *Journal of Biogeography 22(2-3):289-295.*

Plant responsiveness to elevated carbon dioxide (CO2) is a relevant dimension for the definition of functional types in the face of global change. Most traits reported to be associated with high CO2 responsiveness are derived from laboratory experiments on individually grown species. This paper suggests that physiological traits such as photosynthetic pathway and internal sink strength are necessary, but not enough for the prediction of plant responses in mixed stands. A number of examples from the literature are presented to illustrate how predictions based on single-species experiments may not match the behaviour of multi-species assemblages. Individual attributes associated to the interaction of the species with other members of the community should be also considered. Morphogenetic and architectural traits, as well as characteristics related to other trophic levels, such as the presence of root symbionts or the preferential allocation to growth or defences against herbivory, may be useful for a better prediction of plant responsiveness to high CO2 in the field.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, INSECT HERBIVORE, NITROGEN, PHOTOSYNTHESIS, RESPONSES, SEEDLING GROWTH, WATER-STRESS

530
Diaz, S. 1996. Effects of elevated [CO2] at the community level mediated by root symbionts. *Plant and Soil 187(2):309-320.*

This review examines the effects of elevated [CO2] on plant symbioses with mycorrhizal fungi and root nodule bacteria, with emphasis on community and ecosystem processes. The effects of elevated [CO2] on the relationships between single plant species and root symbionts are considered first. There is some evidence that plant infection by and/or biomass of root symbionts are stimulated by elevated [CO2], but growth enhancement of the host seemingly depends on its degree of dependence on symbiosis and on soil nutrient availability. Second, the effects of elevated [CO2] on the relationships between plant multispecies assemblages and soil, and likely impacts on above-ground and belowground diversity, are analysed. Experimental and modelling work have suggested the existence of complex feedbacks in the responses of plants and the rhizosphere to CO2 enrichment. By modifying C inputs from plants to soil, elevated [CO2] may affect the biomass, the infectivity, and the species/isolate composition of root symbionts. This has the potential to alter community structure and ecosystem functioning. Finally, the incorporation of type and degree of symbiotic dependence into the definition of plant functional types, and into experimental work within the context of global change research, are discussed. More experimental work on the effects of elevated [CO2] at the community/ecosystem level, explicitly considering the role of root symbioses, is urgently needed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BOUTELOUA-GRACILIS, ECTOMYCORRHIZAL FUNGI, EXTERNAL HYPHAE, NITROGEN NUTRITION, PLANT COMMUNITY, QUERCUS-ALBA, SEEDLING GROWTH, VESICULAR-ARBUSCULAR MYCORRHIZAS, WATER RELATIONS

531
Diaz, S., and M. Cabido. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science 8(4):463-474.*

Plant functional types (PFTs) bridge the gap between plant physiology and community and ecosystem processes, thus providing a powerful tool in climate change research. We aimed at identifying PFTs within the flora of central-western Argentina, and to explore their possible consequences for ecosystem function. We analyzed 24 vegetative and regenerative traits of the 100 most abundant species along a steep climatic gradient. Based on plant traits and standard multivariate techniques, we identified eight PFTs. Our results confirmed, over a wide range of climatic conditions, the occurrence of broad recurrent patterns of association among plant traits reported for other floras; namely trade-offs between high investment in photosynthesis and growth on the one hand, and preferential allocation to storage and defence on the other. Regenerative traits were only partially coupled with vegetative traits. Using easily-measured plant traits and individual species cover in 63 sites, we predicted main community- ecosystem processes along the regional gradient. We hypothesized likely impacts of global climatic change on PFTs and ecosystems ill situ, and analysed their probabilities of migrating in response to changing climatic conditions. Finally, we discuss the advantages and limitations of this kind of approach in predicting changes in plant distribution and in ecosystem processes over the next century.

KEYWORDS: ATTRIBUTES, CLASSIFICATION, CO2- ENRICHMENT, COMMUNITIES, ECOLOGY, GROWTH RATE, RESPONSES, SEED SIZE, STRATEGIES, VEGETATION

532
Diaz, S., M. Cabido, M. Zak, E.M. Carretero, and J. Aranibar. 1999. Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science 10(5):651-660.*

This paper deals with theoretical concepts, methodological steps, and case studies related to the use of plant functional traits in the assessment of vegetation responses to climate and land use. Trait-environment links are considered, and special emphasis is put on the links between vegetation structure and ecosystem function, and on the role of disturbance history in determining vegetation responses to land use at present. As a basis for discussion, published and new case studies from central-western Argentina are presented. Similar plant traits measured with different levels of precision are utilized in the description of ecosystem structure in different land-use situations along a steep regional climatic gradient. The general protocol followed in the case studies represents a data-driven, non-hierarchical, low-tech approach, that can be applied to a wide range of spatial scales, from plots to regions. Climatic factors (including extreme events and seasonality), disturbance frequency and intensity, and disturbance history are suggested as key factors to be considered in global comparisons of vegetation responses to land use and in predictive models of ecosystem dynamics.

KEYWORDS: ATMOSPHERIC CO2, BIODIVERSITY, COMMUNITIES, GLOBAL CHANGE, GRASSLAND, VEGETATION

533
Diaz, S., L.H. Fraser, J.P. Grime, and V. Falczuk. 1998. The impact of elevated CO2 on plant-herbivore interactions: experimental evidence of moderating effects at the community level. *Oecologia 117(1-2):177-186.*

Surprisingly little research has been published on the responses to elevated [CO2] at the community level, where herbivores can select their preferred food. We investigated the combined effects of atmospheric [CO2] and herbivory on synthesised plant communities growing on soils of different fertility. Factorial combinations of two [CO2] (350 or 700 mu l l(-1)), two fertility (fertilised or non-fertilised), and two herbivory (herbivores present or absent) treatments were applied to a standard mixture of seven fast- and eight slow- growing plants in outdoor microcosms. The herbivores used were the grain aphid (Sitobion avenae) and the garden snail (Helix aspersa). We measured plant biomass, foliar nitrogen and soluble tannin concentration, aphid fecundity, and snail growth, fecundity, and feeding preferences over one growing season. Elevated [CO2] did not have a significant impact on(1)the combined biomass of fast-growing or slow-growing plants, (2) herbivore feeding preferences, or (3) herbivore fitness. There was, however, a significant biomass increase of Carex flacca (which represented in all cases less than 5% of total live biomass), and some chemical changes in unpalatable plants under elevated [CO2]. The herbivory treatment significantly increased the biomass of slow-growing plants over fast-growing plants, whereas fertilisation significantly increased the abundance of fast-growing plants over slow- growing plants. Predictions on the effects of elevated [CO2] based on published single-species experiments were not supported by the results of this microcosm study.

KEYWORDS: ATMOSPHERIC CO2, CALCAREOUS GRASSLAND, CARBON DIOXIDE, CHEMICAL-COMPOSITION, DECOMPOSITION, EXPERIMENTAL MICROCOSMS, INSECT HERBIVORE, PERFORMANCE, RELATIVE GROWTH-RATE, RESPONSES

534

Diaz, S., J.P. Grime, J. Harris, and E. McPherson. 1993. Evidence of a feedback mechanism limiting plant-response to elevated carbon-dioxide. *Nature 364(6438):616-617.*

IN short-term experiments under productive laboratory conditions, native herbaceous plants differ widely in their potential to achieve higher yields at elevated concentrations of atmospheric carbon dioxide1-8. The most responsive species appear to be large fast-growing perennials of recently disturbed fertile soils7,8. These types of plants are currently increasing in abundance9 but it is not known whether this is an effect of rising carbon dioxide or is due to other factors. Doubts concerning the potential of natural vegetation for sustained response to rising carbon dioxide have arisen from experiments on infertile soils, where the stimulus to growth was curtailed by mineral nutrient limitations2,3,10. Here we present evidence that mineral nutrient constraints on the fertilizer effect of elevated carbon dioxide can also occur on fertile soil and in the earliest stages of secondary succession. Our data indicate that there may be a feedback mechanism in which elevated carbon dioxide causes an increase in substrate release into the rhizosphere by non-mycorrhizal plants, leading to mineral nutrient sequestration by the expanded microflora and a consequent nutritional limitation on plant growth.

KEYWORDS: CO2- ENRICHMENT, ECOSYSTEMS, GROWTH, NUTRITION, POPULATIONS, SOIL, TUNDRA

535

Dickson, R.E., M.D. Coleman, D.E. Riemenschneider, J.G. Isebrands, G.D. Hogan, and D.F. Karnosky. 1998. Growth of five hybrid poplar genotypes exposed to interacting elevated CO2 and O-3. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28(11):1706-1716.*

A wide variety of hybrid poplar clones are being introduced for intensive culture biomass production, but the potential clonal or genotypic response to increasing tropospheric carbon dioxide (CO2), ozone (O-3), and their interactions are unknown. To study these effects, we exposed five different hybrid Populus clones to increased concentrations of CO2, O-3, and CO2 + O-3 in open-top chambers for one growing season and determined growth responses. Exposure to elevated CO2 increased height growth, dry mass, and basal area; exposure to O-3 decreased all three of these growth responses. Exposure impact differed among the different plant parts (leaf, stem, and roots) and among the crones. These differences were associated with different growth strategies or carbon allocation patterns inherent in the different clones. The fastest growing clones had the greatest response to O-3 treatment. The addition of CO2 to the O-3 exposure counteracted the negative impact of O-3 in all plant components except leaf mass (e.g., CO2 + O-3 plant mass equaled control plant mass) in all of the clones. But correspondingly, added O-3 negated increased growth from CO2. Genetic variation in response to atmospheric pollutants must be considered even in closely related genotypes found in Populus culture.

KEYWORDS: AIR-POLLUTION, ASPEN CLONES, ATMOSPHERIC CO2, BETULA-PUBESCENS EHRH, CARBON DIOXIDE, ESTABLISHMENT-YEAR, FOREST ECOSYSTEMS, PLANT GROWTH, POPULUS X EURAMERICANA, TROPOSPHERIC OZONE

536

Didham, R.K. 1998. Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia 116(3):397-406.*

The effects of forest fragmentation on leaf-litter decomposition rates were investigated for the first time in an experimentally fragmented tropical forest landscape in Central Amazonia. Leaf-litter decomposition rates were measured at seven distances (0-420 m) along forest edge-to-interior transects in two 100-ha fragments, two continuous forest edges, and at an identical series of distances along two deep continuous forest transects, as well as at the centers of two 1-ha and two 10-ha fragments. Decomposition rates increased significantly towards the edge of 100-ha forest fragments. Litter turnover times were 3-4 times faster within 50 m of the edge of 100-ha fragments than normally found in deep continuous forest. In contrast, there was no significant change in the rate of leaf-litter decomposition from the interior to the edge of continuous forest. It is difficult to account for these very different edge responses. Decomposition rates were not correlated with air temperature differentials, evaporative drying rates, litter depth, biomass or moisture content, or with total invertebrate densities, either within individual edge transects or across all sites. The difference in edge response may be due to chance, particularly the patchy removal of vast quantities of litter by litter-feeding termites, or may be a real, area-dependent phenomenon. Clearly, however, forest fragmentation increases the variability and unpredictability of litter decomposition rates near forest edges. In addition to edge effects, decomposition. rates were strongly affected by decreasing fragment area. While sites at the centers of 10-ha and 100-ha forest fragments and continuous forest had equivalent decomposition rates, rates were markedly lower at the centers of 1-ha fragments. Litter turnover times were 2-3 times slower in I-ha fragments than in continuous forest, and up to 13 times slower than at 100-ha edges. Litter structure and nutrient cycling dynamics are inevitably altered by forest fragmentation.

KEYWORDS: AMAZON, CLEAR-CUT, DECAY-RATES, DOUGLAS-FIR FOREST, ELEVATED CO2, GROWTH, LIGNIN CONTROL, NITROGEN, NUTRIENT DYNAMICS, RAIN FORESTS

537

Diemer, M.C., and C. Korner. 1996. Lifetime leaf carbon balances of herbaceous perennial plants from low and high altitudes in the central Alps. *Functional Ecology 10(1):33-43.*

1. A combination of demographic analysis of leaf growth, age- specific CO2 gas exchange and microclimate were employed to calculate lifetime sums of net photosynthesis and dark respiration, in order to obtain leaf carbon balances (Q(c)) of altitudinally disjunct Ranunculus and Geum species, as well as two altitudinal populations of Potentilla crantzii. If carbon costs for construction of leaf tissue are included, leaves fixed a lifetime carbon surplus ranging from 0.4 to 2.0 mmol CO2 cm(-2) independent of altitude, thereby exceeding initial investments by the plant three- to sixfold. 2. The lack of a consistent difference between the Q(c) of high and related low elevation taxa with similar leaf area ratios (LAR) challenges the view that carbon gain impairs growth and persistence of herbaceous perennials in harsh alpine climates to a greater extent than at low elevation. 3. Evidence from a sensitivity analysis of our carbon balance model as well as rank correlations indicate that the primary determinant of a leaf's carbon balance is its longevity. A comparison of leaf carbon balance data from the literature on wild plants of the temperate zone suggests that daily carbon gain on a leaf area basis is higher in herbaceous plants, compared to deciduous woody shrubs, which could explain the predominance of the herbaceous growth form at high altitudes.

KEYWORDS: COST, LONGEVITY, PHOTOSYNTHETIC CHARACTERISTICS, SEASONAL-CHANGES, SHRUB, SPANS

538

Diemer, M. 1992. Population-dynamics and spatial arrangement of ranunculus- glacialis L, an alpine perennial herb, in permanent plots. *Vegetatio 103(2):159-166.*

In 1986 sixteen permanent plots (625 cm2 each) were established in scree slopes dominated by Ranunculus glacialis at Mt. Glungezer, Austria (2600 m elevation) in order to document the population dynamics of herbaceous perennials near the upper altitudinal limits of plant existence. The abundance and sizes of individual R. glacialis shoots, their leaf numbers and reproductive status were evaluated over a 6-year period. On South-facing slopes the population sizes of adult and juvenile shoots remained constant over the years, while seedling numbers fluctuated significantly. Overall density of all developmental stages of R. glacialis was significantly lower on North-facing slopes and year-to-year fluctuations were greater, than on thermally-favorable Southern slopes. The spatial pattern of adult shoots and seedlings was clumped, while juvenile shoots had a random or clumped distribution. Fertilization had no effects on population dynamics. Proposed greenhouse effects, e.g. increases in CO2 and temperature, should result in population growth on North-facing slopes and may increase mortality on South-facing sites.

KEYWORDS: AREA, FINNISH LAPLAND, PLANTS

539

Diemer, M.W. 1994. Mid-season gas-exchange of an alpine grassland under elevated co2. *Oecologia 98(3-4):429-435.*

Ecosystem net CO2 uptake, evapotranspiration (ET) and night- time CO2 efflux were measured in an alpine grassland dominated by Carex curvula, treated with doubled ambient partial pressure of CO2 via open-top chambers. One quarter of the plots were treated with mineral nutrients to simulate the effect of lowland nitrogen deposition rates. Depending upon fertilizer supply, ecosystem net CO2 uptake per ground area in full sunlight (NCE(max)) was 41-81% higher in open-top chambers supplied with doubled ambient partial pressure (p(a)) of CO2 than in plots receiving ambient CO2. Short-term reversals of the CO2 level suggest that the extent of downward adjustment of canopy photosynthesis under elevated CO2 was 30-40%. ET tended to decline, while water use efficiency (WUE), expressed as the NCE(max):ET ratio, increased more than twofold under elevated CO2. Night-time ecosystem CO2 efflux did not respond to changes in CO2 p(a). NCE(max) and night-time CO2 efflux were more responsive to mineral fertilizer than the doubling of CO2. This suggests that in these alpine plant communities, atmospheric nutrient input may induce equal or greater effects on gas exchange than increased CO2.

KEYWORDS: ATMOSPHERIC CO2, BALANCE, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, RESPONSES, TUSSOCK TUNDRA

540

Diemer, M. 1996. The incidence of herbivory in high-elevation populations of Ranunculus glacialis: A re-evaluation of stress-tolerance in alpine environments. *Oikos 75(3):486-492.*

Growing conditions in the upper alpine zone are characterized by low temperature, low partial pressures of CO2 and, in the temperate zone, a short growing period. The plants which have evolved under these conditions presumably share a number of characteristics that were ascribed to stress-tolerance, namely slow growth, extended longevity, resource limitation and low palatability to herbivores. Hence chronic biomass removals by herbivores should be a threat to plant persistence in alpine environments. as predicted by Grime's C-S-R theory. I tested this hypothesis on populations of an alpine buttercup, Ranunculus glacialis. A survey along an altitudinal transect in the Central Alps of Austria indicated that between 15 and 26% of the R. glacialis plants in each population examined exhibited signs of herbivory damage. Merely a small population, isolated by glaciers, at the highest site (3310 m a.s.l.) showed no traces of herbivory. Ar two sites (2600 m and 3180 m a.s.l.) twenty plants each were tagged and examined for a two- year period. Herbivory damage was considerable: on an average nearly 25% of a plant's total leaf area was removed in 1987. primarily by snow mice (Microtus nivalis). Inflorescences of 65-85% of all flowering plants were removed as well. Ar the lower sire (2600 m, roughly 600 m above the treeline) up to 5 g dry matter and 140 mg nitrogen m(-2) were consumed in one season. Despite the magnitude of these losses both reproductive investment and the number of leaves initiated per plant did not change appreciably in the subsequent year. Since populations of R. glacialis are able to support populations of herbivores at the altitudinal limits of plant growth without obvious reductions in vigor,these plants and other food species (e.g. Oxyria digyna) cannot fit the stress-tolerator scheme proposed by Grime. The widespread occurrence of herbivory at high elevations and plant traits challenge the concept of stress- tolerance as it is commonly applied to alpine environments.

KEYWORDS: AVAILABILITY, DYNAMICS, GRADIENTS, HERB, LEAF, LIFE, PLANTS, SEED, ZONE

541

Diemer, M. 1997. Effects of elevated CO2 on gas exchange characteristics of alpine grassland. *Acta Oecologica-International Journal of Ecology 18(3):177-182.*

The ecosystem-level gas exchange characteristics of an alpine grassland treated with a combination of elevated CO2 and moderate additions of NPK fertilizer during the third season of experimental treatments are described. Mid-season maximum daytime net ecosystem CO2 flux (NEC)increased significantly under elevated CO2 (+45%), whereas nighttime NEC was unaffected by the CO2 treatment. Since daytime NEC under elevated CO2 underwent a seasonal decline, only moderate carbon surpluses accumulated under elevated CO2. The observed seasonal decline in daytime NEC may be due to reduced sink strength once maximum aboveground biomass is attained, and appears to be a reg ulatory mechanism of ecosystem carbon accumulation. Moderate additions of NPK fertilizer stimulated both day- (+39%) and nighttime NEC (+29%) due to increased plant biomass, independent of CO2 treatment. Yet there is no indication that enhanced mineral nutrient

status will increase ecosystem responsiveness to elevated CO2.

KEYWORDS: CARBON BALANCE

542

Diemer, M., and C. Korner. 1998. Transient enhancement of carbon uptake in an alpine grassland ecosystem under elevated CO2. *Arctic and Alpine Research 30(4):381-387.*

We investigated the carbon uptake and release of a Central European alpine grassland community subjected to doubled ambient CO2 during the third (1994) and fourth (1995) season of CO2 enrichment. Within this period net carbon uptake under elevated CO2 declined successively, providing evidence of carbon saturation in this high-elevation environment. Third year data were used to calculate a CO2 balance for the 13-wk growing season and indicated that the grassland still served as net carbon sink in 1994. Integrated over the growth period, plots exposed to doubled ambient CO2 fixed 22% more CO2 than control treatments receiving ambient CO2. Increased carbon uptake under elevated CO2 was entirely due to a stimulation of daytime net CO2 uptake, since nighttime CO2 release remained unaffected. However, enhancement of net canopy CO2 uptake showed a distinct seasonal response: following substantial net CO2 gains from snowmelt until attainment of peak biomass (ca. 6 wk), the relative effect of elevated CO2 declined over the remainder of the season. In contrast to controls, the C balance became negative under CO2 enrichment during the final weeks of the growth period. Estimates of wintertime respiratory CO2 losses of unfertilized plots (ca, 9 mo during which soils remain thawed under the snow) indicate a release of 73 to 89% of the amount of CO2 fixed during the snow-free period. Under elevated CO2 an estimated mean surplus of 41 g C m(-2) accreted during the third year of CO2 enrichment, which we hypothesize must been transferred belowground, since aboveground biomass remained unchanged. Moderate additions of mineral fertilizer (NPK) alone had a strong positive effect on seasonal net CO2 balance (57% increase) mediated by enhanced plant biomass. NPK- treated plots under elevated CO2 had a 38% higher seasonal CO2 balance, relative to NPK-plots at ambient CO2 concentration. Fourth-year (1995) data indicate no further stimulation of daytime net ecosystem CO2 flux under elevated CO2, both in unfertilized plots and plots treated with NPK. Hence, it is unlikely that alpine grasslands will serve as carbon sinks in a CO2-rich world in the long term.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE, ENRICHMENT, ENVIRONMENTAL-CHANGE, GAS-EXCHANGE, GROWTH, HIGH-ALTITUDES, PLANTS, RESPONSES, TUSSOCK TUNDRA

543

Dietz, T., and E.A. Rosa. 1997. Effects of population and affluence on CO2 emissions. *Proceedings of the National Academy of Sciences of the United States of America 94(1):175-179.*

We developed a stochastic version of the Impact = Population Affluence Technology (IPAT) model to estimate the effects of population, affluence, and technology on national CO2 emissions. Our results suggest that, for population, there are diseconomies of scale for the largest nations that are not consistent with the assumption of direct proportionality (log- linear effects) common to most previous research. In contrast, the effects of affluence on CO2 emissions appear to reach a maximum at about $10,000 in per-capita gross domestic product and to decline at higher levels of affluence. These results confirm the general value of the IPAT model as a starting point for understanding the anthropogenic driving forces of global change and suggest that population and economic growth anticipated over the next decade will exacerbate greenhouse gas emissions.

KEYWORDS: ECONOMIC-GROWTH, ENVIRONMENTAL-QUALITY, ROBUST

544

Diiorio, A.A., R.D. Cheetham, and P.J. Weathers. 1992. Carbon-dioxide improves the growth of hairy roots cultured on solid medium and in nutrient mists. *Applied Microbiology and Biotechnology 37(4):463-467.*

The effect of varying CO2 concentrations on the growth of beet and safflower hairy roots was measured for tissues cultured in nutrient mists and on solid media in chambers fed mixtures of humidified air supplemented with different CO2 concentrations. Hairy root tissue grown on solid media in air enriched with CO2 showed increased growth, as measured by dry weight increases vs air-fed controls. Growth increased with CO2 enrichment as much as 2.5 times more than the air-fed control for safflower at 1.0 % CO2 and 1.4 times more than the air-fed control for beets at 1.5 % CO2 over a 12-day period. Beet hairy root tissue was also cultured aeroponically in nutrient mists. Beet hairy root cultured in nutrients mists enriched with 1.0 % CO2 showed a 15 % increase in biomass over a 7-day period vs tissue cultured in nutrient mists (with ambient air) or in shake flasks. The stimulation of root growth via CO2 enrichment reduced the time required for biomass accumulation.

KEYWORDS: ACID

545

Dijkstra, P., A.H.M.C. Schapendonk, K. Groenwold, M. Jansen, and S.C. Van de Geijn. 1999. Seasonal changes in the response of winter wheat to elevated atmospheric CO2 concentration grown in Open-Top Chambers and field tracking enclosures. *Global Change Biology 5(5):563-576.*

Winter wheat was grown at ambient and elevated (ambient plus 350 mu L L-1) CO2 concentrations in open top chambers and in field-tracking sun-lit climatized enclosures (elevated is 718 mu L L-1). There was no significant effect of CO2 concentration on sheath, leaf and root biomass and leaf area in the early spring (January to April). 24-h canopy CO2 exchange rate (CCER) was not significantly affected either. However, elevated CO2 concentration increased CCER at midday, decreased evapotranspiration rate and increased instantaneous water-use-efficiency during early spring. Leaf, sheath and root nitrogen concentration per unit dry weight decreased and nonstructural carbohydrate concentration increased under elevated CO2, and N-uptake per unit ground area decreased significantly (-22%) towards the end of this period. These results contrast with results from the final harvest, when grain yield and biomass were increased by 19% under elevated CO2. N concentration per dry weight was reduced by 5%, but N-uptake per unit ground area was significantly higher (+11%) for the elevated CO2 treatment. 24-h and midday-CCER increased significantly more in late spring (period of 21 April to 30 May) (respectively by + 40% and 53%) than in the early spring (respectively 5% and 19%) in response to elevated CO2. Midday evapotranspiration rate was reduced less by elevated CO2 in the late spring (-13%) than in early spring (-21%). The CO2 response of midday and 24-h CCER decreased again (+ 27% and + 23% resp.) towards the end of the growing season. We conclude that the low response to CO2 concentration during the early spring was associated with a growth-restriction, caused by low temperature and irradiance levels. The reduction of nitrogen concentration, the increase of nonstructural carbohydrate, and the lower evapotranspiration indicated that CO2 did have an effect towards the end of early spring; but not on biomass accumulation. Regression analysis showed that both irradiance and temperature affected the response to CO2.

KEYWORDS: ACCLIMATION, C-3, CARBON DIOXIDE,

CARBOXYLASE-OXYGENASE, ENRICHMENT, LOLIUM-PERENNE, TEMPERATURE, TRITICUM-AESTIVUM L, WATER-USE EFFICIENCY, YIELD

546

Ding, L., C.H. Zhang, K.Z. Bai, and T.Y. Kuang. 1997. Relation between seed size in different plant species and response of their seedlings to double CO2. *Chinese Science Bulletin 42(4):331-333.*

547

Dippery, J.K., D.T. Tissue, R.B. Thomas, and B.R. Strain. 1995. Effects of low and elevated co2 on C-3 and C-4 annuals .1. Growth and biomass allocation. *Oecologia 101(1):13-20.*

In order to study C-3 and C-4 plant growth in atmospheric CO2 levels ranging from past through predicted future levels, Abutilon theophrasti (C-3) and Amaran thus retroflexus (C-4) were grown from seed in growth chambers controlled at CO2 partial pressures of 15 Pa (below Pleistocene minimum) 27 Pa (pre-industrial), 35 Pa (current) and 70 Pa (predicted future). After 35 days of growth, CO2 had no effect on the relative growth rate, total biomass or partitioning of biomass in the C-4 species. However, the C-3 species had greater biomass accumulation with increasing CO2 partial pressure. C-3 plants grown in 15 Pa CO2 for 35 days had only 8% of the total biomass of plants grown in 35 Pa CO2. In 15 Pa CO2, C-3 plants had lower relative growth rates and lower specific leaf mass than plants grown in higher CO2 partial pressures, and aborted reproduction. C-3 plants grown in 70 Pa CO2 had greater root mass and root-to-shoot ratios than plants grown in lower CO2 partial pressures. These findings support other studies that show C-3 plant growth is more responsive to CO2 partial pressure than C-4 plant growth. Differences in growth responses to CO2 levels of the Pleistocene through the future suggest that competitive interactions of C-3 and C-4 annuals have changed through geologic time. This study also provided evidence that C-3 annuals may be operating near a minimum CO2 partial pressure for growth and reproduction at 15 Pa CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COMPETITION, ENRICHMENT, PERENNIALS, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, SUBAMBIENT

548

Dixon, M., D. Lethiec, and J.P. Garrec. 1995. The growth and gas-exchange response of soil-planted norway spruce [picea-abies (L) karst] and red oak (quercus-rubra L) exposed to elevated co2 and to naturally-occurring drought. *New Phytologist 129(2):265-273.*

Norway spruce and red oak trees were planted directly into the soil and exposed to 700 mu mol mol(-1) CO2 in open-top chambers. There were large inter-specific differences in response to naturally occurring drought during the second pear of exposure to elevated CO2. Both species had decreased assimilation rates. CO2-treated red oak had no loss of photosynthetic enhancement when undroughted, whereas CO2- treated Norway spruce showed a relative increase in assimilation rates only when droughted. The effect of CO2 on radial growth of both species was less marked in the second growing season, but this may have been a result of different biomass partitioning as Norway spruce shoot extension had a different pattern of growth in elevated CO2. Stomatal density and chlorophyll content were largely unaffected by the CO2 treatment. A precise method for measuring Norway spruce needle surface area was also developed.

KEYWORDS: ENHANCEMENT, ENRICHMENT, INCREASE, LIMITATIONS, PHOTOSYNTHESIS, SEEDLINGS, SITCHENSIS BONG CARR, STOMATAL DENSITY, WATER-STRESS

549

Dixon, R.K. 1995. Agroforestry systems - sources or sinks of greenhouse gases. *Agroforestry Systems 31(2):99-116.*

The prominent role of forestry and agroforestry systems in the flux and long-term storage of carbon (C) in the terrestrial biosphere has increased global interest in these land-use options to stabilize greenhouse gas (GHG) emissions. Preliminary assessments suggest that some agroforestry systems (e.g., agrosilvicultural) can be CO2 sinks and temporarily store C, while other systems (e.g., ruminant-based silvopastoral systems) are probably sources of GHG (e.g., CH4). Agroforestry;systems can be significant sources of GHG emissions, especially at low latitudes. Practices such as tillage, burning, manuring, chemical fertilization, and frequent disturbance can lead to emission of CO2, CH4, and N2O from soils and vegetation to the atmosphere. Establishment and management of agroforestry systems incompatible with prevailing edaphic and climatic conditions can accelerate soil GHG emissions. Non-sustainable agroforestry systems are quickly degraded, and woody and herbaceous crops can become significant GHG sources. Silvopastoral systems can result in soil compaction and erosion with significant loss of labile C and N compounds to the atmosphere. Ruminant-based silvopastoral systems and rice paddy agrisilvicultural systems are well documented sources of CH4 which significantly contribute to the global CH4 budget. Early assessments of national and global terrestrial CO2 sinks reveal two primary beneficial attributes of agroforestry systems: 1) direct near-term C storage (decades to centuries) in trees and soils, and, 2) potential to offset immediate GHG emissions associated with deforestation and subsequent shifting agriculture. Within the tropical latitudes, it is estimated that one ha of sustainable agroforestry can provide goods and services which potentially offset 5-20 ha of deforestation. At a global scale, agroforestry systems could potentially be established on 585-1275 x 10(6) ha of technically suitable land, and these systems could store 12-228 (median 95) Mg C ha(-1) under current climate and edaphic conditions.

550

Dixon, R.K., S. Brown, R.A. Houghton, A.M. Solomon, M.C. Trexler, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science 263(5144):185-190.*

Forest systems cover more than 4.1 x 10(9) hectares of the Earth's land area. Globally, forest vegetation and soils contain about 1146 petagrams of carbon, with approximately 37 percent of this carbon in low-latitude forests, 14 percent in mid-latitudes, and 49 percent at high latitudes. Over two- thirds of the carbon in forest ecosystems is contained in soils and associated peat deposits. In 1990, deforestation in the low latitudes emitted 1.6 +/- 0.4 petagrams of carbon per year, whereas forest area expansion and growth in mid- and high- latitude forest sequestered 0.7 +/- 0.2 petagrams of carbon per year, for a net flux to the atmosphere of 0.9 +/- 0.4 petagrams of carbon per year. Slowing deforestation, combined with an increase in forestation and other management measures to improve forest ecosystem productivity, could conserve or sequester significant quantities of carbon. Future forest carbon cycling trends attributable to losses and regrowth associated with global climate and land-use change are uncertain. Model projections and some results suggest that forests could be carbon sinks or sources in the future.

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, CLIMATE CHANGE, CO2 CONCENTRATION, ELEVATED CO2, INCREASING CO2, STORAGE, TRANSIENT-RESPONSE, TROPICAL FORESTS, UNITED-STATES

551

Dixon, R.K., J.B. Smith, S. Brown, O. Masera, L.J. Mata, and I.

Buksha. 1999. Simulations of forest system response and feedbacks to global change: experiences and results from the US Country Studies Program. *Ecological Modelling 122(3):289-305.*

Large shifts in the response and feedbacks of forest systems are implied by models and systems analysis driven by global change scenarios of general circulation models (GCMs). Prior climate change analyses and modeling efforts have been reported at a global scale in a few developed countries, but relatively few national assessments have been successfully completed in developing countries. Under the auspices of the U.S. Country Studies Program, analysts from 55 countries employed a common set of methods and models to characterize current carbon (C) pools in forests, future impacts of global change on forest distribution, and management options for conserving and sequestering carbon dioxide (CO2) in forest systems. The analysis revealed that the response and feedbacks of forest systems to global climate change will be profound in the 55 countries studied on five continents. Globally, forest vegetation and soils contain about 1146 Pg C, with approximately 37% of this C in low-latitude forests, 14% in mid-latitudes, and 49% at high latitudes. The impacts of future global change on forest distribution and productivity will be most significant at high latitudes, with more modest changes in distribution and productivity at low latitudes. Future opportunities to conserve and sequester CO2 in forest systems are potentially significant, but land-use practices and global change will influence the size of this C pool and CO2 sink. In the future, a greater proportion of forests at all latitudes could become a greenhouse gas (GHG) source if sustained management and conservation policies are not employed. The timing and magnitude of future changes in forest systems are dependent on global environmental factors (for example, global change, biogeochemical Sulphur and Nitrogen cycles), as well as on human factors such as demographics, economic growth, technology, and resource management policies.

KEYWORDS: AGROFOREST MANAGEMENT-PRACTICES, ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, BUDGET, CO2-INDUCED CLIMATE CHANGE, EMISSIONS, MODEL, SENSITIVITY, STORAGE, TRANSIENT-RESPONSE

552

Dixon, R.K., J.K. Winjum, and P.E. Schroeder. 1993. Conservation and sequestration of carbon - the potential of forest and agroforest management-practices. *Global Environmental Change-Human and Policy Dimensions 3(2):159-173.*

Forests play a major role in Earth's carbon cycle through assimilation, storage, and emission of CO2. Establishment and management of boreal, temperate, and tropical forest and agroforest systems could potentially enhance sequestration of carbon in the terrestrial biosphere. A biological and economic analysis of forest establishment and management options from 94 nations revealed that forestation, agroforestry, and silviculture could be employed to conserve and sequester one Petagram (Pg) of carbon annually over a 50-year period. The marginal cost of implementing these options to sequester 55 Pg of carbon would be approximately $10/Mg.

553

Dixon, R.K., and J. Wisniewski. 1995. Global forest systems: An uncertain response to atmospheric pollutants and global climate change? *Water, Air, and Soil Pollution 85(1):101-110.*

Forest systems cover more than 4.1 x 10(9) ha of the Earth's land area. The future response and feedbacks of forest systems to atmospheric pollutants and projected climate change may be significant. Boreal, temperate and tropical forest systems play a prominent role in carbon (C), nitrogen (N) and sulfur (S) biogeochemical cycles at regional and global scales. The timing and magnitude of future changes in forest systems will depend on environmental factors such as a changing global climate, an accumulation of CO2 in the atmosphere, and increase global mineralization of nutrients such as N and S. The interactive effects of all these factors on the world's forest regions are complex and not intuitively obvious and are likely to differ among geographic regions. Although the potential effects of some atmospheric pollutants on forest systems have been observed or simulated, large uncertainty exists in our ability to project future forest distribution, composition and productivity under transient or nontransient global climate change scenarios. The potential to manage and adapt forests to future global environmental conditions varies widely among nations. Mitigation practices, such as liming or fertilization to ameliorate excess NOx or SOx or forest management to sequester CO2 are now being applied in selected nations worldwide.

KEYWORDS: CARBON, ECOSYSTEMS, ELEVATED CO2, NITROGEN DEPOSITION, SINK

554

Docherty, M., D.K. Hurst, J.K. Holopainen, J.B. Whittaker, P.J. Lea, and A.D. Watt. 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology 2(4):335-341.*

The phenology of Fagus sylvatica was unaffected by exposure to an atmosphere of elevated CO2 (600 mu L L(-1)) after two years of fumigation. Non-significant changes in nitrogen and phenolic content of the leaves decreased the nutritional status of beech for female larvae in elevated CO2 such that they responded by eating in a compensatory manner; males were unaffected. Rates of development, mortality and adult biomass of Rhynchaenus fagi were no different from those in ambient CO2 concentrations (355 mu L L(-1)). It is possible that, with the changes in leaf chemistry affecting the females, fecundity will be altered, with important consequences for populations of beech weevil.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, GROWTH, INSECT HERBIVORE INTERACTIONS, LEAF-MINER, PICEA-SITCHENSIS, RESPONSES, RHYNCHAENUS-FAGI, SITKA SPRUCE, WINTER MOTH

555

Docherty, M., F.A. Wade, D.K. Hurst, J.B. Whittaker, and P.J. Lea. 1997. Responses of tree sap-feeding herbivores to elevated CO2. *Global Change Biology 3(1):51-59.*

Five species of sap-feeding homoptera were studied on Fagus sylvatica and Acer pseudoplatanus and exposed to elevated concentrations of carbon dioxide (600 mu L L(-1)). The concentration of total soluble amino acids in foliage of F. sylvatica was unaffected by growing saplings in elevated atmospheric CO2 concentrations. Although experiments on individual aphids indicated poorer performance of Phyllaphis fagi (fewer, smaller nymphs produced), resultant populations did not differ from those in ambient (350 mu L L(-1)) conditions. The area of beech foliage stippled by the leafhopper Fagocyba cruenta was similar at ambient and elevated CO2 concentrations. The concentration of total amino acids and that of serine of A. pseudoplatanus foliage were significantly lower at elevated CO2 concentrations. However, the relative growth rates of two aphid species Drepanosiphum platanoidis and Periphyllus testudinaceus and one leafhopper Ossiannilssonola callosa were not significantly different in elevated CO2. No evidence was found that, under the conditions of these experiments, populations of aphids and leafhoppers will change as concentrations of CO2 increase.

KEYWORDS: AIR-POLLUTION, CARBON DIOXIDE, GROWTH,

INFESTATION, INSECT PERFORMANCE, PHLOEM SAP, PLANTS, POPULATIONS, REPRODUCTIVE ACTIVITY, SYCAMORE APHID

556

Doi, M., H. Oda, N. Ogasawara, and T. Asahira. 1992. Effects of co2 enrichment on the growth and development of invitro cultured plantlets. *Journal of the Japanese Society for Horticultural Science 60(4):963-970.*

Plantlets of Caladium bicolor (C3 plant), Saccharum officinarum (C4 plant), and Phalaenopsis hybrid (CAM plant) at the preparation stage for acclimatization (the final stage of in vitro culture) were cultured on the medium containing 2% sucrose. The culture vessels were kept under continuous, 16 hr, or 8 hr lighting conditions; half of the vessels were ventilated continuously with 0.8 +/- 0.4% CO2 enriched atmosphere; while the remainder was exposed to ambient atmosphere. The growth of plantlets was promoted with an increase in daylength under both ambient and CO2 enriched atmospheres. When the plantlets were supplied with adequate CO2, dry matter production increased under all daylength treatments except Caladium cultured under continuous lighting. This promotive effect of CO2 enrichment was especially noticeable in root growth. In Caladium and Phalaenopsis, the leaf chlorophyll content of plantlets cultured under CO2 enriched atmosphere was less than that of leaves from plantlets grown in ambient atmosphere. Although the chlorophyll was less concentrated in leaves of plantlets growing under the CO2 enriched treatment, the rate of CO2 uptake of these plantlets measured at the midpoint of the light period was higher than that of leaves exposed to ambient atmosphere. Increasing the O2 concentration in culture vessels to 37% also promoted the growth of Caladium and Dendrobium phalaenopsis (CAM plant) under CO2 enriched condition. Because of the development of photoautotrophy, the Caladium plantlets exposed to enriched CO2 atmosphere and cultured on sugar-free medium using ceramic wool plug system responded with vigorous growth when transplanted into pots.

557

DolcetSanjuan, R., E. Claveria, and A. Huerta. 1997. Androgenesis in Capsicum annuum L - Effects of carbohydrate and carbon dioxide enrichment. *Journal of the American Society for Horticultural Science 122(4):468-475.*

A new and simple protocol for androgenesis in bell pepper is described. The initial medium, a modification of Nitsch and Nitsch's H medium, consisted of a two-phase system of semi- solid and liquid medium and contained maltose as carbon source. The total number of embryos formed was greater with maltose at 40 g . L-1, but embryos developed better at 10 to 20 g . L-1. Depending on the genotype, the number of embryos and plants recovered ranged from 3 to 750 and 0.25 to 8, respectively, per 100 flowers. Further increases in the number of embryos (up to 3561 per 100 flowers) and plants (up to 23 per 100 flowers) could be attained by flushing cultures with air enriched with CO2 at 900 mu L . L-1. The ploidy level and the microspore origin of the recovered plants were determined by flow cytometry and zymograms for isocitrate dehydrogenase. Nearly 65% of the acclimated plants had undergone spontaneous doubling of the chromosome number, as confirmed by flow cytometry of leaf nuclei. Isocitrate dehydrogenase zymograms demonstrated that plants originated from microspores and that the two parental alleles were equally represented among the haploid and dihaploid plants.

KEYWORDS: ACTIVATED-CHARCOAL, ANTHER-CULTURE RESPONSE, GENETIC-MARKERS, HORDEUM VULGARE L, INDUCTION, INHERITANCE, MEDIA, PEPPER, PLANTS, SEGREGATION

558

Donnelly, A., M.B. Jones, J.I. Burke, and B. Schnieders. 1999. Does elevated CO2 protect grain yield of wheat from the effects of ozone stress? *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 54(9-10):802-811.*

This study has investigated the effects of elevated CO2 and elevated O-3, both singly and in combination, on the yield of spring wheat (Triticum aestivum L., cv. Minaret). Plants were grown in open-top chambers and exposed to three CO2 concentrations (ambient, 510 and 680 ppmv) and two O-3 concentrations (ambient and ambient +50 or +90 ppbv) either from anthesis onwards or for the full growing season. To date, experiments that have investigated the interactive effects of these gases have shown a variety of responses, ranging from an amelioration of the damaging effects of high O-3 to a greater sensitivity to O-3, at elevated CO2. The effects on grain yield and yield components were determined. Our results confirm that elevated CO2 provides some protection to a wheat crop against the damaging effects of O-3 On grain yield. However, the level of protection varies from one growing season to the next and also appears to be related particularly to the timing of exposure to elevated O-3.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, LEAF-AREA, OPEN-TOP CHAMBERS, PLANT GROWTH, SPRING WHEAT, TRITICUM-AESTIVUM L, TROPOSPHERIC OZONE, WATER-STRESS

559

Dorais, M., J. Charbonneau, and A. Gosselin. 1993. Gas-exchange in greenhouse tomatoes grown under supplemental light. *Canadian Journal of Plant Science 73(2):577-585.*

This study reports on in situ gas-exchange measurements in tomatoes grown under a sequential intercropping system with supplemental lighting provided by high-pressure sodium-vapour lamps. A supplemental photosynthetic photon flux (PPF) of 150 mumol m-2 s-1 significantly increased the amount of light energy penetrating the canopy of intercropped tomato seedlings. During the day, the supplemental 150 mumol m-2 s-1 light regime increased the photosynthetic rate of leaves 5 and 10 by 67%, while at night the increases were 93 and 12%, respectively. Regression analysis of the photosynthetic rate of leaves 5 and 10 as a function of PPF received accounts for 58 and 45% of the variation, respectively. Hierarchical analysis demonstrated a significant linear relationship between PPF received during the day and photosynthetic activity of leaves 5 and 10 accounting for 46 and 28%, respectively, of the variance in the model. Regression analysis of the photosynthetic activity as a function of PPF received at night accounts for 41 and 32 %, respectively, of the variation in the photosynthetic rate of leaves 5 and 10. Using a high level of supplemental lighting during the day or at night had no significant effect on stomatic conductance or on the transpiration rate of leaves.

KEYWORDS: CO2- ENRICHMENT, LEAF, PHOTOINHIBITION, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSPIRATION, TRANSPORT, YIELD

560

Downing, J.P., and D.A. Cataldo. 1992. Natural sinks of co2 - technical synthesis from the palmas-del- mar workshop. *Water, Air, and Soil Pollution 64(1-2):439-453.*

Natural CO2 sinks in terrestrial and marine environments are important components of the global carbon cycle, yet the sign and magnitudes of key fluxes among them are unknown. The results of the Palmas Del Mar Workshop - Natural Sinks of CO2 presented in this special issue and its companion hard-bound volume of Water, Air, & Soil Pollution, provide

a synthesis of current research on the carbon cycle, CO2 sinks and associated processes and fluxes, and critical research needs to assess the potential role of forest and land-use management in carbon sequestration. The papers in this volume present data, observations, and model simulations that demonstrate: 1) the existence of natural CO2 sinks that could mitigate a significant amount of CO2 emissions from fossil-fuel combustion; 2) probable, human-caused imbalances in C exchanges among vegetation, soils, and the atmosphere; 3) enhanced C storage in vegetation in response to excess atmospheric CO2; 4) strong interactions among carbon, nutrient and hydrological cycles; and 5) an excess of carbon production over consumption in several, large managed forests. Although it appears unlikely that the search for the "missing" C sink required to balance the C budget will end in the open ocean, new estimates of C storage in mangrove wood and peat, suggest that coastal ecosystems have the capacity to store significant amounts of carbon in vegetation and sediments. Convincing analyses are also presented indicating the technical and economical feasibility of managing existing lands to sequester additional carbon. Long-term field studies of CO2 fertilization effects and carbon cycling by plants and soils in geographically important systems, native forests, and coastal ecosystems will go a long way toward meeting the research needs identified at the workshop.

KEYWORDS: MODEL, OCEAN

561

Downton, W.J.S., and W.J.R. Grant. 1994. Photosynthetic and growth-responses of variegated ornamental species to elevated co2. *Australian Journal of Plant Physiology 21(3):273-279.*

Variegated and completely green cultivars of oleander (Nerium oleander L.) and willow myrtle (Agonis flexuosa (Willd.) Sweet) were grown in controlled environment cabinets for 3 and 5 months, respectively, under either ambient levels of CO2 or with supplementary CO2 to a partial pressure of 800 mu bar. Photosynthesis of entirely green leaves and the green portions of variegated leaves on both species was greatly stimulated by high CO2 and there was no evidence of downward adjustment (acclimation) of photosynthetic rates to high CO2 during the experiment. Dark respiration rates of these leaves were lowered by high CO2. The yellow portions of willow myrtle leaves showed a low level of photosynthetic activity which was stimulated by high CO2; however, dark respiration rates showed little response to elevated CO2. Green and yellow areas on variegated leaves of willow myrtle had much lower dark respiration rates than completely green leaves, but this difference was not evident for oleander. Yellow portions of oleander leaves showed little evidence of photosynthetic capacity. This was also confirmed by a low photochemical efficiency as determined by chlorophyll fluorescence. A major effect of variegation was to slow overall plant growth compared with completely green plants. The respective 3-fold and 6-7-fold differences in biomass between fully green and variegated cultivars of oleander and willow myrtle was closely related to estimated net carbon gain per day by the plant canopy. Variegation for both species averaged close to 50:50, green:yellow areas. Variegated plants developed about twice the leaf area ratio and specific leaf area compared with their completely green counterparts. The relative growth response to high CO2 was significantly greater for the variegated plants compared to the completely green plants.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DARK RESPIRATION, LEAVES, PLANTS

562

Drake, B.G. 1992. A field-study of the effects of elevated CO2 on ecosystem processes in a Chesapeake Bay wetland. *Australian Journal of Botany 40(4-5):579-595.*

Open top chambers are being used in a long-term project to determine the effects of elevated CO2 on ecosystem processes on a Chesapeake Bay wetland. Three communities are studied: mono-specific stands of the C3 sedge, Scirpus olneyi, and the C4 grass, Spartina patens, and a mixed community of these two species and the C4 grass, Distichlis spicata. Treatment began in the spring of 1987 and will continue through the 1994 growing season. During the first 4 years of exposure, elevated CO2 had the following effects on mono-specific stands of the C3 sedge, Scirpus olneyi: increased quantum yield and photosynthetic capacity, reduced dark respiration, increased numbers of shoots, roots and rhizomes, reduced nitrogen concentration of all tissues, increased nitrogen fixation and increased ecosystem carbon accumulation. In a mixed community of the sedge and C4 grass species, Spartina patens and Distichlis spicata, biomass of the C3 component increased over 100% and this was accompanied by decreased biomass in the C4 component of the community. Elevated CO2 reduced water loss, increased water potential and delayed senescence in all three species. Many factors contributed to CO2 stimulated carbon accumulation in the plant community dominated by the C3 sedge, Scirpus olneyi, including: sustained high photosynthetic capacity, decreased respiration, delayed senescence, and allocation of the additional carbon to roots and rhizomes. The complex interaction of these diverse responses suggests that the rising atmospheric CO2 may have a significant impact on ecosystem processes.

KEYWORDS: ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE ENRICHMENT, ELECTRON-TRANSPORT CAPACITY, ESTUARINE MARSH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE 1;5-BISPHOSPHATE, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES

563

Drake, B.G. 1992. The impact of rising co2 on ecosystem production. *Water, Air, and Soil Pollution 64(1-2):25-44.*

A fundamental property of green plants is that the rate of photosynthesis is dependent in the ambient CO2 concentration. There is overwhelming experimental evidence that this effect increases plant production in most C3 Plants: hundreds of experiments with many species show that plant growth increases an average 30% to 40% for a doubling of the present normal ambient CO2 concentration (Kimball, 1986). External environmental factors, such as temperature and the availability of nutrients, modify this response. The greatest stimulation of photosynthesis and growth can be expected to occur at high temperatures and much smaller responses at low temperature. Factors which restrict growth, such as low nutrients, will reduce but usually do not eliminate the stimulation of production with increasing CO2 even when nitrogen is severly limiting. There are also reports of direct effects of ambient CO2 concentration on dark respiration which show that there is an immediate reduction in the rate of CO2 efflux or O2 consumption when the CO2 around plant tissues is increased. There have been very few long-term field studies of the effects of increased CO2 on whole plants and ecosystem processes but the data from these studies are consistent in showing an increase in plant production with an increase in CO2 concentration of the ambient air.

KEYWORDS: ABSCISIC- ACID, CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, SOYBEAN LEAVES, STOMATAL CONDUCTANCE, TRANSPIRATION RESPONSES, TUSSOCK TUNDRA

564

Drake, B.G., J. Azcon-Bieto, J. Berry, J. Bunce, P. Dijkstra, J. Farrar, R.M. Gifford, M.A. Gonzalez-Meler, G. Koch, H. Lambers,

J. Siedow, and S. Wullschleger. 1999. Does elevated atmospheric CO2 concentration inhibit mitochondrial respiration in green plants? *Plant, Cell and Environment 22(6):649-657.*

There is abundant evidence that a reduction in mitochondrial respiration of plants occurs when atmospheric CO2 (C-a) is increased. Recent reviews suggest that doubling the present C-a will reduce the respiration rate [per unit dry weight (DW)] by 15 to 18%. The effect has two components: an immediate, reversible effect observed in leaves, stems, and roots of plants as well as soil microbes, and an irreversible effect which occurs as a consequence of growth in elevated C-a and appears to be specific to C-3 species. The direct effect has been correlated with inhibition of certain respiratory enzymes, namely cytochrome-c-oxidase and succinate dehydrogenase, and the indirect or acclimation effect may be related to changes in tissue composition. Although no satisfactory mechanisms to explain these effects have been demonstrated, plausible mechanisms have been proposed and await experimental testing. These are carbamylation of proteins and direct inhibition of enzymes of respiration. A reduction of foliar respiration of 15% by doubling present ambient C-a would represent 3 Gt of carbon per annum in the global carbon budget.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CHEMICAL-COMPOSITION, CONSTRUCTION COSTS, DARK RESPIRATION, GAS-EXCHANGE, GROWTH, LEAF RESPIRATION, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, WHEAT LEAVES

565

Drake, B.G., M.A. GonzalezMeler, and S.P. Long. 1997. More efficient plants: A consequence of rising atmospheric CO2? *Annual Review of Plant Physiology and Plant Molecular Biology 48:609-639.*

The primary effect of the response of plants to rising atmospheric CO2 (C-a) is to increase resource use efficiency. Elevated C-a reduces stomatal conductance and transpiration and improves water use efficiency, and at the same time it stimulates higher rates of photosynthesis and increases light- use efficiency. Acclimation of photosynthesis during long-term exposure to elevated C-a reduces key enzymes of the photosynthetic carbon reduction cycle, and this increases nutrient use efficiency. Improved soil-water balance, increased carbon uptake in the shade, greater carbon to nitrogen ratio, and reduced nutrient quality for insect and animal grazers are all possibilities that have been observed in field studies of the effects of elevated C-a. These effects have major consequences for agriculture and native ecosystems in a world of rising atmospheric C-a and climate change.

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, LEAF GAS- EXCHANGE, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS, WATER-USE EFFICIENCY

566

Drake, B.G., and P.W. Leadley. 1991. Canopy photosynthesis of crops and native plant-communities exposed to long-term elevated CO2. *Plant, Cell and Environment 14(8):853-860.*

There have been seven studies of canopy photosynthesis of plants grown in elevated atmospheric CO2: three of seed crops, two of forage crops and two of native plant ecosystems. Growth in elevated CO2 increased canopy photosynthesis in all cases. The relative effect of CO2 was correlated with increasing temperature: the least stimulation occurred in tundra vegetation grown at an average temperature near 10-degrees-C and the greatest in rice grown at 43-degrees-C. In soybean, effects of CO2 were greater during leaf expansion and pod fill than at other stages of crop maturation. In the longest running experiment with elevated CO2 treatment to date, monospecific stands of a C3 sedge, Scirpus olneyi (Grey), and a C4 grass, Spartina patens (Ait.) Muhl., have been exposed to twice normal ambient CO2 concentrations for four growing seasons, in open top chambers on a Chesapeake Bay salt marsh. Net ecosystem CO2 exchange per unit green biomass (NCE(b)) increased by an average of 48% throughout the growing season of 1988, the second year of treatment. Elevated CO2 increased net ecosystem carbon assimilation by 88% in the Scirpus olneyi community and 40% in the Spartina patens community.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, ENRICHMENT, ESTUARINE MARSH, GROWTH, SALT-MARSH, SOYBEAN PHYSIOLOGY, TEMPERATURE, TRANSPIRATION RESPONSES, TUSSOCK TUNDRA

567

Drake, B.G., M.S. Muehe, G. Peresta, M.A. GonzalezMeler, and R. Matamala. 1996. Acclimation of photosynthesis, respiration and ecosystem carbon flux of a wetland on Chesapeake Bay, Maryland to elevated atmospheric CO2 concentration. *Plant and Soil 187(2):111-118.*

Acclimation of photosynthesis and respiration in shoots and ecosystem carbon dioxide fluxes to rising atmospheric carbon dioxide concentration (C-a) was studied in a brackish wetland. Open top chambers were used to create test atmospheres of normal ambient and elevated C-a(=normal ambient+34 Pa CO2) over mono-specific stands of the C-3 sedge Scirpus olneyi, the dominant C-3 species in the wetland ecosystem, throughout each growing season since April of 1987. Acclimation of photosynthesis and respiration were evaluated by measurements of gas exchange in excised shoots. The impact of elevated C-a on the accumulation of carbon in the ecosystem was determined by ecosystem gas exchange measurements made using the open top chamber as a cuvette. Elevated C-a increased carbohydrate and reduced Rubisco and soluble protein concentrations as well as photosynthetic capacity(A) and dark respiration (R-d; dry weight basis) in excised shoots and canopies (leaf area area basis) of Scirpus olneyi, Nevertheless, the rate of photosynthesis was stimulated 53% in shoots and 30% in canopies growing in elevated C-a compared to normal ambient concentration. Elevated C-a inhibited R-d measured in excised shoots (-19 to -40%) and in seasonally integrated ecosystem respiration (R-e; -36 to -57%). Growth of shoots in elevated C- a was stimulated 14-21%, but this effect was not statistically significant at peak standing biomass in midseason. Although the effect of elevated C-a on growth of shoots was relatively small, the combined effect of increased number of shoots and stimulation of photosynthesis produced a 30% stimulation in seasonally integrated gross primary production (GPP). The stimulation of photosynthesis and inhibition of respiration by elevated C-a increased net ecosystem production (NEP=GPP-R-e) 59% in 1993 and 50% in 1994. While this study consistently showed that elevated C-a produced a significant increase in NEP, we have not identified a correspondingly large pool of carbon below ground.

KEYWORDS: ENRICHMENT, ESTUARINE MARSH, EXPOSURE, FIELD, GAS-EXCHANGE, OPEN-TOP CHAMBERS, PERSPECTIVE, PLANT, SCIRPUS- OLNEYI, TUNDRA

568

Drake, S.R. 1994. Elevated carbon-dioxide storage of anjou pears using purge- controlled atmosphere. *Hortscience 29(4):299-301.*

'Anjou' pears (Pyrus communis L.) were placed in controlled-atmosphere (CA) storage immediately after harvest (<24 hours) or after a 10-day delay in refrigerated storage, and held there for 9 months at 1C. Oxygen in all atmospheres was 1.5% and CO2 was at either 1% or 3%.

Atmospheres in the flow-through system were computer-controlled at +/- 0.1%. After removal from CA storage, pears were evaluated immediately and after ripening at 21C for 8 days. Pears stored in 3% CO2 were firmer, greener, and displayed less scald, internal breakdown, and stem-end decay than pears stored in 1% CO2. In addition, no internal discoloration of 'Anjou' pears was evident when held with 3% CO2. 'Anjou' pears held in 3% CO2 retained the ability to ripen after long-term storage. A 10-day delay in atmosphere establishment had little or no influence on the long-term keeping quality or ripening ability of 'Anjou' pears.

KEYWORDS: DANJOU PEAR

569
Drake, S.R. 1999. Quality of 'Bosc' pears as influenced by elevated carbon dioxide storage. *Journal of Food Quality 22(4):417-425.*

'Bosc' pears (Pyrus communis L.) were placed in a purge-type controlled-atmosphere (CA) storage immediately after harvest (<24 h) and held for 180 days at IC. Oxygen in all atmospheres was 1.5% and CO2 was 1%, 3% or 5%. Pears were evaluated immediately after removal from CA storage and after ripening for an additional 7 days at 21 C. Pears stored in 3% CO2 were firmer, had a superior finish, with significantly reduced decay and internal breakdown than pears stored in 1% CO2. In 3% CO2, pears retained the ability to ripen after long-term storage. A 10 day delay in atmosphere establishment had little or no influence on the long-term keeping quality or ripening ability of 'Bosc 'pears. Firmness, soluble solids content and starch either alone or together were good indices of maturity for 'Bosc 'pears.

KEYWORDS: ATMOSPHERE, DANJOU PEAR

570
Drake, S.R., and D.C. Elfving. 1999. Response of three strains of 'Gala' apples to high carbon dioxide prior to controlled atmosphere storage. *Fruit Varieties Journal 53(1):16-21.*

The postharvest fruit quality of three strains ('Royal Gala: 'Imperial Gala' and 'Crimson Gala') of apples was evaluated over two or three storage seasons. To determine the influence of carbon dioxide treatment on storage quality, apples were stored in normal controlled atmosphere (1% O-2 & 1% CO2), or treated with 12% CO2 for 7 or 14 days prior to normal CA and evaluated after 90 or 150 days of storage. The use of 12% CO2 prior to storage helped to maintain firmness of 'Royal Gala' apples in 1 of 3 seasons. Firmness of 'Imperial Gala' and 'Crimson Gala' apples was not influenced by high CO2 treatment, regardless of storage season. Other quality factors (color, soluble solids, acidity and carbohydrates) were not influenced to the extent that high CO(2)would be a viable option for the quality enhancement of 'Gala' apples during storage, regardless of strain. Use of normal CA maintained 'Gala' apple quality for 150 days of storage. Harvest date had a major influence on 'Gala' apple quality. A delay of one week reduced firmness and acidity, but enhanced color and content of sucrose, glucose and fructose in 'Royal Gala: 'Imperial Gala' and 'Crimson Gala' apples.

KEYWORDS: CA

571
Drake, S.R., and A. Yazdaniha. 1999. Short-term controlled atmosphere storage for shelf-life extension of apricots. *Journal of Food Processing and Preservation 23(1):57-70.*

Shelf-life of 'Perfection' and 'Rival' apricots can be enhanced with the use of controlled atmosphere (CA) storage. Apricots were harvested at commercial maturity and immediately stored in CA at 1 or 2 % O-2 and 3, 6, 9, 12 or 15 % CO2 for 30, 45 and 60 days. No differences in fruit quality were evident between O-2 atmospheres of 1 and 2 %, except that fruit stored in 1 % O-2 displayed less rot development and higher acid content. Apricots stored in 9 % or less CO2 displayed reduced external and internal color, inadequate finish, increased internal breakdown and more rot development with unacceptable firmness retention for additional handling. Apricots stored in 12 or 15 % CO2 retained firmness and displayed enhanced finish with reduced rots and very little internal breakdown with storage duration of 60 days. Color was much slower to develop in apricots stored in 12 or 15 % CO2 for all storage periods.

KEYWORDS: NECTARINES, PHYSIOLOGICAL DISORDERS

572
Drennan, P.M., and P.S. Nobel. 1996. Temperature influences on root growth for Encelia farinosa (Asteraceae), Pleuraphis rigida (Poaceae), and Agave deserti (Agavaceae) under current and doubled CO2 concentrations. *American Journal of Botany 83(2):133-139.*

To help evaluate root distribution patterns, elongation rates of individual roots were measured as a function of soil temperature for Encelia farinosa (a C-3 species), Pleuraphis rigida (C-4), and Agave deserti (CAM), sympatric codominants in the northwestern Sonoran Desert. Measurements were made at current and doubled CO2 concentrations under winter and summer conditions of air temperature (day/night temperatures of 17 C/10 C and 33 C/22 C, respectively). The three species had different optimal temperatures for root elongation (T-opt) under winter conditions (25 C for E. farinosa, 35 C for P. rigida, and 30 C for A. deserti); T-opt increased by 2-3 C under summer conditions for all three species. The limiting temperatures for elongation also acclimated from winter to summer conditions. The rate of root elongation at T-opt was higher under summer than winter conditions for E. farinosa (3 vs. 6 mm d(-1)) and P. rigida (20 vs. 14 mm d(-1)), reflecting conditions for maximum photosynthesis; no difference occurred for A. deserti (9 vs. 10 mm d(-1)). Decreased elongation rates at extreme temperatures were associated with less cell division and reduced cell extension. The doubled CO2 concentration increased average daily root elongation rates for A. deserti under both winter (7%) and summer (12%) conditions, reflecting increased cell extension, but had no effect for the other two species. Simulations of root elongation as a function of soil temperatures showed that maximum elongation would occur at different depths (16-20 cm for E. farinosa, 4-8 cm for P. rigida, and 0-4 cm for A. deserti) and during different seasons (winter to spring for E. farinosa, spring to summer for P. rigida, and all year for A. deserti), contributing to their niche separation. Shading of the soil surface moderated daily variations in soil temperature, reducing seasonal root elongation for winter and spring and increasing elongation for summer. Shading also altered root distribution patterns, e.g., optimal rooting depth for A. deserti and especially P. rigida increased for a hot summer day.

KEYWORDS: C-4, CAM PLANT, CARBON DIOXIDE, COMPETITION, ELEVATED CO2, HILARIA-RIGIDA, RESPONSES, SUCCULENTS, WATER RELATIONS

573
Drennan, P.M., and P.S. Nobel. 1998. Root growth dependence on soil temperature for Opuntia ficus- indica: influences of air temperature and a doubled CO2 concentration. *Functional Ecology 12(6):959-964.*

1. Root elongation as a function of soil temperature was determined for the CAM succulent Opuntia ficus-indica, under three different day/night air temperatures (15 degrees C/5 degrees C, 25 degrees C/15 degrees C and 35 degrees C/25 degrees C) and an ambient (360 mu mol mol(-1)) vs a doubled CO2 concentration (720 mu mol mol(-1)) at 25 degrees

C/15 degrees C, the optimum temperature for net CO2 uptake. 2. Root elongation occurred at soil temperatures from 12 degrees C (at 15 degrees C/5 degrees C) to 43 degrees C (at 35 degrees C/25 degrees C) with optimum temperatures of 27-30 degrees C, similar to other CAM succulents and consistent with the distribution of this shallow-rooted species in warm regions. Although a doubled CO2 concentration did not alter the optimum or limiting soil temperatures, increases of up to 5 degrees C in these temperatures accompanied the 20 degrees C increase in day/night air temperatures. 3. Root elongation rates at optimum soil temperatures ranged from 5.4 mm day(-1) (15 degrees C/5 degrees C), through 6.6 mm day(-1) (25 degrees C/15 degrees C), to 10.4 mm day(-1) (35 degrees C/25 degrees C) with a 25% increase under a doubled CO2 concentration. Highest root elongation rates at 35 degrees C/25 degrees C may reflect changing root vs shoot sink strengths in a species with a highly plastic root system. 4. At limiting soil temperatures, the length of the cell division zone was reduced by an average of 20% and cell length at the mid-point of-the elongation zone by 10%. Increased root elongation rates under a doubled CO2 concentration reflected increased cell elongation. 5. The temperature response for the roots of O. ficus-indica and stimulation of elongation by a doubled CO2 concentration indicate that root growth for this highly productive species should be enhanced by predicted global climate change.

KEYWORDS: CAM PLANT, DESERT SUCCULENTS, ELEVATED CO2, ELONGATION, EXCHANGE, GLOBAL CLIMATE-CHANGE, NITROGEN, RESPONSES, WATER

574

Dube, S.L., and W. Vidaver. 1992. Photosynthetic competence of plantlets grown-invitro - an automated-system for measurement of photosynthesis invitro. *Physiologia Plantarum 84(3):409-416.*

An aseptic gas exchange and hydroponic system (AGEHS) has been developed in an attempt for characterization of physiological requirements for photoautotrophic growth in vitro and alleviation of the needs for ex vitro acclimatization. The AGEHS monitors and controls several parameters relevant to plant growth. Shootlets of Chrysanthemum, x morifolium Ramat. cv. Envy were treated with flow of air or CO2-enriched air under controlled relative humidity, elevated photosynthetic photon flux density (PPFD) and hydroponic irrigation. After 15 days of treatment, plantlets gained more than 3 times as much dry weight as those from a conventional culture tube treatment. This study shows that it is possible to favour photoautotrophic growth when elevated PPFD, enhanced air-exchange and hydroponic medium flow are provided concurrently. This enhancement is achievable through careful increments of light quanta, balanced with increments of humidified air flow and/or CO2 content in air which seem to be necessary to avoid potential photoinhibition and premature water exhaustion from gelled media.

KEYWORDS: ACCLIMATIZATION, CO2- ENRICHMENT, CULTURE, LEAVES, REGENERANTS, SOIL, SOYBEANS

575

Duchein, M.C., A. Bonicel, and T. Betsche. 1993. Photosynthetic net co2 uptake and leaf phosphate concentrations in co2 enriched clover (trifolium-subterraneum L) at 3 levels of phosphate nutrition. *Journal of Experimental Botany 44(258):17-22.*

Net CO2-uptake of sets of clover plants (Trifolium subterraneum L. was measured over three weeks in ambient air and in a highly CO2-enriched atmosphere (400 Pa CO2). Phosphate (P) in the nutrient solution was varied between 0-05 mol m-3 P (reduced P) and 2.0 mol m-3 P (high P). In ambient air, the daily increments of the daily rate of net CO2-uptake (DICU; a parameter related to relative growth) were higher at reduced P than at high P. Stimulation by high CO2 of net CO2-uptake in the first day was less at reduced P than at high P. In the following days, high CO2 markedly inhibited DICU at reduced P, and thus growth stimulation by high CO2 ceased after between 4 and 12 d. By contrast, at high P, DICU increased more than 2- fold upon CO2-enrichment, and thus growth stimulation by high CO2 was maintained. Intermediate results were obtained with half-strength Hoagland's solution (0-5 mol m-3 P). Leaf pools of inorganic ortho P, soluble esterified P, and total P declined markedly in high CO2 when P-nutrition had been reduced. Considerable decline also occurred in high CO2 when P- nutrition had been increased suggesting that P-uptake was not well tuned with net CO2-uptake (growth). It is proposed that high CO2 can perturb the P-metabolism of clover, the impairment being less at high levels of P-nutrition. With regard to high CO2 as a growth stimulus, these results demonstrate that increasing P-nutrition to a level supraoptimal in ambient air can considerably improve the growth of a C3-plant in high CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, GROWTH, PHOSPHORUS, PLANTS, RESPONSES, SOURCE-SINK RELATIONS, SPINACH LEAVES, TEMPERATURE

576

Duff, G.A., C.A. Berryman, and D. Eamus. 1994. Growth, biomass allocation and foliar nutrient contents of 2 eucalyptus species of the wet dry tropics of australia grown under co2 enrichment. *Functional Ecology 8(4):502-508.*

1. Seeds of Eucalyptus tetrodonta and E. miniata were sown in duplicated air-conditioned tents which were ventilated with either ambient or CO2-enriched (700 mumol mol-1) air. Growth, foliar nutrient content, soluble protein and biomass allocation were investigated over the subsequent 32-week experimental period. 2. It was found that CO2 enrichment significantly increased the total biomass and tree height of E. tetrodonta, but had no effect on total biomass or tree height of E. miniata. 3. Allocation of biomass to main-stem wood and main- stem leaf mass increased and allocation to branch wood and branch leaves declined, under CO2 enrichment for E. tetrodonta. No change in allocation patterns for E miniata was observed in response to CO2 enrichment. 4. Foliar nitrogen, manganese and phosphorus contents were decreased under CO2 enrichment in E tetrodonta, but there was no effect of CO2 concentration in E. miniata. Soluble protein contents were not affected by CO2 enrichment in either species. These results are discussed in relation to the competitive relationship between these two species in northern Australia.

577

Dufrene, E., J.Y. Pontailler, and B. Saugier. 1993. A branch bag technique for simultaneous co2 enrichment and assimilation measurements on beech (fagus-sylvatica L). *Plant, Cell and Environment 16(9):1131-1138.*

A cheap CO2 enrichment system was designed to perform continuous gas exchange measurements of branches of mature European beech trees (Fagus sylvatica L.). Branches were grown at ambient (350 cm(3) m(-3)) and elevated CO2 (700 cm(3) m(-3)) during the whole 1992 leafy period. Leaks resulting from airtightness defaults in the system appeared to be low enough to measure accurately net CO2 assimilation and transpiration rates during the day. However, the CO2 exchange rates during the night (respiration) were too low to allow accurate measurements. Elevated CO2 had a great effect on the net assimilation rate of branches via its influence on both the C-3 photosynthetic pathway and the shade-tolerance of beech frees (85% increase). The A/C-a curves showed no acclimation effect to high CO2, both control and enriched branches increasing their net assimilation in the same way. The decrease of net assimilation rates in mature leaves was similar for

both control and enriched branches. The pattern of daily transpiration rates remained the same for both control and enriched branches, hence we can assume that there was no visible CO2 effect on stomata.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, TREES

578

Dugal, A., S. Yelle, and A. Gosselin. 1990. Influence of CO2 enrichment and its method of distribution on the evolution of gas exchanges in greenhouse tomatoes. *Canadian Journal of Plant Science 70(1):345-356.*

579

Dugas, W.A., M.L. Heuer, D. Hunsaker, B.A. Kimball, K.F. Lewin, J. Nagy, and M. Johnson. 1994. Sap flow measurements of transpiration from cotton grown under ambient and enriched co2 concentrations. *Agricultural and Forest Meteorology 70(1-4):231-245.*

Increasing atmospheric CO2 concentration has many implications for agriculture and forestry, one of which is the effect it will have on transpiration (T). The objective of this work was to quantify T of cotton (Gossypium hirsutum L.) grown in the field under ambient (370 mumol mol-1) and enriched (550 mumol mol-1) CO2 concentrations. Measurements were made in 1990 and 1991 at the Maricopa Agricultural Center, Arizona. Constant- power sap flow gauges were used to measure T. In 1990, three plants and in 1991, 10 plants were simultaneously instrumented with gauges in each of the CO2 treatments. Leaf area of plants with gauges was measured. T measured by sap flow was compared with evapotranspiration (ET) calculated by water balance in 1990 and with T calculated by water balance in 1991. Soil evaporation was measured using microlysimeters in 1991, and was found to be essentially equal (approximately 0.8 mm day-1, or about 10% of T) in the two CO2 treatments. There were no consistent differences in leaf area of plants with gauges between the two CO2 treatments. Sap flow, for periods from 15 min to 2 weeks, was not significantly different between the two CO2 treatments in either year, except for a few days in 1990. In 1991, the coefficient of variation of daily sap flow across plants was the same (about 30%) for both CO2 treatments throughout the year. The water balance ET (1990) and T (1991) were similar to sap flow in both years, and also showed no effect of CO2 treatment. These results show that for this crop, grown under well-watered and high-fertility conditions, there was no effect of CO2 on T, on a per unit ground area or per plant basis. These results are relevant for assessing the effects of increasing atmospheric CO2 concentrations on transpiration by cotton.

KEYWORDS: CARBON DIOXIDE, CROP YIELD, ELEVATED CO2, EVAPORATION, HEAT-BALANCE, LEAF CONDUCTANCE, MASS-FLOW, PLANTS, STEM-FLOW, WATER-USE

580

Dugas, W.A., S.A. Prior, and H.H. Rogers. 1997. Transpiration from sorghum and soybean growing under ambient and elevated CO2 concentrations. *Agricultural and Forest Meteorology 83(1-2):37-48.*

The increasing concentration of carbon dioxide in the atmosphere ([CO2]) has several direct effects on plants and these effects may be different for C-3 and C-4 plants. Our objective was to measure hourly and daily whole-plant transpiration rates from the C-4 plant grain sorghum (Sorghum bicolor (L.) Moench) and the C-3 plant soybean (Glycine max (L.) Merr.) grown under ambient (359 mu molCO(2) mol(-1) dry atmospheric air) and elevated (705 mu molmol(-1)) [CO2] values. Transpiration measurements were made for 22 days in August 1994 at Auburn, Alabama, USA, using stem flow gauges on plants growing in open top chambers, n = 8 for each [CO2] and species. Leaf area averaged slightly more than 0.1m(2) per plant for sorghum and about 0.2 m(2) per plant for soybean, Averages (15 min and daily) of transpiration, per unit leaf area, were consistently greater from plants growing under the ambient [CO2,] for both sorghum and soybean. Average daily transpiration from plants growing under the elevated [CO2] was significantly smaller (P = 0.05) on all but 2 days for soybean and on 9 of the 22 days of measurements for sorghum. Average daily sorghum transpiration was 1128 gm(-2) day(-1) and 772 gm(-2) day(-1) from plants growing under an ambient and elevated [CO2], respectively. Corresponding soybean averages were 731 gm(-2) day(-1) and 416 gm(-2) day(-1). The transpiration reduction under elevated [CO2] was greater for the C-3 plant soybean than for the C-4, plant sorghum. These results support previous studies showing that transpiration, per unit leaf area, from sorghum and soybean will both be reduced if atmospheric [CO2] continues to increase, although the reduction may be greater for C-3, plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, COTTON, CROP TRANSPIRATION, HEAT-BALANCE, LEAF CONDUCTANCE, SAP FLOW, STEM-FLOW GAUGE, WATER-USE EFFICIENCY, YIELD

581

Dukes, J.S., and H.A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology and Evolution 14(4):135-139.*

Biological invasions are gaining attention as a major threat to biodiversity and an important element of global change. Recent research indicates that other components of global change, such as increases in nitrogen deposition and atmospheric CO2 concentration, favor groups of species that share certain physiological or life history traits. New evidence suggests that many invasive species share traits that will allow them to capitalize on the various elements of global change. Increases in the prevalence of some of these biological invaders would alter basic ecosystem properties in ways that feed back to affect many components of global change.

KEYWORDS: CARBON DIOXIDE, CLIMATE, COMMUNITY, CONSEQUENCES, DISTURBANCE, ELEVATED CO2, ENRICHMENT, MORPHOLOGY, NITROGEN, VEGETATION

582

Duquesnay, A., N. Breda, M. Stievenard, and J.L. Dupouey. 1998. Changes of tree-ring delta C-13 and water-use efficiency of beech (Fagus sylvatica L.) in north-eastern France during the past century. *Plant, Cell and Environment 21(6):565-572.*

We investigated variation in intrinsic water-use efficiency during the past century by analysing delta(13)C in tree rings of beech growing in north-eastern France. Two different silvicultural systems were studied: high forest and coppice- with-standards, We studied separately effects related to the age of the tree at the time the ring was formed and effects attributable to environmental changes. At young ages, delta(13)C shows an increase of more than 1 parts per thousand. However, age-related trends differ in high forest and coppice- with-standards. Changes in microenvironmental variables during stand maturation, and physiological changes related to structural development of the trees with ageing, could explain these results. During the past century, delta(13)C in tree rings shows a pattern of decline that is not paralleled by air delta(13)C changes. Isotopic discrimination has significantly decreased from 18.1 to 16.4 parts per thousand in high forest and varied insignificantly between 17.4 and 16.9 parts per thousand in coppice-

with-standards, As a consequence, intrinsic water-use efficiency has increased by 44% in high forest and 23% in coppice-with-standards during the past century. These results accord with the increased water-use efficiency observed in controlled experiments under a CO2-enriched atmosphere. However other environmental changes, such as nitrogen deposition, may be responsible for such trends.

KEYWORDS: ANTARCTIC ICE, ATMOSPHERIC CO2 CONCENTRATION, C 13/C 12, CARBON ISOTOPE DISCRIMINATION, CENTURIES, DIOXIDE, DOUGLAS-FIR, GAS-EXCHANGE, POLAR ICE CORES, STOMATAL DENSITY

583

During, H., and M. Harst. 1996. Stomatal behaviour, photosynthesis and photorespiration of in vitro-grown grapevines: Effects of light and CO2. *Vitis 35(4):163-167.*

To improve photosynthesis and growth of grapevines cultivated in vitro (Seyval blanc and SO 4) effects of light intensity, spectral irradiance and CO2 concentration on stomatal behaviour, CO2 fixation and photorespiration were studied. Stomata were shown to respond to changes of light intensity but, unlike photosynthesis, their reactions were delayed and stomatal closure was incomplete in the dark. In contrast, alterations of the CO2 concentration in the headspace (50-2200 ppm) did not cause stomatal reactions. Photosynthesis vs, light intensity relationships indicated lower light compensation points, higher quantum yield and higher rates of light- saturated photosynthesis with "Fluora" lamps (maximal spectral irradiance al 460 and 680 nm) compared to "projector" lamps (maximal spectral irradiance at 620 nm). Photosynthesis vs. intercellular CO2 concentration relationships indicated varietal differences, the carboxylation efficiency and rates of photosynthesis at CO2 saturation being distinctly higher in the more vigorous variety SO 4 compared to Seyval blanc. Under the usual light conditions of our in vitro culture (50-60 mu mol quanta . m(-2). s(-1), Fluora) the headspace CO2 concentration ranged from 145 to 155 ppm while at the end of a 10-hour dark period it increased to values >3000 ppm. Rates of photorespiration were high (>50 % of photosynthesis) due to the relative low CO2 concentrations and, presumably, due to elevated O-2 concentrations in the headspace. It is concluded that the often observed low rates of photosynthesis of in vitro plantlets are mainly due to low light intensity and CO2 concentration in the headspace, the latter depending on the low rates of gas diffusion between ambient air and headspace.

KEYWORDS: CULTURED INVITRO, LEAVES, PLANTLETS, VITIS

584

Dury, S.J., J.E.G. Good, C.M. Perrins, A. Buse, and T. Kaye. 1998. The effects of increasing CO2 and temperature on oak leaf palatability and the implications for herbivorous insects. *Global Change Biology 4(1):55-61.*

Rising levels of atmospheric CO2 are expected to perturb forest ecosystems, although the extent to which specific ecological interactions will be modified is unclear. This research evaluates the effects of elevated CO2 and temperature, alone and in combination, on the leaf nutritional quality of Pendunculate oak (Qeurcus robur L.), and the implications for herbiverous insect defoliators are discussed. A 3 degrees C temperature rise reduced leaf nutritional quality, by reducing foliar nitrogen concentration and increasing condensed tannin content. Doubling atmospheric CO2 temporarily increased total phenolics, but also reduced leaf toughness. The nutritional quality of the second leaf flush (lammas growth) was considerably reduced at elevated CO2. It is concluded that larval development of spring-feeding defoliators and hence adult fecundity may be adversely affected by increased temperatures.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ELEVATED ATMOSPHERIC CO2, LARVAL EMERGENCE, LEPIDOPTERA, MOTH, NUTRIENT BALANCE, PERFORMANCE, PHYTOCHEMISTRY, PLANTS, QUERCUS-ROBUR L

585

Eamus, D. 1991. The interaction of rising CO2 and temperatures with water-use efficiency. *Plant, Cell and Environment 14(8):843-852.*

Recent data concerning the impact of elevated atmospheric CO2 upon water use efficiency (WUE) and the related measure, instantaneous transpiration efficiency (ITE), are reviewed. It is concluded from both short and long-term studies that, at the scale of the individual leaf or plant, an increase in WUE or ITE is generally observed in response to increased atmospheric CO2 levels. However, the magnitude of this increase may decline with time. The opinion that elevated CO2 may substantially decrease transpiration at the regional scale is discussed. The mechanisms by which elevated CO2 may cause a change in these measures are discussed in terms of stomatal conductance, assimilation and respiration responses to elevated CO2. Finally, recent experimental data and model outputs concerning the impact of the interaction of increased temperature with elevated CO2 on WUE, ITE and yield are reviewed. It is concluded that substantially more data is required before reliable predictions about the regional scale response of WUE and catchment hydrology can be made.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GAS-EXCHANGE, LEAF, PLANT GROWTH, RESPONSES, STOMATAL GUARD-CELLS, STRESS

586

Eamus, D. 1996. Tree responses to CO2 enrichment: CO2 and temperature interactions, biomass allocation and stand-scale modeling. *Tree Physiology 16(1-2):43-47.*

In this review, I focus on modeling studies of tree responses to CO2 enrichment. First, I examine leaf-scale models of assimilation with respect to the interaction between low temperature and CO2 enrichment. Second, because changes in allocation within a tree may be significant in determining the growth response of trees to CO2 enrichment and low temperatures, I review models of the control of allocation in plants. Finally, models of stand-scale processes are discussed with respect to their ability to make reliable estimates of likely vegetation responses to predicted climate change. I conclude that our ability to make reliable predictions is hindered by our lack of understanding of several processes, namely: the interaction between increased atmospheric CO2 concentration and low temperatures; the control of allocation in plants; and the modeling of stand-scale processes.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, BALANCE, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, ROOT, SEEDLINGS, TERM

587

Eamus, D., C.A. Berryman, and G.A. Duff. 1993. Assimilation, stomatal conductance, specific leaf-area and chlorophyll responses to elevated co2 of maranthes corymbosa, a tropical monsoon rain-forest species. *Australian Journal of Plant Physiology 20(6):741-755.*

Seeds of Maranthes corymbosa Blume, a monsoon rain forest species of northern Australia, were sown under ambient or elevated CO2 concentrations in tropical Australia. Seedlings were grown under conditions of photon flux density, temperature and atmospheric vapour pressure deficit which followed ambient variations as closely as possible. Specific leaf area, chlorophyll, stomatal density, stomatal conductance

and assimilation responses to photon flux density were measured after 30 weeks growth. Gas exchange characteristics were divided into morning and afternoon data sets and analysed separately. Stomatal density decreased and leaf area:dry weight ratio decreased in response to elevated CO2. In contrast there was no effect of elevated CO2 upon chlorophyll (total or ratio of a:b). Apparent quantum yield and rates of light saturated assimilation (A(max)) increased in response to elevated CO2. There was a significant decline in apparent quantum yield for both treatments between morning and afternoon. Stomatal conductance (g(s)) declined in response to elevated CO2. There was no significant difference in g(s) between morning and afternoon for ambient grown trees, but g(s) declined significantly between morning and afternoon for elevated CO2 grown trees. Instantaneous transpiration efficiency (ITE) was higher for elevated CO2 grown trees compared with control trees. There was a significant increase in ITE between morning and afternoon data for ambient grown trees; in contrast a significant decline in ITE was observed for elevated CO2 grown trees between morning anf afternoon data sets. The slope of the regression between assimilation rate and stomatal conductance increased for plants grown under elevated CO2. These data are discussed and compared with the responses of plants adapting to different photon flux densities.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GROWTH, INCREASES, IRRADIANCE, LIGHT, ORANGE, PHOTOSYNTHESIS, SEEDLINGS, TREES

588

Eamus, D., C.A. Berryman, and G.A. Duff. 1995. The impact of co2 enrichment on water relations in maranthes- corymbosa and eucalyptus-tetrodonta. *Australian Journal of Botany 43(3):273-282.*

Seeds of Maranthes corymbosa Blume and Eucalyptus tetrodonta F.Muell were sown under ambient or CO2 enriched conditions (two replicate tents per treatment) in tropical Australia and allowed to grow, rooted in the ground, for 20 months. For both species, periodic measurements of leaf water potential, stomatal conductance and leaf temperature were made on four replicate leaves on each of four replicate trees within each tent. Measurements were made in November (M. corymbosa) and June (E. tetrodonta). At the same time, atmospheric wet and dry bulb temperatures were recorded and hence leaf-to-air vapour presure difference (LAVPD) calculated. Measurements of pre-dawn leaf water potential were also made on E. tetrodonta. Leaves were also taken to the laboratory, rehydrated to full turgor and pressure-volume analyses undertaken. For M. corymbosa, leaf water potential was lower throughout the day for control leaves compared to leaves growing in CO2 enriched air. Similarly, pre dawn leaf water potential was lower for control E. tetrodonta trees than for trees grown with CO2 enrichment. However, mid- morning and mid-afternoon values of leaf water potential for E. tetrodonta were slightly lower for plants growing in CO, enriched air compared to control plants. In both species, stomatal conductance was consistently lower for trees grown in CO2 enriched air than for controls. Whole plant hydraulic conductivity of both species was significantly lower for trees grown in CO2 enriched air than for control trees. For both species, maximum turgor and bulk volumetric elastic modulus increased and osmotic potential at zero turgor decreased for trees grown in CO2 enriched air.

KEYWORDS: ANATOMY, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, MORPHOLOGY, SEEDLINGS, STRESS

589

Eamus, D., G.A. Duff, and C.A. Berryman. 1995. Photosynthetic responses to temperature, light flux-density, co2 concentration and vapor-pressure deficit in eucalyptus tetrodonta crown under co2 enrichment. *Environmental Pollution 90(1):41-49.*

Seeds of Eucalyptus tetrodonta were sown under ambient or CO2 enriched (700 mu l litre(-1)) conditions in tropical Australia. Four sets of measurements were made, the first two after 12 months, on trees growing either in pots or planted in the ground. The third and fourth set were made after 18 and 30 months exposure to CO2 enrichment, on trees growing in the ground After 12 months exposure to CO2 enrichment, the rate of light-saturated assimilation (A(max)) of plants growing in the ground was determined. Responses of CO2 assimilation to variations in leaf temperature, leaf-to-air vapour,pressure deficit (LAVPD), Eight flux density and CO2 concentration were also measured in the laboratory using plants growing in large pots. There was no significant difference in A(max) between pot and ground located plants. Assimilation of E. tetrodonta was relatively insensitive to changes in LAVPD for both ambient and CO2 enriched plants but the temperature optimum of assimilation was increased in plants grown and measured under CO2 enrichment. Plants grown with CO2 enrichment had an increased rate of light-saturated assimilation and apparent quantum yield I-vas significantly inn eased by CO2 enrichment. rn contrast, carboxylation efficiency was decreased significantly by CO2 enrichment. After 18 months growth with CO2 enrichment, there was no sign of a decline in assimilation I ate compared to measurements undertaken after 12 months, At low LAVPD values, assimilation rate was not influenced by CO2 treatment but at moderate to high LAVPD, plants grown under CO2 enrichment exhibited a larger assimilation rate than control plants. Specific leaf area and chlorophyll contents decreased in response to CO2 enrichment, whilst foliar soluble protein contents and chlorophyll a/b ratios were unaffected by CO2 treatment. Changes in soluble protein and chlorophyll contents in response to CO2 enrichment did not account for changes in assimilation between treatments. After 30 months exposure to CO2 enrichment, the rate of light-saturated assimilation was approximately 50% larger than controls and this enhancement was larger than that observed after 18 months exposure to CO2 enrichment.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, GROWTH, L LEAVES, MARANTHES-CORYMBOSA, PHASEOLUS-VULGARIS L, SEEDLINGS, STOMATAL CONDUCTANCE

590

Eamus, D., and M. Murray. 1991. Photosynthetic and stomatal conductance responses of norway spruce and beech to ozone, acid mist and frost - a conceptual-model. *Environmental Pollution 72(1):23-44.*

Two-year-old beech and Norway spruce seedlings were exposed to a combination of ozone and acid mist treatments in open-top chambers in Scotland during the months of July through to September 1988. Replicate pairs of chambers received charcoal- filtered air (control), ozone-enriched air (140 nl ozone litre- 1) or 140 nl ozone litre-1 plus a synthetic acid mist (pH 2.5) composed of ammonium nitrate and sulphuric acid. Field measurements of assimilation and stomatal conductance were made during August. In addition, measurements of assimilation and conductance were made during September in the laboratory. Light response curves of assimilation and conductance were determined using a GENSTAT non-rectangular hyperbolic model. During February 1988/9 the Norway spruce were subject to a four day warming period at 12-degrees-C and the light response of assimilation determined. The same plants were then subject to a 3-h night-time frost of -10-degrees-C. The following day the time-course of the recovery of assimilation was determined. It was found that ozone fumigation did not influence the light response of assimilation of beech trees in the field, although stomatal conductance was reduced in the ozone-fumigated trees. The rate of light-saturated assimilation of Norway spruce was increased by ozone fumigation when measured in the field. Measurements of assimilation of Norway spruce made during the winter showed that prior to rewarming there was no difference in the rate of light-saturated assimilation for control and ozone-fumigated trees. However, the ozone plus acid mist- treated trees exhibited a significantly

higher rate. The 4-day period of warming to 12-degrees-C increased the rate of light-saturated assimilation in all treatments but only the ozone plus acid mist-treated trees showed a significant increase. Following a 3-h frost to -10-degrees-C the control trees exhibited a reduction in the rate of light-saturated assimilation (A(max)) to 80% of the pre-frost value. In comparison, following the frost, the ozone-fumigated trees showed an A(max) of 74% of the pre-frost value. The ozone plus acid mist-treated trees showed an A(max) of 64% of the pre- frost trees. The time taken for A(max) to attain 50% of the pre-frost value increased from 30 min (control) to 85 min for ozone-fumigated trees to 190 min (ozone plus acid mist). These results are discussed in relation to the impact of mild, short- term frosts, which are known to occur with greater frequency than extreme, more catastrophic frost events. A simple conceptual framework is proposed to explain the variable results obtained in the literature with respect to the impact of ozone upon tree physiology.

KEYWORDS: ABIES L KARST, CO2 ASSIMILATION, FOREST DECLINE, GROWTH, HARDINESS, PINUS SYLVESTRIS, RAIN, SCOTS PINE, SEEDLINGS, TEMPERATURES

591

Easterling, W.E., P.R. Crosson, N.J. Rosenberg, M.S. McKenney, L.A. Katz, and K.M. Lemon. 1993. Agricultural impacts of and responses to climate-change in the missouri-iowa-nebraska-kansas (mink) region. *Climatic Change 24(1-2):23-61.*

The climate of the 1930s was used as an analog of the climate that might occur in Missouri, Iowa, Nebraska and Kansas (the MINK region) as a consequence of global warming. The analog climate was imposed on the agriculture of the region under technological and economic conditions prevailing in 1984/87 and again under a scenario of conditions that might prevail in 2030. The EPIC model of Williams et al. (1984), modified to allow consideration of the yield enhancing effects of CO2 enrichment, was used to evaluate the impacts of the analog climate on the productivity and water use of some 50 representative farm enterprises. Before farm level adjustments and adaptations to the changed climate, and absent CO2 enrichment (from 350 to 450 ppm), production of corn, sorghum and soybeans was depressed by the analog climate in about the same percent under both current and 2030 conditions. Production of dryland wheat was unaffected. Irrigated wheat production actually increased. Farm level adjustments using low-cost currently available technologies, combined with CO2 enrichment, eliminated about 80% of the negative impact of the analog climate on 1984/87 baseline crop production. The same farm level adjustments, plus new technologies developed in response to the analog climate, when combined with CO2 enrichment, converted the negative impact on 2030 crop production to a small increase. The analog climate would have little direct effect on animal production in MINK. The effect, if any, would be by way of the impact on production of feed-grains and soybeans. Since this impact would be small after on-farm adjustments and CO2 enrichment, animal production in MINK would be little affected by the analog climate.

KEYWORDS: CO2, CORN, EPIC MODEL, EROSION, PRODUCTIVITY

592

Easterling, W.E., N.J. Rosenberg, K.M. Lemon, and M.S. McKenney. 1992. Simulations of crop responses to climate change - effects with present technology and currently available adjustments (the smart farmer scenario). *Agricultural and Forest Meteorology 59(1-2):75-102.*

If climate changes, farmers will have to adapt to a new set of climate constraints. In this paper we examine the efficacy of strategies for dealing with climate change that are currently available to farmers and that are inexpensive to use; we refer to this group of strategies as 'adjustments'. Adjustment schemes of various kinds were identified for us by agricultural experts in the Missouri-Iowa-Nebraska-Kansas (MINK) states. These can involve changes in land use, changes in variety and crop selection, changes in planting and harvesting practices, and changes in fertility and pest management. Using the erosion productivity impact calculator (EPIC) model on a small set of representative farms, we tested adjustments of these kinds. The simulations show that earlier planting, longer- season cultivars and the use of furrow diking for moisture conservation would offset some of the yield losses induced by climate change in warm-season crops. Longer-season varieties of wheat (a cool-season crop) and shorter-season varieties of the perennials wheatgrass and alfalfa were also effective. The adjustments to climate change diminished yield losses in all crops but irrigated wheat. Despite the positive effects of adjustments, however, yields of all dryland warm-season crops remained lower than control levels. The adjustments also increased demand for irrigation water. Carbon dioxide enrichment had the same incremental effect on crop yields with or without adjustments (see the fourth paper in this issue), except in the case of alfalfa and sorghum, where a CO2- adjustment interaction was found. We conclude that currently available techniques would partially offset the yield reductions caused by a 1930s-like climate, but that in most crops the yield reductions would still be substantial.

KEYWORDS: AGRICULTURE

593

Edwards, N.T., and R.J. Norby. 1998. Below-ground respiratory responses of sugar maple and red maple saplings to atmospheric CO2 enrichment and elevated air temperature. *Plant and Soil 206(1):85-97.*

The research described in this paper represents a part of a much broader research project with the general objective of describing the effects of elevated [CO2] and temperature on tree growth, physiological processes, and ecosystem-level processes. The specific objective of this research was to examine the below-ground respiratory responses of sugar maple (Acer saccharum Marsh.) and red maple (Acer rubrum L.) seedlings to elevated atmospheric [CO2] and temperature. Red maple and sugar maple seedlings were planted in the ground in each of 12 open-top chambers and exposed from 1994 through 1997 to ambient air or air enriched with 30 Pa CO2, in combination with ambient or elevated (+4 degrees C) air temperatures. Carbon dioxide efflux was measured around the base of the seedlings and from root-exclusion zones at intervals during 1995 and 1996 and early 1997. The CO2 efflux rates averaged 0.4 mu mol CO2 m(-2) s(-1) in the root-exclusion zones and 0.75 mu mol CO2 m(-2) s-1 around the base of the seedlings. Mineral soil respiration in root-exclusion zones averaged 12% higher in the high temperature treatments than at ambient temperature, but was not affected by CO2 treatments. The fraction of total efflux attributable to root + rhizosphere respiration ranged from 14 to 61% in measurements made around red maple plants, and from 35 to 62% around sugar maple plants. Root respiration rates ranged from 0 to 0.94 mu mol CO2 s(-1) m(-2) of soil surface in red maple and from 0 to 1.02 in sugar maple. In both 1995 and 1996 root respiration rates of red maple were highest in high-CO2 treatments and lowest in high temperature treatments. Specific red maple root respiration rates of excised roots from near the soil surface in 1996 were also highest under CO2 enrichment and lowest in high temperature treatments. In sugar maple the highest rates of CO2 efflux were from around the base of plants exposed to both high temperature and high-CO2, even though specific respiration rates were lowest for this species under the high temperature and CO2 enrichment regime. In both species, patterns of response to treatments were similar in root respiration and root mass, indicating that the root respiration responses were due in part to differences in root mass. The results underscore the need for separating the processes occurring in the roots from those in the

forest floor and mineral soil in order to increase our understanding of the effects of global climate change on carbon sequestration and cycling in the below-ground systems of forests.

KEYWORDS: CARBON DIOXIDE, DECIDUOUS FOREST FLOOR, DROUGHT, EVOLUTION, GROWTH, NITROGEN, PONDEROSA PINE, ROOT RESPIRATION, SEEDLINGS, SOIL RESPIRATION

594

Egli, P., and C. Korner. 1997. Growth responses to elevated CO2 and soil quality in beech- spruce model ecosystems. *Acta Oecologica-International Journal of Ecology 18(3):343-349.*

Growth responses of beech (Fagus sylvatica L.) and Norway spruce (Picea abies Karst.) to elevated atmospheric CO2 (366 and 550 mu l CO2 l(-1)) and increased wet deposition of nitrogen (2.5 and 25 kg N ha(-1) a(-1)) in combination with two soil types were studied in open-top chambers. Eight young beech and spruce trees, together with five understory species, were established in each of 32 model ecosystems. We present initial growth responses of trees during the first year of treatment which may set the trends for longer term responses to elevated CO2. Above-ground biomass production at the system level (biometric data) during the first year and root biomass (coring data) did not show significant responses to elevated CO2, irrespectively of other cc-treatments. Increased nitrogen deposition (treatment commencing by mid-season) also had no effect on above-ground biomass, whereas end of season root biomass was significantly increased in the high-nitrogen treated low fertility acidic soil (74 g m(-2) in the high-N versus 49 g m(-2)? in the low N-treatment), but not-in the more fertile calcareous soil. Stem diameter increment of beech was significantly increased (+9%) under elevated CO, in the calcareous soil, but not in the acidic soil. The opposite was found for spruce stems, which responded positively to elevated CO2 in the acidic soil (+ 11%; P < 0.05) but nor in the calcareous soil. These results suggest that soil type co- determines the CO2 response of young forest trees and that these interactions are species specific. These initial differences are likely to affect long-term responses of community structure and ecosystem functioning. Soil type appears to be a key factor in predictions of forest responses to continued atmospheric CO2 enrichment.

KEYWORDS: ATMOSPHERE, COMMUNITIES, PLANTS, TREES

595

Egli, P., S. Maurer, M.S. Gunthardt-Goerg, and C. Korner. 1998. Effects of elevated CO2 and soil quality on leaf gas exchange and above-ground growth in beech-spruce model ecosystems. *New Phytologist 140(2):185-196.*

Responses of leaf gas exchange and above-ground growth of beech (Fagus sylvatica L.) and Norway spruce (Picea abies Karst.) to atmospheric CO2 enrichment (374 mu l l(-1) VS. 590 mu l l(-1)) and increased wet deposition of N (5 vs. 50 kg N ha(-1) a(-1)) in combination with two natural forest soil types ('acidic' and 'calcareous') were studied in large open-top chambers. Eight juvenile beech and spruce trees from different provenances, together with a ground cover composed of five understorey species, were established in each of 32 model ecosystems. Both beech and spruce showed sustained enhancement of photosynthesis in response to atmospheric CO2 enrichment during the first 2 yr of treatment. Nevertheless, switching measurement CO2 concentrations revealed partial downward adjustment of photosynthesis in trees grown in elevated CO2, beech generally showing more pronounced downward adjustment than spruce. The responsiveness of photosynthesis to CO2 enrichment did not vary significantly among trees from different provenances. Stomatal conductance was reduced under elevated CO2 in both tree species. In spruce, the radial growth of the main stem and the annual production of wood (shoot-wood dry mass of current-year lateral shoots), needle dry mass, and assimilation area per tree were stimulated both by CO2 enrichment and increased N deposition, but were not significantly affected by soil type by year 2. In contrast, in beech, the radial growth of the stem and the total leaf number, foliage dry mass, and assimilation area per tree were all not significantly affected by elevated CO2 and increased N deposition when responses of the two soil types were pooled, but were greater on calcareous than on acidic soil by year 2. However, CO2 interacted with soil type in beech: irrespective of the N deposition rate, saplings showed growth stimulation on the calcareous soil but responded negatively to CO2 enrichment on the acidic soil (where growth was slower). Our results suggest that complex interactions between CO2, species and soil quality need to be accounted for when attempting to predict forest development in a future CO2- rich world.

KEYWORDS: ATMOSPHERIC CO2, BRANCH BAG, CARBON DIOXIDE, ENRICHMENT, FAGUS-SYLVATICA, PHOTOSYNTHETIC ACCLIMATION, PINUS-TAEDA, RESPONSES, RISING CO2, TREES

596

Ehler, N., and P. Karlsen. 1993. Optico - a model-based real-time expert-system for dynamic optimization of co2 enrichment of greenhouse vegetable crops. *Journal of Horticultural Science 68(4):485-494.*

To improve the economic yield of CO2 enrichment for greenhouse crops, an expert system (OPTICO) was constructed. The system continually adapts the setpoints of a standard climate computer to the climate, the greenhouse regulation equipment and the crop's physiological status and stage of development. Models describing air loss and photosynthesis were used for selecting an optimized CO2 setpoint by choosing the largest positive difference between expected income and cost. During the autumn of 1991 the sweet pepper (Capsicum annuum L.) cv. Trophy was used as experimental plant in two standard greenhouse compartments. One treatment used the optimized CO2 enrichment, the other a fixed CO2 level of 600 ppm. The optimized treatment resulted in greater yield using less CO2. The results stress the importance of adapting the CO2 level to the immediate irradiance and current leaf area and carbon partitioning behaviour of the crop.

597

Ehleringer, J.R., and T.E. Cerling. 1995. Atmospheric co2 and the ratio of intercellular to ambient co2 concentrations in plants. *Tree Physiology 15(2):105-111.*

Much attention is focused today on predicting how plants will respond to anticipated changes in atmospheric composition and climate, and in particular to increases in CO2 concentration. Here we review the long-term global fluctuations in atmospheric CO2 concentration as a framework for understanding how current trends in atmospheric CO2 concentration fit into a selective, evolutionary context. We then focus on an integrated approach for understanding how gas exchange metabolism responds to current environmental conditions, how it previously responded to glacial-interglacial conditions, and how it may respond to future changes in atmospheric CO2 concentration.

KEYWORDS: CARBON ISOTOPE DISCRIMINATION, GAS-EXCHANGE, LAST 3 CENTURIES, LEAVES, PHOTOSYNTHESIS, SOIL CARBONATE, STOMATAL DENSITY, TRANSPIRATION EFFICIENCY, VOSTOK ICE-CORE, WATER-USE EFFICIENCY

598

Ehleringer, J.R., T.E. Cerling, and B.R. Helliker. 1997. C-4 photosynthesis, atmospheric CO2 and climate. *Oecologia 112(3):285-299.*

The objectives of this synthesis are (1) to review the factors that influence the ecological, geographical, and palaeoecological distributions of plants possessing C-4 photosynthesis and (2) to propose a hypothesis/model to explain both the distribution of C-4 plants with respect to temperature and CO2 and why C-4 photosynthesis is relatively uncommon in dicotyledonous plants (hereafter dicots), especially in comparison with its widespread distribution in monocotyledonous species (hereafter monocots). Our goal is to stimulate discussion of the factors controlling distributions of C-4 plants today, historically, and under future elevated CO2 environments. Understanding the distributions of C-3/C-4 plants impacts not only primary productivity, but also the distribution, evolution, and migration of both invertebrates and vertebrates that graze on these plants. Sixteen separate studies all indicate that the current distributions of C-4 monocots are tightly correlated with temperature: elevated temperatures during the growing season favor C-4 monocots. In contrast, the seven studies on C-4 dicot distributions suggest that a different environmental parameter, such as aridity (combination of temperature and evaporative potential), more closely describes their distributions. Differences in the temperature dependence of the quantum yield for CO2 uptake (light-use efficiency) of C-3 and C-4 species relate well to observed plant distributions and light-use efficiency is the only mechanism that has been proposed to explain distributional differences in C-3/C-4 monocots. Modeling of C-3 and C-4 light- use efficiencies under different combinations of atmospheric CO2 and temperature predicts that C-4-dominated ecosystems should not have expanded until atmospheric CO2 concentrations reached the lower levels that are thought to have existed beginning near the end of the Miocene. At that time, palaeocarbonate and fossil data indicate a simultaneous, global expansion of C-4-dominated grasslands. The C-4 monocots generally have a higher quantum yield than C-4 dicots and it is proposed that leaf venation patterns play a role in increasing the light-use efficiency of most C-4 monocots. The reduced quantum yield of most C-4 dicots is consistent with their rarity, and it is suggested that C-4 dicots may not have been selected until CO2 concentrations reached their lowest levels during glacial maxima in the Quaternary. Given the intrinsic light-use efficiency advantage of C-4 monocots, C-4 dicots may have been limited in their distributions to the warmest ecosystems, saline ecosystems, and/or to highly disturbed ecosystems. All C-4 plants have a significant advantage over C- 3 plants under low atmospheric CO2 conditions and are predicted to have expanded significantly on a global scale during full- glacial periods, especially in tropical regions. Bog and lake sediment cores as well as pedogenic carbonates support the hypothesis that C-4 ecosystems were more extensive during the last glacial maximum and then decreased in abundance following deglaciation as atmospheric CO2 levels increased.

KEYWORDS: BUNDLE-SHEATH, C-4 PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ECOLOGICAL DISTRIBUTION, GEOGRAPHICAL-DISTRIBUTION, ICE CORE, LAST GLACIAL MAXIMUM, LEAF ANATOMY, ORGANIC-MATTER, QUANTUM YIELD

599

Eichelmann, H., and A. Laisk. 1994. Co2 uptake and electron-transport rates in wild-type and a starchless mutant of nicotiana-sylvestris - the role and regulation of starch synthesis at saturating co2 concentrations. *Plant Physiology 106(2):679-687.*

CO2 uptake rate, chlorophyll fluorescence, and 830-nm absorbance were measured in wild-type (wt) Nicotiana sylvestris (Speg. et Comes) and starchless mutant NS 458 leaves at different light intensities and CO2 concentrations. Initial slopes of the relationships between CO2 uptake and light and CO2 were similar, but the maximum rate at CO2 and light saturation was only 30% in the mutant compared with the wt. O-2 enhancement of photosynthesis at CO2 and tight saturation was relatively much greater in the mutant than in the wt. In 21% O- 2, the electron transport rate (ETR) calculated from fluorescence peaked near the beginning of the CO2 saturation of photosynthesis. With the further increase of CO2 concentration ETR remained nearly constant or declined a little in the wt but drastically declined in the mutant. Absorbance measurements at 830 nm indicated photosystem I acceptor side reduction in both plants at saturating CO2 and light. Assimilatory charge (postillumination CO2 uptake) measurements indicated trapping of chloroplast inorganic phosphate, supposedly in hexose phosphates, in the mutant. It is concluded that starch synthesis gradually substitutes for photorespiration as electron acceptor with increasing CO2 concentration in the wt but not in the mutant. It is suggested that starch synthesis is co-controlled by the activity of the chloroplast fructose bisphosphatase.

KEYWORDS: CARBON METABOLISM, CHLOROPLAST, FLUORESCENCE, LEAVES, MATHEMATICAL-MODEL, PHOTOSYNTHESIS, PLASTID PHOSPHOGLUCOMUTASE, REDUCED-ACTIVITY, STEADY-STATE, SUCROSE SYNTHESIS

600

Elhottova, D., J. Triska, H. Santruckova, J. Kveton, J. Santrucek, and M. Simkova. 1997. Rhizosphere microflora of winter wheat plants cultivated under elevated CO2. *Plant and Soil 197(2):251-259.*

We studied an effect of elevated atmospheric CO2 on rhizosphere microorganisms in a hydroponics system where young wheat plants provided the only source of C for microorganisms. Plants were cultivated in mineral solution in sterile silica sand and exposed to control (ambient) and elevated (double) CO2 concentrations for periods of 13, 20, 25 and 34 days. Microbial biomass C (C content in fraction of size 0.3-2.7 mu m) was not affected by the elevated CO2 concentration during the first 25 days of plant growth and was increased after 34 days of plant growth. A content of poly-beta-hydroxybutyrate (PHB) reserve compounds (measured as derivatized product of 3-hydroxy-butyric acid and N-tert-butyldimethylsilyl-N-methyltrifluoracetamide using GC-MS) was lowered significantly ($p<0.001$) in the elevated CO2 after 25 and 34 days. It was accompanied with a shift of bacterial distribution towards the nutritional groups utilising more complex organic material (number of CFUs on media with different sources of C and N). A coincidence of several events connected with plant and microbial carbon economy (decrease of an assimilation rate and relative growth rate of plants, small increase of microbial biomass, PHB decrease and suppression within the bacterial nutritional group requiring the most readily available source of C and energy) was observed in the system under elevated CO2 on the 25th day. A modification of the CC-MS method for the detection of low levels of PHB compounds in natural samples was developed. We excluded the lipids fractionation step and we used EI MS/MS detection of the main fragment ions of the derivatized compound. This guarantees that the ion profiles have high signal-to-noise ratio at correct retention time. The detection limit is then about 30 pg g(-1) of sand or soil. The rhizosphere microflora responded very sensitively to the short- term changes in C partitioning in plants caused by the elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, AZOSPIRILLUM- BRASILENSE, CARBON, GROWTH, METABOLISM, POLY BETA HYDROXYBUTYRATE, RESPONSES

601

Elkohen, A., and M. Mousseau. 1994. Interactive effects of elevated co2 and mineral-nutrition on growth and co2 exchange of sweet chestnut seedlings (castanea- sativa). *Tree Physiology 14(7-9):679-690.*

The effects of elevated atmospheric CO2 (700 mumol mol-1) and

fertilization were investigated on 2-year-old sweet chestnut (Castanea sativa Mill.) seedlings grown outdoors in pots in constantly ventilated open-sided chambers. Plants were divided into four groups: fertilized controls (+F/-CO2), unfertilized controls (-F/-CO2), fertilized + CO2-treated plants (+F/+CO2) and unfertilized + CO2-treated plants (-F/+CO2). Dry matter accumulation and allocation were measured after one growing season and CO2 exchange of whole shoots was measured throughout the growing season. Shoot growth and total leaf area of unfertilized plants were not affected by elevated CO2, whereas both parameters were enhanced by elevated CO2 in fertilized plants. Elevated CO2 increased total biomass by about 20% in both fertilized and unfertilized plants; however, biomass partitioning differed. In unfertilized plants, elevated CO2 caused an increase in root growth, whereas in fertilized plants, it stimulated aboveground growth. At the whole-shoot and leaf levels, photosynthetic activity of both fertilized and unfertilized plants increased in response to elevated CO2, but the seasonal pattern of this enhancement varied with nutrient treatment. In unfertilized plants, a downward acclimation of photosynthesis was observed early in the season (June), and was related to reductions in nitrogen and chlorophyll content and to starch accumulation. The decrease in the slope of the A/Ci curve suggested a decrease in Rubisco activity. In both fertilized and unfertilized plants, shoot respiration decreased during the night in response to elevated CO2 until mid-July. The decrease was not related to changes in sugar concentration.

602

Elkohen, A., J.Y. Pontailler, and M. Mousseau. 1991. Effect of doubling of atmospheric CO2 concentration on dark respiration in aerial parts of young chestnut trees (Castanea sativa mill). *Comptes Rendus De L Academie Des Sciences Serie III-Sciences De La Vie-Life Sciences 312(9):477-481.*

Two-year-old sweet chestnut seedlings were grown in constantly ventilated tunnels at ambient (350 vpm) or double (700 vpm) CO2 concentration during a full growing season. End-of-night dark respiration of aerial parts was measured in each CO2 concentration throughout the growing season. Dark respiration rate of enriched plants showed a net decrease as compared to control plants during the first half of the growing season. This difference decreased with time and became negligible in the fall. Atmospheric CO2 concentration acted instantaneously on the respiration rate: when doubled, it decreased control plant respiration and when decreased, it enhanced CO2 enriched plant respiration. The explanation of these findings remains hypothetical. It is concluded that the rise in carbon dioxide level of the atmosphere will affect the carbon balance of young trees not only through an increase in net photosynthesis during the day, but also at night by reducing respiratory losses.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LEAF

603

Elkohen, A., H. Rouhier, and M. Mousseau. 1992. Changes in dry-weight and nitrogen partitioning induced by elevated co2 depend on soil nutrient availability in sweet chestnut (castanea-sativa mill). *Annales Des Sciences Forestieres 49(2):83-90.*

The effect of 2 levels of atmospheric carbon dioxide (ambient, ie 350 ppm, and double, ie 700 ppm) and 2 contrasting levels of mineral nutrition on dry weight, nitrogen accumulation and partitioning were examined in 2-year-old chestnut seedlings (Castanea sativa Mill), grown in pots outdoors throughout the vegetative season. Fertilization had a pronounced effect on dry weight accumulation, tree height, leaf area, and plant nitrogen content. Carbon dioxide enrichment significantly increased total biomass by about 20%, both on fertilized and on unfertilized forest soil. However, the partitioning of biomass was very different: on the unfertilized soil, only the root biomass was increased, leading to an increase in the root: shoot ratio. Contrastingly, on fertilized soil only stem biomass and diameter but not height were increased. Carbon dioxide enrichment significantly reduced the nitrogen concentration in all organs, irrespective of the nutrient availability. However, the biomass increase made up for this reduction in such a way that the total nitrogen pool per tree remained unchanged.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FORESTS, GROWTH, PLANTS, QUERCUS-ALBA, ROOT, SEEDLINGS

604

Elkohen, A., L. Venet, and M. Mousseau. 1993. Growth and photosynthesis of 2 deciduous forest species at elevated carbon-dioxide. *Functional Ecology 7(4):480-486.*

1. Two-year-old sweet chestnut (Castanea sativa) and beech (Fagus sylvatica) seedlings were grown in large pots of forest soil, at ambient (+/-350 mul l-1) and double (700 mul l-1) atmospheric CO2 Concentration in constantly ventilated.mini- green-houses during an entire growing season. 2. CO2 enrichment caused very different changes in these two temperate deciduous species. A 20% dry weight enhancement was obtained for sweet chestnut, and a 60% enhancement in beech. This greater effect of elevated CO2 in beech was the result of a significant increase of net photosynthesis of the seedlings occurring during the whole season. However, in sweet chestnut, this increase in photosynthesis lasted only a few weeks and then an acclimation process took place. 3. No effect of increased CO2 could be found on sweet chestnut leaf area or leaf number, while a significant effect was found with beech, in which total leaf area per plant increased, owing to a greater number of growth flushes, of progressively larger leaves. 4. The partitioning of the biomass increase due to elevated CO2 was very different in the two species. All additional dry matter was allocated to the roots in sweet chestnut, while it was partitioned equally amongst all organs of the beech seedling. 5. The reactions to elevated CO2 of different tree species is discussed in relation to their specific growth strategy.

605

Ellert, B.H., and H.H. Janzen. 1999. Short-term influence of tillage on CO2 fluxes from a semi-arid soil on the Canadian Prairies. *Soil & Tillage Research 50(1):21-32.*

The flux of CO2 from soil determines the extent to which carbon (C) deposited as plant litter is retained in the soil. Retention of soil C is beneficial for soil physical, chemical and biological properties, and is essential if soils are to be used as a repository of C to mitigate atmospheric CO2 increases. Although tillage is assumed to have a major influence on soil C retention, the extent to which tillage enhances the transfer of soil C to the atmosphere is uncertain. We assessed the short-term (50 h) influence of tillage on CO2 fluxes from Chernozemic soils under a two-year wheat (Triticum aestivum L.)-summerfallow rotation in a semi-arid region of the Canadian Prairie, The tillage effect and its persistence were assessed by using a portable CO2 analyzer to record several temporal series of CO2 fluxes, along undisturbed and tilled transects, at successive time intervals (from -0.5 to 50 h) after a single pass with a heavy-duty cultivator. Immediately after tillage, CO2 fluxes along the tilled transects increased from 2 to 4-fold above pre-tillage fluxes, but the increases were short-lived and fluxes along undisturbed and tilled transects were again similar within 24 h of cultivation. Total amounts of CO2 released by a tillage operation were quantified by: 1. linear interpolations among successive fluxes along tilled and undisturbed transects, and 2. by fitting a model to successive differences between fluxes along the transects. Both methods estimated the amounts of tillage-susceptible CO2 to be in the range of 3.6-7.2 kg C ha(-1). The

tillage-induced flush of CO2 was attributed mainly to enhanced transport of CO2 already in the soil, but enhanced production of CO2 by heterotrophic soil organisms also may have contributed to the flush. Regardless of the sources of CO2 released by single tillage operations, amounts of tillage-susceptible soil C were minor; even 10 passes with a cultivator would account for less than 5% of annual soil CO2 emissions or crop residue production in these cropping systems. Our study suggested that the short- term influence of tillage on the transfer of soil C to atmospheric CO2 is small under semi-arid conditions like those in southern Alberta, Canada.

KEYWORDS: CARBON-DIOXIDE FLUX, COVER, CROPPING SYSTEMS, EVOLUTION, LIGHT FRACTION, MICROORGANISMS, ORGANIC-MATTER, RESPIRATION

606

Ellis, R.H., P.Q. Craufurd, R.J. Summerfield, and E.H. Roberts. 1995. Linear relations between carbon-dioxide concentration and rate - of development towards flowering in sorghum, cowpea and soybean. *Annals of Botany 75(2):193-198.*

Negative linear relations were detected (P < 0.005) between the rate of progress from sowing to panicle initiation and CO2 concentration (210-720 mu mol CO2 mol(-1) air) for two genotypes of sorghum [Sorghum bicolor (L.) Moench]. Relations between CO2 concentration and the rate of progress from sewing to first flowering were also negative in soyabean [Glycine max (L). Merrill] (P < 0.025), but positive in cowpea [Vigna unguiculata (L.) Walp.] (P < 0.025), albeit that in both grain legumes sensitivity was much less than in sorghum. Thus CO2 elevation does not delay flowering in all short-day species. The considerable effect of CO2 concentration on times to panicle initiation resulted in large differences among the sorghum plants at this developmental stage; with increase in CO2 concentration, plants were taller with slightly more leaves and more pronounced apical extension. At the same time after sowing however, sorghum plants were heavier (P < 0.05) at 210 than at 360 mu mol CO2 mol(-1) air. In contrast, relations between the dry masses of the soyabean and cowpea plants and CO2 concentration were positive and curvilinear (P < 0.05). It is suggested that the impact of global environmental change could be severe for sorghum production in the semi-arid tropics.

KEYWORDS: BICOLOR, CLIMATE, CO2- ENRICHMENT, ELEVATED CO2, FLORAL INITIATION, GROWTH, TEMPERATURE, VIGNA UNGUICULATA L, YIELD

607

Ellsworth, D.S. 1999. CO2 enrichment in a maturing pine forest: are CO2 exchange and water status in the canopy affected? *Plant, Cell and Environment 22(5):461-472.*

Elevated CO2 is expected to reduce forest water use as a result of CO2-induced stomatal closure, which has implications for ecosystem-scale phenomena controlled by water availability. Leaf-level CO2 and H2O exchange responses and plant and soil water relations were examined in a maturing loblolly pine (Pinus taeda L,) stand in a free-air CO2 enrichment (FACE) experiment in North Carolina, USA to test if these parameters were affected by elevated CO2, Current-year foliage in the canopy was continuously exposed to elevated CO2 (ambient CO2 + 200 mu mol mol(-1)) in free-air during needle growth and development for lip to 400 d. Photosynthesis in upper canopy foliage was stimulated by 50-60% by elevated CO2 compared with ambient controls. This enhancement was similar in current-year, ambient-grown foliage temporarily measured at elevated CO2 compared with long-term elevated CO2 grown foliage, Significant photosynthetic enhancement by CO2 was maintained over a range of conditions except during peak drought. There was no evidence of water savings in elevated CO2 plots in FACE compared to ambient plots under drought and non-drought conditions. This was supported by evidence from three independent measures. First, stomatal conductance was not significantly different in elevated CO2 versus ambient trees of P. taeda, Calculations of time-integrated c(i)/c(a) ratios from analysis of foliar delta(13)C showed that these ratios were maintained in foliage under elevated CO2. Second, soil moisture was not significantly different between ambient and elevated CO2 plots during drought. Third, pre-dawn and mid-day leaf water potentials were also unaffected by the seasonal CO2 exposure, as were tissue osmotic potentials and turgor loss points. Together the results strongly support the hypothesis that maturing P. taeda trees have low stomatal responsiveness to elevated CO2. Elevated CO2 effects on water relations in loblolly pine-dominated forest ecosystems may be absent or small apart from those mediated by leaf area. Large photosynthetic enhancements in the upper canopy of P. taeda by elevated CO2 indicate that this maturing forest may have a large carbon sequestration capacity with limiting water supply.

KEYWORDS: DROUGHT, ELEVATED CARBON-DIOXIDE, GROWTH, INCREASING ATMOSPHERIC CO2, LEAF GAS-EXCHANGE, LOBLOLLY-PINE, NET PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STOMATAL CONDUCTANCE

608

Ellsworth, D.S., R. Oren, C. Huang, N. Phillips, and G.R. Hendrey. 1995. Leaf and canopy responses to elevated co2 in a pine forest under free-air co2 enrichment. *Oecologia 104(2):139-146.*

Physiological responses to elevated CO2 at the leaf and canopy- level were studied in an intact pine (Pinus taeda) forest ecosystem exposed to elevated CO2 using a free-air CO2 enrichment (FACE) technique. Normalized canopy water-use of trees exposed to elevated CO2 over an 8-day exposure period was similar to that of trees exposed to current ambient CO2 under sunny conditions. During a portion of the exposure period when sky conditions were cloudy, CO2-exposed trees showed minor (less than or equal to 7%) but significant reductions in relative sap flux density compared to trees under ambient CO2 conditions. Short-term (minutes) direct stomatal responses to elevated CO2 were also relatively weak (approximate to 5% reduction in stomatal aperture in response to high CO2 concentrations). We observed no evidence of adjustment in stomatal conductance in foliage grown under elevated CO2 for nearly 80 days compared to foliage grown under current ambient CO2 so intrinsic leaf water-use efficiency at elevated CO2 was enhanced primarily by direct responses of photosynthesis to CO2. We did not detect statistical differences in parameters from photosynthetic responses to intercellular CO2 (A(net)-C-i curves) for Pinus taeda foliage grown under elevated CO2 (550 mu mol mol(-1)) for 50-80 days compared to those for foliage grown under current ambient CO2 from similar-sized reference trees nearby. In both cases, leaf net photosynthetic rate at 550 mu mol mol(-1) CO2 was enhanced by approximately 65% compared to the rate at ambient CO2 (350 mu mol mol(-1)). A similar level of enhancement under elevated CO2 was observed for daily photosynthesis under field conditions on a sunny day. While enhancement of photosynthesis by elevated CO2 during the study period appears to be primarily attributable to direct photosynthetic responses to CO2 in the pine forest, longer-term CO2 responses and feedbacks remain to be evaluated.

KEYWORDS: AREA, CARBON-DIOXIDE ENRICHMENT, CONDUCTANCE, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RISING CO2, SEEDLINGS, TREES, WATER-STRESS

609

Ellsworth, D.S., R. Oren, C. Huang, N. Phillips, and G.R. Hendrey. 1996. Leaf and canopy responses to elevated CO2 in a pine forest under free-air CO2 enrichment (vol 104, pg 139, 1995). *Oecologia*

106(3):416.

610

ElMaayar, M., B. Singh, P. Andre, C.R. Bryant, and J.P. Thouez. 1997. The effects of climatic change and CO2 fertilisation on agriculture in Quebec. *Agricultural and Forest Meteorology 85(3-4):193-208.*

The agricultural sector forms an important part of the economy of Quebec. The risk of global increase of atmospheric CO2 concentration and associated climatic change and their influence on agriculture need to be assessed. Although many studies have been conducted on the effect of climate change on agriculture in various parts of the world, fewer studies have focused on the combined effects of climatic change and CO2 fertilisation on agriculture. This study, using the outputs of the Canadian Climate Centre (CCC) general circulation model coupled with the Food and Agricultural Organization (FAG) crop model, attempts to assess the response of agricultural productivity to both direct (or fertilisation) and indirect (or climatic) effects of increased atmospheric CO2 concentration, for a variety of crops including C-3 and C-4 cereals, legumes, vegetables and special crops grown in Quebec. It appears that C-4 cereal (corn and sorghum) crops would benefit by climate change but would be least favoured by CO2 fertilisation effect. (C) 1997 Published by Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, CROP, DRY-WEIGHT, ENRICHMENT, GROWTH, SCENARIO, TEMPERATURE, UNITED-STATES, WHEAT, YIELD

611

Elmeskaoui, A., J.P. Damont, M.J. Poulin, Y. Piche, and Y. Desjardins. 1995. A tripartite culture system for endomycorrhizal inoculation of micropropagated strawberry plantlets in-vitro. *Mycorrhiza 5(5):313-319.*

The objective of the current investigation was to develop a reliable method to obtain vesicular-arbuscular mycorrhizae (VAM) in micropropagated plantlets and to determine their influence on growth, An in vitro system for culturing the VA mycorrhizal fungus Glomus intraradices with Ri T-DNA- transformed carrot roots or nontransformed tomato roots was used in this study as a potential active source of inoculum for the colonization of micropropagated plantlets. After root induction, micropropagated plantlets grown on cellulose plugs (sorbarod) were placed in contact with the primary mycorrhizae in growth chambers enriched with 5000 ppm CO2 and fed with a minimal medium. After 20 days of tripartite culture, all plantlets placed in contact with the primary symbiosis were colonized by the VAM fungus. As inoculum source, 30-day-old VA mycorrhizal transformed carrot roots had a substantially higher infection potential than 5-, 10- or 20-day-old VAM. Colonized plantlets had more extensive root systems and better shoot growth than control plants. The VAM symbiosis reduced the plantlet osmotic potential. This response may be a useful pre- adaptation for plantlets during transfer to the acclimatization stage.

KEYWORDS: ASPARAGUS, FUNGI, GROWTH, INFECTION, INVITRO, PROPAGATION, SYMBIOSIS, TRANSPORT, VA-MYCORRHIZAL, VESICULAR-ARBUSCULAR MYCORRHIZAE

612

Endo, M., and I. Ikushima. 1997. Effects of CO2 enrichment on yields and preservability of cut flowers in Phalaenopsis. *Journal of the Japanese Society for Horticultural Science 66(1):169-174.*

The effect of CO2 enrichment on Phalaenopsis cut flower production was examined for 30 months throughout five flowering cycles. The plant was cultured in three greenhouses with different CO2 levels of (A) : control, daily mean of ambient air = 438 ppm; (B) : 700 ppm; and (C) : 1000 ppm. 1. The fresh weight of cut flowers, the numbers of inflorescence and flowers per 20 plants varied, depending on the CO2 concentration for each flowering cycle. 2. The preservability (vase life) of cut flowers always improved under higher CO2 levels. Organic acid contents of plants were also higher under higher CO2 levels. The malic acid content in the flowers was higher than in the younger leaf and flower stalk at 1:00 PM and 10:00 PM; and it was also higher in the younger leaf than in the flower stalk at 10:00 PM, but lower at 1:00 PM. The pH value of plants was always lower at higher ambient CO2 levels, and lower in the younger leaf and flower stalk at 1:00 PM than at 10:00 PM, wheras at those same times the sugar content at the higher ambient CO2 levels reached its maximum.

KEYWORDS: LEAF, PHOTOSYNTHESIS

613

Endo, M., and I. Ikusima. 1997. Effects of CO2 enrichment by complete combustion of liquid petroleum gas on growth of Doritaenopsis. *Journal of the Japanese Society for Horticultural Science 66(1):163-168.*

The effects of increasing ambient CO2 levels on the growth of developing Doritaenopsis plants in a greenhouse were studied for 840 days. Leaf area, dry weight, and content of total carbon and total nitrogen in dry matter were measured every three months, and the time course of the relative growth rate (RGR) was investigated. Leaf area and dry weight increased with increasing CO2 concentration from 438 ppm to 946 ppm in the atmosphere. In an initial growth stage when plants were transplanted from flasks to pots, RGR increased as the CO2 level increased. RGR during a later vegetative growth stage was not affected by the CO2 concentration, and its value was 0.006/day. The value of RGR was less than that of the other C- 3, C-4, and CAM plants.

KEYWORDS: LIGHT, PLANTS, RESPONSES

614

Enoch, H.Z., and J.M. Olesen. 1993. Plant-response to irrigation with water enriched with carbon- dioxide. *New Phytologist 125(2):249-258.*

The influence of irrigation with CO2-enriched water on plant development and yield is reviewed. The reason for irrigation with CO2-enriched water was - in most cases - to increase yield. The present evaluation considers results from over a hundred studies performed since the first experiment in 1866. Special emphasis is given to the comparison of 85 experiments made by Mitscherlich in 1910 with 358 irrigation experiments made in the last 80 years. In a statistical analysis of these experiments, the measured plant parameter (often growth and/or gas exchange rates) showed a highly significant mean increase of 2.9 % in plants irrigated with CO2-enriched water as compared with control. Evidence of five mechanisms was found. The subterranean carbon dioxide concentration influences: (a) the rate of nitrification and hence of nitrogen availability; (b) the rate of weathering and pH, and hence the availability of other plant nutrients; (c) the CO2 uptake via roots into the transpiration stream, contributing to the rate of leaf photosynthesis; (d) the hormone levels in the plant; and (e) the rate of pesticide decomposition in soils. After examining the available evidence we found that (a) and (b) in some experiments are important to plant growth, since they change the physiochemical environment of the roots. On the other hand, while (c) could theoretically contribute up to 5% of plant carbon assimilation, it usually contributes less than 1%, while (d) contributes most of the observed effects of CO2-enriched water on plants. In addition, pesticide decomposition in soils can be delayed by supra- or sub-optimal CO2 concentrations.

KEYWORDS: ETHYLENE, GASEOUS CO2 TRANSPORT, GROWTH, ROOT ENVIRONMENT, SEEDLINGS, SOIL, TUBERIZATION

615

Entry, J.A., G.B. Runion, S.A. Prior, R.J. Mitchell, and H.H. Rogers. 1998. Influence of CO2 enrichment and nitrogen fertilization on tissue chemistry and carbon allocation in longleaf pine seedlings. *Plant and Soil 200(1):3-11.*

One-year old, nursery-grown longleaf pine (Pinus palustris Mill.) seedlings were grown in 45-L pots containing a coarse sandy medium and were exposed to two concentrations of atmospheric CO2 (365 or 720 mu mol(-1)) and two levels of nitrogen (N) fertility (40 or 400 kg N ha(-1) yr(-1)) within open top chambers for 20 months. At harvest, needles, stems, coarse roots, and fine roots were separated and weighed. Subsamples of each tissue were frozen in liquid N, lyophilized at -50 degrees C, and ground to pass a 0.2 mm sieve. Tissue samples were analyzed for carbon (C), N, nonpolar extractives (fats, waxes, and oils = FWO), nonstructural carbohydrates (total sugars and starch), and structural carbohydrates (cellulose, lignin, and tannins). Increased dry weights of each tissue were observed under elevated CO2 and with high N; however, main effects of CO2 were significant only on belowground tissues. The high N fertility tended to result in increased partitioning of biomass aboveground, resulting in significantly lower root to shoot ratios. Elevated CO2 did not affect biomass allocation among tissues. Both atmospheric CO2 and N fertility tended to affect concentration of C compounds in belowground, more than aboveground, tissues. Elevated CO2 resulted in lower concentrations of starch, cellulose, and lignin, but increased concentrations of FWO in root tissues. High N fertility increased the concentration of starch, cellulose, and tannins, but resulted in lower concentrations of lignin and FWO in roots. Differences between CO2 concentrations tended to occur only with high N fertility. Atmospheric CO2 did not affect allocation patterns for any compound; however the high N treatment tended to result in a lower percentage of sugars, cellulose, and lignin belowground.

KEYWORDS: ALLELOCHEMICALS, COTTON PLANTS, DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH, PLANT-RESPONSES, PRODUCTIVITY, RESPIRATORY RESPONSES, ROOTS, SOIL

616

Epron, D., E. Dreyer, C. Picon, and J.M. Guehl. 1994. Relationship between co2-dependent o-2 evolution and photosystem-II activity in oak (quercus-petraea) trees grown in the field and in seedlings grown in ambient or elevated co2. *Tree Physiology 14(7-9):725-733.*

The light-response of the apparent quantum yield of photosynthetic O2 evolution (PHI(O2)) under non- photorespiratory conditions was measured together with the photochemical efficiency Of PS II (DELTAF/F(m)'), the photochemical efficiency of open PS II reaction centers (F(v)'/F(m)') and the photochemical fluorescence quenching (q(p)) of leaf disks punched from oak leaves of seedlings grown in ambient (350 mumol mol-1) or elevated (700 mumol mol- 1) CO2 in a greenhouse, and from sunlit leaves of mature oak trees (Quercus petraea (Matt.) Liebl.). There were marked differences between seedlings and trees. In seedlings, CO2 concentration during growth did not modify the light response of photosynthesis or PS II activity. There was a single linear relationship between PHI(O2) and DELTAF/F(m)' in seedling leaves that was independent of the CO2 concentration imposed during growth. In contrast, this relationship was curvilinear in sunlit leaves of adult trees. In seedling leaves, the decrease in q(p) (i.e., the proportion of open PS II reaction centers) largely accounted for the decrease in DELTAF/F(m)', whereas the decrease in DELTAF/F(m)' in sunlit leaves of mature oak trees was dependent on both q(p) and F(v)'/F(m)'.

617

Epron, D., D. Godard, G. Cornic, and B. Genty. 1995. Limitation of net co2 assimilation rate by internal resistances to co2 transfer in the leaves of 2 tree species (fagus- sylvatica L and castanea-sativa mill). *Plant, Cell and Environment 18(1):43-51.*

Using a combination of gas-exchange and chlorophyll fluorescence measurements, low apparent CO2/O-2 specificity factors (1300 mol mol(-1)) were estimated for the leaves of two deciduous tree species (Fagus sylvatica and Castanea sativa), These low values contrasted with those estimated for two herbaceous species and were ascribed to a drop in the CO2 mole fraction between the intercellular airspace (C-i) and the catalytic site of Rubisco (C-c) due to internal resistances to CO2 transfer, C-c was calculated assuming a specificity of Rubisco value of 2560 mol mol(-1). The drop between C-i and C-c was used to calculate the internal conductance for CO2 (g(i)), A good correlation between mean values of net CO2 assimilation rate (A) and g(i) was observed within a set of data obtained using 13 woody plant species, including our own data, We report that the relative limitation of A, which can be ascribed to internal resistances to CO2 transfer, was 24-30%, High internal resistances to CO2 transfer may explain the low apparent maximal rates of carboxylation and electron transport of some woody plant species calculated from A/C-i curves.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, ELEVATED CO2, GAS-EXCHANGE, MESOPHYLL CONDUCTANCE, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PLANTS, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECIFICITY FACTOR, STOMATAL CONDUCTANCE

618

Epron, D., R. Liozon, and M. Mousseau. 1996. Effects of elevated CO2 concentration on leaf characteristics and photosynthetic capacity of beech (Fagus sylvatica) during the growing season. *Tree Physiology 16(4):425-432.*

Two-year-old beech (Fagus sylvatica L.) saplings were planted directly in the ground at high density (100 per m(2)), in an experimental design that realistically mimicked field conditions, and grown for two years in air containing CO2 at either ambient or an elevated (ambient + 350 ppm) concentration. Plant dry mass and leaf area were increased by a two-year exposure to elevated CO2. The saplings produced physiologically distinct types of sun leaves associated with the first and second growth flushes. Leaves of the second flush had a higher leaf mass per unit area and less chlorophyll per unit area, per unit dry mass and per unit nitrogen than leaves of the first flush. Chlorophyll content expressed per unit nitrogen decreased over time in plants grown in elevated CO2, which suggests that, in elevated CO2, less nitrogen was invested in machinery of the photosynthetic light reactions. In early summer, the photosynthetic capacity measured at saturating irradiance and CO2 was slightly but not significantly higher in saplings grown in elevated CO2 than in saplings grown in ambient CO2. However, a decrease in photosynthetic capacity was observed after July in leaves of saplings grown in CO2-enriched air. The results demonstrate that photosynthetic acclimation to elevated CO2 can occur in field-grown saplings in late summer, at the time of growth cessation.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CHLOROPHYLL, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, RESPONSES, SEEDLINGS, SHADE PLANTS

619

Erhardt, A., and H.P. Rusterholz. 1997. Effects of elevated CO2 on flowering phenology and nectar production. *Acta Oecologica-International Journal of Ecology 18(3):249-253.*

Effects of elevated CO2 on flowering phenology and nectar production were studied in five important nectar plants of calcareous grasslands, i.e. Lotus corniculatus, Trifolium pratense, Betonica officinalis, Scabiosa columbaria ia and Centaurea jacea. Glasshouse experiments showed that flowering probability was significantly enhanced in C. jacea. B. officinalis flowered earlier and L. corniculatus produced more flowers under elevated CO2. In contrast, the number of flowers decreased in T. pratense. The amount of nectar produced per flower was not affected in the investigated legumes (T. pratense, L. corniculatus), but was significantly reduced in the other forbs. Elevated CO2 did not significantly affect nectarsugar concentration and sugar composition. However, S. columbaria and C: jacea produced significantly less total sugar per flower under elevated CO2. The nectar amino acid concentration remained unaffected in all investigated plant species whereas the total of amino acids produced per flower was significantly reduced in all nan-legumes. In addition, the amino acid composition changed significantly in all investigated species except for C. jacea. The observed effects are unexpected and are a potential threat to flower visitors such as most butterflies which have no alternative food resources except nectar. Changes in nectar production due to elevated CO2 could also generally have detrimental effects on the interactions of flowers and their pollinators.

620

Erickson, D.J. 1999. Nitrogen deposition, terrestrial carbon uptake and changes in the seasonal cycle of atmospheric CO2. *Geophysical Research Letters 26(21):3313-3316.*

Observational evidence indicates an increasing trend in the amplitude of the seasonal cycle of atmospheric CO2 over the last several decades. Here, the influence of nitrogen deposition on the seasonal cycle of atmospheric CO2 is investigated using a global carbon cycle model embedded in a 3- D general circulation model. We employ a recently published estimate of the enhancement of carbon dioxide uptake induced by the atmospheric deposition of NOy and NHx. We partition the carbon sink related to nitrogen deposition over the seasonal cycle of CO2 uptake. The modeled increase in the amplitude of the seasonal cycle of CO2 in the Northern Hemisphere related to the simulated nitrogen deposition alone is 25%-50% of observed. At Mauna Loa the increased amplitude in the CO2 seasonal cycle due to nitrogen deposition is 50-90% of that observed. The subtle interaction between 3-D atmospheric transport, atmospheric nitrogen deposition, and seasonal CO2 uptake results in significant changes in the amplitude of the seasonal cycle of atmospheric CO2. The magnitude of these nitrogen deposition-induced changes in the atmospheric behavior of CO2 is comparable to other processes that are thought to influence global carbon cycle dynamics.

KEYWORDS: DIOXIDE, EXCHANGE, GROWTH, MODEL, SINK

621

Ericsson, T. 1995. Growth and shoot - root ratio of seedlings in relation to nutrient availability. *Plant and Soil 169:205-214.*

The influence of mineral nutrient availability, light intensity and CO2 on growth and shoot:root ratio in young plants is reviewed. Special emphasis in this evaluation is given to data from laboratory experiments with small Betula pendula plants, in which the concept of steady-state nutrition has been applied. Three distinctly different dry matter allocation patterns were observed when growth was limited by the availability of mineral nutrients: 1, Root growth was favoured when N, P or S were the major growth constraints. 2, The opposite pattern obtained when K, Mg and Mn restricted growth. 3, Shortage of Ca, Fe and Zn had almost no effect on the shoot:root ratio. The light regime had no effect on dry matter allocation except at very low photon flux densities (< 6.5 mol m(-2) day(-1)), in which a small decrease in the root fraction was observed. Shortage of CO2 on the other hand, strongly decreased root development, while an increase of the atmospheric CO2 concentration had no influence on dry matter partitioning. An increased allocation of dry matter to below- ground parts was associated with an increased amount of starch in the tissues. Depletion of the carbohydrate stores occurred under all conditions in which root development was inhibited. It is concluded that the internal balance between labile nitrogen and carbon in the root and the shoot system determines how dry matter is being partitioned in the plant. The consistency of this statement with literature data and existing models for shoot:root regulation is examined.

KEYWORDS: ASSIMILATION, BETULA-PENDULA ROTH, BIRCH SEEDLINGS, ELEVATED CO2, NITROGEN STRESS, PHOTON FLUX-DENSITY, PHOTOSYNTHESIS, PLANT NUTRITION, TRANSLOCATION, WHEAT TRITICUM- AESTIVUM

622

Ershova, A.N., and V.A. Khripach. 1996. Effect of epibrassinolide on lipid peroxidation in Pisum sativum at normal aeration and under oxygen deficiency. *Russian Journal of Plant Physiology 43(6):750-752.*

The effect of epibrassinolide on oxidative lipid degradation in pea seedlings was studied at normal aeration and in oxygen- deprived and CO2-enriched media. The content of various products of lipid peroxidation (POL), including the primary derivatives (conjugated dienoic acids) and end products (malonyl dialdehyde, MDA), was shown to decrease in seedlings treated with epibrassinolide (10 mg/l). Epibrassinolide inhibited POL in pea seedlings more strongly than kinetin. These effects became even more pronounced in plants under hypoxia or in the CO2-enriched medium. The content of conjugated dienes declined by 13 and 21% at hypoxia and in the CO2-medium compared to their content in air-grown seedlings, whereas the content of MDA was 38 and 26% below the level in the untreated plants, respectively. We presume that as a protector, epibrassinolide can inhibit the oxidative degradation of lipids in biological membranes and prevent the disruption of membrane structures. Thus it increases the tolerance of plants to deleterious factors.

623

Esler, K.J., P.W. Rundel, and P. Vorster. 1999. Biogeography of prostrate-leaved geophytes in semi-arid South Africa: hypotheses on functionality. *Plant Ecology 142(1-2):105-120.*

Nowhere is the species diversity of geophytes greater than in the five mediterranean-climate ecosystems of the world. Of these, the Cape mediterranean zone of South Africa is the most speciose. While the relative diversity and importance of geophytes of all of the other four mediterranean regions of the world drops off sharply as one moves into adjacent winter- rainfall desert regions, geophytes in the semi-arid to arid Succulent Karoo (including Namaqualand) remain a very important component of the flora, both in terms of abundance and diversity (comprising 13 to 29% of the regional floras in this region). Apart from species richness, there are also a number of interesting geophyte growth forms in this region. One unusual growth form is geophytes with flattened leaves that lie prostrate on the soil surface. At least eight families (Amaryllidaceae, Colchicaceae, Eriospermaceae, Geraniaceae, Hyacinthaceae, Iridaceae, Orchidaceae and Oxalidaceae) exhibit this growth form. While this growth form is relatively common in many geophyte lineages in the Succulent Karoo biome and the Cape mediterranean zone (Fynbos biome), and occurs infrequently through the summer-rainfall temperate regions of Africa, it is virtually absent in other regions worldwide. A null hypothesis is that the prostrate leaved trait is a neutral characteristic, however biogeographical data do not support this. A neutral trait would be unlikely to show such a clear

pattern of distribution. Several alternative hypotheses on the adaptive significance of this growth form are discussed. These include: avoidance of herbivory, reduction in competition from neighbors, creation of a CO2 enriched environment below the leaves, reduction of water loss around the roots, reduction of water loss through transpiration, precipitation of dew on the leaves and maintenance of optimal leaf temperatures for growth.

KEYWORDS: ALLOCATION, BIOMASS, FLORA, LOWLAND COASTAL FYNBOS, SUBSPECIES PUBESCENS

624

Estiarte, M., J. Penuelas, B.A. Kimball, D.L. Hendrix, P.J. Pinter, G.W. Wall, R.L. LaMorte, and D.J. Hunsaker. 1999. Free-air CO2 enrichment of wheat: leaf flavonoid concentration throughout the growth cycle. *Physiologia Plantarum 105(3):423-433.*

To test the predictions that plants will have a larger flavonoid concentration in a future world with a CO2-enriched atmosphere, wheat (Triticum aestivum L. cv. Yecora Rojo) was grown in a field experiment using FACE (free-air CO2 enrichment) technology under two levels of atmospheric CO2 concentration: ambient (370 pmol mol(-1)) and enriched (550 pmol mol(-1)), and under two levels of irrigation: well-watered (100% replacement of potential evapotranspiration) and half-watered. We also studied the effects of CO2 on the concentration of total non-structural carbohydrates (TNC) and nitrogen (N), two parameters hypothesized to be linked to flavonoid metabolism. Throughout the growth cycle the concentration of isoorientin, the most abundant flavonoid, decreased by 62% (from an average of 12.5 mg g(-1) on day of year (DOY) 41 to an average of 4.8 mg g(-1) on DOY 123), whereas the concentration of tricin, another characteristic flavone, increased by two orders of magnitude (from an average of 0.007 mg g(-1) of isoorientin equivalents on DOY 41 to an average of 0.6 mg g(-1) of isoorientin equivalents on DIOY 123). Although flavonoid concentration was dependent on growth stage, the effects of treatments on phenology did not invalidate the comparisons between treatments. CO2-enriched plants had higher flavonoid concentrations (14% more isoorientin, an average of 7.0 mg g(-1) for ambient CO2 vs an average of 8.0 mg g(-1) for enriched CO2), higher TNC concentrations and lower N concentrations in upper canopy leaves throughout the growth cycle. Well-irrigated plants had higher flavonoid concentrations (11% more isoorientin, an average of 7.1 mg g(-1) for half watered vs an average of 7.9 mg g(-1) for well-watered) throughout the growth cycle, whereas the effect of irrigation treatments on TNC and N was more variable. These results are in accordance with the hypotheses that higher carbon availability promoted by CO2-enrichment provides carbon that can be invested in carbon-based secondary compounds such as flavonoids. The rise in atmospheric CO2 may thus indirectly affect wheat-pest relations, alter the pathogen predisposition and improve the UV-B protection by changing flavonoid concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHEMICAL-COMPOSITION, ELEVATED CO2, LEAVES, N-AVAILABILITY, NITROGEN, NUTRIENT BALANCE, SOURCE-SINK RELATIONS, UV-B, WATER-USE

625

Estiarte, M., J. Penuelas, B.A. Kimball, S.B. Idso, R.L. Lamorte, P.J. Pinter, G.W. Wall, and R.L. Garcia. 1994. Elevated co2 effects on stomatal density of wheat and sour orange trees. *Journal of Experimental Botany 45(280):1665-1668.*

No significant differences were found in stomatal densities or stomatal indices of wheat or sour orange trees grown at high CO2 concentrations in two different CO2 enrichment systems (Free-Air CO2 enrichment for wheat and Open-Top Chambers for orange trees). These results are in accordance with most of the previous results obtained in short-term experimental studies which suggest that plants do not acclimate to increasing CO2 concentration by changing stomatal density within a single generation.

KEYWORDS: ANATOMY, ENRICHMENT, GROWTH

626

Ewert, F., and H. Pleijel. 1999. Phenological development, leaf emergence, tillering and leaf area index, and duration of spring wheat across Europe in response to CO2 and ozone. *European Journal of Agronomy 10(3-4):171-184.*

Phenological development, leaf emergence, tillering and leaf area index (LAI), and duration (LAD) of spring wheat cv. Minaret, grown in open-top chambers at different sites throughout Europe for up to 3 years at each site, were investigated in response to elevated CO2 (ambient CO2 x2) and ozone (ambient ozone x1.5) concentrations. Phenological development varied among experiments and was partly explained by differences in temperature among sites and years. There was a weak positive relationship between the thermal rate of development and the mean daylength for the period from emergence to anthesis. Main stems produced on average 7.7 leaves with little variation among experiments. Variation was higher for the thermal rate of leaf emergence, which was partly explained by differences in the rate of change of daylength at plant emergence among seasons. Phenological development, rate of leaf emergence and final leaf number were not affected by CO2 and ozone exposure. Responses of tillering and LAI to CO2 and ozone exposure were significant only in some experiments. However, the direction of responses was consistent for most experiments. The number of tillers and ears per plant, respectively, was increased as a result of CO2 enrichment by about 13% at the beginning of stem elongation (DC31), at anthesis and at maturity. Exposure to ozone had no effect on tillering. LAI was increased as a result of CO2 elevation by about 11% at DC31 and by about 14% at anthesis. Ozone exposure reduced LAI at anthesis by about 9%. No such effect was observed at DC31. There were very few interactive effects of CO2 and ozone on tillering and LAI. Variations in tillering and LAI, and their responses to CO2 and ozone exposure, were partly explained by single linear relationships considering differences in plant density, tiller density and the duration of developmental phases among experiments. Consideration of temperature and incident photosynthetically active radiation in this analysis did not reduce the unexplained variation. There was a negative effect of ozone exposure on leaf area duration at most sites. Direct effects of elevated CO2 concentration on leaf senescence, both positive and negative, were observed in some experiments. There was evidence in several experiments that elevated CO2 concentration ameliorated the negative effect of ozone on leaf area duration. It was concluded from these results that an analysis of the interactive effects of climate, CO2 and ozone on canopy development requires reference to the physiological processes involved.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROPS, ELEVATED CO2, GRAIN QUALITY, GROWTH, TEMPERATURE, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, WINTER-WHEAT, YIELD COMPONENTS

627

Ewert, F., M. van Oijen, and J.R. Porter. 1999. Simulation of growth and development processes of spring wheat in response to CO2 and ozone for different sites and years in Europe using mechanistic crop simulation models. *European Journal of Agronomy 10(3-4):231-247.*

The response of crop growth and yield to CO2 and ozone is known to depend on climatic conditions and is difficult to quantify due to the complexity of the processes involved. Two modified mechanistic crop

simulation models (AFRCWHEAT2-O3 and LINTULCC), which differ in the levels of mechanistic detail, were used to simulate the effects of CO2 (ambient, ambient x2) and ozone (ambient, ambient x1.5) on growth and developmental processes of spring wheat in response to climatic conditions. Simulations were analysed using data from the ESPACE-wheat project in which spring wheat cv. Minaret was grown in open-top chambers at nine sites throughout Europe and for up to 3 years at each site. Both models closely predicted phenological development and the average measured biomass at maturity. However, intermediate growth variables such as biomass and leaf area index (LAI) at anthesis, seasonal accumulated photosynthetically active radiation intercepted by the crop (Sigma IPAR), the average seasonal light use efficiency (LUE) and the light saturated rate of flag leaf photosynthesis (A(sat)) were predicted differently and less accurately by the two models. The effect of CO2 on the final biomass was underestimated by AFRCWHEAT2-O3 due to its poor simulation of the effect of CO2 on tillering, and LAI.LINTULCC overestimated the response of biomass production to changes in CO2 level due to an overprediction of the effect of CO2 on LUE. The measured effect of ozone exposure on final biomass was predicted closely by the two models. The models also simulated the observed interactive effect of CO2 and ozone on biomass production. However, the effects of ozone on LAI, Sigma IPAR and A(sat) were simulated differently by the models and less accurately with LINTULCC for the ozone effects on LAI and Sigma IPAR. Predictions of the variation between sites and years of growth and development parameters and of their responses to CO2 and ozone were poor for both AFRCWHEAT2-O3 and LINTULCC. It was concluded that other factors than those considered in the models such as chamber design and soil properties may have affected the growth and development of cv. Minaret. An analysis of the relationships between growth parameters calculated from the simulations supported this conclusion. In order to apply models for global change impact assessment studies, the difficulties in simulating biomass production in response to CO2 need to be considered. We suggest that the simulation of leaf area dynamics deserves particular attention in this regard.

KEYWORDS: AIR, CLIMATE, EXPOSURE, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, TRITICUM-AESTIVUM, WINTER-WHEAT, YIELD

628

Fajer, E.D. 1989. The effects of enriched CO2 atmospheres on plant-insect herbivore interactions- growth-responses of larvae of the specialist butterfly, Junonia coenia (lepidoptera, nymphalidae). *Oecologia 81(4):514-520.*

629

Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1991. The effects of enriched CO2 atmospheres on the buckeye butterfly, Junonia coenia. *Ecology 72(2):751-754.*

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CLIMATE, LEPIDOPTERA, NOCTUIDAE

630

Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1991. Performance and allocation patterns of the perennial herb, Plantago lanceolata, in response to simulated herbivory and elevated CO2 environments. *Oecologia 87(1):37-42.*

We tested the prediction that plants grown in elevated CO2 environments are better able to compensate for biomass lost to herbivory than plants grown in ambient CO2 environments. The herbaceous perennial Plantago lanceolata (Plantaginaceae) was grown in either near ambient (380 ppm) or enriched (700 ppm) CO2 atmospheres, and then after 4 weeks, plants experienced either 1) no defoliation; 2) every fourth leaf removed by cutting; or 3) every other leaf removed by cutting. Plants were harvested at week 13 (9 weeks after simulated herbivory treatments). Vegetative and reproductive weights were compared, and seeds were counted, weighed, and germinated to assess viability. Plants grown in enriched CO2 environments had significantly greater shoot weights, leaf areas, and root weights, yet had significantly lower reproductive weights (i.e. stalks + spikes + seeds) and produced fewer seeds, than plants grown in ambient CO2 environments. Relative biomass allocation patterns further illustrated differences in plant responses to enriched CO2 atmospheres: enriched CO2-grown plants only allocated 10% of their carbon resources to reproduction whereas ambient CO2-grown plants allocated over 20%. Effects of simulated herbivory on plant performance were much less dramatic than those induced by enriched CO2 atmospheres. Leaf area removal did not reduce shoot weights or reproductive weights of plants in either CO2 treatment relative to control plants. However, plants from both CO2 treatments experienced reductions in root weights with leaf area removal, indicating that plants compensated for lost above-ground tissues, and maintained comparable levels of reproductive output and seed viability, at the expense of root growth.

KEYWORDS: GROWTH

631

Fajer, E.D., M.D. Bowers, and F.A. Bazzaz. 1992. The effect of nutrients and enriched co2 environments on production of carbon-based allelochemicals in plantago - a test of the carbon nutrient balance hypothesis. *The American Naturalist 140(4):707-723.*

In a test of the carbon/nutrient (C/N) balance hypothesis, we grew the perennial herb Plantago lanceolata in different CO2 and nutrient environments and then (1) measured the total allocation to shoots, roots, and reproductive parts and (2) quantified aucubin, catalpol, and verbascoside contents of replicate plants of six genotypes. Plants grown under low- nutrient conditions do have higher concentrations of carbon-based allelochemicals than plants grown under high-nutrient conditions. However, in contrast to the C/N balance hypothesis, plants grown in elevated (700-mu-L.L-1) CO2 conditions had similar, or lower, concentrations of carbon-based allelochemicals than plants grown in ambient (350-mu-L.L-1) CO2 conditions. We suggest that augmented substrate concentrations (i.e., excess carbohydrates) are a necessary but insufficient trigger for increased secondary metabolism; instead, hormonal and/or direct physical cues (such as light) may be essential to synthesize or activate the appropriate enzyme systems. Moreover, although plant genotype significantly affected plant growth, reproduction, and chemistry, we never observed significant genotype-by-CO2 interactions for these factors, which suggests that changing CO2 environments may not improve the fitness of certain genotypes over others.

KEYWORDS: CHEMICAL DEFENSE, DIOXIDE ATMOSPHERES, EXPERIMENTAL ECOLOGICAL GENETICS, HETEROTHECA-SUBAXILLARIS, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LANCEOLATA L, LIMITING CONDITIONS, REPRODUCTIVE EFFORT, VOLATILE LEAF TERPENES

632

Falge, E., R.J. Ryel, M. Alsheimer, and J.D. Tenhunen. 1997. Effects of stand structure and physiology on forest gas exchange: a simulation study for Norway spruce. *Trees-Structure and Function 11(7):436-448.*

The process-based simulation model STAND-FLUX describes canopy water vapor and carbon dioxide exchange based on rates calculated for

individual trees and as affected by local gradients in photon flux density (PFD), atmospheric humidity, atmospheric carbon dioxide concentration, and air temperature. Direct, diffuse, and reflected PFD incident on foliage elements within compartments of individual trees (defined by vertical layers and a series of concentric cylinders centered on the trunk) is calculated for a 3-dimensional matrix of points. Foliage element gas exchange rates are based on estimates of carboxylation, RuBP regeneration, and respiratory capacities as well as the correlated behavior found between stomatal conductance and assimilation rate. Because of the difficulties associated with effective sampling and description of spatial variation in structure and leaf level gas exchange parameters for trees comprising the forest canopy, the significance for canopy water and carbon dioxide exchange of varied representations of tree foliage distribution and of physiology is examined. The additional interactive effects encountered due to changes in tree density and, thus, spatial aggregation or disaggregation of foliage is also studied. The analysis is conducted within the context of observed structural and physiological variation encountered in Norway spruce (Picea abies) stands in the Fichtelgebirge region of central Germany. Potentials for simplifying the three-dimensional canopy gas exchange model without sizable influence on canopy flux rates were small. A relatively large number of sample points within the tree crowns is necessary to obtain consistent calculations of flux rates because of the nonlinear relationship between PFD and net photosynthesis. Transpiration and net photosynthesis for stands with a low leaf area index (LAI) may be obtained from single tree estimates for each tree class weighted by class frequency, while 30 or more trees per class in differing relation to neighboring trees may be necessary to calculate reliable estimates of net photosynthesis in canopies with high LAI. The complexity in structure assumed for modeled trees was important, especially when overall canopy foliage area was either high or low due to spatial heterogeneity in clumping, e.g., potential canopy overlaps or side-lighting. Effects were greater for calculated net photosynthesis than for transpiration, reflecting higher sensitivity of net photosynthesis to differences in light distribution within individual trees. Accuracy in estimates of physiological parameters is equally important, and these characteristics have profound effects on estimated canopy gas exchange rates. While one-dimensional representations of canopy structure or approximations of tree physiological characteristics from other canopies or species may often be necessary in assessing vegetation/atmosphere exchanges, especially in the study of water balance of landscapes or regions, STANDFLUX provides a tool that can aid in evaluating the limitations of these simpler approaches.

KEYWORDS: CANOPY, CONDUCTANCE, DECIDUOUS FOREST, ELEVATED CO2, LEAF, MODEL, PHOTOSYNTHESIS, SCALING CARBON-DIOXIDE, TUSSOCK GRASSES, WATER-VAPOR EXCHANGE

633

Falloon, P.D., P. Smith, J.U. Smith, J. Szabo, K. Coleman, and S. Marshall. 1998. Regional estimates of carbon sequestration potential: linking the Rothamsted Carbon Model to GIS databases. *Biology and Fertility of Soils 27(3):236-241.*

Soil organic matter (SOM) represents a major pool of carbon within the biosphere. It is estimated at about 1400 Pg globally, which is roughly twice that in atmospheric CO2. The soil can act as both a source and a sink for carbon and nutrients, Changes in agricultural land use and climate can lead to changes in the amount of carbon held in soils, thus, affecting the fluxes of CO2 to and from the atmosphere. Some agricultural management practices will lead to a net sequestration of carbon in the soil. Regional estimates of the carbon sequestration potential of these practices are crucial if policy makers are to plan future land uses to reduce national CO, emissions. In Europe, carbon sequestration potential has previously been estimated using data from the Global Change and Terrestrial Ecosystems Soil Organic Matter Network (GCTE SOMNET). Linear relationships between management practices and yearly changes in soil organic carbon were developed and used to estimate changes in the total carbon stock of European soils. To refine these semi-quantitative estimates, the local soil type, meteorological conditions and land use must also be taken into account. To this end, we have modified the Rothamsted Carbon Model, so that it can be used in a predictive manner. with SOMNET data. The data is then adjusted for local conditions using Geographical Information Systems databases. In this paper, we describe how these developments call be used to estimate carbon sequestration at the regional level using a dynamic simulation model linked to spatially explicit data. Some calculations of the potential effects of afforestation on soil carbon stocks in Central Hungary provide a simple example of the system in use.

KEYWORDS: CLIMATE, CO2, SOILS, STORAGE

634

Fangmeier, A., L. De Temmerman, L. Mortensen, K. Kemp, J. Burke, R. Mitchell, M. van Oijen, and H.J. Weigel. 1999. Effects on nutrients and on grain quality in spring wheat crops grown under elevated CO2 concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. *European Journal of Agronomy 10(3-4):215-229.*

Nutrient element concentrations and grain quality were assessed in spring wheat grown under elevated CO2 concentrations and contrasting levels of tropospheric ozone at different nitrogen supply rates at several European sites. Carbon dioxide enrichment proved to affect nutrient concentrations in a complex manner, In green leaves, all elements (with exception of phosphorus and iron) decreased. In contrast, effects on the element composition of grains were restricted to reductions in nitrogen, calcium, sulphur and iron. Ozone exposure resulted in no significant effects on nutrient element concentrations in different tissues in the overall analysis. The nitrogen demand of green tissues was reduced due to CO2 enrichment as shown by reductions in the critical leaf nitrogen concentration and also enhanced nitrogen use efficiency. Reductions in the content of ribulose-bisphosphate carboxylase/oxygenase and repression of the photorespiratory pathway and reduced nitrogen allocation to enzymes driving the photosynthetic carbon oxidation cycle were chiefly responsible for this effect. Thus, nitrogen acquisition by the crop did not match carbon acquisition under CO2 enrichment, Since crop nitrogen uptake from the soil was already completed at anthesis, nitrogen allocated to the grain after anthesis originated from vegetative poors-causing grain nitrogen concentrations to decrease under CO2 enrichment (on average by 15% when CO2 concentrations increased from 360 to 680 mu mol mol(-1)). Correspondingly, grain quality was reduced by CO2 enrichment. The Zeleny value, Hagberg value and dry/wet gluten content decreased significantly with increasing [CO2]. Despite the beneficial impact of CO2 enrichment on growth and yield of C-3 cereal crops, declines in flour quality due to reduced nitrogen content are likely in a future, [CO2]-rich world.

KEYWORDS: AMBIENT AIR, CLIMATE CHANGE, LITTER QUALITY, MINERAL NUTRITION, NORWAY SPRUCE, RISING ATMOSPHERIC CO2, SPRUCE PICEA-ABIES, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, TROPOSPHERIC OZONE

635

Fangmeier, A., U. Gruters, U. Hertstein, A. SandhageHofmann, B. Vermehren, and H.J. Jager. 1996. Effects of elevated CO2, nitrogen supply and tropospheric ozone on spring wheat .1. Growth and yield. *Environmental Pollution 91(3):381-390.*

Spring wheat (Triticum aestivum L. cv. Minaret) was exposed to three CO2 levels, in combination with two nitrogen fertilizer levels and two

levels of tropospheric ozone, from sowing to ripening in open-top chambers. Three additional nitrogen fertilizer treatments were carried out at the lowest and the highest CO2 level, respectively. Plants were harvested at growth stages 31, 65 and 93 and separated into up to eight fractions to gain information about biomass partitioning. CO2 enrichment (263 mu l litre(-1) above ambient levels) drastically increased biomass of organs serving as long-term carbohydrate pools. Peduncle weight increased by 92%, stem weight by 73% and flag leaf sheath weight by 59% at growth stage 65. Average increase in shoot biomass due to CO2 enrichment amounted to 51% at growth stage 65 and 36% at final harvest. Average yield increase was 34%. Elevated nitrogen application was most effective on biomass of green tissues. Yield was increased by 30% when nitrogen application was increased from 150 to 270 kg N ha(-1). Significant interactions were observed between CO2 enrichment and nitrogen application. Yield increase due to CO2 ranged from 23% at 120 kg N to 47% at 330 kg N. Triticum aestivum cv. Minaret was not very responsive to ozone at 1.5 times ambient levels. 1000 grain weight was slightly decreased, which was compensated by an increased number of grains.

KEYWORDS: CARBOHYDRATE, CARBON DIOXIDE, DRY-MATTER, NUTRITION, RESPONSES, STEMS, STORAGE, STRESS, TEMPERATURE, WINTER-WHEAT

636

Fangmeier, A., U. Gruters, P. Hogy, B. Vermehren, and H.J. Jager. 1997. Effects of elevated CO2 nitrogen supply and tropospheric ozone on spring wheat .2. Nutrients (N, P, K, S, Ca, Mg, Fe, Mn, Zn). *Environmental Pollution 96(1):43-59.*

CO2 enrichment is expected to alter leaf demand for nitrogen and phosphorus in plant species with C-3 carbon dioxide fixation pathway, thus possibly causing nutrient imbalances in the tissues and disturbance of distribution and redistribution patterns within the plants. To test the influence of CO2 enrichment and elevated tropospheric ozone in combination with different nitrogen supply, spring wheat (Tritium aestivum L. cv. Minaret) was exposed to three levels of CO2 (361, 523, and 639 mu l liter(-1), 24 h mean from sowing to final harvest), two levels of ozone (28.4 and 51.3 nl litre(-1)) and two levels of nitrogen supply (150 and 270 kg ha(-1)) in a full-factorial design in open-top field chambers. Additional fertilization experiments (120, 210, and 330 kg N ha(-1)) were carried out at low and high CO2 levels. Macronutrients (N, P, K, S, Ca, Mg) and three micronutrients (Mn, Fe, Zn) were analysed in samples obtained at three different developmental stages: beginning of shoot elongation, anthesis, and ripening. At each harvest, plant samples were separated into different organs (green and senescent leaves, stem sections, ears, grains). According to analyses of tissue concentrations at the beginning of shoot elongation, the plants were sufficiently equipped with nutrients. Elevated ozone levels neither affected tissue concentrations nor shoot uptake of the nutrients. CO2 and nitrogen treatments affected nutrient uptake, distribution and redistribution in a complex manner. CO2 enrichment increased nitrogen-use efficiency and caused a lower demand for nitrogen in green tissues which was reflected in a decrease of critical nitrogen concentrations, lower leaf nitrogen concentrations and lower nitrogen pools in the leaves. Since grain nitrogen uptake during grain filling depended completely on redistribution from vegetative pools in green tissues, grain nitrogen concentrations fell considerably with severe implications for grain quality. Ca, S, Mg and Zn in green tissues were influenced by CO2 enrichment in a similar manner to nitrogen. Phosphorus concentrations in green tissues, on the other hand, were not, or only slightly, affected by elevated CO2. In stems, 'dilution' of all nutrients except manganese was observed, caused by the huge accumulation of water soluble carbohydrates, mainly fructans, in these tissues under CO2 enrichment. Whole shoot uptake was either remarkably increased (K, Mn, P, Mg), nearly unaffected (N, S, Fe, Zn) or decreased (Ca) under CO2 enrichment. Thus, nutrient cycling in plant-soil systems is expected to be altered under CO2 enrichment. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBOHYDRATE, CARBON DIOXIDE, GROWTH-RESPONSE, MINERAL NUTRITION, PHOTOSYNTHESIS, SOURCE-SINK RELATIONS, STRESS, VEGETATION

637

Fangmeier, A., U. Gruters, B. Vermehren, and H.J. Jager. 1996. Responses of some cereal cultivars to CO2 enrichment and tropospheric ozone at different levels of nitrogen supply. *Journal of Applied Botany-Angewandte Botanik 70(1-2):12-18.*

Two cultivars of spring wheat (Triticum aestivum L. cv. 'Nandu' and cv. 'Minaret') and one cultivar of spring barley (Hordeum vulgare L. cv. 'Alexis') were exposed to CO2 enrichment (concentrations ranging from 363 to 650 mu l l(-1)), ozone (ambient and 1.7 times ambient levels) at different levels of nitrogen nutrition in open-top field chambers from sowing to maturity. CO2 increased grain yield and shoot biomass, barley showing the smallest response and wheat 'Nandu' being most responsive. The cultivars were rather insensitive to ozone, however, a decrease of thousand grain weight was observed in one of the wheat cultivars ('Minaret') at high ozone levels. In this cultivar, interactions between CO2 and ozone were observed. Elevated CO2 appeared to be protective against impairments caused by ozone. CO2 and nitrogen supply strongly interacted. CO2 fertilizing effects on grain yield of wheat 'Minaret' ranged from 22.9 % at 120 kg N ha(-1) to 47.4 % at 330 kg N ha(-1). Increase in grain yield by CO2 was accompanied with a decrease of grain nitrogen content. Grain yield increase and grain nitrogen content depression exactly compensated each other and led to constant amounts of nitrogen stored in the grains on an area unit basis independent from the applied CO2 concentration. The grain quality, assessed as nitrogen content, was severely decreased by CO2 enrichment. The regressions obtained from the data suggest that nearly twice the nitrogen supply will be required to maintain the nitrogen content in grains at the same level if CO2 concentrations rise from the current 363 mu l l(-1) (seasonal mean 1994) to 650 mu l l(-1).

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, OPEN-AIR FUMIGATION, PHOTOSYNTHESIS, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L, VEGETATION, WINTER-WHEAT, YIELD

638

Farage, P.K., I.F. McKee, and S.P. Long. 1998. Does a low nitrogen supply necessarily lead to acclimation of photosynthesis to elevated CO2? *Plant Physiology 118(2):573-580.*

Long-term exposure of plants to elevated partial pressures of CO, (pCO(2)) often depresses photosynthetic capacity. The mechanistic basis for this photosynthetic acclimation may involve accumulation of carbohydrate and may be promoted by nutrient limitation. However, our current knowledge is inadequate for making reliable predictions concerning the onset and extent of acclimation. Many studies have sought to investigate the effects of N supply but the methodologies used generally do not allow separation of the direct effects of limited N availability from those caused by a N dilution effect due to accelerated growth at elevated pCO(2). To dissociate these interactions, wheat (Triticum aestivum L.) was grown hydroponically and N was added in direct proportion to plant growth. Photosynthesis did not acclimate to elevated pCO(2) even when growth was restricted by a low-N relative addition rate. Ribulose-l, 5-bisphosphate carboxylase/oxygenase activity and quantity were maintained, there was no evidence for triose phosphate limitation of photosynthesis, and tissue N content remained within the range recorded for healthy wheat plants. In contrast, wheat grown in sand culture with N supplied at a fixed concentration suffered

photosynthetic acclimation at elevated pCO(2) in a low-N treatment. This was accompanied by a significant reduction in the quantity of active ribulose-l, 5- bisphosphate carboxylase/oxygenase and leaf N content.

KEYWORDS: C-3 PLANTS, CARBON, ENRICHMENT, GROWTH, PERSPECTIVE, PRODUCTIVITY, RESPONSES, RISING ATMOSPHERIC CO2, TREES, WHEAT

639

Faria, T., M. Vaz, P. Schwanz, A. Polle, J.S. Pereira, and M.M. Chaves. 1999. Responses of photosynthetic and defence systems to high temperature stress in Quercus suber L-seedlings crown under elevated CO2. *Plant Biology 1(3):365-371.*

Growth in elevated CO2 led to an increase in biomass production per plant as a result of enhanced carbon uptake and lower rates of respiration, compared to ambient CO2-grown plants. No down-regulation of photosynthesis was found after six months of growth under elevated CO2. Photosynthetic rates at 15 degrees C or 35 degrees C were also higher in elevated than in ambient CO2-grown plants, when measured at their respective CO2 growth condition. Stomata of elevated CO2-grown plants were less responsive to temperature as compared to ambient CO2 plants. The after effect of a heat-shock treatment (4 h at 45 degrees C in a chamber with 80% of relative humidity and 800-1000 mu mol m(-2) s(-1) photon flux density) on A(max) was less in elevated than in ambient CO2-grown plants. At the photochemical level, the negative effect of the heat-shock treatment was slightly more pronounced in ambient than in elevated CO2-grown plants. A greater tolerance to oxidative stress caused by high temperatures in elevated CO2-grown plants, in comparison to ambient CO2 plants, is suggested by the increase in superoxide dismutase activity, after 1 h at 45 degrees C, as well as its relatively high activity after 2 and 4 h of the heat shock in the elevated CO2-grown plants in contrast with the decrease to residual levels of superoxide dismutase activity in ambient CO2-grown plants immediately after 1 h at 45 degrees C. The observed increase in catalase after 1 h at 45 degrees C in both ambient and elevated CO2-grown plants, can be ascribed to the higher rates of photorespiration and respiration under this high temperature.

KEYWORDS: ACCLIMATION, ANTIOXIDATIVE ENZYMES, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, DOWN-REGULATION, PHOTOSYSTEM, PICEA-ABIES L, PLANTS, RISING ATMOSPHERIC CO2, SUPEROXIDE-DISMUTASE

640

Faria, T., D. Wilkins, R.T. Besford, M. Vaz, J.S. Pereira, and M.M. Chaves. 1996. Growth at elevated CO2 leads to down-regulation of photosynthesis and altered response to high temperature in Quercus suber L seedlings. *Journal of Experimental Botany 47(304):1755-1761.*

The effects of growth at elevated CO2 on the response to high temperatures in terms of carbon assimilation (net photosynthesis, stomatal conductance, amount and activity of Rubisco, and concentrations of total soluble sugars and starch) and of photochemistry (for example, the efficiency of excitation energy captured by open photosystem II reaction centres) were studied in cork oak (Quercus suber L.). Plants grown in elevated CO2 (700 ppm) showed a down-regulation of photosynthesis and had lower amounts and activity of Rubisco than plants grown at ambient CO2 (350 ppm), after 14 months in the greenhouse. At that time plants were subjected to a heat- shock treatment (4 h at 45 degrees C in a chamber with 80% relative humidity and 800-1000 mu mol m(-2) s(-1) photon flux density). Growth in a CO2-enriched atmosphere seems to protect cork oak leaves from the short-term effects of high temperature. Elevated CO2 plants had positive net carbon uptake rates during the heat shock treatment whereas plants grown at ambient CO2 showed negative rates. Moreover, recovery was faster in high CO2-grown plants which, after 30 min at 25 degrees C, exhibited higher net carbon uptake rates and lower decreases in photosynthetic capacity (A(max) as well as in the efficiency of excitation energy captured by open photosystem II reaction centres (F-v/F-m) than plants grown at ambient CO2. The stomata of elevated CO2 plants were also less responsive when exposed to high temperature.

KEYWORDS: ACCLIMATION, CHLOROPHYLL FLUORESCENCE, ENZYMES, EXPRESSION, GENES, LEAVES, MECHANISM, PROTEINS, RUBISCO, TREES

641

Farnsworth, E.J., and F.A. Bazzaz. 1995. Inter-generic and intra-generic differences in growth, reproduction, and fitness of 9 herbaceous annual species grown in elevated co2 environments. *Oecologia 104(4):454-466.*

In assessing the capacity of plants to adapt to rapidly changing global climate, we must elucidate the impacts of elevated carbon dioxide on reproduction, fitness and evolution. We investigated how elevated CO2 influenced reproduction and growth of plants exhibiting a range of floral morphologies, the implications of shifts in allocation for fitness in these species, and whether related taxa would show similar patterns of response. Three herbaceous, annual species each of the genera Polygonum, Ipomoea, and Cassia were grown under 350 or 700 ppm CO2. Vegetative growth and reproductive output were measured non-destructively throughout the full life span, and vegetative biomass was quantified for a subsample of plants in a harvest at first flowering. Viability and germination studies of seed progeny were conducted to characterize fitness precisely. Early vegetative growth was often enhanced in high- CO2 grown plants of Polygonum and Cassia (but not Ipomoea). However, early vegetative growth was not a strong predictor of subsequent reproduction. Phenology and production of floral buds, flowers, unripe and abscised fruits differed between CO2 treatments, and genera differed in their reproductive and fitness responses to elevated CO2. Polygonum and Cassia species showed accelerated, enhanced reproduction, while Ipomoea species generally declined in reproductive output in elevated CO2. Seed "quality" and fitness (in terms of viability and percentage germination) were not always directly correlated with quantity produced, indicating that output alone may not reliably indicate fitness or evolutionary potential. Species within genera typically responded more consistently to CO2 than unrelated species. Cluster analyses were performed separately on suites of vegetative and reproductive characters. Some species assorted within genera when these reproductive responses were considered, but vegetative responses did not reflect taxonomic affinity in these plants. Congeners may respond similarly in terms of reproductive output under global change, but fitness and prognoses of population persistence and evolutionary performance can be inferred only rarely from examination of vegetative characters alone.

KEYWORDS: ALLOCATION, AMBIENT, CARBON DIOXIDE, CASSIA-FASCICULATA, ENRICHMENT, FECUNDITY, INTRASPECIFIC VARIATION, OVULE ABORTION, PLANTS, SEED PRODUCTION

642

Farnsworth, E.J., A.M. Ellison, and W.K. Gong. 1996. Elevated CO2 alters anatomy, physiology, growth, and reproduction of red mangrove (Rhizophora mangle L). *Oecologia 108(4):599-609.*

Mangroves, woody halophytes restricted to protected tropical coasts, form some of the most productive ecosystems in the world, but their capacity to act as a carbon source or sink under climate change is unknown. Their ability to adjust growth or to function as potential carbon sinks under conditions of rising atmospheric CO2 during global

change may affect global carbon cycling, but as yet has not been investigated experimentally. Halophyte responses to CO2 doubling may be constrained by the need to use carbon conservatively under water-limited conditions, but data are lacking to issue general predictions. We describe the growth, architecture, biomass allocation, anatomy, and photosynthetic physiology of the predominant neotropical mangrove tree, Rhizophora mangle L., grown solitarily in ambient (350 mu ll(-1)) and double-ambient (700 mu ll(-1)) CO2 concentrations for over 1 year. Mangrove seedlings exhibited significantly increased biomass, total stem length, branching activity, and total leaf area in elevated CO2. Enhanced total plant biomass under high CO2 was associated with higher root:shoot ratios, relative growth rates, and net assimilation rates, but few allometric shifts were attributable to CO2 treatment independent of plant size. Maximal photosynthetic rates were enhanced among high-CO2 plants while stomatal conductances were lower, but the magnitude of the treatment difference declined over time, and high-CO2 seedlings showed a lower P-max at 700 mu ll(-1) CO2 than low-CO2 plants transferred to 700 mu ll(-1) CO2: possible evidence of downregulation. The relative thicknesses of leaf cell layers were not affected by treatment. Stomatal density decreased as epidermal cells enlarged in elevated CO2. Foliar chlorophyll, nitrogen, and sodium concentrations were lower in high CO2. Mangroves grown in high CO2 were reproductive after only 1 year of growth (fully 2 years before they typically reproduce in the field), produced aerial roots, and showed extensive lignification of the main stem; hence, elevated CO2 appeared to accelerate maturation as well as growth. Data from this long- term study suggest that certain mangrove growth characters will change flexibly as atmospheric CO2 increases, and accord with responses previously shown in Rhizophora apiculata. Such results must be integrated with data from sea-level rise studies to yield predictions of mangrove performance under changing climate.

KEYWORDS: ATMOSPHERIC CO2, AVICENNIA-MARINA, CARBON DIOXIDE, CARIBBEAN REGION, CLIMATE CHANGE, ECOSYSTEM COLLAPSE, ESTUARINE MARSH, HOLOCENE ANALOGS, INTERSPECIFIC VARIATION, SEA-LEVEL RISE

643

Farrar, J.F., and M.L. Williams. 1991. The effects of increased atmospheric carbon-dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment 14(8):819-830.*

Herbaceous C3 plants grown in elevated CO2 show increases in carbon assimilation and carbohydrate accumulation (particularly starch) within source leaves. Although changes in the partitioning of biomass between root and shoot occur, the proportion of this extra assimilate made available for sink growth is not known. Root:shoot ratios tend to increase for CO2-enriched herbaceous plants and decrease for CO2-enriched trees. Root:shoot ratios for cereals tend to remain constant. In contrast, elevated temperatures decrease carbohydrate accumulation within source and sink regions of a plant and decrease root:shoot ratios. Allometric analysis of at least two species showing changes in root:shoot ratios due to elevated CO2 show no alteration in the whole-plant partitioning of biomass. Little information is available for interactions between temperature and CO2. Cold-adapted plants show little response to elevated levels of CO2, with some species showing a decline in biomass accumulation. In general though, increasing temperature will increase sucrose synthesis, transport and utilization for CO2-enriched plants and decrease carbohydrate accumulation within the leaf. Literature reports are discussed in relation to the hypothesis that sucrose is a major factor in the control of plant carbon partitioning. A model is presented in support.

KEYWORDS: ABSCISIC- ACID, CARBOHYDRATE CONTENT, CO2-ENRICHMENT, DARK RESPIRATION, ELEVATED CO2, PHASEOLUS-VULGARIS, PLANT GROWTH, POTATO-TUBERS, SOYBEAN PHYSIOLOGY, SUGAR-BEET

644

Favis-Mortlock, D.T., and S.J.T. Guerra. 1999. The implications of general circulation model estimates of rainfall for future erosion: a case study from Brazil. *Catena 37(3-4):329-354.*

One consequence of global change will be shifts in the probability of occurrence of soil erosion by water. This could have serious consequences for those areas of the world which are present-day 'hotspots' for erosion. By means of a case study, this paper suggests an approach to quantifying the change in risk of serious erosion for sites in such areas. The case study focuses on future erosion under intensive soya bean cultivation in the Mate Grosso area of Brazil. On the area's highly erodible latosols, current erosion problems are severe. Scenarios of change future climate change are taken from general circulation models (GCMs) and used to perturb current- climate weather data. These are input to an erosion model (water erosion prediction project (WEPP)-CO2), together with local knowledge regarding current and probable future land use, in order to estimate future changes in erosion rates. WEPP- simulated average annual sediment yield increases in one of the scenarios and decreases in the other two, reflecting the range of uncertainty in predictions of future rainfall. Using the 'best-guess' climate scenario from the UK Meteorological Office's HADCM2 GCM, the increase in mean annual sediment yield is 27%. Increases are disproportionately greater in wetter years. Average rates for individual months increase by over 100%. Erosion increases most on those parts of the hillslope profile which are currently hardest-hit by erosion. At present, an annual sediment yield of 5 t ha(-1) is currently exceeded in about 1 year in 2. The HADCM2 simulations suggest that an equal or greater rate will occur in about 70% of years by around 2050. A rate of at least 10 t ha(-1) yr(-1) is currently exceeded in about 1 year in 5. The HADCM2 simulations suggest that this will rise, to about 1 year in 4.

KEYWORDS: ADJUSTMENTS, CLIMATE CHANGE, ELEVATED CO2, FARMER SCENARIO, PRESENT TECHNOLOGY, RESPONSES, SIMULATIONS, SOIL-EROSION, SOUTH-DOWNS, WHEAT YIELD

645

Fearnside, P.M. 1999. Plantation forestry in Brazil: the potential impacts of climatic change. *Biomass & Bioenergy 16(2):91-102.*

Most climatic changes predicted to occur in Brazil would reduce yields of silvicultural plantations, mainly through increased frequency and severity of droughts brought on by global warming and by reduction of water vapor sources in Amazonia caused by deforestation. Some additional negative effects could result from changes in temperature, and positive effects could result from CO2 enrichment. The net effects would be negative, forcing the country to expand plantations onto less-productive land, requiring increased plantation area land consequent economic losses) out of proportion to the climatic change itself. These impacts would affect carbon sequestration and storage consequences of any plans for subsidizing silviculture as a global warming mitigation option. Climate change can be expected to increase the area of plantations needed to supply projected internal demand for and exports of end products from Brazil. June-July-August (dry season) precipitation reductions indicated by simulations reported by the Intergovernmental Panel on Climate Change (IPCC) correspond to rainfall declines in this critical season of approximately 34% in Amazonia, 39% in Southern Brazil and 61% in the Northeast. As an example, if rainfall in Brazilian plantation areas (most of which are now in Southern Brazil) were to decline by 50%, the area needed in 2050 would expand by an estimated 38% over the constant climate case, bringing the total plantation area to 4.5 times the 1991 area. These large areas of additional plantations imply substantial social and environmental impacts. Further addition of

plantation area as a global warming response option would augment these impacts, indicating the need for caution in evaluating carbon sequestration proposals. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: AMAZON BASIN, CARBON

646

Feng, X.H., and S. Epstein. 1996. Climatic trends from isotopic records of tree rings: The past 100-200 years. *Climatic Change 33(4):551-562.*

There has been a great deal of discussion about global warming from accumulation of anthropogenic greenhouse gases in the atmosphere (Houghton et al., 1990). Relatively less attention has been paid to spatial and/or temporal climatic variations that may be associated with a warmer climate (Rind et al., 1989) or with anthropogenic activities (Schneider, 1994). In this article; we show that an increase in climatic variability may have started. Fourteen isotopic time series of tree rings are presented. These trees were randomly collected from world- wide locations and cover time periods of 120 to over 200 years. The isotopic records show increasing delta D values that suggest a consistent and progressive warming occurred in the 19th century in all locations where the trees were sampled. The rate of warming is greater at relatively cold locations than at warm locations with two exceptions. The records also suggest greater climatic variations both temporally and spatially in the 20th century than in the 19th century.

KEYWORDS: ATMOSPHERIC CO2, CELLULOSE, D-H RATIO, D/H RATIOS, ENRICHMENT, LEAF WATER, NON-EXCHANGEABLE HYDROGEN, NORTH-AMERICA, PRECIPITATION, VARIABILITY

647

Ferguson, S.A. 1997. A climate-change scenario for the Columbia River basin. *Usda Forest Service Pacific Northwest Research Station Research Paper (499):CP1-CP&.*

This work describes the method used to generate a climate- change scenario for the Columbia River basin. The scenario considers climate patterns that may change if the atmospheric concentration of carbon dioxide (CO2), or its greenhouse gas equivalent, were to double over pre-Industrial Revolution values. Given the current rate of increase in atmospheric CO2 concentration, doubling could occur within the next 50 to 100 years. The Columbia River basin is in a transition climate zone between predominating maritime to the west, arctic to the north, and continental to the east. Consequently, it is difficult to characterize through means and averages. Therefore, many of the current stochastic methods for developing climate-change scenarios cannot directly apply to the basin. To circumvent this problem, a composite approach was taken to generate a climate scenario that considers knowledge of current regional climate controls, available output from general circulation and regional climate models, and observed changes in climate. The resulting climate-change scenario suggests that precipitation could increase substantially during winter (+20 to +50 percent) and moderately during spring and autumn (+5 to +35 percent). A slight decrease (0 to -5 percent) in summer precipitation is possible, except for the southeastern portions of the basin that may experience an increase in convective precipitation (+5 percent). Low- elevation (<1 kilometer) temperatures throughout the year may increase 1 to 3 degrees C, with greatest increases during winter. This amount of temperature change is possible because of an expected loss of low-elevation snow cover. At high elevations, increased cloud cover could cause average temperatures to decrease during winter but be synchronized with possible warming at low elevations during summer. The diurnal range of temperature could decrease, especially in summer and autumn.

KEYWORDS: INCOMPLETE, MODEL, PRECIPITATION, TEMPERATURE, UNITED-STATES

648

Fernandez, M.D., A. Pieters, C. Donoso, W. Tezara, M. Azkue, C. Herrera, E. Rengifo, and A. Herrera. 1998. Effects of a natural source of very high CO2 concentration on the leaf gas exchange, xylem water potential and stomatal characteristics of plants of Spatiphylum cannifolium and Bauhinia multinervia. *New Phytologist 138(4):689-697.*

The effect of a very high CO2 mole fraction (27 000-35 000 mu mol mol(-1)) on photosynthesis and water relations was studied during the dry and the rainy season in plants of Spatiphylum cannifolium (Dryand.) Schott and Bauhinia multinervia (H.B.K.) DC. growing near natural cold CO2 springs. Xylem water potential in plants of both species was lowered by drought, high CO2 growth-concentration decreasing it further in S. cannifolium. In plants of both species growing under high CO2 concentration photosynthetic rates measured at a CO2 mole fraction of 1000 mu mol mol(-1) were higher than in plants growing at ambient CO2 mole fraction and measured at 350 mu mol mol(-1). The response was the result of a direct effect of CO2 on the photosynthetic machinery. Changes in carboxylation efficiency in response to high CO2 were found during the rainy season, with an increase in S. cannifolium and a decrease in B. multinervia; a significant interaction between growth CO2 concentration and season in B. multinervia resulted from significant effects of both factors. An increase in intrinsic water-use efficiency due to high CO2 was determined in both species by an increase in photosynthetic rate as well as a decrease in leaf conductance. In high-CO2 plants of S. cannifolium a 71 % decrease in stomatal density and 73 % in stomatal index suggested that CO2 affected stomatal initiation, whereas in B. multinervia an 85 % decrease in stomatal index and a 72 % decrease in stomatal density indicated that CO2 influenced stomatal initiation as well as epidermal cell expansion. Our results indicate that very high CO2 concentrations did not inhibit photosynthesis in these species, and that growth under high CO2 allowed plants to attain carbon balances higher than those of plants growing under low CO2. This was particularly so during the dry season, since the photosynthetic rates at the corresponding ambient concentration were higher in plants nearer the springs, and carboxylation efficiency and some stomatal characteristics of both species apparently acclimated to high CO2, but patterns were not consistent and bore no obvious relationship to photosynthetic capacity.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, DENSITY, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHESIS, SCIRPUS- OLNEYI, USE EFFICIENCY

649

FerrarioMery, S., M.C. Thibaud, T. Betsche, M.H. Valadier, and C.H. Foyer. 1997. Modulation of carbon and nitrogen metabolism, and of nitrate reductase, in untransformed and transformed Nicotiana plumbaginifolia during CO2 enrichment of plants grown in pots and in hydroponic culture. *Planta 202(4):510-521.*

Transformed plants of Nicotiana plumbaginifolia Viv. constitutively expressing nitrate reductase (35S-NR) or beta- glucuronidase (35S-GUS) and untransformed controls were grown for two weeks in a CO2-enriched atmosphere. Whereas CO2 enrichment (1000 mu l. 1(-1)) resulted in an increase in the carbon (C) to nitrogen (N) ratio of both the tobacco lines grown in pots with vermiculite, the C/N ratio was only slightly modified when plants were grown in hydroponic culture in high CO2 compared to those grown in air. Constitutive nitrate reductase (NR) expression per se did not change the C/N ratio of the shoots or roots. Biomass accumulation was similar in both types of plant when hydroponic or pot-grown material, grown in air or high CO2, were

compared. Shoot dry matter accumulation was primarily related to the presence of stored carbohydrate (starch and sucrose) in the leaves. In the pot- grown tobacco, growth at elevated CO2 levels caused a concomitant decrease in the N content of the leaves involving losses in NO3- and amino contrast, the N content and composition were similar in all plants grown in hydroponic culture. The 35S-NR plants grown in air had higher foliar maximum extractable NR activities and increased glutamine levels (on a chlorophyll or protein basis) than the untransformed controls. These increases were maintained following CO2 enrichment when the plants were grown in hydroponic culture, suggesting that an increased flux through nitrogen assimilation was possible in the 35S-NR plants. Under CO2 enrichment the NR activation state in the leaves was similar in all plants. When the 35S-NR plants were grown in pots, however, foliar NR activity and glutamine content fell in the 35S-NR transformants to levels similar to those of the untransformed controls. The differences in NR activity between untransformed and 35S-NR leaves were much less pronounced in the hydroponic than in the pst-grown material but the difference in total extractable NR activity was more marked following CO2 enrichment. Foliar NR message levels were decreased by CO2 enrichment in all growth conditions but this was much more pronounced in pot-grown material than in that grown hydroponically. Since beta-glucuronidase (GUS) activity and message levels in 35S-GUS plants grown under the same conditions of CO2 enrichment (to test the effects of CO2 enrichment on the activity of the 35S promoter) were found to be constant, we conclude that NR message turnover was specifically accelerated in the 35S-NR plants as well as in the untransformed controls as a result of CO2 enrichment. The molecular and metabolic signals involved in increased NR message and protein turnover are not known but possible effecters include NO3-, glutamine and asparagine. We conclude that plants grown in hydroponic culture have greater access to N than those grown in pots. Regardless of the culture method, CO2 enrichment has a direct effect on NR mRNA stability.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CONSTITUTIVE EXPRESSION, DIOXIDE ENRICHMENT, ETIOLATED BARLEY LEAVES, GENE-EXPRESSION, GLUTAMINE-SYNTHETASE, LIGHT, PHOTOSYNTHESIS, TOMATO

650

Ferris, R., I. Nijs, T. Behaeghe, and I. Impens. 1996. Contrasting CO2 and temperature effects on leaf growth of perennial ryegrass in spring and summer. *Journal of Experimental Botany 47(301):1033-1043.*

The effects of increased atmospheric carbon dioxide (CO2) of 700 mu mol mol(-1) and increased air temperature of +4 degrees C were examined in Lolium perenne L. cv. Vigor, growing in semi-controlled greenhouses, Leaf growth, segmental elongation rates (SER), water relations, cell wall (tensiometric) extensibility (%P) and epidermal cell lengths (ECL) were measured in expanding leaves in spring and summer. In elevated CO2, shoot dry weight (SDW) increased in mid-summer, In both seasons, SDW decreased in elevated air temperatures with this reduction being greater in summer as compared to spring, Specific leaf area (SLA) decreased in elevated CO2 and in CO2 x temperature in both seasons, In spring, increased leaf extension and SER in elevated CO2 were linked with increased ECL, %P and final leaf size whilst in summer all were reduced, In high temperature, leaf extension, SER, %P and final leaf size were reduced in both seasons. In elevated CO2 x temperature, leaf extension, SER, %P, and ECL increased in spring, but final leaf size remained unaltered, whilst in summer all decreased. Mid-morning water potential did not differ with CO2 or temperature treatments. Leaf turgor pressure increased in elevated CO2 in spring and remained similar to the control in summer whilst solute potential decreased in spring and increased in summer, Contrasting seasonal growth responses of L. perenne in response to elevated CO2 and temperature suggests pasture management may change in the future, The grazing season may be prolonged, but whole season productivity may become more variable than today.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CELL-GROWTH, DIVERSE ALTITUDINAL RANGES, ELEVATED CO2, EXPANSION, GROWING LEAVES, LOLIUM-TEMULENTUM, PLANT GROWTH, RESPONSES, WATER RELATIONS

651

Ferris, R., I. Nijs, T. Behaeghe, and I. Impens. 1996. Elevated CO2 and temperature have different effects on leaf anatomy of perennial ryegrass in spring and summer. *Annals of Botany 78(4):489-497.*

Mature second leaves of Lolium perenne L. cv. Vigor, were sampled in a spring and summer regrowth period. Effects of CO2 enrichment and increased air temperature on stomatal density, stomatal index, guard cell length, epidermal cell density, epidermal cell length and mesophyll cell area were examined for different positions on the leaf and seasons of growth. Leaf stomatal density was smaller in spring but greater in summer in elevated CO2 and higher in both seasons in elevated temperature and in elevated CO2 x temperature relative to the respective controls. In spring, leaf stomatal index was reduced in elevated CO2 but in summer it varied with position on the leaf. In elevated temperature, stomatal index in both seasons was lower at the tip/middle of the leaf but slightly higher at the base. In elevated CO2 x temperature, stomatal index varied with position on the leaf and between seasons. Leaf epidermal cell density was higher in all treatments relative to controls except in elevated CO2 (spring) and elevated CO2 x temperature (summer), it was reduced at the leaf base. In all treatments, stomatal density and epidermal cell density declined from leaf tip to base, whilst guard cell length showed an inverse relationship, increasing towards the base. Leaf epidermal cell length and mesophyll cell area increased in elevated CO2 in spring and decreased in summer. In elevated CO2 x temperature leaf epidermal cell length remained unaltered in spring compared to the control but decreased in summer. Stomatal conductance was lower in all treatments except in summer in elevated CO2 it was higher than in the ambient CO2. These contrasting responses in anatomy to elevated CO2 and temperature provide information that might account. for differences in seasonal leaf area development observed in L. perenne under the same conditions. (C) 1996 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, POPLAR CLONES, RESPONSES, STOMATAL DENSITY, WATER

652

Ferris, R., and G. Taylor. 1993. Contrasting effects of elevated co2 on the root and shoot growth of 4 native herbs commonly found in chalk grassland. *New Phytologist 125(4):855-866.*

The aim of this study was to investigate the impact of ambient (345 mu l l(-1)) and elevated (590 mu l l(-1)) CO2 on the root and shoot growth of four native chalk grassland herbs: Sanguisorba minor Scop. (salad burnet), Lotus corniculatus L. (birdsfoot trefoil), Anthyllis vulneraria L. (kidney vetch) and Plantage media L. (hoary plantain). Elevated CO2 had contrasting effects on both shoot and root growth of the four species studied. Both leaf expansion and production were stimulated by elevated CO2 for S. minor, L. corniculatus and P. media, whilst for A. vulneraria, only leaflet shape appeared to be altered by elevated CO2, with the production of broader leaflets, compared with those produced in ambient CO2. After 100 d shoot biomass was enhanced in elevated CO2 for S. minor and L. corniculatus, whilst there was no effect of elevated CO2 on shoot biomass for A. vulneraria or P. media. Contrasting effects of CO2 were also apparent for measurements of specific leaf area (SLA), which

increased for L. corniculatus, decreased for A. vulneraria and remained unaltered for S. minor and P. media in elevated compared with ambient CO2. Elevated CO2 also had contrasting effects on both the growth and morphology of roots. The accumulation of root biomass was stimulated following exposure to elevated CO2 for S. minor and L. corniculatus whilst there was no effect on root biomass for A. vulneraria or P. media. Root length was measured on three occasions during the 100 d and revealed that exposure to elevated CO2 promoted root extension in S. minor, L. corniculatus and P. media, but not in A. vulneraria. Specific root length (SRL, length per unit dry weight) was increased in elevated CO2 for one species, P. media, whilst the root to shoot ratio of all four species remained unchanged by CO2. These results show that four native herbs differ in their response to CO2, suggesting that the structure of this plant community may be altered in the future.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENRICHMENT, LEAF ANATOMY, PHOTOSYNTHESIS, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE

653

Ferris, R., and G. Taylor. 1994. Elevated co2, water relations and biophysics of leaf extension in 4 chalk grassland herbs. *New Phytologist 127(2):297-307.*

Diurnal measurements of leaf or leaflet extension, water relations and cell wall extensibility (phi) were made on young growing leaves of four chalk downland herbs (Sanguisorba minor Scop., Lotus corniculatus L., Anthyllis vulneraria L. and Plantago media L.) growing in controlled environment cabinets and exposed to either ambient or elevated CO2. This study revealed differences in the effect of CO2 and the control of leaf growth between the four species. Leaf extension rate (LER) increased significantly at night (average over 8 h) in elevated CO2 for S. minor, A. vulneraria and P. media with a significant increase over the first 4 h of darkness for S. mines, L. corniculatus and P. media, whilst for S. minor and P. media average day-time LER (over 16 h) also increased significantly in elevated CO2 as compared with ambient CO2. Water potential (Psi), solute potential (Psi(s)), turgor pressure (P), yield turgor (Y) and the effective turgor for growth (Pe) were measured using psychrometers. Solute potentials of S. minor, A. vulneraria acid P. media decreased significantly following exposure to elevated CO2 with a significant reduction in Psi(s) during the day in A. vulneraria. Turgor pressure increased significantly in elevated CO2 as compared with ambient CO2 in A. vulneraria but there was no effect of elevated CO2 on P in the other species. No effects of CO2 on Psi, Y or Pe were observed. Leaf cell wall extensibility (phi) increased significantly in leaves of S. minor, L. corniculatus and P. media exposed to elevated CO2, whereas in A. vulneraria, there was no effect of CO2 on extensibility. These results suggest that the mechanism by which elevated CO2 promotes leaf growth differs between species since in S. minor, L. corniculatus and P. media, CO2 promoted growth through an influence on cell wall properties, whilst in A. vulneraria, higher values of P explain the increased leaf growth in elevated CO2 for this species.

KEYWORDS: EXPANSION, LEAVES, PHOTOSYNTHESIS, PLANT-CELL GROWTH, PRODUCTIVITY, SALIX-VIMINALIS, TEMPERATURE, WALL EXTENSIBILITY, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD TURGOR

654

Ferris, R., and G. Taylor. 1994. Increased root-growth in elevated co2 - a biophysical analysis of root cell elongation. *Journal of Experimental Botany 45(280):1603-1612.*

A biophysical analysis of root expansion was conducted in four chalk downland herbs (Sanguisorba minor Scop., Lotus corniculatus L., Anthyllis vulneraria L. and Plantago media L.) exposed to either ambient or elevated CO, in controlled environment cabinets. Measurements of fine (F) and extra-fine (EF) root extension rate (RER), water relations, and cell wall tensiometric extensibility revealed differences in the diurnal pattern of root growth between species. After 35 d of exposure to elevated CO2, RER of both F and EF roots increased significantly in darkness and on illumination for S. minor, whilst for A. vulneraria (EF roots only) and L. corniculatus a significant increase occurred at night whereas for P. media a significant increase occurred during the day. Cells measured in the zone of elongation were longer in all species exposed to elevated CO2. Water potential (Psi), solute potential (Psi(s)), turgor pressure (P), yield turgor (Y) and effective turgor (Pe) were measured by stress-relaxation of excised root tips placed in psychrometers. Solute potentials decreased significantly for all species following exposure to elevated CO2. In S. minor and L. corniculatus, P and Pe, respectively, were higher in elevated CO2. No significant effects of CO2 on Y were observed (not shown). Root cell wall tensiometric extensibility, measured as % plasticity, increased in all species exposed to elevated CO2. These results suggest that root growth is enhanced following increased cell expansion and that increased P and cell wall tensiometric extensibility are both important for root growth in elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, LEAF GROWTH, MAIZE ROOTS, PLANTS, PRESSURE PROBE, TURGOR, WALL EXTENSIBILITY, WATER RELATIONS, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD THRESHOLD

655

Ferris, R., and G. Taylor. 1994. Stomatal characteristics of 4 native herbs following exposure to elevated co2. *Annals of Botany 73(4):447-453.*

KEYWORDS: ALLIUM, CARBON DIOXIDE, CELLS, DENSITY, ENRICHMENT, GROWTH, INCREASES, LEAF ANATOMY, NUMBERS, POPLAR CLONES

656

Ferris, R., and G. Taylor. 1995. Contrasting effects of elevated CO2 and water deficit on two native herbs. *New Phytologist 131(4):491-501.*

This study investigated the effects of carbon dioxide (CO2) enrichment and soil water deficit on the water use efficiency (WUE) and growth of Sanguisorba minor Scop. (salad burnet) and Anthyllis vulneraria L. (kidney vetch), growing in controlled environments. Instantaneous WUE (IWUE) increased in both species in elevated CO2, with a higher average increase in unwatered (UW) A. vulneraria over the drying cycle. Total plant WUE of A. vulneraria increased in elevated CO2 and under water deficit: the UW plants in elevated CO2 had higher WUE and reduced water loss. By contrast, thee was only an effect of water supply on S. minor: total plant WUE increased and water loss decreased in the UW plants in both CO2 treatments. Total apparent root length (ARL) of both species increased with CO2 enrichment and in UW S. minor total ARL was increased. By contrast, for A. vulneraria, total ARL of UW plants increased in ambient CO2, but decreased in elevated CO2 as compared with well-watered (WW) plants. Shoot dry weight (SDW) and root dry weight increased in both species (WW and UW) with CO2 enrichment. For UW S. minor, SDW decreased relative to WW plants in both CO2 treatments. By contrast, ANOVA showed no significant effect of water supply on SDW of A. vulneraria. Leaflet length increased in both species in elevated CO2 and decreased following drought. Cell wall tensiometric extensibility (%P) increased in expanding leaves of S. minor in elevated CO2 and for both species %P decreased in the UW plants as compared with those WW. Leaf water potential (Psi) of both species was lower in growing leaves of WW plants in elevated CO2. Water deficit reduced the Psi of growing leaves in both CO2 treatments.

The different responses of these species suggest that in a drier, enriched CO2 environment survival in a community might depend on their ability to maintain growth at the same time as conserving water.

KEYWORDS: BETULA, CARBON DIOXIDE, DROUGHT, ENRICHMENT, GROWTH, LIMITED CONDITIONS, SEEDLINGS, STRESS, USE EFFICIENCY, YIELD

657

Ferris, R., T.R. Wheeler, R.H. Ellis, and P. Hadley. 1999. Seed yield after environmental stress in soybean grown under elevated CO2. *Crop Science 39(3):710-718.*

Episodes of high temperature and drought are predicted to occur more frequently under conditions of future climate change, This study investigated whether an episode of high air temperature (HT + 15 degrees C), water deficit (WD), or both (HTWD), for 8 d, had the same effects on the yield of soybean [Glycine max (L.) Merrill, cv. Fiskeby V] grown under either ambient (aCO(2); 360 mu mol mol(-1) CO2) or elevated (eCO(2); 700 mu mol mol(-1) CO2) CO2 concentrations. Plants were grown in a glasshouse at either aCO(2) or at eCO(2) until 52 d after sowing (DAS). The 8-d stress treatments were then imposed before the plants were returned to their original environments. Across harvests, total biomass was 41% greater under eCO(2) than under aCO(2) but reduced by HT, WD, and HTWD under both CO2 concentrations, The relative response of total biomass to HT,WD, and HTWD episodes was the same for plants grown under either aCO(2) or eCO(2). At maturity, seed dry weight and number per plant under eCO(2) were increased by an average of 32 and 22%, respectively, compared with aCO(2). The same parameters were reduced after HTWD by 29 and 30%, respectively, in aCO(2) and eCO(2), Seed filling was earlier under HT and HTWD The rate of change in harvest index was unaltered by CO2 while under HTWD, it decreased. Seed number explained 85% of the variation in yield, but yield was also related linearly to photosynthesis during seed filling, suggesting both are important determinants of yields under stress.

KEYWORDS: CARBON DIOXIDE, CLIMATIC VARIABILITY, CROP YIELDS, LONG-TERM, LUPINUS-ANGUSTIFOLIUS L, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TRANSIENT HIGH-TEMPERATURES, WATER-STRESS

658

Ferris, R., T.R. Wheeler, P. Hadley, and R.H. Ellis. 1998. Recovery of photosynthesis after environmental stress in soybean grown under elevated CO2. *Crop Science 38(4):948-955.*

Episodes of high temperature and water deficit may be more frequent under predicted future climates of warmer mean temperatures and elevated CO2. This study investigated whether the effects of an episode of high sir temperature (HT, 43 degrees C as a daily maximum), water deficit (WD), or both, had the same effect on the recovery of photosynthesis and on leaf water relations of soybean [Glycine max (L.) Merr., cv. Fiskeby V] grown at ambient CO2 (aCO(2)) or elevated CO2 (eCO(2)). An 8-d period of HT, WD, or both (HTWD) were imposed during early seed filling of soybean grown in glasshouses at either 362 or 685 mu mol mol(-1) CO2. Photosynthesis (Amax), stomatal conductance (g(s)), and water relations were measured in fully expanded upper-canopy leaves. Immediately after the 8-d treatments at 60 d after sowing (DAS), Amax was reduced by 31, 48, and 64% in aCO(2) and by 28, 39, and 49% in eCO(2) under HT, WD, and HTWD, respectively, but no significant interactions were detected. At 60 DAS, g(s) was reduced by WD and HTWD in aCO(2) but not by HT while there was little change in g(s) by WD, HT, and HTWD under eCO(2). Amar fully recovered under WD in eCO(2) by 66 DAS, while Amax remained reduced under WD in aCO(2). Under each CO2 concentration, almost full recovery of Amar occurred under HT by 75 DAS but under HTWD Amar never attained control values. At 60 DAS, early morning leaf water potential (Psi) was lower after HT, WD, and HTWD and Amax was a negative function of Psi, at each CO2 concentration. The results suggest that full recovery of Amax from WD was only possible under eCO(2), because at aCO(2), immediately after the stress episode, Psi was below the threshold for chloroplast damage.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC VARIABILITY, CROP YIELDS, ENRICHMENT, GAS-EXCHANGE, LEAF WATER POTENTIALS, PERENNIAL RYEGRASS, PLANTS, RESPONSES, TEMPERATURE

659

Field, C.B. 1994. Carbon-cycle - arctic chill for co2 uptake. *Nature 371(6497):472-473.*

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, ELEVATED CO2, TUSSOCK TUNDRA

660

Field, C.B., F.S. Chapin, P.A. Matson, and H.A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere - a resource-based approach. *Annual Review of Ecology and Systematics 23:201-235.*

KEYWORDS: ALASKAN TUSSOCK TUNDRA, ALPINE LIFE ZONE, CARBON NUTRIENT BALANCE, ELEVATED CO2 CONCENTRATIONS, HARDWOOD LEAF LITTER, L KARST STANDS, NITROGEN-USE EFFICIENCY, SOURCE-SINK RELATIONS, TEMPERATE FOREST ECOSYSTEMS, WATER-USE EFFICIENCY

661

Field, C.B., R.B. Jackson, and H.A. Mooney. 1995. Stomatal responses to increased co2 - implications from the plant to the global-scale. *Plant, Cell and Environment 18(10):1214-1225.*

Increased atmospheric CO2 Often but not always leads to large decreases in leaf conductance, Decreased leaf conductance has important implications for a number of components of CO2 responses, from the plant to the global scale, All of the factors that are sensitive to a change in soil moisture, either amount or timing, may be affected by increased CO2. The list of potentially sensitive processes includes soil evaporation, run- off, decomposition, and physiological adjustments of plants, as well as factors such as canopy development and the composition of the plant and microbial communities, Experimental evidence concerning ecosystem-scale consequences of the effects of CO2 on water use is only beginning to accumulate, but the initial indication is that, in water-limited areas, the effects of CO2- induced changes in leaf conductance are comparable in importance to those of CO2-induced changes in photosynthesis, Above the leaf scale, a number of processes interact to modulate the response of canopy or regional evapotranspiration to increased CO2. While some components of these processes tend to amplify the sensitivity of evapotranspiration to altered leaf conductance, the most likely overall pattern is one in which the responses of canopy and regional evapotranspiration are substantially smaller than the responses of canopy conductance, The effects of increased CO2 on canopy evapotranspiration are likely to be smallest in aerodynamically smooth canopies with high leaf conductances, Under these circumstances, which are largely restricted to agriculture, decreases in evapotranspiration may be only one-fourth as large as decreases in canopy conductance, Decreased canopy conductances over large regions may lead to altered climate, including increased temperature and decreased precipitation, The simulation experiments to date predict small effects globally, but these could be important regionally, especially

in combination with radiative (greenhouse) effects of increased CO2.

KEYWORDS: ATMOSPHERIC CO2, CONDUCTANCE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAF-AREA, PHOTOSYNTHESIS, SCIRPUS- OLNEYI, TRANSPIRATION, WATER-STRESS

662

Field, C.B., C.P. Lund, N.R. Chiariello, and B.E. Mortimer. 1997. CO2 effects on the water budget of grassland microcosm communities. *Global Change Biology 3(3):197-206.*

Experimental grassland ecosystems, in microcosms 0.2 m in diameter and with a 0.95 m soil column, varied in their responses to elevated partial pressure of CO2 (pCO(2)) and altered moisture inputs. Ecosystems on moderately fertile sandstone soil and with a typical mix of moderately fast- growing sandstone species, responded to elevated pCO(2) with decreases in mid-season evapotranspiration of nearly 50%. This pattern reversed at the end of the growing season, and sandstone ecosystems under elevated pCO(2) continued active transpiration farther into the summer drought. The sandstone ecosystems appeared to convert mid-season water conservation into increased late-season growth. Effects of increased pCO(2) on ecosystem evapotranspiration were much smaller in ecosystems with very infertile serpentine soil and a diverse mixture of slow-growing serpentine species.

KEYWORDS: AMBIENT, COTTON, ELEVATED CO2, ENRICHMENT, EVAPOTRANSPIRATION, INCREASES, RESPONSES, SIMULATIONS, STOMATAL CONDUCTANCE, TRANSPIRATION

663

Field, C.D. 1995. Impact of expected climate-change on mangroves. *Hydrobiologia 295(1-3):75-81.*

There is a consensus of scientific opinion that the activities of man will cause a significant change in the global climate over the next hundred years. The rising level of carbon dioxide and other industrial gases in the atmosphere may lead to global warming with an accompanying rise in sea-level. Mangrove ecosystems grow in the intertidal zones in tropical and sub- tropical regions and are likely to be early indicators of the effects of climate change. The best estimates of predicted climate change in the literature are presented. It is suggested that a rise in mean sea-level may be the most important factor influencing the future distribution of mangroves but that the effect will vary dramatically depending on the local rate of sea-level rise and the availability of sediment to support reestablishment of the mangroves. The predicted rise in mean air temperature will probably be of little consequence to the development of mangroves in general but it may mean that the presence of mangroves will move further north and south, though this will depend on a number of additional factors. The effect of enhanced atmospheric CO2 on the growth of mangroves is unknown at this time but that there is some evidence that not all species of mangroves will respond similarly. The socio- economic impacts of the effects of climate change on mangrove ecosystems may include increased risk of flooding, increased erosion of coast lines, saline intrusion and increased storm surges.

KEYWORDS: AVICENNIA-MARINA, ELEVATED CO2, GREY MANGROVE, GROWTH, PLANT-RESPONSES, SALINITY, SEA-LEVEL, STOMATAL RESPONSES

664

Fierro, A., N. Tremblay, and A. Gosselin. 1994. Supplemental carbon-dioxide and light improved tomato and pepper seedling growth and yield. *Hortscience 29(3):152-154.*

The experiment was conducted to determine the effects of CO2 enrichment (900 mul.liter-1, 8 hours/day) in combination with supplementary lighting of 100 mumol.s-1.m-2 (16-h photoperiod) on tomato (Lycopersicon esculentum Mill.) and sweet pepper (Capsicum annuum L.) seedling growth in the greenhouse and subsequent yield in the field. Enrichment with CO2 and supplementary lighting for almost-equal-to 3 weeks before transplanting increased accumulation of dry matter in shoots by almost-equal-to 50% compared with the control, while root dry weight increased 49% for tomato and 62% for pepper. Early yields increased by almost-equal-to 15% and 11% for tomato and pepper, respectively.

KEYWORDS: CO2, NITROGEN- FERTILIZATION, VEGETABLE TRANSPLANT PRODUCTION

665

Figueira, A., and J. Janick. 1994. Optimizing carbon-dioxide and light levels during in-vitro culture of theobroma-cacao. *Journal of the American Society for Horticultural Science 119(4):865-871.*

In vitro culture of axillary cotyledonary shoots of Theobroma cacao L. (cacao) under increasing CO2 concentration from ambient to 24,000 ppm (culture tube levels) significantly increased total shoot elongation, number of leaves, leaf area per explant, and shoot dry and fresh weight. Although light was necessary for the CO2 response, the effect of various photon fluxes was not significant for the measured growth parameters. Net photosynthesis estimated on the basis of CO2 depletion in culture tubes increased 3.5 times from 463 to 2639 ppm CO2, and increased 1.5 times from 2639 to 14,849 ppm CO2, but declined from 14,849 to 24,015 ppm CO2. Ethylene concentration in culture vessels increased under enriched CO2 conditions. Depletion of nutrients (fructose, K, Ca, Mg, and P) from the medium was increased under enriched CO2 conditions.

KEYWORDS: AMELONADO, CO2- ENRICHMENT, GROWTH, PLANTLETS, SHOOT PROLIFERATION, STRAWBERRY, TISSUE

666

Figueira, A., A. Whipkey, and J. Janick. 1991. Increased co2 and light promote invitro shoot growth and development of theobroma-cacao. *Journal of the American Society for Horticultural Science 116(3):585-589.*

Axillary shoots of cacao (Theobroma cacao L.), induced in vitro with cytokinins (BA or TDZ), elongated and produced leaves only in the presence of cotyledons and/or roots. Detached axillary shoots, which do not grow in vitro under conventional tissue culture protocols, rooted with auxin and developed normally in vivo. Detached axillary shoots from cotyledonary nodes and single-node cuttings from mature plants were induced to elongate and produce normal leaves in the presence of 20,000 ppm CO2 and a photosynthetic photon flux density (PPFD) of 150 to 200-mu-mol.s-1.m-2. Subcultured nodal cuttings continued to elongate and produce leaves under elevated CO2 and light levels, and some formed roots. Subculture of microcuttings under CO2 enrichment could be the basis for a rapid system of micropropagation for cacao. Chemical names used: N- (phenylmethyl)-1H-purin-6-amine (BA); 1H-indole-3-butyric acid (IBA); alpha-naphthaleneacetic acid (NAA); thidiazuron (TDZ).

KEYWORDS: CULTIVATED INVITRO, L VAR AMELONADO, PROLIFERATION, PROPAGATION, TISSUES

667

Finlayson, S.A., and D.M. Reid. 1996. The effect of CO2 On ethylene evolution and elongation rate in roots of sunflower (Helianthus annuus)

seedlings. *Physiologia Plantarum 98(4):875-881.*

Both carbon dioxide and ethylene can affect the rate of root elongation. Carbon dioxide can also promote ethylene biosynthesis by enhancing the activity of 1-aminocylopropane-1- carboxylic acid (ACC) oxidase. Since the amount of CO2 in the soil air, and in the atmosphere surrounding roots held in enclosed containers, is known to vary widely, we investigated the effects of varying CO2 concentrations on ethylene production by excised and intact sunflower roots (Helianthus annuus L. cv. Dahlgren 131). Seedlings were germinated in an aeroponic system in which the roots hung freely in a chamber and were misted with nutrient solution. This allowed for treatment, manipulation and harvest of undamaged and minimally disturbed roots. While exposure of excised roots to 0.5% CO2 could produce a small increase in ethylene production (compared to roots in ambient CO2), CO2 concentrations of 2% and above always inhibited ethylene evolution. This inhibition of ethylene production by CO2 was attributed to a reduction in the availability of ACC; however, elevated CO2 had no effect on ACC oxidase activity. ACC levels in excised roots were depressed by CO2 at a concentration of 2% (as compared to ambient CO2), but n-malonyl-ACC (MACC) levels were not affected. Treating intact roots with 2% CO2 inhibited elongation by over 50%. Maximum inhibition of elongation occurred 1 h after the CO2 treatment began, but elongation rates returned to untreated values by 6 h. Supplying these same intact roots with 2% CO2 did not alter ethylene evolution. Thus, in excised sunflower roots 2% CO2 treatment reduces ethylene evolution by lowering the availability of ACC. Intact seedlings respond differently in that 2% CO2 does not affect ethylene production in roots. These intact roots also temporarily exhibit a significantly reduced rate of elongation in response to 2% CO2.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLATE OXIDASE, ACC OXIDASE, ACTIVATION, CARBON DIOXIDE, FORMING ENZYME, GROWTH, PLANTS, RESPIRATION, SOIL O2, WATER

668

Firbank, L.G., A.R. Watkinson, L.R. Norton, and T.W. Ashenden. 1995. Plant-populations and global environmental-change - the effects of different temperature, carbon-dioxide and nutrient regimes on density-dependence in populations of vulpia-ciliata. *Functional Ecology 9(3):432-441.*

1. Monocultures of Vulpia ciliata spp. ambigua were subjected to a range of temperatures, CO2, nutrient and density regimes in a factorial design housed within solar-domes. Temperature treatments were imposed at ambient and +3 degrees C levels, CO2 at ambient and +340 ppm, and there were three levels of nutrients and eight levels of densities ranging from 156 to 31250 seeds m(-2). The abiotic treatments were imposed after emergence. 2. There was little mortality and this was unrelated to the treatments. Plants grew more quickly at the high temperature, high nutrient and low density regimes, and flowering was earlier at the high temperature regime. 3. At seed set, biomass per plant and seed production per plant were analysed by analysis of variance and by fitting mean yield- density models expanded to account for different environmental conditions. Biomass and fecundity were greatest at high temperature, high nutrient and low density regimes. Allocation of biomass to shoots was greater at the high temperatures, as were seed number/shoot biomass ratios. Any effects of CO2 were negligible. The parameter b describing the nature of the relationship between seed production per plant and density was always less than unity but was greater at the higher temperature regime. The response to density was therefore undercompensating in all conditions, implying that populations would display monotonic damping to equilibrium densities. 4. Under proposed future environmental regimes, V. ciliata has the capacity for more rapid population growth from low levels and for a northwards range shift. However, if open ground is not maintained, its habitat may become dominated by species that are more competitive or that have a higher rate of increase.

KEYWORDS: BRECKLAND, CLIMATE, CO2- ENRICHMENT, ELEVATED CO2, FASCICULATA, GROWTH-RESPONSES, PHYSIOLOGY, SIMULATION, SINGLE-SPECIES POPULATIONS, SOURCE-SINK RELATIONS

669

Fischer, B.U., M. Frehner, T. Hebeisen, S. Zanetti, F. Stadelmann, A. Luscher, U.A. Hartwig, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Source-sink relations in Lolium perenne L. as reflected by carbohydrate concentrations in leaves and pseudo-stems during regrowth in a free air carbon dioxide enrichment (FACE) experiment. *Plant, Cell and Environment 20(7):945-952.*

The effect of an elevated partial pressure of CO2 (P-CO2) on carbohydrate concentrations in source leaves and pseudostems (stubble) of Lolium perenne L., (perennial ryegrass) during regrowth was studied in a regularly defoliated grass sward in the field, The free air carbon dioxide enrichment (FACE) technology enabled natural environmental conditions to be provided, Two levels of nitrogen (N) supply were used to modulate potential plant growth. Carbohydrate concentrations in source leaves were increased at elevated P-CO2, particularly at low N supply, Elevated leaf carbohydrate concentrations were related to an increased structural carbon (C) to N ratio and thus reflected an increased C availability together with a N- dependent sink limitation, Immediately after defoliation, apparent assimilate export rates (differences in the carbohydrate concentrations of young source leaves measured in the evening and on the following morning) showed a greater increase at elevated p(CO2) than at ambient p(CO2); however, replenishment of carbohydrate reserves was not accelerated Distinct, treatment-dependent carbohydrate concentrations in pseudo-stems suggested an increasing degree of C-sink limitation from the treatment at ambient p(CO2) with high N supply to that at elevated P-CO2 With low N supply. During two growing seasons, no evidence of a substantial change in the response of the carbohydrate source in L. perenne to elevated p(CO2) was found, Our results support the view that the response of L. perenne to elevated p(CO2) is restricted by a C- sink limitation, which is particularly severe at low N supply.

KEYWORDS: ELEVATED CO2, GROWTH, LEAF, PASTURE TURVES, PLANTS, RESPIRATION, RYEGRASS, SIMULATED SEASONAL-CHANGES, TEMPERATURE, TRIFOLIUM- REPENS

670

Fischer, M., D. Matthies, and B. Schmid. 1997. Responses of rare calcareous grassland plants to elevated CO2: a field experiment with Gentianella germanica and Gentiana cruciata. *Journal of Ecology 85(5):681-691.*

1 Endangered plant species may be particularly vulnerable to global change. We investigated differences in the behaviour of the rare calcareous grassland species Gentiana cruciata and Gentianella germanica under ambient (360 mu l l(-1)) and elevated CO2 (600 mu l l(-1)) in a field experiment. 2 Rosettes of G. germanica and C. cruciata were planted into grassland plots with 29 other plant species. Each of the 30 rosettes of G. germanica in a plot represented a different maternal seed family, whereas G. cruciata was grown from a mixture of seeds from one field site. After overwintering, eight of the 12 plots were equipped with open-top chambers, four of which were run at ambient and four at elevated CO2 concentrations; the remaining four plots were left without chambers. 3 CO2 concentration did not significantly affect growth and survival of G. cruciata. Rosette diameter increased by 70% over 1 year. 4 Overall only 13.6% of transplanted G. germanica survived for 1 year. Elevated CO2 reduced survival by 57% (this reduction was

only marginally significant due to large variation between plots) and seed set by 46%. Both these effects appeared to be mediated by competition from other species since survival and seed set were negatively correlated with total plot biomass at the time of fastest growth in June 1994 and at the time of fruit set in October, respectively. Compared with plots under ambient CO2, population growth rate (based on survival and reproduction) was reduced by 56% under elevated CO2. 5 There were no significant effects of elevated CO2 on leaf characters in either species. 6 The sugar concentration of the nectar of G. germanica was increased by 36% under elevated CO2 but its composition remained unchanged. 7 Significant interactions between the effects of seed family and CO2 concentration on demographic parameters in G. germanica indicated large genetic variation in the response to elevated CO2, which represents evolutionary potential. Although predictions based on mean responses are therefore unreliable, the majority of genotypes reacted negatively to elevated CO2, suggesting that competitive exclusion and extinction of G. germanica would occur at many sites before populations could adapt to increased concentrations of CO2.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS PRODUCTION, CHALK GRASSLANDS, CLOVER TRIFOLIUM-REPENS, GROWTH, PERFORMANCE, RYEGRASS LOLIUM-PERENNE, SHORT-LIVED FORBS, TEMPERATURE, WHITE CLOVER

671

Fiscus, E.L., and C.D. Reid. 1995. Pollutant ozone does not affect stomatal limitation to photosynthesis in soybean in ambient or elevated co2. *Plant Physiology 108(2):63.*

672

Fiscus, E.L., C.D. Reid, J.E. Miller, and A.S. Heagle. 1997. Elevated CO2 reduces O-3 flux and O-3-induced yield losses in soybeans: Possible implications for elevated CO2 studies. *Journal of Experimental Botany 48(307):307-313.*

Soybeans were grown for three seasons in open-top field chambers to determine (1) whether elevated CO2 (360 Versus 700 mu mol mol(-1)) alleviates some of the yield loss due to pollutant O-3, (2) whether the partial stomatal closure resulting froth chronic O-3 exposure (charcoal-filtered air versus 1.5 x ambient concentrations) is a cause or result of decreased photosynthesis, and (3) possible implications of CO2/O-3 interactions to climate change studies using elevated CO2. Leaf conductance was reduced by elevated CO2, regardless of O-3 level, or by exposure to O-3 alone. AS a result of these effects on conductance, high CO2 reduced estimated midday O-3 flux into the leaf by an average of 50% in charcoal-filtered air and 35% in the high O-3 treatment. However, while exposure to O-3 reduced seed yields by 41% at ambient CO2 levels, the yield reduction was completely ameliorated by elevated CO2. The threshold midday O-3 flux for yield loss appears to be 20-30 nmol m(-2) s(-1) in this study. Although elevated CO2 increased total biomass production, it did not increase seed yields. A/C- i curves show a large reduction in the stomatal limitation to photosynthesis due to elevated CO2, but no effect of O-3. These data demonstrate that (1) reduced conductance due to O-3 is the result, and not the cause, of reduced photosynthesis, (2) 700 mu mol mol(-1) CO2 can completely ameliorate yield losses due to O-3 within the limits of these experiments, and (3) some reports of increased yields under elevated CO2 treatments may, at least in part, reflect the amelioration of unrecognized suppression of yield by O-3 or other stresses.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, B RADIATION, CONDUCTANCE, ENRICHMENT, GROWTH, LEAF RESPIRATION, OZONE, PHOTOSYNTHESIS, POLLUTANTS, WATER DEFICIT

673

Fitter, A.H., J.D. Graves, J. Wolfenden, G.K. Self, T.K. Brown, D. Bogie, and T.A. Mansfield. 1997. Root production and turnover and carbon budgets of two contrasting grasslands under ambient and elevated atmospheric carbon dioxide concentrations. *New Phytologist 137(2):247-255.*

Monoliths of two contrasting vegetation types, a species-rich grassland on a brown earth soil over limestone and a species- poor community on a peaty gley, were transferred to solardomes and grown under ambient (350 mu l l(-1)) and elevated (600 mu l l(-1)) CO2 for 2 yr. Shoot biomass was unaltered but root biomass increased by 40-50% under elevated CO2. Root production was increased by elevated CO2 in the peat soil, measured both as instantaneous and cumulative rates, but only the latter measure was increased in the limestone soil. Root growth was stimulated more at 6 cm depth than at 10 cm in the limestone soil. Turnover was faster under elevated CO2 in the peat soil, but there was only a small effect on turnover in the limestone soil. Elevated CO, reduced nitrogen concentration in roots and might have increased mycorrhizal colonization. Respiration rate was correlated with N concentration, and was therefore lower in roots grown at elevated CO2. Estimates of the C budget of the two communities, based upon root production and on net C uptake, suggest that C sequestration in the peat soil increases by c. 0.2 kg C m(-2) yr(-1) (= 2 t ha yr(-1)) under elevated CO2.

KEYWORDS: BIOMASS, CO2- ENRICHMENT, GROWTH, STORAGE

674

Fitter, A.H., G.K. Self, J. Wolfenden, M.M.I. vanVuuren, T.K. Brown, L. Williamson, J.D. Graves, and D. Robinson. 1996. Root production and mortality under elevated atmospheric carbon dioxide. *Plant and Soil 187(2):299-306.*

An essential component of an understanding of carbon flux is the quantification of movement through the root carbon pool. Although estimates have been made using radiocarbon, the use of minirhizotrons provides a direct measurement of rates of root birth and death. We have measured root demographic parameters under a semi-natural grassland and for wheat. The grassland was studied along a natural altitudinal gradient in northern England, and similar turf from the site was grown in elevated CO2 in solardomes. Root biomass was enhanced under elevated CO2. Root birth and death rates were both increased to a similar extent in elevated CO2, so that the throughput of carbon was greater than in ambient CO2, but root half-lives were shorter under elevated CO2 only under a Juncus/Nardus sward on a peaty gley soil, and not under a Festuca turf on a brown earth soil. In a separate experiment, wheat also responded to elevated CO2 by increased root production, and there was a marked shift towards surface rooting: root development at a depth of 80-85 cm was both reduced and delayed. In conjunction with published results for trees, these data suggest that the impact of elevated CO2 will be system- dependent, affecting the spatio-temporal pattern of root growth in some ecosystems and the rate of turnover in others. Turrnover is also sensitive to temperature, soil fertility and other environmental variables, all of which are likely to change in tandem with atmospheric CO2 concentrations. Differences in turnover and time and location of rhizodeposition may have a large effect on rates of carbon cycling.

KEYWORDS: CO2- ENRICHMENT, FORESTS, GRASSES, GROWTH, PATTERNS, RESPONSES, TURNOVER

675

Flagella, Z., R.G. Campanile, M.C. Stoppelli, A. De Caro, and N. Di Fonzo. 1998. Drought tolerance of photosynthetic electron transport under CO2-enriched and normal air in cereal species. *Physiologia*

Plantarum 104(4):753-759.

The quantum yield of photosynthetic electron transport (Phi PSII), evaluated by means of chlorophyll (Chl) fluorescence analysis, has proven to be a useful screening test for drought tolerance in durum wheat (Triticum durum Desf.). To explore the potential of this parameter further in detecting drought- tolerant genotypes, three cereal species were studied; Phi PSII measurements were carried out under two different gas mixtures, at three points of the induction curve (to obtain the maximal Phi PSII and both the transient and steady-state actual Phi PSII), and at three different water stress levels (moderate, severe and drastic). The species investigated were durum and bread wheat (Triticum aestivum L.) and barley (Hordeum vulgare L.); two cultivars per species, characterized by different levels of drought tolerance, were tested. The two gas mixtures used were normal air (21% O-2, 0.035% CO2 in N-2) to monitor the whole photosynthetic process under physiological conditions, and CO2 enriched-low O-2 air (1% O-2, 5% CO2 in N- 2) to monitor Phi PSII reduction under stress mainly related to Calvin cycle activity. When Phi PSII related to both assimilatory and non-assimilatory metabolism was evaluated, the cultivar differences observed under normal air were more representative of the agronomic performance upon drought stress than under high CO2-low O-2 air. Maximal Phi PSII showed no difference among either cultivars, gas mixtures or stress levels, the efficiency of excitation capture being highly resistant to drought. The Phi PSII evaluated during the transient yielded predictable values in respect of drought tolerance for durum wheat and barley cultivars, highlighting the key role of regulatory processes such as the Mehler peroxidase reaction and possibly also cyclic electron transport, in preventing overreduction under stress. The results clearly show that when Chi fluorescence analysis is used as a parameter in plant breeding, different experimental conditions should be used depending on the physiological mechanism that is bred or selected for.

KEYWORDS: CARBON ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CULTIVARS, DURUM-WHEAT, EFFICIENCIES, LIGHT, PHOTOINHIBITION, PHOTOSYSTEM, QUANTUM YIELD, WATER

676

Flanagan, L.B., S.L. Phillips, J.R. Ehleringer, J. Lloyd, and G.D. Farquhar. 1994. Effect of changes in leaf water oxygen isotopic composition on discrimination against (coo)-o-18-o-16 during photosynthetic gas-exchange. *Australian Journal of Plant Physiology 21(2):221-234.*

Photosynthetic gas exchange measurements were combined with measurements of the carbon and oxygen stable isotopic composition of CO2 after it passed over a leaf of Phaseolus vulgaris or Senecio spp. plants held in a controlled environment chamber. Calculations were then made of discrimination by the leaf against (CO2)-C-13 and (COO)-O-18-O- 16. Leaves were maintained at different vapour pressure gradients in order to generate a range of leaf water O-18/O-16 ratios. The O-18 content of leaf water increased when plants were exposed to higher vapour pressure deficits. The observed (COO)-O-18-O-16 discrimination values also increased with an increase in the leaf-air vapour pressure gradient and the associated change in leaf water 18/(OO)-O-16 values. In addition, the observed (COO)-O-18-O-16 discrimination values were strongly correlated with values predicted by a mechanistic model of isotopic fractionation.

KEYWORDS: CARBONIC-ANHYDRASE, CO2 DIFFUSION, DEUTERIUM, ENRICHMENT, HYDROGEN, LEAVES, O-18, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STABLE OXYGEN

677

Flexas, J., M. Badger, W.S. Chow, H. Medrano, and C.B. Osmond. 1999. Analysis of the relative increase in photosynthetic O-2 uptake when photosynthesis in grapevine leaves is inhibited following low night temperatures and/or water stress. *Plant Physiology 121(2):675-684.*

We found similarities between the effects of low night temperatures (5 degrees C-10 degrees C) and slowly imposed water stress on photosynthesis in grapevine (Vitis vinifera L.) leaves. Exposure of plants growing outdoors to successive chilling nights caused light- and CO2 saturated photosynthetic O-2 evolution to decline to zero within 5 d. Plants recovered after four warm nights. These photosynthetic responses were confirmed in potted plants, even when roots were heated. The inhibitory effects of chilling were greater after a period of illumination, probably because transpiration induced higher water deficit. Stomatal closure only accounted for part of the inhibition of photosynthesis. Fluorescence measurements showed no evidence of photoinhibition, but nonphotochemical quenching increased in stressed plants. The most characteristic response to both stresses was an increase in the ratio of electron transport to net O-2 evolution, even at high external CO2 concentrations. Oxygen isotope exchange revealed that this imbalance was due to increased O-2 uptake, which probably has two components: photorespiration and the Mehler reaction. Chilling- and drought-induced water stress enhanced both O-2 uptake processes, and both processes maintained relatively high rates of electron flow as CO2 exchange approached zero in stressed leaves. Presumably, high electron transport associated with O-2 uptake processes also maintained a high Delta pH, thus affording photoprotection.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CO2 ASSIMILATION, ELECTRON-TRANSPORT, LIGHT, MEHLER-PEROXIDASE REACTION, OXYGEN- EXCHANGE, PHOTOINHIBITION, PLANTS, QUANTUM YIELD, VITIS-VINIFERA L

678

Foley, J.A., S. Levis, I.C. Prentice, D. Pollard, and S.L. Thompson. 1998. Coupling dynamic models of climate and vegetation. *Global Change Biology 4(5):561-579.*

Numerous studies have underscored the importance of terrestrial ecosystems as an integral component of the Earth's climate system. This realization has already led to efforts to link simple equilibrium vegetation models with Atmospheric General Circulation Models through iterative coupling procedures. While these linked models have pointed to several possible climate- vegetation feedback mechanisms, they have been limited by two shortcomings: (i) they only consider the equilibrium response of vegetation to shifting climatic conditions and therefore cannot be used to explore transient interactions between climate and vegetation; and (ii) the representations of vegetation processes and land-atmosphere exchange processes are still treated by two separate models and, as a result, may contain physical or ecological inconsistencies. Here we present, as a proof concept, a more tightly integrated framework for simulating global climate and vegetation interactions. The prototype coupled model consists of the GENESIS (version 2) Atmospheric General Circulation Model and the IBIS (version 1) Dynamic Global Vegetation Model. The two models are directly coupled through a common treatment of land surface and ecophysiological processes, which is used to calculate the energy, water, carbon, and momentum fluxes between vegetation, soils, and the atmosphere. On one side of the interface, GENESIS simulates the physics and general circulation of the atmosphere. On the other side, IBIS predicts transient changes in the vegetation structure through changes in the carbon balance and competition among plants within terrestrial ecosystems. As an initial test of this modelling framework, we perform a 30 year simulation in which the coupled model is supplied with modern CO2 concentrations, observed ocean temperatures, and modern insolation. In this exploratory study, we run the GENESIS atmospheric model at relatively coarse horizontal resolution (4.50

latitude by 7.5 degrees longitude) and IBIS at moderate resolution (2 degrees latitude by 2 degrees longitude). We initialize the models with globally uniform climatic conditions and the modern distribution of potential vegetation cover. While the simulation does not fully reach equilibrium by the end of the run, several general features of the coupled model behaviour emerge. We compare the results of the coupled model against the observed patterns of modern climate. The model correctly simulates the basic zonal distribution of temperature and precipitation, but several important regional biases remain. In particular, there is a significant warm bias in the high northern latitudes, and cooler than observed conditions over the Himalayas, central South America, and north-central Africa. In terms of precipitation, the model simulates drier than observed conditions in much of South America, equatorial Africa and Indonesia, with wetter than observed conditions in northern Africa and China. Comparing the model results against observed patterns of vegetation coves shows that the general placement of forests and grasslands is roughly captured by the model. In addition, the model simulates a roughly correct separation of evergreen and deciduous forests in the tropical, temperate and boreal zones. However, the general patterns of global vegetation cover are only approximately correct: there are still significant regional biases in the simulation. In particular, forest cover is not simulated correctly in large portions of central Canada and southern South America, and grasslands extend too far into northern Africa. These preliminary results demonstrate the feasibility of coupling climate models with fully dynamic representations of the terrestrial biosphere. Continued development of fully coupled climate-vegetation models will facilitate the exploration of a broad range of global change issues, including the potential role of vegetation feedbacks within the climate system, and the impact of climate variability and transient climate change on the terrestrial biosphere.

KEYWORDS: ATMOSPHERIC CO2, GENERAL-CIRCULATION MODELS, LEAF, PHOTOSYNTHESIS, PLANT FUNCTIONAL TYPES, SENSITIVITY, STOMATAL CONDUCTANCE, TERRESTRIAL BIOSPHERE, TRANSFER SCHEME LSX, TRANSPIRATION

679

Fonseca, F., C.G. Bowsher, and I. Stulen. 1997. Impact of elevated atmospheric CO2 on nitrate reductase transcription and activity in leaves and roots of Plantago major. *Physiologia Plantarum 100(4):940-948.*

Vegetative plants of an inbred line, A4, of Plantage major ssp. pleiosperma (L.) Pilger were grown at 350 mu l 1(-1) or at elevated (700 mu l l(-1)) CO2 in non-limiting nutrient solution with nitrate. Both the relative growth rate (RGR) and the root to total plant weight ratio (RWR) were increased by elevated CO2. However, the stimulation of both RGR and RWR was transient and did not last longer than 8 days. To investigate the physiological mechanisms involved in this stimulation, related changes in C/N metabolism were examined. In the roots soluble sugar concentration increased during the transient period of RGR stimulation (up to 23%), as did the root respiration rate. Changes in nitrogen metabolism were also restricted to this period and consisted of an increase in (1) in vivo and in vitro root nitrate reductase (EC 1.6.6.1) activity, (2) in vitro leaf nitrate reductase activity, (3) leaf and root nitrate reductase mRNA and (4) reduced nitrogen concentration in the roots. The elevated CO2-related signal for the increase in nitrate reductase transcript levels in the roots is discussed in terms of the increased availability of soluble sugars. The results suggest that the short-term enhancement of root carbon and nitrogen metabolism may be responsible for the transient effect of elevated CO, on whole plant RGR.

KEYWORDS: ASSIMILATION, CARBOHYDRATE CONTENT, CARBON DIOXIDE, EXPRESSION, GROWTH, MAIZE, METABOLISM, NITRITE-REDUCTASE, PHOTOSYNTHESIS, RAPID MODULATION

680

Fonseca, F., J. DenHertog, and I. Stulen. 1996. The response of Plantago major ssp pleiosperma to elevated CO2 is modulated by the formation of secondary shoots. *New Phytologist 133(4):627-635.*

The effect of elevated CO2 on the relative growth rate (RGR) of Plantago major ssp. pleiosperma was studied during the vegetative stage, in relation to plant development, by growing plants at 350 mu l l(-1) or at 700 mu l l(-1) CO2 in non- limiting nutrient solution with nitrate. To minimize interference by the accumulation of non-structural carbohydrates in the interpretation of results, RGR was expressed on a f. wt basis (RGR(FW)), as were all plant weight ratios. Stimulation of the RGR(FW) Of the whole plant by elevated CO2 was transient, and did not last longer than 8 d. At the same time a transient increase in root weight ratio (RWR) was observed. In order to investigate whether the transient effect of elevated CO2 on RGR(FW) was size-dependent, the data were plotted versus total f. wt (log(e) transformed). The transient period of stimulation of RGR(FW) and of RWR by elevated CO2 was still found, but in both CO2 treatments RGR(FW) decreased after a certain plant size had been reached. This size coincided with the stage at which secondary shoots started to develop, and was reached earlier in plants grown at elevated CO2. The RGR of these secondary shoots (RGR(see)) was Still increased when the period of whole plant stimulation of RGR(FW) had ended, indicating that the development of these new sinks took priority over a continuation of the stimulation of RWR. It is hypothesized that in this Plantago subspecies the response of the RGR(FW) of the whole plants to elevated CO2 is modulated by the formation of secondary shoots. Apparently, partitioning of the extra soluble carbohydrates at elevated CO2 to this tissue takes precedence over partitioning to the roots. resulting in a cessation of stimulation of plant RGR(FW) by elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COTTON, ENRICHMENT, PHOTOSYNTHESIS, PHYSIOLOGY, RELATIVE GROWTH-RATE, RESPIRATION, SEEDLINGS, TEMPERATURE

681

Fordham, M., J.D. Barnes, I. Bettarini, A. Polle, N. Slee, C. Raines, F. Miglietta, and A. Raschi. 1997. The impact of elevated CO2 on growth and photosynthesis in Agrostis canina L ssp monteluccii adapted to contrasting atmospheric CO2 concentrations. *Oecologia 110(2):169-178.*

The aim of this study was to characterise growth and photosynthetic capacity in plants adapted to long-term contrasting atmospheric CO2 concentrations (C-a). Seeds of Agrostis canina L. ssp. monteluccii were collected from a natural CO2 transect in central-western Italy and plants grown in controlled environment chambers at both ambient and elevated CO2 (350 and 700 mu mol mol(-1)) in nutrient-rich soil. Seasonal mean C-a at the source of the plant material ranged from 610 to 451 mu mol CO2 mol(-1), derived from C-4 leaf stable carbon isotope discrimination (delta(13)C). Under chamber conditions, CO2 enrichment stimulated the growth of all populations. However, plants originating from elevated C-a exhibited higher initial relative growth rates (RGRs) irrespective of chamber CO2 concentrations and a positive relationship was found between RGR and C-a at the seed source. Seed weight was positively correlated with C-a, but differences in seed weight were found to explain no more than 34% of the variation in RGRs at elevated CO2. Longer-term experiments (over 98 days) on two populations originating from the extremes of the transect (451 and 610 mu mol CO2 mol(-1)) indicated that differences in growth between populations were maintained when plants were grown at both 350 and 700 mu mol CO2 mol(-1). Analysis of leaf material revealed an increase in the cell wall fraction (CWF) in plants grown at elevated CO2, with plants originating from high C-a exhibiting constitutively lower levels but a variable response in terms of the degree of lignification. In vivo gas exchange measurements revealed

no significant differences in light and CO2 saturated rates of photosynthesis and carboxylation efficiency between populations or with CO2 treatment. Moreover, SDS-PAGE/LISA quantification of leaf ribulose bisphosphate carboxylase/oxygenase (Rubisco) showed no difference in Rubisco content between populations or CO2 treatments. These findings suggest that long-term adaptation to growth at elevated CO2 may be associated with a potential for increased growth, but this does not appear to be linked with differences in the intrinsic capacity for photosynthesis.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ECOSYSTEMS, EFFICIENCY, ENRICHMENT, ENVIRONMENT, PLANTS, PROTEINS, RESPONSES, WHEAT

682

Fournioux, J.C., and R. Bessis. 1993. Use of carbon-dioxide enrichment to obtain adult morphology of grapevine invitro. *Plant Cell Tissue and Organ Culture 33(1):51-57.*

A procedure has been developed for in vitro propagation of Vitis vinifera 'Pinot noir' from lateral-bud cuttings under high CO2 concentration (1200 mumol mol-1). Because of inhibition of rooting by CO2, this procedure requires a rooting pre-culture of explants on medium with sucrose before the CO2- enriched culture on sucrose-free medium. Shoot growth was enhanced by CO2 enrichment as a result of both a higher rate of leaf production and greater internode elongation. Leaf expansion and tendril growth were promoted and better rooting was obtained. The more significant effect of CO2 enrichment was to promote adult morphology with, in particular, the tendril pattern. Thus, for the first time, grapevine plants have been produced in vitro without typical juvenile characteristics. CO2 enrichment appears to be an interesting process to improve the in vitro propagation of grapevines.

KEYWORDS: CULTURE, MORPHOGENESIS, VITIS-VINIFERA L

683

Fowler, D., J.N. Cape, M. Coyle, C. Flechard, J. Kuylenstierna, K. Hicks, D. Derwent, C. Johnson, and D. Stevenson. 1999. The global exposure of forests to air pollutants. *Water, Air, and Soil Pollution 116(1-2):5-32.*

The tall, aerodynamically rough surfaces of forests provide for the efficient exchange of heat and momentum between terrestrial surfaces and the atmosphere. The same properties of forests also provide for large potential rates of deposition of pollutant gases, aerosols and cloud droplets. For some reactive pollutant gases, including SO2, HNO3 and NH3, rates of deposition may be large and substantially larger than onto shorter vegetation and is the cause of the so called "filtering effect" of forest canopies. Pollutant inputs to moorland and forest have been compared using measured ambient concentrations from an unpolluted site in southern Scotland and a more polluted site in south eastern Germany. The inputs of S and N to forest at the Scottish site exceed moorland by 16% and 31% respectively with inputs of 7.3 kg S ha(-1) y and 10.6 kg N ha(-1) y(-1). At the continental site inputs to the forest were 43% and 48% larger than over moorland for S and N deposition with totals of 53.6 kg S ha(-1) y(-1) and 69.5 kg N ha(-)1 y(-)1 respectively. The inputs of acidity to global forests show that in 1985 most of the areas receiving > 1 kg H+ ha(-1) y(-1) as S are in the temperate latitudes, with 8% of total global forest exceeding this threshold. By 2050, 17% of global forest will be receiving > 1 kg H-1 ha(-1) as S and most of the increase is in tropical and sub-tropical countries. Forests throughout the world are also exposed to elevated concentrations of ozone. Taking 60 ppb O-3 as a concentration likely to be phytotoxic to sensitive forest species, a global model has been used to simulate the global exposure of forests to potentially phytotoxic O-3 concentrations for the years 1860, 1950, 1970, 1990 and 2100. The model shows no exposure to concentrations in excess of 60 ppb in 1860, and of the 6% of global forest exposed to concentrations > 60 ppb in 1950, 75% were in temperate latitudes and 25% in the tropics. By 1990 24% of global forest is exposed to O-3 concentrates > 60 ppb, and this increases to almost 50% of global forest by 2100. While the uncertainty in the future pollution climate of global forest is considerable, the likely impact of O-3 and acid deposition is even more difficult to assess because of interactions between these pollutants and substantial changes in ambient CO2 concentration, N deposition and climate over the same period, but the effects are unlikely to be beneficial overall.

KEYWORDS: ATMOSPHERIC AMMONIA, DIOXIDE, DRY DEPOSITION, EXCHANGE, MOORLAND, NITROGEN, POLLUTION, TEMPERATE, TROPOSPHERIC OZONE, VEGETATED SURFACES

684

Franchito, S.H., V.B. Rao, and R.R. da Silva. 1998. A parameterization of radiative fluxes suitable for use in a statistical-dynamical model. *Meteorology and Atmospheric Physics 69(1-2):23-38.*

A parameterization of shortwave and longwave radiation fluxes derived from detailed radiative transfer models is included in a global primitive equation statistical-dynamical model (SDM) with two bulk atmospheric layers. The model is validated comparing the model simulations with the observed mean annual and seasonal zonally averaged climate. The results show that the simulation of the shortwave and longwave radiation fluxes matches well with the observations. The SDM variables such as surface and 500hPa temperatures, zonal winds at 250hPa and 750 hPa, vertical velocity at 500 hPa and precipitation are also in good agreement with the observations. A comparison between the results obtained with the present SDM and those with the previous version of the model indicates that the model results improved when the parameterization of the radiative fluxes based on detailed radiative transfer models are included into the SDM. The SDM is used to investigate its response to the greenhouse effect. Sensitivity experiments regarding the doubling of CO2 and the changing of the cloud amount and height an performed. In the case 2xCO(2) the model results are consistent with those obtained from GCMs, showing a warming of the climate system. An enhancement of the greenhouse effect is also noted when the cloud layer is higher. However, an increase of the cloud amount in all the latitude belts provokes an increase of the surface temperature near poles and a decrease in all the other regions. This suggests that the greenhouse effect overcomes the albedo effect in the polar latitudes and the opposite occurs in other regions. In all the experiments the changes in the surface temperature an larger near poles, mainly in the Southern Hemisphere.

KEYWORDS: CLIMATE MODEL, CO2, EARTH, ENERGY-BALANCE, GENERAL-CIRCULATION MODEL, MACROCLIMATE, SEASONAL CYCLE, SENSITIVITY, SOLAR RADIATION, SURFACE-TEMPERATURE

685

Franck, V.M., B.A. Hungate, F.S. Chapin, and C.B. Field. 1997. Decomposition of litter produced under elevated CO2: Dependence on plant species and nutrient supply. *Biogeochemistry 36(3):223-237.*

We investigated the effect of CO2 concentration and soil nutrient availability during growth on the subsequent decomposition and nitrogen (N) release from litter of four annual grasses that differ in resource requirements and native habitat. Vulpia microstachys is a native grass found on California serpentine soils, whereas Avena fatua, Bromus hordaceus, and Lolium multiflorum are introduced grasses restricted to more fertile sandstone soils (Hobbs & Mooney 1991). Growth in elevated CO2 altered litter C:N ratio, decomposition, and N release, but the direction and magnitude of the changes differed among plant species and nutrient treatments, Elevated CO2 had relatively

modest effects on C:N ratio of litter, increasing this ratio in Lolium roots (and shoots at high nutrients), but decreasing C:N ratio in Avena shoots. Growth of plants under elevated CO2 decreased the decomposition rate of Vulpia litter, but increased decomposition of Avena litter from the high-nutrient treatment. The impact of elevated CO2 on N loss from litter also differed among species, with Vulpia litter from high-CO2 plants releasing N more slowly than ambient-CO2 litter, whereas growth under elevated CO2 caused increased N loss from Avena litter. CO2 effects on N release in Lolium and Bromus depended on the nutrient regime in which plants were grown. There was no overall relationship between litter C:N ratio and decomposition rate or N release across species and treatments. Based on our study and the literature, we conclude chat the effects of elevated CO2 on decomposition and N release from litter are highly species-specific. These results do not support the hypothesis that CO2 effects on litter quality consistently lead to decreased nutrient availability in nutrient-limited ecosystems exposed to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, LEAF LITTER, NITROGEN, QUALITY, RESPONSES, SERPENTINE GRASSLAND

686

Frank, A.B., and A. Bauer. 1996. Temperature, nitrogen, and carbon dioxide effects on spring wheat development and spikelet numbers. *Crop Science 36(3):659-665.*

Spring wheat (Triticum aestivum L.) responds favorably to elevated atmospheric carbon dioxide concentration ([CO2]) at optimum temperatures. Predictions are for air temperatures to increase as global [CO2] increases. Since spring wheat grain yields generally decline as temperature increases, there is a need to understand the effects of both [CO2] and temperature on spring wheat growth, development, and yield potential. Objectives were to evaluate combinations of [CO2], air temperature, and applied N levels on leaf and apex development, spike components, tiller numbers, dry matter, plant height, and water use in spring wheat. 'Amidon' spring wheat was grown in controlled environment chambers at all combinations of 350, 650, and 950 mu L L(-1) [CO2], 0, 100, and 300 kg N ha(-1), and 14/18 degrees C and 22/26 degrees C night/day air temperatures. Temperature affected the Haun stage by growth degree-days (GDD) relationship more than N or [CO2]. The phyllochron in GDD was greater for plants grown at 22/26 degrees C (433 GDD) than at 14/18 degrees C (345 GDD). The Haun stage at apex double ridge and terminal spikelet increased as applied N and [CO2] increased. Fertile spikelet numbers increased as [CO2] and N level increased at 14/18 degrees C, but at 22/26 degrees C, spikelets increased as N increased and decreased as [CO2] increased. Fertile spikelets were greatest at 14/18 degrees C and 650 mu L L(-1) [CO2]. Results suggest that at elevated [CO2] and adequate soil water, air temperature is more important than [CO2] in controlling grain yield potential. Because wheat yield potential at higher temperatures decreased as [CO2] increased, a northly shift in the spring wheat growing areas may occur if global temperatures increased in concert with [CO2].

KEYWORDS: AIR- TEMPERATURE, CO2- ENRICHMENT, GROWTH, PHYSIOLOGY, PLANTS, RATES, RESPONSES, SOIL-WATER, WINTER-WHEAT, YIELD

687

Fredeen, A.L., and C.B. Field. 1995. Contrasting leaf and ecosystem co2 and h2o exchange in avena- fatua monoculture - growth at ambient and elevated co2. *Photosynthesis Research 43(3):263-271.*

Elevated CO2 (ambient + 35 Pa) increased shoot dry mass production in Avena fatua by similar to 68% at maturity. This increase in shoot biomass was paralleled by an 81% increase in average net CO2 uptake (A) per unit of leaf area and a 65% increase in average A at the 'ecosystem' level per unit of ground area. Elevated CO2 also increased 'ecosystem' A per unit of biomass. However, the products of total leaf area and light- saturated leaf A divided by the ground surface area over time appeared to lie on a single response curve for both CO2 treatments. The approximate slope of the response suggests that the integrated light saturated capacity for leaf photosynthesis is similar to 10-fold greater than the 'ecosystem' rate. 'Ecosystem' respiration (night) per unit of ground area, which includes soil and plant respiration, ranged from -20 (at day 19) to -18 (at day 40) mu mol m(-2) s(-1) for both elevated and ambient CO2 Avena. 'Ecosystem' below-ground respiration at the time of seedling emergence was similar to -10 mu mol m(-2) s(- 1), while that occuring after shoot removal at the termination of the experiment ranged from -5 to -6 mu mol m(-2) s(-1). Hence, no significant differences between elevated and ambient CO2 treatments were found in any respiration measure on a ground area basis, though 'ecosystem' respiration on a shoot biomass basis was clearly reduced by elevated CO2. Significant differences existed between leaf and 'ecosystem' water flux. In general, leaf transpiration (E) decreased over the course of the experiment, possibly in response to leaf aging, while 'ecosystem' rates of evapotranspiration (ET) remained constant, probably because falling leaf rates were offset by an increasing total leaf biomass. Transpiration was lower in plants grown at elevated CO2, though variation was high because of variability in leaf age and ambient light conditions and differences were not significant. In contrast, 'ecosystem' evapotranspiration (ET) was significantly decreased by elevated CO2 on 5 out of 8 measurement dates. Photosynthetic water use efficiencies (A/E at the leaf level, A/ET at the 'ecosystem' level) were increased by elevated CO2. Increases were due to both increased A at leaf and 'ecosystem' level and decreased leaf E and 'ecosystem' ET.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, LIMITATION, NUTRIENTS, PHOTOSYNTHESIS, PLANTS, RESPONSES, WATER-USE EFFICIENCY

688

Fredeen, A.L., G.W. Koch, and C.B. Field. 1995. Effects of atmospheric CO2 enrichment on ecosystem CO2 exchange in a nutrient and water limited grassland. *Journal of Biogeography 22(2-3):215-219.*

We have completed 3 years of a study aimed at understanding the impact of elevated atmospheric CO2 on ecosystem properties of annual grasslands at the Jasper Ridge Biological Preserve, Stanford, CA, U.S.A. Measurements of net ecosystem CO2 uptake were made on intact grassland (on serpentine and sandstone derived soils grown in open-top chambers since December 1991). We measured CO2 exchange in the field with transparent Teflon- lined acrylic chambers coupled to an open gas exchange system. Net ecosystem CO2 uptake for both the high productivity sandstone and the low productivity serpentine grassland communities ranged from 2 to 11 mu mol m(-2) ground s(-1) in 1992 and 1993, similar to rates obtained with eddy covariance techniques on the sandstone and serpentine grasslands at Jasper Ridge in a previous study. There was a significant effect of elevated CO2 on net ecosystem CO2 uptake rate (40-48% increase in 1992 and 17-117% increase in 1993: ANOVA P = 0.018). Although elevated CO2 consistently enhanced net ecosystem CO2 uptake at the growth CO2 concentrations, acclimation occurred such that elevated CO2-grown ecosystems had reduced rates of CO2 uptake relative to ambient CO2-grown ecosystems at either ambient or elevated CO2 measurement concentrations of CO2. The reduction in ecosystem level photosynthetic capacity in elevated CO2 treatments was accompanied by decreased foliar ribulose-bis-phosphate carboxylase (rubisco) activity on a weight basis in the species dominant in both grassland communities. Decreases in rubisco activity resulted largely from increases in leaf mass per area in elevated CO2 plants. In general, net ecosystem CO2 uptake was positively correlated with peak biomass. However, the data suggest that biomass yield for a

given level of net ecosystem CO2 uptake may be lower in elevated CO2 chambers, especially in the higher productivity sandstone community.

KEYWORDS: AVAILABILITY, CARBON DIOXIDE, ELEVATED CO2, NITROGEN, PHOTOSYNTHESIS, RESPONSES

689

Fredeen, A.L., G.W. Koch, and C.B. Field. 1998. Influence of fertilization and atmospheric CO2 enrichment on ecosystem CO2 and H2O exchanges in single- and multiple-species grassland microcosms. *Environmental and Experimental Botany 40(2):147-157.*

This paper reports on measurements of net CO2 and H2O exchange from single- and multiple-species microcosms composed of California annual grassland species grown at either ambient or elevated (ambient + 36 Pa) CO2. Microcosms consisted of grassland species grown in PVC tubes (similar to 0.95 m deep x 0.2 m diameter) containing similar to 45 kg of either serpentine or sandstone derived soil or parent material in open-top enclosures under ambient meteorological conditions. Half of the microcosms were left unfertilized (low nutrient) while the other half received an intermediate level of a slow- release (N,P,K) fertilizer (high nutrient). Gas exchange was performed by sealing individual microcosms within a transparent chamber (on clear sunny days) and coupling this to an open gas- exchange system. In fertilized single-species microcosms, elevated CO2 consistently enhanced net 'ecosystem' CO2 exchange (NCE) on a ground area basis in both early and late spring. Among unfertilized single-species microcosms, no significant trends or differences were observed in NCE between those grown at ambient versus elevated CO2. The NCE in sandstone and serpentine multiple-species microcosms was monitored seasonally over a majority of the 1993-1994 growing season. Rates were largely unaffected by growth CO2 or fertilization until after mid-February, 1994. Water-use efficiency (WUE = NCE/evapotranspiration (ET)) was generally enhanced by elevated CO2, but this was primarily a result of enhancements in NCE as opposed to decreases in ET. Enhancements in NCE by elevated CO2 in fertilized single-species microcosms at the growth-CO2, concentration were partially explained by higher above-ground biomass in elevated CO2 microcosms. However, ecosystem-level 'acclimation' occurred such that microcosms grown at elevated CO2 consistently had lower NCE than ambient CO2 treatments at a single measurement CO2 concentration (ambient or elevated). The reduction in apparent ecosystem-level photosynthetic capacity in elevated CO2 microcosms was accompanied by decreases in foliar Rubisco activity, such that NCE measured at ambient CO2 was highly correlated (r = 0.98) with foliar Rubisco activity across the three single-species microcosms in which it was measured.

KEYWORDS: ALPINE GRASSLAND, AVAILABILITY, CARBON DIOXIDE, ELEVATED CO2, GROWTH-RESPONSES, NITROGEN, PHOTOSYNTHESIS, PLANTS, USE EFFICIENCY, WATER-LIMITED GRASSLAND

690

Fredeen, A.L., J.T. Randerson, N.M. Holbrook, and C.B. Field. 1997. Elevated atmospheric CO2 increases water availability in a water-limited grassland ecosystem. *Journal of the American Water Resources Association 33(5):1033-1039.*

Californian annual grassland on sandstone (moderately fertile) and serpentine (very infertile) soils at the Jasper Ridge Biological Preserve, Stanford, California, were exposed to ambient or elevated (ambient + 36 Pa CO2) atmospheric CO2 in open-top chambers since December 1991. We measured ecosystem evapotranspiration with open gas-exchange systems, and soil moisture with time-domain reflectometry (TDR) over 0-15 cm (serpentine) and 0-30 cm (sandstone) depths, at times of peak above ground physiological activity. Evapotranspiration decreased by 12 to 63 percent under elevated CO2 in three consecutive years in the sandstone ecosystem (p = 0.053, p = 0.162, p = 0.082 in 1992, 1993, and 1994, respectively). In correspondence with decreased evapotranspiration, late-season soil moisture reserves in the sandstone were extended temporally by 10 +/- 3 days in 1993 and by 28 +/- 11 days in 1994. The effect of elevated CO2 on soil moisture was greater in the drier spring of 1994 (419 mm annual rainfall) than in 1993 (905 mm annual rainfall). In the serpentine ecosystem, evapotranspiration and soil moisture reserves were not clearly affected by elevated CO2. Soil water may be conserved in drought-affected ecosystems exposed to elevated CO2, but the amount of conservation appears to depend on the relative importance of transpiration and soil evaporation in controlling water flux.

KEYWORDS: AMBIENT, ELECTROMAGNETIC DETERMINATION, EVAPORATION, EXCHANGE, PATTERNS, PLANT, RESPONSES, SCALE, STOMATAL CONTROL, TRANSPIRATION

691

Frederick, J.R., D.M. Alm, J.D. Hesketh, and F.E. Below. 1990. Overcoming drought-induced decreases in soybean leaf photosynthesis by measuring with co2-enriched air. *Photosynthesis Research 25(1):49-57.*

692

Frederick, K.D. 1993. Climate-change impacts on water-resources and possible responses in the mink region. *Climatic Change 24(1-2):83-115.*

The capacity to supply both instream and offstream water uses under alternative climate conditions and likely future changes in population, technology, and water-using practices are examined through an adaptation of the framework developed in the Second National Water Assessment. Two measures of the adequacy of water supplies - the availability of renewable supplies to provide for withdrawal and instream uses and the relation between desired instream flows and current streamflows - are used to examine the impact of the 1931-1940 analog climate (with and without CO2 enrichment) on Missouri, Iowa, Nebraska, and Kansas (MINK). The impacts of the analog climate on water supplies are estimated from actual streamflow data and estimates of the differences in reservoir evaporation under the 1931-1940 analog and the 1951-1980 control climates. A modification of the Erosion Productivity Inventory Calculator (EPIC) model is used to estimate the impacts of the analog climate (with and without CO2 enrichment) on irrigation water use. Water, which is already a scarce resource in the MINK region, would become much scarcer if the climate of the 1930s were to become the norm. Mean assessed total streamflow would drop to 69% of the control climate level for the Missouri River Basin, 71% for the Upper Mississippi, and 93% for the Arkansas. Even in the absence of climate change, MINK will have less water in the year 2030 than it does today because groundwater stocks are being depleted and increased upstream diversions would reduce surface flows into these states. Irrigation and instream uses such as navigation, hydroelectric power production, recreation, and fish and wildlife habitat would be most adversely, impacted by the climate-induced changes in water supplies.

693

Freeman, C., R. Baxter, J.F. Farrar, S.E. Jones, S. Plum, T.W. Ashendon, and C. Stirling. 1998. Could competition between plants and microbes regulate plant nutrition and atmospheric CO2 concentrations? *The Science of the Total Environment 220(2-3):181-184.*

It has been proposed that under high CO2, soil microbes may outcompete plants for access to inorganic nutrients, leading to a negative feedback to the fertilising effects of that CO2. However, tests of the hypothesis using radioisotope tracers indicate that, in the competition for inorganic nutrients, higher CO2 concentrations may actually favour the plants rather than the microflora. The relatively lower microbial metabolism could, however, have an indirect adverse effect on plant nutrition by restricting nutrient cycling in soils, and has the potential to induce negative feedback to rising atmospheric CO2 concentrations.

KEYWORDS: DISSOLVED ORGANIC-MATTER, ELEVATED CARBON-DIOXIDE

694

Frehner, M., A. Luscher, T. Hebeisen, S. Zanetti, F. Schubiger, and M. Scalet. 1997. Effects of elevated partial pressure of carbon dioxide and season of the year on forage quality and cyanide concentration of Trifolium repens L. from a FACE experiment. *Acta Oecologica-International Journal of Ecology 18(3):297-304.*

Differently managed (cutting frequency and N fertilization) Trifolium repens monocultures were grown at 60 Pa and 35 Pa of pCO(2) (partial pressure of CO2) in a Free Air Carbon dioxide Enrichment (FACE) array. The concentrations of cyanide, digestible organic matter, crude protein and net energy for lactation were measured at different harvests throughout the growing season. The average cyanide concentrations differed significantly in the years and the seasons within the year; however, the concentrations were not affected by CO2. Digestible organic matter, crude protein and net energy for lactation differed significantly with the seasons of the year and cutting frequencies. While digestible organic matter and net energy for lactation were not affected by elevated pCO(2), the concentration of crude protein decreased from 288 g kg(-1) at ambient to 251 g kg(-1) at elevated pCO(2). Since the crude protein concentration in herbage from Trifolium monocultures was very high even at elevated CO2, it is suggested that this decrease in crude protein concentration does not negatively affect forage quality. We conclude that, in Trifolium herbage, the seasons of the year and management practices are more decisive for forage quality than changes in pCO(2). We shall discuss how forage quality and cyanide intake by ruminants may, however, be affected by CO2-induced shifts in the proportion of species in mixed plant communities.

KEYWORDS: ECOSYSTEM, HERBIVORE INTERACTIONS, INSECT HERBIVORE, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES, RISING CO2, ROOT FRACTION, TEMPERATURE

695

Frick, J., S.S. Nielsen, and C.A. Mitchell. 1994. Yield and seed oil content response of dwarf, rapid-cycling brassica to nitrogen treatments, planting density, and carbon- dioxide enrichment. *Journal of the American Society for Horticultural Science 119(6):1137-1143.*

Effects of N level (15 to 30 mM), time of N increase (14 to 28 days after planting), and planting density (1163 to 2093 plants/m(2)) were determined for crop yield responses of dwarf, rapid-cycling brassica (Brassica napus L., CrGC 5-2, Genome: ACaacc). Crops were grown in solid-matrix hydroponic systems and under controlled-environment conditions, including nonsupplemented (ambient) or elevated CO2 concentrations (998 +/- 12 mumol mol(-1)). The highest seed yield rate obtained (4.4 g.m(-2).day(-1)) occurred with the lowest N level (15 mM) applied at the latest treatment time (day 28). In all trials, CO2 enrichment reduced seed yield rate and harvest index by delaying the onset of flowering and senescence and stimulating vegetative shoot growth. The highest shoot biomass accumulation rate (55.5 g.m-2.day(-1)) occurred with the highest N level (30 mM) applied at the earliest time (day 14). Seed oil content was not significantly affected by CO2 enrichment. Maximum seed oil content (30% to 34%, dry weight basis) was obtained using the lowest N level (15 mM) initiated at the latest treatment time (day 28). In general, an increase in seed oil content was accompanied by a decrease in seed protein. Seed carbohydrate, moisture, and ash contents did not vary significantly in response to experimental treatments. Effects of N level and time of N increase were consistently significant for most crop responses. Planting density was significant only under elevated CO2 conditions.

KEYWORDS: AUTUMN, GROWTH, NAPUS, OILSEED RAPE, SIZE

696

Friedlingstein, P., I. Fung, E. Holland, J. John, G. Brasseur, D. Erickson, and D. Schimel. 1995. On the contribution of co2 fertilization to the missing biospheric sink. *Global Biogeochemical Cycles 9(4):541-556.*

A gridded biospheric carbon model is used to investigate the impact of the atmospheric CO2 increase on terrestrial carbon storage. The analysis shows that the calculated CO2 fertilization sink is dependent not just on the mathematical formulation of the "beta factor" but also on the relative controls of net primary productivity (NPP), carbon residence times, and resource availability. The modeled evolution of the biosphere for the period 1850-1990 shows an increasing lag between NPP and the heterotrophic respiration. The time evolution of the modeled biospheric sink (i.e., difference between enhanced NPP and enhanced respiration) does not match that obtained by deconvolution of the ice core CO2 time series. Agreement between the two is reasonable for the first half of the period, but during the recent decades the deconvoluted CO2 increase is much too fast to be explained by the CO2 fertilization effect only. Therefore other mechanisms than CO2 fertilization should also contribute to the missing sink. Our results suggest that about two thirds to three fourths of the 1850-1990 integrated missing sink is due to the CO2 greening of the biosphere. The remainder may be due to the increased level of nitrogen deposition starting around 1950.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, DECOMPOSITION DYNAMICS, ECOSYSTEMS, ELEVATED CO2, MODEL, NITROGEN, RESPONSES, SIMULATION, TROPICAL DEFORESTATION

697

Friedlingstein, P., G. Joel, C.B. Field, and I.Y. Fung. 1999. Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology 5(7):755-770.*

The distribution of assimilated carbon among the plant parts has a profound effect on plant growth, and at a larger scale, on terrestrial biogeochemistry. Although important progress has been made in modelling photosynthesis, less effort has been spent on understanding the carbon allocation, especially at large spatial scales. Whereas several individual-level models of plant growth include an allocation scheme, most global terrestrial models still assume constant allocation of net primary production (NPP) among plant parts, without any environmental coupling. Here, we use the CASA biosphere model as a platform for exploring a new global allocation scheme that estimates allocation of photosynthesis products among leaves, stems, and roots depending on resource availability. The philosophy underlying the model is that-allocation patterns result from evolved responses that adjust carbon investments to facilitate capture of the most limiting resources, i.e. light, water, and mineral nitrogen. In addition, we allow allocation of NPP to vary in response to changes in atmospheric CO2. The relative magnitudes of changes in NPP and resource-use efficiency control the response of root:shoot allocation. For ambient CO2, the model produces realistic changes in above- ground allocation along productivity

gradients. In comparison to the CASA standard estimate using fixed allocation ratios, the new allocation scheme tends to favour root allocation, leading to a 10% lower global biomass. Elevated CO2, which alters the balance between growth and available resources, generally leads to reduced water stress and consequently, decreased root:shoot ratio. The major exception is forest ecosystems, where increased nitrogen stress induces a larger root allocation.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, BIOMASS ALLOCATION, BIOSPHERE-MODEL, INTERNAL NITROGEN CONCENTRATION, LONG-TERM ELEVATION, NET PRIMARY PRODUCTION, PARTITIONING MODEL, PLANT-RESPONSES, SHOOT RATIOS, SURFACE PARAMETERIZATION SIB2

698

Friend, A.D., and P.M. Cox. 1995. Modeling the effects of atmospheric co2 on vegetation atmosphere interactions. *Agricultural and Forest Meteorology 73(3-4):285-295.*

The effect of doubling atmospheric CO2 concentration (C-a) on climate and vegetation is investigated using a combined climate-vegetation model. The vegetation model predicts the response of leaf area index, canopy transpiration (E(T)) and whole-plant carbon balance to changes in climate, soil moisture, and atmospheric CO2 forcing. This model has been embedded in the UK Meteorological Office Single Column Model (SCM), which provides the climate feedback to the vegetation. The vegetation model uses an optimisation approach to predict stomatal resistance, a biochemical model to predict photosynthesis and a simple carbon balance model to predict leaf area. Respiration is calculated as a function of leaf area and vegetation height. Clouds are assumed to be radiatively passive in the SCM to avoid unrealistic feedbacks. Simulations were performed with the fully interactive vegetation-climate model for an Amazon location with the present-day value of C-a (1 x CO2), and twice this value (2 x CO2). In addition, two other types of simulation were performed at both CO2 concentrations: one in which the vegetation component was forced only with 1 x CO2, and one using a fixed surface resistance. The latter case is equivalent to simulations using most current general circulation models. In all the simulations, increased atmospheric CO2 caused an increase in surface temperature owing to increased radiative forcing. With a fixed resistance, mean E(T) was increased by 5.6% and sensible heat flux was reduced by 3.8%. The fully interactive model had significant effects on the response of both climate and productivity to C-a. Increased C-a caused stomatal closure, which resulted in a reduction in mean E(T) Of 25%. The effect of C-a on E(T) was amplified by the positive feedback resulting from the effect of increased air humidity deficit on stomatal resistance.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, FIELD, PHOTOSYNTHESIS, SEEDLINGS, STOMATAL CONDUCTANCE, TRANSPIRATION

699

Fritschi, F.B., K.J. Boote, L.E. Sollenberger, and L.H. Allen. 1999. Carbon dioxide and temperature effects on forage establishment: tissue composition and nutritive value. *Global Change Biology 5(7):743-753.*

Atmospheric CO2 concentration ([CO2]) and temperature are likely to increase in the future and may change plant growth and composition characteristics. Rhizoma peanut (Arachis glabrata Benth.) and bahiagrass (Paspalum notatum Flugge) were grown on a natural field soil in temperature-gradient greenhouses to evaluate the effects of elevated [CO2] and temperature on tissue composition and digestibility during the establishment year. Carbon dioxide levels were maintained at 365 (ambient) and 640 mu L CO2 L-1 air. The temperature- gradient greenhouses were regulated to obtain air temperature sectors of 0.2, 1.5, 2.9, and 4.5 degrees C above ambient. Samples were taken of previously undefoliated herbage at 57, 86, 121, 148, and 217 days after planting and entire plots were harvested at 218 days after planting. Elevated [CO2] increased total nonstructural carbohydrate concentration in rhizoma peanut leaves by almost 50%. Rhizoma peanut leaf N concentration was 6% lower at elevated than at ambient [CO2]. The N concentration in new rhizomes of rhizoma peanut was increased by high [CO2], while the N concentration in bahiagrass was not affected by temperature or [CO2]. No effects of [CO2] and temperature were found on neutral detergent fibre in rhizoma peanut leaves or stems; however, elevated [CO2] increased neutral detergent fibre in bahiagrass leaves. Only at season end was in vitro organic matter digestion of rhizoma peanut higher at ambient (623 g kg(-1)) than at elevated [CO2] (609 g kg(-1)). Elevated [CO2] had a greater effect on tissue composition of rhizoma peanut than of bahiagrass. These data suggest that elevated temperature and CO2-induced changes in chemical composition of forage species adapted to humid subtropics will be relatively small, particularly for C4 species.

KEYWORDS: DECIDUOUS TREES, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, GRACILIS C-4, INSECT PERFORMANCE, LEAF, NITROGEN, PASCOPYRUM-SMITHII C-3, PLANT, ROOT FRACTION

700

Fritschi, F.B., K.J. Boote, L.E. Sollenberger, L.H. Allen, and T.R. Sinclair. 1999. Carbon dioxide and temperature effects on forage establishment: photosynthesis and biomass production. *Global Change Biology 5(4):441-453.*

Concerns about climatic change have stimulated interest in the response of plants to increasing CO2 concentration ([CO2]), temperature, and their possible interactions. The purpose of this study was to determine the effects of elevated [CO2] and air temperature on photosynthesis, development, and biomass production of rhizoma peanut (Arachis glabrata Benth.) and bahiagrass (Paspalum notatum Flugge) during the establishment year. Forages were grown in four temperature-gradient greenhouses on a natural Grossarenic Paleudult soil profile at temperatures of 0.2, 1.5, 2.9, and 4.5 degrees C above ambient, and at [CO2] of 365 and 640 mu L CO2 L-1 air. Elevated [CO2] accelerated establishment and ground cover of both species. Leaf and canopy photosynthesis of both species increased at elevated [CO2], with greater increases in rhizoma peanut than bahiagrass. Averaged across five sampling dates, total biomass production of rhizoma peanut and bahiagrass responded to elevated [CO2] with a 52 and 9% increase, respectively. Increasing temperature enhanced biomass production of bahiagrass but not rhizoma peanut. Forage yield at the end of the growing season in CO2-enriched treatments was increased over that in ambient [CO2] treatments (385 vs. 318 g m(-2) for rhizoma peanut and 376 vs. 321 g m(-2) for bahiagrass). Overall, the enhancement of rhizoma peanut under elevated [CO2] was greater than that of bahiagrass; however, bahiagrass responded more positively to increasing temperature.

KEYWORDS: AIR CO-2 ENRICHMENT, CLIMATE, ELEVATED ATMOSPHERIC CO2, GRACILIS C-4, GROWTH, LEAF GAS-EXCHANGE, LEAVES, LOLIUM, PASCOPYRUM-SMITHII C-3, RESPONSES

701

Fujii, N., M. Watanabe, Y. Watanabe, and N. Shimada. 1994. Relationship between oxalate synthesis and glycolate cycle in spinach. *Journal of the Japanese Society for Horticultural Science 62(4):789-794.*

The relationship between oxalate synthesis and glycolate pathway in spinach (Spinacia oleracea L. cv. Sunlight) was studied by exposing

seedling to 1,000 PPM CO2-enriched atmosphere. It was observed that CO2-enrichment increased the content of ascorbic acid but decreased that of oxalate. It was presumed that reducing the rate of glycolate synthesis would reduce the content of oxalate. Mature leaves of spinach grown under normal conditions, were fed with [2-C-14] glycolate and [1-C-14] ascorbic acid to compare their contribution as a precursor of oxalate. Using the values of the C-14 distribution to oxalate, photorespiratory glycolate metabolic rate and the turnover rate of ascorbic acid, the rate of oxalate synthesis was calculated. It was observed that glycolate was more efficient as a precursor of oxalate synthesis than it was for ascorbic acid. From these results, we postulate that the oxalate synthesis is closely related to the glycolate cycle.

KEYWORDS: CALCIUM

702

Gahrooee, F.R. 1998. Impacts of elevated atmospheric CO2 on litter quality, litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. *Global Change Biology 4(6):667-677.*

Elevated CO2 may affect litter quality of plants, and subsequently C and N cycling in terrestrial ecosystems, but changes in litter quality associated with elevated CO2 are poorly known. Abscised leaf litter of two oak species (Quercus cerris L. and a. pubescens Willd.) exposed to long-term elevated CO2 around a natural CO2 spring in Tuscany (Italy) was used to study the impact of increasing concentration of atmospheric CO2 on litter quality and C and N turnover rates in a Mediterranean-type ecosystem. Litter samples were collected in an area with elevated CO2 (>500 ppm) and in an area with ambient CO2 concentration (360 ppm). Leaf samples were analysed for concentrations of total C, N, lignin, cellulose, acid detergent residue (ADR) and polyphenol. The decomposition rate of litter was studied using a litter bag experiment (12 months) and laboratory incubations (3 months). In the laboratory incubations, N mineralization in litter samples was measured as well (125 days). Litter quality was expressed in terms of chemical composition and element ratios. None of the litter quality parameters was affected by elevated CO2 for the two Quercus species. Remaining mass in a. cerris and Q. pubescens litter from elevated CO2 was similar to that from ambient conditions. C mineralization in Q. pubescens litter from elevated CO2 was lower than that from ambient CO2, but the difference was insignificant. This effect was not observed for Q. cerris. N mineralization was higher from litter grown at elevated CO2, but this difference disappeared at the end of the incubation. Litter of a. pubescens had a higher quality than Q. cerris, and indeed mineralized more rapidly in the laboratory, but not under field conditions.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECOMPOSITION, GROWTH, LEAF LITTER, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SOIL, TERRESTRIAL ECOSYSTEMS

703

Gallardo, A., and J. Merino. 1998. Soil nitrogen dynamics in response to carbon increase in a Mediterranean shrubland of SW Spain. *Soil Biology and Biochemistry 30(10-11):1349-1358.*

Most models predict that high atmospheric CO2 concentrations will lead to an increase in the C-to-N ratio of litter production in terrestrial ecosystems. The effect of an increase in the soil C-to-N ratio on the nitrogen dynamics in a Mediterranean shrubland was simulated by mixing with the lifter layer wood shavings with a high C-to-N ratio. Samples of mineral soil, taken subsequently eight times during 404 d, were analyzed for total C, total N, total soil carbohydrates, potential net N mineralization, potential net nitrification and microbial biomass-N. We found significant increases in the concentration of total carbohydrates, C-to-N ratio and microbial biomass N in amended soils during the experiment, while potential net N mineralization rate and net nitrification rate significantly decreased; amounts of available nitrogen (NH4+-N + NO3-N) were unaffected by the amendment treatment. However, by the end of the experiment, no significant differences between amended and control soil samples were found. The total carbohydrates-to-K2SO4-extractable total-N ratio was the best predictor of both net mineralization rate and microbial biomass N, showing that the available C-to- available-N ratio is a better indicator of N dynamics than the total C to total N ratio. Our results support the hypothesis that increasing C availability in soils leads to a decrease in N availability for plants through the immobilization of N in microbial biomass and to an increase in the temporal heterogeneity of soil properties in a Mediterranean shrubland. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ANNUAL GRASSLAND, DIOXIDE, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO2, MICROBIAL BIOMASS, MINERAL-SOIL, NITRIFICATION, OLD-GROWTH FOREST, PLANTS, TALLGRASS PRAIRIE

704

Galtier, N., C.H. Foyer, E. Murchie, R. Alred, P. Quick, T.A. Voelker, C. Thepenier, G. Lasceve, and T. Betsche. 1995. Effects of light and atmospheric carbon-dioxide enrichment on photosynthesis and carbon partitioning in the leaves of tomato (lycopersicon-esculentum L) plants over-expressing sucrose- phosphate synthase. *Journal of Experimental Botany 46:1335-1344.*

Photosynthetic carbon assimilation, carbon partitioning and foliar carbon budgets were measured in the leaves of transformed tomato plants expressing a maize sucrose-phosphate synthase (SPS) gene in addition to the native enzyme, and in untransformed controls. The maize SPS gene was expressed under control of either the promoter of the small subunit of ribulose 1,5-bisphosphate carboxylase (rbcS promoter; lines 2, 9 and 18) or the 35S promoter from cauliflower mosaic virus (CaMV promoter; line 13). The rate of sucrose synthesis was increased relative to that of starch and sucrose/starch ratios were higher throughout the photoperiod in the leaves of all plants expressing high SPS activity. The leaf carbon budget over the day/night cycle in air at low irradiance (180 mu mol photon m(- 2) s(-1)) was similar in all plants. Net photosynthesis measured in air and at elevated CO2 (800-1500 mu l I-1) on whole plants grown in air at 400 mu mol m(-2) s(-1) irradiance was significantly increased in the high SPS expressors compared to the untransformed controls and was highest where SPS activity was greatest. At high CO2 the stimulation of photosynthesis was more pronounced, We conclude that SPS activity is a major point of control of photosynthesis particularly under saturating light and CO2.

KEYWORDS: ACCLIMATION, BIOSYNTHESIS, CARBOHYDRATE, ELEVATED CO2, GROWTH, INHIBITION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPINACH LEAVES, STARCH

705

Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano, and M. Kiyohara. 1991. Enhanced growth of the red alga porphyra-yezoensis ueda in high co2 concentrations. *Journal of Applied Phycology 3(4):355-362.*

Leafy thalli of the red alga Porphyra yezoensis Ueda, initiated from conchospores released from free-living conchocelis, were cultured using aeration with high CO2. It was found that the higher the CO2 concentration, the faster the growth of the thalli. Aeration with elevated CO2 lowered pH in dark, but raised pH remarkably in light with the thalli, because the photosynthetic conversion of HCO3- to OH- and CO2 proceeded much faster than the dissociation of hydrated CO2 releasing

H+. Photosynthesis of the alga was found to be enhanced in the seawater of elevated dissolved inorganic carbon (DIC, CO2 + HC O3- + CO3-). It is concluded that the increased pH in the light resulted in the increase of DIC in the culture media, thus enhancing photosynthesis and growth. The relevance of the results to removal of atmospheric CO2 by marine algae is discussed.

KEYWORDS: ASSIMILATION, CHONDRUS-CRISPUS, DIATOM, INORGANIC-CARBON UPTAKE, MARINE MACROALGAE, PHAEOPHYTA, PHOTOSYNTHESIS, PLANTS, TRANSPORT, WATER

706

Gao, K., Y. Aruga, K. Asada, T. Ishihara, T. Akano, and M. Kiyohara. 1993. Calcification in the articulated coralline alga corallina-pilulifera, with special reference to the effect of elevated co2 concentration. *Marine Biology 117(1):129-132.*

Calcification in Corallina pilulifera Postels et Ruprecht displayed diurnal variations in aerated (350 ppm CO2) culture media, with faster rates during the light than during the dark period. Addition of CO2 (air + 1250 ppm) inhibited calcification. This was attributable to the decreased pH resulting from CO2 addition. Both photosynthesis and calcification were enhanced in seawater, with elevated dissolved inorganic carbon concentrations at a constant pH of 8.2.

KEYWORDS: CAULERPALES, CHLOROPHYCEAE, GROWTH, HALIMEDA, MARINE PLANTS, PHOTOSYNTHESIS, RESPIRATION

707

Gao, K., Y. Aruga, K. Asada, and M. Kiyohara. 1993. Influence of enhanced co2 on growth and photosynthesis of the red algae gracilaria sp and g-chilensis. *Journal of Applied Phycology 5(6):563-571.*

The influence of elevated CO2 concentrations on growth and photosynthesis of Gracilaria sp. and G. chilensis was investigated in order to procure information on the effective utilization of CO2. Growth of both was enhanced by CO2 enrichment (air + 650 ppm CO2, air + 1250 ppm CO2), the enhancement being greater in Gracilaria sp. Both species increased uptake of NO, with CO, enrichment. Photosynthetic inorganic carbon uptake was depressed in G. chilensis by pre- culture (15 days) with CO2 enrichment, but little affected in Gracilaria sp. Mass spectrometric analysis showed that O-2 uptake was higher in the light than in the dark for both species and in both cases was higher in Gracilaria sp. The higher growth enhancement in Gracilaria sp. was attributed to greater depression of photorespiration by the enrichment of CO2 in culture.

KEYWORDS: ANHYDRASE, INORGANIC CARBON, MARINE MACROALGAE, PHYSIOLOGY

708

Gao, Q., and M. Yu. 1998. A model of regional vegetation dynamics and its application to the study of Northeast China Transect (NECT) responses to global change. *Global Biogeochemical Cycles 12(2):329-344.*

We developed a dynamic regional vegetation model to address problems of responses of regional vegetation to elevated ambient CO2 and climatic change. The model takes into consideration both local ecosystem processes within a patch or grid cell, such as plant growth and death, and mass and energy flow, such as plant migration, across adjacent grid cells. The model is able to couple vegetation structure dynamics and primary production processes. The normalized differential vegetation index from meteorological satellite AVHRR was used to parameterize the model. Plant migration rates were derived based on effective seedling distribution around parent plants. The model was applied to Northeast China Transect at a spatial resolution of 10 min latitude by 10 min longitude per grid cell and a temporal resolution of 1 month. The results indicated that with doubled CO2 concentration, a 20% increase in precipitation and a 4 degrees C increase in temperature, the model predicted that net primary productivity (NPP) of Larix forests, conifer-broadleaf mixed forests, Aneurolepidium chinense steppes, Stipa grandis steppes, and wetland and salty meadows would decrease by 15% to 20%. However, NPP of deciduous broadleaf forests, woodland and shrubs, Stipa baicalensis meadow steppes, and desert grasslands would increase by 20% to 115%, as predicted by the model for the same climatic scenario. The average NPP of natural vegetation over the whole transect would decrease slightly, largely because of the compensation between the positive effects of increased CO2 and precipitation and the negative effect of increased evapotranspiration induced by increased temperature.

KEYWORDS: BIOMASS, CLIMATE, FOREST ECOSYSTEM PROCESSES, GENERAL-MODEL, NET PRIMARY PRODUCTIVITY, PHOTOSYNTHESIS, SATELLITE, SENSITIVITY, SIMULATION, TERRESTRIAL BIOSPHERE

709

Gao, Q., and X.S. Zhang. 1997. A simulation study of responses of the northeast China transect to elevated CO2 and climate change. *Ecological Applications 7(2):470-483.*

The spatiotemporal variations of vegetation biomass of the ecological transect in northeast China were simulated. Slate variables of the model included green biomass and nongreen biomass of 12 vegetation categories and water contents of three soil layers. The simulated monthly green biomass was converted into NDVI, or Normalized Differential Vegetation Index of AVHRR (Advanced Very High Resolution Radiometry). A comparison between the modeled and the observed NDVI was made at 10' spatial resolution, Atmospheric CO2 concentration and montiiiy precipitation were used as two driving variables for global change simulation. Effects of precipitation increments on percentage sunshine, relative humidity, radiation, evapotranspiration, and eventually soil water and plant growth, were considered, Two levers of CO2 concentration (present, doubled) and seven levels of precipitation increments (0, 0.05, 0.1, 0.15, 0.2, 0.25, and 0.30) were prescribed for a total of 14 simulation runs. A steady-state solution was obtained for each simulation run. The results of simulation showed that with the present climate conditions, doubling atmospheric CO2 concentration led approximately to a 20.3% increase in green biomass, 11.0% increase in nongreen biomass, 19,0% increase in green NPP, 12.8% increase in nongreen NPP, and 24.9% increase in overall average NPP at steady state, These increases go, respectively, to 32.9, 13.9, 30.0, 20.1, and 23.4% when a 30% precipitation increase was superimposed on the doubled CO2 concentration.

KEYWORDS: FORESTS, LEAF-AREA INDEX, MODEL, PHOTOSYNTHESIS, PRODUCTIVITY, SATELLITE, VEGETATION

710

Garbutt, K., W.E. Williams, and F.A. Bazzaz. 1990. Analysis of the differential response of 5 annuals to elevated CO2 during growth. *Ecology 71(3):1185-1194.*

711

Garcia, J.M. 1993. Effect of co2 in fruit storage atmosphere on olive oil quality. *Grasas Y Aceites 44(3):169-174.*

Olive fruits (Olea europaea, cv. "Picual") were stored at 5- degrees-C and

four different atmospheres (% CO2/% O2/%N2: 0/21/78: 5/20/75; 10/19/71 and 20/17/63). At 5-degrees-C the enrichment of the fruit storage atmosphere with concentrations of CO2 above 5% resulted in a linear increase of the acidity of extracted oils after 60 days of fruit storage time. This fact showed a strong relationship with the appearence of fruit decay. Simple refrigeration of fruits at 5-degrees-C for 60 days was sufficient to mantain the commercial quality of "virgin extra" in oil extracted from them. Oils obtained from fruits stored at 5-degrees-C in CO2 enriched atmospheres showed lower peroxide index and UV absorbance (270 nm), but developed off-flavor. Therefore, greater-than-or-equal-to 5% CO2 concentrations in storage atmosphere of olive fruits for oil production at 5-degrees-C must be avoided.

712

Garcia, J.M., and J. Streif. 1993. Quality and storage potential of pear .1. Influence of ca- storage and ulo-storage conditions. *Gartenbauwissenschaft 58(1):36-41.*

In a CA experiment the storage potential of different pear cultivars was investigated, especially the behaviour of the fruits against elevated CO2 concentrations and/or ultra low oxygen (ULO).The following CA combinations were tested: < 1 % CO2 + 3 % O2; 3 % CO2 + 3 % O2; < 1 % CO2 + 1 % O2; 3 % CO2 + 1 % O2, and refrigerated storage at -1-degrees-C 'Packham's Triumph' showed the best storage potential of all tested cultivars followed by 'Conference' and 'Doyenne' du Comice. The keepability of 'General Leclerc' was only slightly improved by CA conditions compared with cold stored pears. CA storage of 'Alexander Lucas' and 'Bristol Cross' didn't show an obvious advantage because of high CO2 damages. Therefore, CO2 concentrations in CA storage of these two cultivars should be < 1 %. 'Conference' and 'General Leclerc' tolerate up to 2 % CO2, 'Doyenne du Comice' and 'Packham's Triumph' up to 3 % CO2. ULO conditions amplified the CO2 damages in the CO2 sensitive cultivars, but improved the keepability of 'Doyenne du Comice' and 'Packham's Triumph'.

713

Garcia, R.L., S.B. Idso, and B.A. Kimball. 1994. Net photosynthesis as a function of carbon-dioxide concentration in pine trees grown at ambient and elevated co2. *Environmental and Experimental Botany 34(3):337-341.*

Pinus eldarica seedlings were grown in a field of Avondale loam at Phoenix, Arizona within transparent open-top enclosures maintained for 15 months at mean CO2 concentrations of 402 and 788 mu l 1(-1), after which whole-tree net photosynthetic rates were measured at a number of CO2 concentrations ranging from ambient (360 mu l 1(-1)) to 3000 mu l 1(-1). Rates of the low- CO2-treatment trees saturated at approximately five times their ambient-concentration value; while rates of the high-CO2- treatment trees rose linearly across the entire CO2 range investigated to more than 10 times their value al 360 mu l 1(- 1). These findings suggest that long-term exposure to elevated CO2 can increase the ability of trees with unrestricted root systems to respond positively to still higher CO2 concentrations.

KEYWORDS: ACCLIMATION, ENRICHMENT, PLANTS, RESPIRATION

714

Garcia, R.L., S.B. Idso, G.W. Wall, and B.A. Kimball. 1994. Changes in net photosynthesis and growth of pinus-eldarica seedlings in response to atmospheric co2 enrichment. *Plant, Cell and Environment 17(8):971-978.*

Pinus eldarica L. trees, rooted in the natural soil of an agricultural field at Phoenix, Arizona, were grown from the seedling stage in clear-plastic-wall open-top enclosures maintained at four different atmospheric CO2 concentrations for 15 months. Light response functions were determined for one tree from each treatment by means of whole-tree net CO2 exchange measurements at the end of this period, after which rates of carbon assimilation of an ambient-treatment tree were measured across a range of atmospheric COP concentrations. The first of these data sets incorporates the consequences of both the CO2-induced enhancement of net photosynthesis per unit needle area and the CO2-induced enhancement of needle area itself (due primarily to the production of more needles), whereas the second data set reflects only the first of these effects. Hence the division of the normalized results of the first data set by the normalized results of the second set yields a representation of the increase in whole-tree net photosynthesis due to enhanced needle production caused by atmospheric CO2 enrichment. In the solitary trees we studied, the relative contribution of this effect increased rapidly with the CO2 concentration of the air to increase whole-tree net photosynthesis by nearly 50% at a CO2 concentration approximately 300 mu mol mol(-1) above ambient.

KEYWORDS: AMBIENT, CARBON DIOXIDE, ELEVATED CO2, FIELD, LIGHT, PRODUCTIVITY, SCIRPUS- OLNEYI, SOUR ORANGE TREES, TEMPERATURE, YIELD

715

Garcia, R.L., S.P. Long, G.W. Wall, C.P. Osborne, B.A. Kimball, G.Y. Nie, P.J. Pinter, R.L. Lamorte, and F. Wechsung. 1998. Photosynthesis and conductance of spring-wheat leaves: field response to continuous free-air atmospheric CO2 enrichment. *Plant, Cell and Environment 21(7):659-669.*

Spring wheat was grown from emergence to grain maturity in two partial pressures of CO2 (pCO(2)): ambient air of nominally 37 Pa and air enriched with CO2 to 55 Pa using a free-air CO2 enrichment (FACE) apparatus. This experiment was the first of its kind to be conducted within a cereal field without the modifications or disturbance of microclimate and rooting environment that accompanied previous studies, It provided a unique opportunity to examine the hypothesis that continuous exposure of wheat to elevated pCO(2) will lead to acclimatory loss of photosynthetic capacity. The diurnal courses of photosynthesis and conductance for upper canopy leaves were followed throughout the development of the crop and compared to model-predicted rates of photosynthesis. The seasonal average of midday photosynthesis rates was 28% greater in plants exposed to elevated pCO(2) than in contols and the seasonal average of the daily integrals of photosynthesis was 21% greater in elevated pCO(2) than in ambient air. The mean conductance at midday was reduced by 36%. The observed enhancement of photosynthesis in elevated pCO(2) agreed closely with that predicted from a mechanistic biochemical model that assumed no acclimation of photosynthetic capacity. Measured values fell below predicted only in the flag leaves in the mid afternoon before the onset of grain-filling and over the whole diurnal course at the end of grain-filling. The loss of enhancement at this final stage was attributed to the earlier senescence of flag leaves in elevated pCO(2). In contrast to some controlled-environment and field-enclosure studies, this field-scale study of wheat using free-air CO2 enrichment found little evidence of acclimatory loss of photosynthetic capacity with growth in elevated pCO(2) and a significant and substantial increase in leaf photosynthesis throughout the life of the crop.

KEYWORDS: ACCLIMATION, CAPACITY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, LEAF, PRODUCTIVITY, PROTEINS, WATER-USE EFFICIENCY, WINTER-WHEAT

716

Garcia-Ibilcieta, D., and J.C. Pushnik. 1997. Differential gene displays from Pinus ponderosa seedlings experiencing elevated CO2 stress. *Faseb Journal 11(9):A1104.*

717

Gardner, S.D.L., G. Taylor, and C. Bosac. 1995. Leaf growth of hybrid poplar following exposure to elevated co2. *New Phytologist 131(1):81-90.*

Leaf extension was stimulated following exposure of three interamerican hybrid poplar clones (Populus trichocarpa x P. deltoides); 'Unal', 'Boelare', and 'Beaupre' and a euramerican clone 'Primo' (Populus nigra x P. deltoides) to elevated CO2 in controlled environment chambers. For all three interamerican clones the evidence suggests that this was the result of increased leaf cell expansion associated with enhanced cell wall extensibility (WEx), measured as tensiometric increases in cell wall plasticity. For the interamerican clone 'Boelare', there was also a significant increase in cell wall elasticity following exposure to elevated CO2 (P less than or equal to 0.001). The effect of elevated CO2 in stimulating cell wall extensibility was confirmed in a detailed spatial analysis of extensibility made across the lamina of expanding leaves of the clone 'Boelare'. For two of the interamerican hybrids, 'Unal' and 'Beaupre', both leaf cell water potential (psi) and turgor pressure (P) were lower in elevated than in ambient CO2 By contrast, no significant effects on the cell wall properties or leaf water relations for the euramerican hybrid 'Primo' were observed following exposure to elevated CO2, suggesting that the mechanism for increased leaf extension in elevated CO2 differed, depending on clone. The cumulative total length of leaves of 'Boelare' grown in elevated CO2 was significantly increased (P less than or equal to 0.05) and since leaf number was not significantly increased in any inter-american clone it is hypothesized that final leaf size was stimulated in elevated CO2 for these clones. By contrast, there was no significant effect of CO2 on cumulative total leaf length for the euramerican clone 'Primo', but leaf number was significantly increased by elevated CO2. The measurements suggest that total tree leaf area was stimulated for a range of poplar hybrids exposed to elevated CO2. Given the short rotation of a coppiced crop, it is likely that increased leaf areas will result in enhanced stemwood production when hybrid poplars are grown in the CO2 concentrations predicted for the next century.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOPHYSICS, ENRICHMENT, FORESTS, PLANT-CELL GROWTH, SALIX-VIMINALIS, SEEDLINGS, WALL EXTENSIBILITY, WATER-LIMITED CONDITIONS, YIELD

718

Gary, C., N. Bertin, J.S. Frossard, and J. Le Bot. 1998. High mineral contents explain the low construction cost of leaves, stems and fruits of tomato plants. *Journal of Experimental Botany 49(318):49-57.*

The construction cost of plant tissues is used in crop models to convert the products of photosynthesis into biomass. As for other greenhouse crops, tomato tissues are specific in that they have a high mineral content. The consequences of this accumulation of minerals on the construction cost of the tissues and the possible interactions with the physiological age of the organs and with the CO2 concentration in the atmosphere was examined. For that purpose, three methods of estimating the construction cost were used and compared. Large quantities of minerals accumulated in the tissues of tomato plants (ranging from 0.05 in fruits to 0.26 g g(-1) DM in leaves). The subsequent dilution of the organic matter explained why the estimated construction cost of the dry matter (organic matter + minerals) was fairly low in comparison to that of other crop species. The construction cost was higher in fruits than in vegetative organs, partly because of a lower mineral content. It decreased by 7-12% from top to bottom of the canopy, following the increase in the physiological age of the tissues. This ontogenic drift was partly explained by the accumulation of minerals in the older organs. In the conditions of CO2 enrichment of a commercial greenhouse, no effect of CO2 concentration on the mineral content and on the construction cost of tissues was observed. Such a variability of the construction cost of tomato plant tissues due to the accumulation of minerals or to the ontogeny questions the use of standard values in crop models.

KEYWORDS: CARBON CONTENT, COMBUSTION, CROP, DARK RESPIRATION, EFFICIENCY, ELEVATED CO2, GRAIN-SORGHUM, GREENHOUSE TOMATO, GROWTH, TEMPERATURE

719

Gay, A.P., and B. Hauck. 1994. Acclimation of lolium-temulentum to enhanced carbon-dioxide concentration. *Journal of Experimental Botany 45(277):1133-1141.*

Acclimation of single plants of Lolium temulentum to changing [CO2] was studied on plants grown in controlled environments at 20 degrees C with an 8 h photoperiod. In the first experiment plants were grown at 135 mu mol m(-2) s(-1) photosynthetic photon flux density (PPFD) at m s 415 mu l l(-1) or 550 mu l l(-1) [CO2] with some plants transferred from the lower to the higher [CO2] at emergence of leaf 4. In the second experiment plants were grown at 135 and 500 mu mol m(-2) s(-1) PPFD at 345 and 575 mu l l(-1) [CO2]. High [CO2] during growth had little effect on stomatal density, total soluble proteins, chlorophyll a content, amount of Rubisco or cytochrome f. However, increasing [CO2] during measurement increased photosynthetic rates, particularly in high light. Plants grown in the higher [CO2] had greater leaf extension, leaf and plant growth rates in low but not in high light. The results are discussed in relation to the limitation of growth by sink capacity and the modifications in the plant which allow the storage of extra assimilates at high [CO2].

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, FESTUCA-PRATENSIS, GROWTH, LEAF, LEAVES, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, PROTEINS, STOMATAL DENSITY

720

Gebauer, R.L.E., J.F. Reynolds, and B.R. Strain. 1996. Allometric relations and growth in Pinus taeda: The effect of elevated CO2 and changing N availability. *New Phytologist 134(1):85-93.*

Loblolly pine (Pinus taeda L.) seedlings were grown for 138 d at two CO2 partial pressures (35 and 70 Pa CO2) and four N solution concentrations (0.5, 1.5, 3.5 and 6.5 mM NH4NO3). Allometric regression analysis was used to determine whether patterns of biomass allocation among functionally distinct plant-parts were directly controlled by CO2 and N availability or whether differences between treatments were the result of size-dependent changes in allocation. Both CO2 and N availability affected growth of loblolly pine. Growth stimulation by CO2 at nonlimiting N solution concentrations (3.5 and 6.5 mM NH4NO3) was c. 90%. At the lowest N solution concentration (0.5 mM NH4NO3), total plant biomass was still enhanced by 35% under elevated CO2. Relative growth rates were highly correlated with net assimilation rates, whereas leaf mass ratio remained unchanged under the wide range of CO2 and N solution concentrations. When differences in plant size were adjusted apparent CO2 effects on biomass allocation among different plant parts disappeared, indicating that CO2 only indirectly affected allocation through accelerated growth. N availability, by contrast, had a direct effect on biomass allocation, but primarily at the lowest N solution concentration (0.5 mM NH4NO3). Loblolly pine compensated for N limitation by increasing specific lateral root length and proportional biomass allocation to the lateral root system. The results emphasize the significance of distinguishing size-dependent effects on biomass allocation from functional adjustments

made in direct response to changing resource availability.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, LOBLOLLY-PINE, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, ROOT LENGTH, SEEDLINGS, SHOOT, WOODY-PLANTS

721

Gebauer, R.L.E., B.R. Strain, and J.P. Reynolds. 1998. The effect of elevated CO2 and N availability on tissue concentrations and whole plant pools of carbon-based secondary compounds in loblolly pine (Pinus taeda). *Oecologia 113(1):29-36.*

We examined the extent to which carbon investment into secondary compounds in loblolly pine (Pinus taeda L.) is changed by the interactive effect of elevated CO2 and N availability and whether differences among treatments are the result of size-dependent changes. Seedlings were grown for 138 days at two CO2 partial pressures (35 and 70 Pa CO2) and four N solution concentrations (0.5, 1.5, 3.5, and 6.5 mmol l(-1) NO3NH4) and concentrations of total phenolics and condensed tannins were determined four times during plant development in primary and fascicular needles, stems and lateral and tap roots. Concentrations of total phenolics in lateral roots and condensed tannins in tap roots were relatively high regardless of treatment. In the smallest seedlings secondary compound concentrations were relatively high and decreased in the initial growth phase. Thereafter condensed tannins accumulated strongly during plant maturation in all plant parts except in lateral roots, where concentrations did not change. Concentrations of total phenolics continued to decrease in lateral roots while they remained constant in all other plant parts. At the final harvest plants grown at elevated CO2 or low N availability showed increased concentrations of condensed tannins in aboveground parts. The CO2 effect, however, disappeared when size differences were adjusted for, indicating that CO2 only indirectly affected concentrations of condensed tannins through accelerating growth. Concentrations of total phenolics increased directly in response to low N availability and elevated CO2 in primary and fascicular needles and in lateral roots, which is consistent with predictions of the carbon-nutrient balance (CNB) hypothesis. The CNB hypothesis is also supported by the strong positive correlations between soluble sugar and total phenolics and between starch and condensed tannins. The results suggest that predictions of the CNB hypothesis could be improved if developmentally induced changes of secondary compounds were included.

KEYWORDS: DECOMPOSITION, DEFENSE, GROWTH, HERBIVORY, METABOLISM, NITROGEN, NUTRIENT BALANCE, PAPER BIRCH, PERFORMANCE, PHENOLIC-COMPOUNDS

722

Gedroc, J.J., K.D.M. McConnaughay, and J.S. Coleman. 1996. Plasticity in root shoot partitioning: Optimal, ontogenetic, or both? *Functional Ecology 10(1):44-50.*

1. We tested whether plants increase root,shoot ratios to compensate for limitations of below-ground resources in a manner consistent with optimal partitioning theory or whether the relative production of roots and shoots is controlled by species-specific developmental patterns. Individuals of two annual plant species, Abutilon theophrasti and Chenopodium album, were grown from seed in controlled greenhouse conditions under high- or low-nutrient regimes. Mid-way through the experiment, a sub-set of low-nutrient-grown plants were given high nutrient availability and a sub-set of high-nutrient-grown plants were transferred to a low nutrient environment. 2. Under continuous nutrient regimes: (1) high-nutrient-grown plants of both species grew faster and had a lower root:shoot ratio than low-nutrient-grown plants, consistent with optimal partitioning theory; (2) both species exhibited a substantial amount of ontogenetic drift as root:shoot ratios decreased through ontogeny (subsequent to an initial increase in R/S shortly after germination); (3) allometric analyses revealed that increased allocation to roots occurred very early in ontogeny for both species, after which the relative growth of shoots exceeded that of roots in low-nutrient-grown plants compared to their high nutrient-grown counterparts - a result inconsistent with optimal partitioning theory. 3. Under temporally varying nutrient regimes: (1) growth substantially increased in low-nutrient-grown plants that were switched to a high-nutrient environment without a change in root:shoot partitioning; (2) there was no change in growth or partitioning when plants were switched from a high- to a low-nutrient regime. 4. We conclude that, for these annual species, root/shoot partitioning is partially consistent with optimal partitioning theory but that is also highly ontogenetically constrained. This constraint is evident both in substantive ontogenetic drift in partitioning and in the period during development that plasticity in partitioning can be expressed.

KEYWORDS: CARBON DIOXIDE, CONSEQUENCES, ELEVATED CO2, FRAGMENTATION, GROWTH, NITROGEN CONCENTRATION, PERFORMANCE, PLANT, SIZE, SPACE

723

Geethakumari, V.L., and K. Shivashankar. 1991. Studies on organic amendment and CO2 enrichment in ragi soybean intercropping systems. *Indian Journal of Agronomy 36(2):202-206.*

Organic amendment comprising of ragi husk and FYM mixed in 1:1 ratio by weight promoted organic carbon content and available P status of the soil. A level of 4 t/ha of organic amendment promoted the uptake of N significantly by both ragi and soybean. Availability of P and K were also favourably influenced. Uptake of nutrients by soybean was promoted by CO2 enrichment. Available P status was higher in intercropped ragi and soybean as compared to pure crops but nutrient uptake was higher by pure crops.

724

Geiger, M., V. Haake, F. Ludewig, U. Sonnewald, and M. Stitt. 1999. The nitrate and ammonium nitrate supply have a major influence on the response of photosynthesis, carbon metabolism, nitrogen metabolism and growth to elevated carbon dioxide in tobacco. *Plant, Cell and Environment 22(10):1177-1199.*

The effect of elevated [CO2] on biomass, nitrate, ammonium, amino acids, protein, nitrate reductase activity, carbohydrates, photosynthesis, the activities of Rubisco and Sig other Calvin cycle enzymes, and transcripts for Rubisco small subunit, Rubisco activase, chlorophyll a binding protein, NADP-glyceraldehyde-3-phosphate dehydrogenase, aldolase, transketolase, plastid fructose-1,6-bisphosphatase and ADP-glucose pyrophosphorylase was investigated in tobacco growing an 2, 6 and 20 mM nitrate and 1, 3 and 10 mM ammonium nitate. (i) The growth stimulation in elevated [CO2] was attenuated in intermediate and abolished in low nitrogen. (ii) Elevated [CO2] led to a decline of nitrate, ammonium, amino acids especially glutamine, and protein in low nitrogen and a dramatic decrease in intermediate nitrogen, but not in high nitrogen. (iii) Elevated [CO2] led to a decrease of nitrate reductase activity in low, intermediate and high ammonium nitrate and in intermediate nitrate, but not in high nitrate, (iii) At low nitrogen, starch increased relative to sugars. Elevated [CO2] exaggerated this shift. ADP-glucose pyrophosphorylase transcript increased in low nitrogen, and in elevated [CO2]. (iv) In high nitrogen, sugars rose in elevated [CO2], but there was no acclimation of photosynthetic rate, only a small decrease of Rubisco and no decrease of other Calvin cycle enzymes and no decrease of the corresponding transcripts. In lower nitrogen, there was a marked acclimation of photosynthetic rate and a general decrease of Calvin cycle enzymes, even though sugar levels did not increase. The

decreased activities were due to a general decrease of leaf protein. The corresponding transcripts did not decrease except at very low nitrogen. (v) It is concluded that many of the effects of elevated [CO2] on nitrate metabolism, photosynthate allocation, photosynthetic acclimation and growth are due to a shift in nitrogen status.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, ATMOSPHERIC CO2 ENRICHMENT, GAS-EXCHANGE, LOBLOLLY-PINE, MINERAL NUTRITION, PINUS-TAEDA, PLANT GROWTH, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOUR ORANGE TREES, TAEDA L SEEDLINGS

725

Geiger, M., P. Walch-Liu, C. Engels, J. Harnecker, E.D. Schulze, F. Ludewig, U. Sonnewald, W.R. Scheible, and M. Stitt. 1998. Enhanced carbon dioxide leads to a modified diurnal rhythm of nitrate reductase activity in older plants, and a large stimulation of nitrate reductase activity and higher levels of amino acids in young tobacco plants. *Plant, Cell and Environment 21(3):253-268.*

Higher rates of nitrate assimilation are required to support faster growth in enhanced carbon dioxide. To investigate how this is achieved, tobacco plants were grown on high nitrate and high light in ambient and enhanced (700 mu mol mol(-1)) carbon dioxide. Surprisingly, enhanced carbon dioxide did not increase leaf nitrate reductase (MR) activity in the middle of the photoperiod. Possible reasons for this anomalous result were investigated. (a) Measurements of biomass, nitrate, amino acids and glutamine in plants fertilized once and twice daily with 12 mol m(-3) nitrate showed that enhanced carbon dioxide did not lead to a nitrate limitation in these plants. (b) Enhanced carbon dioxide modified the diurnal regulation of NR activity in source leaves. The transcript for nia declined during the light period in a similar manner in ambient and enhanced carbon dioxide. The decline of the transcript correlated with a decrease of nitrate in the leaf, and was temporarily reversed after re-irrigating with nitrate in the second part of the photoperiod. The decline of the transcript was not correlated with changes of sugars or glutamine. NR activity and protein decline in the second part of the photoperiod, and NR is inactivated in the dark in ambient carbon dioxide. The decline of NR activity was smaller and dark inactivation was partially reversed in enhanced carbon dioxide, indicating that post- transcriptional or post-translational regulation of NR has been modified. The increased activation and stability of NR in enhanced carbon dioxide was correlated with higher sugars and lower glutamine in the leaves. (c) Enhanced carbon dioxide led to increased levels of the minor amino acids in leaves. (d) Enhanced carbon dioxide led to a large decrease of glycine and a small decrease of serine in leaves of mature plants. The glycine:serine ratio decreased in source leaves of older plants and seedlings. The consequences of a lower rate of photorespiration for the levels of glutamine and the regulation of nitrogen metabolism are discussed. (e) Enhanced carbon dioxide also modified the diurnal regulation of NR in roots. The nia transcript increased after nitrate fertilization in the early and the second part of the photoperiod. The response of the transcript was not accentuated in enhanced carbon dioxide. NR activity declined slightly during the photoperiod in ambient carbon dioxide, whereas it increased 2-fold in enhanced carbon dioxide. The increase of root NR activity in enhanced carbon dioxide was preceded by a transient increase of sugars, and was followed by a decline of sugars, a faster decrease of nitrate than in ambient carbon dioxide, and an increase of nitrite in the roots. (f) To interpret the physiological significance of these changes-in nitrate metabolism, they were compared with the current growth rate of the plants. (g) In 4-5-week-old plants, the current rate of growth was similar in ambient and enhanced carbon dioxide (approximate to 0.4 g(-1) d(-1)). Enhanced carbon dioxide only led to small changes of NR activity, nitrate decreased, and overall amino acids were not significantly increased. (h) Young seedlings had a high growth rate (0.5 g(-1) d(-1)) in ambient carbon dioxide, that was increased by another 20% in enhanced carbon dioxide. Enhanced carbon dioxide led to larger increases of NR activity and NR activation, a 2-3-fold increase of glutamine, a 50% increase of glutamate, and a 2-3-fold increase in minor amino acids. It also led to a higher nitrate level. It is argued that enhanced carbon dioxide leads to a very effective stimulation of nitrate uptake, nitrate assimilation and amino acid synthesis in seedlings. This will play an important role in allowing faster growth rates in enhanced carbon dioxide at this stage.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, ELEVATED CO2, ENRICHMENT, GROWTH, MINERAL NUTRITION, NITRITE-REDUCTASE, NITROGEN, POSTTRANSLATIONAL REGULATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SINK REGULATION

726

GenoudGourichon, C., H. Sallanon, and A. Coudret. 1996. Effects of sucrose, agar, irradiance and CO2 concentration during the rooting phase on the acclimation of Rosa hybrida plantlets to ex vitro conditions. *Photosynthetica 32(2):263-270.*

Plantlets of Rosa hybrida cv. Deladel Madame Delbard were grown in vitro under different CO2 concentrations and irradiances, The medium was solid or liquid with or without sucrose, Morphological (shoot length, leaf number, leaf area, root number and root length) and photosynthetic parameters (photosynthesis/irradiance curves and phosphoenolpyruvate carboxylase and ribulose-1,5-bisphosphate carboxylase/oxygenase activities) were measured. Sucrose was necessary for root formation but not for root initiation, Culture in sucrose-free and liquid medium, under CO2 enrichment and high photosynthetic photon flux density increased the photosynthetic abilities and improved acclimation of plantlets to ex vitro conditions even if these plants had no roots after the rooting initiation phase.

KEYWORDS: CULTURED INVITRO, PHOTOSYNTHESIS

727

George, V., D. Cantin, D. Gerant, and P. Dizengremel. 1997. Long-term effects of elevated CO2 concentration on respiratory enzymes and dark respiration in pedunculate oak leaves. *Plant Physiology 114(3):657.*

728

George, V., D. Gerant, and P. Dizengremel. 1996. Photosynthesis, Rubisco activity and mitochondrial malate oxidation in pedunculate oak (Quercus robur L) seedlings grown under present and elevated atmospheric CO2 concentrations. *Annales Des Sciences Forestieres 53(2-3):469-474.*

Pedunculate oak seedlings were grown at 350 and 700 mu L/L CO2 in controlled chambers. After 130 days at elevated CO2, the biomass of the whole plant did not significantly increase. Photosynthesis, Rubisco activity, mitochondrial malate oxidation, carbohydrates and nitrogen contents were examined in the fourth growth flush. At 700 mu L/L CO2, the leaf net photosynthetic rate was 220% higher than at 350 mu L/L CO2. The decreased activity of Rubisco was accompanied by an accumulation of sucrose and glucose. The decreased oxidative capacity of crude leaf mitochondria from elevated CO2 plants was driven by the lower nitrogen and protein contents rather than by the higher carbohydrates contents in the leaves. Nevertheless, direct effects of elevated CO2 on the respiratory biochemistry cannot be excluded.

KEYWORDS: RESPIRATION, TREES

729

Gesch, R.W., K.J. Boote, J.C.V. Vu, L.H. Allen, and G. Bowes. 1998. Changes in growth CO2 result in rapid adjustments of ribulose- 1,5-bisphosphate carboxylase/oxygenase small subunit gene expression in expanding and mature leaves of rice. *Plant Physiology 118(2):521-529.*

The accumulation of soluble carbohydrates resulting from growth under elevated CO2 may potentially signal the repression of gene activity for the small subunit of ribulose-1,5- bisphosphate carboxylase/oxygenase (rbcS). To test this hypothesis we grew rice (Oryza sativa L.) under ambient (350 mu L L-1) and high (700 mu L L-1) CO2 in outdoor, sunlit, environment-controlled chambers and performed a cross-switching of growth CO2 concentration at the late-vegetative phase. Within 24 h, plants switched to high CO2 showed a 15% and 23% decrease in rbcS mRNA, whereas plants switched to ambient CO2 increased 27% and 11% in expanding and mature leaves, respectively. Ribulose-1,5-bisphosphate carboxylase/oxygenase total activity and protein content 8 d after the switch increased up to 27% and 20%, respectively, in plants switched to ambient CO2, but changed very little in plants switched to high CO2. Plants maintained at high CO2 showed greater carbohydrate pool sizes and lower rbcS transcript levels than plants kept at ambient CO2. However, after switching growth CO2 concentration, there was not a simple correlation between carbohydrate and rbcS transcript levels. We conclude that although carbohydrates may be important in the regulation of rbcS expression, changes in total pool size alone could not predict the rapid changes in expression that we observed.

KEYWORDS: ACCLIMATION, ACCUMULATION, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, HIGHER-PLANTS, MECHANISM, PHOTOSYNTHESIS, RUBISCO, SOURCE-SINK RELATIONS, TEMPERATURE

730

Ghannoum, O., and J.P. Conroy. 1998. Nitrogen deficiency precludes a growth response to CO2 enrichment in C-3 and C-4 Panicum grasses. *Australian Journal of Plant Physiology 25(5):627-636.*

We investigated the interaction of nitrogen (N) supply and CO2 enrichment on the growth and photosynthesis of Panicum laxum (C-3), P. coloratum (C-4) and P. antidotale (C-4). Plants were grown at ambient CO2 partial pressures (p(a)) of either 36 (low) or 71 (high) Pa, in potted soil supplied with 0 (low) or 60 (high) mg N kg(-1) soil week(-1). Elevated CO2 enhanced total plant dry mass of all three species by approximately 28% under high N supply, but had no effect on biomass accumulation under N deficiency. CO2 enrichment resulted in reductions of CO2 assimilation rates (A; measured at comparable p(a)) of P. laxum, indicating acclimation of photosynthesis. This acclimation, which was more pronounced under N stress, was unrelated to changes in leaf N or non-structural carbohydrate concentrations, because neither were affected by CO2 enrichment. In the C-4 grasses grown at low N, A were fully saturated at the current ambient p(a), whereas at high N, A increased slightly when CO2 was raised to 71 Pa. N deficiency reduced the initial slope of the CO2 response curve of A in P. antidotale, and this effect was more pronounced at high CO2. In conclusion, the preclusion of a growth response to CO2 enrichment by N deficiency was correlated with a strong inhibition of A in the C-3 species, and the saturation of A at below current atmospheric p(a) in C-4 species.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, DRY-MATTER, ELEVATED CO2, NUTRITION, PHOTOSYNTHESIS, RESPIRATION, SOURCE-SINK RELATIONS, TEMPERATURE

731

Ghannoum, O., K. Siebke, S. Von Caemmerer, and J.P. Conroy. 1998. The photosynthesis of young Panicum C-4 leaves is not C-3-like. *Plant, Cell and Environment 21(11):1123-1131.*

Evidence is presented contrary to the suggestion that C-4 plants grow larger at elevated CO2 because the C-4 pathway of young C-4 leaves has C-3-like characteristics, making their photosynthesis O-2 sensitive and responsive to high CO2, We combined PAM fluorescence with gas exchange measurements to examine the O-2 dependence of photosynthesis in young and mature leaves of Panicum antidotale (C-4, NADP-ME) and P. coloratum (C4, NAD-ME), at an intercellular CO2 concentration of 5 Pa. P. laxum (C-3) was used for comparison, The young C, leaves had COL and light response curves typical of C-4 photosynthesis. When the O-2 concentration was gradually increased between 2 and 40%, CO2 assimilation rates (A) of both mature and young C-4 leaves were little affected, while the ratio of the quantum yield of photosystem II to that of CO2 assimilation (Phi(PSII)/Phi(CO2)) increased more in young (up to 31%) than mature (up to 10%) C-4 leaves. A of C-3 leaves decreased by 1.3 and Phi(PSII)/Phi(CO2) increased by 9-fold, over the same range of O-2 concentrations. Larger increases in electron transport requirements in young, relative to mature, C-4 leaves at low CO2 are indicative of greater O-2 sensitivity of photorespiration, Photosynthesis modelling showed that young C-4 leaves have lower bundle sheath CO2 concentration, brought about by higher bundle sheath conductance relative to the activity of the C-4 and C-3 cycles and/or lower ratio of activities of the C-4 to C-3 cycles.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON ASSIMILATION, CHLOROPHYLL FLUORESCENCE, DEVELOPING MAIZE LEAVES, ELECTRON-TRANSPORT, GENE-EXPRESSION, IRRADIANCE, LEAF DEVELOPMENT, PHOTOSYSTEM, QUANTUM YIELD

732

Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1996. Effect of CO2 enrichment on growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass grown at two irradiance levels. *Plant Physiology 111(2):211.*

733

Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1997. The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass. *Australian Journal of Plant Physiology 24(2):227-237.*

The effect of CO2 enrichment and irradiance on the growth and gas exchange of two tropical grasses, Panicum laxum (C-3) and Panicum antidotale (C-4) were investigated. The two species were grown at either 350 (low) or 700 (high) mu L L-1 CO2 concentration, under 40% (low) or 100% (high) of direct sunlight and supplied with ample water and nutrition. Elevated CO2 enhanced plant dry weight at both irradiances in the C-3 species (1.41-fold and 1.71-fold increase at low and high light, respectively) but only at high light in the C-4 species (1.28 fold increase). CO2 enrichment had no effect on the dry weight of P. antidotale, when stem development was suppressed by growth under artificial lighting. When measured at the CO2 concentration at which they were grown, assimilation rates were similar in the low and high CO2 grown plants, for both species. However, when measurements made at low CO2 were compared, CO2 assimilation rates of the high light, high CO2 grown C-3 and C- 4 species were lower than those of their low CO2 grown counterparts. High CO2 strongly reduced the stomatal conductance of both species, while it affected the Rubisco content (30% decrease) of the high light C-3 species only. This work shows clearly that C-4 species can respond to CO2 enrichment under favourable growth conditions, and that acclimation to elevated CO2 in pasture grasses does not necessarily involve accumulation of non-structural

carbohydrates or reduction of total N or soluble proteins in source leaves.

KEYWORDS: ACCLIMATION, ASSIMILATION, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, NITROGEN-USE EFFICIENCY, PARTIAL-PRESSURE, PHOTOSYNTHETIC CAPACITY, PLANTS, RESPONSES, TEMPERATURE

734

Ghannoum, O., S. vonCaemmerer, E.W.R. Barlow, and J.P. Conroy. 1997. The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C-3 (Panicum laxum) and a C-4 (Panicum antidotale) grass (vol 24, pg 227, 1997). *Australian Journal of Plant Physiology 24(3):U2.*

735

Gifford, R.M. 1992. Implications of the globally increasing atmospheric CO2 concentration and temperature for the Australian terrestrial carbon budget - integration using a simple-model. *Australian Journal of Botany 40(4-5):527-543.*

A simple continentally aggregated model of the Australian terrestrial carbon budget (CQUESTA) integrates information on CO2 and temperature effects and is applied to evaluating whether vegetation is absorbing anthropogenic CO2. Information from the literature is used to parameterise CQUESTA. A standard set of parameters is adopted for exploratory purposes. Historical information is used to describe the average CO2 concentration and temperature over the southern hemisphere from 1750 AD to the present. From the present to 2050 AD the 'business-as-usual' scenario described by the Intergovernmental Panel on Climate Change (IPCC) is applied. The standard parameterisation of the model suggests that the changing CO2 concentration and temperature regime since 1750 AD has been causing continuous net sequestration of carbon into Australian live vegetation and soils. The present modelled rate of net sequestration is of a similar magnitude to CO2 emissions from continental fossil fuel burning and land clearing combined. The rate of sequestration is predicted to continue to increase until 2050 AD and beyond if atmospheric CO2 concentration and temperature continue to increase. However, there remains considerable experimental uncertainty about the correct parameterisation of the model. The findings have implications for policies on greenhouse effect gas emissions.

KEYWORDS: ACCLIMATION, DIOXIDE, DYNAMICS, ELEVATED CO2, GROWTH, NITROGEN, PHOTOSYNTHESIS, SOIL, TUSSOCK TUNDRA, WATER

736

Gifford, R.M. 1994. The global carbon-cycle - a viewpoint on the missing sink. *Australian Journal of Plant Physiology 21(1):1-15.*

Atmospheric carbon budgets that ignore the possibility of terrestrial ecosystem responses to global atmospheric change do not balance; there is a 'missing sink' of about 0.4 - 4 Gt C yr(-1). This paper argues a case that mechanistically it is well within the bounds of possibility that increasing carbon storage in vegetation and soils in response to the globally increasing CO2 concentration, temperature and nitrogen deposition can account for the missing C sink. Global warming conditions considered alone would be unlikely to cause most ecosystems to emit CO2, because the N mineralised by any enhanced soil organic matter decomposition would be largely taken up by plants and reconverted into organic matter having a much higher C:N ratio than that in the soil. Models of the global terrestrial C cycle indicate that an extra 0.5 - 4 Gt C yr(-1) could well be being stored in soils and vegetation today in response to the CO2 fertilising effect, having regard for the interactions with growth restricting water, light and nitrogen levels. To obtain direct proof as to whether that this is happening or not is a major challenge.

KEYWORDS: BIOSPHERE, BUDGET, CLIMATE, DIOXIDE, ECOSYSTEMS, ELEVATED CO2, INCREASING ATMOSPHERIC CO2, PLANT GROWTH, RESPONSES, TEMPERATURE

737

Gifford, R.M. 1995. Whole plant respiration and photosynthesis of wheat under increased CO2 concentration and temperature: Long-term vs short-term distinctions for modelling. *Global Change Biology 1(6):385-396.*

Short- and long-term effects of elevated CO2 concentration and temperature on whole plant respiratory relationships are examined for wheat grown at four constant temperatures and at two CO2 concentrations. Whole plant CO2 exchange was measured on a 24 h basis and measurement conditions varied both to observe short-term effects and to determine the growth respiration coefficient (r(g))r dry weight maintenance coefficient (r(g)), basal (i.e. dark acclimated) respiration coefficient (r(b)), and 24 h respiration:photosynthesis ratio (R:P). There was no response of r(b) to short-term variation in CO2 concentration. For plants with adequate N-supply, r(g) was unaffected by the growth-CO2 despite a 10% reduction in the plant's N concentration (%N). However, r(m) was decreased 13%, and r(b) was decreased 20% by growth in elevated CO2 concentration relative to ambient. Nevertheless, R:P was not affected by growth in elevated CO2. Whole plant respiration responded to short-term variation of + 5 degrees C around the growth temperature with low sensitivity (Q(10) = 1.8 at 15 degrees C, 1.3 at 30 degrees C). The shape of the response of whole plant respiration to growth temperature was different from that of the short term response, being a slanted S-shape declining between 25 and 30 degrees C. While r(m) increased, r(g) decreased when growth temperature increased between 15 and 20 degrees C. Above 20 degrees C r(m) became temperature insensitive while r(g) increased with growth temperature. Despite these complex component responses, R:P increased only from 0.40 to 0.43 between 15 degrees and 30 degrees C growth temperatures. Giving the plants a step increase in temperature caused a transient increase in R:P which recovered to the pre- transient value in 3 days. It is concluded that use of a constant R:P with respect to average temperature and CO2 concentration may be a more simple and accurate way to model the responses of wheat crop respiration to 'climate change' than the more complex and mechanistically dubious functional analysis into growth and maintenance components.

KEYWORDS: ELEVATED CO2, GROWTH

738

Gifford, R.M., J.L. Lutze, and D. Barrett. 1996. Global atmospheric change effects on terrestrial carbon sequestration: Exploration with a global C- and N-cycle model (CQUESTN). *Plant and Soil 187(2):369-387.*

A model of the interacting global carbon and nitrogen cycles (CQUESTN) is developed to explore the possible history of C-sequestration into the terrestrial biosphere in response to the global increases (past and possible future) in atmospheric CO2 concentration, temperature and N-deposition. The model is based on published estimates of pre-industrial C and N pools and fluxes into vegetation, litter and soil compartments. It was found necessary to assign low estimates of N pools and fluxes to be compatible with the more firmly established C-cycle data. Net primary production was made responsive to phytomass N level, and to CO2 and temperature deviation from preindustrial values with sensitivities covering the ranges in the

literature. Biological N-fixation could be made either unresponsive to soil C:N ratio, or could act to tend to restore the preindustrial C:N of humus with different N-fixation intensities. As for all such simulation models, uncertainties in both data and functional relationships render it more useful for qualitative evaluation than for quantitative prediction. With the N-fixation response turned off, the historic CO2 increase led to standard-model sequestration into terrestrial ecosystems in 1995AD of 1.8 Ct C yr(-1). With N-fixation restoring humus C:N strongly, C sequestration was 3 Ct yr(-1) in 1995. In both cases C:N of phytomass and litter increased with time and these increases were plausible when compared with experimental data on CO2 effects. The temperature increase also caused net C sequestration in the model biosphere because decrease in soil organic matter was more than offset by the increase in phytomass deriving from the extra N mineralised. For temperature increase to reduce system C pool size, the biosphere "leakiness" to N would have to increase substantially with temperature. Assuming a constant N-loss coefficient, the historic temperature increase alone caused standard-model net C sequestration to be about 0.6 Gt C in 1995. Given the disparity of plant and microbial C:N, the modelled impact of anthropogenic N-deposition on C- sequestration depends substantially on whether the deposited N is initially taken up by plants or by soil microorganisms. Assuming the latter, standard-model net sequestration in 1995 was 0.2 Ct C in 1995 from the N-deposition effect alone. Combining the effects of the historic courses of CO2, temperature and N-deposition, the standard-model gave C- sequestration of 3.5 Ct in 1995. This involved an assumed weak response of biological N-fixation to the increased carbon status of the ecosystem. For N-fixation to track ecosystem C- fixation in the long term however, more phosphorus must enter the biological cycle. New experimental evidence shows that plants in elevated CO2 have the capacity to mobilize more phosphorus from so-called "unavailable" sources using mechanisms involving exudation of organic acids and phosphatases.

KEYWORDS: BIOSPHERE, CO2 CONCENTRATION, ELEVATED CO2, LITTER DECOMPOSITION, NITROGEN, ORGANIC-ACIDS, PLANT, SOIL, STORAGE, TEMPERATURE-DEPENDENCE

739

Gil, M.I., D.M. Holcroft, and A.A. Kader. 1997. Changes in strawberry anthocyanins and other polyphenols in response to carbon dioxide treatments. *Journal of Agricultural and Food Chemistry 45(5):1662-1667.*

Carbon dioxide-enriched atmospheres are used to reduce the incidence and severity of decay and to extend the postharvest life of strawberries. The influence of CO2 on the postharvest quality parameters of strawberries, particularly the stability of anthocyanins and other phenolic compounds, was investigated. Freshly harvested strawberries were placed in jars ventilated continuously with air or air enriched with 10%, 20%, or 40% CO2 at 5 degrees C for 10 days. Samples were taken initially, and after 5 and 10 days of storage, and color (L* a* b* color space), pH, TA, TSS, and firmness were measured. Anthocyanins and other phenolics were analyzed by HPLC. Elevated CO2 degraded internal color while air-treated fruit remained red. Internal and external tissues differed in composition and concentration of phenolic compounds. CO2 had a minimal effect on the anthocyanin content of external tissues but induced a remarkable decrease in anthocyanin content of internal tissues. Factors, such as pH and copigmentation, that could explain this degradation are discussed.

KEYWORDS: COLOR, FIRMNESS, FRUITS, JUICE, MODIFIED ATMOSPHERES, QUALITY

740

Gilmanov, T.G., and W.C. Oechel. 1995. New estimates of organic matter reserves and net primary productivity of the North American tundra ecosystems. *Journal of Biogeography 22(4-5):723-741.*

The reserves and fluxes of carbon in ecosystems of the circumpolar tundra biome should be among the most responsive to climatic change, including their transformation from a CO2 sink to a CO2 source with respect to the atmosphere. To estimate accurately the significance of Arctic tundra to global carbon stocks and balances, quantitative geographically referenced estimates of the masses and fluxes of carbon are needed. Although new empirically based estimates of reserves and productivity were recently obtained for the Eurasian part of the tundra biome using GIS technology, the figures currently used for carbon reserves and productivity of the North American tundra ecosystems are based on earlier expert estimates or large scale models based on data primarily for non-tundra areas. To obtain new more empirically based estimates of the reserves and fluxes of carbon in North American tundra ecosystems a set of records of North American tundra ecosystems was obtained from the Global Arctic/Alpine Climate/Soil/Plant Productivity Data Base (Global Change Research Group, San Diego State University). This data base contains phytomass, productivity, climatic and soil characteristics for nearly fifty tundra-type ecosystems studied during the past 30 years in Alaska and Northern Canada. This information was used to interpolate the necessary data for all the tundra cells (1 X 1 degree) of the simple GIS, based on the Global Vegetation Map and the FAO/UNESCO Soil Map of the World. By integrating the corresponding maps of phytomass and productivity the quantitative estimates of the reserves and. productivity fluxes of organic matter in tundra ecosystems of North America and Greenland (4.12 x 10(6) km(2) total area) were obtained: 2.26 Gt above-ground phytomass, 4.99 Gt total phytomass, 91.3 Gt soil organic matter of the active layer; 0.56 Gt/yr above- ground net primary production; 0.98 Gt/yrotal net primary production. As an alternative means of determining the productivity totals for North American tundra ecosystems, the phenomenological model of the form: NPP=f(T,H,G), relating net primary production of tundra ecosystems to climatic, soil and vegetation factors, was applied to the GIS layers of mean annual temperature (T), soil organic matter content (H), and above-ground phytomass density (G) to produce a map of modelled NPP estimates for North American tundra ecosystems. The subroutine of spatial integration of the local production estimates takes into account geographical changes in the landscape composition (proportions of the zonal, meadow, mire and aquatic ecosystem types) and results in totals of 0.58 Gt/yr for above-ground and 1.16 Gt/yr for total net primary production of tundra ecosystems of North America and Greenland.

KEYWORDS: ACCUMULATION, ALASKA, ARCTIC TUNDRA, BIOMASS, CLIMATE, NUTRIENT, PLANT, SOIL PROPERTIES, VEGETATION TYPES

741

Gimenez, C., V.J. Mitchell, and D.W. Lawlor. 1992. Regulation of photosynthetic rate of 2 sunflower hybrids under water-stress. *Plant Physiology 98(2):516-524.*

The effect of short-term water stress on photosynthesis of two sunflower hybrids (Helianthus annuus L. cv Sungro-380 and cv SH-3622), differing in productivity under field conditions, was measured. The rate of CO2 assimilation of young, mature leaves of SH-3622 under well-watered conditions was approximately 30% greater than that of Sungro-380 in bright light and elevated CO2; the carboxylation efficiency was also larger. Growth at large photon flux increased assimilation rates of both hybrids. The changes in leaf composition, including cell numbers and sizes, chlorophyll content, and amounts of total soluble and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) protein, and in Rubisco activity and amount of ribulose-1,5- bisphosphate (RuBP) were determined to assess the factors regulating the differences in assimilation of the hybrids at high and low water potentials. The amounts of chlorophyll, soluble protein, Rubisco protein and the initial activity of

Rubisco and its activation state did not differ significantly between hybrids. However, unstressed leaves of SH-3622 had more, smaller cells per unit area and 60% more RuBP per unit leaf area than that of Sungro-380. Water stress developing over 4 days decreased the assimilation of both hybrids similarly. Changes in the amounts of chlorophyll, soluble and Rubisco protein, and Rubisco activity and activation state were small and were not sufficient to explain the decrease in photosynthesis; neither was decreased stomatal conductance (or stomatal "patchiness"). Reduction of photosynthesis per unit leaf area from 25 to 5 micromoles CO2 per square meter per second in both hybrids was caused by a decrease in the amount of RuBP from approximately 130 to 40 micromoles per square meter in SH-3622 and from 80 to 40 micromoles per square meter in Sungro. Differences between hybrids and their response to water stress is discussed in relation to control of RuBP regeneration.

KEYWORDS: BISPHOSPHATE CARBOXYLASE ACTIVITY, C-3, INHIBITION, LEAVES, OXYGENASE, PLANTS, POTENTIALS, PROTEIN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, WHEAT GENOTYPES

742

Giordano, M., J.S. Davis, and G. Bowes. 1994. Organic-carbon release by dunaliella-salina (chlorophyta) under different growth-conditions of co2, nitrogen, and salinity. *Journal of Phycology 30(2):249-257.*

Two strains of Dunaliella salina (Dunal) Teod., UTEX 1644 and UTEX 200, were cultured under different growth regimes, including 10 mM NO3- or NH4+, 1.5 or 3.0 M NaCl, and low (0.035%) or high (5%) CO2 in air. The release of C-14-labeled dissolved organic carbon (DOC), expressed as a rate and as a percentage of photo synthetic (CO2)-C-14, assimilation, was subsequently determined. The percentage of DOC released was inversely related to cell density in the assay medium, but photosynthesis on a per-cell basis was not. Release of DOC was low, in the range of 1-5% of photosynthesis, but during acclimation to growth on NH4+, it rose to 11%. The presence of NH4+ rather than NO3- in the growth medium increased the rate of release by both strains, but the percentage release was stimulated only in UTEX 200 cells, because their photosynthetic ra te was depressed by NH4+. For UTEX 1644, high, as compared to low, CO2-grown cells, had somewhat higher rates a nd percentages of DOC release, but release from UTEX 200 cells was unaffected by the growth-CO2. The rate of DOC release by high CO2-grown cells was not enhanced at a low concentration of dissolved inorganic carbon, indicating that the released material did not originate from the photorespiratory pathway. The effects of NaCl on DOC release varied with strain a nd growth conditions. For UTEX 200, the cells in NO3-, but not NH4+, exhibited a doubling or more in percentage Of release with a doubling in NaCl concentration, irrespective of growth-CO2. With UTEX 1644 the low CO2-grown cells showed the greatest enhancement in 3.0 M NaCl. Organic matter accumulated on the external surface of the cell membrane and constituted a well- defined cell-coat, which was more dense in NH4+ than in NO3-- grown cells. Microtubules, which may play a role in maintaining cell shape, were observed just below the plasma membrane. From a practical viewpoint, the presence of organic material in the hypersaline ponds of salt-works is detrimental to salt production. When D. salina cells become abundant in such ponds, the attendant, continuous release of DOC may make a significant contribution to the problem.

KEYWORDS: BIOCULATA, COAT, EXCRETION, GREEN-ALGA, HEALTHY CELLS, INTRACELLULAR GLYCEROL, MARINE-PHYTOPLANKTON, METABOLISM, TEMPERATURE, TERTIOLECTA

743

Gleadow, R.M., W.J. Foley, and I.E. Woodrow. 1998. Enhanced CO2 alters the relationship between photosynthesis and defence in cyanogenic Eucalyptus cladocalyx F. Muell. *Plant, Cell and Environment 21(1):12-22.*

The effect of elevated CO2 and different levels of nitrogen on the partitioning of nitrogen between photosynthesis and a constitutive nitrogen-based secondary metabolite (the cyanogenic glycoside prunasin) was examined in Eucalyptus cladocalyx. Our hypothesis was that the expected increase in photosynthetic nitrogen-use efficiency of plants grown at elevated CO2 concentrations would lead to an effective reallocation of available nitrogen from photosynthesis to prunasin, Seedlings were grown at two concentrations of CO2 and nitrogen, and the proportion of leaf nitrogen allocated to photosynthesis, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), protein and prunasin compared, Up to 20% of leaf nitrogen was allocated to the cyanogenic glycoside, although this proportion varied with leaf age, position and growth conditions, Leaf prunasin concentration,vas strongly affected by nitrogen supply, but did not increase, on a dry weight basis, in the leaves from the elevated CO2 treatments, However, the proportion of nitrogen allocated to prunasin increased significantly, in spite of a decreasing pool of leaf nitrogen, in the plants grown at elevated concentrations of CO2. There was less protein in leaves of plants grown at elevated CO2 in both nitrogen treatments, while the concentration of active sites of Rubisco only decreased in plants from the low-nitrogen treatment. These changes in leaf chemistry may have significant implications in terms of the palatability of foliage and defence against herbivores.

KEYWORDS: ACCLIMATION, C-3 PLANTS, CARBON NUTRIENT BALANCE, ELEVATED ATMOSPHERIC CO2, GAS-EXCHANGE, GROWTH, HERBIVORE INTERACTIONS, NITROGEN, RISING CO2, TOMATO PLANTS

744

Glenn, D.M., and W.V. Welker. 1997. Effects of rhizosphere carbon dioxide on the nutrition and growth of peach trees. *Hortscience 32(7):1197-1199.*

Our objectives in this study were to measure the effects of low levels of root system carbon dioxide on peach tree growth (Prunus persica L. Batsch) and nutrient uptake. Using soil and hydroponic systems, we found that increased root CO2: 1) increased root growth without increasing shoot growth, 2) increased leaf P concentration, 3) decreased leaf N concentration, and 4) reduced water use relative to air injection or no treatment.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, INORGANIC CARBON, METABOLISM, PLANTS, RESPIRATION, RESPONSES, ROOT-GROWTH, SEEDLINGS, SOIL, WATER

745

Gloser, J., and M. Bartak. 1994. Net photosynthesis, growth-rate and biomass allocation in a rhizomatous grass calamagrostis-epigejos grown at elevated co2 concentration. *Photosynthetica 30(1):143-150.*

Young plants of Calamagrostis epigejos (L.) Roth were grown in controlled environments with two regimes of CO2 in the air: normal (350 cm(3) m(-3)) and elevated (700 cm(3) m(-3)). The relative growth rate of plants grown at elevated CO2 was increased by about 20 % in comparison with control plants cultivated at ambient CO2 concentration. Partitioning of assimilates into roots (+ rhizomes) and shoots was the same in both treatments. Slightly lower values of specific leaf area, leaf mass ratio and leaf area ratio were found in the plants grown at elevated CO2. The net photosynthetic rate (P-N) was measured gasometrically in plants from both treatments at 350 and 700 cm(3) m(-3) CO2 in the leaf chamber. There were no significant differences between plants grown at either CO2 concentration in their responses to radiation and CO2 conditions during measurements, i.e., no regulation of photosynthetic

processes in response to elevated CO2 was detectable. P-N at saturating irradiance and maximum apparent quantum yield of photosynthesis were always considerably higher at doubled CO2 concentration during measurements.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, PLANTS, PRODUCTIVITY, RESPIRATION, RESPONSES, TEMPERATURE

746

Godbold, D.L., and G.M. Berntson. 1997. Elevated atmospheric CO2 concentration changes ectomycorrhizal morphotype assemblages in Betula papyrifera. *Tree Physiology 17(5):347-350.*

Ectomycorrhizae are extremely diverse, with different species of fungi having very different physiologies and morphologies that, in turn, confer a range of different benefits to the host plant. To test the hypothesis that elevated CO2 leads to changes in the assemblage of ectomycorrhizae associated with trees, we examined the number and frequency of ectomycorrhizal morphotypes colonizing roots of Betula papyrifera Marsh. saplings grown at an ambient or elevated (700 ppm) atmospheric CO2 concentration for 24 weeks. Elevated CO2 resulted in significant changes in the composition of the ectomycorrhizal assemblage toward morphotypes with a higher incidence of emanating hyphae and rhizomorphs. We conclude that B. papyrifera saplings will be able to support a more costly mycorrhization in future elevated-CO2 atmospheres.

KEYWORDS: CARBON DIOXIDE, FUNGI, GROWTH, INFECTION, MYCELIUM, PINE, RESPONSES, ROOTS, SEEDLINGS

747

Godbold, D.L., G.M. Berntson, and F.A. Bazzaz. 1997. Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric CO2. *New Phytologist 137(3):433-440.*

We investigated the effect of elevated CO2 on the growth and mycorrhizal colonization of three tree species native to north- eastern American forests (Betula papyrifera Marsh., Pinus strobus L. and Tsuga canadensis L. Carr). Saplings of the tree species were collected from Harvard Forest, Massachusetts, and grown in forest soil under ambient (c. 375 ppm) and elevated (700 ppm) atmospheric CO2 concentrations for 27-35 wk. In all three species there was a trend to increasing whole-plant, total-root and fine-root biomass in elevated CO2, and a significant increase in the degree of ectomycorrhizal colonization in B. papyrifera and P. strobus, but not in T. canadensis. However, in T. canadensis the degree of colonization with arbuscular mycorrhizas increased significantly. In both the ambient and elevated environments, on the roots of B. papyrifera and P. strobus 12 distinct ectomycorrhizal morphotypes were identified. Distinct changes in the ectomycorrhizal morphotype assemblage of B. papyrifera were observed under CO2 enrichment. This change resulted in an increase in the frequency of ectomycorrhizas with a higher incidence of emanating hyphae and rhizomorphs, and resulted in a higher density of fungal hyphae in a root exclusion chamber.

KEYWORDS: CARBON DIOXIDE, ECTOMYCORRHIZAL PLANTS, ENRICHMENT, FUNGI, LOBLOLLY-PINE, NUTRIENT, RESPONSES, ROOTS, SEEDLINGS, VEGETATIVE MYCELIUM

748

Goettel, M.S., G.M. Duke, and D.W. Goerzen. 1997. Pathogenicity of Ascosphaera larvis to larvae of the alfalfa leafcutting bee, Megachile rotundata. *Canadian Entomologist 129(6):1059-1065.*

Laboratory assays and field surveys showed that Ascosphaera larvis (Bissett) is a pathogen of alfalfa leafcutting bee larvae, capable of causing high mortality in commercial populations. In one population over 21% of bees were found to be infected by A. larvis. However, overall levels of the disease are low and it is unlikely that this pathogen poses an immediate threat to commercial leafcutting bee populations in Canada. The LD50 was determined to be 1.9 x 10(5) spores/bee. Elevated levels of CO2 are required for in vitro spore germination. The disease can easily be diagnosed within bee cells by X-ray radiography, thereby enabling disease levels to be monitored using conventional methods utilized by the industry to monitor leafcutting bee quality.

KEYWORDS: CHALKBROOD

749

Goldewijk, K.K., J.G. Vanminnen, G.J.J. Kreileman, M. Vloedbeld, and R. Leemans. 1994. Simulating the carbon flux between the terrestrial environment and the atmosphere. *Water, Air, and Soil Pollution 76(1-2):199-230.*

A Terrestrial C Cycle model that is incorporated in the Integrated Model to Assess the Greenhouse Effect (IMAGE 2.0) is described. The model is a geographically explicit implementation of a model that simulates the major C fluxes in different compartments of the terrestrial biosphere and between the biosphere and the atmosphere. Climatic parameters, land cover and atmospheric C concentrations determine the result of the dynamic C simulations. The impact of changing land cover patterns, caused by anthropogenic activities (shifting agriculture, de- and afforestation) and climatic change are modeled implicitly. Feedback processes such as CO2 fertilization and temperature effects on photosynthesis, respiration and decomposition are modeled explicitly. The major innovation of this approach is that the consequences of climate change are taken into account instantly and that their results can be quantified on a global medium-resolution grid. The objectives of this paper are to describe the C cycle model in detail, present the linkages with other parts of the IMAGE 2.0 framework, and give an array of different simulations to validate and test the robustness of this modeling approach. The computed global net primary production (NPP) for the terrestrial biosphere in 1990 was 60.6 Gt C a-1, with a global net ecosystem production (NEP) of 2.4 Gt C a-1. The simulated C flux as result from land cover changes was 1.1 Gt C a-1, so that the terrestrial biosphere in 1990 acted as a C sink of 1.3 Gt C a-1. Global phytomass amounted 567.5 Gt C and the dead biomass pool was 1517.7 Gt C. IMAGE 2.0 simulated for the period 1970 - 2050 a global average temperature increase of 1.6-degrees-C and a global average precipitation increase of 0.1 mm/day. The CO2 concentration in 2050 was 522.2 ppm. The computed NPP for the year 2050 is 82.5 Gt C a-1, with a NEP of 8.1 Gt C a-1. Projected land cover changes result in a C flux of 0.9 Gt C a-1, so that the terrestrial biosphere will be a strong sink of 7.2 Gt C a-1. The amount of phytomass hardly changed (600.7 Gt C) but the distribution over the different regions had. Dead biomass increased significantly to 1667.2 Gt C.

KEYWORDS: BIOSPHERE, CO2 CONCENTRATIONS, ELEVATED CO2, FEEDBACK PROCESSES, GLOBAL CHANGE, LAND-USE, MANAGED FORESTS, MODEL, STORAGE, WATER-USE EFFICIENCY

750

Gong, H., S. Nilsen, and J.F. Allen. 1993. Photoinhibition of photosynthesis invivo - involvement of multiple sites in a photodamage process under co2-free and o2- free conditions. *Biochimica Et Biophysica Acta 1142(1-2):115-122.*

Intact Lemna gibba plants were illuminated by photoinhibitory light in air, in air minus O2, in air minus CO2, and in pure N2. In pure N2, the degree of photoinhibition increased 3-5- times compared with that in air.

This high degree of photoinhibition is described as photodamage. Photodamage was found to constitute a syndrome, that is, it is due to inactivation of multiple sites. These sites include RC II component(s) from P680 to Q(A); the Q(B)-Site; and a component of PS I. In photodamage, the donor side of PS II and PS II excitation energy transfer remain unimpaired, but the size of the PS I antenna seems to decrease. Photodamage is distinguishable from photoinactivation. Photoinactivation occurred in air and could be attributed to inhibition of electron transport from Q(A)- to Q(B). During photoinactivation the D1 protein of RC II became degraded faster than the detectable inhibition of Q(B) reduction. The photoinhibition- induced rise in F0 occurred only during the process of photodamage but not during that of photoinactivation, and was a secondary event which arose as a consequence of photodamage. Atmospheric O2 alleviated photodamage but increased photoinactivation. The light-induced Dl degradation and inhibition of Q(A) to Q(B) electron transfer were enhanced in vivo not only by O2 but also by depletion of CO2.

KEYWORDS: ANAEROBIC CONDITIONS, CHLAMYDOMONAS-REINHARDTII, CHLOROPHYLL FLUORESCENCE, D1 PROTEIN, DEGRADATION, ENERGY-DISTRIBUTION, ISOLATED-CHLOROPLASTS, MECHANISM, PHOTOSYSTEM, REACTION CENTERS

751

GonzalezMeler, M.A., M. RibasCarbo, J.N. Siedow, and B.G. Drake. 1996. Direct inhibition of plant mitochondrial respiration by elevated CO2. *Plant Physiology 112(3):1349-1355.*

Doubling the concentration of atmospheric CO2 often inhibits plant respiration, but the mechanistic basis of this effect is unknown. We investigated the direct effects of increasing the concentration of CO2 by 360 mu L L(-1) above ambient on O-2 uptake in isolated mitochondria from soybean (Glycine max L. cv Ransom) cotyledons. Increasing the CO2 concentration inhibited the oxidation of succinate, external NADH, and succinate and external NADH combined. The inhibition was greater when mitochondria were preincubated for 10 min in the presence of the elevated CO2 concentration prior to the measurement of O-2 uptake. Elevated CO2 concentration inhibited the salicylhydroxamic acid-resistant cytochrome pathway, but had no direct effect on the cyanide-resistant alternative pathway. We also investigated the direct effects of elevated CO2 concentration on the activities of cytochrome c oxidase and succinate dehydrogenase (SDH) and found that the activity of both enzymes was inhibited. The kinetics of inhibition of cytochrome c oxidase were time-dependent. The level of SDH inhibition depended on the concentration of succinate in the reaction mixture. Direct inhibition of respiration by elevated CO2 in plants and intact tissues may be due at least in part to the inhibition of cytochrome c oxidase and SDH.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PATHWAYS, PEAR FRUIT, ROOT RESPIRATION, SHORT- TERM, SOIL

752

Gonzalez-Meler, M.A., and J.N. Siedow. 1999. Direct inhibition of mitochondrial respiratory enzymes by elevated CO2: does it matter at the tissue or whole-plant level? *Tree Physiology 19(4-5):253-259.*

On average, a doubling in current atmospheric [CO2] results in a 15 to 20% direct inhibition of respiration, although the variability associated with this value is large within and among species. Direct effects of CO2 on respiration may also be relevant to tree canopies because of dynamic fluctuations between nighttime and daytime [CO2] throughout the growing season. The mechanism by which CO2 inhibits respiration is not known. A doubling of ambient [CO2] inhibits the activity of the mitochondrial enzymes, cytochrome c oxidase and succinate dehydrogenase. If inhibition of these enzymes is the only factor involved in the direct inhibition of respiration, the overall inhibition of specific respiration will be proportional to the control that such enzymes exert on the overall respiratory rate. We analyzed the effects of [CO2] on respiration in an attempt to scale the direct effects of CO2 on respiratory enzymes to the whole-plant level. Sensitivity analysis showed that inhibition of mitochondrial enzymes by doubling current atmospheric [CO2] does not explain entirely the CO2 inhibition of tissue or whole-plant respiration. We conclude that CO2-dependent suppression of respiratory enzymatic activity will be minimal when cytochrome c oxidase inhibition is scaled up from the mitochondria to the whole tree and that the primary mechanism for the direct inhibitory effect remains to be identified.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE STATUS, CARBON-DIOXIDE CONCENTRATIONS, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PHOTOSYNTHESIS, RESPONSES, ROOT RESPIRATION, SHORT- TERM

753

Goodale, C.L., J.D. Aber, and E.P. Farrell. 1998. Predicting the relative sensitivity of forest production in Ireland to site quality and climate change. *Climate Research 10(1):51-67.*

Most model-based predictions of climate change effects on forest ecosystems have used either potential or static descriptions of vegetation and site, removing the effects of direct management or land use. In this paper we use a previously developed and validated model of carbon and water balances in forest ecosystems (PnET-II) to assess the relative sensitivity of forest production in Ireland to predicted climate change and to ambient variability in site quality. After validating the model against measured productivity for 2 sets of stands, we ran the model using existing variation in site quality, represented as differences in foliar N concentration, and also for predicted changes in climate and atmospheric CO2. Resulting variations in productivity were compared with those due to potential errors in the specification of input parameters and to variation in current ambient climate across the region. The effects on net primary production (NPP) and wood production of either ambient variation in climate or predicted changes in temperature, precipitation and CO2 are quite small (0 to 30%) relative to the effects of ambient variability in site quality (up to 400%). The range of possible variation in other user-specified physiological parameters resulted in changes of less than 10% in model predictions. We conclude that site-specific conditions and management practices result in a range of forest productivity that is much greater than any likely to be induced by climate change or CO2 enrichment. We also suggest that it is essential to understand and map spatial variability in site quality, as well as to understand how the productive capacity of landscapes will change in response to management and pollution loading, if we are to predict the actual role that climate change will play in altering forest productivity and global biogeochemistry.

KEYWORDS: BIOMASS DISTRIBUTION, GENERAL-CIRCULATION MODEL, LEAF CO2 EXCHANGE, NET PRIMARY PRODUCTION, PACIFIC NORTHWEST, PHOTOSYNTHESIS- NITROGEN RELATIONS, PICEA-SITCHENSIS, SITCHENSIS BONG CARR, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

754

Goodfellow, J., D. Eamus, and G. Duff. 1997. Diurnal and seasonal changes in the impact of CO2 enrichment on assimilation, stomatal conductance and growth in a long-term study of Mangifera indica in the wet-dry tropics of Australia. *Tree Physiology 17(5):291-299.*

We studied assimilation, stomatal conductance and growth of Mangifera indica L. saplings during long-term exposure to a CO2-enriched

atmosphere in the seasonally wet-dry tropics of northern Australia. Grafted saplings of M. indica were planted in the ground in four air-conditioned, sunlit, plastic-covered chambers and exposed to CO2 at the ambient or an elevated (700 mu mol mol(-1)) concentration for 28 months. Light-saturating assimilation (A(max)), stomatal conductance (g(s)), apparent quantum yield (phi), biomass and leaf area were measured periodically. After 28 months, the CO2 treatments were changed in all four chambers from ambient to the elevated concentration or vice versa, and A(max) and g(s) were remeasured during a two-week exposure to the new regime. Throughout the 28-month period of exposure, A(max) and apparent quantum yield of leaves in the elevated CO2 treatment were enhanced, whereas stomatal conductance and stomatal density of leaves were reduced. The relative impacts of atmospheric CO2 enrichment on assimilation and stomatal conductance were significantly larger in the dry season than in the wet season. Total tree biomass was substantially increased in response to atmospheric CO2 enrichment throughout the experimental period, but total canopy area did not differ between CO2 treatments at either the first or the last harvest. During the two-week period following the change in CO2 concentration, A(max) of plants grown in ambient air but measured in CO2-enriched air was significantly larger than that of trees grown and measured in CO2-enriched air. There was no difference in A(max) between trees grown and measured in ambient air compared to trees grown in CO2-enriched air but measured in ambient air. No evidence of down-regulation of assimilation in response to atmospheric CO2 enrichment was observed when rates of assimilation were compared at a common intercellular CO2 concentration. Reduced stomatal conductance in response to atmospheric CO2 enrichment was attributed to a decline in both stomatal aperture and stomatal density.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FIELD, FOLIAR GAS-EXCHANGE, LEAF, MARANTHES-CORYMBOSA, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC RESPONSE, PLANTS, TREES

755

Goodfellow, J.E., D. Eamus, and G.A. Duff. 1997. The impact of CO2 enrichment on assimilation, stomatal conductance and growth in a long-term study of Mangifera indica in the wet-dry tropics of Australia. *Plant Physiology 114(3):480.*

756

Gordon, D.C., M.M.I. VanVuuren, B. Marshall, and D. Robinson. 1995. Plant growth chambers for the simultaneous control of soil and air temperatures, and of atmospheric carbon dioxide concentration. *Global Change Biology 1(6):455-464.*

Many facilities for growing plants at elevated atmospheric concentrations of CO2 ([CO2]) neglect the control of temperature, especially of the soil. Soil and root temperatures in conventional, free-standing pots often exceed those which would occur in the field at a given air temperature. A plant growth facility is described in which atmospheric CO2 can be maintained at different concentrations while soil and air temperatures mimic spatial and temporal patterns seen in the field. It consists of glasshouse-located chambers in which [CO2] is monitored by an infra-red gas analyser and maintained by injection of CO2 from a cylinder. Air is cooled by a heat exchange unit. Plants grow in soil in 1.2 m long containers that are surrounded by cooling coils and thermal insulation. Both [CO2] and temperature are controlled by customized software. Air temperature is programmed to follow a sine function of diurnal time. Soil temperature at a depth of 0.55 m is programmed to be constant. Temperature at 0.1 m depth varies as a damped, lagged function of air temperature; that at 1.0 m as a similar function of the 0.55 m temperature. [CO2] is maintained within 20 mu mol mol(-1) of target concentrations during daylight. A feature of the system is that plant material is labelled with a C-13 enrichment different from that of carbon in soil organic matter. The operation of the system is illustrated with data collected in an experiment with spring wheat (Triticum aestivum L., cv Tonic) grown at ambient [CO2] and at [CO2] 350 mu mol mol(-1) greater than ambient.

KEYWORDS: CO2

757

Gordon, H.B., P.H. Whetton, A.B. Pittock, A.M. Fowler, and M.R. Haylock. 1992. Simulated changes in daily rainfall intensity due to the enhanced greenhouse-effect - implications for extreme rainfall events. *Climate Dynamics 8(2):83-102.*

In this study we present rainfall results from equilibrium 1 x - and 2 x CO2 experiments with the CSIRO 4-level general circulation model. The 1 X CO2 results are discussed in relation to observed climate. Discussion of the 2 x CO2 results focuses upon changes in convective and non-convective rainfall as simulated in the model, and the consequences these changes have for simulated daily rainfall intensity and the frequency of heavy rainfall events. In doing this analysis, we recognize the significant shortcomings of GCM simulations of precipitation processes. However, because of the potential significance of any changes in heavy rainfall events as a result of the enhanced greenhouse effect, we believe a first examination of relevant GCM rainfall results is warranted. Generally, the model results show a marked increase in rainfall originating from penetrative convection and, in the mid- latitudes, a decline in large-scale (non-convective) rainfall. It is argued that these changes in rainfall type are a consequence of the increased moisture holding capacity of the warmer atmosphere simulated for 2 x CO2 conditions. Related to changes in rainfall type, rainfall intensity (rain per rain day) increases in the model for most regions of the globe. Increases extend even to regions where total rainfall decreases. Indeed, the greater intensity of daily rainfall is a much clearer response of the model to increased greenhouse gases than the changes in total rainfall. We also find a decrease in the number of rainy days in the middle latitudes of both the Northern and Southern Hemispheres. To further elucidate these results daily rainfall frequency distributions are examined globally and for four selected regions of interest. In all regions the frequency of high rainfall events increases, and the return period of such events decreases markedly. If realistic, the findings have potentially serious practical implications in terms of an increased frequency and severity of floods in most regions. However, we discuss various important sources of uncertainty in the results presented, and indicate the need for rainfall intensity results to be examined in enhanced greenhouse experiments with other GCMs.

KEYWORDS: CLIMATE VARIABILITY, CO2, GENERAL-CIRCULATION MODEL, OCEAN, TEMPERATURE, WATER-VAPOR

758

Gorissen, A. 1996. Elevated CO2 evokes quantitative and qualitative changes in carbon dynamics in a plant/soil system: Mechanisms and implications. *Plant and Soil 187(2):289-298.*

It is hypothesized that carbon storage in soil will increase under an elevated atmospheric CO2 concentration due to a combination of an increased net CO2 uptake, a shift in carbon allocation pattern in the plant/soil system and a decreased decomposition rate of plant residues. An overview of several studies, performed in our laboratory, on the effects of elevated CO2 on net carbon uptake, allocation to the soil and decomposition of roots is given to test this hypothesis. The studies included wheat, ryegrass and Douglas-fir and comprised both short-term and long-term studies. Total dry weight of the plants increased up to 62%, but depended on nutrient availability. These results were supported by the data on net (CO2)-C-14 uptake. A shift in C-14-carbon

distribution from shoots to roots was found in perennial species, although this depended on nutrient availability. The decomposition experiments showed that roots cultivated at 700 mu L L-1 CO2 were decomposed more slowly than those cultivated at 350 mu L L-1 CO2. Even after two growing seasons differences up to 13% were observed, although this was found to be dependent on the nitrogen level at which the roots were grown. Both an increased carbon allocation to the soil due to an increased carbon uptake, whether or not combined with a shift in distribution pattern, and a decreased decomposition of root residues will enhance the possibilities of carbon sequestration in soil, thus supporting our hypothesis. However, nutrient availability and the response of the soil microbial biomass (size and activity) play a major role in the processes involved and require attention to clarify plant/soil responses in the long term with regard to sustained stimulation of carbon input into soils and the decomposability of roots and rhizodeposition. Soil texture will also have a strong effect on decomposition rates as a result of differences in the protecting capacity for organic matter. More detailed information on these changes is needed for a proper use of models simulating soil carbon dynamics in the long term.

KEYWORDS: ATMOSPHERIC CO2, DECOMPOSITION, FINE ROOTS, LEAF LITTER, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER, ROOT-DERIVED MATERIAL, SOIL SYSTEM, TURNOVER

759

Gorissen, A., P.J. Kuikman, and H. Vandebeek. 1995. Carbon allocation and water-use in juvenile douglas-fir under elevated co2. *New Phytologist 129(2):275-282.*

In this study the impact of an elevated CO2 level on allocation of assimilates and water use efficiency of Douglas fir [Pseudotsuga menziesii (Mirb.) France] was investigated. Juvenile Douglas firs were exposed to a long-term treatment at 350 and 700 pi l(-1) CO2 for 14 months and subsequently crosswise transferred to phytotrons for a short-term treatment with 350 and 700 mu l l(-1) CO2 for 4 wk in an atmosphere continuously labelled with (CO2)-C-14. No interactive effects on total net uptake of (CO2)-C-14 between long-term treatment and short-term treatment were observed. The short-term treatment with 700 mu l l(-1) CO2 increased the total net uptake of (CO2)-C-14 by 22%, compared with the 350 mu l l(-1) CO2 treatment. The long-term pretreatment did not affect the total net uptake, suggesting that photosynthetic acclimation had not occurred. However, expressed per unit of needle mass a 14% reduction was observed in the trees pretreated at 700 mu l l(-1) CO2. This was not because of a reduced sink strength of the root system. This reduced uptake per unit of needle mass after long-term treatment may have implications for carbon storage in forest ecosystems. The results showed that an initial growth stimulation can eventually be annulled by developing physiological or morphological adaptions. (CO2)-C-14 the root/soil respiration increased in the short-term treatment with 700 mu l l(-1) CO2, indicating a stimulated use of current carbon compounds either by roots or microorganisms. The water use efficiency during the short-term treatment with 700 mu l l(-1) CO2 increased by 32%, but was not affected by the long- term pretreatment. Water use per unit needle mass during the short-term treatment was decreased both by the short-term treatment and by the long-term pretreatment by about 15%. Some of the observed effects appeared to be persistent, such as decreased water use per unit needle mass, whereas others, stimulation of total net (CO2)-C-14 uptake and water use efficiency, were transient.

KEYWORDS: BLACK SPRUCE SEEDLINGS, DIOXIDE, ECOSYSTEMS, ENRICHMENT, GROWTH, LIQUIDAMBAR-STYRACIFLUA, PHOTOSYNTHETIC ACCLIMATION, PINUS-TAEDA SEEDLINGS, RESPONSES, ROOT-DERIVED MATERIAL

760

Gorissen, A., P.J. Kuikman, J.H. vanGinkel, H. vandeBeek, and A.G. Jansen. 1996. ESPAS - An advanced phytotron for measuring carbon dynamics in a whole plant-soil system. *Plant and Soil 179(1):81-87.*

The use of carbon isotopes as tracers is essential for measuring carbon flows in an intact whole plant-soil system. Here, we describe an Experimental Soil Plant Atmosphere System (ESPAS) to perform pulse-labelling and steady-state labelling experiments with (CO2)-C-13 and (CO2)-C-14. The ESPAS facility is an environmental research tool that is used to measure the carbon fluxes from the atmosphere to the roots and into the soil and the microbial biomass and to study decomposition of plant residues and soil organic matter. The influence of environmental conditions in the atmosphere or in soil on the carbon allocation and turnover in the plant-soil ecosystem can be quantified. The design and the technical description of the phytotrons is presented and evidence is provided that the phytotrons are equivalent. For this purpose, Triticum aestivum plants were cultivated in the phytotrons for 39 days and shoot growth, root growth and water use were compared. No significant differences were observed for plant growth and water use. As an example of the practical application of the equipment, an experiment with elevated atmospheric CO2 is presented. Data are given on the uptake of C-14 under ambient (350 mu L L(-1)) and elevated (700 mu L L(-1)CO(2) in Lolium perenne and Festuca arundinacea and the distribution of C-14 among different plant- soil compartments i.e. shoot, root, root-soil respiration, and soil. We conclude that these phytotrons yield detailed information on gross carbon flows in a whole plant-soil system that can not be obtained without sensitive carbon tracers. Such data are important for proper calibration of simulation models on soil organic matter.

KEYWORDS: DIOXIDE, DOUGLAS-FIR, OZONE, RHIZOSPHERE, ROOT-DERIVED MATERIAL, TRANSLOCATION, TURNOVER, WHEAT

761

Gorissen, A., J.H. Vanginkel, J.J.B. Keurentjes, and J.A. Vanveen. 1995. Grass root decomposition is retarded when grass has been grown under elevated co2. *Soil Biology and Biochemistry 27(1):117-120.*

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CYCLE, INCREASE, LEAF LITTER, NITROGEN, SOIL

762

Gorny, J.R., and A.A. Kader. 1996. Controlled-atmosphere suppression of ACC synthase and ACC oxidase in 'Golden Delicious' apples during long-term cold storage. *Journal of the American Society for Horticultural Science 121(4):751-755.*

Preclimacteric 'Golden Delicious' apples (Malus domestica Borkh.) were stored at 0 degrees C in: air; air + 5% CO2; 2% O- 2 + 98% N-2; or 2% O-2 + 5% CO2 + 93% N-2, and sampled monthly for 4 months to investigate the mechanism(s) by which reduced O-2 and/or elevated CO2 atmospheres inhibit C2H4 biosynthesis. Ethylene biosynthesis rates and in vitro ACS activity were closely correlated in all treatments, while in vitro ACO activity significantly increased over time regardless of the treatment. Only a small amount of C2H4 biosynthesis inhibition by lowered O-2 and/or elevated CO2 atmospheres could be accounted for by suppressed induction of ACO activity, Western blot analysis demonstrated that apples held for 2 months in lowered O-2 and/or elevated CO2 atmospheres had significantly reduced abundance of ACO protein, compared to fruit held in air. Northern blot analysis of ACS and ACO transcript abundance revealed that reduced O-2 and/or elevated CO2 atmospheres delay induction and reduce the abundance of both transcripts, Reduced O-2 and/or elevated CO2 atmospheres reduce

C2H4 biosynthesis by delaying and suppressing expression of ACS at the transcriptional level and by reducing the abundance of active ACO protein. Chemical names used: 1-aminocyclopropane-1- carboxylic acid (ACC), ACC synthase (ACS), ACC oxidase (ACO), ethylene (C2H4), S-adenosylmethionine (AdoMet).

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ETHYLENE PRODUCTION, EXPRESSION, FRUIT, PROTEIN, PURIFICATION

763

Gorny, J.R., and A.A. Kader. 1996. Regulation of ethylene biosynthesis in climacteric apple fruit by elevated CO2 and reduced O-2 atmospheres. *Postharvest Biology and Technology 9(3):311-323.*

Autocatalytic (System II) C2H4 biosynthesis in climacteric 'Golden Delicious' apples (Malus domestica Borkh) was effectively inhibited at 20 degrees C by atmospheres of 20% CO2-enriched air (17% O-2 + 63% N-2) or 0.25% O-2 (balance N- 2). In vitro 1-aminocyclopropane-1-carboxylic acid (ACC) synthase (ACC-S) activity of apples held in atmospheres of air + 20% CO2 or 0.25% O-2 was significantly inhibited when compared to apples kept in air, and correlated well with fruit C2H4 production rates. In vivo and in vitro ACC oxidase (ACC-O) activity of fruit held in atmospheres of air, air + 20% CO2 or 0.25% O-2 were similar when the assays were performed under standard assay conditions (i.e., in vivo assay performed in air, in vitro assay performed in air + 6% CO2). However, if the in vivo or in vitro ACC-O enzyme activity assays were performed in an atmosphere of 0.25% O-2, ACC-O catalytic competency and activity were significantly reduced. When the in vivo or in vitro ACC-O enzyme activity assays were performed in an atmosphere of air + 20% CO2, ACC-O enzyme activity was actually stimulated. These data indicate that elevated levels of CO2 do not inhibit ACC-O catalytic competency. Western blot analysis revealed that ACC-O protein abundance was not significantly affected by any of the treatments tested, and only the 0.25% O- 2 atmosphere significantly inhibited ACC-O activity. ACC-S activity was significantly reduced by atmospheres of air + 20% CO2 or 0.25% O-2 but not via direct inhibition of ACC-S catalytic competency.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, CARBON DIOXIDE, OXIDASE, PH, PURIFICATION, SYNTHASE

764

Gorny, J.R., and A.A. Kader. 1997. Low oxygen and elevated carbon dioxide atmospheres inhibit ethylene biosynthesis in preclimacteric and climacteric apple fruit. *Journal of the American Society for Horticultural Science 122(4):542-546.*

Autocatalytic C2H4 biosynthesis in preclimacteric apple fruit (Malus domestica Borkh, 'Golden Delicious') was prevented by storage in atmospheres of 20% CO2-enriched air (17% O-2+ 63% N- 2) or 0.25% O-2 (balance N-2). In preclimacteric fruit, both treatments inhibited C2H4 biosynthesis by suppressing expression of ACC synthase (ACC-S) at the mRNA level. ACC oxidase (ACC-O) mRNA abundance and in vitro enzyme activity also were impaired by these treatments. However, the conversion of ACC to C2H4 never became the rate limiting step in C2H4 biosynthesis, C2H4 biosynthesis also was effectively inhibited in climacteric apple fruit kept in air + 20% CO2 or 0.25% O-2. Climacteric apples also exhibited suppressed expression of ACC- S at the mRNA level, while ACC-O transcript abundance, enzyme activity, and protein abundance mere reduced only slightly. ACC-S is the key regulatory enzyme of C2H4 biosynthesis and is the major site at which elevated CO2 and reduced O-2 atmospheres inhibit C2H4 biosynthesis, irrespective of fruit physiological maturity. Chemical names used: 1-aminocyclopropane-1-carboxcylic acid (ACC).

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, EXPRESSION, OXIDASE, PROPYLENE, PROTEIN, PURIFICATION, SYNTHASE, TOMATO

765

Goudriaan, J. 1992. Where goes the carbon-dioxide - the role of vegetation. *Recherche 23(243):597.*

KEYWORDS: AGRICULTURAL YIELD, ASSEMBLAGE, CO2-ENRICHMENT, PLANT, SOYBEAN LEAVES

766

Gouk, S.S., J. He, and C.S. Hew. 1999. Changes in photosynthetic capability and carbohydrate production in an epiphytic CAM orchid plantlet exposed to super-elevated CO2. *Environmental and Experimental Botany 41(3):219-230.*

The effects on growth in super-elevated (1%) CO2 in terms of photosynthetic capability and carbohydrate production were studied in an epiphytic CAM (Crassulacean acid metabolism) orchid plantlet, Mokara Yellow (Arachmis hookeriana x Ascocenda Madame Kenny). The growth of the plantlets was greatly enhanced after growing for 3 months at 1% CO2 compared with the control plantlets (0.035% CO2). CO2 enrichment produced more than a 2- fold increase in dry matter production. The enhanced root growth at 1% CO2 led to a higher root:shoot ratio. Plantlets grown at super-elevated CO2 had higher F-v/F-m values, a higher photochemical quenching (q(P)) and a relatively lower non- photochemical quenching (q(N)). CO2 at 1% appeared to enhance the utilization of captured light energy in the orchid plantlets. CO2 enrichment also increased contents of soluble sugars (glucose and sucrose) and starch in the orchid plantlets. The extra starch formed under 1% CO, did not cause a disruption of the chloroplasts. Chlorophyll content was higher and a clear granal stacking was evident in young leaves and roots of plantlets grown at 1% CO2. An extensive thylakoid system was observed in the young leaf chloroplasts of the CO2- enriched plantlets indicating an improved development of the photosynthetic apparatus when compared to that of the control plantlets. The increased photosynthetic capacity and enhanced growth of the epiphytic roots under CO, enrichment would facilitate the generation of more photoassimilates and acquisition of essential resources, thereby increasing the survival rate of orchid plantlets under stressful field conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHLOROPHYLL FLUORESCENCE, CULTURE, ENRICHMENT, GROWTH, INVITRO, RESPONSES, ROOTS, STRAWBERRY PLANTLETS, ULTRASTRUCTURE

767

Gouk, S.S., J.W.H. Yong, and C.S. Hew. 1997. Effects of super-elevated CO2 on the growth and carboxylating enzymes in an epiphytic CAM orchid plantlet. *Journal of Plant Physiology 151(2):129-136.*

Responses of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPCase) to super-elevated CO2 were determined along with dry mass production, chlorophyll, soluble protein and nocturnal malate increases (NMI) for an epiphytic Crassulacean acid metabolism (CAM) orchid plantlet, Mokara Yellow. After S-month culture period, the total dry mass under super-elevated CO2 was 170% higher than the plantlets grown in 0.03% CO2; young leaf dry mass was 4-fold higher while the root dry mass increased 278% and 344% under 1% and 5% CO2 respectively. Higher root:shoot ratio was observed under super-elevated CO2; 0.22 in 0.03% CO2, 0.32 in 1% CO2 and 0.38 in 5% CO2. The averaged increase in total young leaf area was 244% and 373% under 1% and 5% CO2 respectively Leaf

chlorophyll expressed per unit fresh weight was reduced under 5% CO2 but it increased 19% and 67% in old and young leaves of 3-month plantlets under 1% CO2. The root chlorophyll content increased 108% and 154% under 1%;, and 5% CO2 respectively. Soluble protein in young leaves increased 32% under 1% CO2 and 75% under 5% CO2, while the increase in root protein varied from 36% to 100%. The activities of Rubisco and PEPCase el:pressed per unit protein were reduced under super- elevated CO2, particularly in 5% CO2, the decreases ranged from 12% to 90% in Rubisco and 27% to 90% in PEPCase. Nevertheless, the leaf Rubisco:PEPCase ratio increased 110% to 362% under super-elevated CO2. Increased NMI, ranged from 23% to 182% under super-elevated CO2, contributed to the increased dry matter accumulation in Mokara plantlets. Throughout the S-month culture period, the CO2-enriched plantlets showed enhanced growth particularly under 1% CO2 in terms of biomass production, chlorophyll, soluble protein and NMI despite a concomitant decrease in the activities of the carboxylating enzymes.

KEYWORDS: CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ENRICHMENT, INVITRO, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, STRAWBERRY PLANTLETS, SUCROSE, TEMPERATURE, TISSUE-CULTURE

768

Goulart, B.L., P.E. Hammer, K.B. Evensen, W. Janisiewicz, and F. Takeda. 1992. Pyrrolnitrin, captan + benomyl, and high co2 enhance raspberry shelf-life at 0C or 18C. *Journal of the American Society for Horticultural Science 117(2):265-270.*

The effects of preharvest applications of pyrrolnitrin (a biologically derived fungicide) on postharvest longevity of 'Bristol' black raspberry (Rubus occidentalis L.) and 'Heritage' red raspberry [R. idaeus L. var. strigosus (Michx.) Maxim] were evaluated at two storage temperatures. Preharvest fungicide treatments were 200 mg pyrrolnitrin/liter, a standard fungicide treatment (captan + benomyl or iprodione) or a distilled water control applied 1 day before first harvest. Black raspberries were stored at 18 or 0 +/- 1C in air or 20% CO2. Red raspberries were stored at the same temperatures in air only. Pyrrolnitrin-treated berries often had less gray mold (Botrytis cinerea Pers. ex Fr.) in storage than the control but more than berries treated with the standard fungicides. Storage in a modified atmosphere of 20% CO2 greatly improved postharvest quality of black raspberries at both storage temperatures by reducing gray mold development. The combination of standard fungicide or pyrrolnitrin, high CO2, and low temperature resulted in more than 2 weeks of storage with less than 5% disease on black raspberries; however, discoloration limited marketability after almost- equal-to 8 days under these conditions. Chemical names used: 3-chloro-4-(2'-nitro-3'-chlorophenyl)-pyrrole (pyrrolnitrin); N-trichloromethylthio-4-cyclohexene-1,2-dicarboximide (captan); methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate) (benomyl); 3-(3,5-dichlorophenyl)-N-(1-methylethyl)-2,4-dioxo-1-imidazolidinecarboxamide (Rovral, iprodione).

KEYWORDS: STRAWBERRIES

769

Graham, E.A., and P.S. Nobel. 1996. Long-term effects of a doubled atmospheric CO2 concentration on the CAM species Agave deserti. *Journal of Experimental Botany 47(294):61-69.*

To examine the effects of a doubled atmospheric CO2 concentration and other aspects of global climate change on a common CAM species native to the Sonoran Desert, Agave deserti was grown under 370 and 750 mu mol CO2 mol(-1) air and gas exchange was measured under various environmental conditions. Doubling the CO2 concentration increased daily net CO2 uptake by 49% throughout the 17 months and decreased daily transpiration by 24%, leading to a 110% increase in water-use efficiency, Under the doubled CO2 concentration, the activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) was 11% lower, phosphoenolpyruvate carboxylase was 34% lower, and the activated:total ratio for Rubisco was 25% greater than under the current CO2 concentration. Less leaf epicuticular wax occurred on plants under the doubled CO2 concentration, which decreased the reflectance of photosynthetic photon flux (PPF); the chlorophyll content per unit leaf area was also less, The enhancement of daily net CO2 uptake by doubling the CO2 concentration increased when the PPF was decreased below 25 mol m(-2) d(-1), when water was withheld, and when day/night temperatures were below 17/12 degrees C, More leaves, each with a greater surface area, were produced per plant under the doubled CO2 concentration. The combination of increased total leaf surface area and increased daily net CO2 uptake led to an 88% stimulation of dry mass accumulation under the doubled CO2 concentration, A rising atmospheric CO2 concentration, together with accompanying changes in temperature, precipitation, and PPF, should increase growth and productivity of native populations of A. deserti.

KEYWORDS: CROP RESPONSES, ELEVATED CARBON-DIOXIDE, ENRICHMENT, ENVIRONMENTAL PHYSIOLOGY, EPICUTICULAR WAX LOAD, GROWTH, PHOTOSYNTHESIS, PLANT, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RISING CO2

770

Grams, T.E.E., S. Anegg, K.H. Haberle, C. Langebartels, and R. Matyssek. 1999. Interactions of chronic exposure to elevated CO2 and O-3 levels in the photosynthetic light and dark reactions of European beech (Fagus sylvatica). *New Phytologist 144(1):95-107.*

Young trees of European beech (Fagus sylvatica) acclimated for one growing season to ambient (c. 367 mu l l(-1)) or elevated CO2 levels (c. 660 mu l l(-1)) were exposed during the subsequent year to combinations of the same CO2 regimes and ambient or twice-ambient ozone (O-3) levels (generated from the database of a rural site). By the end of June, before the development of macroscopic leaf injury, the raised O-3 levels had not affected the light and dark reactions of photosynthesis. However, acclimation to elevated CO2 had resulted in lowered chlorophyll and nitrogen concentrations, whereas photosynthetic performance, examined over a wide range of parameters from light and dark reactions, remained unchanged or showed only slight reductions (e.g. apparent electron transport rate, ETR; apparent quantum yield of CO2 gas exchange, Phi(CO2); apparent carboxylation efficiency, CE; and photosynthetic capacity at light and CO2 saturation, PC). In August, after the appearance of leaf necroses, plants grown under ambient CO2 and twice-ambient O-3 conditions declined in both the photosynthetic light reactions (optimum electron quantum yield, Fv/F-m, non-photochemical energy quenching, NPQ, reduction state of Q(A), apparent electron quantum yield, Phi(PSI)I, maximum electron transport rates) and the dark reactions as reflected by CE, Phi(CO2), as well as the maximum CO2 uptake rate (i.e. PC). CE, Phi(CO2) and PC were reduced by c. 75, 40 and 75%, respectively, relative to plants exposed to ambient CO2 and O-3 levels. By contrast, plants exposed to twice-ambient O-3 and elevated CO2 levels maintained a photosynthetic performance similar to individuals grown either under ambient CO2 and ambient O-3, or elevated CO2 and ambient O-3 conditions. The long-term exposure to elevated CO2 therefore tended to counteract adverse chronic effects of enhanced O-3 levels on photosynthesis. Possible reasons for this compensatory effect in F. sylvatica are discussed.

KEYWORDS: ATMOSPHERIC CO2, BETULA-PENDULA, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, LEAF GAS-EXCHANGE, LOW OZONE CONCENTRATIONS, NORWAY SPRUCE, PHOTOSYSTEM, SPRUCE PICEA-ABIES, TROPOSPHERIC OZONE

771

Grams, T.E.E., and R. Matyssek. 1999. Elevated CO2 counteracts the limitation by chronic ozone exposure on photosynthesis in Fagus sylvatica L.: Comparison between chlorophyll fluorescence and leaf gas exchange. *Phyton-Annales Rei Botanicae 39(4):31-39.*

The interaction of elevated CO2 and enhanced chronic ozone (O- 3) impact was analysed throughout the growing season in the photosynthetic response (chlorophyll fluorescence and leaf gas exchange) of beech saplings (Fagus sylvatica) which had been acclimated to CO2 supply during the year prior to the experiment. Both light and dark reactions (i.e. electron transport rate and photosynthetic capacity) of plants grown at ambient CO2 and twice-ambient O-3 concentrations were distinctly reduced by August. The O-3-induced decline was counteracted by elevated CO2 supply (i.e. ambient +300 ppm). Plants grown at high CO2 supply and ambient or twice-ambient O- 3 concentrations displayed a photosynthetic performance similar to plants exposed to ambient CO2 and O-3 conditions. Responses in chlorophyll fluorescence were found to be consistent with those in leaf gas exchange.

KEYWORDS: BEECH, CARBON DIOXIDE, GROWTH, LEAVES, NORWAY SPRUCE, O-3, RESPONSES, SPRING WHEAT, TROPOSPHERIC OZONE, YIELD

772

Grant, R.F. 1998. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. *Ecological Modelling 107(2-3):237-264.*

If mathematical models of plant growth are to perform reliably under diverse conditions of soil and climate, then the effects of these conditions on root growth must be represented. A mathematical model of root and mycorrhizal growth is proposed to represent the effects of soil and climate on growth using the hypothesis that a functional equilibrium exists among root axes and shoot branches. In this model access to growth resources (C, N, P, water) by different axes or branches depends upon (1) proximity of the axis or branch to the point of resource acquisition, and (2) the rate at which resources are consumed by the axis or branch in relation to that by other axes or branches. This model was coupled to a plant growth model as part of the ecosystem simulation model ecosys, and its sensitivity to changes in model parameters and soil boundary conditions was tested. Simulated root growth was less sensitive to changes in soil water and nitrogen than was simulated shoot growth. This lower sensitivity allowed the model to simulate changes in root,shoot ratios with changes in soil water and nitrogen that were consistent with those commonly reported in the literature. Changes in soil water also caused changes in vertical distributions of root length density to be simulated that were also consistent with those reported. Changes in root,shoot partitioning and in root density distributions allowed improved access by plants in the model to limiting growth resources. The root model was parameterized from basic root growth studies conducted independently of the model, and without reference to site-specific patterns of seasonal root growth. Consequently the model is likely to be of general value in the simulation of root growth under diverse soil conditions, although such generality needs to be established through further testing under different soils, climates and crops. The precision of some of the model parameters is uncertain and the sensitivity of the model to this uncertainty is discussed.

KEYWORDS: AIR CO-2 ENRICHMENT, CARBON DIOXIDE, FACE EXPERIMENT, MODEL, MYCORRHIZAL FUNGI, PHOSPHORUS, PLANTS, SHOOT DEVELOPMENT, WINTER-WHEAT, ZEA-MAYS

773

Grant, R.F., T.A. Black, G. den Hartog, J.A. Berry, H.H. Neumann, P.D. Blanken, P.C. Yang, C. Russell, and I.A. Nalder. 1999. Diurnal and annual exchanges of mass and energy between an aspen-hazelnut forest and the atmosphere: Testing the mathematical model Ecosys with data from the BOREAS experiment. *Journal of Geophysical Research-Atmospheres 104(D22):27699-27717.*

There is much uncertainty about the net carbon (C) exchange of boreal forest ecosystems, although this exchange may be an important part of global C dynamics. To resolve this uncertainty, net C exchange has been measured at several sites in the boreal forest of Canada as part of the Boreal Ecosystem- Atmosphere Study (BOREAS). One of these sites is the Southern Old Aspen site at which diurnal CO2 and energy (radiation, latent, and sensible heat) fluxes were measured during 1994 using eddy correlation techniques at different positions within a mixed 70 year old aspen-hazelnut forest. These measurements were used to test a complex ecosystem model "ecosys" in which mass and energy exchanges between terrestrial ecosystems and the atmosphere are simulated hourly under diverse conditions of soil, management, and climate. These simulations explained between 70% and 80% of diurnal variation in ecosystem CO2 and energy fluxes measured during three 1 week intervals in late April, early June, and mid-July. Total annual CO2 fluxes indicated that during 1994, aspen was a net sink of 540 (modeled) versus 670 (measured) g C m(-2) yr(-1), while hazelnut plus soil were a net source of 472 (modeled) versus 540 (measured) g C m(-2) yr(-1). The aspen-hazelnut forest at the BOREAS site was therefore estimated to be a net sink of about 68 (modeled) versus 130 (measured) g C m(-2) yr(-1) during 1994. Long-term simulations indicated that this sink may be larger during cooler years and smaller during warmer years because C fixation in the model was less sensitive to temperature than respiration. These simulations also indicated that the magnitude of this sink declines with forest age because respiration increases with respect to fixation as standing phytomass grows. Confidence in the predictive capabilities of ecosystem models at decadal or centennial timescales is improved by well-constrained tests of these models at hourly timescales.

KEYWORDS: BLACK SPRUCE, CO2- ENRICHMENT, ELEVATED CARBON-DIOXIDE, JACK PINE, NITROUS-OXIDE, PHOSPHORUS UPTAKE, ROOT-GROWTH, SIMULATION-MODEL, SOIL ORGANIC MATTER, TREMBLING ASPEN

774

Grant, R.F., R.L. Garcia, P.J. Pinter, D. Hunsaker, G.W. Wall, B.A. Kimball, and R.L. LaMorte. 1995. Interaction between atmospheric CO2 concentration and water deficit on gas exchange and crop growth: Testing of ecosys with data from the Free Air CO2 Enrichment (FACE) experiment. *Global Change Biology 1(6):443-454.*

Soil water deficits are likely to influence the response of crop growth and yield to changes in atmospheric CO2 concentrations (C-a), but the extent of this influence is uncertain. To study the interaction of water deficits and C-a on crop growth, the ecosystem simulation model ecosys was tested with data for diurnal gas exchange and seasonal wheat growth measured during 1993 under high and low irrigation at C- a = 370 and 550 mu mol mol(-1) in the Free Air CO2 Enrichment (FACE) experiment near Phoenix, AZ. The model, supported by the data from canopy gas exchange enclosures, indicated that under high irrigation canopy conductance (g(c)) at C-a = 550 mu mol mol(-1) was reduced to about 0.75 that at C-a = 370 mu mol mol(-1), but that under low irrigation, g(c) was reduced less. Consequently when C-a was increased from 370 to 550 mu mol mol(-1), canopy transpiration was reduced less, and net CO2 fixation was increased more, under low irrigation than under high irrigation. The simulated effects of C-a and irrigation on diurnal gas exchange were also apparent on seasonal water use and grain yield. Simulated vs. measured seasonal water use by wheat under high irrigation was reduced by 6% vs. 4% at C-a = 550 vs. 370 mu mol mol(-1), but that under low irrigation was increased by 3% vs. 5%. Simulated

vs. measured grain yield of wheat under high irrigation was increased by 16% vs. 8%, but that under low irrigation was increased by 38% vs. 21%. In ecosys, the interaction between C-a and irrigation on diurnal gas exchange, and hence on seasonal crop growth and water use, was attributed to a convergence of simulated g(c) towards common values under both C-a as canopy turgor declined. This convergence caused transpiration to decrease comparatively less, but CO2 fixation to increase comparatively more, under high vs. low C-a. Convergence of g(c) was in turn attributed to improved turgor maintenance under elevated C-a caused by greater storage C concentrations in the leaves, and by greater rooting density in the soil.

KEYWORDS: BIOCHEMICAL-MODEL, CANOPY PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ELEVATED CARBON-DIOXIDE, MAIZE, ROOT-GROWTH, SIMULATION-MODEL, SOYBEAN LEAVES, TEMPERATURE, WINTER-WHEAT

775

Grant, R.F., B.A. Kimball, P.J. Pinter, G.W. Wall, R.L. Garcia, R.L. Lamorte, and D.J. Hunsaker. 1995. Carbon-dioxide effects on crop energy-balance - testing ecosys with a free-air co2 enrichment (face) experiment. *Agronomy Journal 87(3):446-457.*

Elevated CO2 concentrations (C-e) have been observed to decrease short-term plant water use under controlled conditions by increasing stomatal resistance. The extent to which this decrease occurs over a growing season in the held is uncertain, however, because stomatal resistance is only one of many mechanisms that control water use. In this study, we tested the ecosystem simulation model ecosys, which reproduces an hourly energy balance through soil-vegetation systems under defined atmospheric boundary renditions, using energy exchange data measured as part of the Free-Air CO2 Enrichment (FACE) experiment at C-e = 550 vs. 370 mu mol mol(-1). The model reproduced reductions in measured upward latent heat fluxes that varied from -10 to +40 W m(-2), depending on atmospheric conditions. In the model, the primary effect of elevated C-e on latent heat fluxes was through canopy stomatal conductance. This effect was largely offset by secondary effects through canopy temperature that enabled the model to reproduce measured changes in sensible heat fluxes. The total effect simulated by ecosys of C-e = 550 vs. 370 mu mol mol(-1) on evapotranspiration during the entire PACE experiment was a reduction of 7%. This reduction compares with one of 11% estimated from accumulated daily measurements of latent heat flux. In the model, the different effects of C-e on plant water use depend on atmosphere and soil boundary conditions, and are highly dynamic. Consequently the simulated C-e-water use relationship is likely to be site-specific. The use of models such as ecosys allows site-specific boundary conditions to be considered in the study of C-e effects on plant growth and water use.

KEYWORDS: BIOCHEMICAL-MODEL, CANOPY PHOTOSYNTHESIS, EXPERIMENTAL- VERIFICATION, OSMOTIC ADJUSTMENT, PLANT GROWTH, ROOT-GROWTH, SIMULATION-MODEL, SOIL COMPACTION, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

776

Grant, R.F., G.W. Wall, B.A. Kimball, K.F.A. Frumau, P.J. Pinter, D.J. Hunsaker, and R.L. Lamorte. 1999. Crop water relations under different CO2 and irrigation: testing of ecosys with the free air CO2 enrichment (FACE) experiment. *Agricultural and Forest Meteorology 95(1):27-51.*

Increases in crop growth under elevated atmospheric CO2 concentration (C-A) have frequently been observed to be greater under water-limited versus non-limited conditions. Crop simulation models used in climate change studies should be capable of reproducing such changes in growth response to C-A with changes in environmental conditions. We propose that changes with soil water status in crop growth response to C-A can be simulated if stomatal resistance is considered to vary directly with air-leaf C-A gradient, inversely with leaf carboxylation rate, and exponentially with leaf turgor. Resistance simulated in this way increases with C-A relatively less, and CO2 fixation increases with C-A relatively more, under water-limited versus non-limited conditions. As part of the ecosystem model ecosys, this simulation technique caused changes in leaf conductance and CO2 fixation, and in canopy water potential, temperature and energy balance in a modelling experiment that were consistent with changes measured under 355 versus 550 mu mol mol(-1) C-A and low versus high irrigation in a free air CO2 enrichment (FACE) experiment on wheat. Changes with C-A in simulated crop water relations allowed the model to reproduce under 550 mu mol mol(-1) C-A and low versus high irrigation a measured increase of 20 versus 10% in seasonal wheat biomass, and a measured decrease of 2 versus 5% in seasonal evapotranspiration, The basic nature of the processes simulated in this model is intended to enable its use under a wide range of soil, management and climate conditions.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ENERGY-BALANCE, EXPERIMENTAL-VERIFICATION, GAS-EXCHANGE, ROOT-GROWTH, SIMULATION-MODEL, SOIL TEMPERATURE, STOMATAL CONDUCTANCE, USE EFFICIENCY

777

Grant, W.J.R., H.M. Fan, W.J.S. Downton, and B.R. Loveys. 1992. Effects of co2 enrichment on the physiology and propagation of 2 australian ornamental plants, chamelaucium-uncinatum (schauer) X chamelaucium-floriferum (ms) and correa- schlechtendalii (behr). *Scientia Horticulturae 52(4):337-342.*

Root formation on both Chamelaucium and Correa cuttings maintained at high humidity in an enclosed fog tunnel was significantly enhanced when ambient CO2 was increased from 350 to 800 mubar. CO2 enrichment resulted in decreased transpiration and increased water potential of cuttings implying an effect of CO2 on stomatal conductance. CO2 enrichment led to increased starch levels in cuttings of both species probably by raising the intercellular partial pressure of CO2. Increased starch content with CO2 enrichment was able to account for 70-90% of the dry weight increase in Correa, but only for 10-30% of the dry weight increase in Chamelaucium. It is suggested that the stimulation of rooting associated with CO2 enrichment probably derives from the improved water relations of the cuttings rather than from increased carbohydrate levels.

KEYWORDS: CUTTINGS

778

Grant, W.J.R., and B.R. Loveys. 1996. Controlling rootstock sprouts of Agonis flexuosa (Willd) Sweet at ambient and elevated CO2 by multiple applications of low concentration NAA. *Australian Journal of Experimental Agriculture 36(5):619-624.*

A method for grafting variegated scion material to green leafed Agonis flexuosa (Willd.) Sweet stock was developed to overcome the difficulty of striking cuttings. However sprouting of both seedling and cutting-grown A. flexuosa rootstocks was a significant problem. Microwedge grafting of actively growing leafy scions and stocks in fog at 32/22 degrees C gave 90-100% success and scion bud activity was stimulated within 2 weeks. Weekly or fortnightly spray applications of 100 mg NAA/L (napthaleneacetic acid), starting at the time of grafting, gave effective sprout control whereas a single pregraft spray of 200 mg NAA/L was not effective. CO2 enrichment of the fog environment was

investigated as a means of enhancing scion growth. CO2 at 80 kPa increased scion dry weight (DW), leaf and branch numbers, but had no effect on rootstock sprout or stem DW or sprout numbers. Optimum NAA concentrations for rootstock sprout suppression under elevated CO2 with fog, were 50-100 mg/L, which were not deleterious to scion shoot length, when sprayed on the stock portion only. Stock sprout numbers, scion leaf and branch numbers were negatively correlated with NAA concentration. Sprout growth at 100 mg NAA/L was about 5% of control sprout growth. Concentrations greater than or equal to 200 mg NAA/L caused leaf tip necrosis and excess stem callusing. Scion growth was inversely related to the degree of resprouting in control treatments.

KEYWORDS: ENRICHMENT, GROWTH, TREES

779

Grashoff, C., P. Dijkstra, S. Nonhebel, A.H.C.M. Schapendonk, and S.C. VandeGeijn. 1995. Effects of climate change on productivity of cereals and legumes; model evaluation of observed year-to-year variability of the CO2 response. *Global Change Biology 1(6):417-428.*

The effect of elevated [CO2] on the productivity of spring wheat, winter wheat and faba bean was studied in experiments in climatized crop enclosures in the Wageningen Rhizolab in 1991- 93. Simulation models for crop growth were used to explore possible causes for the observed differences in the CO2 response. Measurements of the canopy gas exchange (CO2 and water vapour) were made continuously from emergence until harvest. At an external [CO2] of 700 mu mol mol(-1), Maximum Canopy CO2 Exchange Rate (CCFRmax) at canopy closure was stimulated by 51% for spring wheat and by 71% for faba bean. At the end of the growing season, above ground biomass increase at 700 mu mol mol(-1) was 58% (faba bean), 35% (spring wheat) and 19% (winter wheat) and the harvest index did not change. For model exploration, weather data sets for the period 1975-88 and 1991-93 were used, assuming adequate water supply and [CO2] at 350 and 700 mu mol mol(-1). For spring wheat the simulated responses (35-50%) were at the upper end of the experimental results. In agreement with experiments, simulations showed smaller responses for winter wheat and larger responses for faba bean. Further model explorations showed that this differential effect in the CO2 response may not be primarily due to fundamental physiological differences between the crops, but may be at least partly due to differences in the daily air temperatures during comparable stages of growth of these crops. Simulations also showed that variations between years in CO2 response can be largely explained by differences in weather conditions (especially temperature) between growing seasons.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, GROWTH, PATTERN, PHOTOSYNTHESIS, VICIA-FABA L, WHEAT, YIELD VARIABILITY

780

Graumlich, L.J. 1991. Sub-alpine tree growth, climate, and increasing CO2 - an assessment of recent growth trends. *Ecology 72(1):1-11.*

LaMarche et al. (1984) hypothesized that recent trends of increasing ring widths in subalpine conifers may be due to the fertilizing effects of increased atmospheric CO2. Five tree- ring series from foxtail pine (Pinus balfouriana), lodgepole pine (P. murrayana), and western juniper (Juniperus occidentalis) collected in the Sierra Nevada, California, were analyzed to determine if the temporal and spatial patterns of recent growth were consistent with the hypothesized CO2-induced growth enhancement. Specifically, I address the following questions: (1) Can growth trends be explained solely in terms of climatic variation? (2) Are recent growth trends unusual with respect to long-term growth records? For three of the five sites, 20th-century growth variation can be adequately modeled as a function of climatic variation. For the remaining two sites, trends in the residuals from the growth/climate models indicate systematic underestimation of growth during the past decade that could be interpreted as either CO2 fertilization or as a response to extreme climatic events during the mid 1970s. At all five sites, current growth levels have been equalled or exceeded during some preindustrial periods. Taken together, these results do not indicate that CO2-induced growth enhancement is occurring among subalpine conifers in the Sierra Nevada. While the results presented here offer no support for the hypothesized CO2 fertilization effect, they do provide insights into the response of subalpine conifers to climatic variation. Response surfaces demonstrate that precipitation during previous winter and temperature during the current summer interact in controlling growth and that the response can be nonlinear. Although maximum growth rates occur under conditions of high winter precipitation and warm summers for all three species, substantial species-to-species variation occurs in the response to these two variables.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CALIFORNIA, FORESTS, PINE, RESPONSES, SIERRA NEVADA

781

Graybill, D.A., and S.B. Idso. 1993. Detecting the aerial fertilization effect of atmospheric co2 enrichment in tree-ring chronologies. *Global Biogeochemical Cycles 7(1):81-95.*

The growth-promoting effects of the historical increase in the air's CO2 content are not yet evident in tree-ring records where yearly biomass additions are apportioned among all plant parts. When almost all new biomass goes into cambial enlargement, however, a growth increase of 60% or more is observed over the past two centuries. As a result, calibration of tree-ring records of this nature with instrumental climate records may not be feasible because of such growth changes. However, climate signals prior to about the mid-19th century may yet be discovered by calibrating such tree-ring series with independently derived proxy climate records for those times.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH TRENDS, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, SOUR ORANGE TREES

782

Grayston, S.J., C.D. Campbell, J.L. Lutze, and R.M. Gifford. 1998. Impact of elevated CO2 on the metabolic diversity of microbial communities in N-limited grass swards. *Plant and Soil 203(2):289-300.*

The impact of elevated atmospheric CO2 on qualitative and quantitative changes in rhizosphere carbon flow will have important consequences for nutrient cycling and storage in soil, through the effect on the activity, biomass size and composition of soil microbial communities. We hypothesized that microbial communities from the rhizosphere of Danthonia richardsonii, a native C3 Australian grass, growing at ambient and twice ambient CO2 and varying rates of low N application (20, 60, 180 kg N ha(-1)) will be different as a consequence of qualitative and quantitative change in rhizosphere carbon flow. We used the Biolog(TM) system to construct sole carbon source utilisation profiles of these communities from the rhizosphere of D. richardsonii. Biolog(TM) GN and MT plates, the latter to which more ecologically relevant root exudate carbon sources were added, were used to characterise the communities. Microbial communities from the rhizosphere of D. richardsonii grown for four years at twice ambient CO2 had significantly greater utilisation of all carbon sources except those with a low C:N ratio (neutral and acidic amino acids, amides, N-heterocycles, long chain aliphatic acids) than communities from plants grown at ambient CO2. This indicates a change in microbial community composition suggesting that under elevated CO2 compounds with a higher C:N ratio were exuded. Enumeration of microorganisms, using

plate counts, indicated that there was a preferential stimulation of fungal growth at elevated CO2 and confirmed that bacterial metabolic activity (C utilisation rates), not population size (counts), were stimulated by additional C flow at elevated CO2. Nitrogen was an additional rate-limiting factor for microbial growth in soil and had a significant impact on the microbial response to elevated CO2. Microbial populations were higher in the rhizosphere of plants receiving the highest N application, but the communities receiving the lowest N application were most active. These results have important implications for carbon turnover and storage in soils where changes in soil microbial community structure and stimulation of the activity of microorganisms which prefer to grow on rhizodeposits may lead to a decrease in the composition of organic matter and result in an accumulation of soil carbon.

KEYWORDS: ATMOSPHERIC CO2, C SOURCE UTILIZATION, CARBON-SOURCE UTILIZATION, DIOXIDE, ENRICHMENT, GROWTH, NITROGEN, PLANT-RESPONSES, RHIZOSPHERE, SOIL

783

Greaves, A.J., and J.G. Buwalda. 1996. Observations of diurnal decline of photosynthetic gas exchange in kiwifruit and the effect of external CO2 concentration. *New Zealand Journal of Crop and Horticultural Science 24(4):361-369.*

The prevalence of diurnal decline of photosynthesis in field- grown kiwifruit (Actinidia deliciosa (A. Chev.) C.F. Liang et A.R. Ferguson var. deliciosa 'Hayward') and the effects of elevated CO2 concentration during decline were studied. During the seasonal period from soon after fruit set to harvest, marked diurnal reductions of photosynthesis rate were found that could not be correlated with levels of photosynthetically active radiation (PAR), temperature, and transpiration. Declines of photosynthesis were observed only on clear days characterised by benign environmental conditions other than sustained irradiance at saturating or near saturating levels. Elevation of CO2 concentration to 200 mu mol/mol above ambient during photosynthesis decline overcame the decline effect, allowing photosynthesis to track irradiance levels throughout the day. Possible mechanisms generating the diurnal decline and the alleviation by elevation of CO2 concentration are discussed.

KEYWORDS: ACTINIDIA-DELICIOSA VINES, C-3 PLANTS, CAPACITY, DEPRESSION, FIELD, GROWTH, LEAVES, RADIATION

784

Greer, D.H., W.A. Laing, and B.D. Campbell. 1995. Photosynthetic responses of 13 pasture species to elevated co2 and temperature. *Australian Journal of Plant Physiology 22(5):713-722.*

Thirteen common pasture species, (eleven C-3 and two C-4), were grown in controlled environments at 12/7, 18/13 and 28/23 degrees C and at 350 and 700 ppm CO2 to evaluate the effects of elevated CO2 on their photosynthetic responses. Photosynthesis was measured at the growth temperatures and at both 350 and 700 ppm CO2. In C-3 species, short-term (within minutes) increases in CO2 had the greatest effect on photosynthesis, with an average of 50-60% higher rates in plants exposed to 700 ppm CO2 at each temperature. However, there was a continuum of response between the C-3 species whereas C-4 species were unaffected by short-term changes in CO2 There was also a long-term (4-8 weeks) response to high CO2, with an average of about 40-50% higher rates of photosynthesis, with some response by C-4 species. Both short- and long-term responses were negatively correlated with the photosynthetic rate of each species at 350 ppm CO2 and all species were less efficient at converting photosynthate to dry matter at elevated CO2. These data show clearly that photosynthesis of these cool temperate pasture species can respond to elevated CO2, especially at low temperatures. This will have consequences for predicting the potential effects of climate change, accompanied by rising CO2, on pasture ecosystems.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENVIRONMENTS, GROWTH, PERENNIAL RYEGRASS, PRODUCTIVITY, RESPIRATION, SOURCE-SINK RELATIONS, WHITE CLOVER, YIELD

785

Gregor, H.D. 1992. The potential role of temperate forests as sinks for co2 - examples from the german environmental-policy against global warming. *Water, Air, and Soil Pollution 64(1-2):197-212.*

Among industrialized nations Germany ranks fourth in CO2 emissions. Most of these originate from the use of fossil fuels. Based on reports of a parliamentary study commission, established in 1987, and other expert groups in Germany this article adresses possible environmental effects of increasing atmospheric CO2, the sink potential of temperate forests and the influence of forest damage on this potential. A strategy for a 25 to 30% or 250 to 300 X 10(6) t yr-1 CO2 emissions reduction by 2005 (which Germany has itself committed to) is described in which measures to enhance C sequestration by forests play an important role. Expansion of forest area, a further increase of C storage by appropriate management and the restoration and protection of forest health impaired by air pollution would result in an additional storage of 17 to 20 x 10(6) t yr-1 of CO2, equaling 6 to 8% of the reduction target.

786

Gregory, K.M. 1996. Are paleoclimate estimates biased by foliar physiognomic responses to increased atmospheric CO2? *Palaeogeography Palaeoclimatology Palaeoecology 124(1-2):39-51.*

Physiognomic analysis of fossil angiosperm leaves has provided an important quantitative database of Tertiary terrestrial paleoclimate. However, atmospheric CO2 level, a critical control on plant growth, may have been higher in the Tertiary. It is thus crucial to investigate whether elevated CO2 affects leaf physiognomy. In this study, leaves were collected from white oak (Quercus alba L.) seedlings grown in open-top growth chambers at Oak Ridge National Laboratory. The only physiognomic change noted is an increase in length to width ratio with increasing CO2. In the literature, leaf size has been observed to increase, decrease or remain unchanged for woody C-3 species grown in elevated CO2. Typically, one sees more variation due to microsite or phenotype than due to CO2 level. By applying these observed physiognomic trends to two fossil floras, it is argued that estimates of mean annual temperature and growing season precipitation may be biased on the order of 1 degrees C and 20 cm, respectively. These are relatively small effects, as the values are similar to the standard errors of the regression models used to estimate paleoclimate. The lack of data, the variability of response to CO2 associated with microsite and phenotype, and the question of whether observed short-term trends with elevated CO2 are sustained make it impossible to propose a correction factor. Adequate sample size and sampling of several sites are the best way to attempt to compensate for CO2 effects on a given fossil flora until response to CO2 is better understood.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, LEAF ANATOMY, LEAVES, LIRIODENDRON-TULIPIFERA L, NORTH-AMERICA, SEEDLINGS, TREE GROWTH, WATER-USE

787

Gregory, P.J., J.A. Palta, and G.R. Batts. 1996. Root systems and root:mass ratio - Carbon allocation under current and projected atmospheric conditions in arable crops. *Plant and Soil 187(2):221-228.*

Roots of annual crop plants are a major sink for carbon particularly during early, vegetative growth when up to one- half of all assimilated carbon may be translocated belowground. Flowering marks a particularly important change in resource allocation, especially in determinate species, with considerably less allocation to roots and, depending on environmental conditions, there may be insufficient for maintenance. Studies with C-14 indicate the rapid transfer belowground of assimilates with typically 50% translocated in young cereal plants of which 50% is respired; exudation/rhizodeposition is generally <5% of the fixed carbon. Root:total plant mass decreases through the season and is affected by soil and atmospheric conditions. Limited water availability increased the allocation of C-13 to roots of wheat grown in columns so that at booting 0.38 of shoot C (ignoring shoot respiration) was belowground compared to 0.31 in well- watered plants. Elevated CO2 (700 mu mol CO2 mol(-1) air) increased the proportion of root:total mass by 55% compared with normal concentration, while increasing the air temperature by a mean of 3 degrees C decreased the proportion from 0.093 in the cool treatment to 0.055 in the warm treatment.

KEYWORDS: CO2- ENRICHMENT, DUPLEX SOIL, FIELD CONDITIONS, GRAIN-SORGHUM, PLANT-RESPONSES, SHOOT GROWTH, SOWING DATE, VULGARE L CULTIVARS, WATER-USE, WINTER-WHEAT

788

Grieb, B., U. Gross, E. Pleschka, B. Arnholdtschmitt, and K.H. Neumann. 1994. Embryogenesis of photoautotrophic cell-cultures of daucus- carota L. *Plant Cell Tissue and Organ Culture 38(2-3):115-122.*

In this paper photoautotrophic carrot (Daucus carota L.) suspension cultures are described which are able to produce somatic embryos. The development of somatic embryos, however, requires a sucrose supplement. Although an elevation of the CO2 concentration up to 2.3% results in the same level of dry weight production as with sucrose in the medium, somatic embryos could not be observed. Results on the influence of sucrose on some aspects of the photosynthetic apparatus of cultured cells are discussed.

KEYWORDS: CARROT, EMBRYOS, PHOTOSYNTHESIS, SOMATIC EMBRYOGENESIS, STORAGE PROTEINS, SUSPENSION

789

Gries, C., B.A. Kimball, and S.B. Idso. 1993. Nutrient-uptake during the course of a year by sour orange trees growing in ambient and elevated atmospheric carbon- dioxide concentrations. *Journal of Plant Nutrition 16(1):129-147.*

During the third year of a long-term carbon dioxide (CO2) enrichment study, macro- and micro-nutrient concentrations in leaves and roots of sour orange trees were analyzed. Data for yearly courses of the macronutrients Ca, Mg, N, P, K, Na, and S and the micronutrients B, Cu, Fe, Mn, and Zn are presented. Significantly higher concentrations of N, K, Ca, and Mn were found in leaves of the control trees. The degree of difference varied seasonally: the greatest differences occured in summer, whereas essentially no differences were found in spring and winter.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITROGEN, PLANTS, RESPONSES, SEEDLINGS, YIELD

790

Griffin, K.L., J.T. Ball, and B.R. Strain. 1996. Direct and indirect effects of elevated CO2 on whole-shoot respiration in ponderosa pine seedlings. *Tree Physiology 16(1-2):33-41.*

We determined the short-term direct and longterm indirect effects of CO2 on apparent dark respiration (CO2 efflux in the dark) in ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings grown in 35 or 70 Pa CO2 partial pressure for 163 days in naturally lit, controlled-environment chambers. Two soil N treatments (7 and 107 ppm total N, low-N and high-N treatments, respectively) were imposed by watering half the plants every 2 weeks with 15/15/18 fertilizer (N,P,K) and the other half with demineralized water. Direct effects of ambient CO2 partial pressure on apparent dark respiration were measured during short-term manipulations (from minutes to hours) of the CO2 environment surrounding the aboveground portion of individual seedlings. Shea-term increases in the ambient CO2 partial pressure consistently resulted in significant decreases in CO2 efflux of seedling in all treatments. Efflux of CO2 decreased by 3 to 13% when measurement CO2 partial pressure was increased from 35 to 70 Pa, and by 8 to 46% over the entire measurement range from 0 to 100 Pa. No significant interactions between the indirect effects of growth CO2 partial pressure and the direct effects of the measurement CO2 partial pressure were found. Seedlings grown in the high-N treatment were significantly less sensitive to short-term changes in CO2 partial pressures than seedlings grown in the low-N treatment. Apparent respiration tended to decrease in seedlings grown in elevated CO2, but the decrease was not significant. Nitrogen had a large effect on CO2 efflux, increasing apparent respiration more than twofold on both a leaf area and a leaf or shoot mass basis. Both the direct and indirect effects of elevated CO2 were correlated with change's in the C/N ratio. A model of cumulative CO2 efflux for a 160-day period demonstrated that, despite a 49% increase in total plant biomass, seedlings grown in the high-N + high-CO2 treatment lost only 2% more carbon than seedlings grown in the high-N + low-CO2 treatment, suggesting increased carbon use efficiency in plants grown in elevated CO2. We conclude that small changes in instantaneous CO2 efflux, such as those observed in ponderosa pine seedlings, could scale to large changes in carbon sequestration.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEMS, GROWTH, LEAVES, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, TREES

791

Griffin, K.L., M.A. Bashkin, R.B. Thomas, and B.R. Strain. 1997. Interactive effects of soil nitrogen and atmospheric carbon dioxide on root/rhizosphere carbon dioxide efflux from loblolly and ponderosa pine seedlings. *Plant and Soil 190(1):11-18.*

We measured CO2 efflux from intact root/rhizosphere systems of 155 day old loblolly (Pinus taeda L.) and ponderosa (Pinus ponderosa Dougl, ex Laws.) pine seedlings in order to study the effects of elevated atmospheric CO2 on the below-ground carbon balance of coniferous tree seedlings. Seedlings were grown in sterilized sand culture, watered daily with either 1, 3.5 or 7 mM NH4+, and maintained in an atmosphere of either 35 or 70 Pa CO2. Carbon dioxide efflux (mu mol CO2 plant(-1) s(-1)) from the root/rhizosphere system of both species significantly increased when seedlings were grown in elevated CO2, primarily due to large increases in root mass. Specific CO2 efflux (mu mol CO2 g root(-1) s(-1)) responded to CO2 only under conditions of adequate soil nitrogen availability (3.5 mM). Under these conditions, CO2 efflux rates from loblolly pine increased 70% from 0.0089 to 0.0151 mu mol g(-1) s(-1) with elevated CO2 while ponderosa pine responded with a 59% decrease, from 0.0187 to 0.0077 mu mol g(-1) s(-1). Although below ground CO2 efflux from seedlings grown in either sub- optimal (I mM) or supra-optimal (7 mM) nitrogen availability did not respond to CO2, there was a significant nitrogen treatment effect. Seedlings grown in supra-optimal soil nitrogen had significantly increased specific CO2 efflux rates, and significantly lower total biomass compared to either of the other two nitrogen treatments. These results indicate that carbon losses from the root/rhizosphere systems are responsive to environmental

resource availability, that the magnitude and direction of these responses are species dependent, and may lead to significantly different effects on whole plant carbon balance of these two forest tree species.

KEYWORDS: ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, FEEDBACK, GROWTH, PLANT, RESPONSES, RHIZOSPHERE, ROOT RESPIRATION, TAEDA L SEEDLINGS

792

Griffin, K.L., and Y.Q. Luo. 1999. Sensitivity and acclimation of Glycine max (L.) Merr. leaf gas exchange to CO2 partial pressure. *Environmental and Experimental Botany 42(2):141-153.*

Theoretical studies suggest that partitioning leaf photosynthetic responses to CO2 partial pressures into two components, sensitivity and acclimation, facilitates both scaling-up photosynthetic responses and predicting global terrestrial carbon influx. Here, we experimentally examine these two components by growing soybean (Glycine max) in two CO2 partial pressures, 35 and 70 Pa, and making a suite of ecophysiological measurements on expanding and fully expanded leaves. These CO2 treatments resulted in a variety of acclimation responses, including changes in net photosynthetic rate and capacity, stomatal conductance, transpiration, and respiration. These responses were strongly dependent on leaf age. Despite the wide variety of acclimation responses, the experimentally derived photosynthetic sensitivity did not vary with CO2 treatments or leaf age. In addition, the photosynthetic sensitivity to ambient CO2 partial pressure was consistent with the sensitivity to intercellular CO2 partial pressure, indicating little effect of stomatal conductance on photosynthetic sensitivity. This study supports the theoretical conclusion that photosynthetic sensitivity is independent of growth environment and leaf age, as well as photosynthetic acclimation, even though the latter varies with both environmental and developmental factors. Accordingly, photosynthetic sensitivity may be directly extrapolated from leaf to globe to predict the increment in terrestrial carbon influx stimulated by the yearly increase in atmospheric CO2, whereas the acclimation component must be used to adjust the overall global estimate. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, CONDUCTANCE, ELEVATED CO2, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC ACCLIMATION, TEMPERATURE, WATER-STRESS

793

Griffin, K.L., P.D. Ross, D.A. Sims, Y. Luo, J.R. Seemann, C.A. Fox, and J.T. Ball. 1996. EcoCELLs: Tools for mesocosm scale measurements of gas exchange. *Plant, Cell and Environment 19(10):1210-1221.*

We describe the use of a unique plant growth facility, which has as its centerpiece four 'EcoCELLs', or 5x7 m mesocosms designed as open-flow, mass-balance systems for the measurement of carbon, water and trace gas fluxes. This system is unique in that it was conceived specifically to bridge the gap between measurement scales during long-term experiments examining the function and development of model ecosystems. There are several advantages to using EcoCELLs, including (i) the same theory of operation as leaf level gas exchange systems, but with continuous operation at a much larger scale; (ii) the ability to independently evaluate canopy-level and ecosystem models; (iii) simultaneous manipulation of environmental factors and measurement of system-level responses, and (iv) maximum access to, and manipulation of, a large rooting volume. In addition to discussing the theory, construction and relative merits of EcoCELLs, we describe the calibration and use of the EcoCELLs during a 'proof of concept' experiment, This experiment involved growing soybeans under two ambient CO2 concentrations (similar to 360 and 710 mu mol mol(-1)). During this experiment, we asked 'How accurate is the simplest model that can be used to scale from leaf-level to canopy-level responses?' in order to illustrate the utility of the EcoCELLs in validating canopy-scale models.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, BRANCH BAG, CLIMATE CHANGE, ELEVATED CO2, FIELD, OPEN-TOP CHAMBERS, PLANT-RESPONSES, TRACE GASES, TUSSOCK TUNDRA

794

Griffin, K.L., and J.R. Seemann. 1996. Plants, CO2 and photosynthesis in the 21st century. *Chemistry & Biology 3(4):245-254.*

Human activity in the last 200 years has led to a marked increase in the level of CO2 in the atmosphere. Plants sense increases in CO2 levels and initially respond with an increase in photosynthetic rate, which may then slow as the plant adapts. This increase in photosynthetic rate may account in part for the 'disappearance' of an estimated 1.8 gigatons of carbon per year.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE CHANGE, ELEVATED CO2, GAS-EXCHANGE, LONG-TERM EXPOSURE, METABOLITE LEVELS, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, TUSSOCK TUNDRA

795

Griffin, K.L., D.A. Sims, and J.R. Seemann. 1999. Altered night-time CO2 concentration affects the growth, physiology and biochemistry of soybean. *Plant, Cell and Environment 22(1):91-99.*

Soybean plants (Glycine max (L.) Merr. c. v. Williams) were grown in CO2 controlled, natural-light growth chambers under one of four atmospheric CO2 concentrations ([CO2]): (1) 250 mu mol mol(-1) 24 h d(-1) [250/250]; (2) 1000 mu mol mol(-1) 24 h d(-1) [1000/1000]; (3) 250 mu mol mol(-1) during daylight hours and 1000 mmol mol(-1) during nighttime hours [250/1000] or (4) 1000 mu mol mol(-1) during daylight hours and 250 mmol mol(-1) during night-time hours [1000/250]. During the vegetative growth phase few physiological differences were observed between plants exposed to a constant 24 h [CO2] (250/250 and 1000/1000) and those that were switched to a higher or lower [CO2] at night (250/1000 and 1000/250), suggesting that the primary physiological responses of plants to growth in elevated [CO2] is apparently a response to daytime [CO2] only. However, by the end of the reproductive growth phase, major differences were observed. Plants grown in the 1000/250 regime, when compared with those in the 1000/1000 regime, had significantly more leaf area and leaf mass, 27% more total plant dry mass, but only 18% of the fruit mass. After 12 weeks of growth these plants also had 19% higher respiration rates and 32% lower photosynthetic rates than the 1000/1000 plants. As a result the ratio of carbon gain to carbon loss was reduced significantly in the plants exposed to the reduced night-time [CO2]. Plants grown in the opposite switching environment, 250/1000 versus 250/250, showed no major differences in biomass accumulation or allocation with the exception of a significant increase in the amount of leaf mass per unit area. Physiologically, those plants exposed to elevated night-time [CO2] had 21% lower respiration rates, 14% lower photosynthetic rates and a significant increase in the ratio of carbon gain to carbon loss, again when compared with the 250/250 plants. Biochemical differences also were found. Ribulose-1,5-bisphosphate carboxylase/ oxygenase concentrations decreased in the 250/1000 treatment compared with the 250/250 plants, and phosphoenolpyruvate carboxylase activity decreased in the 1000/250 compared with the 1000/1000 plants. Glucose, fructose and to a lesser extent sucrose concentrations also were reduced in the 1000/250 treatment compared with the 1000/1000 plants. These results

indicate that experimental protocols that do not maintain elevated CO2 levels 24 h d(-1) can have significant effects on plant biomass, carbon allocation and physiology, at least for fast-growing annual crop plants. Furthermore, the results suggest some plant processes other than photosynthesis are sensitive to [CO2] and under ecologically relevant conditions, such as high night-time [CO2], whole plant carbon balance can be affected.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, DARK RESPIRATION, ELEVATED ATMOSPHERIC CO2, HIGH AMBIENT CO2, MAX L MERR, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHOTOSYNTHESIS, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SHORT- TERM

796

Griffin, K.L., R.B. Thomas, and B.R. Strain. 1993. Effects of nitrogen supply and elevated carbon-dioxide on construction cost in leaves of pinus-taeda (L) seedlings. *Oecologia 95(4):575-580.*

Seedlings of loblolly pine (Pinus taeda L.) were grown under varying conditions of soil nitrogen and atmospheric carbon dioxide availability to investigate the interactive effects of these resources on the energetic requirements for leaf growth. Increasing the ambient CO2 partial pressure from 35 to 65 Pa increased seedling growth only when soil nitrogen was high. Biomass increased by 55% and photosynthesis increased by 13% after 100 days of CO2 enrichment. Leaves from seedlings grown in high soil nitrogen were 7.0% more expensive on a g glucose g-1 dry mass basis to produce than those grown in low nitrogen, while elevated CO2 decreased leaf cost by 3.5%. Nitrogen and CO2 availability had an interactive effect on leaf construction cost expressed on an area basis, reflecting source-sink interactions. When both resources were abundant, leaf construction cost on an area basis was relatively high (81.8 +/- 3.0 g glucose m-2) compared to leaves from high nitrogen, low CO2 seedlings (56.3 +/- 3.0 g glucose m-2) and low nitrogen, low CO2 seedlings (67.1 +/- 2.7 g glucose m-2). Leaf construction cost appears to respond to alterations in the utilization of photoassimilates mediated by resource availability.

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, CHLOROPHYLL CONTENT, GROWTH, LONG-TERM EXPOSURE, MAINTENANCE RESPIRATION, PHOTOSYNTHETIC INHIBITION, RESPONSES, WATER

797

Griffin, K.L., W.E. Winner, and B.R. Strain. 1995. Growth and dry-matter partitioning in loblolly and ponderosa pine-seedlings in response to carbon and nitrogen availability. *New Phytologist 129(4):547-556.*

We grew loblolly pine (Pinus taeda L.) and ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings in a factorial experiment with two CO2 partial pressures (35 and 70 Pa) and two nitrogen treatments (1.0 and 3.5 mM NH4+) for one growing season in a 'common garden' experiment designed to examine the extent that dry matter and nitrogen accumulation and partitioning are environmentally controlled. Ponderosa pine seedlings grown in 35 Pa CO2 and 3.5 mM NH4+ showed symptoms of nitrogen toxicity, characterized by greatly reduced growth, and moderately reduced total plant N. With the exception of this treatment combination, there were no significant differences between species in total plant dry matter or total plant nitrogen, suggesting that responses of growth to environmental conditions were stronger than heritable responses. There were however large differences in dry matter and N partitioning between the two species. Increases in leaf mass were largest in loblolly pine, whilst ponderosa pine tended to have higher root:shoot (R:S) ratios. R:S ratio of loblolly increased in response to C availability and decreased in response to N availability, whilst R: S ratio of ponderosa pine was much less responsive to resource availability. Total plant N varied with N supply, and N partitioning was related to plant growth and carbon partitioning. Carbon and N were interactive, such that an increase in the accumulation of either resource was always accompanied by an increase in the other. Over several seasons the different patterns of resource acquisition and biomass allocation that we observed in a uniform environment could potentially result in different growth rates at most resource levels. In the first season, contrary to our expectations, heritable differences in growth rate did not appear.

KEYWORDS: ATMOSPHERIC CO2, DIFFERENT IRRADIANCE LEVELS, DIOXIDE, ECOSYSTEMS, ENRICHMENT, FORESTS, LIQUIDAMBAR- STYRACIFLUA, NITRATE, TAEDA SEEDLINGS, WATER-STRESS

798

Griffin, K.L., W.E. Winner, and B.R. Strain. 1996. Construction cost of loblolly and ponderosa pine leaves grown with varying carbon and nitrogen availability. *Plant, Cell and Environment 19(6):729-739.*

We grew loblolly and ponderosa pine seedlings in a factorial experiment with two CO2 partial pressures (35 and 70 Pa), and two nitrogen treatments (1 . 0 and 3 . 5 mol m(-3) NH4+), for one growing season to examine the effects of carbon and nitrogen availability on leaf construction cost, Growth in elevated CO2 reduced leaf nitrogen concentrations by 17 to 40%, and increased C:N by 22 to 68%. Elevated N availability increased leaf N concentrations and decreased C:N, Non-structural carbohydrates increased in high-CO2-grown loblolly seedlings, except in fascicles from low N, and in ponderosa primary and fascicle leaves grown in high N, In loblolly, increases in starch were nearly 2-fold greater than the increases in soluble sugars, In ponderosa, only the soluble sugars were affected by CO2. Leaf construction cost (g glucose g(-1) dm) varied by 9 . 3% across all treatments, All of the variation in loblolly leaf construction cost could be explained by changes in non-structural carbohydrates. A model of the response of construction cost to changes in the mass of different biochemical fractions suggests that the remainder of the variation in ponderosa, not explained by non-structural carbohydrates, is probably attributable to changes in lignin, phenolic or protein concentrations.

KEYWORDS: ALLOCATION, BIOMASS, DIOXIDE, ENERGY, NUTRIENTS, PLANTS, SEEDLINGS, TAEDA

799

Griffiths, B.S., K. Ritz, N. Ebblewhite, and G. Dobson. 1999. Soil microbial community structure: Effects of substrate loading rates. *Soil Biology and Biochemistry 31(1):145-153.*

A fuller understanding of the interactions which affect rhizosphere microbial community structure requires experimental manipulation of the individual components of that interaction (e.g. amount and composition of exudate, soil moisture and soil nutrient status). We describe an experiment where a synthetic root exudate was applied continuously to a soil held at constant water potential. The solution contained compounds characteristic of root exudates (fructose, glucose, sucrose, succinic acid, malic acid, arginine, serine and cysteine), which were added at a range of concentrations. After 14 d of such substrate addition, a central portion of soil, known to be influenced by the added substrate, was removed for analysis. Microbial community structure of this central core was determined by the broad-scale measurements; community DNA hybridisation and %G + C profiling, and phospholipid-fatty acid analysis (PLFA). The trend was that microbial community structure changed consistently as substrate loading increased, and that fungi dominated over bacteria at high substrate loading rates. The DNA and the PLFA analyses both indicated that there was a coherent gradient of changes with increased substrate loading. This may have arisen as a consequence of the competitive ability of soil microorganisms being

dependent on the quantity of available substrate. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: BACTERIOPLANKTON, BIOMASS, CARBON, DNA HYBRIDIZATION, ELEVATED ATMOSPHERIC CO2, FATTY-ACIDS, GLUCOSE, MASS- SPECTROMETRY, PROFILES, RHIZOSPHERE

800

Griffiths, B.S., K. Ritz, N. Ebblewhite, E. Paterson, and K. Killham. 1998. Ryegrass rhizosphere microbial community structure under elevated carbon dioxide concentrations, with observations on wheat rhizosphere. *Soil Biology and Biochemistry 30(3):315-321.*

The structure of microbial communities in the rhizospheres of ryegrass and wheat, growing at an elevated atmospheric CO2 concentration, was investigated using broad-scale DNA techniques. Community DNA hybridisation and %G + C base profiling by thermal denaturation assess changes at the whole microbial community level. DNA analysis of the rhizosphere of ryegrass grown in soil microcosms for 28 or 42 d, showed only minor differences between plants grown at 450 or 720 mu l CO2 l(-1). In a second experiment with ryegrass, 5 of 10 replicate microcosms were pulse labelled with (CO2)-C-14 and 5 simultaneously sampled for DNA analysis. Carbon partitioning below ground showed changes due to the elevated CO2, notably an increased proportion of fi?ted carbon in non-microbial biomass residue in the rhizosphere. There was again no effect of elevated CO2 on rhizosphere microbial community structure. Community DNA hybridisation indicated that the rhizosphere communities under ambient and elevated CO2 were 86% similar (unlikely to be a biologically relevant change), with indistinguishable %G + C profiles. Wheat was grown to maturity (129 d) in a different soil microcosm design, and rhizosphere microbial communities from plants grown at 350 and 700 mu l CO2 l(-1) were identical according to the DNA analyses. In these experiments rhizosphere microbial community structure at the broad scale was unaffected by the interactions occurring below ground as a result of elevated concentrations of CO2. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, DNA HYBRIDIZATION, ENRICHMENT, FEEDBACK, GROWTH, HYBRIDIZATION TECHNIQUE, POPULATIONS, RESPONSES, ROOTS, SOIL

801

Grime, J.P., K. Thompson, R. Hunt, J.G. Hodgson, J.H.C. Cornelissen, I.H. Rorison, G.A.F. Hendry, T.W. Ashenden, A.P. Askew, S.R. Band, R.E. Booth, C.C. Bossard, B.D. Campbell, J.E.L. Cooper, A.W. Davison, P.L. Gupta, W. Hall, D.W. Hand, M.A. Hannah, S.H. Hillier, D.J. Hodkinson, A. Jalili, Z. Liu, J.M.L. Mackey, N. Matthews, M.A. Mowforth, A.M. Neal, R.J. Reader, K. Reiling, W. RossFraser, R.E. Spencer, F. Sutton, D.E. Tasker, P.C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos 79(2):259-281.*

Standardised procedures have been used to measure 67 traits in 43 common plants of the British flora. This paper provides an interpretation of the most consistent patterns in the resulting matrix by means of correlation, ordination and classification analyses. Only a weak coupling was observed between attributes of the regenerative and established phases of the life history. However, within each phase, attributes were strongly aggregated into sets and a high proportion of the variation between species coincided with a single axis. Attributes of the established phase displayed remarkably consistent trends, with a strong 'Axis 1' being identified by three different multivariate methods. There was a marked correlation between foliar concentrations of N, P, K, Ca and Mg, high concentrations of which coincided with the capacity for rapid growth in productive conditions and an inability to sustain yield under limiting supplies of nutrients. A diverse array of other traits, less immediately involving mineral nutrients, were also entrained in Axis 1; these included life history, root and shoot foraging, the morphology, longevity, tensile strength and palatability of leaves, and the decomposition rate of leaf litter. This pattern occurred in both monocotyledons and dicotyledons and appeared to reflect a tradeoff between attributes conferring an ability for high rates of resource acquisition in productive habitats and those responsible for retention of resource capital in unproductive conditions. The second axis of variation evident in the established phase was related to phylogeny and distinguished between monocotyledons and dicotyledons on the basis of a diverse set of traits including genome size, cell size, root and shoot foraging characteristics and vascular tissues. A third axis was detected in which ephemerals and perennials were separated by differences in attributes such as breeding system, leaf decomposition rate and a set of traits reflecting the small stature of many short-lived plants. In the regenerative phase, the leading axis was clearly related to the widely recognised tradeoff between seed size and seed number and was consistent with current understanding of seed banks, and with modern theories explaining species coexistence in terms of complementary responses to temporal and spatial variation in vegetation gap dynamics. The data provide strong evidence of functional integration between evolutionary specialisations in root and shoot and support Donald's unified theory of competitive ability. The data are not consistent with theories of functional types based upon evolutionary tradeoffs in allocation between root and shoot. We suggest that the evidence assembled here and elsewhere in the current literature points to the existence of primary functional types, including those recognised by Ramenskii and Grime. These functional types can be reconciled with the individuality of plant ecologies in the field and provide an effective basis For interpretation and prediction at various scales from the plant community to regional floras. There are particular opportunities for prediction of successional trajectories, the role of herbivores in vegetation succession and the response of vegetation to eutrophication and extreme climatic events. It is also suggested that aspects of this investigation may provide a Darwinian underpinning for Odum's theory of ecosystem maturation.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, COMPETITION, ECOLOGICAL STRATEGIES, GERMINATION CHARACTERISTICS, LIFE-HISTORY STRATEGIES, LOCAL FLORA, RELATIVE GROWTH-RATE, SUCCESSION, VEGETATION

802

Grimm, A.G., and J. Fuhrer. 1992. The response of spring wheat (triticum-aestivum L) to ozone at higher elevations .1. Measurement of ozone and carbon-dioxide fluxes in open-top field chambers. *New Phytologist 121(2):201-210.*

The flux of O3 was determined in open-top chambers (OTC) used to investigate its effect on spring wheat (Triticum aestivum L., cv. Albis) in 1989 and 1990. The experimental site was located at 900 m above sea level at Zimmerwald, near Bern (Switzerland). The aims were to evaluate the use of OTCs for O3 flux measurements under field conditions, to assess the role of stomata in controlling the O3 fluxes, and to establish a quantitative relationship between radiation-weighted O3 concentrations and O3 flux. Measurements were carried out from full expansion of flag leaves until the onset of senescence. Ozone flux was determined by mass balance using the concentrations of O3 measured at the inlet and outlet of the OTC. The CO2 exchange rate was corrected for soil-borne CO2 and used as a reference. Measurements of temperature, photosynthetically active radiation (PAR), saturated water vapour pressure deficit (SVPD), and boundary layer conductance were used to describe the microclimate inside OTCs. In the warmer microclimate in 1989, the plant canopy was characterized by a smaller leaf area index (LAI) than in 1990, while the fluxes of O3 and CO2 during daytime were generally larger in 1989. The diurnal patterns of

fluxes of O3 and CO2 in OTCs supplied with unfiltered air were similar. It is estimated that O3 absorption via the stomata contributed 50-70 % of its total flux. Identical relationships between leaf conductance for O3 measured by porometry and leaf conductance calculated from O3 flux were found in both years, but measured leaf conductance during daytime was generally smaller in 1990 than in 1989. The results indicate that stomatal conductance largely controlled O3 flux, and that the canopy structure has an influence on the overall conductance of the canopy. Different linear functions were obtained for the relationship between radiation-weighted O3 concentration and O3 flux, using data from OTCs supplied with either charcoal-filtered air, unfiltered air or unfiltered air enriched with O3 (two levels). These relationships form the basis for the calculation of mean O3 fluxes which can be used as an exposure index in the exposure-response analysis.

KEYWORDS: ABIES L KARST, BARLEY, CROP YIELD, DEPOSITION, GAS-EXCHANGE, INJURY, PHOTOSYNTHESIS, RESISTANCES, SITCHENSIS BONG CARR, TRANSPIRATION

803

Grimmer, C., T. Bachfischer, and E. Komor. 1999. Carbohydrate partitioning into starch in leaves of Ricinus communis L-grown under elevated CO2 is controlled by sucrose. *Plant, Cell and Environment 22(10):1275-1280.*

Ricinus communis plants were grown. under normal (350 ppm) and elevated (700 ppm) CO2 atmosphere and the growth and carbohydrate status of leaf 2 (first leaf above the pair of primary leaves) was studied. Elevated carbon dioxide stimulated the growth of leaves 1.7-fold. The glucose and fructose concentrations exhibited the same diurnal rhythm under both growth conditions. The sucrose concentrations stayed relatively constant and at 700 ppm were one-third higher than at 350 ppm. The starch content increased steadily during the day and disappeared overnight at 350 ppm CO2, but remained partially in plants at 700 ppm CO2, Consequently at 700 ppm CO2, the leaves accumulated starch continuously over their life time, The rate of starch synthesis was correlated to the activity of ADP- glucose pyrophosphorylase, which was related to the sucrose concentration in the leaf, It is concluded that sucrose controls the expression of ADP-glucose pyrophosphorylase, leading to a shift of carbohydrate partitioning into starch when more sucrose is produced than consumed or exported, a situation which is especially pertinent at elevated CO2, These results show that the previously experimentally observed transscriptional regulation of starch synthesis by sucrose occurs in vivo in the daily life of a leaf.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CARBON DIOXIDE, GENES, PLANTS, POTATO, TUBERS

804

Grimmer, C., and E. Komor. 1999. Assimilate export by leaves of Ricinus communis L. growing under normal and elevated carbon dioxide concentrations: the same rate during the day, a different rate at night. *Planta 209(3):275-281.*

Castor bean (Ricinus communis L.) plants were grown for 5-7 weeks in a controlled environment at 350 mu l l(-1) or 700 mu l l(-1) CO2. Carbon assimilation, assimilate deposition, dark respiration and assimilate mobilization were measured in leaves 2, 3 and 4 (counted from the base of the plant), and a balance sheet of carbon input and export was elaborated for both CO2 concentrations. Carbon dioxide assimilation was nearly constant over the illumination period, with only a slight depression occurring at the end of the day in mature source leaves, not in young source leaves, Assimilation was ca. 40% higher at 700 mu l l(-1) than at 350 mu l l(-1) CO2. The source leaves increased steadily in weight per unit area during the first 3 weeks, more at 700 mu l l(-1) than at 350 mu l l(-1) CO2. On top of an irreversible weight increase, there was a large gain in dry weight during the day, which was reversed during the night. This reversible weight gain was constant over the life time of the leaf and ca. 80% higher at 700 mu l l(-1) than at 350 yl l(-1). Most of it was due to carbohydrates. The carbon content (as a percentage) was not altered by the CO2 treatment. Respiration was 25% higher in high-CO2 plants when based on leaf area, but the same when based on dry weight. The rate of carbon export via the phloem was the same during the daytime in plants grown at 350 mu l l(-1) and 700 mu l l(-1) CO2. During the night the low-CO2 plants had only 50% of the daytime export rate, in contrast to the high-CO2 plants which maintained the high export rate. It was concluded that the phloem loading system is saturated during the daytime in both CO2 regimes, whereas during the night the assimilate supply is reduced in plants in the normal CO2 concentration. Two-thirds of the carbon exported from the leaves was permanently incorporated as plant dry matter in the residual plant parts. This "assimilation efficiency" was the same for both CO2 regimes. It is speculated that under 350 mu l l(-1) CO2 the growing Ricinus plant operates at sink limitation during the day and at source limitation during the night.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, GROWTH, PHOTOSYNTHESIS, PLANTS, STARCH, SUCROSE

805

Grobbelaar, N., W.M. Chou, and T.C. Huang. 1992. Effect of co2, o2, dcmu, fccp, and dl-glyceraldehyde on the nitrogenase activity of synechococcus rf-1. *Botanical Bulletin of Academia Sinica 33(2):167-174.*

Elevated atmospheric CO2 concentrations drastically inhibit nitrogenase activity of the unicellular Synechococcus RF-1 but stimulate photosynthetic CO2 assimilation. The inhibitory effect on nitrogenase activity is stronger in the light than in the dark. During three hours, 1% CO2 in air can reduce nitrogenase activity in the light by about 50% compared to that in unenriched air. The inhibitory effect of elevated CO2 concentrations on nitrogenase activity persists for many hours after the organism has been returned to air not enriched with CO2. The nitrogenase activity of heterocystous cyanobacteria, generally, does not appear to be affected by 5% CO2 in the air. DCMU strongly enhanced nitrogenase activity and inhibited the assimilation of CO2 by Synechococcus RF-1 in the light, and elevated atmospheric O2 concentrations reduced the nitrogenase activity, especially in the dark. DL-glyceraldehyde at a concentration of 19.4 mM strongly inhibited nitrogenase activity, dark respiration, and photosynthesis. FCCP had no effect on dark respiration but depressed nitrogenase activity and photosynthesis of Synechococcus RF-1. The inhibitory effect of FCCP on nitrogenase activity was stronger in the dark than in the light.

KEYWORDS: BLUE GREEN ALGA, DINITROGEN, LIGHT, PHOTOSYNTHESIS, RHYTHM

806

Grodzinski, B. 1992. Plant nutrition and growth-regulation by co2 enrichment. *BioScience 42(7):517-525.*

KEYWORDS: ABSCISIC- ACID, ACCLIMATION, ATMOSPHERIC CO2, CARBONIC-ANHYDRASE, CARBOXYLASE, ETHYLENE, EXCHANGE, PHOTOSYNTHESIS, STOMATAL DENSITY, WHOLE PLANT

807

Grodzinski, B., J.R. Jiao, and E.D. Leonardos. 1998. Estimating photosynthesis and concurrent export rates in C-3 and C-4 species at ambient and elevated CO2. *Plant Physiology 117(1):207-215.*

The ability of 21 C-3 and C-4 monocot and dicot species to rapidly export newly fixed C in the light at both ambient and enriched CO2 levels was compared. Photosynthesis and concurrent export rates were estimated during isotopic equilibrium of the transport sugars using a steady-state (CO2)-C-14-labeling procedure. At ambient CO2 photosynthesis and export rates for C-3 species were 5 to 15 and 1 to 10 mu mol C m(-2) s(-1), respectively, and 20 to 30 and 15 to 22 mu mol C m(-2) s(-1), respectively, for C-4 species. A linear regression plot of export on photosynthesis rate of all species had a correlation coefficient of 0.87. When concurrent export was expressed as a percentage of photosynthesis, several C-3 dicots that produced transport sugars other than Suc had high efflux rates relative to photosynthesis, comparable to those of C-4 species. At high CO2 photosynthetic and export rates were only slightly altered in C, species, and photosynthesis increased but export rates did not in all C(3)species. The C-3 species that had high efflux rates relative to photosynthesis at ambient CO2 exported at rates comparable to those of C-4 species on both an absolute basis and as a percentage of photosynthesis. At ambient CO2 there were strong linear relationships between photosynthesis, sugar synthesis, and concurrent export. However, at high CO2 the relationships between photosynthesis and export rate and between sugar synthesis and export rate were not as strong because sugars and starch were accumulated.

KEYWORDS: HIGHER-PLANTS, LEAF, LEAVES, SALVIA-SPLENDENS, STARCH, STEADY-STATE PHOTOSYNTHESIS, SUCROSE, TEMPERATURE

808

Grodzinski, B., L. Woodrow, E.D. Leonardos, M. Dixon, and M.J. Tsujita. UNKNOWN YEAR. Plant responses to short- and long-term exposures to high carbon dioxide levels in closed environments. *Natural and Artificial Ecosystems :203-211.*

When higher plants are exposed to elevated levels of CO2 for both short- and long-term periods photosynthetic C-gain and photoassimilate export from leaves are generally increased. Water use efficiency is increased on a leaf area basis. During long-term exposures, photosynthesis rates on leaf and whole plant bases are altered in a species specific manner. The most common pattern in C-3 plants is an enhanced rate of whole plant photosynthesis in a well irradiated canopy. Nevertheless, in some herbaceous species prolonged exposure to high CO2 results in remobilization of nitrogenous reserves (i.e., leaf protein degradation) and reduced rates of mature leaf photosynthesis when assayed at ambient CO2 and O-2 levels. Both short- and long-term exposures to those CO2 levels (i.e., 100 to 2,000 mu l.l(-1)) which modify photosynthesis and export, also modify both endogenous ethylene gas (C2H4) release, and substrate, 1- aminocyclopropane-1-carboxylic acid (ACC), saturated C2H4 release rates from irradiated leaves. Photosynthetically active canopy leaves contribute most of the C2H4 released from the canopy. Prolonged growth at high CO2 results in a persistent increase in the rate of endogenous C2H4 release from leaves which can, only in part, be attributed to the increase of the endogenous pools of C2H4 pathway intermediates (e.g., methionine, M-ACC, and ACC). The capacity for increasing the rate of C2H4 release in response to short-term exposures to varying CO2 levels does not decline after prolonged growth at high CO2. When leaves, whole plants, and model canopies of tomato plants are exposed to exogenous C2H4 a reduction in the rate of photosynthesis can, in each case, be attributed to the classical effects of C2H4 on plant development and morphology. The effect of C2H4 on CO2 gas exchange of plant canopies is shown to be dependent on the canopy leaf area index.

KEYWORDS: INCOMPLETE, ACCLIMATION, ATMOSPHERIC CO2, ETHYLENE RELEASE, GAS-EXCHANGE, LEAVES, LYCOPERSICON-ESCULENTUM MILL, PHOTOSYNTHESIS, TOMATO, XANTHIUM-STRUMARIUM L, ZEA-MAYS

809

Groninger, J.W., K.H. Johnsen, J.R. Seiler, R.E. Will, D.S. Ellsworth, and C.A. Maier. 1999. Elevated carbon dioxide in the atmosphere - What might it mean for loblolly pine plantation forestry? *Journal of Forestry 97(7):4-10.*

Research with loblolly pine suggests that projected increases iii atmospheric CO2 concentration will accelerate early growth and could result in shouter rotation length, reduced time until first commercial thinning, higher optimal planting density, and possibly higher maximum stocking level in managed stands. We discuss some of the physiological processes and stand dynamics that underlie these changes, as well as silvicultural strategies that may serve to ensure sustainability of intensively managed forest systems in the face of increasing CO2 and possible climate change.

KEYWORDS: CO2 CONCENTRATIONS, GAS-EXCHANGE, GROWTH, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC CAPACITY, ROOT RESTRICTION, SEEDLINGS, STOMATAL CONDUCTANCE, TAEDA TREES, WATER

810

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1995. Effects of elevated co2, water-stress, and nitrogen level on competitive interactions of simulated loblolly-pine and sweetgum stands. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(7):1077-1083.*

Loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) were grown in mixed stands and in monocultures at 2.54 X 2.54 cm spacing in controlled-environment chambers. Treatments consisted of present (ambient) and projected future (ambient + 400 ppm) carbon dioxide (CO2) concentrations, drought-stressed, and well-watered conditions, and low (20 kg N/ha) and high (474 kg N/ha) nitrogen application rates. After two accelerated growing cycles, total biomass of both species was significantly greater under elevated CO2. No significant interactions between CO2 concentration and water availability, nitrogen availability, or stand type were observed. Competitive interactions between loblolly pine and sweetgum were strongly influenced by water availability, but not CO2 concentration. Assessment of species response to CO2 was dependent upon growth in monoculture or mixture. Under low water availability, data from monocultures suggested that sweetgum had a stronger growth response to elevated CO2 concentrations than loblolly pine. In contrast, results from mixed-species stands showed that the competitive status of loblolly pine and sweetgum did not change under the high CO2 concentration. These results underscore the value of growing co-occurring species in mixed stands under varying levels of multiple resources for the determination of relative performance under future environments.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FIELD, GROWTH, INTERFERENCE, LIQUIDAMBAR- STYRACIFLUA, PLANTS, RESPONSES, TAEDA SEEDLINGS

811

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1996. Effects of CO2 concentration and water availability on growth and gas exchange in greenhouse-grown miniature stands of Loblolly Pine and Red Maple. *Functional Ecology 10(6):708-716.*

1. The study assesses the effects of atmospheric CO2 concentration and water availability on stand development and photosynthetic characteristics of Loblolly Pine (Pinus taeda) and Red Maple (Acer rubrum). Miniature stands of these species were grown from seed in monoculture and in a 50:50 replacement mixture for two accelerated growing seasons. 2. Both species had greater biomass under the higher

levels of CO2 and water availability. Biomass of Loblolly Pine seedlings in mixed stands exceeded that in monocultures, while the opposite was true for Red Maple. No significant treatment interactions were detected for total biomass. Significant main effects for water and stand type were detected for stem height of Loblolly Pine. CO2, water and stand type interactions were observed for height of Red Maple. 3. Net photosynthetic rates were measured on miniature stand canopies and constituent seedlings from these stands. Both species exhibited higher photosynthetic rates under elevated CO2. However, expression of photosynthesis on a leaf mass or soil area basis affected conclusions regarding the role of water availability on stand-level response to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BEECH STANDS, ELEVATED CARBON-DIOXIDE, ENRICHMENT, INTERFERENCE INTERACTIONS, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, STRESS, TAEDA SEEDLINGS, TREE SEEDLINGS

812

Groninger, J.W., J.R. Seiler, S.M. Zedaker, and P.C. Berrang. 1996. Photosynthetic response of loblolly pine and sweetgum seedling stands to elevated carbon dioxide, water stress, and nitrogen level. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(1):95-102.*

Seedling stands of loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) were grown in monoculture or mixed stands for two growing cycles in controlled-environment chambers. Treatments consisted of ambient (408 ppm) and elevated (806 ppm) CO2 concentrations, water-stressed and well- watered conditions, and low (20 kg N/ha) and high (215 kg N/ha) nitrogen application rates. Photosynthesis rates were measured under ambient and elevated cuvette CO2 concentrations for both whole stands and individual seedlings from these stands. Significant interactions between CO2 and water suggested that elevated CO2 concentration compensated for low water availability in individually measured loblolly pine and in whole seedling stands regardless of stand type. Expressing photosynthesis on a soil area versus a leaf-mass basis influenced the photosynthetic rankings of the three stand types relative to one another. Net photosynthetic rates per unit leaf mass were 390 and 880% higher in individually measured seedlings than in whole monoculture stands for loblolly pine and sweetgum, respectively. Lower photosynthetic contributions from lower canopy leaves in whole seedling stands compared with the upper canopy leaves used in individual-seedling measurements were thought to be responsible for lower photosynthetic rates in seedling stands. These results suggest that photosynthetic response is influenced by canopy dynamics that are unaccounted for by individual-seedling measurements of photosynthesis. Differences in photosynthetic response between loblolly pine and sweetgum stands and individuals are thought to be largely due to species-specific differences in canopy light extinction characteristics.

KEYWORDS: CO2- ENRICHMENT, FORESTS, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR- STYRACIFLUA, RUBISCO, TAEDA SEEDLINGS

813

Gross, U., F. Gilles, L. Bender, P. Berghofer, and K.H. Neumann. 1993. The influence of sucrose and an elevated co2 concentration on photosynthesis of photoautotrophic peanut (arachis-hypogaea L) cell-cultures. *Plant Cell Tissue and Organ Culture 33(2):143-150.*

Using photoautotrophic cells of Arachis hypogaea (L.) growing at ambient CO2, it was shown that exogenous sucrose supplied to the liquid medium reduced (CO2)-C-14 fixation (supplied as NaH (CO3)-C-14) . This was mostly due to a reduced labelling in P-esters, and to a lesser extent, in the serine/glycine moiety. However, radioactivity in the neutral sugar fraction was increased upon supplement of exogenous sucrose. The reduced labelling of P-esters and serine/glycine agrees with a lower concentration and specific activity of Rubisco in the sucrose supplied treatments as compared to the control. Following a transfer into a sugar free nutrient medium the concentration and activity of Rubisco is increased. The concentration of PEPCase was not influenced by sucrose application, although its specific activity was increased. At elevated CO2 concentration (2.34% v/v) the Rubisco concentration and specific activity was at the same level as in the control (0.03% V/V CO2). However, the concentration and the specific activity of PEPCase was increased and dry weight increase was about 8-9-fold higher than at ambient CO2.

KEYWORDS: ENZYME, FLAGELLATE CHLOROGONIUM-ELONGATUM, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SUBUNITS

814

Grossman, S., T. Kartschall, B.A. Kimball, D.J. Hunsaker, R.L. LaMorte, R.L. Garcia, G.W. Wall, and P.J. Pinter. 1995. Simulated responses of energy and water fluxes to ambient atmosphere and free-air carbon dioxide enrichment in wheat. *Journal of Biogeography 22(4-5):601-609.*

Increased ambient carbon dioxide has been associated with CO2-induced stomatal closure which affects growth and evapotranspiration of crop canopies. This results in changes of the energy balance components of the soil-plant-atmosphere system. The agroecosystem wheat model DEMETER was linked to a soil-vegetation-atmosphere-transfer module which includes the energy balance of the crop canopy and the energy balance of the soil surface. Thus, it was possible to calculate evapotranspiration, canopy temperature and the changed ratio of sensible and latent heat fluxes in response to elevated atmospheric CO2 concentrations. The free-air carbon dioxide enrichment (FACE) technique provided a largely undisturbed regime for atmospheric exchange. During the FACE wheat experiment at Maricopa in 1992-93, the effects of elevated atmospheric CO2 concentrations on energy balance and evapotranspiration of the wheat canopy at about 350-370 mu mol/mol (control) and 550 mu mol/mol (FACE) were investigated. The recorded data were used for model validation. Diurnal trends of all energy balance components and the canopy temperature were simulated for FACE and control conditions using hourly weather data. Results were compared with the observed data on 16 March 1993. Simulated cumulative seasonal evapotranspiration was found in good accordance to the observed one. Consistent with observations, the simulations suggest that there was a small reduction in evapotranspiration of about 4%. Of course, with the observed increases in growth, there were even larger increases in water use efficiency.

KEYWORDS: TEMPERATURE

815

Grossman-Clarke, S., B.A. Kimball, D.J. Hunsaker, S.P. Long, R.L. Garcia, T. Kartschall, G.W. Wall, P.J. Printer, F. Wechsung, and R.L. LaMorte. 1999. Effects of elevated atmospheric CO2 on canopy transpiration in senescent spring wheat. *Agricultural and Forest Meteorology 93(2):95-109.*

The seasonal course of canopy transpiration and the diurnal courses of latent heat flux of a spring wheat crop were simulated for atmospheric CO2 concentrations of 370 and 550 mu mol mol(-1). The hourly weather data, soil parameters and the irrigation and fertilizer treatments of the Free-Air Carbon Dioxide Enrichment wheat experiment in Arizona (1992-1993) were used to drive the model. The simulation results were tested against field measurements with special emphasis on the period

between anthesis and maturity. A model integrating leaf photosynthesis and stomatal conductance was scaled to canopy level in order to be used in the wheat growth model. The simulated intercellular CO2 concentration, C-i, was determined from the ratio of C-i to the CO2 concentration at the leaf surface, C-s, the leaf-to-air specific humidity deficit and a possibly unfulfilled transpiration demand, After anthesis, the measured assimilation rates of the flag leaves decreased more rapidly than their stomatal conductances, leading to a rise in the C-i/C-s ratio. In order to describe this observation, an empirical model approach was developed which took into account the leaf nitrogen content for the calculation of the C-i/C-s ratio. Simulation results obtained with the new model version were in good agreement with the measurements. If changes in the C-i/C-s ratio in accordance with the decrease in leaf nitrogen content during leaf senescence were not considered in the model, simulations revealed an underestimation of the daily canopy transpiration of up to 20% and a decrease in simulated seasonal canopy transpiration by 10%. The measured reduction in the seasonal sum of canopy transpiration and soil evaporation owing to CO2 enrichment, in comparison, was only about 5%. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: AMBIENT ATMOSPHERE, C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, LEAF, LEAVES, MODEL, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, WATER-USE

816

Grotenhuis, T.P., and B. Bugbee. 1997. Super-optimal CO2 reduces seed yield but not vegetative growth in wheat. *Crop Science 37(4):1215-1222.*

Although terrestrial atmospheric CO2 levels will not reach 1000 mu mol mol(-1) (0.1%) for decades, CO2 levels in growth chambers and greenhouses routinely exceed that concentration. CO2 levels in life support systems in space can exceed 10 000 mu mol mol(-1)(1%). Numerous studies have examined CO2 effects up to 1000 mu mol mol(-1), but biochemical measurements indicate that the beneficial effects of CO2 can continue beyond this concentration. We studied the effects of near-optimal (approximate to 1200 mu mol mol(-1)) and super-optimal CO2 levels (2400 mu mol mol(-1)) on yield of two cultivars of hydroponically grown wheat (Triticum aestivum L.) in 12 trials in growth chambers. Increasing CO2 from sub-optimal to near- optimal (350-1200 mu mol mol(-1)) increased vegetative growth by 25% and seed yield by 15% in both cultivars. Yield increases were primarily the result of an increased number of heads per square meter. Further elevation of CO2 to 2500 mu mol mol(-1) reduced seed yield by 22% (P < 0.001) in cv. Veery-10 and by 15% (P < 0.001) in cv. USU-Apogee. Super-optimal CO2 did not decrease the number of heads per square meter, but reduced seeds per head by 10% and mass per seed by 11%. The toxic effect of CO2 was similar over a range of light levels from half to full sunlight. Subsequent trials revealed that super- optimal CO2 during the interval between 2 wk before and after anthesis mimicked the effect of constant super-optimal CO2. Furthermore, near-optimal CO2 during the same interval mimicked the effect of constant near-optimal CO2. Nutrient concentration of leaves and heads was not affected by CO2. These results suggest that super optimal CO2 inhibits some process that occurs near the time of seed set resulting in decreased seed set, seed mass, and yield.

KEYWORDS: CARBON DIOXIDE, EFFICIENCY, ENRICHMENT, ETHYLENE BIOSYNTHESIS, GAS-EXCHANGE, INTACT SUNFLOWER PLANTS, LEAVES, LIGHT, PHOTOSYNTHETIC ACCLIMATION, RESPIRATION

817

Grotenhuis, T., J. Reuveni, and B. Bugbee. UNKNOWN YEAR. Super-optimal CO2 reduces wheat yield in growth chamber and greenhouse environments. *Life Sciences: Life Support Systems Studies-I :1901-1904.*

Seven growth chamber trials (six replicate trials using 0.035, 0.12, and 0.25 % CO2 in air and one trial using 0.12, 0.80, and 2.0% CO2 in air) and three replicate greenhouse trials (0.035, 0.10, 0.18, 0.26, 0.50, and 1.0% CO2 in air) compare the effects of super-optimal CO2 on the seed yield, harvest index, and vegetative growth rate of wheat (Triticum aestivum L. cvs. USU-Apogee and Veery-10). Plants in the growth chamber trials were grown hydroponically under fluorescent lamps, while the greenhouse trials were grown under sunlight and high pressure sodium lamps and in soilless media. Plants in the greenhouse trials responded similarly to those in the growth chamber trials; maximum yields occurred near 0.10 and 0.12 % CO2 and decreased significantly thereafter. This research indicates that the toxic effects of elevated CO2 are not specific to only one environment and has important implications for the design of bio-regenerative life support systems in space, and for the future of terrestrial agriculture. (C) 1997 COSPAR. Published by Elsevier Science Ltd.

KEYWORDS: INCOMPLETE, ETHYLENE

818

Grulke, N.E., J.L. Hom, and S.W. Roberts. 1993. Physiological adjustment of 2 full-sib families of ponderosa pine to elevated co2. *Tree Physiology 12(4):391-401.*

Seeds from two full-sib families of ponderosa pine (Pinus ponderosa) with known differences in growth rates were germinated and grown in an ambient (350 mul l-1) or elevated (700 mul l-1) CO2 concentration. Gas exchange at both ambient and elevated CO2 concentrations was measured 1, 6,39, and 112 days after the seed coat was shed. Initial stimulation of CO2 exchange rate (CER) by elevated CO2 was large (> 100%). On Day 1, CER of seedlings grown in elevated CO2 and measured at ambient CO2 was significantly lower than the CER of seedlings grown and measured at ambient CO2, indicating physiological adjustment of the seedlings exposed to elevated CO2. Physiological acclimation to elevated CO2 was complete by Day 39 when there was no significant difference in CER between seedlings grown and measured at ambient CO2 and seedlings grown and measured at elevated CO2. After 4 months, the light response of seedlings in the two treatments was determined at both ambient and elevated CO2. Light compensation point, CER at light saturation, and apparent quantum efficiency of seedlings grown and measured at ambient CO2 were not significantly different from those of seedlings grown and measured at elevated CO2. With a short-term increase in CO2, CER at light saturation (5.16 +/- 0.52 versus 3.13 +/- 0.30 mumol CO2 m-2 s- 1) and apparent quantum efficiency (0.082 +/- 0.011 versus 0.045 +/- 0.003 mumol CO2 mumol-1 quanta) were significantly increased. Leaf C/N ratio was significantly increased in the elevated CO2 treatment. There were few significant differences between families for any response to elevated CO2. Under the experimental conditions, high growth rate was not correlated with a greater response to elevated CO2.

819

Grulke, N.E., G.H. Riechers, W.C. Oechel, U. Hjelm, and C. Jaeger. 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO2. *Oecologia 83(4):485-494.*

820

Gruters, U. 1999. On the role of wheat stem reserves when source-sink balance is disturbed by elevated CO2. *Journal of Applied Botany-Angewandte Botanik 73(1-2):55-62.*

Spring wheat (Triticum aestivum L. cv. Minaret) was exposed to 360 and 680 mu mol mol(-1) CO2 in open top chambers during the vegetation periods of 1994/1995. In 1994 fractionated harvests were carried out at weekly intervals from the onset of stem elongation,. At final harvest CO, enhanced aboveground biomass and yield by 49.7 and 43.2%, respectively. From all plant organs stem dry weights showed the largest increases under doubled CO2, whereas leaf-blade dry weights increased only slightly. Since stems are known as sites of intermediary carbohydrate-storage, carbohydrate composition was analysed in the internodes of the main stem. Carbohydrates were determined as fructans, sucrose and reducing sugars. CO2 stimulated the amounts per organ of all components, but fructans showed the largest increases. Fructan accumulation lasted about one week longer and remobilisation was faster under elevated CO2. The results are consistent with current knowledge, that temporary storage pools accomodate source photosynthate supply to sink demand and suggested a predominant role of the intermediary stem reserves, when source-sink relations are changed under elevated CO2. The contribution of the main stem reserves to the main stem yield was also enhanced by elevated CO2 (6.1-8.7% compared to 10.0-14.2%). In 1995 growth and yield increase due to elevated CO2 (50.6 and 53%) was comparable to 1994. A functional growth analysis of the stem dry weight was carried out in this year. There was only a slightly longer accumulation phase in response to elevated CO2. Combined stem reserves contributed 12-18% to the final grain yield thereby contradicting, the suggestions based on the results of the year 1994.

KEYWORDS: FRUCTAN ACCUMULATION, GROWTH, PLANTS, SPRING WHEAT, TEMPERATURE, YIELD

821

Guak, S., D.M. Olsyzk, L.H. Fuchigami, and D.T. Tingey. 1998. Effects of elevated CO2 and temperature on cold hardiness and spring bud burst and growth in Douglas-fir (Pseudotsuga menziesii). *Tree Physiology 18(10):671-679.*

We examined effects of elevated CO2 and temperature on cold hardiness and bud burst of Douglas-fir (Pseudotsuga menziesii (Mirb.) France) seedlings. Two-year-old seedlings were grown for 2.5 years in semi-closed, sunlit chambers at either ambient or elevated (ambient + approximate to 4 degrees C) air temperature in the presence of an ambient or elevated (ambient + approximate to 200 ppm) CO2 concentration. The elevated temperature treatment delayed needle cold hardening in the autumn and slowed dehardening in the spring. At maximum hardiness, trees in the elevated temperature treatment were less hardy by about 7 degrees C than trees in the ambient temperature treatment. In general, trees exposed to elevated CO2 were slightly less hardy during hardening and dehardening than trees exposed to ambient CO2. For trees in the elevated temperature treatments, date to 30% burst of branch terminal buds was advanced by about 6 and 15 days in the presence of elevated CO2 and ambient CO2, respectively. After bud burst started, however, the rate of increase in % bud burst was slower in the elevated temperature treatments than in the ambient temperature treatments. Time of bud burst was more synchronous and bud burst was completed within a shorter period in trees at ambient temperature (with and without elevated CO2) than in trees at elevated temperature. Exposure to elevated temperature reduced final % bud burst of both leader and branch terminal buds and reduced growth of the leader shoot. We conclude that climatic warming will influence the physiological processes of dormancy and cold hardiness development in Douglas-fir growing in the relatively mild temperate region of western Oregon, reducing bud burst and shoot growth.

KEYWORDS: BUDBURST, DORMANCY, FROST DAMAGE, PICEA-SITCHENSIS, PROBABILITY, RISK, TREES

822

Guehl, J.M., C. Picon, G. Aussenac, and P. Gross. 1994. Interactive effects of elevated co2 and soil drought on growth and transpiration efficiency and its determinants in 2 european forest tree species. *Tree Physiology 14(7-9):707-724.*

The responses of growth and transpiration efficiency (W = biomass accumulation/water consumption) to ambient and elevated atmospheric CO2 concentrations (350 and 700 mumol mol-1, respectively) were investigated under optimal nutrient supply in well-watered and in drought conditions in two temperate- forest tree species: Quercus petraea Liebl. and Pinus pinaster Ait. Under well-watered conditions, doubling the CO2 concentration for one growing season increased biomass growth by 138% in Q. petraea and by 63% in P. pinaster. In contrast, under drought conditions, elevated CO2 increased biomass growth by only 47% in Q. petraea and had no significant effect on biomass growth in P. pinaster. Transpiration efficiency was higher in Q. petraea than in P. pinaster in all treatments. This difference was linked (i) to lower carbon isotope discrimination (DELTA), and thus lower values of the intercellular/ambient CO2 concentration (c(i)/c(a)) ratio, in Q. petraea, (ii) to lower values of leaf mass ratio (LMR, leaf mass/whole plant mass), which we suggest was positively related to the proportion of daytime carbon fixation lost by respiration (PHI), in Q. petraea, and (iii) to slightly lower C concentrations in Q. petraea than in P. pinaster. The CO2- promoted increase in W was higher in Q. petraea (+80%) than in P. pinaster (+50%), and the difference was associated with a more pronounced decrease in PHI in response to elevated CO2 in Q. petraea than in P. pinaster, which could be linked with the N dilution effect observed in Q. petraea. Because PHI also directly affects growth, the CO2-induced enhancement of PHI in Q. petraea is a crucial determinant of the growth stimulation observed in this species. Leaf gas exchange regulation was not the only factor involved in the responses of growth and W to elevated CO2 and drought, other physiological processes that have crucial roles include carbon and N allocation and respiration.

823

Gunderson, C.A., R.J. Norby, and S.D. Wullschleger. 1993. Foliar gas-exchange responses of 2 deciduous hardwoods during 3 years of growth in elevated co2 - no loss of photosynthetic enhancement. *Plant, Cell and Environment 16(7):797-807.*

Responses of photosynthesis and stomatal conductance were monitored throughout a 3-year field exposure of Liriodendron tulipifera (yellow-poplar) and Quercus alba (white oak) to elevated concentrations of atmospheric CO2. Exposure to atmospheres enriched with +150 and +300 mumol mol-1 CO2 increased net photosynthesis by 12-144% over the course of the study. Net photosynthesis was consistently higher at +300 than at +150 mumol mol-1 CO2. The effect Of CO2 enrichment on stomatal conductance was limited, but instantaneous leaf-level water use efficiency increased significantly. No decrease in the responsiveness of photosynthesis to CO2 enrichment over time was detected, and the responses were consistent throughout the canopy and across successive growth flushes and seasons. The relationships between internal CO2 concentration and photosynthesis (e.g. photosynthetic capacity and carboxylation efficiency) were not altered by growth at elevated concentrations of CO2. No alteration in the timing of leaf senescence or abscission was detected, suggesting that the seasonal duration of effective gas-exchange was unaffected by CO2 treatment. These results are consistent with data previously reported for these species in controlled-environment studies, and suggest that leaf-level photosynthesis does not down-regulate in these species as a result of acclimation to CO2 enrichment in the field. This sustained enhancement of photosynthesis provides the opportunity for increased growth and carbon storage by trees as the atmospheric concentration of CO2 rises, but many additional factors interact in determining whole-plant and forest responses to global change.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHED ATMOSPHERES, LEAVES, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, SCIRPUS- OLNEYI, SEEDLINGS, TUSSOCK TUNDRA, WATER-USE

824

Gunderson, C.A., and S.D. Wullschleger. 1994. Photosynthetic acclimation in trees to rising atmospheric co2 - a broader perspective. *Photosynthesis Research 39(3):369-388.*

Analysis of leaf-level photosynthetic responses of 39 tree species grown in elevated concentrations of atmospheric CO2 indicated an average photosynthetic enhancement of 44% when measured at the growth [CO2]. When photosynthesis was measured at a common ambient [CO2], photosynthesis of plants grown at elevated [CO2] was reduced, on average, 21% relative to ambient-grown trees, but variability was high. The evidence linking photosynthetic acclimation in trees with changes at the biochemical level is examined, along with anatomical and morphological changes in trees that impact leaf- and canopy- level photosynthetic response to CO2 enrichment. Nutrient limitations and variations in sink strength appear to influence photosynthetic acclimation, but the evidence in trees for one predominant factor controlling acclimation is lacking. Regardless of the mechanisms that underlie photosynthetic acclimation, it is doubtful that this response will be complete. A new focus on adjustments to rising [CO2] at canopy, stand, and forest scales is needed to predict ecosystem response to a changing environment.

KEYWORDS: CASTANEA-SATIVA MILL, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, PLANT-RESPONSES, POPLAR CLONES, RADIATA D-DON, STOMATAL CONDUCTANCE, WATER-STRESS

825

Gunn, S., S.J. Bailey, and J.F. Farrar. 1999. Partitioning of dry mass and leaf area within plants of three species grown at elevated CO2. *Functional Ecology 13:3-11.*

1. We tested the hypothesis that the net partitioning of dry mass and dry mass:area relationships is unaltered when plants are grown at elevated atmospheric CO2 concentrations. 2. The total dry mass of Dactylis glomerata, Bellis perennis and Trifolium repens was higher for plants in 700 compared to 350 mu mol CO2 mol(-1) when grown hydroponically in controlled- environment cabinets. 3. Shoot:root ratios were higher and leaf area ratios and specific leaf areas lower in all species grown at elevated CO2. Leaf mass ratio was higher in plants of B. perennis and D. glomerata grown at elevated CO2. 4. Whilst these data suggest that CO2 alters the net partitioning of dry mass and dry mass:leaf area relationships, allometric comparisons of the components of dry mass and leaf area suggest at most a small effect of CO2. CO2 changed only two of a total of 12 allometric coefficients we calculated for the three species: v relating shoot to root dry mass was higher in D. glomerata, whilst v relating leaf area to total dry mass was lower in T. repens. 5. CO2 alone has very little effect on partitioning when the size of the plant is taken into account.

KEYWORDS: ALLOCATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, CROP RESPONSES, ENRICHMENT, MATTER, NITROGEN, RESPIRATION, ROOT, TEMPERATURE

826

GunthardtGoerg, M.S. 1997. Leaf and shoot formation of young spruce and beech exposed to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):335-341.*

Sixteen open-top chambers (divided into two halves each containing either calcareous or acidic soil) were supplied in four combinations with either 366 or 550 mu l CO2 L-1, and either 2.5 or 25 kg N ha-(1) y(-1) (ammonium nitrate by irrigation). The development of young spruce (Picea abies) and beech (Fagus sylvatica) trees planted in the chambers together with understory plants will be studied over four years. The presented data are preliminary results from the first year of this experiment and refer to 64 spruce and 64 beech trees from two different Swiss spruce and beech provenances; two trees each per soil type, sampled in July and September in each chamber. Specific current-year spruce nee die length (length/dry mass) was reduced by elevated CO2 due to an increase in dry mass. Beech specific leaf area was only temporarily reduced in July. Elevated CO2 induced an earlier autumnal leaf discoloration. Total current-year shoot length per spruce and total number of leaves per beech tree were not influenced by the first year treatment with elevated CO2. N deposition had no effect on these parameters, but soil type influenced spruce needle colour Spruce, in contrast to beech, may therefore profit from elevated CO2 (when other resources are unlimited) by increasing shoot and needle dry mass.

KEYWORDS: ACCLIMATION, GROWTH, PLANT-RESPONSES, PRODUCTIVITY, TREES

827

Guy, M., G. Granoth, and J. Gale. 1990. Cultivation of Lemna gibba under desert conditions .2. the effect of raised winter temperature, CO2 enrichment and shading on productivity. *Biomass 23(1):1-11.*

828

GwynnJones, D., J.A. Lee, and T.V. Callaghan. 1997. Effects of enhanced UV-B radiation and elevated carbon dioxide concentrations on a sub-Arctic forest heath ecosystem. *Plant Ecology 128(1-2):242-249.*

An experiment is described which studies the effects of enhanced UV-B radiation (simulating a 15% reduction in the Ozone layer) and elevated atmospheric concentrations of CO2 (600 ppm) on the dwarf shrub layer of a sub-arctic forest heath ecosystem at Abisko, North Sweden. The experimental treatments were first applied in 1993, and have covered most of the snow- free season (late May to early September) 1993-1995. Effects of the treatments on the four dwarf shrub species have been recorded largely using non-destructive measures (Vaccinium uliginosum, Vaccinium myrtillus - deciduous species and Vaccinium vitis-idaea and Empetrum hermaphroditum - evergreen species). Effects of the treatments on stem growth and leaf thickness have so far been small, although CO2 treatments initially stimulated stem extension in Vaccinium myrtillus 1993 and depressed growth in V. vitis idaea in 1994 and E. hermaphroditum during 1995. UV-B treatments stimulated fruit production in V. myrtillus in both 1994 and 1995, but there was no effect on reproductive phenology. There were also marked effects of UV-B treatments on insect herbivory in the deciduous dwarf shrubs; with leaf area loss being greater than the control in the UV-B treatment in V. myrtillus and less in V. uliginosum. The results point to the possibility of important effects of the treatments on physiological and chemical processes within the plants. The ecological results of such effects may not be immediately apparent, but may be far reaching, pointing to the need for long-term in situ experimentation in predicting the effects of these global change variables.

KEYWORDS: CO2, DWARF SHRUBS, GROWTH, PEA, PLANTS, RESPONSES, ULTRAVIOLET-RADIATION

829

Habash, D.Z., M.A.J. Parry, S. Parmar, M.J. Paul, S. Driscoll, J. Knight, J.C. Gray, and D.W. Lawlor. 1996. The regulation of

component processes of photosynthesis in transgenic tobacco with decreased phosphoribulokinase activity. *Photosynthesis Research 49(2):159-167.*

Tobacco plants (Nicotiana tabacum L.) transformed with an inverted cDNA encoding ribulose 5-phosphate kinase (phosphoribulokinase,PRK;EC 2.7.1.19) were employed to study the in vivo relationship between photosynthetic electron transport and the partitioning of electron transport products to major carbon metabolism sinks under conditions of elevated ATP concentrations and limited ribulose 1,5-bisphosphate (RuBP) regeneration. Simultaneous measurements of room temperature chlorophyll fluorescence and CO2 gas exchange were conducted on intact leaves. Under ambient CO2 concentrations and light intensities above those at which the plants were grown, transformants with only 5% of PRK activity showed 'down-regulation' of PS II activity and electron transport in response to a decrease in net carbon assimilation when compared to wild-type. This was manifested as a decline in the efficiency of PS II electron transport (Phi(PS II)), an increase in dissipation of excess absorbed light in the antennae of PS II and a decline in : total linear electron transport (J(1)), electron transport dedicated to carbon assimilation (J(A)) and electron transport allocated to photorespiration (J(L)). The transformants showed no alteration in the Rubisco specificity factor measured in vitro and calculated in vivo but had a relatively smaller ratio of RuBP oxygenation to carboxylation rates (v(o)/v(c)), due to a higher CO2 concentration at the carboxylation site (C-c). The relationship between Phi(PS II) and Phi(CO2) was similar in transformants and wild-type under photorespiratory conditions demonstrating no change in the intrinsic relationship between PS II function and carbon assimilation, however, a novel result of this study is that this similar relationship occurred at different values of quantum flux, J(1), J(A), J(L) and v(o)/v(c) in the transformant. For both wild-type and transformants, an assessment was made of the possible presence of a third major sink for electron transport products, beside RuBP oxygenation and carboxylation, the data provided no evidence for such a sink.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, DROUGHT STRESS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, NET CO2 ASSIMILATION, PHOTORESPIRATION, REDUCTION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO

830

Habash, D.Z., M.J. Paul, M.A.J. Parry, A.J. Keys, and D.W. Lawlor. 1995. Increased capacity for photosynthesis in wheat grown at elevated co2 - the relationship between electron-transport and carbon metabolism. *Planta 197(3):482-489.*

Spring wheat (Triticum aestivum L.) was grown under optimal nutrition for six weeks at 700 and 350 mu mol . mol(-1) CO2 and simultaneous measurements of photosystem-II (PSII) chlorophyll fluorescence and gas exchange were conducted on intact attached leaves. Plants grown at elevated CO2 had double the concentration of CO2 at the carboxylation site (C-c) despite a lowered stomatal (g(s)) and mesophyll (g(m)) conductance compared with ambient-grown plants. Plants grown at elevated CO2 had a higher relative quantum yield of PSII electron transport (Phi(PSII)) and a higher relative quantum yield of CO2 fixation (Phi CO2). The higher Phi(PSII) was due to a larger proportion of open PSII centres, estimated by the coefficient of photochemical quenching of fluorescence (q(p)), with no change in the efficiency of light harvesting and energy transduction by open PSII centres (F'(v)/F'(m)). Analysis of the relationship between Phi(PSII) and Phi(CO2) conducted under various CO2 and O-2 concentrations showed that the higher Phi(CO2) for a given Phi(PSII) in leaves developed under elevated CO2 was similar to that obtained in leaves upon a partial reduction in photorespiration. Calculation of the allocation of photosynthetic electron-transport products to CO2 and O-2 showed that for leaves developed in elevated CO2, there was an increase in both total linear electron flow and electron flow to CO2 and a decrease in electron flow to O-2. Plants developed under elevated CO, showed positive acclimation manifested by a higher Phi(CO2) when measured under ambient CO2 and higher assimilation rates in A/C-i curves. Initial and to tal activity of ribulose-1,5- bisphosphate carboxylase- oxygenase (Rubisco EC 4.1.1.39) measured in vitro increased by 16 and 15% respectively in leaves from plants grown in elevated CO2, which was in agreement with a 15% higher in vivo carboxylation efficiency. It is concluded that growth of spring wheat at elevated CO2 enhances photosynthesis due to a change in the balance of component processes manifested as an increased capacity for carbon fixation, total electron transport and Rubisco activity, and a concomitant partial reduction of photorespiration.

KEYWORDS: CARBOXYLASE, CHLOROPHYLL FLUORESCENCE, FIELD, GAS-EXCHANGE, LEAVES, PHYSIOLOGY, QUANTUM YIELD, STRESS

831

Hadley, P., G.R. Batts, R.H. Ellis, J.I.L. Morison, S. Pearson, and T.R. Wheeler. 1995. Temperature-gradient chambers for research on global environment change .2. a twin-wall tunnel system for low- stature, field-grown crops using a split heat-pump. *Plant, Cell and Environment 18(9):1055-1063.*

A temperature gradient chamber (TGC) is described which enables elevated CO2 concentrations and a dynamic temperature gradient to be imposed on field crops throughout their life cycle under standard husbandry. Air is circulated through two double-walled polyethylene-covered tunnels connected to a split heat pump system to give a near-linear temperature gradient along each tunnel, Solar energy gain along each tunnel and exchange with outer tunnel air flow contribute to the temperature gradient and also produce diurnal and seasonal temperature fluctuations corresponding to ambient conditions, Mean temperature gradients of between 3 and 5 degrees C have been recorded throughout the growing seasons of crops of lettuce, carrot, cauliflower and winter wheat, Elevated or present CO2 concentrations are maintained in each of two pairs of tunnels throughout the cropping season using pure CO2 injected through motorized needle valves. This system can realistically simulate aspects of the effects of projected future environmental change on crop growth, development and yield, and in particular the possible interaction of the effects of increased CO2 and temperature.

KEYWORDS: CO2

832

Hager, C., G. Wurth, and G.H. Kohlmaier. 1999. Biomass of forest stands under climatic change: a German case study with the Frankfurt biosphere model (FBM). *Tellus Series B-Chemical and Physical Meteorology 51(2):385-401.*

In this contribution, we perform a case study of the German forests. We couple the Frankfurt biosphere model (FBM) with a model of the age class development (AGEDYN). The coupled model is applied to simulate the temporal development of carbon pools in German forests under the influence of climate change taking into account changes in the age class structure. In the base case, the growth of forest stands is simulated using a temporally averaged climate dataset, being representative for the contemporary climate conditions. To assess the sensitivity of forest growth to changes in environmental conditions, the FBM is run in several scenarios. In these simulations the effects both of climate change and of the direct effect of increased levels of atmospheric CO2 on photosynthesis (CO2 fertilization) on forest growth are assessed. In another simulation run with the FBM both effects - climate change and CO2 fertilization are combined. In simulations under present day's

climate conditions a good agreement is gained between simulation results and statistical data of the present standing stock carbon density of Germany's forests. A pure climate change leads to a decrease of the annual increments as well as to the climax standing stocks. The negative effect of climate change alone is overcompensated by enhanced photosynthesis in the simulations with combined climate change and CO2 fertilization. In the transient case, the coupled model is used in two scenarios describing first a continuation of present day's climate conditions and second a transient climate change from present conditions (1990) to 2 x CO2 conditions in 2090. Here, the simulations indicate that changes in the forest's age class structure can have a stronger influence on the future carbon balance of the forests in the considered region than the combined effect of climate change and CO2 fertilization.

KEYWORDS: ATMOSPHERE, BOREAL FORESTS, CARBON DYNAMICS, CO2, EXCHANGE, GLOBAL VEGETATION, PRODUCTIVITY, RESPONSES, TERRESTRIAL ECOSYSTEMS

833

Hakala, K. 1998. Growth and yield potential of spring wheat in a simulated changed climate with increased CO2 and higher temperature. *European Journal of Agronomy 9(1):41-52.*

The effects of climatic change on the growth, yield and nitrogen content of spring wheat (Triticum aestivum L., cv. Polkka) were studied from 1992 to 1994. The crop was sown directly in the field, at a normal sowing density. Leaf canopies were exposed to CO2 concentrations of 700 mu l l(-1) and temperatures 3 degrees C higher than ambient throughout the growing season. CO2 concentrations were elevated in open-top chambers 3m in diameter. Temperatures were elevated in an automatically controlled greenhouse built over the experimental field. To simulate conditions predicted for a future warmer climate, the wheat crop was sown 2-3 weeks earlier in the elevated temperature (future warmer climate) than in the ambient temperature treatment (present climate). In the elevated temperature experiment, the average temperatures and development rates were not increased during the period from sowing to anthesis, but from anthesis to maturity, both temperatures and development rates were increased. The small increase in the development rate after anthesis at elevated temperatures in 1992 and 1994 did not affect the grain weight, but the considerable increase in development rate in 1993 was accompanied by a decrease in grain weight. CO2 enrichment had no effect on development rate. The total biomass at harvest was significantly higher in CO2 enrichment in both temperature treatments. Although the mean increase in grain yield was not significant, the yields tended to be higher in CO2 enrichment. The magnitude of the increase in biomass and grain yield in CO2 enrichment ranged from about 5 to 60%. The increase in yield was mainly attributed to an increase in the number of ear- bearing shoots m(-2). Seed number per main shoot and seed weight were in general not increased with CO2 enrichment unless these were exceptionally low in the ambient CO2 conditions (in 1993). The harvest index was decreased at elevated temperatures, but there was no significant effect of CO2 enrichment. There was a small (7%) but significant decrease in the nitrogen content of the grain in CO2 enrichment at ambient temperatures. (C) 1998 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, ENRICHMENT, FIELD, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES

834

Hakala, K., and T. Mela. 1996. The effects of prolonged exposure to elevated temperatures and elevated CO2 levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. *Agricultural and Food Science in Finland 5(3):285-298.*

Field-sown meadow fescue (Festuca pratensis, cv. Kalevi) stands were exposed to elevated temperatures (+3 degrees C) and elevated CO2 (700 ppm) levels in two experiments conducted in 1992-1993 (experiment 1) and in 1994-1995 (experiment 2). Total aboveground yield was, on average, 38% higher at elevated than at ambient temperatures. At ambient temperatures elevated CO2 increased the number of tillers by 63% in 1992, 24% in 1993, 90% in 1994 and 14% in 1995. At elevated temperatures, the increase in tiller number in elevated CO2 was seen only in the first growing seasons after sowing. The total yield in a growing season was about 10% higher in elevated CO2 in experiment 1. In experiment 2 the yield was more than 20% higher in elevated CO2 at elevated temperatures, whereas at ambient temperatures the rise in CO2 level had no effect on the yield; the root biomass, however, increased by more than 30%. In elevated CO2 at ambient temperatures the root biomass also increased in experiment 1, but at elevated temperatures there was no consistent change. The soluble carbohydrate content of above-ground biomass was 5-48% higher in elevated CO2 at most of the measuring times during the growing season, but the nitrogen content did not show a clear decrease. The reasons for the lack of a marked increase in biomass in elevated CO2 despite a 40-60% increase in photosynthesis are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, LOLIUM-PERENNE, NITROGEN, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, RESPONSES

835

Hakala, K., T. Mela, H. Laurila, and T. Kaukoranta. 1996. Arrangement of experiments for simulating the effects of elevated temperatures and elevated CO2 levels on field-sown crops in Finland. *Agricultural and Food Science in Finland 5(1):25-47.*

The experimental plants: spring wheat, winter wheat, spring barley, meadow fescue, potato, strawberry and black currant were sown or planted directly in the field, part of which was covered by an automatically controlled greenhouse to elevate the temperature by 3 degrees C. The temperature of the other part of the field (open field) was not elevated, but the field was covered with the same plastic film as the greenhouse to achieve radiation and rainfall conditions comparable to those in the greenhouse. To elevate the CO2 concentrations, four open top chambers (OTC) were built for the greenhouse, and four for the open field. Two of these, both in the greenhouse and in the open field, were supplied with pure CO2 to elevate their CO2 level to 700 ppm. The temperatures inside the greenhouse followed accurately the desired level. The relative humidity was somewhat higher in the greenhouse and in the OTC:s than in the open field, especially after the modifications in the ventilation of the greenhouse and in the OTC:s in 1994. Because the OTC:s were large (3 m in diameter), the temperatures inside them differed very little from the surrounding air temperature. The short-term variation in the CO2 concentrations in the OTC:s with elevated CO2 was, however, quite high. The control of the CO2 concentrations improved each year from 1992 to 1994, as the CO2 supplying system was modified. The effects of the experimental conditions on plant growth and phenology are discussed.

KEYWORDS: PHOTOSYNTHESIS, PLANTS

836

Hall, D.O., D.S. Ojima, W.J. Parton, and J.M.O. Scurlock. 1995. Response of temperate and tropical grasslands to CO2 and climate change. *Journal of Biogeography 22(2-3):537-547.*

Under a recent SCOPE collaborative project, longterm data from eleven tropical and temperate grassland sites were used (a) to validate the CENTURY model of plant-soil ecosystems and (b) to model climate

change and CO2 effects for thirty-one temperate and tropical grassland sites, representing seven ecoregions of the world. Model calibration and testing showed that soil carbon and nitrogen dynamics can be well simulated for the grassland biome worldwide, over a wide range of climate and soil types. The interannual response of above ground biomass and plant residue to variation in climate resulted in a good correspondence between simulated and observed dynamics on a monthly basis. These results are useful for analysis and description of grassland carbon dynamics, and as a reference point for testing predictions of net primary production (NPP) and biomass dynamics from levels of more physiologically based models. Prediction of plant and soil organic matter C and N dynamics requires knowledge of climate, soil texture, N inputs and fire and grazing patterns. CENTURY simulations of climate change and CO2 effects showed increased NPP for climate change alone, except in cold desert steppe regions, and CO2 increased production everywhere. Climate changes, predominantly a warming of these ecosystems, caused soil carbon to decrease overall, especially in cold desert and temperate steppes. Increased production due to elevated CO2 tended to ameliorate soil carbon losses and tropical savannas were actually soil carbon sinks. Climate change alone projected a carbon loss of 3-4 Pg after 50 years, and 1-2 Pg for the combined climate change and CO2 simulated effects. We analysed the dynamic response of some of the major CENTURY output parameters (e.g. NPP, soil organic matter, N mineralization and decomposition) for their sensitivity to climate change and increasing CO2 for one of the two general circulation models (GFHI scenario). This analysis was limited to a subset of five well-known study sites, representing five of the seven ecoregions.

KEYWORDS: BIOMASS, CARBON, CONIFEROUS FORESTS, DECOMPOSITION, DYNAMICS, MODEL, PRODUCTIVITY, SOIL

837

Hall, D.O., and J.M.O. Scurlock. 1991. Climate change and productivity of natural grasslands. *Annals of Botany 67:49-55.*

KEYWORDS: BIOSPHERE, CARBON, DYNAMICS, ELEVATED CO2, ESTUARINE MARSH, NITROGEN, PLANTS

838

Hall, F.G. 1999. Introduction to special section: BOREAS in 1999: Experiment and science overview. *Journal of Geophysical Research-Atmospheres 104(D22):27627-27639.*

The goal of BOREAS is to improve our understanding of the interactions between the boreal forest biome and the atmosphere in order to clarify their roles in global change. This overview briefly reviews the science background and motivations for the Boreal Ecosystem-Atmosphere Study (BOREAS). The findings of the 27 papers in this journal special issue are reviewed. Important scientific results of the project to date are summarized, and future research directions are identified.

KEYWORDS: ATMOSPHERE INTERACTIONS, BALANCE, CARBON DIOXIDE, CO2, FOREST, HIGH-LATITUDES, LAND-ATMOSPHERE, MODEL, NORTHERN, WATER

839

Hall, J.M., E. Paterson, and K. Killham. 1998. The effect of elevated CO2 concentration and soil pH on the relationship between plant growth and rhizosphere denitrification potential. *Global Change Biology 4(2):209-216.*

The effect of CO2 concentration on plant growth and the size of the rhizosphere denitrifier population was investigated for ryegrass grown at 3 different soil pH values (pH 4.3, 5.9 and 7.0). Soil microcosms were planted with ryegrass and maintained under constant growth conditions at either ambient (450ppm) or elevated (720ppm) CO2 concentration. At harvest, the rhizosphere soil was collected and subjected to a potential denitrification assay to provide an estimate of the size of the denitrifier population present. Ryegrass dry matter production varied across the pH range studied and contrary to other studies, elevated CO2 concentration did not consistently increase growth. Plant growth was reduced by approximate to 35% and 23% at pH 4.3 and pH 5.9, respectively, under elevated CO2 concentration. At pH 7.0, however, plant growth was increased by approximate to 45% under elevated CO2. Potential denitrification rates within the rhizosphere followed a similar pattern to plant growth in the different treatments, suggesting that plant growth and the size of denitrifier population within the rhizosphere are coupled. This study investigates the relationship between plant growth and rhizosphere denitrification potential, thereby providing an estimate of the size of the denitrifier population under increased CO2 concentration and soil pH.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FIELD, FLOW, LOLIUM-PERENNE, MICROBIAL BIOMASS, NITROGEN, PHOTOSYNTHESIS, RESPONSES, ROOTS

840

Halloy, S.R.P., and A.F. Mark. 1996. Comparative leaf morphology spectra of plant communities in New Zealand, the Andes and the European Alps. *Journal of the Royal Society of New Zealand 26(1):41-78.*

Leaf morphology of native vegetation tias often been interpreted as a sensitive indicator of environmental conditions, presumably as a result of natural selection. If environmental pressures act as a selective force on community leaf morphology, then we would expect a high degree of similarity in similar environments, regardless of biogeographic origin of the flora. A comparative study of full regional floras of alpine vascular plants was undertaken to test the sensitivity of leaf morphology to macro-environmental conditions. Five alpine sites and one lowland (control) site were selected in southern New Zealand spanning 1.5 degrees latitude and 2323 m. Three sites with equivalent alpine environments were selected in South America across a 60 degrees latitudinal and 4200 m altitudinal span with subtropical forest used as a control. A further alpine site from the European Alps was included as an outlier. Twenty leaf parameters were obtained for 2143 taxonomic entities x sites. Both the mean and the frequency distribution of leaf size and shape parameters were distinctive for each locality. Several morphological trends were found. Means of New Zealand contiguous low-alpine and high-alpine site pairs differed in. length -33%, width -14%, length/width -20%, leaf area -44%, entire margin -2% (variable), coriaceousness -18%, folded +22%, pubescence +40%. At higher elevations, leaves become smaller but rounder, considerably softer, are more often folded into crypts or similar structures and are more often pubescent. These changes corresponded to reductions of 2-3 degrees C in mean annual air temperature, c. 10% in mean minimum relative humidity and 7% in CO2 partial pressure. Despite the biogeographic and environmental differences, New Zealand and South American low-alpine sites were consistently similar in their morphological parameters and consistently different from high-alpine sites (except in Tierra del Fuego). High alpine sites were also consistently similar across the Pacific. Several parameters were found to have multimodal frequency distributions that were not significantly different in widely separate localities with different floras. The results suggest that plant community morphology is an emergent property, the magnitude of which is environmentally constrained.

KEYWORDS: ALPINE LIFE ZONE, ALTITUDINAL VARIATION, ANATOMY, CLIMATE, CONDUCTANCE, FLORA, FOSSILS, LATITUDINAL GRADIENT, RADIATION, SIZE

841

Ham, J.M., C.E. Owensby, and P.I. Coyne. 1993. Technique for measuring air-flow and carbon-dioxide flux in large, open-top chambers. *Journal of Environmental Quality 22(4):759-766.*

Open-Top Chambers (OTCs) are commonly used to evaluate the effect of CO2, O3, and other trace gases on vegetation. A study was conducted to develop and test a new technique for measuring forced air flow and net CO2 flux from OTCs. Experiments were performed with a 4.5-m diam. OTC that had a sealed floor and a specialized air delivery system. Air flow through the chamber was computed with the Bernoulli equation using measurements of the pressure differential between the air delivery ducts and the chamber interior. An independent measurement of air flow was made simultaneously to calibrate and verify the accuracy of the Bernoulli relationship. The CO2 flux density was calculated as the product of chamber air flow and the difference in CO2 concentration between the air entering and exhausting from the OTC (C(in) - C(out)). Accuracy of the system was evaluated by releasing CO2 within the OTC at known rates to emulate respiration from the field surface. Data were collected with OTCs at ambient and elevated CO2 (almost-equal-to 700 mumol mol-1). Results showed that the Bernoulli equation, with a flow coefficient of 0.7, accurately measured air flow in the OTC to within +/- 5% regardless of flow rate and air duct geometry. Experiments in ambient OTCs showed that CO2 flux density (mumol m-2 s-1), computed from 2-min averages of air flow and C(in) - C(out), was typically within +/- 10% of actual flux, provided that the exit air velocity at the top of the OTC was greater than 0.6 m s-1. Obtaining the same level of accuracy in CO2- enriched OTCs, however, required a critical exit velocity near 1.2 m s-1 to minimize the incursion of ambient air and prevent contamination of the exit gas sample. When flux data were integrated over time to estimate daily CO2 flux (mumol m-2 d- 1), actual and measured values agreed to within +/- 2% for both ambient and CO2-enriched chambers, suggesting that accurate measurements of daily net C exchange are possible with this technique.

KEYWORDS: CO2, EXCHANGE, FIELD CHAMBERS, WIND-TUNNEL

842

Ham, J.M., C.E. Owensby, P.I. Coyne, and D.J. Bremer. 1995. Fluxes of co2 and water-vapor from a prairie ecosystem exposed to ambient and elevated atmospheric co2. *Agricultural and Forest Meteorology 77(1-2):73-93.*

Increasing concentrations of atmospheric CO2 may alter the carbon and water relations of prairie ecosystems. A C-4- dominated tallgrass prairie near Manhattan, KS, was exposed to 2x ambient CO2 concentrations using 4.5 m-diameter open-top chambers. Whole-chamber net CO2 exchange (NCE) and evapotranspiration (ET) were continuously monitored in CO2- enriched and ambient (no enrichment) plots over a 34-d period encompassing the time of peak biomass in July and August, 1993. Soil-surface CO2 fluxes were measured with a portable surface chamber, and sap flow (water transport in xylem) in individual grass culms was monitored with heat balance techniques. Environmental measurements were used to determine the effect of CO2 on the surface energy balance and canopy resistances to vapor flux. In 1993, frequent rainfall kept soil water near field capacity and minimized plant water stress. Over the 34-d measurement period, average daily NCE (canopy photosynthesis - soil and canopy respiration) was 9.3 g CO2 m(-2) in the ambient treatment and 11.4 g CO2 m(-2) under CO2 enrichment. However, differences in NCE were caused mainly by delayed senescence in the CO2-enriched plots at the end of the growing season. At earlier stages of growth, elevated CO2 had no effect on NCE. Soil-surface CO2 fluxes typically ranged from 0.4 to 0.66 mg CO2 m(-2) s(-1), but were slightly greater in the CO2-enriched chambers. CO2 enrichment reduced daily ET by 22%, reduced sap flow by 18%, and increased canopy resistance to vapor flux by 24 s m(-1). Greater NCE and lower ET resulted in higher daytime water use efficiency (WUE) under CO2 enrichment vs. ambient (9.84 vs. 7.26 g CO2 kg(-1) H2O). However, record high precipitation during the 1993 season moderated the effect of WUE on plant growth, and elevated CO2 had no effect on peak aboveground biomass. CO2-induced stomatal closure also affected the energy balance of the surface by reducing latent heat flux (LE), thereby causing a consequent change in sensible heat flux (H). The daytime Bowen ratio (H/LE) for the study period was near zero for the ambient treatment and 0.21 under CO2 enrichment.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CROP, EXCHANGE, FLOW, RESPONSES

843

Hamerlynck, E.P., C.A. McAllister, A.K. Knapp, J.M. Ham, and C.E. Owensby. 1997. Photosynthetic gas exchange and water relation responses of three tallgrass prairie species to elevated carbon dioxide and moderate drought. *International Journal of Plant Science 158(5):608-616.*

Undisturbed tallgrass prairie was exposed to ambient and elevated (twice-ambient) levels of atmospheric CO, and experimental dry periods. Seasonal and diurnal midday leaf water potential (Psi(leaf)), net photosynthesis (A(net)), and stomatal conductance (g(s)) responses of three tallgrass prairie growth forms-a C-4 grass, Andropogon gerardii; a broad- leaved woody C, shrub, Symphiocarpos orbiculatus; and a C-3 perennial forb, Salvia pitcheri-were assessed. Psi(leaf) in A. gerardii and S, orbiculatus was higher under elevated CO2, regardless of soil moisture, while Psi(leaf) in S. pitcheri responded only to drought. Elevated CO2 always stimulated A(net) in the C-3 species, while A. gerardii A(net) increased only under dry conditions. However, A(net) under elevated CO2 in the C-3 species declined with drought but not in the C,grass, Under wet conditions, g(s) reduced in elevated CO2 for all species. During dry periods, g, at elevated CO, was sometimes higher than in ambient CO2. Our results support claims that elevated CO2 will stimulate tallgrass prairie productivity during dry periods and possibly reduce temporal and spatial variability in productivity in these grasslands.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, BIOMASS PRODUCTION, BOUTELOUA-GRACILIS, C-4 GRASS, GRASS ANDROPOGON-GERARDII, NITROGEN, PASCOPYRUM-SMITHII, SOIL MOISTURE, TOPOGRAPHIC POSITION

844

Hanba, Y.T., E. Wada, M. Osaki, and T. Nakamura. 1996. Growth and delta C-13 responses to increasing atmospheric carbon dioxide concentrations for several crop species. *Isotopes in Environmental and Health Studies 32(1):41-54.*

The responses of plant growth and carbon isotope discrimination (Delta) to elevated atmospheric CO2 concentrations for several crop species (lettuce: Lactuca sativa L.; corn: Zea mays L. var. P3540; wheat: Triticum aestivum L. var Haruyutaka; and soybean: Glycine max (L). Merr. var. Kitamusume) were investigated. Shoot relative growth rate was used to indicate plant growth, and delta(13)C value of leaf materials in corn (C4 species) was used to calculate Delta for C3 species. Plant growth was stimulated by enriched CO2, while Delta remained almost constant as CO2 concentration changed. Delta showed interspecific difference, and the plant species of larger Delta had larger relative growth rates. Relative growth rates of the plants of larger Delta were stimulated by CO2 enrichment more than those of the plants of smaller Delta. We propose that plant Delta could be a possible parameter to assess the interspecific difference of plant response to the increasing atmospheric CO2 concentrations.

KEYWORDS: CO2 CONCENTRATIONS, COOL-SEASON GRASSES,

ELEVATED CO2, ENVIRONMENTS, GAS-EXCHANGE, ISOTOPE DISCRIMINATION, PHOTOSYNTHESIS, PLANTS, SPRING WHEAT, WATER-USE EFFICIENCY

845

Hand, D.W., J.W. Wilson, and B. Acock. 1993. Effects of light and co2 on net photosynthetic rates of stands of aubergine and amaranthus. *Annals of Botany 71(3):209-216.*

KEYWORDS: CARBON DIOXIDE, CROP PHOTOSYNTHESIS, ENRICHMENT, ENVIRONMENT, PLANT GROWTH, RESPONSES

846

Handel, M.D., and J.S. Risbey. 1992. An annotated-bibliography on the greenhouse-effect and climate change. *Climatic Change 21(2):97-253.*

The literature on climate change from an enhanced greenhouse effect is large and growing rapidly. The problems considered are increasingly interdisciplinary. For these reasons many workers will find useful pointers to the literature in the fields interacting with, but outside of, their own. We present here an annotated bibliography on issues relating to changes in the concentrations of Earth's greenhouse gases. The areas covered include theory and numerical modelling of climate change; cycles involving carbon dioxide and other radiatively important trace gases; observations of climate change and the problems associated with those observations; paleoclimatology as it relates to previous changes in the greenhouse gases; the impacts on and interactions with managed and natural ecosystems from climate change; policy issues related to climate change and to the limitation of climate change; history of the study of the greenhouse effect; and some other causes of climate change. Selection of papers has been made to facilitate rapid introduction to most of the important issues and findings in an area. Over 600 articles, reports, and books are discussed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DOUBLED CO2 CLIMATE, EARTHS RADIATION BUDGET, GENERAL-CIRCULATION MODEL, GLOBAL CLIMATE, NORTH-ATLANTIC OCEAN, RISING SEA-LEVEL, SURFACE AIR-TEMPERATURE, TRACE GASES, VOSTOK ICE-CORE

847

Hanninen, H. 1995. Effects of climatic-change on trees from cool and temperate regions - an ecophysiological approach to modeling of bud burst phenology. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):183-199.*

A framework is presented for meddling bud burst phenology of trees from the cool and temperate regions. Three ecophysiological aspects affecting the timing of bud burst are considered: (i) effects of environmental factors on the rest status of the bud, (ii) effect of rest status on the ability for bud burst, and (iii) direct effect of air temperature on the rate of development towards bud burst. Any model for bud burst phenology can be presented within the framework with three submodels, each of them addressing one of the corresponding three ecophysiological aspects. A total of 96 hypothetical models were synthesized by combining submodels presented in the literature. The models were tested in two experiments with saplings of Pinus sylvestris L. growing in experimental chambers at their natural site in eastern Finland. In the first experiment, air temperature and (or) concentration of atmospheric CO2 was elevated. Elevation of the air temperature hastened bud burst, whereas elevation of the concentration of CO2 did not affect it. Several models accurately predicted the timing of bud burst for natural conditions but too early for bud burst at the elevated temperatures. This finding suggests that (i) the risk of a premature bud burst with subsequent frost damage, as a result of climatic warming, was overestimated in a recent simulation study, and (ii) bud burst observations in natural conditions alone are not sufficient for the testing of these mechanistic models. Several models did predict the timing of bud burst accurately for all treatments, but none of them obtained sufficiently strong support from the findings to stand out as superior or uniquely correct. In the second experiment a photoperiod submodel for rest break was tested by exposing the saplings to short-day conditions. The short-day treatment had only a minor effect on the timing of bud burst. These results demonstrated the importance of the concept of model realism: the accuracy of a model can be lost in new conditions (e.g., global warming), unless the model correctly addresses the essential ecophysiological aspects of the regulation of timing of bud burst.

KEYWORDS: BUDBURST, CORNUS-SERICEA L, DORMANCY RELEASE, DOUGLAS-FIR, FLUSHING TEMPERATURE, FROST DAMAGE, PHOTOPERIOD, PLANTS, SEEDLINGS, THERMAL TIME

848

Hanson, J.D., B.B. Baker, and R.M. Bourdon. 1993. Comparison of the effects of different climate change scenarios on rangeland livestock production. *Agricultural Systems 41(4):487-502.*

The effect of climate change on plant and livestock production in the Great Plains of North America is an important issue. The purpose of this study was to modify an existing rangeland ecosystem model and to simulate a cow/calf production system under different climate scenarios. The project required the capability of simulating rangeland livestock production under different ambient CO2 concentrations, temperatures and precipitation patterns. Climate change scenarios were created from three general circulation models (GCMs): GISS (Goddard Institute for Space Studies model), GFDL (Geophysical Fluid Dynamic Laboratory model), and UKMO (United Kingdom Meteorological Office model). Results from the GCMs were used to modify the climate record for a site in northeastern Colorado. Concomitantly, modifications were made to the SPUR model to help predict the effect of predicted climate change on selected variables of the range/livestock ecosystem. Simulation runs showed that predicted climate change will affect plant and animal production for rangelands. Changes in production were more closely related to changes in temperature and precipitation than to enhanced [CO2] alone. The effect of climate change on livestock production was very complex and results were dependent on the particular GCM scenario being simulated.

KEYWORDS: BIOMASS, MODEL

849

Hao, X.M., B.A. Hale, and D.P. Ormrod. 1997. The effects of ultraviolet-B radiation and carbon dioxide on growth and photosynthesis of tomato. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(2):213-219.*

Tomato (Lycopersicon esculentum Mill.) plants were exposed, in controlled environments with 2.7 Wi(m(2).day) background ultraviolet-B (UV-B) radiation from fluorescent and incandescent lamps, to ambient (380 mu L.L-1) or elevated (600 mu L.L-1) CO2 combined with a total of 7.2 or 13.1 kJ/(m(2).day) UV-B radiation to determine effects on growth and photosynthesis. Ten consecutive days of exposure to the higher level of UV-B significantly reduced total and stem dry weight, leaf area, and plant height compared with the lower level. Only leaf area and plant height were significantly reduced after 19 consecutive days of exposure. To investigate whether plants recover from UV-B damage, the UV-B exposures were halted for 3 days after 19 days of UV-B exposure and then restarted for a further 2 days. The largest reduction in plant growth was found after 3 days with no UV-B followed by 2 days of the higher level of UV-B. Plants did not recover from UV-B damage during

the 3 days with background UV-B. Significant CO(2)xUV-B interactions were detected on stem dry weight after 10 consecutive days of the higher level of UV-B and on total dry weight, leaf dry weight, stem dry weight, and plant height after 3 days with no UV-B followed by 2 days of the higher level of UV-B. The higher dose of enhanced UV-B resulted in more severe damage at 600 mu L.L-1 CO than at ambient CO2. The higher level of UV-B did not affect the leaf net photosynthesis rate on a leaf area basis, although this UV-B level may have inhibited tomato growth through reducing the photosynthetic area. UV-absorbing compounds in leaves in the highest UV-B radiation level for 19 days were greater than for leaves with the lower dose. These UV-absorbing compounds in the higher UV-B dose diminished more than in the lower dose plants during the 3 days without UV-B. The UV-absorbing compounds maintained by plants exposed to the highest level of UV-B radiation may have protected plants from UV-B damage, particularly between 10 and 19 consecutive days of exposure.

KEYWORDS: CO2, EXPOSURE, IRRADIATION, MUTANTS, N,N-DIMETHYLFORMAMIDE, OZONE, PLANTS, QUALITY, RICE, YIELD

850

Hao, Y.Y., and R.E. Brackett. 1993. Influence of modified atmosphere on growth of vegetable spoilage bacteria in media. *Journal of Food Protection 56(3):223-228.*

Six gas mixtures (CO2/O2/N2: 0/5/95, 0/10/90, 5/10/85, 5/20/75, 10/5/85, and 10/20/70) and air were used to investigate the effect of modified atmosphere (MA) on growth of four vegetable spoilage bacteria. In addition, we determined the ability of the MA which most inhibited spoilage bacteria to reduce spoilage in bell peppers inoculated with the respective bacteria. In general, MA did not significantly affect growth of the bacteria tested. Growth of Erwinia, Pseudomonas, Xanthomonas, and Pepper # 15 (a pectinolytic Pseudomonas) at 10 and 20-degrees-C was not significantly affected regardless of gas mixtures. At 5-degrees-C, growth of Erwinia, Xanthomonas, and Pepper # 15 was slightly reduced by some gas mixtures (CO2/O2/N2: 0/5/95, 0/10/90, and 10/5/85; 10/5/85; 0/5/95 and 10/5/85, respectively). Modified atmosphere containing 10% CO2, 5% O2, and 85% N2 did not reduce the ability of bacteria tested to grow at elevated concentrations of sodium chloride. In addition, this MA composition did not change the percentage of bell peppers spoiled by test bacteria inoculated. However, overall visual quality was enhanced by MA.

KEYWORDS: BACILLUS-CEREUS, CARBON DIOXIDE, CO2, MARKET QUALITY, MINIMALLY PROCESSED FRUITS, PSEUDOMONAS- FLUORESCENS, SHELF-LIFE, STORAGE LIFE, STORED BROCCOLI, ZUCCHINI SQUASH

851

Harley, P.C., R.B. Thomas, J.F. Reynolds, and B.R. Strain. 1992. Modeling photosynthesis of cotton grown in elevated co2. *Plant, Cell and Environment 15(3):271-282.*

Cotton plants were grown in CO2-controlled growth chambers in atmospheres of either 35 or 65 Pa CO2. A widely accepted model of C3 leaf photosynthesis was parameterized for leaves from both CO2 treatments using non-linear least squares regression techniques, but in order to achieve reasonable fits, it was necessary to include a phosphate limitation resulting from inadequate triose phosphate utilization. Despite the accumulation of large amounts of starch (> 50 g m-2) in the high CO2 plants, the photosynthetic characteristics of leaves in both treatments were similar, although the maximum rate of Rubisco activity (Vc(max)), estimated from A versus C(i) response curves measured at 29-degrees-C, was almost-equal-to 10% lower in leaves from plants grown in high CO2. The relationship between key model parameters and total leaf N was linear, the only difference between CO2 treatments being a slight reduction in the slope of the line relating Vc(max) to leaf N in plants grown at high CO2, Stomatal conductance of leaves of plants grown and measured at 65 Pa CO2 was approximately 32% lower than that of plants grown and measured at 35 Pa. Because photosynthetic capacity of leaves grown in high CO2 was only slightly less than that of leaves grown in 35Pa CO2, net photosynthesis measured at the growth CO2, light and temperature conditions was approximately 25% greater in leaves of plants grown in high CO2, despite the reduction in leaf conductance. Greater assimilation rate was one factor allowing plants grown in high CO2 to incorporate 30% more biomass during the first 36 d of growth.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, DEPENDENCE, ENRICHMENT, GAS-EXCHANGE, LEAVES, LIMITATIONS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SPECIFICITY, TEMPERATURE

852

Harrison, K., W. Broecker, and G. Bonani. 1993. A strategy for estimating the impact of co2 fertilization on soil carbon storage. *Global Biogeochemical Cycles 7(1):69-80.*

As soils are a likely candidate for the so-called missing carbon sink, we explore the possible impact of CO2 fertilization on the global humus inventory. For any given greening-induced enhancement of plant growth, the increase in soil carbon inventory will depend on the spectrum of turnover times with respect to oxidation. Here we develop estimates of carbon turnover rates based on soil radiocarbon measurements.

KEYWORDS: BOMB-PRODUCED C-14, DIOXIDE, DISTRIBUTIONS, DYNAMICS, ORGANIC-MATTER, RADIOCARBON, SIMULATIONS, TURNOVER, WORLD OCEAN MODEL, ZEALAND

853

Harrison, P.A., and R.E. Butterfield. 1996. Effects of climate change on Europe-wide winter wheat and sunflower productivity. *Climate Research 7(3):225-241.*

Spatially explicit crop models were developed from mechanistic principles to investigate the regional impacts of climate change. The approach highlights the spatial variability of crop responses to altered environmental conditions. The mechanistic nature of the models allows some confidence to be placed in the results that are produced under climate change scenarios. Two crop models have been constructed and applied across a large European region: EuroWheat (winter wheat) and EuroSunfl (sunflower). Model results were compared with observed phenology and yield across a variety of scales and found to capture the current spatial variability in wheat and sunflower productivity. Climate change scenarios from both equilibrium and transient general circulation model experiments were applied to each crop model. Wheat yields are predicted to increase throughout Europe for all climate change scenarios. Conversely, water-limited sunflower yields decrease in most regions and scenarios. More positive effects are predicted for winter wheat than sunflower due to a lower sensitivity to increased temperature and a higher sensitivity to elevated concentrations of CO2. The lowest yield increases for wheat and the largest yield decreases for sunflower are found in western Europe, whilst the most positive responses for both crops occur in central and eastern Europe. Predictions for southern Europe are highly sensitive both within the region and between the scenarios. The old generation of equilibrium climate change scenarios gives the worst predictions (lowest yield increases or highest yield decreases). More beneficial responses are observed for the new generation of transient scenarios for both wheat and sunflower. Area averaged results for Europe, based on the United Kingdom Meterorological Office transient experiment (UKTR), indicate a rate of increase in winter wheat yields of 0.2 t ha(-1) decade(-1) up to the 2020s

and 0.36 t ha(-1) decade(-1) beyond. Smaller changes are predicted for sunflower: a rate of decrease of 0.05 t ha(-1) decade(-1) up to the 2020s followed by an increase of 0.05 t ha(-1) decade(-1).

KEYWORDS: CO2 CONCENTRATION, GRADUAL CHANGES, GROWTH, INCREASING CARBON-DIOXIDE, OCEAN-ATMOSPHERE MODEL, PHENOLOGY, SIMULATION-MODEL, TEMPERATURE, TRANSIENT RESPONSES, WATER

854

Hartz, T.K., A. Baameur, and D.B. Holt. 1991. Carbon-dioxide enrichment of high-value crops under tunnel culture. *Journal of the American Society for Horticultural Science 116(6):970-973.*

The feasibility of field-scale CO2 enrichment of vegetable crops grown under tunnel culture was studied with cucumber (Cucumis sativus L. cv. Dasher II, summer squash (Cucurbita pepo L. cv. Gold Bar), and tomato (Lycopersicon esculentum Mill. cv. Bingo) grown under polyethylene tunnels. The drip irrigation system was used to uniformly deliver a CO2-enriched air stream independent of irrigation. Carbon dioxide was maintained between 700 and 1000-mu-l.liter-1 during daylight hours. Enrichment began immediately after crop establishment and continued for almost-equal-to 4 weeks. At the end of the treatment phase, enrichment had significantly increased plant dry weight in the 2 years of tests. This growth advantage continued through harvest, with enriched cucumber, squash, and tomato plots yielding 30%, 20%, and 32% more fruit, respectively, in 1989. In 1990, cucumber and squash yields were increased 20%, and 16%, respectively. As performed, the expense of CO2 enrichment represented less than a 10% increase in total preharvest costs. A similar test was conducted on fall-planted strawberries (Fragaria X ananassa Duch. cvs. Irvine and Chandler). Carbon dioxide enrichment under tunnel culture modestly increased 'Irvine' yields but did not affect 'Chandler'.

KEYWORDS: CO2, GROWTH, POTATO PLANTS, RESPONSES, ROOT ZONE

855

Harvey, L.D.D. 1996. Development of a risk-hedging CO2-emission policy .2. Risks associated with measures to limit emissions, synthesis, and conclusions. *Climatic Change 34(1):41-71.*

This paper is Part II of a two-part series in which the risks associated with unrestrained greenhouse-gas emissions, and with measures to limit emissions, are reviewed. A sustained limitation of global CO2 emissions requires global population stabilization, a reduction in per capita emissions in the developed world, and a limitation of the increase in per capita emissions in the developing world. Reducing or limiting per capita emissions requires a major effort to improve the efficiency with which energy is transformed and used; urban development which minimizes the need for the private automobile and facilitates district heating, cooling, and cogeneration systems; and accelerated development of renewable energy. The following risks associated with these efforts to limit CO2 emissions are reviewed here: (i) resources might be diverted from other urgent needs; (ii) economic growth might be reduced; (iii) reduction measures might cost more than expected; (iv) early action might cost more than later action; (v) reduction measures might have undesired side effects; (vi) reduction measures might require heavy-handed government intervention; and (vii) reduction measures might not work. With gradual implementation of a diversified portfolio of measures, these risks can be greatly reduced. Net risk is further reduced by the fact that a number of non-climatic benefits would result from measures to limit CO2 emissions. Based on the review of risks associated with measures to limit emissions here, and the review of the risks associated with unrestrained emissions presented in Part I, it is concluded that a reasonable near- term (20-30 year) risk hedging strategy is one which seeks to stabilize global fossil CO2 emissions at the present (early 1990's) level. This in turn implies an emission reduction of 26% for industrialized countries as a whole and 40-50% for Canada and the USA if developing country emissions are to increase by no more than 60%, which in itself would require major assistance from the industrialized countries. The effectiveness of global CO2-emission stabilization in slowing down the buildup of atmospheric CO2 is enhanced by the fact that the airborne fraction (ratio of annual atmospheric CO2 increase to total annual anthropogenic emissions) decreases if emissions are stabilized, whereas it increases if emissions continue to grow exponentially. The framework and conclusions presented here are critically compared with so-called optimization frameworks.

KEYWORDS: CO2 EMISSIONS, CONSERVATION, ELECTRICITY, ENERGY EFFICIENCY, FUTURE, GLOBAL CLIMATE-CHANGE, GREENHOUSE, PERSPECTIVES, REDUCTION, UNITED-STATES

856

Harwood, K.G., J.S. Gillon, A. Roberts, and H. Griffiths. 1999. Determinants of isotopic coupling of CO2 and water vapour within a Quercus petraea forest canopy. *Oecologia 119(1):109-119.*

Concentration and isotopic composition (delta(13)C and delta(18)O) of ambient CO2 and water vapour were determined within a Quercus petraea canopy, Northumberland, UK. From continuous measurements made across a 36-h period from three heights within the forest canopy, we generated mixing lines (Keeling plots) for delta(a) (CO2)-C-13, delta(a) (COO)-O-18-O- 16 and delta(a) (H2O)-O-18, to derive the isotopic composition of the signal being released from forest to atmosphere. These were compared directly with measurements of different respective pools within the forest system, i.e. delta(13)C of organic matter input for delta(a) (CO2)-C-13 delta(18)O Of exchangeable water for delta(a) (COO)-O-18-O-16 and transpired water vapour for delta(a) (H2O)-O-18. [CO2] and delta(a) (CO2)- C-13 showed strong coupling, where the released CO2 was, on average, 4 per mil enriched compared to the organic matter of plant material in the system? suggesting either fractionation of organic material before eventual release as soil-respired CO2, or temporal differences in ecosystem discrimination. delta(a) (COO)-O-18-O-16 was less well coupled to [CO2], probably due to the heterogeneity and transient nature of water pools (soil, leaf and moss) within the forest. Similarly, delta(a) (H2O)-O-18 was less coupled to [H2O], again reflecting the transient nature of water transpired to the forest, seen as uncoupling during times of large changes in vapour pressure deficit. The delta(18)O of transpired water vapour, inferred from both mixing lines at the canopy scale and direct measurement at the leaf level, approximated that of source water, confirming that an isotopic steady state held for the forest integrated over the daily cycle. This demonstrates that isotopic coupling of CO2 and water vapour within a forest canopy will depend on absolute differences in the isotopic composition of the respective pools involved in exchange and on the stability of each of these pools with time.

KEYWORDS: 3-DIMENSIONAL SYNTHESIS, ATMOSPHERIC CO2, CARBON DIOXIDE, DISCRIMINATION, LEAF WATER, O-18 CONTENT, RAIN-FOREST, RESPIRED CO2, SPATIAL VARIATIONS, STABLE OXYGEN

857

Haszpra, L. 1999. On the representativeness of carbon dioxide measurements. *Journal of Geophysical Research-Atmospheres 104(D21):26953-26960.*

On the basis of the measurements at two monitoring sites located close to each other (220 km) in plain regions in Hungary, the representativeness of low-elevation continental CO2 measurements is

estimated. It is shown that under such conditions only the measurements carried out in the early afternoon hours can be considered as regionally representative for the CO2 content of the planetary boundary layer (PBL). Filtering the data in this way, it is calculated that the characteristic CO2 mixing ratio in the PBL may be about 2.5 ppm higher over this part of Europe than at the Mauna Loa Observatory (National Oceanic and Atmospheric Administration), Hawaii.

KEYWORDS: ATMOSPHERIC CO2, BUDGET, LATITUDINAL DISTRIBUTION, MODEL, OCEANIC UPTAKE, SINKS

858

Hattenschwiler, S., S. Buhler, and C. Korner. 1999. Quality, decomposition and isopod consumption of tree litter produced under elevated CO2. *Oikos 85(2):271-281.*

Rising atmospheric CO2 is expected to alter plant tissue quality which in turn could affect litter quality, decomposition, and carbon and nutrient turnover. We tested this hypothesis using leaf litter of beech (Fagus sylvatica) and branchlets (wood + bark) of spruce (Picea abies) produced under contrasting CO2 concentrations in model ecosystems. Both types of litter produced under elevated CO2 had significantly lower N concentrations, but showed no CO2-related differences in carbon and lignin concentrations. Decomposition rates (mass loss) assessed in a natural temperate forest were significantly slower in litter produced at high CO2. However, this effect became stronger in beech leaves but gradually disappeared in spruce branchlets over the 331-d exposure period. Irrespective of CO2 treatment beech leaf litter lost 16% of its initial N content. Spruce branchlets produced at low CO2 lost 50% of their initial N content, and those produced at high CO2 lost 26%. Two isopod species representing native macro-decomposers consumed 36% more of the high CO2-produced beech litter than they did of low CO2-produced beech litter. Only small, and non- significant increases in consumption of high CO2-produced spruce branchlets were observed. Isopods feeding on high CO, litter also produced more feces than those feeding litter from low CO2. Our results indicate that CO2-induced litter quality changes influence only certain stages of decomposition. and that these stages differ between different litter types. Inhibitory effects of elevated CO2, however, may be compensated by the positive feed-back of intensified "litter processing" of low quality litter by macro-decomposers. Consequently, the entire cycle of litter production and decomposition must be included in the analysis of the potential effects of rising CO2 on litter decomposition. This includes both micro- and macro- decomposer specific effects.

KEYWORDS: ATMOSPHERIC CO2, FOREST LITTER, HARDWOOD LEAF LITTER, LEAVES, LIGNIN CONTENT, NEEDLE LITTER, NITROGEN DYNAMICS, RATES, SPRUCE MODEL-ECOSYSTEMS, TERRESTRIAL ISOPODS

859

Hattenschwiler, S., and C. Korner. 1996. Effects of elevated CO2 and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia 106(2):172-180.*

We studied the effects of-atmospheric CO, enrichment (280, 420 and 560 mu l CO2 l(-1)) and increased N deposition (0.30 and 90 kg ha(-1) year(-1)) on the spruce-forest understory species Oxalis acetosella, Homogyne alpina and Rubus hirtus. Clones of these species formed the ground cover in nine 0.7 m(2) model ecosystems with 5-year-old Picea abies trees (leaf area index of approx. 2.2). Communities grew on natural forest soil in a simulated montane climate. Independently of N deposition, the rate of light-saturated net photosynthesis of leaves grown and measured at 420 mu l CO2 l(-1) was higher in Oxalis and in Homogyne, but was not significantly different in Rubus compared to leaves grown and measured at the pre-industrial CO2 concentration of 280 mu l l(-1). Remark ably, further CO2 enrichment to 560 mu l l(-1) caused no additional increase of CO2 uptake. With increasing CO2 supply concentrations of non- structural carbohydrates in leaves increased and N concentrations decreased in all species, whereas N deposition had no significant effect on these traits. Above-ground biomass and leaf area production were not significantly affected by elevated CO2 in the more vigorously growing species O. acetosella and R. hirtus, but the "slow growing" H. alpina produced almost twice as much biomass and 50% more leaf area per plant under 420 mu l CO2 l(-1) compared to 280 mu l l(-1) (again no further stimulation at 560 mu l l(-1)). In contrast, increased N addition stimulated growth in Oxalis and Rubus but had no effect on Homogyne. in Oxalis (only) biomass per plant was positively correlated with microhabitat quantum flux density at low CO2, but not at high CO2 indicating carbon saturation. On the other hand, the less shade-tolerant Homogyne profited from CO2 enrichment at all understory light levels facilitating its spread into more shady micro-habitats under elevated CO2. These species-specific responses to CO2 and N deposition will affect community structure. The non-linear responses to elevated CO2 of several of the traits studied here suggest that the largest responses to rising atmospheric CO2 are under way now or have already occurred and possible future responses to further increases in CO2 concentration are likely to be much smaller in these understory species.

KEYWORDS: ATMOSPHERIC DEPOSITION, CARBON, DECIDUOUS FOREST, HERB, LEAVES, LIGHT, RESPONSES, VEGETATION

860

Hattenschwiler, S., and C. Korner. 1996. System-level adjustments to elevated CO2 in model spruce ecosystems. *Global Change Biology 2(4):377-387.*

Atmospheric carbon dioxide enrichment and increasing nitrogen deposition are often predicted to increase forest productivity based on currently available data for isolated forest tree seedlings or their leaves. However, it is highly uncertain whether such seedling responses will scale to the stand level. Therefore, we studied the effects of increasing CO2 (280, 420 and 560 mu L L(-1)) and increasing rates of wet N deposition (0, 30 and 90 kg ha(-1) y(-1)) on whole stands of 4-year-old spruce trees (Picea abies). One tree from each of six clones, together with two herbaceous understory species, were established in each of nine 0.7 m(2) model ecosystems in nutrient poor forest soil and grown in a simulated montane climate for two years. Shoot level light-saturated net photosynthesis measured at growth CO2 concentrations increased with increasing CO2, as well as with increasing N deposition. However, predawn shoot respiration was unaffected by treatments. When measured at a common CO2 concentration of 420 mu L L(-1) 37% down-regulation of photosynthesis was observed in plants grown at 560 mu L CO2 L(-1). Length growth of shoots and stem diameter were not affected by CO2 or N deposition. Bud burst was delayed, leaf area index (LAI) was lower, needle litter fall increased and soil CO2 efflux increased with increasing CO2. N deposition had no effect on these traits. At the ecosystem level the rate of net CO2 exchange was not significantly different between CO2 and N treatments. Most of the responses to CO2 studied here were non-linear with the most significant differences between 280 and 420 mu L CO2 L(-1) and relatively small changes between 420 and 560 mu L CO2 L(-1). Our results suggest that the lack of above-ground growth responses to elevated CO2 is due to the combined effects of physiological down-regulation of photosynthesis at the leaf level, allometric adjustment at the canopy level (reduced LAI), and increasing strength of below-ground carbon sinks. The non- linearity of treatment effects further suggests that major responses of coniferous forests to atmospheric CO2 enrichment might already be under way and that future responses may be comparatively smaller.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON

DIOXIDE, COMMUNITIES, DECIDUOUS FOREST, GLOBAL CHANGE, PLANT GROWTH, RESPONSES, SEEDLINGS, TREES

861

Hattenschwiler, S., and C. Korner. 1997. Annual CO2 budget of spruce model ecosystems in the third year of exposure to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):319-325.*

Clones of 4-year-old spruce trees (Picea abies) were grown in competition in model ecosystems with nutrient-poor natural forest soil and natural understory vegetation and were exposed to three CO, concentrations (280, 420 and 560 mu mol mol(-1)) for three years. Diurnal net ecosystem CO2 uptake (NECd), nocturnal net ecosystem CO2 loss (NECn) and soil CO2 efflux were measured repeatedly in the third year of CO2 exposure and were used to estimate an annual ecosystem CO2 budget. The CO2 induced stimulation of NECd varied over the year with no measurable stimulation in spring and fall but a high mid-season CO2 stimulation. Respiratory losses of whole ecosystems and soil CO2 efflux alone were both progressively increased with increasing CO2, thus counteracting the CO2 stimulation of photosynthesis per unit ground area. Consequently, the annual net ecosystem CO2 uptake was only moderately and non-linearly stimulated by CO2 (+8% = 84 g C m(-2) a(-1) at 420 and +9% = 90 g C m(-2) a(-1) at 560 compared to 280 mu mol CO2 mol(-1)). We conclude that the rising atmospheric CO2 concentration may lead to an increase in annual net ecosystem carbon gain of rather nutrient-poor spruce communities. Our results further suggest that CO2 fertilization effects may be greatest under current CO2 concentration and that relative increases of net ecosystem CO2 uptake will become relatively smaller as atmospheric CO2 will continue to rise.

KEYWORDS: ALPINE GRASSLAND, CARBON DIOXIDE, CYCLE, RESPONSES

862

Hattenschwiler, S., and C. Korner. 1997. Growth of autotrophic and root-hemiparasitic understory plants under elevated CO2 and increased N deposition. *Acta Oecologica-International Journal of Ecology 18(3):327-333.*

Effects of atmospheric CO2 enrichment (280, 420 and 560 mu mol CO2 mol(-1)) and increased N deposition (0, 30 and 90 kg ha(-1) a(-1)) on Oxalis acetosella, Homogyne alpina, and Melampyrum sylvaticum, growing in model ecosystems beneath spruce stands, were studied. Aboveground biomass in the less-shade-tolerant Homogyne and in the annual hemiparasite Melampyrum was strongly increased with increasing CO2, but not in the more shade- adapted Oxalis. In contrast, increased N deposition stimulated growth in Oxalis, but had no effect on Homogyne and Melampyrum. Due to spruce canopy closure Homogyne,le became light limited and its survivorship was strongly correlated with spruce canopy LAI in the second year of the experiment. Our results suggest, that elevated CO2 facilitates the expansion of Hamogyne into less favourable micro-habitats (deeper shade) and that increasing N deposition enables more vigorously growing species like Oxalis to increase in abundance. Growth of the hemiparasite Melampyrum was stimulated indirectly by increased heterotrophic carbon supply (carbon isotope data) from the host (Picea abies), and thus, this species may also increase in abundance with increasing CO2. However, possible indirect effects (canopy feedbacks) make predictions of long-term understory development difficult.

KEYWORDS: CARBON, ECOSYSTEMS

863

Hattenschwiler, S., and C. Korner. 1998. Biomass allocation and canopy development in spruce model ecosystems under elevated CO2 and increased N deposition. *Oecologia 113(1):104-114.*

Ecosystem-level experiments on the effects of atmospheric CO2 enrichment and N deposition on forest trees are urgently needed. Here we present data for nine model ecosystems of spruce (Picea abies) on natural nutrient-poor montane forest soil (0.7 m(2) of ground and 350 kg weight). Each system was composed of six 7-year-old (at harvest) trees each representing a different genotype, and a herbaceous understory layer (three species). The model ecosystems were exposed to three different CO2 concentrations (280, 420, 560 mu l l(-1)) and three different rates of wet N deposition (0, 30, 90 kg ha(-1) year(- 1)) in a simulated annual course of Swiss montane climate for 3 years. The total ecosystem biomass was not affected by CO2 concentration, but increased with increasing N deposition. However, biomass allocation to roots increased with increasing CO2 leading to significantly lower leaf mass ratios (LMRs) and leaf area ratios (LARs) in trees grown at elevated CO2. In contrast to CO2 enrichment, N deposition increased biomass allocation to the aboveground plant parts, and thus LMR and LAR were higher with increasing N deposition. We observed no CO2 x N interactions on growth, biomass production, or allocation, and there were also no genotype x treatment interactions. The final leaf area index (LAI) of the spruce canopies was 19% smaller at 420 and 27% smaller at 560 than that measured at 280 mu l CO2 l(-1), but was not significantly altered by increasing N deposition. Lower LAIs at elevated CO2 largely resulted from shorter branches (less needles per individual tree) and partially from increased needle litterfall. Independently of N deposition, total aboveground N content in the spruce communities declined with increasing CO2 (-18% at 420 and -31% at 560 compared to 280 mu l CO2 l(-1)). N deposition had the opposite effect on total above ground N content (+18% at 30 and +52% at 90 compared to 0 kg N ha(-1) year(-1)). Our results suggest that under competitive conditions on natural forest soil, atmospheric CO2 enrichment may not lead to higher ecosystem biomass production, but N deposition is likely to do so. The reduction in LAI under elevated CO2 suggests allometric down-regulation of photosynthetic carbon uptake at the canopy level. The strong decline in the tree nitrogen mass per unit ground area in response to elevated CO2 may indicate CO2- induced reductions of soil N availability.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, COMPENSATORY RESPONSES, GLOBAL CHANGE, LEAF-AREA, MINERAL NUTRITION, NITROGEN DEPOSITION, NORWAY SPRUCE, TERRESTRIAL ECOSYSTEMS

864

Hattenschwiler, S., F. Miglietta, A. Raschi, and C. Korner. 1997. Morphological adjustments of mature Quercus ilex trees to elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):361-365.*

It is still not known whether mature forest trees. respond to increasing atmospheric CO2 concentrations in similar ways as seedlings do. Mature Mediterranean oaks (Quercus ilex) growing in a CO2 enriched atmosphere around natural CO2 vents since the seedling stage showed a moderate, age dependent increase in stem biomass production, but had significantly lower biomass of 6-year-old branches, decreased branching, and lower leaf area per unit branch biomass, compared to control trees at a nearby unenriched site. Our data indicate that trees in natural forest stands morphologically adjust to increasing CO2 and reduce CO2 induced initial growth stimulations. Allometric adjustments such as reduction in leaf area may be regarded as a "down- regulation" of canopy photosynthesis and may be an effective mechanism for saving water.

KEYWORDS: ENRICHMENT, GROWTH, SEEDLINGS

865

Hattenschwiler, S., F. Miglietta, A. Raschi, and C. Korner. 1997. Thirty years of in situ tree growth under elevated CO2: a model for future forest responses? *Global Change Biology 3(5):463-471.*

Rising concentrations of atmospheric carbon dioxide have been predicted to stimulate the growth of forest trees. However, long-term effects on trees growing to maturity and to canopy closure while exposed to elevated CO2 have never been examined. We compared tree ring chronologies of Mediterranean Quercus ilex which have been continuously exposed to elevated CO2 (around 650 mu mol mol(-1)) since they were seedlings, near two separate natural CO2 springs with those from trees at nearby ambient-CO2 'control' sites. Trees grown under high CO2 for 30 years (1964-93) showed a 12% greater final radial stem width than those growing at the ambient-CO2 control sites. However, this stimulation was largely due to responses when trees were young. By the time trees were 25-30 y old the annual difference in tree ring width between low and high CO2 grown trees had disappeared. At any given tree age, elevated CO2 had a relatively greater positive effect on tree ring width in years with a dry spring compared to years with more rainfall between April and May. This indicates a beneficial effect of elevated CO2 on tree water relations under drought stress. Our data suggest that the early regeneration phase of forest stands can be accelerated in CO2-enriched atmospheres and that maximum biomass per land area may be reached sooner than under lower CO2 concentrations. In our study, high CO2 grown Q. ilex trees reached the same stem basal area at the age of 26 y as control trees at 29 y,i.e. three years earlier (faster turnover of carbon?). Reliable predictions of the future development of forests need to account for the variable responses of trees over their entire lifetime. Such responses to elevated CO2 can presently only be assessed at such unique field sites.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CHRONOLOGIES, CLIMATE, ECOSYSTEMS, PLANTS, PRODUCTIVITY, RING-WIDTH, VEGETATION

866

Hattenschwiler, S., and C. Schafellner. 1999. Opposing effects of elevated CO2 and N deposition on Lymantria monacha larvae feeding on spruce trees. *Oecologia 118(2):210-217.*

The effects of elevated atmospheric CO and increased wet N deposition on leaf quality and insect herbivory were evaluated in nine model ecosystems composed of 7-year-old spruce trees (Picea abies) and three understorey species established on natural forest soil. Each model ecosystem was grown in a simulated montane climate, and was exposed to one of three CO2 concentrations (280, 420, and 560 mu l l(-1)) and to one of three levels of N deposition (0, 30, and 90 kg ha(-1) year(-1)) for 3 years. In the 3rd year of the experiment second to third instars of the nun moth (Lymantria monacha) were allowed to feed directly on current-year needles of top canopy branches of each tree for 13 days. Specific leaf area (SLA), water content, and N concentration decreased in needles exposed to elevated CO2, whereas the concentrations of starch, condensed tannins, and total phenolics increased. Increased N deposition had no significant effect on SLA, and water content, but the concentrations of starch, condensed tannins, and total phenolics decreased, and sugar and N concentrations increased. Despite higher relative consumption rates (RCRs) larvae consumed 33% less N per unit larval biomass and per day at the two high CO2 treatments, compared to those feeding on 280 mu l l(-1)-needles, but they maintained similar N accumulation rates due to increased N utilization efficiencies (NUE). However, over the 12-day experimental period larvae gained less N overall and reached a 35% lower biomass in the two high-CO2 treatments compared to those at 280 mu l l(-1). The effects of increased N deposition on needle quality and insect performance were generally opposite to those of CO enrichment, but were lower in magnitude. We conclude that altered needle quality in response to elevated CO2 will impair the growth and development of L. monacha larvae. Increasing N deposition may mitigate these effects, which could lead to altered insect herbivore distributions depending on regional patterns of N deposition.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECIDUOUS TREES, FOLIAGE, FOOD PLANTS, GROWTH, INSECT HERBIVORE INTERACTIONS, NITROGEN, PERFORMANCE, RESPONSES

867

Hattenschwiler, S., F.H. Schweingruber, and C. Korner. 1996. Tree ring responses to elevated CO2 and increased N deposition in Picea abies. *Plant, Cell and Environment 19(12):1369-1378.*

Four- to seven-year-old spruce trees (Picea abies) were exposed to three CO2 concentrations (280, 420 and 560 cm(3) m(-3)) and three rates of wet N deposition (0, 30 and 90 kg ha(-1) year(- 1)) for 3 years in a simulated montane forest climate, Six trees from each of six clones were grown in competition in each of nine 100 x 70 x 36 cm model ecosystems with nutrient-poor natural forest soil, Stem discs were analysed using X-ray densitometry, The radial stem increment was not affected by [CO2] but increased with increasing rates of N deposition, Wood density was increased by [CO2], but decreased by N deposition, Woodstarch concentration increased, and wood nitrogen concentration decreased with increasing [CO2], but neither was affected by N deposition, The lignin concentration in wood was affected by neither [CO2] nor N deposition, Our results suggest that, under natural growth conditions, rising atmospheric [CO2] will not lead to enhanced radial stem growth of spruce, but atmospheric N deposition will, and in some regions is probably already doing so, Elevated [CO2], however, will lead to denser wood unless this effect is compensated by massive atmospheric N deposition, It can be speculated that greater wood density under elevated [CO2] may alter the mechanical properties of wood, and higher ratios of C/N and lignin/N in wood grown at elevated [CO2] may affect nutrient cycles of forest ecosystems.

KEYWORDS: CARBON DIOXIDE, CHRONOLOGIES, COMMUNITIES, DECOMPOSITION, FOREST, GROWTH, NORTH-AMERICA, PLANTS, RISING ATMOSPHERIC CO2, SUMMER TEMPERATURES

868

Hatton, T.J., J. Walker, W.R. Dawes, and F.X. Dunin. 1992. Simulations of hydroecological responses to elevated CO2 at the catchment scale. *Australian Journal of Botany 40(4-5):679-696.*

A spatially explicit hydroecological landscape model of water, carbon and energy balances (Topog-IRM) is described. The landscape is envisaged as a catchment forested with a single stratum comprising Eucalyptus maculata trees. The model was used to simulate the direct effects of a 2X elevation in atmospheric carbon dioxide at two levels of nitrogen on catchment water yield, soil moisture status and tree growth, Experimental results used to parameterise the model are detailed. Key features of the model are (1) an ability to scale hydrological processes at the catchment scale in three dimensions, and (2) a means to integrate multiple factors/stresses on plant growth. The effects of CO2 on catchment hydrology (water yield or soil moisture content) and forest growth (expressed as leaf area index, LAI) were modelled for a 2-year period, and contrasted with the effects of added nitrogen. Results were expressed as totals for the catchment or spatially distributed across the catchment. For the total catchment, water yield increased in the order: high CO2 with low N, high CO2 with high N, ambient CO2 with low N, ambient CO2 with high N. LAI increased from 3.3 to 5.7 in the order: ambient CO2 with low N, ambient CO2 with high N, high CO2 with low N, high CO2 with high N. These results agree with previous data. New findings are: (1) with elevated CO2 a new equilibrium in transpiration is established in which leaf area increases offset decreases in stomatal

conductance; (2) the addition of nitrogen increases transpiration without any indication of a new equilibrium being reached during the simulated period; (3) the spatial distribution of soil moisture changes, presenting a new resource base for spatial changes to species composition and growth rates. The major hydroecological responses to elevated CO2 are seen as increased maximum upper canopy leaf area, increased litter inputs, especially at times of drought (hence changed fire regimes), changes in the composition of the understorey (hence litter composition, soil microfauna, and the spatial expression of biological diversity) and a slight increase in water yield.

KEYWORDS: ASSIMILATION, CARBON BALANCE, CLIMATE CHANGE, FOREST ECOSYSTEM PROCESSES, GENERAL-MODEL, LEAF CONDUCTANCE, PARTIAL-PRESSURE, PHOTOSYNTHESIS, REGIONAL APPLICATIONS, TRANSPIRATION

869

Hausler, R.E., P.J. Lea, and R.C. Leegood. 1994. Control of photosynthesis in barley leaves with reduced activities of glutamine-synthetase or glutamate synthase .2. Control of electron-transport and co2 assimilation. *Planta 194(3):418-435.*

Heterozygous plants of barley (Hordeum vulgare L. cv. Maris Mink) with activities of chloroplastic glutamine synthetase (GS) between 47% and 97% of the wild-type and ferredoxin- dependent glutamate synthase (Fd-GOGAT) activities down to 63% of the wild-type have been used to study the control of photosynthetic fluxes. Rates of CO2 assimilation measured over a range of intercellular CO2 concentrations and photon flux densities (PFDs) were little different in the wild-type and a mutant with 47% GS, although total activities of ribulose-1, 5- bisphosphate carboxylase/oxygenase (Rubisco) decreased by about 20% with a decrease in GS to 50% of the wild-type. The quantum efficiencies of photosystem II electron transport (Phi PSII) and CO2 assimilation (Phi CO2) were determined. Phi PSII was lower than expected in mutants with 50% less GS under conditions which enhance the photorespiratory flux, but were identical to the wildtype under non-photorespiratory conditions, suggesting that at high rates of photorespiration the electron requirement for net CO2 assimilation declines in plants with decreased GS. This discrepancy in the electron requirement between the wild-type and the 47% GS mutant was enhanced at high temperatures and low CO2, conditions which favour oxygenation by Rubisco. Photochemical and non- photochemical chlorophyll a fluorescence quenching as well as the quantum efficiency of excitation-energy capture by open photosystem II reaction centres were differentially affected in mutants with less GS relative to the wild-type when CO2 was lowered or the PFD was varied. The quantum efficiencies of electron transport in photosystems I and II were closely correlated under a range of PFDs and CO2 concentrations, confirming that the rate of linear electron transport was much lower in plants with less GS. It is shown that GS exerts considerable control (flux control coefficients between 0.5 and 1.0) on the electron requirement for CO2 assimilation at high fluxes of photorespiration relative to CO2 assimilation. Apart from the control of GS on protein and Rubisco contents, GS in the wild-type has also some direct positive control on CO2 assimilation. However, negative control on CO2 assimilation was found in mutants with 50% less GS. These data, taken with the data on electron requirements for CO2 assimilation, suggest that CO2-fixing processes other than that catalysed by Rubisco, such as carboxylation of phosphoenolpyruvate, or an inhibition of photorespiration (e.g. glycine decarboxylation), may contribute to the observed CO2 exchange and photosystem II electron transport in plants with less GS. In the 63%-Fd-GOGAT mutant, rates of CO2 assimilation were appreciably lower than in the wild-type under a range of PFDs and CO2 concentrations, which largely reflected lower contents of Rubisco in the Fd- GOGAT mutants. Assimilation of CO2 was inhibited appreciably at high CO2 concentrations. There was little difference in the electron requirement for CO2 assimilation between the wild-type and mutants with less Fd-GOGAT, although there were indications that a triose-phosphate/glycerate-3-phosphate shuttle or cyclic electron transport operates to balance ATP generation and NADP reduction. The latter was supported by a curvilinear relationship of photosystem I and II electron transport in the 63% Fd-GOGAT mutant. A positive control is exerted by Fd-GOGAT on the amounts of protein and Rubisco and on CO2 assimilation.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, LIGHT, PHOTOSYSTEM, QUANTUM YIELDS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SERINE, SPECIFICITY, SPINACH-CHLOROPLASTS, TOBACCO-LEAVES

870

Havstrom, M., T.V. Callaghan, and S. Jonasson. 1993. Differential growth-responses of cassiope-tetragona, an arctic dwarf-shrub, to environmental perturbations among 3 contrasting high sites and sub-arctic sites. *Oikos 66(3):389-402.*

Three populations of Cassiope tetragona (Ericaceae) were subjected to in situ environmental perturbations simulating predictions of global warming. The populations were selected to represent different parts of the range of the species, one growing in a high arctic coastal heath at Ny-Alesund (Svalbard, northern part of the species' range), one at a subarctic fellfield at 1150 m a.s.l. at Abisko, Swedish Lapland, and one in a subarctic tree-line heath at 450 m a.s.l. at Abisko, southern part of the species' range. The manipulations included nutrient addition, shading and two levels of temperature enhancement using passive greenhouses. The micrometeorological effects of the shading treatment was similar to that of a mountain birch canopy and the temperature enhancement treatments had the desired effect to increase the average air temperature by 2-4-degrees-C. Greenhouses which had a gap between the soil and the greenhouse plastic were particularly successful in creating the desired climatic perturbation without causing extreme maximum temperatures or other unwanted side-effects. The environmental manipulations caused strikingly different responses in the vegetative growth pattern of main shoots of C. tetragona among the three populations: at the subarctic tree-line heath, nutrient addition caused a substantial increase in growth, whereas it was the temperature enhancement treatments that caused increases, although smaller, at the subarctic fellfield and the high arctic heath sites. At the high arctic site, we also found growth reduced in response to shading, but at the subarctic sites, and particularly at the tree-line heath site, shading caused a marked etiolation of the shoots. Hence, different factors seem to produce very different responses in the vegetative growth of C. tetragona in different parts of its geographical range. We conclude that competition for nutrients and light are the main limiting factors for the growth of Cassiope tetragona near the lower distributional limit (LODIL) of the species, but that temperature is the main limiting factor in the northern parts of its range, and at high altitudes in the southern parts of its range. We also suggest that the direct effect of predicted future climatic warming on the growth of Cassiope tetragona will increase towards the north, whereas a possible indirect effect of increasing nutrient availability following a temperature increase will be the main effect in the southern and lower parts of its range. These responses could, however, be modified by shading from other species responding to environmental change by increased growth.

KEYWORDS: CLIMATIC CHANGE, ELEVATED CO2 CONCENTRATIONS, GREENHOUSE, PLANT- COMMUNITIES, TUSSOCK TUNDRA

871

Haxeltine, A., and I.C. Prentice. 1996. A general model for the light-use efficiency of primary production. *Functional Ecology 10(5):551-561.*

1. Net primary production (NPP) by terrestrial ecosystems appears to be proportional to absorbed photosynthetically active radiation (APAR) on a seasonal and annual basis. This observation has been used in 'diagnostic' models that estimate NPP from remotely sensed vegetation indices. In 'prognostic' process-based models carbon fluxes are more commonly integrated with respect to leaf area index assuming invariant leaf photosynthetic parameters. This approach does not lead to a proportional relationship between NPP and APAR. However, leaf nitrogen content and Rubisco activity are known to vary seasonally and with canopy position, and there is evidence that this variation takes place in such a way as to nearly optimize total canopy net photosynthesis. 2. Using standard formulations for the instantaneous response of leaf net photosynthesis to APAR, we show that the optimized canopy net photosynthesis is proportional to APAR. This theory leads to reasonable values for the maximum (unstressed) light-use efficiency of gross and net primary production of C-3 plants at current ambient CO2, comparable with empirical estimates for agricultural crops and forest plantations. 3. By relating the standard formulations to the Collatz-Farquhar model of photosynthesis, we show that a range of observed physiological responses to temperature and CO2 can be understood as consequences of the optimization. These responses include the CO2 fertilization response and stomatal closure in C-3 plants, the increase of leaf N concentration with decreasing growing season temperature, and the downward acclimation of leaf respiration and N content with increasing ambient CO2. The theory provides a way to integrate diverse experimental observations into a general framework for modelling terrestrial primary production.

KEYWORDS: ATMOSPHERIC CO2, CARBON GAIN, CLIMATE CHANGE, CO2 CONCENTRATIONS, DAILY CANOPY PHOTOSYNTHESIS, ELEVATED CO2, LEAF NITROGEN DISTRIBUTION, PLANTS, SOLAR RADIATION, STOMATAL CONDUCTANCE

872

Hdider, C., L.P. Vezina, and Y. Desjardins. 1994. Short-term studies of (no3-)-n-15 and (nh4+)-n-15 uptake by micropropagated strawberry shoots cultured with or without co2 enrichment. *Plant Cell Tissue and Organ Culture 37(2):185-191.*

The uptake of (NO3-)-N-15 and (NH4+)-N-15 has been examined in 5-,10- and 28-day-old micropropagated strawberry (Fragaria x ananassa Duch. cv. Kent) shoots rooted in one-half strength Murashige and Skoog (MS) liquid medium on cellulose plugs (Sorbarods). The results indicated that the plantlets absorbed both NO3- and NH4+ during the culture with a greater uptake of NH4+ at 5 days of culture. Furthermore, a pronounced reduction in NO3- and NH4+ uptake at 10 and 28 days of culture Ras observed within 6 h of the short-term uptake study. This reduction could be explained by the low CO2 concentration in test tubes during the photoperiod, since no reduction in nitrogen uptake occurred in the CO2 enriched condition. The results are interpreted as an indication of the important role for photosynthetic CO2 fixation in the process of nitrogen uptake by the plantlets during the rooting stage.

KEYWORDS: GROWTH, INVITRO, NITROGEN, PLANTLETS

873

He, P., K.P. Bader, A. Radunz, U. Kahmann, G.H. Ruppel, and G.H. Schmid. 1998. Gas exchange characteristics in leaves of the Euphorbiacea Aleurites montana as consequence of growth under 700 ppm CO2 in air - A study on photosynthesis and photorespiration in the Chinese tung-oil tree. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 53(3-4):151-158.*

Three months old plants of the Chinese tung-oil tree Aleurites montana (Euphorbiaceae) were cultivated for 4 months in air containing 700 ppm CO2. These plants, which grow substantially better in the CO2-enriched atmosphere, were analyzed by mass spectrometry for photosynthesis and photorespiration together with control plants grown all the lime in normal (350 ppm CO2) air. Thereafter part of the plants was subjected for two weeks to 0.3 ppm SO2 in the atmosphere and again analyzed for photosynthesis and photorespiration. Aleurites montana exhibits a strongly CO2-dependent photosynthesis which partially explains the observed stimulatory effect of 700 ppm CO2 on growth of the plant. In control plants grown in normal air, photorespiration measured simultaneously with photosynthesis via the uptake of O-18(2) in the light, is much lower than in C-3-plants like tobacco (He et at, 1995, Z. Naturforsch. 50c, 781-788). In Aleurites grown in 700 ppm CO2, however, photorespiration is completely absent in contrast to tobacco when grown under 700 ppm CO2. In tobacco, photorespiration is not inhibited to the extent of the in vitro experiments in which plants grown at 350 ppm CO2 are measured under the increased CO2 content of 700 ppm. Gas exchange measurements carried out by mass spectrometry show that the ratio of O-2 evolved to CO2 fixed is about 0.5. Apparently, part of the CO2 fixed is channelled into a metabolic path without concomitant O-2-evolution. Although the plant has no succulent appearance (its leaves somehow resemble maple leaves) apparently a Crassulacean type metabolism is performed. When Aleurites plants grown all the time in normal air with 350 ppm, are exposed for two weeks to 0.3 ppm SO2 the treatment completely inhibits this CO2-fixing portion which is tentatively attributed to a Crassulacean type of metabolism. This is demonstrated by a normal C-3-type ratio O-2 evolved/CO2 fixed of 1. When Aleurites plants, grown for 4 months in a CO2- enriched atmosphere of 700 ppm CO2, are subjected for two weeks to 0.3 ppm SO2, the features of control plants show up again. When these plants are tested under 350 ppm CO2 the Crassulacean type CO2-fixation apparently is not inhibited by SO2. Photorespiration, although low is present in the same activity as in the controls. Seemingly, an increased level of CO2 in air tends to alleviate the impact of the SO2 at least in the Chinese lung-oil tree.

KEYWORDS: LIGHT, RATES, TOBACCO MUTANTS

874

He, P., K.P. Bader, A. Radunz, and G.H. Schmid. 1995. Consequences of high CO2-concentrations in air on growth and gas-exchange rates in tobacco mutants. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 50(11-12):781-788.*

Wild type tobacco N. tabacum var. John William's Broadleaf and the tobacco aurea mutant Su/su were permanently grown under 700 ppm CO2 in air. In comparison to plants grown under 350 ppm CO2 in air but under otherwise identical conditions growth was substantially enhanced. Gas exchange measurements carried out by mass spectrometry show that the rate of photosynthesis in the wild type and in the mutant is increased by more than 100%. The photorespiratory rate in the wild type measured;as O-18(2)- uptake in the light in the "700 ppm CO2-plants" is not reduced to the extent expected or deduced from experiments in which the 350 ppm system responds under in vitro conditions to 700 ppm CO2. An analysis of the induction kinetics of room temperature fluorescence kinetics of the adapted (700 ppm CO2) system and the control system (350 ppm CO2) under various CO2-partial pressures shows that permanent growth under the elevated CO2-partial pressure leads to a structural modification of the photosynthetic apparatus.

KEYWORDS: AUREA MUTANT, LIGHT, PARAMETERS, PHOTOSYNTHESIS, RESPIRATION

875

He, P., A. Radunz, K.P. Bader, and G.H. Schmid. 1996. Influence of CO2 and SO2 on growth and structure of photosystem II of the Chinese

tung-oil tree Aleurites montana. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 51(7-8):441-453.*

Three months old plants of the Chinese tung-oil tree Alenrites montana were cultivated for 4 months in air containing an increased amount of 700 ppm CO2. During the exposure to 700 ppm CO2 the plants exhibited a considerably stronger growth (30- 40%) in comparison to the control plants (grown in normal air). In these CO2-plants during the entire analyzing period the amount of soluble proteins, of soluble sugars and the chlorophyll content were lower than in control plants. The protein content, referred to leaf area, increased during this time in both plant types by approx. 50% but with a different time course. The increase is faster in CO2-plants compared to control plants, and ends up with similar values in both plants after 4 months. No difference is seen between sun and shade leaves. The chlorophyll content in both sun and shade leaves is 20% lower in CO2-plants. Whereas the chlorophyll content in sun leaves stays constant during development, it has increased in shade leaves by 20% at the end of the 4 months period. The content of soluble sugars is lower in CO2-plants compared to control plants. The difference is bigger in sun leaves than in shade leaves. The ribulose 1.5-bisphosphate carboxylase/oxygenase content almost doubles within the experimentation period, but seems to be subject to large variations. CO2-plants contain in general less ribulose 1.5- bisphosphate carboxylase/oxygenase than control plants. The content of coupling factor of photophosphorylation is 20% lower in CO2-plants when compared to control plants and remains during development more constant in CO2-plants. The molecular structure of the photosystem II-complex undergoes under the influence of the increased CO2-content a quantitative modification. The light harvesting complex (LHCP) and the extrinsic peptide with the molecular mass of 33 kDa increase in CO2-plants. Gassing with SO2 (0.3 ppm in air) leads to a strong damage of the plants. The damaging influence is already seen after 6 days and leads to a partial leaf-shedding of the tree. In the visually still intact remaining leaves the chlorophyll content referred to unit leaf area decreases by 63%, that of soluble sugars by 65%, the content of soluble proteins and that of Rubisco decrease by 26% and 36% respectively. The light harvesting complex and the chlorophyll-binding peptides (43 and 47 kDa) increase whereas the extrinsic peptides decrease. It looks as if the simultaneous application of SO2 (0.3 ppm) and increased CO2 (700 ppm) releaves the damaging effect of SO2. Plant growth does not exhibit a difference in comparison to control plants. Soluble proteins and chlorophyll increase by 27% and 33% and the ribulose 1.5-bisphosphate carboxylase/oxygenase content as well as that of soluble sugars increases by 18 respectively 14%. The peptide composition of photosystem II shows a quantitative modification. The LHCP increases and the chlorophyll-binding peptides and the peptides with a molecular mass smaller than 24 kDa are reduced. The quantity of extrinsic peptides appears unchanged. Ribulose 1,5- bisphosphate carboxylase/oxygenase and the CF1-complex of Aleurites are immunochemically only partially identical to the corresponding enzymes of Nicotiana tabacum as demonstrated by tandem-cross-immune electrophoresis.

KEYWORDS: ACCLIMATION, ELEVATED CO2, LEAVES, NICOTIANA-TABACUM, ORGANIZATION, PHOTOSYNTHETIC APPARATUS, RUBISCO, SHADE PLANTS, SUN, THYLAKOID MEMBRANES

876

He, X.Q., Y.H. Lin, J.X. Lin, and Y.X. Hu. 1998. Relationship between stomatal density and the changes of atmospheric CO2 concentrations. *Chinese Science Bulletin 43(11):928-930.*

The relationship between the stomatal density of five woody plants endemic to China, i.e. Eucommia ulmoides, Quercus liaotungensis, Q. glandulifera var. brevipetiolata, Cyclocarya paliurus and Ficus heteromorpha, and the atmospheric CO2 concentrations was studied by observations on leaves of the herbarium-stored specimens(1920s-1990s). The results showed that the stomatal density in Eucommia ulmoides, Quercus liaotungensis and Q. glandulifera var. brevipetiolata decreased significantly in response to the elevated atmospheric CO2 concentrations, while in Cyclocarya paliurus it decreased slightly and in Ficus heteromorpha there were no responses.

KEYWORDS: INCREASE, NUMBERS

877

He, Y., X.S. Yang, D.R. Miller, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1996. Effects of face system operation on the micrometeorology of a loblolly pine stand. *Transactions of the Asae 39(4):1551-1556.*

The effects of the gas injection operation on air movement in the loblolly pine stand at the Duke Forest prototype BNL-FACE User Facility were investigated The micrometeorological conditions were measured using three-dimensional sonic anemometers in the center of the FACE ring at two heights, one just above the canopy (median height of the canopy = 9 m) at 11.6 m and another at 6.8 m above the ground where the canopy war the most dense. While the micrometeorological parameters were sampled continuously at 10 Hz, the gas injection system was turned alternatively on and off every 5 min for about 100 h. The analyses indicated that the system operation had little effect on the micrometeorology processes above the canopy. There were small magnitude but detectable changes in some of the micrometeorological parameters within the canopy, primarily during stable atmospheric conditions, in response to this 5-min alternation. The gas injection operation created a slightly diverging windfield in the top half of the canopy in the enclosed stand A slight dampening of the vertical wind and air temperature fluctuations was detected No detectable effects on the mean, or accumulated, heat and momentum fluxes at the measurement locations were found. in general, the system was shown to cause minimal disturbances to the natural environment compared to traditional carbon dioxide (CO2) enrichment facilities and it provides a better alternative for long-term ecological studies.

KEYWORDS: CO2- ENRICHMENT

878

He, Z.L., S. von Caemmerer, G.S. Hudson, G.D. Price, M.R. Badger, and T.J. Andrews. 1997. Ribulose-1,5-bisphosphate carboxylase/oxygenase activase deficiency delays senescence of ribulose-1,5-bisphosphate carboxylase/oxygenase but progressively impairs its catalysis during tobacco leaf development. *Plant Physiology 115(4):1569-1580.*

Transgenic tobacco (Nicotiana tabacum L. cv W38) plants with an antisense gene directed against the mRNA of ribulose-1,5- biphosphate carboxylase/oxygenase (Rubisco) activase grew more slowly than wild-type plants in a CO2-enriched atmosphere, but eventually attained the same height and number of leaves. Compared with the wild type, the anti-activase plants had reduced CO2 assimilation rates, normal contents of chlorophyll and soluble leaf protein, and much higher Rubisco contents, particularly in older leaves. Activase deficiency greatly delayed the usual developmental decline in Rubisco content seen in wild-type leaves. This effect was much less obvious in another transgenic tobacco with an antisense gene directed against chloroplast-located glyceraldehyde-3-phosphate dehydrogenase, which also had reduced photosynthetic rates and delayed development. Although Rubisco carbamylation was reduced in the anti-activase plants, the reduction was not sufficient to explain the reduced photosynthetic rate of older anti-activase leaves. Instead, up to a 10-fold reduction in the catalytic turnover rate of carbamylated Rubisco in vivo appeared to be the main cause. Slower catalytic turnover by carbamylated Rubisco was particularly obvious in high-CO2-grown leaves but was also detectable in air-grown leaves. Rubisco activity measured immediately after rapid

extraction of anti- activase leaves was not much less than that predicted from its degree of carbamylation, ruling out slow release of an inhibitor from carbamylated sites as a major cause of the phenomenon. Nor could substrate scarcity or product inhibition account for the impairment. We conclude that activase must have a role in vivo, direct or indirect, in promoting the activity of carbamylated Rubisco in addition to its role in promoting carbamylation.

KEYWORDS: 1,5-BISPHOSPHATE CARBOXYLASE, CARBAMYLATION, GAS-EXCHANGE, GENE-EXPRESSION, INHIBITION, LEAVES, OXYGENASE, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE

879

Heagle, A.S., F.L. Booker, J.E. Miller, W.A. Pursley, and L.A. Stefanski. 1999. Influence of daily carbon dioxide exposure duration and root environment on soybean response to elevated carbon dioxide. *Journal of Environmental Quality 28(2):666-675.*

Little is known about effects of daily CO2 enrichment duration and root environment on plant response to elevated CO2. Two experiments were performed,vith Essex soybean (Glycine max L, Merr,) in open-top field chambers to address these questions. In one experiment, effects of 12 and 24 h d(-1) exposures to double-ambient CO2 were compared for plants grown in 14 L pots that were either insulated to moderate soil temperature or not insulated. Although never significant statistically, trends at some growth stages suggested that nighttime CO2 enrichment contributed to growth and yield. Plants grew and yielded more in insulated than noninsulated pots, but there were no significant CO2 enrichment X insulation interactions. In the second experiment, response to approximately 1.3, 1.6, and 1.9 times ambient CO2 was compared for plants grown in the ground or 14 L pots. Enhancement of photosynthesis, growth, and yield by CO2 enrichment was similar in pots and in the ground. Linear responses to different CO2 concentrations were significant for all yield components in both root environments, whereas quadratic responses were significant for plants in pots but not for plants in the ground. Tests of proportionality of response for yield components shelved no evidence of significant differences between plants in pots and in the ground except weight per 100 seeds. Seed yield enhancement at 1.9 times ambient CO2 was 36% for plants in pots and 33% for plants in the ground. Overall, proportional response of soybean to CO2 enrichment was relatively uniform in spite of large differences in baseline growth and yield.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CHAMBERS, ENHANCEMENT, FIELD, GROWTH, OZONE, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, YIELD RESPONSE

880

Heagle, A.S., R.L. Brandenburg, J.C. Burns, and J.E. Miller. 1994. Ozone and carbon-dioxide effects on spider-mites in white clover and peanut. *Journal of Environmental Quality 23(6):1168-1176.*

Effects of O-3 and/or elevated CO2 on two-spotted spider mites (Tetranychus urticae Koch) grown on an On-sensitive and an O-3-resistant clone of white clover (Trifolium repens L.) were measured in greenhouse and field experiments. Peanut (Arachis hypogeae L.) 'NC-9' was used in one greenhouse study with O-3. In field studies, O-3 treatments were charcoal filtered air (CF), nonfiltered air (NF), and two NF treatments with On added for 12 h d(-1) at proportions of approximate to 1.25 and 1.50 times the ambient O-3 concentration. In greenhouse studies, constant amounts of O-3 were added to CF for 6 h d(-1) to achieve mean concentrations ranging from 5 to 100 nL L(-1). For the greenhouse O-3 X CO2 experiment, CO2 concentrations were ambient and approximately twice-ambient for 24 h d(-1). Plants were exposed to O-3 and/or CO2 for approximate to 7 d before infestation with mites; daily exposures continued for 14 to 28 d to allow reproduction for at least two generations. Leaves were sampled to count eggs, larvae, nymphs, and adults. Ozone caused more chlorosis and necrosis on the O-3-sensitive clover clone (NC-S) than on the Oa-resistant clone (NC-R). Carbon dioxide enrichment increased shoot growth of both clones by approximate to 33%. Statistical analyses indicated significant O-3 effects in some experiments and nonsignificant O-3 effects in others. A trend toward increased mite populations with increased O-3 occurred, however, on NC-S in all trials. No consistent trends occurred with NC-R. With peanut, a significant linear increase in mite population occurred with increased O-3. Carbon dioxide enrichment increased the rate of population increase on both clover clones, but more so on NC-R. At 22 to 28 d after infestation, the total population in the twice-ambient CO2 treatment was 65% greater than in the ambient treatment for NC-R and 22% greater than in the ambient treatment for NC-S. There were no statistically significant interactive effects between CO2 and O-3 On mite population growth. The apparent clone effects on mite population response to O-3 and CO2 strongly suggest that responses were mediated through the host plants.

KEYWORDS: ALTERED FEEDING PREFERENCE, AMBIENT AIR-POLLUTION, APHID INFESTATION, BEETLE EPILACHNA-VARIVESTIS, GROWTH, HERBIVORE INTERACTIONS, HOST PLANTS, INSECT HERBIVORE, RESPONSES, TOP FIELD CHAMBERS

881

Heagle, A.S., J.E. Miller, and F.L. Booker. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: I. Foliar properties. *Crop Science 38(1):113-121.*

Tropospheric O-3 can cause foliar injury, decreased growth, and decreased yield, whereas CO2 enrichment generally causes opposite effects. Little is known about plant response to mixtures of O-3 and CO2. Open-top field chambers were ere used to determine if foliar responses of soybean [Glycine max (L.) Merr.] to CO2 enrichment are affected by O-3 stress and vice versa. Plants were grown in 14-L pots and exposed to four CO2 and three O-3 concentrations in 12 combinations. The CO2 treatments were ambient (366 mu L L-1) and three treatments with CO2 added for 24 h d(-1) at approximately 1.3, 1.6, and 2.0 times ambient. The O-3 treatments were charcoal-filtered air (CF), nonfiltered air (NF), and NF with O-3 added for 12 h d(-1) (NF+), resulting in seasonal concentrations of approximately 20, 46, and 75 nL L-1. Foliar effects of CO2 enrichment were dependent on the amount of stress caused by O-3 In the CF treatment, plants were not stressed by O-3, and CO2 enrichment caused chlorosis and decreased chlorophyll. In the IVF and NF+ treatments, plants were stressed by O-3, and CO2 enrichment suppressed chlorosis and increased chlorophyll. Ozone decreased specific leaf weight, increased foliar N and C, and decreased C/N ratios, whereas CO2 caused opposite responses for these measures. Ozone increased foliar S and B but did not affect P or K concentrations. Conversely, CO2 enrichment suppressed foliar S, B, P, and K concentrations. These interactions between O-3 and CO2 emphasize a need to consider the amount of plant stress caused by O-3 in studies to measure effects of CO2 enrichment.

KEYWORDS: AGRICULTURAL CROPS, ASSESSING IMPACTS, ATMOSPHERIC CO2 ENRICHMENT, CHLOROPHYLL CONTENT, ELEVATED CO2, EXCHANGE-RATE, GAS-EXCHANGE, GROWTH, NITROGEN NUTRITION, PLANT-RESPONSES

882

Heagle, A.S., J.E. Miller, F.L. Booker, and W.A. Pursley. 1999. Ozone stress, carbon dioxide enrichment, and nitrogen fertility interactions in cotton. *Crop Science 39(3):731-741.*

Ozone (O-3) in the troposphere can cause plant stress leading to foliar injury and suppressed growth and yield, whereas elevated CO2 generally enhances growth and yield. Numerous studies have been performed to determine effects of O-3 and CO2 separately, but relatively few have been performed to determine if O-3 can affect plant response to CO2 or vice versa. Open-top field chambers were used to determine if such interactions occur for cotton (Gossypium hirsutum L.), which is relatively sensitive to O-3. Nitrogen nutrition is especially important in cotton production so N nutrition was included as an experimental factor. Plants were grown in 14-L pots at low, medium, and high soil N levels and exposed to three CO2 and two or three O-3 treatments in all combinations during two seasons. The CO2 treatments were ambient (370 mu L L-1) and two treatments with CO2 added for 24 h d(-1) at approximately 1.5 and 2.0 Limes ambient. In 1995, the O-3 treatments were charcoal filtered air (CP), and nonfiltered air (NF) with O-3 added for 12 h d(-1) (NF+). In 1996, a NF treatment was also included to represent ambient O-3 conditions. The CF, NF, and NF+ treatments resulted in seasonal O-3 concentrations of approximately 23, 51, and 75 nL L-1. Carbon dioxide enrichment generally stimulated growth and yield whereas O-3 exposure suppressed growth. and yield. Stimulation induced by CO2 increased as O-3 stress increased. For example, in 1995 at medium N, the percentage increase in yield caused by doubling CO2 in CF air was 0%, but was 52% in NF+ air. Comparable values for 1996 were 23% in CF air and 140% in NF+ air. These interactions occurred for a range of soil N levels, and were probably caused by CO2-induced prevention of O-3 stress. The results emphasize the need to consider O-3 x CO2 interactions to ensure correct interpretation of cause-effect relationships in CO2 enrichment studies with crops that are sensitive to O-3.

KEYWORDS: ATMOSPHERIC CO2, CHAMBERS, ELEVATED CO2, FACE, GROWTH, INJURY, PLANT-RESPONSES, SOIL MOISTURE, SOYBEAN RESPONSE, YIELD RESPONSE

883

Heagle, A.S., J.E. Miller, and W.A. Pursley. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: III. Yield and seed quality. *Crop Science 38(1):128-134.*

Ozone in the troposphere can cause plant stress, whereas elevated CO2 generally causes positive responses. Little is known of how these gases interact to affect plant response. Interactive effects on yield and seed quality of soybean [Glycine max (L.) Merr.] grown in 14-L pots were measured in open-top field chambers. Essex was tested in 1993, and Essex, Holladay, and NK 6955 were tested in 1994. Plants were exposed from emergence to maturity to four CO2 levels (ambient and 1.3, 1.6, and 2.0 times ambient) and three O-3 levels (0.4, 0.9, and 1.5 times ambient) in 12 combinations. Increasing O-3 suppressed growth and yield, whereas CO2 enrichment stimulated growth and yield. Carbon dioxide-induced stimulation was greater for plants stressed by O-3 than for non stressed plants. For example, CO2 at 2.0 times ambient increased 2-yr mean seed yield of Essex by 16, 24, and 81% at O-3 levels of O.4, 0.9, and 1.5 times ambient, respectively. Effects of O-3 and CO2 on seed oil content were variable with numerous cultivar differences. Seed protein content was never affected. Elevated O-3 suppressed oleic acid content in seeds, whereas CO2 increased it; the nature of the O-3 x CO2 interaction for oleic acid was similar to that observed for most yield measures. Carbon dioxide-induced stimulation of plants stressed by O-3 was apparently caused partly by amelioration of O-3 stress. Interactions between O-3 and CO2 must be considered for proper interpretation of cause-effect relationships in CO2 enrichment studies.

KEYWORDS: CHAMBERS, CO2, FIELD, GROWTH, O-3

884

Heagle, A.S., J.E. Miller, D.E. Sherrill, and J.O. Rawlings. 1993. Effects of ozone and carbon-dioxide mixtures on 2 clones of white clover. *New Phytologist 123(4):751-762.*

The effects of mixtures of ozone and carbon dioxide on growth and physiology of an O3-sensitive (NC-S) and an O3-resistant (NC-R) clone of white clover (Trifolium repens L.) were determined. The experiment was performed in a greenhouse with O3 treatments of 5 and 82 nl l-1 (ppb) for 6 h d-1 and CO2 treatments of 380 (ambient), 490,600, and 710 mul l-1 (ppm) for 24 h d-1. Enrichment with CO2 decreased foliar gas exchange (measured as stomatal resistance) of NC-R more than that of NC- S whereas O3 decreased gas exchange of NC-S more than that of NC-R. Ozone caused extensive foliar injury of NC-S but caused only slight injury of NC-R. CO2 enrichment suppressed O3- induced foliar injury of NC-S as measured after 4 wk of exposure, but this effect diminished after 8 wk of exposure. CO2 enrichment decreased the relative chlorophyll content (mug of chlorophyll mg-1 of leaf tissue sampled) but not the total chlorophyll (total chlorophyll in the leaves sampled). There were no O3 x CO2 interactions for foliar chlorophyll. High concentrations of CO2 caused reddening of new leaves near the end of the 8 wk exposure period. CO2 enrichment decreased foliar concentrations of N, P, K, S, Cu, B, and Fe, increased foliar concentrations of Mn, but did not affect Zn, Ca, or Mg. Ozone exposure did not modify the CO2 effects on foliar nutrient concentration. Ozone decreased growth of NC-S but not NC-R while CO2 enrichment stimulated growth of both clones. The highest CO2 concentration appeared to decrease the effects of O3 on growth of NC-S. However, except for a transitory effect on foliar injury, there was no evidence that CO2, at concentrations less than the highest used in this study, will protect white clover from the effects of tropospheric O3.

KEYWORDS: AGRICULTURAL CROPS, ASSESSING IMPACTS, ATMOSPHERIC CO2 ENRICHMENT, ELEVATED CO2, GROWTH, LADINO CLOVER, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, TALL FESCUE PASTURE, WATER-USE

885

Heath, J. 1998. Stomata of trees growing in CO2-enriched air show reduced sensitivity to vapour pressure deficit and drought. *Plant, Cell and Environment 21(11):1077-1088.*

Stomatal conductance (g(s)) and photosynthetic rate (A) mere measured in young beech (Fagus sylvatica), chestnut (Castanea sativa) and oak (Quercus robur) growing in ambient or CO2- enriched air. In oak, g(s) was consistently reduced in elevated CO2, However, in beech and chestnut, the stomata of trees growing in elevated CO2 failed to close normally in response to increased leaf-to-air vapour pressure deficit (LAVPD). Consequently, while g(s) was reduced in elevated CO2 on days with low LAVPD, on warm sunny days (with correspondingly high LAVPD) g(s) was unchanged or even slightly higher in elevated CO2. Furthermore, during drought, g(s) of beech and chestnut was unresponsive to [CO2], over a wide range of ambient LAVPD, whereas in oak g(s) was reduced by an average of 50% in elevated CO2. Stimulation of A by elevated CO2 in beech and chestnut was restricted to days with high irradiance, and was greatest in beech during drought. Hence, most of the additional carbon gain in elevated CO2 was made at the expense of water economy, at precisely those times (drought, high evaporative demand) when mater conservation was most important. Such effects could have serious consequences for drought tolerance, growth and, ultimately, survival as atmospheric [CO2] increases.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, FAGUS-SYLVATICA, GUARD-CELL, HYDRAULIC CONDUCTANCE, LEAF GAS- EXCHANGE, RESPONSES, SIGNAL-TRANSDUCTION, WATER-LOSS REGULATION

886

Heath, J., and G. Kerstiens. 1997. Effects of elevated CO2 on leaf gas exchange in beech and oak at two levels of nutrient supply: Consequences for sensitivity to drought in beech. *Plant, Cell and Environment 20(1):57-67.*

Beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L,) were grown from seed for two whole seasons at two CO, concentrations (ambient and ambient + 250 mu mol mol(-1)) with two levels of soil nutrient supply, Measurements of net leaf photosynthetic rate (A) and stomatal conductance (g(s)) of well-watered plants were taken over both seasons; a drought treatment was applied in the middle of the second growing season to a separate sample of beech drawn from the same population, The net leaf photosynthetic rate of well-watered plants was stimulated in elevated CO2 by an average of 75% in beech and 33% in oak; the effect continued through both growing seasons at both nutrient levels, There were no interactive effects of CO2 concentration and nutrient level on A or g(s) in beech or oak, Stomatal conductance was reduced in elevated CO2 by an average of 34% in oak, but in beech there were no significant reductions in g(s) except under cloudy conditions (-22% in elevated CO2), During drought, there was no effect of CO2 concentration on g(s) in beech grown with high nutrients, but for beech grown with low nutrients, g(s) was significantly higher in elevated CO2, causing more rapid soil drying, With high nutrient supply, soil drying was more rapid at elevated CO2 due to increased leaf area, It appears that beech may substantially increase whole-plant water consumption in elevated CO2, especially under conditions of high temperature and irradiance when damage due to high evaporative demand is most likely to occur, thereby putting itself at risk during periods of drought.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, FAGUS-SYLVATICA L, FOREST, GROWTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, WATER-USE EFFICIENCY

887

Heath, J., G. Kerstiens, and M.T. Tyree. 1997. Stem hydraulic conductance of European beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L.) grown in elevated CO2. *Journal of Experimental Botany 48(312):1487-1489.*

Over two seasons in c. 600 ppm CO2, oak had lower stomatal conductance in CO2-enriched compared to ambient air, Beech showed no response to CO2 concentration on sunny days, Mirroring this pattern, exposure to elevated CO2 reduced whole- shoot hydraulic conductance per unit leaf area in oak, but not in beech.

KEYWORDS: CARBON DIOXIDE, DROUGHT, PLANTS, SEEDLINGS, WATER-USE

888

Hebeisen, T., A. Luscher, and J. Nosberger. 1997. Effects of elevated atmospheric CO2 and nitrogen fertilisation on yield of Trifolium repens and Lolium perenne. *Acta Oecologica-International Journal of Ecology 18(3):277-284.*

Trifolium repens L. and Lolium perenne L. were grown in monocultures and bi-species mixture in a Free Air Carbon Dioxide Enrichment (FACE) experiment at elevated (60 Pa) and ambient (35 Pa) CO2 partial pressure (pCO(2)) for two years. The effects of nitrogen fertilisation (10 and 42 g N m(-2) a(- 1) in 1993; 14 and 56 g N m(-2) a(-1) in 1994) on the growth response to pCO, were investigated in frequently defoliated (7 cuts in 1993; 8 cuts in 1994) swards. The yield of Trifolium in monocultures increased by 22% when grown at elevated pCO(2). In contrast, the yield of Lolium monocultures was not affected (2%) by elevated pCO(2), whereas Lolium increased its root mass considerably. The consequence of these interspecific differences in the CO2 response was an increase in the proportion of Trifolium in the mixed swards from 39% at ambient to 50% at elevated pCO(2). However, the proportion of the species was more strongly affected by N fertilisation than by elevated pCO(2). Based on these 2' results, we conclude that the species proportion in managed grassland may change as the CO2 concentration increases. However, an adapted management may, at least partially, counteract such CO2 induced changes in the proportion of the species.

KEYWORDS: CARBON, ENRICHMENT, GRASSLAND, GROWTH, RYEGRASS, WHITE CLOVER

889

Hebeisen, T., A. Luscher, S. Zanetti, B.U. Fischer, U.A. Hartwig, M. Frehner, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Growth response of Trifolium repens L and Lolium perenne L as monocultures and bi-species mixture to free air CO2 enrichment and management. *Global Change Biology 3(2):149-160.*

Trifolium repens L. and Lolium perenne L. were grown in monocultures and bi-species mixture in a Free Air Carbon Dioxide Enrichment (FACE) experiment at elevated (60 Pa) and ambient (35 Pa) CO2 partial pressure (pCO(2)) for three years. The effects of defoliation frequencies (4 and 7 cuts in 1993; 4 and 8 cuts in 1994/95) and nitrogen fertilization (10 and 42 g m(-2) y(-1) N in 1993; 14 and 56 g m(-2) y(-1) in 1994/95) on the growth response to pCO(2) were investigated. There were significant interspecific differences in the CO2 responses during the first two years, while in the third growing season, these interspecific differences disappeared. Yield of T. repens in monocultures increased in the first two years by 20% when grown at elevated pCO(2). This CO2 response was independent of defoliation frequency and nitrogen fertilization. In the third year, the CO2 response of T. repens declined to 11%. In contrast, yield of L. perenne monocultures increased by only 7% on average over three years at elevated pCO(2). The yield response of L. perenne to CO2 changed according to defoliation frequency and nitrogen fertilization, mainly in the second and third year. The ratio of root/yield of L. perenne increased under elevated pCO(2), low N fertilizer rate, and frequent defoliation, but it remained unchanged in T. repens. We suggest that the more abundant root growth of L. perenne was related to increased N limitation under elevated pCO(2). The consequence of these interspecific differences in the CO2 response was a higher proportion of T. repens in the mixed swards at elevated pCO(2). This was evident in all combinations of defoliation and nitrogen treatments. However, the proportion of the species was more strongly affected by N fertilization and defoliation frequency than by elevated pCO(2). Based on these results, we conclude that the species proportion in managed grassland may change as the CO2 concentration increases. However, an adapted management could, at least partially, counteract such CO2 induced changes in the proportion of the species. Since the availability of mineral N in the soil may be important for the species' responses to elevated pCO(2), more long-term studies, particularly of processes in the soil, are required to predict the entire ecosystem response.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GRASS, MINERAL NUTRITION, NITROGEN-FERTILIZER, ROOT-GROWTH, RYEGRASS, TALLGRASS PRAIRIE, WHITE CLOVER

890

Hedges, L.V., J. Gurevitch, and P.S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology 80(4):1150-1156.*

Meta-analysis provides formal statistical techniques for summarizing the results of independent experiments and is increasingly being used in ecology. The response ratio (the ratio of mean outcome in the experimental group to that in the control group) and closely related measures of proportionate change are often used as measures of effect

magnitude in ecology. Using these metrics for meta-analysis requires knowledge of their statistical properties, but these have not been previously derived. We give the approximate sampling distribution of the log response ratio, discuss why it is a particularly useful metric for many applications in ecology, and demonstrate how to use it in meta-analysis. The meta- analysis of response-ratio data is illustrated using experimental data on the effects of increased atmospheric CO2 on plant biomass responses.

KEYWORDS: CO2, METAANALYSIS

891

Heifetz, P.B., A. Lers, D.H. Turpin, N.W. Gillham, J.E. Boynton, and C.B. Osmond. 1997. dr and spr/sr mutations of Chlamydomonas reinhardtii affecting D1 protein function and synthesis define two independent steps leading to chronic photoinhibition and confer differential fitness. *Plant, Cell and Environment 20(9):1145-1157.*

The effects of introduced chloroplast gene mutations affecting D1 synthesis, turnover and function on photosynthesis, growth and competitive ability were examined in autotrophic cultures of Chlamydomonas reinhardtii (Chlorophyta) adapted to low or high irradiance. Few discernible effects were evident when the mutants were grown in low light (LL, 70 mu mol m(-2) s(-1)). The herbicide-resistant psbA mutation Ser(264) --> Ala (dr) slowed electron transfer and accelerated D1 degradation in cells grown under high light (HL, 600 mu mol m(-2) s(-1)). The maximum rate of light- and CO2-saturated photosynthesis, cell growth rate and competitive ability in the dr mutant were reduced compared to wild type under HL. However, the wild-type rate of D1 synthesis in dr was adequate to compensate for accelerated D1 degradation. 16S rRNA mutations conferring resistance to streptomycin and spectinomycin (spr/sr) that altered chloroplast ribosome structure and assembly were used to inhibit chloroplast protein synthesis. In spr/sr cells grown under HL, D1 synthesis was reduced by 40-60% compared to wild type and D1 degradation was accelerated, leading to a 4-fold reduction in D1 pool size. The reduced D1 levels were accompanied by an elevation of F-o and a decline in F-v/F-m, quantum yield and maximum rate of CO2-saturated photosynthesis. Chemostat experiments showed that the growth rate and competitive ability of spr/sr were reduced against both wild type and dr.

KEYWORDS: 32-KILODALTON PROTEIN, CHLOROPHYLL FLUORESCENCE, CHLOROPLAST, LIGHT-INTENSITY, PHALARIS-PARADOXA, PHOTOSYNTHESIS, PHOTOSYSTEM, RIBOSOMAL-RNA GENES, TRIAZINE RESISTANCE, ULVA-ROTUNDATA

892

Heilman, J.L., D.R. Cobos, F.A. Heinsch, C.S. Campbell, and K.J. McInnes. 1999. Tower-based conditional sampling for measuring ecosystem-scale carbon dioxide exchange in coastal wetlands. *Estuaries 22(3A):584-591.*

Long-term measurements of CO2 exchange between coastal wetlands and the atmosphere are necessary to improve our understanding of the role these ecosystems play in the global carbon cycle, and the response of these systems to environmental change. We conducted research to adapt and evaluate tower-based conditional sampling as a method for measuring net CO2 exchange (NCE) at the ecosystem scale on a continuous basis. With conditional sampling, NCE is determined from the product of the standard deviation of vertical wind velocity, the difference in CO2 concentration between updrafts and downdrafts in the constant flux portion of the boundary layer above the surface, and an empirical coefficient. We constructed a system that used a sonic anemometer to measure vertical wind velocity (w) and control a high-speed three-way valve that diverted air from updrafts and down,drafts into separate sample lines, depending on the direction of w. An infrared gas analyzer was used to measure the concentration difference. The conditional sampling system was installed and tested in a marsh in the Nueces River Delta near Corpus Christi, Texas, as part of a long-term study of effects of freshwater inflow on CO2 flux. System accuracy was evaluated by comparing conditional sampling measurements of water vapor flux with independent estimates obtained with the Bowen ratio method. Average daily flux estimates for the two methods agreed to within 13%. Measurements showed that freshwater inflow due to flooding of the Nueces River increased NCE by increasing CO2 assimilation and decreasing CO2 efflux. Over a 65-d period, daily NCE varied from a maximum gain of 0.16 mol CO2 m(-2) d(-1) during flooding to a maximum loss of - 0.14 mol CO2 m(-2) d(-1) when the marsh dried. Our study showed that conditional sampling was well suited for quantifying CO2 exchange in coastal wetlands on a diel, daily, and seasonal basis.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CANOPY PHOTOSYNTHESIS, CHESAPEAKE BAY, CROP, ELEVATED CO2, FIELD, FLUX MEASUREMENT, SEQUESTRATION, USE EFFICIENCY, WATER

893

Heineke, D., F. Kauder, W. Frommer, C. Kuhn, B. Gillissen, F. Ludewig, and U. Sonnewald. 1999. Application of transgenic plants in understanding responses to atmospheric change. *Plant, Cell and Environment 22(6):623-628.*

Acclimation of plants to an increase in atmospheric carbon dioxide concentration is a well described phenomenon, It is characterized by an increase in leaf carbohydrates and a degradation of ribulose 1,5-bisphosphate carboxylase protein (Rubisco) leading in the long term to a lower rate of CO2 assimilation than expected from the kinetic constants of Rubisco, This article summarizes studies with transgenic plants grown in elevated pCO(2) which are modified in their capacity of CO2 fixation, of sucrose and starch synthesis, of triosephosphate and sucrose transport and of sink metabolism of sucrose, These studies show that a feedback accumulation of carbohydrates in leaves play only a minor role in acclimation, because leaf starch synthesis functions as an efficient buffer for photoassimilates. There is some evidence that in elevated pCO(2), plants grow faster and senescence is induced earlier.

KEYWORDS: ANTISENSE REPRESSION, ELEVATED CO2, EXPRESSION, INHIBITION, PHOTOSYNTHETIC ACCLIMATION, POTATO PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOBACCO, TRIOSE-PHOSPHATE TRANSLOCATOR, YEAST- DERIVED INVERTASE

894

Heissner, A. 1996. A simple model of greenhouse climate for short term control of temperature, air humidity, and CO2 concentration. *Gartenbauwissenschaft 61(6):289-300.*

A simple greenhouse climate model was designed for short term control of temperature, air humidity, and CO2 concentration. The model is based on the balances of thermal energy, water vapour, and carbon dioxide and is represented by a system of three nonlinear differential equations of the first order. The reaction of the canopy is taken into consideration through empirical models of CO2 gas exchange and transpiration of tomato plants. Model inputs are the meteorological conditions in the open (temperature, air humidity, CO2 concentration, global radiation, and wind velocity), the temperature of the ground surface in the greenhouse, and the temperature on the greenhouse cover as well as four control variables (heating, ventilation, CO2 enrichment, and moistening of the air). Measurements were carried out in two greenhouses with glass and plastic film cover under conditions of ventilation to estimate model quantities and to test the suitability of the

model fort prognosis. By means of simulations possibilities for the comparison of control strategies were demonstrated.

KEYWORDS: SYSTEM, TRANSPIRATION

895

Hemming, J.D.C., and R.L. Lindroth. 1999. Effects of light and nutrient availability on aspen: Growth, phytochemistry, and insect performance. *Journal of Chemical Ecology 25(7):1687-1714.*

This study explored the effect of resource availability on plant phytochemical composition within the framework of carbon- nutrient balance (CNB) theory. We grew quaking aspen (Populus tremuloides) under two levels of light and three levels of nutrient availability and measured photosynthesis, productivity, and foliar chemistry [water, total nonstructural carbohydrates (TNC), condensed tannins, and phenolic glycosides]. Gypsy moths (Lymantria dispar) and forest tent caterpillars (Malacosoma disstria) were reared on foliage from each of the treatments to determine effects on insect performance. Photosynthetic rates increased under high light, but were not influenced by nutrient availability. Tree growth increased in response to both the direct and interactive effects of light and nutrient availability. Increasing light reduced foliar nitrogen, while increasing nutrient availability increased foliar nitrogen. TNC levels were elevated under high light conditions, but were not influenced by nutrient availability. Starch and condensed tannins responded to changes in resource availability in a manner consistent with CNB theory; levels were highest under conditions where tree growth was limited more than photosynthesis (i.e., high light-low nutrient availability). Concentrations of phenolic glycosides, however, were only moderately influenced by resource availability. In general, insect performance varied relatively little among treatments. Both species performed most poorly on the high light-low nutrient availability treatment. Because phenolic glycosides are the primary factor determining aspen quality for these insects, and because levels of these compounds were minimally affected by the treatments, the limited response of the insects was not surprising. Thus, the ability of CNB theory to accurately predict allocation to defense compounds depends on the response of specific allelochemicals to changes in resource availability. Moreover, whether allelochemicals serve to defend the plant depends on the response of insects to specific allelochemicals. Finally, in contrast to predictions of CNB theory, we found substantial allocation to storage and defense compounds under conditions in which growth was carbon-limited (e.g., low light), suggesting a cost to defense in terms of reduced growth.

KEYWORDS: BETULA-PENDULA ROTH, CLONAL VARIATION, ELEVATED ATMOSPHERIC CO2, FOLIAR CHEMISTRY, FOREST TENT CATERPILLARS, HARDWOOD SEEDLINGS, MINERAL NUTRITION, NO3 AVAILABILITY, POPULUS-TREMULOIDES MICHX, SUCCESSIONAL STATUS

896

Hendrey, G.R. 1992. Global greenhouse studies - need for a new approach to ecosystem manipulation. *Critical Reviews in Plant Sciences 11(2-3):61-74.*

KEYWORDS: BALANCE, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, FIELD, GROWTH, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TUSSOCK TUNDRA

897

Hendrey, G.R., D.S. Ellsworth, K.F. Lewin, and J. Nagy. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO2. *Global Change Biology 5(3):293-309.*

A free-air CO2 enrichment (FACE) system was designed to permit the experimental exposure of tall vegetation such as stands of forest trees to elevated atmospheric CO2 concentrations ([CO2](a)) without enclosures that alter tree microenvironment. We describe a prototype FACE system currently in operation in forest plots in a maturing loblolly pine(Pinus taeda L.) stand in North Carolina, USA. The system uses feedback control technology to control [CO2] in a 26 m diameter forest plot that is over 10 m tall, while monitoring the 3D plot volume to characterize the whole-stand CO2 regime achieved during enrichment. in the second summer season of operation of the FACE system, atmospheric CO2 enrichment was conducted in the forest during all daylight hours for 96.7% of the scheduled running time from 23 May to 14 October with a preset target [CO2] of 550 mu mol mol(-1), approximate to 200 mu mol mol(-1) above ambient [CO2]. The system provided spatial and temporal control of [CO2] similar to that reported for open-top chambers over trees, but without enclosing the vegetation. The daily average daytime [CO2] within the upper forest canopy at the centre of the FACE plot was 552 +/- 9 mu mol mol-l (mean +/- SD). The FACE system maintained I-minute average [CO2] to within +/- 110 mu mol mol(-1) of the target [CO2] for 92% of the operating time. Deviations of [CO2] outside of this range were short-lived (most lasting < 60 s) and rare, with fewer than 4 excursion events of a minute or longer per day. Acceptable spatial control of [CO2] by the system was achieved,,with over 90% of the entire canopy volume within +/- 10% of the target [CO2] over the exposure season. CO2 consumption by the FACE system was much higher than for open- top chambers on an absolute basis, but similar to that of open- top chambers and branch bag chambers on a per unit volume basis. CO2 consumption by the FACE system was strongly related to windspeed, averaging 50 g CO2 m(-3) h(-1) for thestand for an average windspeed of 1.5 m s(-1) during summer. The [CO2] control results show that the free-air approach is a tractable way to study long-term and short-term alterations in trace gases, even within entire tall forest ecosystems. The FACE approach permits the study of a wide range of forest stand and ecosystem processes under manipulated [CO2](a) that were previously impossible or intractable to study in true forest ecosystems.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, FACE, FIELD CROPS, GROWTH, OPEN-TOP CHAMBERS, PHOTOSYNTHESIS, PINE PINUS- TAEDA, SHORT- TERM, STOMATAL CONDUCTANCE, TEMPERATE TREES

898

Hendrey, G.R., and B.A. Kimball. 1994. The face program. *Agricultural and Forest Meteorology 70(1-4):3-14.*

A large, cooperative, integrated experimental program utilizing free-air CO2 enrichment (FACE) is being conducted to expose plants to elevated concentrations of CO2. The goals are to evaluate the effects of increasing atmospheric CO2 on plants and ecosystems and, in the long run, to contribute to the evaluation of terrestrial plant feedback regulation on the rate of change of CO2 in the atmosphere. Having no walls, the FACE system allows plants to be grown under realistic microclimate and CO2 conditions expected to prevail in the mid-twenty-first century. Data obtained under such conditions are needed for validation of models being developed to predict the effects of increasing CO2 and changing climate variables on plants, ecosystems, agricultural productivity and water resources. Setup costs for the FACE systems used in these experiments are similar to the costs of field chamber systems. Although annual operating costs are about three times the cost of field chambers, FACE plots are relatively large, leading to an economy of scale, so that per unit of treated plant material, FACE systems are the least expensive approach for well- integrated field experiments. These features have provided an incentive to conduct comprehensive FACE experiments with many cooperating scientists working together to measure numerous plant, soil and micrometeorological parameters, as described in the collection of papers in this special issue of 'Agricultural

and Forest Meterology'.

KEYWORDS: AIR CO-2 ENRICHMENT, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ELEVATED CO2, EXPOSURE, FIELD, OPEN-TOP CHAMBER, PHOTOSYNTHESIS, POPULATIONS, VEGETATION

899

Hendrey, G.R., K.F. Lewin, and J. Nagy. 1993. Free air carbon-dioxide enrichment - development, progress, results. *Vegetatio 104:17-31.*

Credible predictions of climate change depend in part on predictions of future CO2 concentrations in the atmosphere. Terrestrial plants are a large sink for atmospheric CO2 and the sink rate is influenced by the atmospheric CO2 concentration. Reliable field experiments are needed to evaluate how terrestrial plants will adjust to increasing CO2 and thereby influence the rate of change of atmospheric CO2. Brookhaven National Laboratory (BNL) has developed a unique Free-Air CO2 Enrichment (FACE) system for a cooperative research program sponsored by the U.S. Department of Energy and U.S. Department of Agriculture, currently operating as the FACE User Facility at the Maricopa Agricultural Center (MAC) of the University of Arizona. The BNL FACE system is a tool for studying the effects of CO2 enrichment on vegetation and natural ecosystems, and the exchange of carbon between the biosphere and the atmosphere, in open-air settings without any containment. The FACE system provides stable control of CO2 at 550 ppm +/- 10%, based on 1- min averages, over 90% of the time. In 1990, this level of control was achieved over an area as large as 380 m2, at an annual operating cost of $668 m-2. During two field seasons of enrichment with cotton (Gossypium hirsutum) as the test plant, enrichment to 550 ppm CO2 resulted in significant increases in photosynthesis and biomass of leaves, stems and roots, reduced evapotranspiration, and changes in root morphology. In addition, soil respiration increased and evapotranspiration decreased.

KEYWORDS: FIELD CROPS, FUMIGATION, POLLUTION, SYSTEM

900

Hendrey, G.R., S.P. Long, I.F. McKee, and N.R. Baker. 1997. Can photosynthesis respond to short-term fluctuations in atmospheric carbon dioxide? *Photosynthesis Research 51(3):179-184.*

Rapid and irregular variations of atmospheric CO2 concentrations (c(a)) occur in nature but are often very much more pronounced and frequent when artificially enriching CO2 concentrations in simulating the future atmosphere. Therefore, there is the danger that plant responses at elevated CO2 in fumigation experiments might reflect the increased Frequency and amplitude of fluctuation in concentration as well as the increase in average concentration. Tests were conducted to determine whether the photosynthetic process could sense such fluctuations in c(a). Instantaneous chlorophyll fluorescence (F-t) was monitored for wheat leaves (Triticum aestivum cv. Hereward) exposed to c(a) oscillating symmetrically by 225 mu mol mol(-1) about a c(a) set point concentration of 575 or 650 mu mol mol(-1). No F-t response was detected to half-cycle step changes in c(a) lasting less than two seconds, but at half- cycles of two seconds or longer, the response of F-t was pronounced. In order to determine the in vivo linear electron transport rate (J) the O-2 concentration was maintained at 21 mmol mol(-1) to eliminate photorespiration. J which is directly proportional to the rate of CO2 uptake under these conditions, was not significantly changed at half-cycles of 30 s or less but was decreased by half-cycles of 60 s or longer. It was inferred that if duration of an oscillation is less than 1 minute and is symmetrical with respect to mean CO2 concentration, then there is no effect on current carbon uptake, but oscillations of 1 minute or more decrease photosynthetic CO2 uptake in wheat.

KEYWORDS: ELECTRON-TRANSPORT, LEAVES, MESOPHYLL CONDUCTANCE, ZEA-MAYS

901

Hendrix, D.L., J.R. Mauney, B.A. Kimball, K. Lewin, J. Nagy, and G.R. Hendrey. 1994. Influence of elevated co2 and mild water-stress on nonstructural carbohydrates in field-grown cotton tissues. *Agricultural and Forest Meteorology 70(1-4):153-162.*

Root, stem and leaf tissues, from cotton plants exposed to CO2 at ambient (370 mumol mol-1 (control)) or elevated (550 mumol mol-1 (FACE; free-air carbon dioxide enrichment)) levels in the field during the 1990 and 1991 growing seasons, were analyzed for nonstructural carbohydrates (glucose, fructose, sucrose and starch). Besides the FACE treatment, these plants were also exposed to two irrigation levels: 100% and 67% replacement of evapotranspiration. FACE had a greater effect upon cotton plant nonstructural carbohydrates than did irrigation treatments. Leaf carbohydrate content was increased by FACE, but this increase was much more pronounced in the stems and roots. Starch and soluble sugars in leaves in FACE plots tended to be consistently greater than in control leaves, without much change in carbohydrate content during the growing season. In contrast, root and stem, starch and soluble sugar pools were strongly increased by FACE and fluctuated strongly during the growing season. In both seasons, stem and taproot nonstructural carbohydrate content passed through a minimum during periods of heavy boll set. The fluctuations in stem and root carbohydrate content were therefore probably caused by the varying metabolic demands of the developing plant. These results suggest that a significant effect of CO2 enrichment on starch-accumulating plants is an increase of nonstructural carbohydrate, especially starch, in nonleaf storage pools. This buildup occurs somewhat independently of the water status of the plant, and these enlarged pools can be drawn upon by the growing plant to maintain growth during periods of high metabolic demand.

KEYWORDS: ATMOSPHERIC CO2, CO2, ENRICHMENT, EXPORT, PLANT GROWTH, TEMPERATURE, TUSSOCK TUNDRA, YIELD

902

Hendry, M.J., C.A. Mendoza, R.A. Kirkland, and J.R. Lawrence. 1999. Quantification of transient CO2 production in a sandy unsaturated zone. *Water Resources Research 35(7):2189-2198.*

Temporal and spatial respiration rates were determined in a 5.7-m thick, sandy, unsaturated zone over a 550-day period using measured CO2 concentrations, CO2 fluxes to the atmosphere, moisture contents, and temperatures. Cyclical patterns in CO2 concentrations were measured in duplicate nests of nine gas samplers. Maximum CO2 gas concentrations occurred during the summer (0.85-1.22%), and minimum concentrations occurred during the winter (0.04-0.24%). CO2 gas concentrations decreased with increasing depth during the summer and increased with depth during the winter. A one-dimensional finite element model was developed to quantify transient respiration rates through the unsaturated zone. The model was calibrated to the measured CO2 concentrations. Temperature and moisture content variations were represented with an analytical expression and linear interpolation of field-measured values, respectively, in the model. Simulation results provided very good approximations to the field-measured CO2 concentrations, but predicted CO2 fluxes to the atmosphere were higher than measured. Respiration rates ranged from 5 mu g C g(-1) d(-1) in the soil horizon during the summer to about <10(-4) mu g C g(-1) d(-1) in unsaturated sections of the C horizon. A sensitivity analysis showed that the respiration rates in the C horizon must be <10(-3) mu g C g(-1) d(-1) and that the majority of the elevated CO2 concentrations in this thick unsaturated zone are the result of respiration in the soil horizon. Overall, roots contribute about 75% of the CO2 in the summer months. O-2 gas, microbial analyses, and the distribution of root biomass supported this conclusion. These

observations also imply that although microorganisms are present in subsurface environments their in situ activity in this sandy unsaturated zone may be very low.

KEYWORDS: AQUIFER, ATMOSPHERE, BIODEGRADATION, CARBON DIOXIDE, FIELD CONDITIONS, FOREST, MICROBIAL ACTIVITY, SOIL RESPIRATION, TEMPERATURES, TRANSPORT

903

Henning, F.P., C.W. Wood, H.H. Rogers, G.B. Runion, and S.A. Prior. 1996. Composition and decomposition of soybean and sorghum tissues grown under elevated atmospheric carbon dioxide. *Journal of Environmental Quality 25(4):822-827.*

It has been hypothesized that changes in both quantity and quality of plant residue inputs to soils as atmospheric carbon dioxide (CO2) concentration increases may alter carbon (C) and nitrogen (N) turnover rates and pool sizes, We determined the effect of elevated atmospheric CO2 on plant tissue quality, and flow modifications in tissue quality affect C and N mineralization. Soybean [C-3; Glycine max (L.) Merr. cv. Stonewall] and sorghum [C-4; Sorghum bicolor (L.) Moen, cv. Savanna 5] were grown under elevated (704.96 +/- 0.33 mu mol CO2 mol(-1)) and ambient (357.44 +/- 0.12 mu mol CO2 mol(-1)) atmospheric CO2 in open-top chambers, Leaf and stem tissues were separated from harvested plants and analyzed for C, N, lignin, and cellulose. Tissues were applied to Norfolk loamy sand (fine-loamy, siliceous, thermic Typic Kandiudult) and aerobically incubated for 70-d to determine C and N mineralization, C turnover, relative N mineralization, and C/N mineralized. Elevated CO2 had no effect on plant residue C concentration, but N concentration of soybean leaves and stems and sorghum stems was reduced; however, CO2 enrichment increased C/N ratio and lignin concentration for only sorghum stems and soybean leaves, respectively. Source of plant residue (i.e., produced under either elevated or ambient CO2) had no impact on soil C turnover, relative N mineralization, cumulative C and N mineralization, and C/N mineralized, These data suggest that increasing atmospheric CO2 will have little effect on composition or decomposition of field crop residues. Thus, since CO2 enrichment results in increased photosynthetic C fixation, the possibility exists For increased soil C storage under field crops in an elevated CO2 world.

KEYWORDS: CO2 LEVELS, DYNAMICS, NITROGEN, ORGANIC-MATTER, RESPONSES, SYSTEMS

904

Herbert, D.A., E.B. Rastetter, G.R. Shaver, and G.I. Agren. 1999. Effects of plant growth characteristics on biogeochemistry and community composition in a changing climate. *Ecosystems 2(4):367-382.*

Vegetation growth characteristics influence ecosystem biogeochemistry and must be incorporated in models used to project biogeochemical responses to climate variations. We used a multiple-element limitation model (MEL) to examine how variations in nutrient use efficiency (NUE) and net primary production to biomass ratio (nPBR) affect changes in ecosystem C stocks after an increase in temperature and atmospheric CO2. nPBR influences the initial rates of response, but the magnitude and direction of long-term responses are determined NUE. MEL was used to simulate responses to climate change in communities composed of two species differing in nPBR and/or NUE. When only nPBR differed between the species, the high-nPBR species outgrew the low-nPBR species early in the simulations, but the shift in dominance was transitory because of secondary N limitations. High-NUE and were therefore favored under elevated CO2. Increased temperature stimulated N release from soil organic matter (SOM) and therefore favored low-NUE species. The combined release from C and N limitation under the combination of increased temperature and elevated CO2 favored high-NUE species. High C:N litter from high-NUE species limited the N-supply rate from SOM, which favors the dominance of the high-NUE species in the short term. However, in the long term increased litter production resulted in SOM accumulation, which reestablished a N supply rate favorable to the reestablishment and dominance of the low-NUE species. Conditions then reverted to a state favorable to the high-NUE species.

KEYWORDS: ALASKAN TUNDRA, BIOLOGICAL INVASION, CARBON STORAGE, GLOBAL CHANGE, MYRICA-FAYA, NITROGEN, RESPONSES, TERRESTRIAL ECOSYSTEMS, TROPICAL FORESTS, VEGETATION TYPES

905

Herbst, M., and G. Hormann. 1998. Predicting effects of temperature increase on the water balance of beech forest - An application of the 'KAUSHA' model. *Climatic Change 40(3-4):683-698.*

The water balance model 'KAUSHA' (Halldin, 1989) was applied to a 100-year-old beech (Fagus sylvatica L.) forest in northern Germany. Overall, a satisfying agreement between modelled evapotranspiration values and independent micrometeorological measurements (Bowen ratio energy balance method) could be observed, although for rainy days KAUSHA showed a tendency to overestimate evapotranspiration. The model was used to predict the effects of a climate warming on the water budgets of the forest. It is shown that a temperature increase of 2 degrees C due to a rising CO2 content of the atmosphere will not change the yearly totals of evapotranspiration significantly, but could have serious effects on the soil water balance during the vegetation period. Because under climate change conditions a higher amount of the available soil water has already been evaporated in winter and spring, soil water content will limit the transpiration of the trees from July to September much more strongly. Therefore, the yield of beech forest might also suffer from drought effects. It can be concluded that a better knowledge of the seasonal distribution of rainfall under climate change conditions is indispensable for predicting effects of rising temperatures and CO2 concentrations on ecosystems.

KEYWORDS: CLIMATE-CHANGE SCENARIOS, CO2- ENRICHMENT, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, EVAPOTRANSPIRATION, GROWTH, OCEAN-ATMOSPHERE MODEL, RESPONSES, SCOTS PINE, SIMULATION

906

Herrick, J.D., and R.B. Thomas. 1999. Effects of CO2 enrichment on the photosynthetic light response of sun and shade leaves of canopy sweetgum trees (Liquidambar styraciflua) in a forest ecosystem. *Tree Physiology 19(12):779-786.*

To investigate whether sun and shade leaves respond differently to CO2 enrichment, we examined photosynthetic light response of sun and shade leaves in canopy sweetgum (Liquidambar styraciflua L.) trees growing at ambient and elevated (ambient + 200 mu l l(-1)) atmospheric CO2 in the Brookhaven National Laboratory/Duke University Free Air CO2 Enrichment (FACE) experiment. The sweetgum trees were naturally established in a 15-year-old forest dominated by loblolly pine (Pinus taeda L.). Measurements were made in early June and late August 1997 during the first full year of CO2 fumigation in the Duke Forest FACE experiment. Sun leaves had a 68% greater leaf mass per unit area, 63% more leaf N per unit leaf area, 27% more chlorophyll per unit leaf area and 77% greater light-saturated photosynthetic rates than shade leaves. Elevated CO2 strongly stimulated light-saturated photosynthesis of sun and shade leaves in June and August; however, the relative photosynthetic enhancement by elevated CO2 for sun leaves was mon than double the relative enhancement of shade leaves. Elevated CO2

stimulated apparent quantum yield by 30%. but there was no interaction between CO2 and leaf position. Daytime leaf-level carbon gain extrapolated from photosynthetic light response curves indicated that sun leaves were enhanced 98% by elevated CO2, whereas shade leaves were enhanced 41%. Elevated CO2 did not significantly affect leaf N per unit area in sun or shade leaves during either measurement period. Thus, the greater CO2 enhancement of light-saturated photosynthesis in sun leaves than in shade leaves was probably a result of a greater amount of nitrogen per unit leaf area in sun leaves. A full understanding of the effects of increasing atmospheric CO2 concentrations on forest ecosystems must take account of the complex nature of the light environment through the canopy and how light interacts with CO2 to affect photosynthesis.

KEYWORDS: ATMOSPHERIC CO2, DECIDUOUS FOREST, DIFFERENT IRRADIANCE LEVELS, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, LOBLOLLY-PINE, LONG-TERM ELEVATION, NITROGEN LEVEL, PINUS-TAEDA SEEDLINGS, WATER-STRESS

907

Herrmann, B., and U. Feller. 1998. CO2, light and temperature influence senescence and protein degradation in wheat leaf segments. *Physiologia Plantarum 103(3):320-326.*

Effects of environmental conditions influencing photosynthesis and photorespiration on senescence and net protein degradation were investigated in segments from the first leaf of young wheat (Triticum aestivum cv. Arina) plants. The segments were floated on H2O at 25, 30 or 35 degrees C in continuous light (PAR: 50 or 150 mu mol m(-2) s(-1)) in ambient air and in CO2- depleted air. Stromal enzymes, including phosphoglycolate phosphatase, glutamine synthetase, ferredoxin-dependent glutamate synthase, phosphoribulokinase, and the peroxisomal enzyme, glycolate oxidase, were detected by SDS-PAGE followed by immunoblotting with specific antibodies. In general, the net degradation of proteins and chlorophylls was delayed in CO2- depleted air. However, little effect of CO2 on protein degradation was observed at 25 degrees C under the lower level of irradiance. The senescence retardation by the removal of CO2 was most pronounced at 30 degrees C and at the higher irradiance. The stromal enzymes declined in a coordinated manner. Immunoreactive fragments from the degraded polypeptides were in most cases not detectable. However, an insolubilized fragment of glycolate oxidase accumulated in vivo, especially at 25 degrees C in the presence of CO2. Detection of this fragment was minimal after incubation at 30 degrees C and completely absent on blots from segments kept at 35 degrees C. In CO2-depleted air, the fragment was only weakly detectable after incubation at 25 degrees C. The results from these investigations indicate that environmental conditions that influence photosynthesis may interfere with senescence and protein catabolism in wheat leaves.

KEYWORDS: ACCLIMATION, ACCUMULATION, CALVIN-CYCLE, DETACHED LEAVES, ELEVATED CO2, EXPRESSION, GLUTAMINE-SYNTHETASE, LIMITING CO2, PHOTOSYNTHESIS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

908

Hertstein, U., J. Colls, F. Ewert, and M. van Oijen. 1999. Climatic conditions and concentrations of carbon dioxide and air pollutants during 'ESPACE-wheat' experiments. *European Journal of Agronomy 10(3-4):163-169.*

A major objective of the ESPACE-wheat programme was to perform by means of open-top chambers (OTCs) 'standardised' experimental investigations of spring wheat responses to increased atmospheric CO2 and O-3 concentrations and to other environmental stresses at different locations in Europe, representing a broad range of different climatic conditions. From 1994 to 1996 a total number of 25 OTC experiments were carried out. In addition, four growth chamber experiments focusing on key physiological processes of wheat growth in CO2- enriched air were performed. According to the specific needs for subsequent modelling purposes, environmental data were collected during experiments, i.e. air temperature, global radiation, humidity and trace gas concentrations. In the present paper results of these measurements are summarised. It was shown, that the OTC-experiments covered a considerable range of growing season mean-air-temperatures (13.0-23.4 degrees C) and global irradiances (10.8-18.1 MJ m(-2) d(-1)), the most important driving variables for crop growth simulation models. Mean concentrations of CO2 and O-3 in ambient air and in different treatments illustrated the observed variability of trace gas exposures between different experiments. Implications for subsequent analyses of biological response data are discussed.

909

Hertstein, U., A. Fangmeier, and H.J. Jager. 1996. ESPACE-wheat (European Stress Physiology and Climate Experiment-project 1: Wheat): Objectives, general approach, and first results. *Journal of Applied Botany-Angewandte Botanik 70(5-6):172-180.*

The "European Stress Physiology and Climate Experiment - project 1: wheat" (acronym: ESPACE-wheat) is funded by the EU since 1994. In the present paper the projects goals, the general methodological approach, and a summary of the experimental work performed in 1994 and 1995 are described. Main objectives of the project are 1) to investigate experimentally the sensitivity of wheat growth, development and productivity to changes in CO2 concentration, climatic variables and other physiological stresses, 2) to use experimental data for extension, improvement and validation of process-based wheat growth simulation models, and 3) to use models for assessments of the influences on crops of climatic change, increasing CO2 concentration and additional physiological stresses in Europe. Most experimental investigations are being performed by means of open-top chambers (OTC's) according to a common standard protocol to meet specific data requirements for model construction and validation. ESPACE-wheat OTC-experiments in 1994 and 1995 are summarized and the principal methods of data evaluation are presented by analyzing responses of grain yield and aboveground biomass of spring wheat, cv. Minaret, to CO2 enrichment and other factors varied in experiments at different sites. The mean observed CO2-doubling responses was about 1.4, i.e. grain yield and biomass production were increased by about 40% compared to growth in ambient CO2 concentration. However, there was a large variability of responses between sites and years. Results are discussed with respect to modeling attempts.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CROP RESPONSES, IMPACTS, OZONE, PLANTS, VEGETATION

910

Hew, C.S., S.E. Hin, J.W.H. Yong, S.S. Gouk, and M. Tanaka. 1995. In-vitro co2 enrichment of cam orchid plantlets. *Journal of Horticultural Science 70(5):721-736.*

Increased growth of an in vitro-propagated CAM orchid hybrid Mokara 'White' was obtained using a novel method of COP enrichment in an optimized photoautotrophic open system compared with the conventional closed system of culture. The optimization process for the open system involved the manipulation of external CO2 concentrations (0.03%, 1% and 10%), sucrose requirements, light intensities (80 and 200 mu mol m(-2) s(-1)) and the venting of headspace ethylene from the culture vessels. The physiological basis for increased growth in these CAM orchid plantlets after three months was attributed to the direct

effects of elevated CO2 resulting in higher CAM activity for the plantlets and to the elevated CO2 present in the system which might interact with the ethylene present thereby reducing the inhibition of growth of plantlets due to ethylene.

KEYWORDS: FIXATION, GROWTH, INVITRO

911

Heyworth, C.J., G.R. Iason, V. Temperton, P.G. Jarvis, and A.J. Duncan. 1998. The effect of elevated CO2 concentration and nutrient supply on carbon-based plant secondary metabolites in Pinus sylvestris L. *Oecologia 115(3):344-350.*

This study investigated changes in carbon-based plant secondary metabolite concentrations in the needles of Pinus sylvestris saplings, in response to longterm elevation of atmospheric CO?, at two rates of nutrient supply. Experimental trees were grown for 3 years in eight open-top chambers (OTCs), four of which were maintained at ambient (similar to 350 mu mol mol(-1)) and four at elevated (700 mu mol mol(-1)) CO2 concentrations, plus four open air control plots. Within each of these treatments, plants received either high (7.0 g N m(-2) year(-1) added) or low (no nutrients added) races of nutrient supply for two years. Needles from lateral branches were analysed chemically for concentrations of condensed tannins and monoterpenes. Biochemical determinations of cellulase digestibility and protein precipitating capacity of their phenolic extracts were made because of their potential of importance in ecological interactions between pine and other organisms including herbivores and decomposers. Elevated CO2 concentration caused an increase ($P < 0.05$) in dry mass per needle, tree height and the concentration of the monoterpene alpha-pinene, but there were no direct effects of CO2 concentration on any of the other chemical measurements made. High nutrient availability increased cellulase digestibility of pine needles. There was a significant negative effect of the OTCs on protein precipitating capacity of the needle extracts in comparison to the open-air controls. Results suggest that predicted changes in atmospheric CO2 concentration will be insufficient to produce large changes in the concentration of condensed tannins and monoterpenes in Scots pine. Processes which are influenced by these compounds, such as decomposition and herbivore food selection; along with their effects on ecosystem functioning, are therefore unlikely to be directly affected through changes in these secondary metabolites.

KEYWORDS: ALLELOCHEMICALS, ATMOSPHERIC CO2, BALANCE, CONTORTA, DIOXIDE CONCENTRATION, ECOSYSTEMS, FERTILIZATION, PERFORMANCE, RESPONSES, TANNIN

912

Hibberd, J.M., P. Richardson, R. Whitbread, and J.F. Farrar. 1996. Effects of leaf age, basal meristem and infection with powdery mildew on photosynthesis in barley grown in 700 mu mol mol(-1) CO2. *New Phytologist 134(2):317-325.*

The rate of net photosynthesis in the second leaf of barley was higher in 700 than 350 mu mol mol(-1) CO2 when measured in the CO2 concentration in which the plants were grown, but the magnitude of this difference decreased as the leaf aged. Infection by powdery mildew accelerated the decline in net photosynthesis of leaves grown in either 350 or 700 mu mol mol(-1) CO2. A/C-i curves allowed the reduction in net photosynthesis of plants exposed to 700 mu mol mol(-1) CO2 or after infection by powdery mildew to be related to changes in the carboxylation efficiency or in the regeneration of ribulose 1,5-bisphosphate. The carboxylation efficiency declined in plants exposed to 700 mu mol mol(-1) CO2. In plants infected with powdery mildew, the reduction in net photosynthesis was associated with both reduced carboxylation efficiency and reduced ability to regenerate ribulose 1,5-bisphosphate. Reduced carboxylation efficiency of the second leaf of plants grown in 700 mu mol mol(-1) CO2 was not associated with a reduction in the concentration of rubisco within the leaf. In contrast to the presence of a close exogenous sink, leaf age had large effects on the acclimation of photosynthesis to 700 mu mol mol(-1) CO2.

KEYWORDS: ACCLIMATION, BROWN RUST, CARBON DIOXIDE, GAS-EXCHANGE, LEAVES, PROTEIN, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STOMATAL CONDUCTANCE, TOMATO PLANTS

913

Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Carbohydrate metabolism in source leaves of barley grown in 700 mu mol mol(-1) CO2 and infected with powdery mildew. *New Phytologist 133(4):659-671.*

Soluble carbohydrate accumulated faster in second leaf blades of barley when plants were grown in 700 mu mol mol(-1) CO2 rather than 350 mu mol mol(-1) CO2. Infection of the second leaf blade by powdery mildew had no effect on the concentration of soluble carbohydrate until 6 d after inoculation when it was lower than in controls. The accumulation of soluble carbohydrate in the second leaf of uninfected plants grown in 700 mu mol mol(-1) CO2 was due largely to earlier and faster accumulation of fructan. TLC showed that the series of fructan was not different in plants grown in 700 mu mol mu mol(-1) CO2 relative to plants grown in 350 mu mol mol(-1) CO2, neither did infection by powdery mildew affect the series of fructan present in the second leaf blade. The rate constant for phloem loading obtained by compartmental analysis of C-14 efflux from the leaf blade was not reduced in plants grown in 700 mu mol mol(-1) CO2, indicating that carbohydrate accumulation was not caused by reduced ability of the leaf to export carbon.

KEYWORDS: CARBON, COMPARTMENTAL ANALYSIS, ELEVATED CO2, FLUXES, FRUCTAN ACCUMULATION, LEAF BLADES, PLANTS, STARCH, SUCROSE

914

Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Effect of 700 mu mol mol(-1) CO2 and infection with powdery mildew on the growth and carbon partitioning of barley. *New Phytologist 134(2):309-315.*

The dry weight of barley plants in 700 mu mol mol(-1) CO2 was increased by 19 d after planting relative to plants grown in 350 mu mol mol(-1) CO2. Infection of the second leaf by powdery mildew led to reduced growth rates in both 350 and 700 mu mol mol(-1) CO2, but the reduction in growth was transitory in 350 mu mol mol(-1) CO2. Neither the alIometric coefficient k between shoot and root, nor the leaf weight ratio, was altered by growth in 700 mu mol mol(-1) CO2 or by infection with powdery mildew. The number of tillers produced increased per plant but not per unit d. wt in 700 mu mol mol(-1) CO2. The growth response of barley to increased concentrations of CO2 and/or to infection with powdery mildew was not associated with alterations in net carbon partitioning, so a change in the ratio of photosynthetic to non-photosynthetic tissue, contributed to neither the growth response of barley to 700 mu mol mol(-1) CO2 nor to infection with powdery mildew. The increase in the growth rate of barley in 700 mu mol mol(-1) CO2 and the reduction in the growth rate after infection occurred at the same time as increased and reduced rates of net photosynthesis respectively.

KEYWORDS: DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, ROOT, RUST, TEMPERATURE

915

Hibberd, J.M., R. Whitbread, and J.F. Farrar. 1996. Effect of elevated concentrations of CO2 on infection of barley by Erysiphe graminis. *Physiological and Molecular Plant Pathology 48(1):37-53.*

Although there was no difference in the percentage of powdery mildew conidia that germinated on the second leaf of barley plants grown in either 350 or 700 ppm CO2, the percentage of conidia that progressed to produce colonies was lower in plants grown in 700 than in 350 ppm CO2. The lower percentage of conidia producing hyphae in 700 ppm CO2 was due to a higher proportion of the spores being arrested at the appressorial stage. The reduction in penetration of spores in 700 ppm CO2 was due neither to 700 ppm CO2 per se, nor to ontogenetic changes in the host tissue. Removing the epicuticular waxes from the surface of the leaf had no effect on the development of conidia on the surface of leaves in 350 or 700 ppm CO2, showing that increased epicuticular waxes were not causing the increased resistance to primary penetration of powdery mildew in 700 ppm CO2. We relate reduced rates of primary penetration in barley grown in 700 ppm CO2 to higher rates of net photosynthesis allowing increased mobilisation of resources into resistance including the production of papillae and accumulation of silicon at the sites of appressorial penetration. Established colonies of powdery mildew grew faster in 700 ppm CO2 than in 350 ppm CO2, coincident with accumulation of host carbohydrate in the source leaf.

KEYWORDS: AGE, CARBON DIOXIDE, GERMLING DEVELOPMENT, INSOLUBLE SILICON, LEAVES, POWDERY MILDEW, PRIMARY PENETRATION, RESISTANCE, SPRING BARLEY, WHEAT

916

Hibbs, D.E., S.S. Chan, M. Castellano, and C.H. Niu. 1995. Response of red alder seedlings to co2 enrichment and water- stress. *New Phytologist 129(4):569-577.*

Red alder (Alnus rubra Bong.) is a nitrogen-fixing pioneer tree species of the Pacific Northwest of North America. We investigated the response of different seed sources of red alder to elevated atmospheric CO2 and to varied levels of water stress. Seeds were stratified, germinated and grown for up to 147 d under ambient (350 mu l l(-1)) or elevated (700 mu l l(- 1)) CO2. There were no significant interactions of seed source latitude with either treatment, although seedlings from more northerly sources were larger. Elevated CO2 and low moisture stress resulted in larger plants with more leaf area; effects of the two factors appeared additive. Effects of both factors on biomass allocation, including root:shoot ratios, were small or nonsignificant. Elevated CO2 decreased specific nitrogenase activity and generally increased photosynthesis (A) and stomatal conductance (g). The ratio A:g, potential water use efficiency, also increased when plants were under water stress. Elevated CO2 appears to improve drought tolerance in red alder. Overall, these results indicate that red alder would benefit in total plant growth from increased ambient CO2 and could tolerate changes in precipitation.

KEYWORDS: ALLOCATION, ALNUS-RUBRA, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, GROWTH, NODULATION

917

Hikosaka, K. 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C-3 plants with respect to nitrogen use. *Annals of Botany 80(6):721-730.*

A new hypothesis for temperature acclimation by the photosynthetic apparatus is presented. An optimization model is developed to examined effects of changes in the organization of photosynthetic components on leaf photosynthesis under various growth temperatures where the photosynthetic apparatus is not damaged. In this model, photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP), or by the capacity of RuBP regeneration. For temperature dependence of the RuBPCase activity, data from Spinacia oleracea L., which have a temperature optimum of 30 degrees C, are used. For temperature dependence of the capacity of RuBP regeneration, two contrasting curves that have temperature optima of 30 degrees C (Eucalyptus pauciflora Sieb. ex Spreng) and 40 degrees C (Larrea divaricata Cav.) are applied. The temperature dependence of each process is fixed for respective species, but the rate of each process varies with changes in the amounts of components. The cost of proteins, in terms of nitrogen, required to carry out each process is calculated when nitrogen is partitioned differently among photosynthetic components. The optimal nitrogen partitioning that maximizes daily photosynthesis at a given temperature is obtained. The predicted temperature optimum of the photosynthetic rate in Larrea divaricata exhibits large shifts with changes in target temperature, while shifts are negligible in Eucalyptus pauciflora. It is suggested that the shift in temperature optimum of photosynthetic rate is large when the temperature dependences of the capacities of RuBPCase and RuBP regeneration differ from each other. (C) 1997 Annals of Botany Company.

KEYWORDS: CO2/O2 SPECIFICITY, DESERT SHRUB, ELECTRON-TRANSPORT, ELEVATED CO2, GAS-EXCHANGE, GROWTH TEMPERATURE, INTACT LEAVES, LARREA- DIVARICATA, NERIUM-OLEANDER, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE

918

Hikosaka, K., and T. Hirose. 1998. Leaf and canopy photosynthesis of C-3 plants at elevated CO2 in relation to optimal partitioning of nitrogen among photosynthetic components: theoretical prediction. *Ecological Modelling 106(2-3):247-259.*

Effects of changes in the organization of photosynthetic components on leaf photosynthesis under contrasting atmospheric CO2 conditions (35 and 70 Pa) are evaluated using an optimization model, in which the photosynthetic rate is limited either by the capacity of ribulose bisphosphate carboxylase (RuBPCase) to consume ribulose bisphosphate (RuBP) or by the capacity of RuBP regeneration. The nitrogen cost of photosynthetic components to carry out each process is calculated for the optimal partitioning of nitrogen among the components. The model predicts that nitrogen allocation to the components carrying out RuBP regeneration should be increased with reduction in allocation to RuBPCase to maximize daily photosynthesis at 70 Pa CO2. Al a temperature of 25 degrees C, doubling the current CO2 level increases daily photosynthesis by 60% with optimal reallocation of the nitrogen partitioning while the increase without reallocation of nitrogen is 40%. However, at lower growth irradiance, the advantage in daily photosynthesis due to the reallocation decreases with increasing nitrogen content. The ratio of photosynthesis at 70 Pa to that at 35 Pa increases with increasing temperature. The effects of CO2 levels on photosynthesis of a canopy in which nitrogen is optimally allocated among leaf layers are also examined. At 25 degrees C, canopy photosynthesis at the doubled CO2 level is predicted to increase 60 and 40% with and without the optimization of nitrogen partitioning among photosynthetic components, respectively. Doubling the CO2 level does not affect the optimal nitrogen distribution among leaf layers in the canopy irrespective of optimization of nitrogen partitioning among photosynthetic components. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCLIMATION, ALLOCATION, ASSIMILATION, ATMOSPHERIC CO2, LEAVES, LIMITATIONS, MODEL, RESPECT, SYSTEM, TEMPERATURE

919

Hilbert, D.W., A. Larigauderie, and J.F. Reynolds. 1991. The influence of carbon-dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root - shoot ratio. *Annals of Botany 68(4):365-376.*

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, GROWTH, LEAVES, LIGHT, PHOTOSYNTHETIC CHARACTERISTICS, SEEDLINGS, SHADE PLANTS, STOMATAL CONDUCTANCE, USE EFFICIENCY

920

Hileman, D.R., N.C. Bhattacharya, P.P. Ghosh, P.K. Biswas, K.F. Lewin, and G.R. Hendrey. 1992. Responses of photosynthesis and stomatal conductance to elevated carbon-dioxide in field-grown cotton. *Critical Reviews in Plant Sciences 11(2-3):227-231.*

KEYWORDS: BEHAVIOR, CO2- ENRICHMENT, NITROGEN DEFICIENCY, PLANTS, SORGHUM, SUNFLOWER, WATER RELATIONS

921

Hileman, D.R., G. Huluka, P.K. Kenjige, N. Sinha, N.C. Bhattacharya, P.K. Biswas, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Canopy photosynthesis and transpiration of field-grown cotton exposed to free-air co2 enrichment (face) and differential irrigation. *Agricultural and Forest Meteorology 70(1-4):189-207.*

Growth, yield and leaf photosynthetic rates of cotton (Gossypium hirsutum L.) all respond strongly to CO2 enrichment, but the gas exchange of whole cotton canopies grown under elevated CO2 has not been investigated. We compared the effects of CO2 enrichment on both single-leaf and whole-canopy photosynthetic rates in cotton. We also determined whole- canopy photosynthetic and transpiration rates in cotton in response to CO2 enrichment and differential irrigation. Field-grown cotton was exposed to either 550 mumol mol-1 of CO2 using the free-air carbon dioxide enrichment (FACE) system or to 370 mumol mol-1 in control plots. In the second year of the experiment, half of each plot received reduced levels of irrigation. Rates of photosynthesis and stomatal conductance of single leaves were determined using a portable photosynthesis system and a portable steady-state porometer, respectively. Rates of whole-canopy photosynthesis and transpiration were determined using a custom-built chamber (about 1 m x 1 m). Midday net photosynthesis rates of both leaves and canopies were 19-41% higher in the CO2-enriched plots than in control plots. The CO2 effect on leaf photosynthesis was greatest in July, whereas the CO2 effect on canopy photosynthesis was greatest in June and decreased thereafter as mutual shading of leaves and the amount of non-photosynthetic biomass increased. Midday stomatal conductance values of leaves were 13-44% greater in control plants than in CO2-enriched plants. Except for late in the second season, canopy transpiration rates were not affected by the CO2 treatment because the decrease in stomatal conductance was offset by an increase in plant size. Differential irrigation led to no significant differences in either canopy photosynthesis or transpiration, possibly because differential irrigation was applied only during the second half of the season. It appears that cotton crops grown in a future, higher-CO2 climate may have increased photosynthetic rates, but water requirements may not be reduced.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, LEAF, NITROGEN DEFICIENCY, PLANTS, RESPONSES, STOMATAL CONDUCTANCE, STRESS, WATER-USE EFFICIENCY, YIELD

922

Hirose, T., D.D. Ackerly, M.B. Traw, and F.A. Bazzaz. 1996. Effects of CO2 elevation on canopy development in the stands of two co-occurring annuals. *Oecologia 108(2):215-223.*

Elevated CO2 may increase dry mass production of canopies directly through increasing net assimilation rate of leaves and also indirectly through increasing leaf area index (LAI). We studied the effects of CO2 elevation on canopy productivity and development in monospecific and mixed (1:1) stands of two co- occurring C-3 annual species, Abutilon theophrasti and Ambrosia artemisiifolia. The stands were established in the glasshouse with two CO2 levels (360 and 700 mu l/l) under natural light conditions. The planting density was 100 per m(2) and LAI increased up to 2.6 in 53 days of growth. Root competition was excluded by growing each plant in an individual pot. However, interference was apparent in the amount of photons absorbed by the plants and in photon absorption per unit leaf area. Greater photon absorption by Abutilon in the mixed stand was due to different canopy structures: Abutilon distributed leaves in the upper layers in the canopy while Ambrosia distributed leaves more to the lower layers. CO2 elevation did not affect the relative performance and light interception of the two species in mixed stands. Total aboveground dry mass was significantly increased with CO2 elevation, while no significant effects on leaf area development were observed. CO2 elevation increased dry mass production by 30-50%, which was mediated by 35-38% increase in the net assimilation rate (NAR) and 37-60% increase in the nitrogen use efficiency (NUE, net assimilation rate per unit leaf nitrogen). Since there was a strong overall correlation between LAI and aboveground nitrogen and no significant difference was found in the regression of LAI against aboveground nitrogen between the two CO2 levels, we hypothesized that leaf area development was controlled by the amount of nitrogen taken up from the soil. This hypothesis suggests that the increased LAI with CO2 elevation observed by several authors might be due to increased uptake of nitrogen with increased root growth.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-4 ANNUALS, GAS-EXCHANGE, GROWTH, LEAF, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, TEMPERATURE, TUSSOCK TUNDRA

923

Hirose, T., D.D. Ackerly, M.B. Traw, D. Ramseier, and F.A. Bazzaz. 1997. CO2 elevation, canopy photosynthesis, and optimal leaf area index. *Ecology 78(8):2339-2350.*

We studied the effects of CO2 elevation on leaf and canopy photosynthesis and optimal leaf area index (LAI) for stands of the annual species Abutilon theophrasti and Ambrosia artemisiifolia. Leaf photosynthesis was modeled as a function of photosynthetic photon flux density (PPFD) and nitrogen content per unit leaf area (N-L). There was a curvilinear relationship between the light-saturated rates of leaf photosynthesis (P-max) and N-L. CO2 elevation significantly increased P-max as a function of N, in both species. Dark respiration (R-d) was linearly correlated with N-L. CO2 elevation slightly but significantly increased R-d in Abutilon, while it had no significant effect on R-d in Ambrosia. The initial slope of a light-response curve was determined from quantum yield (phi(abs)) multiplied by leaf absorptance and then calibrated against N-L. Daily canopy photosynthesis, calculated by integration of leaf photosynthesis with the actual distribution of leaf area, leaf N, and PPFD within a canopy, showed fairly good agreement with the canopy photosynthesis estimated from growth analysis. CO2 elevation increased canopy photosynthesis by 30-50%. Based on the leaf photosynthesis model for Abutilon, we calculated daily canopy photosynthesis for a given LAI and N availability, in which N was assumed to be distributed optimally within a leaf canopy to maximize daily canopy photosynthesis. An optimal LAI to maximize daily canopy photosynthesis was obtained for each level of N availability and this optimum increased with increasing N availability. Contrary to the often predicted increase in LAI with CO2 elevation, the optimum LAI did not

increase at high CO2 when N availability was limited. Two factors were suggested to be involved in counteracting the increase in LAI in a high-CO2 world. One is the higher phi(abs) of plants grown in elevated CO2, which makes leaves in the canopy more N limited, favors higher N-L and thus lowers optimal LAI. The other is the higher R-d in elevated CO2, which leads to higher light compensation points, and lowers optimal LAI.

KEYWORDS: ANNUALS, C-3, CARBON-DIOXIDE CONCENTRATION, ECOSYSTEMS, GAS-EXCHANGE, GROWTH, NITROGEN DISTRIBUTION, RESPIRATION, RESPONSES, TEMPERATURE

924

Hirose, T., and F.A. Bazzaz. 1998. Trade-off between light- and nitrogen-use efficiency in canopy photosynthesis. *Annals of Botany 82(2):195-202.*

If the light-use efficiency (LUE) of species in a canopy is constant, canopy photosynthesis (CP) is proportional to the number of photons (Phi) absorbed by the canopy (CP = LUE x Phi). Likewise, if nitrogen-use efficiency (NUE) is constant, canopy photosynthesis is proportional to the amount of total leaf nitrogen (LN) (CP = NUE x LN). We applied these concepts to monospecific and mixed (1:1) stands of annuals (Abutilon theophrasti and Ambrosia artemisiifolia) at two stages, established in an ambient (360 mu l l(-1)) or elevated (700 mu l l(-1)) CO2 atmosphere. In both CO2 concentrations, across the two species, daily canopy photosynthesis gave strong linear regressions with zero intercepts both against the number of absorbed photons and against total leaf nitrogen in the canopy. Doubling CO2 increased LUE by 20-80 % and NUE by 20-100 %. LUE tended to be higher in Ambrosia than in Abutilon, and also higher in the later stage of canopy development than in the younger stage. Interference by Abutilon increased the LUE of Ambrosia. On the other hand, NUE tended to be higher in Abutilon than in Ambrosia, and to be higher in younger than in later stages. Interference by Abutilon decreased the NUE of Ambrosia. Thus, there are trade-offs (negative correlations) between LUE and NUE, which result from differences in leaf nitrogen per unit leaf area and from differences in leaf area development in the canopy. LUE increased with increasing leaf nitrogen concentration, while NUE increased with increasing light availability in the canopy. (C) 1998 Annals of Botany Company.

KEYWORDS: ABSORPTION, ALLOCATION, AREA, C-3 PLANTS, CARBON GAIN, CO2 ELEVATION, LEAF NITROGEN, LEAVES, MODEL, RADIATION

925

Hirschel, G., C. Korner, and J.A. Arnone. 1997. Will rising atmospheric CO2 affect leaf litter quality and in situ decomposition rates in native plant communities? *Oecologia 110(3):387-392.*

Though field data for naturally senesced leaf litter are rare, it is commonly assumed that rising atmospheric CO2 concentrations will reduce leaf litter quality and decomposition rates in terrestrial ecosystems and that this will lead to decreased rates of nutrient cycling and increased carbon sequestration in native ecosystems. We generally found that the quality of naturally senesced leaf litter (i.e. concentrations of C, N and lignin; C:N, lignin:N) of a variety of native plant species produced in alpine, temperate and tropical communities maintained at elevated CO2 (600-680 mu l(- 1)) was not significantly different from that produced in similar communities maintained at current ambient CO2 concentrations (340-355 mu l l(-1)). When this litter was allowed to decompose in situ in a humid tropical forest in Panama (Cecropia peltata, Elettaria cardamomum, and Ficus benjamina, 130 days exposure) and in a lowland temperate calcareous grassland in Switzerland (Carex flacca and a graminoid species mixture; 261 days exposure), decomposition rates of litter produced under ambient and elevated CO2 did not differ significantly. The one exception to this pattern occurred in the high alpine sedge, Carex curvula, growing in the Swiss Alps. Decomposition of litter produced in situ under elevated CO2 was significantly slower than that of litter produced under ambient CO2 (14% vs. 21% of the initial litter mass had decomposed over a 61-day exposure period, respectively). Overall, our results indicate that relatively little or no change in leaf litter quality can be expected in plant communities growing under soil fertilities common in many native ecosystems as atmospheric CO2 concentrations continue to rise. Even in situations where small reductions in litter quality do occur, these may not necessarily lead to significantly slower rates of decomposition. Hence in many native species in situ litter decomposition rates, and the time course of decomposition, may remain relatively unaffected by rising CO2.

KEYWORDS: BIOMASS, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ELEVATED CO2, FOREST, GRASSLAND, NITROGEN, PRODUCTIVITY, RESPONSES

926

Hobbie, J.E., B.L. Kwiatkowski, E.B. Rastetter, D.A. Walker, and R.B. McKane. 1998. Carbon cycling in the Kuparuk basin: Plant production, carbon storage, and sensitivity to future changes. *Journal of Geophysical Research-Atmospheres 103(D22):29065-29073.*

The Marine Biological Laboratory General Ecosystem Model was calibrated for an arctic tussock tundra system using data from long-term observations and experiments at Toolik Lake, Alaska. These experiments include the effects of changes in temperature, light, CO2, and nutrients, so the model could be applied to five regions comprising the entire Kuparuk River basin. Met primary production, averaged for the entire basin, was 92 g C m(-2) yr(-1). A 150 year simulation of carbon storage under a doubling of CO2 (slow ramp-up) and a temperature increase of 3.5 degrees C gave an estimate of +400 g C m(-2) when soil moisture increased and +500 g C m(-2) when soil moisture decreased. Drier soils stimulated decomposition producing an increase in nitrogen availability; the increased N led to increased net primary production. If this result is applicable to other arctic ecosystems, then it is unlikely that warming will enhance carbon loss to the atmosphere to further enhance warming.

KEYWORDS: ARCTIC TUNDRA, BALANCE, CLIMATE CHANGE, CO2, DIOXIDE, GLOBAL CHANGE, MODEL, RESPONSES, TERRESTRIAL ECOSYSTEMS

927

Hocking, P.J., and C.P. Meyer. 1991. Carbon-dioxide enrichment decreases critical nitrate and nitrogen concentrations in wheat. *Journal of Plant Nutrition 14(6):571-584.*

Atmospheric carbon dioxide (CO2) levels are increasing. In a glasshouse experiment with wheat grown at 5 levels of nitrate (NO3) supply, CO2 enrichment (1500 cm3/m3) substantially decreased critical concentrations of NO3-N and total-N in stem bases and leaves. For example, critical NO3-N concentrations in stem bases at Feekes Stages 1.5, 5, and 10.3, were 4.5, 2.0, and 2.0 mg/g dry wt, respectively, for CO2-enriched plants, compared with 7.5, 6.2 and 6.4 mg/g dry wt, respectively, for control plants grown at the ambient level of CO2. However, concentrations of NO3-N in the rooting medium required to produce maximum dry matter accumulation by CO2-enriched plants were similar to those of control plants at the three growth stages. Critical concentrations of NO3-N and total-N declined with time in stem bases and leaves of plants grown at both ambient and elevated CO2 levels, but the decline was greater for CO2-enriched plants. It was concluded that diagnostic criteria based on current critical N concentrations may

become invalid as the atmospheric level of CO2 increases.

KEYWORDS: AVAILABILITY, CO2- ENRICHMENT, DEFICIENCY, DRY-MATTER, GROWTH, NUTRITION, SOIL, SPRING WHEAT, YIELD

928

Hocking, P.J., and C.P. Meyer. 1991. Effects of CO2 enrichment and nitrogen stress on growth, and partitioning of dry-matter and nitrogen in wheat and maize. *Australian Journal of Plant Physiology 18(4):339-356.*

Atmospheric CO2 levels are increasing, but little is known about how this will affect tissue concentrations and the partitioning of agriculturally important nutrients such as nitrogen (N) within crop plants. To investigate this, a glasshouse experiment was conducted in which wheat, a C3 species, and maize, a C4 species, were grown for 8 weeks at high CO2 (1500 cm3 m-3) on N supplies ranging from deficient (0.5 mol m-3) to more than adequate for maximum growth (25 mol m-3). Wheat responded to both CO2 enrichment and N supply; maize responded only to N supply. CO2-enriched wheat produced about twice the dry matter of control plants at all levels of N supply. Tiller and ear numbers were increased by CO2 enrichment irrespective of N supply. Enriched wheat plants had a lower Leaf Area Ratio but higher Net Assimilation Rate and Relative Growth Rate than control plants. There was no effect of CO2 enrichment on specific leaf weight. The enriched plants had lower shoot to root dry matter ratios than thecontrols at 6 mol m-3 N and higher. Shoot to root dry matter ratios of both wheat and maize increased with increasing N supply. CO2-enriched wheat plants accumulated more N than the controls but the proportional increase in N content was not as great as that in dry matter, with the result that concentrations of total-N and nitrate-N were lower in all organs of enriched plants, including ears. Nitrate reductase activity was lower in enriched than in control wheat plants. N-use efficiency by wheat was increased by CO2 enrichment. From a practical point of view, the study indicates that critical total-N and NO3-N concentrations used to diagnose the N status of wheat will need to be reassessed as global CO2 levels increase. Elevated CO2 may also reduce the protein content of grain and thus the baking quality of hard wheats.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, MINERAL NUTRITION, NITRATE, NUTRIENT CONCENTRATION, PHOSPHORUS, PHOTOSYNTHESIS, PLANT GROWTH, USE EFFICIENCY, WATER, YIELD

929

Hoddinott, J., and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species .1. Growth responses. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(3):383-390.*

Plant growth responds to light quality, as evaluated by the red/far-red (R/FR) quantum flux ratio, and to the level of CO2. Pinus banksiana, Picea mariana and Picea glauca seedlings were raised at 350, 700, or 1050 at mu L . L(-1) CO2 and high or low R/FR ratios and growth was measured over a 16-week growth period. Far-red rich light enhanced the whole plant and height relative growth rates of Pinus banksiana. The three species showed species specific responses in plant organ relative growth rates and partitioning ratios. On the basis of their biomass partitioning the species would be ranked Pinus banksiana < Picea mariana < Picea glauca for shade tolerance. In commercial operations, seedlings grown for outplanting are selected, in part, on the basis of plant form as described by the stem height/diameter ratio. More desirable ratios were obtained at ambient CO2 concentrations for Pinus banksiana and Picea mariana in red rich light and for Picea glauca in far-red rich light.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BLACK SPRUCE SEEDLINGS, FORESTS, NATURAL- ENVIRONMENT, PHYTOCHROME

930

Hoddinott, J., and R. Scott. 1996. The influence of light quality and carbon dioxide enrichment on the growth and physiology of seedlings of three conifer species .2. Physiological responses. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(3):391-402.*

Pinus banksiana, Picea mariana, and Picea glauca were grown at 350, 700, or 1050 mu L . L(-1) CO2 and either high or low red/far-red quantum flux ratios. After a 16-week, long day growth period, seedlings were subjected sequentially to short daylengths, then short days with low temperatures. Various physiological parameters were determined at the end of each treatment phase to monitor how those treatments influenced the onset of seedling dormancy. After the long day treatments, high ratios increased the total chlorophyll content and reduced the original level of chlorophyll fluorescence and the shoot total nonstructural carbohydrate content in very shade-intolerant Pinus banksiana. In shade-tolerant Picea mariana, high CO2 levels caused the main effects on these parameters while neither light quality or CO2 had significant effects on them in shade-tolerant Picea glauca. Short days and low temperature induced a proportional increase in the partitioning of total nonstructural carbohydrate to the roots in all species and produced other species and treatment-specific responses.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BLACK SPRUCE SEEDLINGS, CHLOROPHYLL FLUORESCENCE, FORESTS, FROST HARDINESS, PHOTOSYNTHESIS, PHYTOCHROME, PINUS-RADIATA, PLANTS, TEMPERATURE

931

Hodge, A. 1996. Impact of elevated CO2 on mycorrhizal associations and implications for plant growth. *Biology and Fertility of Soils 23(4):388-398.*

The impact of increasing concentrations of atmospheric CO2 upon plant physiology has been widely investigated. Plant, and in particular root, growth is nearly always enhanced as a direct consequence of CO2 enrichment, with C-3 species generally more responsive than C-4 species. Such alterations in plant productivity will have consequence for below-ground processes and increased carbon allocation to the roots may favour symbiotic relationships. This paper discusses the current information available for the consequences of these changes upon mycorrhizal relationships. Generally mycorrhizal plants grown under CO2 enrichment show enhanced phosphorus uptake but nitrogen uptake is unaffected. This increased nutrient uptake is not correlated with increased mycorrhizal colonization of the roots. Similarly root exudation does not increase under CO2 enrichment but qualitative differences have yet to be assessed. However, it is predicted that total rhizodeposition of materials will increase as will litter inputs, although mineral and biochemical alterations to these plant derived inputs may occur. The consequences of such changes within the rhizosphere are discussed and future research priorities identified.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BOUTELOUA-GRACILIS, CASTANEA-SATIVA MILL, ECTOMYCORRHIZAL FUNGI, GAS-EXCHANGE, GLOMUS-MOSSEAE, NUTRIENT-UPTAKE, PHOTOSYNTHETIC ACCLIMATION, SEEDLING GROWTH, WOODY-PLANTS

932

Hodge, A., and P. Millard. 1998. Effect of elevated CO2 on carbon partitioning and exudate release from Plantago lanceolata seedlings.

Physiologia Plantarum 103(2):280-286.

Plantago lanceolata L. seedlings were grown in sand microcosm units over a 43-day experimental period under two CO2 regimes (800 or 400 mu mol mol(-1)) to investigate the effect of elevated atmospheric CO2 concentration on carbon partitioning and exudate release. Total organic carbon (TOC) content of the collected exudate material was measured throughout the experimental period. After 42 days growth the seedlings were labelled with [C-14]-CO2 and the fate of the label within the plant and its release by the roots monitored. Elevated CO2 significantly (P less than or equal to 0.001) enhanced shoot, root and total dry matter production although the R:S ratio was unaltered, suggesting no alteration in press carbon partitioning. The cumulative release of TOC (in mg C) over 0-42 days was unaltered by CO2 treatment however, when expressed as a percentage of net assimilated C, ambient-grown plants released a significantly (P less than or equal to 0.001) higher percentage from their roots compared to elevated CO2-grown plants (i.e. 8 vs 3%). The distribution of C-14-label was markedly altered by CO2 treatment with significantly (P less than or equal to 0.001) greater per cent label partitioned to the roots under elevated CO2. This indicates increased partitioning of recent assimilate belowground under elevated CO2 treatment although there was no significant difference in the percentage of C-14-label released by the roots. Comparison of plant C budgets based on C-14-pulse-chase methodology and TOC measurements is discussed.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, FLOW, GROWTH, MAIZE, RESPONSES, RHIZOSPHERE, ROOT EXUDATION, SOIL BIOTA, ZEA MAYS L

933

Hodge, A., E. Paterson, S.J. Grayston, C.D. Campbell, B.G. Ord, and K. Killham. 1998. Characterisation and microbial utilisation of exudate material from the rhizosphere of Lolium perenne grown under CO2 enrichment. *Soil Biology and Biochemistry 30(8-9):1033-1043.*

The effects of elevated atmospheric CO2 concentration on alterations, both qualitatively and quantitatively, of exuded compounds from the roots of Lolium perenne seedlings were investigated by growing plants in a sterilised sand microcosm unit. In addition, the effect of CO2 treatment on carbon substrate utilisation of microbial populations extracted from the rhizosphere of L. perenne seedlings grown in soil microcosm units was examined and alterations on microbial activity and diversity assessed using a commercially-available redox-based sole C source utilisation test (Biolog(R)) including additional exudate compounds. Both types of microcosm units (sand and soil) were maintained at specific growth conditions under two CO2 regimes (450 and 720 mu mol mol(-1)). Growth of L. perenne seedlings from both types of microcosm units was enhanced under elevated atmospheric CO2 although the root-to-shoot ratios were not significantly altered, indicating no gross change in dry matter partitioning. Cumulative total organic carbon (TOC) release in the exudate material over the duration of the experiment was significantly (P less than or equal to 0.05) higher from ambient-grown seedlings despite a significant (P less than or equal to 0.05) increase in the dry weight of roots of the elevated CO2 grown seedlings as determined at harvest. Over the individual sampling periods TOC release was significantly (P less than or equal to 0.05) higher from elevated CO2 grown seedlings on only one occasion (21 d). Qualitative differences, measured between d 1-6 and 14-18, also occurred with elevated CO2 treatment decreasing the amount of phenolic acids and total sugars at the latter sampling period compared to ambient CO2 seedlings. Total numbers of bacteria were significantly (P less than or equal to 0.05) decreased under elevated CO2 although culturable numbers significantly (P less than or equal to 0.05) increased. This increase in culturable microorganisms may explain the faster carbon source utilisation rates of the elevated CO2 treatment. No change in morphotypes of microbial colonies were observed suggesting a quantitative difference due to elevated CO2 treatment only.

KEYWORDS: BIOMASS, CARBON DIOXIDE, COMMUNITIES, ELEVATED ATMOSPHERIC CO2, NITROGEN, PLANT-RESPONSES, ROOTS, SEEDLINGS, SOIL BIOTA, ZEA MAYS L

934

Hoen, H.F., and B. Solberg. 1994. Potential and economic-efficiency of carbon sequestration in forest biomass through silvicultural management. *Forest Science 40(3):429-451.*

This paper has two main objectives: First, to discuss in principle some vital methodological issues which have to be considered when analyzing bow preferable measures in forestry are to decrease the atmospheric concentration of greenhouse gases (GHGs). Economic evaluation of the flow of carbon in and out of the atmosphere is discussed, related particularly to two important problems: (1) the determination of the utility of reducing the quantity of CO2 in the atmosphere at a given point in time; and (2) the intertemporal evaluation of a flow of atmospheric CO2 reductions. The marginal cost, measured as the change in net present value, is proposed as a proper measure for ranking of alternative projects. Secondly, a case study is reported. The case study is based on forest-level optimization with a model estimating carbon flows related to forest biomass growth and decay, linked to a long-range forest management planning (LFMP) model. Alternative stand treatment schedules are simulated, and the forest management problem is solved by linear programming in a model I type LFMP model for the county of Buskerud, with a forest area of 574,000 ha. The potential for increasing the net carbon sequestration related to timber production by changes in the forest management over a time period of 30 yr is studied. A total of 253 stand treatment schedules was calculated for the 40 stand types, allowing for the following stand treatment options, (1) continued growth, (2) release thinnings of young growth, (3) thinning, (4) fertilization, (5) clear felling, (6) clear felling with retention of seed trees, and (7) planting or natural regeneration depending on the felling regime. The study shows that there is a significant potential for increasing the present value of the flow of net CO2 fixations (NPV(CO2)) by changing the forest management on the productive forest area of Buskerud. Compared with the NPV(CO2) obtained when the net present value of the timber cash flow (NPV(NOK)) for the area is maximized (BASE problem), an increase between 8.4%-17.9% in NPV(CO2) can be obtained. The potential for increasing the NPV(CO2) depends on the real rate of discount. The corresponding decrease in the NPV(NOK) lies between 8.1% and 14.9%. The results further indicate that a large proportion of the increase in NPV(CO2) can be obtained by changes in forest management at a moderate marginal cost. If we assume that 80% of the maximum potential increase in NPV(CO2) is obtained, this gives a yearly increase (30-yr annuity) in net CO2 fixation in the range from 145,000 to 250,000 tons (depending on the real rate of discount and assumptions about fertilization) by changing the management of the 574,000 ha of productive forestland in Buskerud, compared to the current forest management practice (BASE problem). Obtaining 80% of the maximum potential increase in NPV(CO2) imposes a decrease in the NPV(NOK) in the range of 22% to 65% of the total potential difference in NPV(NOK) between the BASE problem and the NPV(CO2) maximizing problem. The annual decrease (30-yr annuity) in NPV(NOK) corresponding to the 80% of the maximum potential NPV(CO2) increase, is ranging between 7.6 and 25 million NOK. The results indicate that at a RRD of 4%, 5%, and 7% p.a., 80% of the increase in NPV(CO2) can be reached at a marginal cost (shadow price) below 150 NOK (21/US$) per ton NPV(CO2). Measured per ton C, the corresponding marginal cost is 551 NOK (79 US$) per ton C. For RRDs at 3% p.a. and 2% p.a., the marginal costs are significantly higher, but relaxing the NPV(CO2) constraint to 60% of the total increase brings the marginal costs down and below half of this level (59 NOK or 8 US$ per ton NPV(CO2)) for 3% p.a. and to a comparable level (182 NOK or 26

US$ per ton NPV(CO2)) for 2% p.a. These results are related to changes in the management of the forested area in even-aged stands and do not take into account measures such as afforestation of marginal agricultural land or changes of tree species. Fertilization, avoiding release thinning in young growth, and changes in clear felling priorities were the most cost-efficient changes in stand treatment management in order to increase the net CO2 fixation.

KEYWORDS: ELEVATED CO2, RESPONSES

935

Hogan, K.P., I. Fleck, R. Bungard, J.M. Cheeseman, and D. Whitehead. 1997. Effect of elevated CO2 on the utilization of light energy in Nothofagus fusca and Pinus radiata. *Journal of Experimental Botany 48(311):1289-1297.*

Red beech (Nothofagus fusca (Hook. F.) Oerst.; Fagaceae) and radiata pine (Pinus radiata D. non; Pinaceae) were grown for 16 months in large open-top chambers at ambient (37 Pa) and elevated (66 Pa) atmospheric partial pressure of CO2, and in control plots (no chamber). Summer-time measurements showed that photosynthetic capacity was similar at elevated CO2 (light and CO2-saturated value of 17.2 mu mol m(-2) s(-1) for beech, 13.5 mu mol m(-2) s(-1) for pine), plants grown at ambient CO2 (beech 21.0 mu mol m(-2) s(-1), pine 14.9 mu mol m(-2) s(-1)) or control plants grown without chambers (beech 23.2 mu mol m(- 2) s(-1), pine 12.9 mu mol m(-2) s(-1)). However, the higher CO2 partial pressure had a direct effect on photosynthetic rate, such that under their respective growth conditions, photosynthesis for the elevated CO2 treatment (measured at 70 Pa CO2 partial pressure: beech 14.1 mu mol m(-2) s(-1) pine 10.3) was greater than in ambient (measured at 35 Pa CO2: beech 9.7 mu mol m(-2) s(-1), pine 7.0 mu mol m(-2) s(-1)) or control plants (beech 10.3 mu mol m(-2) s(-1), pine 7.2 mu mol m(-2) s(-1)). Measurements of chlorophyll fluorescence revealed no evidence of photodamage in any treatment for either species. the quantity of the photoprotective xanthophyll cycle pigments and their degree of de-epoxidation at midday did not differ among treatments for either species. The photochemical efficiency of photosystem II (yield) was lower in control plants than in chamber-grown plants, and was higher in chamber plants at ambient than at elevated CO2. These results suggest that at lower (ambient) CO2 partial pressure, beech plants may have dissipated excess energy by a mechanism that does not involve the xanthophyll cycle pigments.

KEYWORDS: CARBON METABOLISM, CAROTENOIDS, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, INHIBITION, PHOTOINHIBITION, PHOTOSYNTHESIS, PLANTS, RESPONSES, TEMPERATURE

936

Hogan, K.P., A.P. Smith, and L.H. Ziska. 1991. Potential effects of elevated CO2 and changes in temperature on tropical plants. *Plant, Cell and Environment 14(8):763-778.*

Very little attention has been directed at the responses of tropical plants to increases in global atmospheric CO2 concentrations and the potential climatic changes. The available data, from greenhouse and laboratory studies, indicate that the photosynthesis, growth and water use efficiency of tropical plants can increase at higher CO2 Concentrations. However, under field conditions abiotic (light, water or nutrients) or biotic (competition or herbivory) factors might limit these responses. In general, elevated atmospheric CO2 concentrations seem to increase plant tolerance to stress, including low water availability, high or low temperature, and photoinhibition. Thus, some species may be able to extend their ranges into physically less favourable sites, and biological interactions may become relatively more important in determining the distribution and abundance of species. Tropical plants may be more narrowly adapted to prevailing temperature regimes than are temperate plants, so expected changes in temperature might be relatively more important in the tropics. Reduced transpiration due to decreased stomatal conductance could modify the effects of water stress as a cue for vegetative or reproductive phenology of plants of seasonal tropical areas. The available information suggests that changes in atmospheric CO2 concentrations could affect processes as varied as plant/herbivore interactions, decomposition and nutrient cycling, local and geographic distributions of species and community types, and ecosystem productivity. However, data on tropical plants are few, and there seem to be no published tropical studies carried out in the field. Immediate steps should be undertaken to reduce our ignorance of this critical area.

KEYWORDS: AMAZON DEFORESTATION, ATMOSPHERIC CO2, CLIMATE CHANGE, COSTA-RICA, GLOBAL CARBON-CYCLE, INSECT HERBIVORE, PHOTOSYNTHETIC RESPONSES, RAIN-FOREST, ULTRAVIOLET-B RADIATION, WATER RELATIONS

937

Hogan, K.P., D. Whitehead, J. Kallarackal, J.G. Buwalda, J. Meekings, and G.N.D. Rogers. 1996. Photosynthetic activity of leaves of Pinus radiata and Nothofagus fusca after 1 year of growth at elevated CO2. *Australian Journal of Plant Physiology 23(5):623-630.*

Radiata pine (Pinus radiata D.Don) and red beech (Nothofagus fused (Hook.f.) Oerst.) were grown for over 1 year at elevated (ELEV, 64 Pa) and ambient (AMB, 38 Pa) CO2 partial pressure in open-top chambers. Springtime measurements of overwintering leaves showed that light- and CO2-saturated photosynthetic rates (A,,) of pine leaves were similar for the two treatments (AMB: 6.7 +/- 1.08 mu mol m(-2) s(-1), mean +/- 1 s.e.; ELEV: 6.6 +/- 0.47) but, for beech leaves, A(max) was greater for AMB plants (8.8 +/- 0.90 mu mol m(-2) s(-1)) than for ELEV plants (6.10 +/- 0.71). Summertime measurements of leaves grown that spring showed that for pine, A(max) was similar in the two CO2 treatments (AMB 14.9 mu mol m(-2) s(-1) +/- 0.80; ELEV: 13.5 +/- 1.9) while, for beech, A(max) was higher in AMB plants (21.0 +/- 1.1) than in ELEV plants (17.2 +/- 1.9), although the difference was not statistically significant. These results indicate downregulation of photosynthetic capacity of beech but not pine. V-cmax did not differ between treatments within species, suggesting that there was no acclimation of rubisco activity. Triose phosphate utilisation limitation may have contributed to the downregulation of A(max) in beech. For pine, photosynthesis at treatment CO2 partial pressures was greater in ELEV plants in both spring and summer. For beech measured at treatment CO2 partial pressures, photosynthesis was greater in ELEV plants in summer, but was similar between treatments in the springtime.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, ENHANCEMENT, LIMITATIONS, LOBLOLLY-PINE, NUTRITION, SENESCENCE

938

Holbrook, G.P., J. Hansen, K. Wallick, and T.M. Zinnen. 1993. Starch accumulation during hydroponic growth of spinach and basil plants under carbon-dioxide enrichment. *Environmental and Experimental Botany 33(2):313-321.*

The effects of CO2 enrichment, photoperiod duration, and inorganic phosphate levels on growth and starch accumulation by spinach and basil plants were studied in a commercial hydroponic facility. During a 3-week growth period, both species exhibited increased whole-plant fresh weight as a result of an increase in atmospheric CO2 concentration from 400 to 1500 mul/l. However, basil leaves exhibited a 1.5- to 2-fold greater increase in specific leaf weight (SLW), and accumulated starch to much greater levels than did leaves of spinach. At 1500 mul CO2/l, starch accounted for up to 38% of SLW with basil compared to < 10%

of SLW with spinach. The maximum ratio of starch/chlorophyll was 55.0 in basil leaves vs 8.0 in spinach leaves. High ratio values were associated with the appearance of chlorotic symptoms in leaves of basil grown under CO2 enrichment (WALLICK and ZINNEN (1990) Plant Disease 74, 171-173), whereas spinach did not exhibit chlorosis. Increasing inorganic phosphate concentrations from 0.7 to 1.8 mM in the hydroponic medium did not appreciably affect leaf starch accumulation in either species. Starch accumulation in basil leaves was not consistently related to the duration of the photoperiod. However, photoperiod-induced changes in leaf starch levels were much greater in basil than spinach. The results clearly indicate that different horticultural crops can show diverse responses to CO2 enrichment, and thus highlight the need to develop individual growth strategies to optimize production quality of each species.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERES, CO2-ENRICHMENT, CROP RESPONSES, LEAVES, PHOTOSYNTHESIS, SUCROSE PHOSPHATE SYNTHASE, TOMATO, YIELD

939

Holcroft, D.M., M.I. Gil, and A.A. Kader. 1998. Effect of carbon dioxide on anthocyanins, phenylalanine ammonia lyase and glucosyltransferase in the arils of stored pomegranates. *Journal of the American Society for Horticultural Science 123(1):136-140.*

Wonderful' Pomegranates (Punica granatum L.) were placed in jars ventilated continuously with air or air enriched with 10 or 20 kPa CO2 at 10 degrees C for 6 weeks. Samples were taken initially and after 1, 2, 4, and 6 weeks, and postharvest quality attributes were measured. The arils of the pomegranates stored in air were deeper red than the initial controls and than those stored in CO2-enriched atmospheres. This increased color was associated with increased anthocyanin concentration. Arils from fruit stored in air enriched with 10 kPa CO2 had a lower anthocyanin concentration than air-stored fruit, and atmospheres enriched with 20 kPa CO2 had even lower levels, possibly from suppressed anthocyanin biosynthesis. Anthocyanin concentration correlated well with the activity of phenylalanine ammonia lyase but not with glucosyltransferase activity. Moderate CO2 atmospheres (10 kPa) prolong the storage life and maintain quality of pomegranates, including adequate red color intensity of the arils.

KEYWORDS: APPLE, ATMOSPHERE, BIOSYNTHESIS, CO2, CULTIVARS, LETTUCE TISSUE, PHENOLICS, PIGMENTATION, STORAGE, STRAWBERRY FRUIT

940

Holcroft, D.M., and A.A. Kader. 1999. Carbon dioxide-induced changes in color and anthocyanin synthesis of stored strawberry fruit. *Hortscience 34(7):1244-1248.*

Anthocyanin concentrations increased in both external and internal tissues of 'Selva' strawberries (Fragaria xananassa Duch.) stored in air at 5 degrees C for 10 days, but the increase was lower in fruit stored in air enriched with 10 or 20 kPa CO2. Flesh red color was less intense in CO2 storage than in air storage. Activities of phenylalanine ammonia lyase (PAL) and UDP glucose : flavonoid glucosyltransferase (GT) decreased during storage, with decreases being greater in both external and internal tissues of strawberry fruit stored in air + 20 kPa CO2 than in those kept in air. Activities of both PAL and GT in external tissues of strawberries stored in air + 10 kPa CO2 were similar to those in fruit stored in air, while enzyme activities in internal tissues more closely resembled those from fruit stored in air +20 kPa CO2. Phenolic compounds increased during storage but were not affected by the storage atmosphere. The pH increased and titratable acidity decreased during storage; these effects were enhanced in internal tissues by the CO2 treatments, and may in turn have influenced anthocyanin expression.

KEYWORDS: BIOSYNTHESIS, CULTIVARS, PHENYLALANINE AMMONIA-LYASE

941

Holland, E.A., A.R. Townsend, and P.M. Vitousek. 1995. Variability in temperature regulation of co2 fluxes and n mineralization from 5 hawaiian soils - implications for a changing climate. *Global Change Biology 1(2):115-123.*

We examined the possibility that microbial adaptation to temperature could affect rates of CO2, N2O and CH4 release from soils. Laboratory incubations were used to determine the functional relationship between temperature and CO2, N2O and CH4 fluxes for five soils collected across an elevational range in Hawaii. Initial rates of CO2 production and net N mineralization increased exponentially from 15 degrees C to 55 degrees C; initial rates of CH4 and N2O release were more complex. No optimum temperature (in which rates decline at higher and lower temperatures) was apparent for any of the gases, but respiration declined with time at higher temperatures, suggesting rapid depletion of readily available substrate. Mean Q(10)s for respiration varied from 1.4 to 2.0, a typical range for tropical soils. The functional relationship between CO2 production and temperature was consistent among all five soils, despite the substantial differences in mean annual temperature, soils, and land-use among the sites. Temperature responses of N2O and CH4 fluxes did not follow simple Q(10) relationships suggesting that temperature functions developed for CO2 release from heterotrophic respiration cannot be simply extrapolated. Expanding this study to tropical heterotrophic respiration, the flux is more sensitive to changes in Q(10) than to changes in temperature on a per unit basis: the partial derivative with respect to temperature is 2.4 Gt C . degrees C- 1, with respect to Q(10) it is 3.5 Gt C . Q(10) unit(-1). Therefore, what appears to be minor variability might still produce substantial uncertainty in regional estimates of gas exchange.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, EMISSIONS, GRASSLANDS, MODEL, VEGETATION

942

Hollander, B., and H. Krug. 1991. Effects of high CO2 concentrations on vegetable species .1. Symptoms, ranges of injuries, and reactions of species. *Gartenbauwissenschaft 56(5):193-205.*

To test the reactions of various vegetable species to high CO2-concentrations, the plants were treated with 1-3% technical CO2 day and night for 10-42 days in growth chambers (table 1). The development of CO2 injury symptoms as well as growth rates were noted and measured. With exception of spinach and sweet pepper, which showed no symptoms in the range tested, CO2 injuries occurred in the form of morphological alterations (epinastic and hyponastic rolling of the leaves, crisping, reduction and thickening of the leaf lamina), chlorosis (marginal or in areas between the veins), necrosis, wilting, drying up and browning ot the veins (kohlrabi). The symptoms mentioned varied between the species and between the cultivars. The injuries occurred at young leaves only (beans), at older leaves (kohlrabi) or at all leaves (fig. 1-5, table 6). Moreover, high CO2-concentrations caused a remarkable reduction of growth (fig. 6). Ensuring favourable growth conditions the cold-season species tolerated concentrations of 1% CO2 for 4-6 weeks showing only week (radish var. niger, kohlrabi, corn salad) or no significant growth reductions (radish, var. sativus, lettuce). Light injuries and morphological alterations were identifiable after 2-3 weeks. Higher concentrations caused stronger growth reductions, injuries appeared after 1 week using 2% CO2 and after 2-3 days using 3% CO2. The warm-season species tested reacted more sensitive. Cucumbers tolerated 1% CO2 for 2-3 weeks, using 2% CO2 wilting and driving injuries occurred already after 1 day table 2). In case of disturbances of the water status of the plants by transplanting, top dressing or sharp decrease of air

humidity cucumber wilted with 1% CO2 already after a few days. Equal reactions were observed with radish, var. sativus. With tomatoes strong injuries of the leaves causing leaf death were observed after 7 days with 1% CO2 and after 5 days with 2% CO2. Bush beans reacted by a distinct reduction of leaf area growth and by chlorotic discolorations.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, MONOECIOUS CUCUMBERS, PHARBITIS, PLANT GROWTH

943

Hollander, B., and H. Krug. 1992. Effects of high co2-concentrations on vegetable species .2. Growth, co2-gas-exchange and stomata resistance. *Gartenbauwissenschaft 57(1):32-43.*

In the climatic conditions tested the growth of young cucumber plants (3-7 leaf stage) was slightly promoted as well by day as by continuous enrichment with 5000-mu-l/l CO2 compared to the control (400-mu-l/l CO2). A definite effect of enrichment during the night was not evident. The analysis of the growth components and gas exchange measurements revealed, that CO2 enrichment during the day as well as during day and night increased net assimilation rate and dark respiration distinctly. Enrichment during the night showed no effect on net assimilation rate and increased dark respiration only slightly. The specific leaf area was strongly reduced by the high CO2 concentration, but leaf weight ratio was rarely changed. By these morphogenetic effects growth promotion by an increased net assimilation rate was diminished. Continuous CO2 enrichment to cucumber plants with CO2 concentrations greater- than-or-equal-to 1000-mu-l/l decreased stomata resistance. This effect increased with higher CO2 concentrations and longer treatments. The stomata remained open even at night and at low air humidity. Also with CO2 enrichment up to 5000-mu-l/l during the day or during the night only the stomata remained wider open than in the control plants. The reaction of stomata to high CO2-concentrations is reversible. The regeneration proceeds all the faster as lower the proceeding concentration and shorter the exposition. The actions of high CO2-concentrations on stomata movement of cucumbers were confirmed with other species.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CO2-ENRICHMENT, DARK RESPIRATION, DRY-MATTER PRODUCTION, LEAVES, PHOTOSYNTHETIC RATE, PLANT GROWTH, RESPONSES, TRANSPIRATION, VICIA-FABA

944

Homma, K., H. Nakagawa, T. Horie, H. Ohnishi, H.Y. Kim, and M. Ohnishi. 1999. Energy budget and transpiration characteristics of rice grown under elevated CO2 and high temperature conditions as determined by remotely sensed canopy temperatures. *Japanese Journal of Crop Science 68(1):137-145.*

The effects of elevated CO2 concentration and high temperatures on transpiration and gaseous diffusive resistances of rice canopy were investigated. Akihikari and IR36 cultivars were grown under two CO2 concentrations ([CO2], 365 and 700 mu L L- 1) X three temperatures (29.8, 30.4 and 32.5 degrees C on average over the experimental period), created by two Temperature Gradient Chambers. From 2 August (panicle initiation) to 22 August (booting), measurements were made of dry and wet bulb temperatures, canopy surface temperatures (T- c) and net radiation along with evapotranspiration (E) measurements by microlysimeters. Aerodynamic resistance (r(a)), obtained from the measured E and microclimate data, showed a fairly constant value (11.7 s m(-1). Then, r(a), T-c and microclimates data were substituted into energy budget equations to obtain E and canopy resistance (r(c)). In all plots, calculated E was in good agreement with measurement by lysimeters, and r(c) reached minimum values (r(c,min)) at solar radiation above 500 W m(-2). Elevated [CO2] at the lowest temperature plot increased r(c,min) by 40-49% and T-c by 1.4- 1.6 degrees C and it reduced E by 14-16% of those under ambient CO2 conditions. With the rising growth temperature, these effects of elevated [CO2] drastically decreased. The observed r(c,min) responses to temperature and [CO2] seemed to have reflected a long-term acclimation of rice to these environments. These results indicate that anticipated global warming significantly reduces the advantageous effects of elevated [CO2] on plant water use.

KEYWORDS: CARBON DIOXIDE

945

Hopkins, D.W., J.A. Chudek, E.A. Webster, and D. Barraclough. 1997. Following the decomposition of ryegrass labelled with C-13 and N-15 in soil by solid-state nuclear magnetic resonance spectroscopy. *European Journal of Soil Science 48(4):623-631.*

Investigating the biogeochemistry of plant material decomposition in soil has been restricted by difficulties extracting and identifying organic compounds. In this study the decomposition of C-13- and N-15-labelled Lolium perenne leaves mixed with mineral soil has been investigated over 224 days of incubation under laboratory conditions. Decomposition was followed using short-term rates of CO2 evolution, the amounts of C-13 and N-15 remaining were determined by mass spectrometry, and C-13 and N-15 solid-state nuclear magnetic resonance (NMR) spectroscopy was used to characterize chemically the plant material as it decomposed. After 224 days 48% of the added C-13 had been lost with a rapid period of CO2 evolution over the first 56 days. The fraction of cross- polarization magic angle spinning (CP MAS) C-13 NMR spectra represented by O-alkyl-C signal probably in carbohydrates (chemical shift, 60-90 p.p.m.) declined from 60 to 20% of the spectrum (chemical shift, 0-200 p.p.m.) over 224 days. The rate of decline of the total C-13 exceeded that of the 60-90 p.p.m. signal during the first 56 days and was similar thereafter. The fraction of the CP MAS C-13 NMR spectra represented by the alkyl- and methyl-C (chemical shift, 10-45 p.p.m.) signal increased from 5 to 14% over the first 14 days and was 19% after 224 days. CP MAS C-13 NMR of C-13- and N-15-L. perenne contained in 100-mu m aperture mesh bags incubated in the soil for 56 days indicated that the remaining material was mainly carbohydrate but there was an increase in the alkyl-and methyl- C associated with the bag's contents. After 224 days incubation of the labelled C-13- and N-15-L. perenne mixed with the soil, 40% of the added N-15 had been lost. Throughout the incubation there was only one signal centred around 100 p.p.m, detectable in the CP MAS N-15 NMR spectra. This signal corresponded to amide N-15 in peptides and may have been of plant or microbial origin or both. Although there had been substantial interaction between the added N-15 and the soil microorganisms, the associated redistribution of N-15 from plant to microbial tissues occurred within the amide region. The feasibility of following some of the component processes of plant material decomposition in soil using NMR has been demonstrated in this study and evidence that microbial synthesis contributes to the increase in alkyl- and methyl-C content of soil during decomposition has been represented.

KEYWORDS: CPMAS, ELEVATED CO2, IMMOBILIZATION, MICROBIAL BIOMASS, MINERALIZATION, NMR-SPECTROSCOPY, ORGANIC-MATTER, PARTICLE-SIZE, PLANT- MATERIAL, WHOLE SOILS

946

Horie, T., H. Nakagawa, J. Nakano, K. Hamotani, and H.Y. Kim. 1995. Temperature-gradient chambers for research on global environment change .3. a system designed for rice in kyoto, japan. *Plant, Cell and Environment 18(9):1064-1069.*

Synthesis and validation of crop models for assessment of of the impact

of elevated atmospheric CO2 concentration and anticipated global warming on crop production require crop response data obtained under field-like conditions, The temperature gradient chamber (TGC) with the facility for CO2 enrichment allows the creation of various CO2 and temperature regimes for crops over the entire growth period with relatively inexpensive construction and running costs, The TGC develops a temperature gradient along its longitudinal axis using solar energy during the day and heating at night while maintaining the natural diurnal cycle, The temperature gradient and the CO2 concentration in the TGC are regulated by computer control of the air ventilation rate through the TGC and of the CO2 release rate, Longitudinal gradients of CO2 concentration and water vapour pressure deficit of air in the TGC were generally less than 5% and +/-0.2 kPa, respectively. A CO2 enrichment experiment on rice in the TGC showed that a doubling of the CO2 concentration markedly enhanced crop dry matter production, Temperature had less effect on dry matter production, although panicle dry weight was greatly decreased at higher temperature as a result of high-temperature-induced sterility of rice spikelets, Since rice spikelets are most sensitive to high temperature at the moment of flowering, and their flowering habit is highly synchronized with the diurnal courses of environmental conditions, the TGC is a useful tool in understanding rice responses to changes in atmosphere and temperature.

KEYWORDS: CARBON DIOXIDE, RESPONSES

947

Horn, M.E., and J.M. Widholm. 1994. Photoautotrophic growth of soybean cells in suspension-culture .3. Characterization of carbon fixation products under high and low co2 levels. *Plant Cell Tissue and Organ Culture 39(3):239-244.*

A photoautotrophic soybean suspension culture (SB-P) was used to study CO2 assimilation while exposed to elevated or ambient CO2 levels. These studies showed that under elevated CO2 (5% v/v) malate is the dominant fixation product, strongly suggesting that phosphoenolpyruvate carboxylase (PEPCase) is the primary enzyme involved in carbon fixation in these cells under their normal growth conditions. Citrate and [aspartate + glutamate] were also significant fixation products during fifteen minutes of exposure to (CO2)-C-14. During the ten minute unlabeled CO2 chase however, C-14-malate continued to increase while citrate and [aspartate + glutamate] declined. Fixation of (CO2)-C-14 under ambient CO2 levels (0.037%) showed a very different product pattern as 3-phosphoglycerate was very high in the first one to two minutes followed by increases in [serine + glycine] and [aspartate + glutamate]. Hexose phosphates were also quite high initially but then declined relatively rapidly. Thus, the carbon fixation pattern at ambient CO2 levels resembles somewhat that seen in C3 leaf cells while that seen at elevated CO2 levels more closely resembles that of a C-4 plant. The initial fixation product of C-3 plants, 3-PGA, was never detectable under high CO2 conditions. These data suggest that an in vitro photoautotrophic system would be suitable for studying carbon fixation physiology during photosynthetic and non- photosynthetic growth.

KEYWORDS: CHENOPODIUM-RUBRUM, METABOLISM, PHOTOSYNTHESIS

948

Hostetler, S.W., and F. Giorgi. 1995. Effects of a 2-times-co2 climate on 2 large lake systems - pyramid lake, nevada, and yellowstone lake, wyoming. *Global and Planetary Change 10(1-4):43-54.*

The possible effects of trace-gas induced climatic changes on Pyramid and Yellowstone Lakes are assessed using a model of lake temperature. The model is driven by 3 1/2 years of hourly meteorological data obtained directly from the output of doubled-CO2 experiments (2 x CO2) conducted with a regional climate model nested in a general circulation model. The regional atmospheric model is the climate version of the National Center for Atmospheric Research/Pennsylvania State University mesoscale model, MM4. Average annual surface temperature of Pyramid Lake for the 2 X CO2 climate is 15.5 +/- 5.4 degrees C (+/- 1 sigma), 2.8 degrees C higher than the control. Annual overturn of the lake ceases as a result of these higher temperatures for the 2 x CO2 climate. Evaporation increases from 1400 mm yr(-1) in the control to 1595 mm yr(-1) in the 2 X CO2 simulation, but net water supplied to the Pyramid Lake basin increases from -6 mm yr(-1) in the control to +27 mm yr(-1) in the 2 x CO2 simulation due to increased precipitation. For the open water periods, the average annual surface temperature of Yellowstone Lake is 13.2 +/- 5.1 degrees C for the 2 x CO2 climate, a temperature 1.6 degrees C higher than the control. The annual duration of ice cover on the lake is 152 days in the 2 X CO2 simulation, a reduction of 44 days relative to the control, Warming of the lake for the 2 x CO2 climate is mostly confined to the near-surface. Simulated spring overturn for the 2 X CO2 climate occurs earlier in the year and fall overturn later than in the control. Evaporation increases from 544 mm yr(-1) to 600 mm yr(-1) in the 2 X CO2 simulation, but net water supplied to the Yellowstone Lake basin increases from +373 mm yr(-1) in the control to +619 mm yr(-1) due to increased precipitation. The effects of these climatic changes suggest possible deterioration of water quality and productivity in Pyramid Lake and possible enhancement of productivity in Yellowstone Lake.

KEYWORDS: EVAPORATION, FISH, MODEL, POTENTIAL CHANGES, SIMULATION, THERMAL HABITAT

949

Houghton, R.A. 1996. Converting terrestrial ecosystems from sources to sinks of carbon. *Ambio 25(4):267-272.*

It may be possible to sequester carbon in forests and forest products, but to date global trends in land management have resulted in a release of terrestrial carbon to the atmosphere. Over 100 PgC were released between 1850 and 1980, and during the 1980s global changes in land use (predominantly deforestation) caused a net release of 1.6 PgC yr(-1), about 25% of the total emissions of carbon dioxide from human activities and about 15% of the enhanced radiative forcing. Management practices that could change this release of terrestrial carbon to an accumulation include (i) a halt to deforestation; (ii) an expansion in the land area of forests; (iii) an increase in the stocks of carbon in existing forests; (iv) more efficient harvest and greater use of wood in long-lasting products; and (v) the substitution of wood fuels for fossil fuels. However, the rate of global warming needs management as well. Unless the warming is gradual enough to avoid widespread mortality of forests, the additional releases of carbon caused by the warming itself, through increased respiration, decay, and fires, may cancel the intended effects of forest management.

KEYWORDS: CLIMATE, CO2, DEFORESTATION, DIOXIDE, FLUX, LAND-USE CHANGE, SEQUESTRATION, TRANSIENT-RESPONSE, TROPICAL FORESTS, VEGETATION

950

Houpis, J.L.J., P.D. Anderson, J.C. Pushnik, and D.J. Anschel. 1999. Among-provenance variability of gas exchange and growth in response to long-term elevated CO2 exposure. *Water, Air, and Soil Pollution 116(1-2):403-412.*

Genetic variability can have profound effects on the interpretation of results from elevated CO2 studies, and future forest management decisions. Information on which varieties are best suited to future atmospheric conditions is needed to develop future forest management practices. A large-scale screening study of the effects of elevated CO2

on 15 half- sibling sources of genetically superior ponderosa pine (Pinus ponderosa Dougl ex P. Laws.) is presented. These sources represent multiple elevations and latitudes throughout California. Among-provenance variability in the effects of elevated CO2 on gas exchange and growth, and their correlation with geographic origin were investigated in ponderosa pine seedlings subjected to ambient or elevated CO2 concentrations (525 mu mol mol(-1) CO2, and 700 mu mol mol(-1) CO2) for more than two years in open-top chambers. Substantial among- provenance variability in growth response to elevated CO2 was evident, with 8 sources demonstrating no significant growth response to elevated CO2 while 7 sources responded positively. For all sources, elevated CO2 increased photosynthesis (ranging from 19% increase at 525 mu mol mol(-1) CO2 to 49% increase at 700 mu mol mol(-1) CO2). A modest correlation existed between geographic origin and above ground growth response to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, FAMILIES, LEAVES, PHOTOSYNTHESIS, PLANT-RESPONSES, PONDEROSA PINE

951

Houpis, J.L.J., J. Pushnik, D. Anschel, P. Anderson, and R. Demaree. 1995. Intraspecific variability of photosynthetic traits of pinus- ponderosa subjected to long-term exposure to elevated co2. *Plant Physiology 108(2):62.*

952

Howden, S.M., G.M. McKeon, L. Walker, J.O. Carter, J.P. Conroy, K.A. Day, W.B. Hall, A.J. Ash, and O. Ghannoum. 1999. Global change impacts on native pastures in south-east Queensland, Australia. *Environmental Modelling & Software 14(4):307-316.*

Increases in atmospheric concentrations of greenhouse gases such as carbon dioxide (CO2) are likely to impact on grazing industries through direct effects on plant growth and through possible changes in climate. Assessment of the likely direction and magnitude of these impacts requires development of appropriate modelling capacities linked with experimental work. This paper documents the adaptation of an existing soil- pasture-livestock model, GRASP, to simulate system responses to changes in CO2. The adapted model is then used to compare these responses under current climate and CO2 conditions with four possible future scenarios: (1) doubled CO2; (2) doubled CO2 and increased temperature; (3) as in the previous scenario but with a drier climate; and (4) as in (2) but with a wetter climate. These studies suggest that CO2 changes alone are likely to have beneficial effects, with increased pasture growth, increased and less variable liveweight gain, and increased ground cover. However, subsoil drainage is likely to increase. Growth responses to CO2 are likely to be greater in drier years than in wetter years partly due to nitrogen limitations in the soils of the region. Increases in temperature in combination with CO2 further increased animal production due to the increased number of growing days in the cooler months. The increased rainfall scenario had few additional positive effects but further increased subsoil drainage. In contrast, the drier scenario had reduced plant and animal production when compared with current conditions even though seasonal transpiration efficiency was increased by 20% due to increased CO2. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, BOUTELOUA-GRACILIS C-4, CLIMATE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GRASS, GROWTH, PASCOPYRUM-SMITHII C-3, RESPONSES, WATER-USE

953

Hu, S.J., M.K. Firestone, and F.S. Chapin. 1998. Elevated atmospheric CO2 and soil biota. *Science 281(5376):518.*

954

Hu, S.J., M.K. Firestone, and F.S. Chapin. 1999. Soil microbial feedbacks to atmospheric CO2 enrichment. *Trends in Ecology and Evolution 14(11):433-437.*

Increased atmospheric CO2 concentration often stimulates plant photosynthesis, enhances carbon (C) allocation belowground, increases plant nutrient uptake and improves the efficiency of plant water use. Recent studies suggest that microbial responses to CO2-induced alterations in soil C, water and nutrient availability play an important role in determining ecosystem feedback to CO2 elevation. However, to date, most of the published results have been obtained from short-term experiments or from studies using high-nutrient or disturbed soils. Information on microbial responses to CO2-induced changes in natural and/or mature ecosystems with nutrient limitations is critical to predict changes in terrestrial ecosystem C storage under future CO2 scenarios.

KEYWORDS: DECOMPOSITION RATES, ELEVATED CARBON-DIOXIDE, LITTER QUALITY, MODEL ECOSYSTEM, N-AVAILABILITY, NITROGEN CYCLES, ORGANIC-MATTER, TALLGRASS PRAIRIE, TERRESTRIAL ECOSYSTEMS, WHITE CLOVER

955

Huang, B.R., J.W. Johnson, and D.S. NeSmith. 1997. Responses to root-zone CO2 enrichment and hypoxia of wheat genotypes differing in waterlogging tolerance. *Crop Science 37(2):464-468.*

Knowledge of wheat (Triticum aestivum L.) responses to CO2 and O-2 in the root environment could improve understanding of the mechanisms of waterlogging tolerance and thus help develop waterlogging-tolerant wheat plants. This experiment was designed to investigate the responses to elevated CO2 and hypoxia of two wheat genotypes, Bayles and Savannah, which differ in waterlogging tolerance. Plants were grown in a growth chamber in nutrient solutions. Nutrient solutions were bubbled with ambient air (control), N-2 containing 5 kPa O-2 and ambient CO2 (hypoxia), N-2 containing 10 kPa CO2 and ambient O- 2 (high CO2, ambient O-2), and N-2 containing 10 kPa CO2 and 5 kPa O-2 (high CO2, low O-2). Hypoxia alone had adverse effects on net photosynthesis (P-n), stomatal conductance (g(s)), water relations, leaf chlorophyll (chi) content, and shoot and root growth. The effects were greater for waterlogging-sensitive Bayles. When compared with the aerated control, the combination of elevated CO2 and hypoxia caused significant reductions in P- n, g(s), leaf water potential, and leaf chi content for Bayles, and in shoot and root growth for both Bayles and Savannah. Photosynthetic rate and leaf chi content of Savannah were increased when roots of hypoxic plants were exposed to elevated CO2, but this was not true for Bayles. Root-zone CO2 enrichment at ambient O-2 had no significant effects on shoot growth, but reduced root growth In both genotypes. The results showed that CO2 enrichment under root hypoxia can alleviate some negative effects of hypoxia on P-n, leaf chl content, and shoot growth, the effect being larger for waterlogging-tolerant Savannah.

KEYWORDS: AERENCHYMA, O2, RESPIRATION, SOIL CARBON-DIOXIDE, TOMATO PLANTS, TRANSPORT, WATER RELATIONS

956

Huang, Y.S., F.A. Street-Perrott, R.A. Perrot, P. Metzger, and G. Eglinton. 1999. Glacial-interglacial environmental changes inferred

from molecular and compound-specific delta C-13 analyses of sediments from Sacred Lake, Mt. Kenya. *Geochimica et Cosmochimica Acta 63(9):1383-1404.*

Molecular Stratigraphic analyses, including lipid distributions and compound-specific delta(13)C measurements, have been performed at 15 levels in a sediment core from Sacred Lake, Mt. Kenya, a high-altitude (2350 m a.s.l.) freshwater lake with a record extending from the last glacial (>40,000 cal. yr BP) through the present interglacial; Terrestrial and aquatic organic-matter sources were independently assessed using source-specific biomarkers. delta(13)C values of long-chain n- alkyl lipids from terrestrial higher plants exhibit large glacial to interglacial shifts: those from the last glacial maximum (LGM) (-20 to -18 parts per thousand) indicate a terrestrial vegetation dominated by C-4 grasses or sedges, whereas those from the early Holocene (-34 to -27 parts per thousand) reflect recolonization of the catchment area by C-3 plants, consistent with a rapid rise in the upper treeline. Specific algal biomarkers, including five unsaturated hydrocarbons of novel structure ascribed to the microalga Botryococcus braunii, were abundant, as confirmed by scanning electronic microscopy (SEM). An extreme delta(13)C shift of over 25 parts per thousand is displayed by the algal biomarkers, an elevated value of -5.1 parts per thousand at the last glacial maximum (LGM) contrasting with a minimum value of -30.3 parts per thousand at the beginning of the Holocene. A major change in the molecular distributions of the algal biomarkers parallels this large delta(13)C shift, with acyclic isoprenoid hydrocarbons dominating the last glacial and cyclic isoprenoid hydrocarbons the Holocene. The low atmospheric partial pressure of CO2 (pCO(2)) at the LGM would favour photosynthetic organisms possessing CO2-concentrating mechanisms, including terrestrial C-4 grasses and freshwater green algae. Hence, glacial/interglacial changes in pCO(2), and in the CO2:O-2 ratio in particular, had a significant impact on both terrestrial and aquatic ecosystems on Mt. Kenya, in addition to the effects of climate and local environmental factors. Copyright (C) 1999 Elsevier Science Ltd.

KEYWORDS: ALGA BOTRYOCOCCUS-BRAUNII, ATMOSPHERIC CO2, C-4 GRASSES, CARBON-ISOTOPE FRACTIONATION, DIOXIDE METABOLISMS, FRESH- WATER PLANTS, MOUNT KENYA, N-ALKANES, ORGANIC-MATTER, VEGETATION CHANGE

957

Hufton, C.A., R.T. Besford, and A.R. Wellburn. 1996. Effects of NO (+NO2) pollution on growth, nitrate reductase activities and associated protein contents in glasshouse lettuce grown hydroponically in winter with CO2 enrichment. *New Phytologist 133(3):495-501.*

Winter hydroponic growth of several lettuce cultivars under glass showed considerable inhibition (up to 47%) of growth after 6 wk exposure to concentrations of NO (+ NO2; 450 nl l(- 1) in total) typical of emissions from propane burners used for direct heating and CO2 enrichment. After a further 4 wk under similar conditions, however, these growth depressions were replaced by a swing into benefit so that, by harvest, pollutant-exposed lettuces were bigger and had faster assimilation rates than those growing in clean CO2-enriched air. This adaptation may partly be explained by enhanced use of NO2-derived N by lettuce leaves, a consequence of increased nitrate reductase (NaR) activities and amounts of associated NaR proteins, despite adequate nitrate also being available in the hydroponic fluid. Rates of NaR activity in the roots, by contrast, were depressed by NO (+ NO2) pollution. NaR activities were highest in early afternoon in clean or polluted air but these daily patterns did not coincide with the content of NaR-associated proteins determined by ELISA. Other mechanisms of modulating NaR activity must therefore be responsible.

KEYWORDS: DIOXIDE, EXPRESSION, GENES, LIGHT-DARK MODULATION, LONG-TERM EXPOSURES, NITRITE-REDUCTASE, NITROGEN- METABOLISM, OXIDES, PLANTS, TOMATO

958

Hughes, L., and F.A. Bazzaz. 1997. Effect of elevated CO2 on interactions between the western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae) and the common milkweed, Asclepias syriaca. *Oecologia 109(2):286-290.*

We measured the effect of elevated CO2 on populations of the western flower thrips, Frankliniella occidentalis and on the amount of leaf damage inflicted by the thrips to one of its host plants, the common milkweed, Asclepias syriaca. Plants grown at elevated CO2 had significantly greater aboveground biomass and C:N ratios, and significantly reduced percentage nitrogen. The number of thrips per plant was not affected by CO2 treatment, but the density of thrips (numbers per gram aboveground biomass), was significantly reduced at high CO2. Consumption by thrips, expressed as the amount of damaged leaf area per capita, was significantly greater at high CO2, and the amount of leaf area damaged by thrips was increased by 33%. However overall leaf area at elevated CO2 increased by 62%, more than compensating for the increase in thrips consumption. The net outcome was that plants at elevated CO2 had 3.6 times more undamaged leaf area available for photosynthesis than plants at ambient CO2, even though they had only 1.6 times the overall amount of leaf area. This study highlights the need for measuring the effects of herbivory at the whole-plant level and also the importance of taking herbivory into account when predicting plant responses to elevated CO2.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CHAMBERS, GROWTH, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, NOCTUIDAE, PAPER BIRCH, PERFORMANCE, PLANTS, RESPONSES

959

Huluka, G., D.R. Hileman, P.K. Biswas, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Effects of elevated co2 and water-stress on mineral concentration of cotton. *Agricultural and Forest Meteorology 70(1-4):141-152.*

Projected increases in atmospheric CO2 concentrations may alter mineral and protein levels in plant tissues, systematically affecting growth, nutrient cycling and utilization, residue decomposition, and insect-plant interactions in the future. The free-air CO2 enrichment (FACE) system provided an opportunity to monitor seasonal trends in nutrient status and crude protein content of cotton (Gossypium hirsutum L. cv. Deltapine 77) grown in a natural field setting without the limitations often imposed by growth chambers or reduced rooting volumes. In 1990, plants were exposed to two levels of atmospheric CO2 (FACE, almost-equal-to 550 mumol mol-1 and CONTROL, almost-equal-to 370 mumol mol-1) and two irrigation regimes (100% and 75% replacement of evapotranspiration) beginning in early July. Cotton leaves, stem, and roots were sampled at different times during the season and analyzed for C, N, Ca, K, Mg, P, Cu, Fe, Mn, Zn, B, Mo, Si and protein. The N and protein concentrations of leaves, stems and roots were significantly lower in FACE plants than in CONTROL plants, but C:N ratios were higher for the FACE plants than the CONTROL plants. Some other elements were significantly affected by CO2 enrichment, but not for all dates and all plant tissues. There were no significant effects in any of the data because of the irrigation treatment or the irrigation-CO2 interaction. Reductions in tissue N and protein concentrations and the increases in the C:N with CO2 enrichment have important implications for agricultural and natural systems and demand additional research.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, LEPIDOPTERA, NITROGEN, NUTRIENT CONCENTRATIONS, PLANTS, STARCH

960

Humphries, S.W., and S.P. Long. 1995. Wimovac - a software package for modeling the dynamics of plant leaf and canopy photosynthesis. *Computer Applications in the Biosciences 11(4):361-371.*

The ability to predict net carbon exchange and production of vegetation in response to predicted atmospheric and climate change is critical to assessing the potential impacts of these changes. Mathematical models provide an important tool in the study of whole plant, canopy and ecosystem responses to global environmental change. Because this requires prediction beyond experience, mechanistic rather than empirical models are needed. The uniformity and strong understanding of the photosynthetic process, which is the primary point of response of plant production to global atmospheric change, provides a basis for such an approach. Existing modelling systems have been developed primarily for expert modellers and have not been easily accessible to experimentalists, managers and students. Here we describe a modular modelling system operating within Winnows to provide this access. WIMOVAC (Windows Intuitive Model of Vegetation response to Atmosphere and Climate Change) is designed to facilitate the modelling of various aspects of plant photosynthesis with particular emphasis on the effects of global climate change. WIMOVAC has been designed to run on IBM PC-compatible computers running Microsoft Windows. The package allows the sophisticated control of the simulation processes for photosynthesis through a standardized Windows user interface and provides automatically formatted results as either tabulated data or as a range of customizable graphs. WIMOVAC has been written in Microsoft Visual Basic, to facilitate the rapid development of user-friendly modules within the familiar Windows framework, while allowing a structured development. The highly interactive nature of controls adopted by WIMOVAC makes it suitable for research, management and educational purposes.

KEYWORDS: C-3, CARBON DIOXIDE, ELEVATED CO2, RESPONSES, YIELD

961

Hungate, B.A., J. Canadell, and F.S. Chapin. 1996. Plant species mediate changes in soil microbial N in response to elevated CO2. *Ecology 77(8):2505-2515.*

The effect of elevated CO2 on plant-microbial interactions and nitrogen (N) cycling is critical to predicting plant growth responses to elevated CO2, because plant growth is often N- limited. We investigated whether the effects of elevated CO2 on plant-microbial N dynamics differed among six annual plant species: three European grasses that have invaded California grasslands, and one grass and two forbs native to California serpentine grassland. Elevated CO2 altered plant N pools and (NH4+)-N-15 uptake, but the direction and magnitude of the changes were species dependent. The introduced grasses showed increased plant N pools and (NH4+)-N-15 uptake, whereas the native species showed smaller increases or even decreases in plant N pools and N-15(4)+ uptake. Under nutrient enrichment, soil microbial N and (NH4+)-N-15 uptake differed among soils with different plant species, but they were not affected by elevated CO2. At low nutrients, elevated CO2 altered soil microbial N and (NH4+)-N-15 uptake, but the direction and magnitude of the changes were species dependent. The changes in soil microbial N were positively correlated with changes in the plant N pool, suggesting that there was no trade-off in N uptake between plants and microbes. These results also suggest that plant species composition will partly determine the direction of changes in soil N cycling in response to elevated CO2.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERIC CO2, CARBON DIOXIDE, DECOMPOSITION, DYNAMICS, ECOSYSTEMS, FOREST, GROWTH, LEAF LITTER, NITROGEN CYCLES

962

Hungate, B.A., F.S. Chapin, H. Zhong, E.A. Holland, and C.B. Field. 1997. Stimulation of grassland nitrogen cycling under carbon dioxide enrichment. *Oecologia 109(1):149-153.*

Nitrogen (N) limits plant growth in many terrestrial ecosystems, potentially constraining terrestrial ecosystem response to elevated CO2. In this study, elevated CO2 stimulated gross N mineralization and plant N uptake in two annual grasslands. In contrast to other studies that have invoked increased C input to soil as the mechanism altering soil N cycling in response to elevated CO2, increased soil moisture, due to decreased plant transpiration in elevated CO2, best explains the changes we observed. This study suggests that atmospheric CO2 concentration may influence ecosystem biogeochemistry through plant control of soil moisture.

KEYWORDS: ATMOSPHERIC CO2, BACTERIA, ECOSYSTEMS, FEEDBACK, MINERALIZATION, NITRATE, NITRIFICATION, PLANT, RESPONSES, SOILS

963

Hungate, B.A., P. Dijkstra, D.W. Johnson, C.R. Hinkle, and B.G. Drake. 1999. Elevated CO2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology 5(7):781-789.*

We report changes in nitrogen cycling in Florida scrub oak in response to elevated atmospheric CO2 during the first 14 months of experimental treatment. Elevated CO2 stimulated above-ground growth, nitrogen mass, and root nodule production of the nitrogen-fixing vine, Galactia elliottii Nuttall. During this period, elevated CO2 reduced rates of gross nitrogen mineralization in soil, and resulted in lower recovery of nitrate on resin lysimeters. Elevated CO2 did not alter nitrogen in the soil microbial biomass, but increased the specific rate of ammonium immobilization (NH4+ immobilized per unit microbial N) measured over a 24-h period. Increased carbon input to soil through greater root growth combined with a decrease in the quality of that carbon in elevated CO2 best explains these changes. These results demonstrate that atmospheric CO2 concentration influences both the internal cycling of nitrogen (mineralization, immobilization, and nitrification) as well as the processes that regulate total ecosystem nitrogen mass (nitrogen fixation and nitrate leaching) in Florida coastal scrub oak. If these changes in nitrogen cycling are sustained, they could cause long-term feedbacks to the growth responses of plants to elevated CO2. Greater nitrogen fixation and reduced leaching could stimulate nitrogen-limited plant growth by increasing the mass of labile nitrogen in the ecosystem. By contrast, reduced nitrogen mineralization and increased immobilization will restrict the supply rate of plant-available nitrogen, potentially reducing plant growth. Thus, the net feedback to plant growth will depend on the balance of these effects through time.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, LONG-TERM, PLANTS, ROOT NODULE ACTIVITY, SYMBIOTIC N-2 FIXATION, TRIFOLIUM- REPENS, WHITE CLOVER

964

Hungate, B.A., E.A. Holland, R.B. Jackson, F.S. Chapin, H.A. Mooney, and C.B. Field. 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature 388(6642):576-579.*

The concentration of carbon dioxide (CO2) in the Earth's atmosphere is rising rapidly(1), with the potential to alter many ecosystem processes. Elevated CO2 often stimulates photosynthesis(2), creating the possibility that the terrestrial biosphere will sequester carbon in response to rising atmospheric CO2 concentration, partly offsetting emissions from fossil-

fuel combustion, cement manufacture, and deforestation(3,4). However, the responses of intact ecosystems to elevated CO2 concentration, particularly the below-ground responses, are not well understood. Here we present an annual budget focusing on below-ground carbon cycling for two grassland ecosystems exposed to elevated CO2 concentrations. Three years of experimental CO2 doubling increased ecosystem carbon uptake, but greatly increased carbon partitioning to rapidly cycling carbon pools below ground, This provides an explanation for the imbalance observed in numerous CO2 experiments, where the carbon increment from increased photosynthesis is greater than the increments in ecosystem carbon stocks. The shift in ecosystem carbon partitioning suggests that elevated CO2 concentration causes a greater increase in carbon cycling than in carbon storage in grasslands.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BUDGET, GROWTH, IMPACT, NITROGEN, PHOTOSYNTHESIS, RESPONSES, ROOT, TERRESTRIAL ECOSYSTEMS, WATER

965

Hungate, B.A., R.B. Jackson, C.B. Field, and F.S. Chapin. 1996. Detecting changes in soil carbon in CO2 enrichment experiments. *Plant and Soil 187(2):135-145.*

After four growing seasons, elevated CO did not significantly alter surface soil C pools in two intact annual grasslands. However, soil C pools in these systems are large compared to the likely changes caused by elevated CO2. We calculated statistical power to detect changes in soil C, using an approach applicable to all elevated CO2 experiments. The distinctive isotopic signature of the fossil-fuel-derived CO2 added to the elevated CO2 treatment provides a C tracer to determine the rate of incorporation of newly-fixed C into soil. This rate constrains the size of the possible effect of elevated CO2 on soil C, Even after four years of treatment, statistical power to detect plausible changes in soil C under elevated CO2 is quite low. Analysis of other elevated CO2 experiments in the literature indicates that either CO2 does not affect soil C content, or that reported CO2 effects on soil C are too large to be a simple consequence of increased plant carbon inputs, suggesting that other mechanisms are involved, or that the differences are due to chance. Determining the effects of elevated CO2 on total soil C and long-term C storage requires more powerful experimental techniques or experiments of longer duration.

KEYWORDS: AMBIENT, BIOMASS PRODUCTION, DYNAMICS, ELEVATED CO2, GRASSLAND, NITROGEN, PLANTS, RESPONSES, TALLGRASS PRAIRIE, TEMPERATURE

966

Hungate, B.A., T.E. Jordan, R.B. Jackson, and B.G. Drake. 1997. Atmospheric nitrogen deposition. *Science 275(5301):739-740.*

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GROWTH, PISUM-SATIVUM, PLANTS

967

Hungate, B.A., C.P. Lund, H.L. Pearson, and F.S. Chapin. 1997. Elevated CO2 and nutrient addition alter soil N cycling and N trace gas fluxes with early season wet-up in a California annual grassland. *Biogeochemistry 37(2):89-109.*

We examined the effects of growth carbon dioxide (CO2) concentration and soil nutrient availability on nitrogen (N) transformations and N trace gas fluxes in California grassland microcosms during early-season wet-up, a time when rates of N transformation and N trace gas flux are high. After plant senescence and summer drought, we simulated the first fall rains and examined N cycling. Growth at elevated CO2 increased root production and root carbon:nitrogen ratio, Under nutrient enrichment, elevated CO2 increased microbial N immobilization during wet-up, leading to a 43% reduction in gross nitrification and a 55% reduction in NO emission from soil. Elevated CO2 increased microbial N immobilization at ambient nutrients, but did not alter nitrification or NO emission. Elevated CO2 did not alter soil emission of N2O at either nutrient level. Addition of NPK fertilizer (1:1:1) stimulated N mineralization and nitrification, leading to increased N2O and NO emission from soil, The results of our study support a mechanistic model in which elevated CO2 alters soil N cycling and NO emission: increased root production and increased C:N ratio in elevated CO2 stimulate N immobilization, thereby decreasing nitrification and associated NO emission when nutrients are abundant. This model is consistent with OUT basic understanding of how C availability influences soil N cycling and thus may apply to many terrestrial ecosystems.

KEYWORDS: DECOMPOSITION, DRY SOIL, EMISSIONS, FOREST, LITTER QUALITY, MICROBIAL BIOMASS, NITRIC-OXIDE, NITROGEN

968

Hunsaker, D.J., G.R. Hendrey, B.A. Kimball, K.F. Lewin, J.R. Mauney, and J. Nagy. 1994. Cotton evapotranspiration under field conditions with co2 enrichment and variable soil-moisture regimes. *Agricultural and Forest Meteorology 70(1-4):247-258.*

The CO2 concentration of the atmosphere is predicted to double by the next century, and this is expected to increase significantly the growth and yield of many important agricultural crops. One consequence of larger and more vigorous plants may be increased crop evapotranspiration (ET) and irrigation water requirements. The objective of this work was to determine ET of cotton (Gossypium hirsutum L. cv. 'Deltapine 77') grown under ambient (about 370 mumol mol-1) and enriched (550 mumol mol-1) CO2 concentrations for both well- watered and water-stress irrigation managements. Studies were conducted in 1990 and 1991 within a large, drip-irrigated cotton field in central Arizona. Cotton ET was measured during the growing seasons using a soil water balance, based on neutron gauge soil water measurements. ET, for periods from 7 to 14 days, was not significantly different between ambient and enriched CO2 treatments at the 0.05 probability level, and the total seasonal ET for the CO2 treatments varied by 2% or less in either year. However, water-stress treatments, which were initiated on 3 July (day of year (DOY) 184) in 1990 and on 20 May (DOY 128) in 1991, had significantly lower ($P < 0.05$) ET than well-watered treatments starting at the end of July in 1990 and in early July in 1991 when the plants were about 75-90 days old. The result that CO2 enrichment to 550 mumol mol-1 did not significantly change the ET of cotton was consistent with the results of co-investigators who measured ET in the same experiments using stem flow gauges and an energy balance. This result implies that irrigation water use would not have to be increased to produce cotton in a future high-CO2 world. However, if a concomitant change in climate occurs, such as global warming, cotton evapotranspiration may change in response to the changed weather condition.

KEYWORDS: CARBON DIOXIDE, WATER-USE, YIELD

969

Hunsaker, D.J., B.A. Kimball, P.J. Pinter, R.L. LaMorte, and G.W. Wall. 1996. Carbon dioxide enrichment and irrigation effects on wheat evapotranspiration and water use efficiency. *Transactions of the Asae 39(4):1345-1355.*

Evapotranspiration (ET) and water use efficiency were evaluated for two spring wheat crops, grown in a drip-irrigated field under ambient (about 370 mu mol mol(-1)) and enriched (550 mu mol mol(-1)) carbon dioxide

(CO2) concentrations during the 1992-1993, and 1993-1994, Free-Air CO Enrichment (FACE) experiments in central Arizona. CO2-enriched (FACE) and ambient CO2 (CONTROL) treatments were replicated in four circular plots, 25 m in diameter, and well-watered (WET) and water- stressed (DRY) irrigation treatments were imposed on one-half of each plot. Wheat ET, measured over discrete time periods of several days by a soil water balance, was significantly higher for WET than DRY irrigation treatments after the first week in March in both years. Differences in ET between CO2 treatments during the season were generally small, although there was a consistent trend towards decreased ET for the FACE over CONTROL under the well-watered irrigation regime. The two-year average reduction in seasonal ET owing to the FACE treatment was about 5% under WET irrigation and was consistent with the results from two parallel investigations that used an energy balance and sap flow measurements. Under the DRY irrigation treatment, seasonal ET was 5 and 0.9% higher for the FACE treatment in the first and second years, respectively. Water use efficiency (grain yield per unit seasonal ET) was significantly higher for FACE treatments; 15 and 24% higher than CONTROL under DRY irrigation, and 13 and 18% higher than CONTROL under WET irrigation. The results indicate that irrigation requirements for fully irrigated wheat may be slightly lower in the future high-CO2 environment.

KEYWORDS: CO2- ENRICHMENT, COTTON, FACILITY, FIELD, TRANSPIRATION, YIELD

970

Hunt, H.W., E.T. Elliott, J.K. Detling, J.A. Morgan, and D.X. Chen. 1996. Responses of a C-3 and a C-4 perennial grass to elevated CO2 and temperature under different water regimes. *Global Change Biology 2(1):35-47.*

An experiment was carried out to determine the effects of elevated CO2, elevated temperatures, and altered water regimes in native shortgrass steppe. Intact soil cores dominated by Bouteloua gracilis, a C-4 perennial grass, or Pascopyrum smithii, a C-3 perennial grass, were placed in growth chambers with 350 or 700 mu L L(-1) atmospheric CO2, and under either normal or elevated temperatures. The normal regime mimicked field patterns of diurnal and seasonal temperatures, and the high-temperature regime was 4 degrees C warmer. Water was supplied at three different levels in a seasonal pattern similar to that observed in the field. Total biomass after two growing seasons was 19% greater under elevated CO2, with no significant difference between the C-3 and C-4 grass. The effect of elevated CO2 on biomass was greatest at the intermediate water level. The positive effect of elevated CO2 on shoot biomass was greater at normal temperatures in B. gracilis, and greater at elevated temperatures in P. smithii. Neither root-to-shoot ratio nor production of seed heads was affected by elevated CO2. Plant tissue N and soil inorganic N concentrations were lower under elevated CO2, but no more so in the C-3 than the C-4 plant. Elevated CO2 appeared to increase plant N limitation, but there was no strong evidence for an increase in N limitation or a decrease in the size of the CO2 effect from the first to the second growing season. Autumn samples of large roots plus crowns, the perennial organs, had 11% greater total N under elevated CO2, in spite of greater N limitation.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, GROWTH-RESPONSE, NITROGEN CONCENTRATION, PHOTOSYNTHESIS, RISING CO2, ROOT, SHORTGRASS PRAIRIE, TALLGRASS PRAIRIE, TUSSOCK TUNDRA

971

Hunt, H.W., J.A. Morgan, and J.J. Read. 1998. Simulating growth and root-shoot partitioning in prairie grasses under elevated atmospheric CO2 and water stress. *Annals of Botany 81(4):489-501.*

We constructed a model simulating growth, shoot-root partitioning, plant nitrogen (N) concentration and total nonstructural carbohydrates in perennial grasses. Carbon (C) allocation was based on the concept of a functional balance between root and shoot growth, which responded to variable plant C and N supplies. Interactions between the plant and environment were made explicit by way of variables for soil water and soil inorganic N. The model was fitted to data on the growth of two species of perennial grass subjected to elevated atmospheric CO2 and water stress treatments. The model exhibited complex feedbacks between plant and environment, and the indirect effects of CO2 and water treatments on soil water and soil inorganic N supplies were important in interpreting observed plant responses. Growth was surprisingly insensitive to shoot-root partitioning in the model, apparently because of the limited soil N supply, which weakened the expected positive relationship between root growth and total N uptake. Alternative models for the regulation of allocation between shoots and roots were objectively compared by using optimization to find the least squares fit of each model to the data. Regulation by various combinations of C and N uptake rates, C and N substrate concentrations, and shoot and root biomass gave nearly equivalent fits to the data, apparently because these variables were correlated with each other. A partitioning function that maximized growth predicted too high a root to shoot ratio, suggesting that partitioning did not serve to maximize growth under the conditions of the experiment (C) 1998 Annals of Botany Company.

KEYWORDS: ALLOCATION, C-4 PLANTS, CARBON, CLIMATE CHANGE, MODEL, NITROGEN, PLANT GROWTH, RESPONSES, SHORTGRASS PRAIRIE, SOIL

972

Hunt, H.W., M.J. Trlica, E.F. Redente, J.C. Moore, J.K. Detling, T.G.F. Kittel, D.E. Walter, M.C. Fowler, D.A. Klein, and E.T. Elliott. 1991. Simulation-model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling 53(3-4):205-246.*

We studied the responses of temperate grasslands to climate change using a grassland ecosystem model which simulates seasonal dynamics of shoots, roots, soil water, mycorrhizal fungi, saprophytic microbes, soil fauna, inorganic nitrogen, plant residues and soil organic matter. Forty-year simulations were made for several climate change scenarios. The model was driven with observed weather and with combinations of elevated atmospheric CO2, elevated temperature, and either increased or decreased precipitation. Precipitation and CO2 level accounted for most of the variation among climate change treatments in the responses of soil, plants, animals and microbes. Elevated temperature extended the growing season but depressed photosynthesis in the summer, with little net effect on annual primary production. Doubling CO2 (1) caused persistent increases in primary production, in spite of greater nitrogen limitation, and (2) led to greater storage of carbon in plant residues and soil organic matter. The increased carbon storage was not great enough to keep pace with the present rate of increase in atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BIOMASS DYNAMICS, BLUE-GRAMA, BOUTELOUA-GRACILIS, CARBON DIOXIDE, CRESTED WHEATGRASS, ELEVATED CO2, NATIVE SHORTGRASS ECOSYSTEM, SOIL-WATER, USE EFFICIENCY

973

Hunt, R., and G.M. Constable. 1993. Multifactorial growth-responses in holcus-lanatus - optima and limiting factors. *Annals of Botany 71(4):357-368.*

KEYWORDS: CO2- ENRICHMENT, INTEGRATED ANALYSIS, LIGHT INTERCEPTION, LOCAL FLORA, PLANT GROWTH, TEMPERATURE, WEIGHT, WHEAT, YIELD

974

Hunt, R., and J.H.C. Cornelissen. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist 135(3):395-417.*

Three groups of species (21 herbaceous monocotyledons, 22 herbaceous dicotyledons and 16 woody dicotyledons), including representatives of a wide range of natural habitats and life forms in inland Britain, were grown in the seedling phase in a resource-rich controlled environment and assessed over a 14-day period (21 d in the case of woody species). Mean values of relative growth rate (RGR), Unit leaf rate (ULR), leaf area ratio (LAR), leaf weight fraction (LWF), specific leaf area (SLA), and the root-shoot allometric coefficient were derived. In herbaceous species, the grand mean RGR was 0.20 d(-1), comparable to values previously recorded. For woody species, the mean was 0.09 d(-1). An existing assumption linking high RGR to high allocation to photosynthetic biomass was upheld by comparisons made between groups. Within groups, however, no pattern of this kind could be demonstrated. When photosynthetically active radiation was increased from 125 to 250 mu mol m(-2) s(-1), ULR was increased almost pro rata. The parallel response in RGR was only slight, being offset by considerable reductions in LAR. The apparent mean quantum yield for photosynthesis in herbaceous species (whole-plant d. wt basis) was 0.60 g mol(-1). There was no significant dependence of RGR on ULR in any of the three groups of species, although the absolute magnitude of ULR declined in the order: herbaceous monocotyledons > herbaceous dicotyledons > woody dicotyledons. In all three groups, RGR was strongly dependent upon LAR but no differences emerged in absolute scale of LAR. The absolute scale of mean LWF decreased from herbaceous to woody species, but the dependence of LAR on LWF strengthened. Groups showed no systematic differences in magnitude of SLA, but the correlation of LAR with SLA was strong throughout. Multiple regression showed that the leading determinants of RGR were ULR and SLA in herbaceous species and LWF in woody species. Principal components analyses (PCA) on each of the three groups explained at least 77% of variation and agreed closely with an optimal (non-hierarchical) classification. Only six cluster 'types' were recognized out of the 16 theoretically possible combinations of 'high' or 'low' values of the four growth parameters. Strong evidence of evolutionary trade-offs emerged, most strikingly in that high RGR was never seen in combination with low SLA. The morphological/physiological types identified by an all-groups PCA separated woody from the herbaceous species, but dicotyledons were almost congruent with the monocotyledons. The non-growth-analytical attributes most strongly correlated with mean RGR were percentage yield at a low level of mineral nutrients, leaf nitrogen concentration, and seed weight. It was concluded that mean RGR plays a central role in the identification of pathways of evolutionary specialization in herbaceous species.

KEYWORDS: ALLOCATION PATTERNS, CARBON DIOXIDE, CHEMICAL-COMPOSITION, CO2- ENRICHMENT, EMERGENT MACROPHYTES, GRASS, LEAF, ROOT, SEED, STRATEGIES

975

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1991. Response to CO2 enrichment in 27 herbaceous species. *Functional Ecology 5(3):410-421.*

CO2-enrichment experiments were performed on 25 British native species of widely differing ecology. Two crops, one C3 (sunflower) and one C4 (maize), were also included. The background regime involved full-light, glasshouse conditions, non-limiting supplies of water and mineral nutrients and a daytime mean temperature of 18-degrees-C. Four CO2 treatments were maintained at nominal concentrations of 350, 500, 650 or 800 v.p.m. over a 56-day period. Hyperbolic functions were fitted to yield vs CO2 concentration. The functions were then used to generate predictions of Q540/350 (the quotient of present yield under the CO2 regime predicted for the year 2050) and Q700/350 (the quotient of present yield predicted for a doubling of ambient CO2 concentration). Values of Q540/350 for whole-plant dry weight ranged from below 1.01 to 1.49, the upper values being at least similar in magnitude to those already observed in C3 crops. The mean value of whole-plant Q700/350 for 11 species of near-competitive strategy was 1.43. Four species of stress-tolerant or ruderal strategy had a mean Q700/350 of only 1.05. High CO2 responsiveness was common only within the competitive strategy and its close relations. The fitted Q540/350 for species of the pure strategy was 1.38. In the centre of the strategic range the fitted value was 1.12, and at the far extreme, the value for species of ruderal or stress-tolerant strategy was only 1.03.

976

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1993. Further responses to co2 enrichment in british herbaceous species. *Functional Ecology 7(6):661-668.*

1. CO2-enrichment experiments have been performed on 15 British herbaceous species of widely differing ecology The conditions of growth were very similar to those used in a previous study and involved full-light glasshouse conditions, non-Limiting supplies of water and mineral nutrients and a daytime mean temperature of 18 degrees C. Four CO2 treatments were maintained (350, 500, 650 or 800 vpm) over periods of 49 or 52 days. 2. Hyperbolic functions were fitted to yield vs CO2 concentration. The functions were used to generate predictions of Q(540/350) (the quotient of the 'present' yield which is predicted for the CO2 regime expected by the year 2050) and Q(700/350) (the quotient predicted for a doubling of the present ambient CO2 concentration). Values of Q(540/350) for whole-plant dry weight ranged from below 1.00 to 1.19. The mean Value of whole-plant Q(700/350) for eight species of 'competitive' functional type was 1.13. Six species of 'stress-tolerant' or 'ruderal' type had a mean Q(700/350) Of only 1.07. 3. The new data support and amplify an earlier conclusion that high CO2 responsiveness is normal only within the competitive functional type (or 'strategy') and its close relations. A simplified and more broadly based general prediction now gives a fitted percentage increase after approximately 7 weeks' growth of 27% for species of broadly competitive strategy In the centre of the range of functional types the fitted values now range from 13 to 20%, and at the far extremes, the value for species of either the ruderal or the stress-tolerant type is now 6%. The gradient of this response is statistically significant, but less steep than that previously reported.

977

Hunt, R., D.W. Hand, M.A. Hannah, and A.M. Neal. 1995. Temporal and nutritional influences on the response to elevated co2 in selected british grasses. *Annals of Botany 75(2):207-216.*

To investigate the duration of the CO2 response and its interaction with mineral nutrition, CO2-enrichment experiments were performed on four British grasses of differing ecology and functional type: Arrhenatherum elatius (L.) Beauv., Festuca ovina L., Festuca rubra L. and Poa annua L. Naturally-lit, glasshouse cabinets were used, with a non-limiting water supply and a daytime mean temperature of 18 degrees C. Two CO2 treatments were maintained at nominal concentrations of 350 and 700 vpm and were combined factorially with two levels of balanced mineral nutrition at conductivities of 0.1 and 1 mS cm(-1). Harvests took place at planting-out, and at 16, 37 and 58 d thereafter. Fitted curves were used to derive instantaneous values of total dry weight, relative growth rate (RGR), shoot weight fraction (SWF) and unit shoot rate (USR) for all combinations of species, CO2 level, nutrient level and time of harvesting. At the higher nutrient level there was a reasonably close

agreement with previous estimates of the CO2 response in the four species. The response, if any, most often arose from an increase in USR being accompanied by a less than proportionate decline in SWF. Responses were sustained throughout the period studied. At the lower nutrient level, all species showed a CO2 response initially, but this declined at a rate which was inversely related to the CO2-responsiveness of the species at the higher nutrient level. The underlying ontogenetic drift appeared to be markedly towards adjustment in SWF and away from that of USR. However, this drift was retarded, suspended or even reversed by low-nutrient conditions and/or by high CO2 responsiveness in the species itself.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH-ANALYSIS, NITROGEN, PLANT GROWTH, RATIO, ROOT, SEEDLINGS, SHOOT, TREES

978

Huntley, B. 1995. Plant-species response to climate-change - implications for the conservation of european birds. *Ibis 137:S127-S138.*

Wildlife conservation faces new and extreme challenges in adapting to the accelerating dynamics of a world responding to global change, The Quaternary record shows that migration has been the usual response of organisms to environmental change, This record also reveals that forecast future climate changes are of a magnitude and in a direction unprecedented in recent earth history: the rate of these changes is likely also to surpass that of any comparable change during the last 2.4 million years, The relationship between a species' geographical distribution and present climate may be modelled by a surface representing the probability of encountering that species under given combinations of climate conditions, This 'climate response surface' then may be used to simulate potential future distributions of the species in response to forecast climate scenarios, Such simulations reveal the magnitude of the impacts of these forecast climate changes. Although to date this approach has been applied in Europe only to plants, it promises to be valuable also for other groups of organisms, including birds. Some bird species, however, may respond more directly to either habitat structure or presence of specific food plants; such factors may be incorporated into the models when required, The magnitude of likely vegetation changes necessitates a global approach to conservation if there is to be any hope of long-term success, Successful conservation of global biodiversity will depend upon conservation of the global environment and limitation of the human population much more than upon parochial efforts to conserve locally rare organisms or habitats.

KEYWORDS: CO2, COMMUNITIES, GRADIENTS, MIGRATION, MODEL, NORTH-AMERICA, POLLEN, SURFACES

979

Huntley, B., P.M. Berry, W. Cramer, and A.P. McDonald. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography 22(6):967-1001.*

It is hypothesized that the principal features of higher plant distributions at continental scales are determined by the macroclimate. Bioclimate data have been computed on a 50 km grid across Europe. Along with published maps of higher plant distributions based upon the same grid, these data have been used to derive climate response surfaces that model the relationship between a species' distribution and the present climate. Eight species representative of a variety of phytogeographic patterns have been investigated. The results support the hypothesis that the European distributions of all eight species are principally determined by macroclimate and illustrate the nature of the climatic constraints upon each species. Simulated future distributions in equilibrium with 2 x CO2 climate scenarios derived from two alternative GCMs show that all of the species are likely to experience major shifts in their potential range if such climatic changes take place. Some species may suffer substantial range and population reductions and others may face the threat of extinction. The rate of the forecast climate changes is such that few, if any, species may be able to maintain their ranges in equilibrium with the changing climate. In consequence, the transient impacts upon ecosystems will be varied but often may lead to a period of dominance by opportunist, early-successional species. Our simulations of potential ranges take no account of such factors as photoperiod or the direct effects of CO2, both of which may substantially alter the realized future equilibrium.

KEYWORDS: BRITISH-ISLES, GRADIENTS, MIGRATION, NORTH-AMERICA, POLLEN, REGRESSION, SPECIES RESPONSE, TILIA-CORDATA, VEGETATION

980

Hurry, V., M. Tobiaeson, S. Kromer, P. Gardestrom, and G. Oquist. 1995. Mitochondria contribute to increased photosynthetic capacity of leaves of winter rye (secale-cereale L) following cold- hardening. *Plant, Cell and Environment 18(1):69-76.*

Cold-hardening of winter rye (Secale cereale L. cv. Musketeer) increased dark respiration from -2.2 to -3.9 mu mol O-2 m(- 2)s(-1) and doubled light- and CO2-saturated photosynthesis at 20 degrees C from 18.1 to 37.0 mu mol O-2 m(-2) s(-1). We added oligomycin at a concentration that specifically inhibits oxidative phosphorylation to see whether the observed increase in dark respiration reflected an increase in respiration in the light, and whether this contributed to the enhanced photosynthesis of cold-hardened leaves, Oligomycin inhibited light- and CO2-saturated rates of photosynthesis in non- hardened and cold-hardened leaves by 14 and 25%, respectively, and decreased photochemical quenching of chlorophyll a fluorescence to a greater degree in cold-hardened than in non- hardened leaves, These data indicate an increase both in the rate of respiration in the light, and in the importance of respiration to photosynthesis following cold-hardening, Analysis of metabolite pools indicated that oligomycin inhibited photosynthesis by limiting regeneration of ribulose- 1,5-bisphosphate, This limitation was particularly severe in cold-hardened leaves, and the resulting low 3-phosphoglycerate pools led to a feed-forward inhibition of sucrose-phosphate synthase activity, Thus, it does not appear that oxidative phosphorylation supports the increase in photosynthetic O-2 evolution following cold-hardening by increasing the availability of cytosolic ATP, The data instead support the hypothesis that the mitochondria function in the light by using the reducing equivalents generated by nan-cyclic photosynthetic electron transport.

KEYWORDS: ACCUMULATION, BARLEY HORDEUM-VULGARE, LOW-TEMPERATURE, METABOLISM, OXIDATIVE-PHOSPHORYLATION, PROTOPLASTS, RESPIRATION, SUCROSE PHOSPHATE SYNTHASE, TERM PHOTOINHIBITION, WHEAT

981

Hussain, M.W., L.H. Allen, and G. Bowes. 1999. Up-regulation of sucrose phosphate synthase in rice grown under elevated CO2 and temperature. *Photosynthesis Research 60(2-3):199-208.*

Rice (Oryza sativa L. cv. IR-30) was grown season-long in outdoor, controlled-environment chambers at 33 Pa CO2 with day/night/paddy-water temperatures of 28/21/25 degrees C, and at 66 Pa CO2 with five different day/night/paddy-water temperature regimes (25/18/21, 28/21/25, 31/24/28, 34/27/31 and 37/30/34 degrees C). Sucrose phosphate synthase (SPS) activities in leaf extracts at 21, 48 and 81 days after planting (DAP) were assayed under saturating and selective (limiting) conditions. Diel SPS activity data indicated that rice SPS was light regulated; with up to 2.2-fold higher rates during the day.

Throughout the growth season, leaf SPS activities were up-regulated in the CO2-enriched plants, averaging 20 and 12% higher than in ambient-CO2 grown plants in selective and saturating assays, respectively. Similarly, SPS activities increased 2.4% for each 1 degrees C rise in growth temperature from 25 to 34 degrees C, but decreased 11.5% at 37 degrees C. Leaf sucrose content was higher, and mirrored SPS activity better, than starch, although starch was more responsive to CO2 treatment. Leaf sucrose and starch contents were significantly higher throughout the season in plants at elevated CO2, but the N content averaged 6.5% lower. Increasing growth temperatures from 25 to 37 degrees C caused a linear decrease (62%) in leaf starch content, but not in sucrose. Consequently, the starch:sucrose ratio declined with growth temperature. The data are consistent with the hypothesis that the up-regulation of leaf SPS may be an acclimation response of rice to optimize the utilization and export of organic-C with the increased rates of inorganic-C fixation in elevated CO2 or temperature growth regimes.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, GENE-EXPRESSION, LEAVES, METABOLISM, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES

982

Hutchin, P.R., M.C. Press, J.A. Lee, and T.W. Ashenden. 1995. Elevated concentrations of co2 may double methane emissions from mires. *Global Change Biology 1(2):125-128.*

The potential impact of an increase in methane emissions from natural wetlands on climate change models could be very large. We report a profound increase in methane emissions from cores of mire peat and vegetation as a direct result of increasing the CO2 concentration from 355 to 550 mu mol mol(-1) (a 60% increase). Increased CH4 fluxes were observed throughout the four month period of study. Seasonal variation in CH4 flux, consistent with that seen in the field, was observed under both ambient and elevated CO2. Under ambient CO2 methane fluxes rose from 0.02 mu mol m(-2) s(-1) in May to 0.11 mu mol m(-2) s(-3) in July before declining again in August. Under elevated CO2, methane fluxes were at least 100% greater throughout the experiment, rising from 0.05 mu mol m(-2) s(-1) in May to a peak of 0.27 mu mol m(-2) s(-1) in July. The stimulation of CH4 emissions was accompanied by a 100% increase in rates of photosynthesis from 4.6 (+/- 0.3) under ambient CO2 to 9.3 (+/- 0.7) mu mol m(-2) s(-1). Root and shoot biomass were unaffected.

KEYWORDS: PADDY FIELDS, RICE PADDY, SOIL TEMPERATURE, TUNDRA, WETLANDS

983

Hutjes, R.W.A., P. Kabat, S.W. Running, W.J. Shuttleworth, C. Field, B. Bass, M.A.F.D. Dias, R. Avissar, A. Becker, M. Claussen, A.J. Dolman, R.A. Feddes, M. Fosberg, Y. Fukushima, J.H.C. Gash, L. Guenni, H. Hoff, P.G. Jarvis, I. Kayane, A.N. Krenke, C. Liu, M. Meybeck, C.A. Nobre, L. Oyebande, A. Pitman, R.A. Pielke, M. Raupach, B. Saugier, E.D. Schulze, P.J. Sellers, J.D. Tenhunen, R. Valentini, R.L. Victoria, and C.J. Vorosmarty. 1998. Biospheric aspects of the hydrological cycle - Preface. *Journal of Hydrology 213(1-4):1-21.*

The Core Project Biospheric Aspects of the Hydrological Cycle (BAHC) of the International Geosphere Biosphere Programme (IGBP) addresses the biospheric aspects of the hydrological cycle through experiments and modelling of energy, water, carbon dioxide and sediment fluxes in the soil-vegetation- atmosphere system at a variety of spatial and temporal scales. Active regulation of water, energy and carbon dioxide fluxes by the vegetation make it an important factor in regulating the Earth's hydrological cycle and in the formation of the climate. Consequently, human induced conversion of vegetation cover is an important driver for climate change. A number of recent studies, discussed in this paper, emphasise the importance of the terrestrial biosphere for the climate system. Initially, these studies demonstrate the influence of the land surface on tropical weather and climate, revealing the mechanisms, acting at various scales, that connect increasing temperatures and decreasing rainfall to large-scale deforestation and other forms of land degradation. More recently, the significance of the land surface processes for water cycle and for weather and climate in temperate and boreal zones was demonstrated. In addition the terrestrial biosphere plays a significant role in the carbon dioxide fluxes and in global carbon balance. Recent work suggests that many ecosystems both in the tropics and in temperate zones may act as a substantial sink for carbon dioxide, though the temporal variability of this sink strength is yet unclear. Further, carbon dioxide uptake and evaporation by vegetation are intrinsically coupled leading to Links and feedbacks between land surface and climate that are hardly explored yet. Earth's vegetation cover and its changes owing to human impact have a profound influence on a lateral redistribution of water and transported constituents, such as nutrients and sediments, and acts therefore as an important moderator of Earth's biogeochemical cycles. In the BAHC science programme, the importance of studying the influence of climate and human activities on mobilisation and river-borne transport of constituents is explicitly articulated. The terrestrial water and associated material cycles are studied as highly dynamic in space and time, and reflect a complex interplay among climatic forcing, topography, land cover and vegetation dynamics. Despite a large progress in our understanding of how the terrestrial biosphere interacts with Earth's and climate system and with the terrestrial part of its hydrological cycle, a number of basic issues still remain unresolved. Limited to the scope of BAHC, the paper briefly assesses the present status and identifies the most important outstanding issues, which require further research. Two, arguably most important outstanding issues are identified: a limited understanding of natural variability, especially with respect to seasonal to inter-annual cycles, and of a complex ecosystem behaviour resulting from multiple feedbacks and multiple coupled biogeochemical cycles within the overall climate system. This leads to two major challenges for the future science agenda related to global change research. First, there is a need for a strong multidisciplinary integration of research efforts in both modelling and experiments, the latter extending to inter- annual timescales. Second, the ever increasing complexity in characterisation and modelling of the climate system, which is mainly owing to incorporation of the biosphere's and human feedbacks, may call for a new approach in global change impact studies. Methodologies need to be developed to identify risks to, and vulnerability of environmental systems, taking into account all important interactions between atmospheric, ecological and hydrological processes at relevant scales. With respect to the influence of climate and human activities on mobilisation and river-borne transport of constituents, the main issues for the future are related to declining availability and quality of ground data for quantity and quality of water discharge. Such assessments presented in this paper, in combination with community wide science evaluation, has lead to an update of the science agenda for BAHC, a summary of which is provided in the appendix. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, CLIMATIC IMPACTS, DROUGHT, FIELD EXPERIMENT, FLUXES, GENERAL-CIRCULATION MODEL, SCALING CHARACTERISTICS, SEMI-ARID REGIONS, TERRESTRIAL ECOSYSTEMS, VEGETATION

984

Huxman, K.A., S.D. Smith, and D.S. Neuman. 1999. Root hydraulic conductivity of Larrea tridentata and Helianthus annuus under elevated CO2. *Plant, Cell and Environment 22(3):325-330.*

While investigations into shoot responses to elevated atmospheric CO2

are extensive, few studies have focused on how an elevated atmospheric CO2 environment might impact root functions such as water uptake and transport. Knowledge of functional root responses may be particularly important in ecosystems where water is limiting if predictions about global climate change are true. In this study we investigated the effect of elevated CO2 on the root hydraulic conductivity (L-p) of a C-3 perennial, Lawea tridentata, and a C-3 annual, Helianthus annuus. The plants were grown in a glasshouse under ambient (360 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2. The L-p through intact root systems was measured using a hydrostatic pressure-induced flow system. Leaf gas exchange was also determined for both species and leaf water potential (psi(leaf)) was determined in L, tridentata, The L-p of L, tridentata roots was unchanged by an elevated CO2 growth environment. Stomatal conductance (g(s)) and transpiration (E) decreased and photosynthetic rate (A(net)) and psi(leaf) increased in L, tridentata, There were no changes in biomass, leaf area, stem diameter or root : shoot (R : S) ratio for L, tridentata. In H, annuus, elevated CO2 induced a nearly two- fold decrease in root L-p. There was no effect of growth under elevated CO2 on A(net), g(s), E, above- and below-ground dry mass, R : S ratio, leaf area, root length or stem diameter in this species. The results demonstrate that rising atmospheric CO2 can impact water uptake and transport in roots in a species-specific manner. Possible mechanisms for the observed decrease in root L-p in H, annuus under elevated CO2 are currently under investigation and may relate to either axial or radial components of root L-p.

KEYWORDS: ANATOMY, C-3, CARBON-DIOXIDE CONCENTRATION, CONDUCTANCE, ENRICHMENT, ENVIRONMENT, GROWTH, PLANTS, RESPONSES, WHEAT

985

Huxman, T.E., E.P. Hamerlynck, D.N. Jordan, K.J. Salsman, and S.D. Smith. 1998. The effects of parental CO2 environment on seed quality and subsequent seedling performance in Bromus rubens. *Oecologia 114(2):202-208.*

Seeds were collected and compared from parent plants of Bromus rubens L. (Poaceae), an exotic Mojave Desert annual grass, grown in ambient (360 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2 to determine if parental CO2 growth conditions affected seed quality. Performance of seeds developed on the above plants was evaluated to determine the influence of parental CO2 growth conditions on germination, growth rate, and leaf production, Seeds of B. rubens developed oil parents grown in elevated CO2 had a larger pericarp surface area, higher C:N ratio, and less total mass than ambient-developed seeds, Parental CO2 environment did not have an effect on germination percentage or mean germination timer as determined by radicle emergence. Seedlings from elevated-CO2-developed seeds had a reduced relative growth rate and achieved smaller final mass over the same growth period. Elevated-CO2-developed seeds had smaller seed reset-yes than ambient seeds, as determined by growing seedlings in sterile media and monitoring senescence. It appears that increased seed C:N ratios associated with plants grown under elevated CO2 may have a major effect on seed quality (morphology, nutrition) and seedling performance (e.g., growth rate and leaf production). Since the invasive success of B. rubens is primarily due to its ability to rapidly germinate, increase leaf area and maintain a relatively high growth rate compared to native annuals and perennial grasses, reductions in seed duality and seedling performance in elevated CO2 may have significant impacts on future community composition in the Mojave Desert.

KEYWORDS: ALLOCATION, ELEVATED CO2, ENRICHMENT, GERMINATION, GRASSLAND, GROWTH, PLANTS, RESPONSES

986

Huxman, T.E., E.P. Hamerlynck, M.E. Loik, and S.D. Smith. 1998. Gas exchange and chlorophyll fluorescence responses of three south-western Yucca species to elevated CO2 and high temperature. *Plant, Cell and Environment 21(12):1275-1283.*

The ability of seedlings to tolerate temperature extremes is important in determining the distribution of perennial plants in the arid south-western USA, and the manner in which elevated CO2 impacts the ability of plants to tolerate high temperatures is relatively unknown, Whereas the effects of chronic high temperature (30-38 degrees C) and elevated CO2 are comparatively well understood, little research has assessed plant performance in elevated CO2 during extreme (> 45 degrees C) temperature events, We exposed three species of Yucca to 360 and 700 mu mol CO, mol(-1) for 8 months, then 9 d of high temperature (up to 53 degrees C) to evaluate the impacts of elevated CO2 on the potential for photosynthetic function during external high temperature. Seedlings of a coastal C-3 species (Yucca whipplei), a desert C-3 species (Yucca brevifolia), and a desert CAM species (Yucca schidigera), were used to test for differences among functional groups. In general, Yuccas exposed to elevated CO2 showed decreases in carboxylation efficiency as compared with plants grown at ambient before the initiation of high temperature, The coastal species (Y. whipplei) showed significant reductions (33%) in CO2 saturated maximum assimilation rate (A(max)), but the desert species (Y. brevifolia and Y. schidigera) showed no such reductions in A(max). Stomatal conductance was lower in elevated CO2 as compared with ambient throughout the temperature event; however, there were species-specific differences over time. Elevated CO2 enhanced photosynthesis in Y. whipplei at high temperatures for a period of 4 d, but not for Y. brevifolia or Y. schidigera, Elevated CO2 offset photoinhibition (measured as F-v/F-m) in Y. whipplei as compared with ambient CO2, depending on exposure time to high temperature. Stable F-v/F-m in Y. whipplei occurred in parallel with increases in the quantum yield of photosystem II (Phi PSII) at high temperatures in elevated CO2. The value of Phi PSII remained constant or decreased with increasing temperature in all other treatment and species combinations, This suggests that the reductions in F-v/F-m resulted from thermal energy dissipation in the pigment bed for Y. brevifolia and Y. schidigera, The greater efficiency of photosystem II in Y. whipplei helped to maintain photosynthetic function at high temperatures in elevated CO2. These patterns are in contrast to the hypothesis that high temperatures in elevated CO2 would increase the potential for photoinhibition, Our results suggest that elevated CO2 may offset high-temperature stress in coastal Yucca, but not in those species native to drier systems, Therefore, in the case of Y. whipplei, elevated CO2 may allow plants to survive extreme temperature events, potentially relaxing the effects of high temperature on the establishment in novel habitats.

KEYWORDS: ACCLIMATION, AGAVE-DESERTI, ATMOSPHERIC CO2, AVAILABILITY, BREVIFOLIA, GROWTH, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, STRESS

987

Huxman, T.E., E.P. Hamerlynck, B.D. Moore, S.D. Smith, D.N. Jordan, S.F. Zitzer, R.S. Nowak, J.S. Coleman, and J.R. Seemann. 1998. Photosynthetic down-regulation in Larrea tridentata exposed to elevated atmospheric CO2: interaction with drought under glasshouse and field (FACE) exposure. *Plant, Cell and Environment 21(11):1153-1161.*

The photosynthetic response of Larrea tridentata Cav,, an evergreen Mojave Desert shrub, to elevated atmospheric CO2 and drought was examined to assist in the understanding of how plants from water-limited ecosystems will respond to rising CO2, We hypothesized that photosynthetic down-regulation would disappear during periods of water Limitation, and would, therefore, likely be a seasonally transient event. To test this we measured photosynthetic, water relations and fluorescence responses during periods of increased and decreased mater

availability in two different treatment implementations: (1) from seedlings exposed to 360, 550, and 700 mu mol mol(-1) CO2 in a glasshouse; and (2) from intact adults exposed to 360 and 550 mu mol mol(-1) CO2 at the Nevada Desert FACE (Free Air CO2 Enrichment) Facility. FACE and glasshouse wed-watered Larrea significantly down-regulated photosynthesis at elevated CO2, reducing maximum photosynthetic rate (A(max)), carboxylation efficiency (CE), and Rubisco catalytic sites, whereas droughted Larrea showed a differing response depending on treatment technique. A(max) and CE were lower in droughted Larrea compared with well-watered plants, and CO2 had no effect on these reduced photosynthetic parameters. However, Rubisco catalytic sites decreased in droughted Larrea at elevated CO2. Operating C-i increased at elevated CO2 in droughted plants, resulting in greater photosynthetic rates at elevated CO2 as compared with ambient CO2. In well-watered plants, the changes in operating C-i, CE andA(max) resulted in similar photosynthetic rates across CO2 treatments. Our results suggest that drought can diminish photosynthetic down-regulation to elevated CO2 in Larrea, resulting in seasonally transient patterns of enhanced carbon gain. These results suggest that water status may ultimately control the photosynthetic response of desert systems to rising CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DESERT, ECOSYSTEMS, GAS-EXCHANGE, GROWTH, INTACT LEAVES, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

988

Hymus, G.J., D.S. Ellsworth, N.R. Baker, and S.P. Long. 1999. Does free-air carbon dioxide enrichment affect photochemical energy use by evergreen trees in different seasons? A chlorophyll fluorescence study of mature loblolly pine. *Plant Physiology 120(4):1183-1191.*

Previous studies of the effects of growth at elevated CO2 on energy partitioning in the photosynthetic apparatus have produced conflicting results. The hypothesis was developed and tested that elevated CO2 increases photochemical energy use when there is a high demand for assimilates and decreases usage when demand is low. Modulated chlorophyll a fluorescence and leaf gas exchange were measured on needles at the top of a mature, 12-m loblolly pine (Pinus taeda L.) forest. Trees were exposed to ambient CO2 or ambient plus 20 Pa CO2 using free-air CO2 enrichment. During April and August, periods of shoot growth, light-saturated photosynthesis and linear electron transport were increased by elevated CO2. In November, when growth had ceased but temperatures were still moderate, CO2 treatment had no significant effect on linear electron transport. In February, when low temperatures were likely to inhibit translocation, CO2 treatment caused a significant decrease in linear electron transport. This coincided with a slower recovery of the maximum photosystem II efficiency on transfer of needles to the shade, indicating that growth in elevated CO2 induced a more persistent photoinhibition. Both the summer increase and the winter decrease in linear electron transport in elevated CO2 resulted from a change in photochemical quenching, not in the efficiency of energy transfer within the photosystem II antenna. There was no evidence of any effect of CO2 on photochemical energy sinks other than carbon metabolism. Our results suggest that elevated CO2 may increase the effects of winter stress on evergreen foliage.

KEYWORDS: ANTIOXIDATIVE ENZYMES, ASSIMILATION, ELEVATED CO2, LEAVES, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC ELECTRON-TRANSPORT, PHOTOSYSTEM-II ACTIVITY, QUANTUM YIELD, RISING ATMOSPHERIC CO2

989

Hyodo, H., C. Hashimoto, S. Morozumi, W.Z. Hu, and K. Tanaka. 1993. Characterization and induction of the activity of 1-aminocyclopropane-1-carboxylate oxidase in the wounded mesocarp tissue of cucurbita-maxima. *Plant and Cell Physiology 34(5):667-671.*

1-Aminocyclopropane-1-carboxylate (ACC) oxidase (ethylene- forming enzyme) was isolated from wounded mesocarp tissue of Cucurbita maxima (winter squash) fruit, and its enzymatic properties were investigated. The enzyme required Fe2+ and ascorbate for its activity as well as ACC and O2 as substrates. The in vitro enzyme activity was enhanced by CO2. The apparent K(m) value for ACC was 175 muM under atmospheric conditions. The enzyme activity was inhibited by sulfhydryl inhibitors and divalent cations such as Co2+, Cu2+, and Zn2+. ACC oxidase activity was induced at a rapid rate by wounding in parallel with an increase in the rate of ethylene production. The exposure of excised discs of mesocarp to 2,5-norbornadiene (NBD), an inhibitor of ethylene action, strongly suppressed induction of the enzyme, and the application of ethylene significantly accelerated the induction of the activity of ACC oxidase in the wounded mesocarp tissue. These results suggests that endogenous ethylene produced in response to wounding may function in promoting the induction of ACC oxidase.

KEYWORDS: ACID SYNTHASE, APPLE FRUIT, BIOSYNTHESIS, CANTALOUPE, CONVERSION, ETHYLENE-FORMING ENZYME, WINTER SQUASH FRUIT

990

Idso, C.D., S.B. Idso, and R.C. Balling. 1998. The urban CO2 dome of Phoenix, Arizona. *Physical Geography 19(2):95-108.*

Air temperatures, relative humidities, and atmospheric carbon dioxide concentrations were measured at a height of 2 m at approximate 1.6-km intervals prior to sunrise and in the middle of the afternoon on five days in January along a number of different transects through the extended metropolitan area of Phoenix, Arizona. Spatially interpolated maps of the data indicate the presence of an "urban CO2 dome" that reaches concentrations as high as 555 ppmv in the city center and decreases to a value of approximately 370 ppmv on the outskirts of the city at this time of year. Pre-dawn CO2 values inside the dome are considerably higher than mid-afternoon values, suggesting that solar-induced convective mixing and the photosynthetic uptake of CO2 by urban vegetation may play significant roles in diurnally redistributing the anthropogenically produced CO2 that, together with that produced by plant respiration, accumulates near the ground during the night and early morning hours. Temperature and relative humidity appear to have little influence on either the concentration or location of the CO2 dome, but variations in wind speed and direction at times may disrupt the pattern that develops under normally fair conditions. The high CO2 concentrations within the dome may help to ameliorate the deleterious effects of urban air pollution on vegetation growing within the city. Together with the urban heat island phenomenon, they may also provide a natural laboratory for studying the effects of contemporaneous warming and atmospheric CO2 enrichment within the context of predicted future global change.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, HEAT-ISLAND, NET PHOTOSYNTHESIS, PLANT-RESPONSES, RURAL TRANSECT, SULFUR-DIOXIDE, TEMPORAL ANALYSIS, WATER-USE, YIELD

991

Idso, K.E., and S.B. Idso. 1994. Plant-responses to atmospheric co2 enrichment in the face of environmental constraints - a review of the past 10 years research. *Agricultural and Forest Meteorology 69(3-4):153-203.*

This paper presents a detailed analysis of several hundred plant carbon

exchange rate (CER) and dry weight (DW) responses to atmospheric CO2 enrichment determined over the past 10 years. It demonstrates that the percentage increase in plant growth produced by raising the air's CO2 content is generally not reduced by less than optimal levels of light, water or soil nutrients, nor by high temperatures, salinity or gaseous air pollution. More often than not, in fact, the data show the relative growth-enhancing effects of atmospheric CO2 enrichment to be greatest when resource limitations and environmental stresses are most severe.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELEVATED CO2, GAS-EXCHANGE, NET PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RADIATA D-DON, SOUR ORANGE TREES, SOYBEAN CANOPY PHOTOSYNTHESIS, WATER-USE EFFICIENCY

992

Idso, S.B. 1991. A general relationship between CO2-induced increases in net photosynthesis and concomitant reductions in stomatal conductance. *Environmental and Experimental Botany 31(4):381-383.*

Simultaneous measurements of net photosynthesis and stomatal conductance of leaves of sour orange trees growing in normal and CO2-enriched air, together with similar data for cotton, cotton, soybeans and water hyacinth, suggest that a plant's photosynthetic response to atmospheric CO2 enrichment is inversely proportional to its degree of CO2-induced stomatal closure.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT

993

Idso, S.B. 1992. Net photosynthesis - corrections required of leaf chamber measurements. *Agricultural and Forest Meteorology 58(1-2):35-42.*

Direct measurements of trunk and branch volumes and fine-root biomass confirm that the growth rate of sour orange trees supplied with an extra 300 cm3 of CO2 m-3 of air is approximately 2.8 times greater than that of similar trees growing in ambient air. Net CO2 exchange measurements made on individual leaves over three 24 h periods in May, June and July 1990, however, suggest a relative growth enhancement for the CO2-enriched trees of the order of five to seven, which is clearly impossible on the basis of the direct growth measurements. It is shown that this discrepancy is due to a problem inherent in the act of enclosing a leaf in a leaf chamber, but that its effects can be removed by means of a simple correction procedure.

KEYWORDS: BASE-LINE ANALYSIS, COMPATIBILITY, HUMIDITY, POROMETRY, TEMPERATURE, WATER-STRESS

994

Idso, S.B. 1992. Shrubland expansion in the american southwest. *Climatic Change 22(1):85-86.*

KEYWORDS: CARBON DIOXIDE, CO2, ENRICHMENT, SOUR ORANGE TREES

995

Idso, S.B. 1997. The poor man's biosphere, including simple techniques for conducting CO2 enrichment and depletion experiments on aquatic and terrestrial plants. *Environmental and Experimental Botany 38(1):15-38.*

This paper reports the results of a 3-year experimental program designed to develop an inexpensive, low-technology approach for conducting atmospheric CO2 enrichment and depletion studies of aquatic and terrestrial plants. It begins by demonstrating the effectiveness of a number of simple techniques for creating a wide range of sub-and supra-ambient atmospheric CO2 concentrations in a set of low-cost experimental enclosures. It then describes the utilization of this approach in a variety of experiments that lead to the derivation of CO2-growth response relationships for a common terrestrial plant and for both a submerged and a floating aquatic species. Finally, it provides a description of a simple procedure for obtaining accurate assessments of atmospheric CO, concentrations in such experiments. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, GROWTH, TEMPERATURE

996

Idso, S.B. 1998. CO2-induced global warming: a skeptic's view of potential climate change. *Climate Research 10(1):69-82.*

Over the course of the past 2 decades, I have analyzed a number of natural phenomena that reveal how Earth's near-surface air temperature responds to surface radiative perturbations. These studies all suggest that a 300 to 600 ppm doubling of the atmosphere's CO2 concentration could raise the planet's mean surface air temperature by only about 0.4 degrees C. Even this modicum of warming may never be realized, however, for it could be negated by a number of planetary cooling forces that are intensified by warmer temperatures and by the strengthening of biological processes that are enhanced by the same rise in atmospheric CO2 concentration that drives the warming. Several of these cooling forces have individually been estimated to be of equivalent magnitude, but of opposite sign, to the typically predicted greenhouse effect of a doubling of the air's CO2 content, which suggests to me that little net temperature change will ultimately result from the ongoing buildup of CO2 in Earth's atmosphere. Consequently, I am skeptical of the predictions of significant CO2-induced global warming that are being made by state-of-the-art climate models and believe that much more work on a wide variety of research fronts will be required to properly resolve the issue.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, DIMETHYL SULFIDE, EQUATORIAL PACIFIC-OCEAN, ICE-FORMING NUCLEI, INORGANIC CARBON, RADIATION BUDGET EXPERIMENT, SOLAR IRRADIANCE, SUBMERSED MACROPHYTE GROWTH, SURFACE AIR-TEMPERATURE

997

Idso, S.B. 1999. The long-term response of trees to atmospheric CO2 enrichment. *Global Change Biology 5(4):493-495.*

KEYWORDS: GROWTH, PLANTS

998

Idso, S.B., S.G. Allen, and B.A. Kimball. 1990. Growth-response of water lily to atmospheric CO2 enrichment. *Aquatic Botany 37(1):87-92.*

999

Idso, S.B., and R.C. Balling. 1992. United-states drought trends of the past century. *Agricultural and Forest Meteorology 60(3-4):279-284.*

One of the primary concerns about potential global change is that the steadily rising CO2 content of earth's atmosphere may lead to significant increases in the severity and frequency of drought, especially in the agricultural heartland of the USA (Manabe et al., 1981; Gleick, 1987;

Manabe and Wetherald, 1986, 1987, McCabe et al., 1990). This consequence has been postulated to result from minor changes in the atmospheric supply of moisture (precipitation) and major changes in the atmospheric demand for moisture (potential evapotranspiration), as a result of increased surface temperatures. Waggoner (1989), for example, has shown how a 10% drop in precipitation can lead to a 46% increase in the frequency of drought; while Rind et al. (1990) have demonstrated that CO2-induced global warming, if it occurs as projected, could raise the frequency of severe drought in the USA from 5 to 50% by the year 2050. If drought is truly this responsive to changes in precipitation and potential evapotranspiration, and there is little reason to believe it is not, it could serve as a sensitive indicator of global warming and as a reliable test for identifying its onset. Hence, as the effective CO2 content of the atmosphere has already risen by nearly 50% above its pre-industrial level (Michaels, 1990; Houghton et al., 1990), studies of drought trends of the past century might even now provide evidence for the reality of global warming. However, there are three separate factors that could complicate this simple test.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, INCREASE, PRECIPITATION, RECORD

1000

Idso, S.B., K.E. Idso, R.L. Garcia, B.A. Kimball, and J.K. Hoober. 1995. Effects of atmospheric co2 enrichment and foliar methanol application on net photosynthesis of sour orange tree (citrus- aurantium, rutaceae) leaves. *American Journal of Botany 82(1):26-30.*

Foliar spray applications of 40% aqueous methanol were made to sunlit leaves of sour orange trees that had been grown continuously in clear-plastic-wall open-top enclosures maintained out-of-doors at Phoenix, Arizona, for over 5.5 years in ambient air of approximately 400 mu mol mol(-1) CO2 and in air enriched with CO2 to a concentration of approximately 700 mu mol mol(-1). No unambiguous effects of the methanol applications were detected in net photosynthesis measurements made on foliage in either of the two CO2 treatments. The 75% increase in CO2 however, raised the upper-limiting leaf temperature for positive net photosynthesis by approximately 7 C, which resulted in a 75% enhancement in net photosynthesis at a leaf temperature of 31 C, a 100% enhancement at a leaf temperature of 35 C, and a 200% enhancement at 42 C.

KEYWORDS: ELEVATED CO2, FIELD, GAS-EXCHANGE, GROWTH, TEMPERATURE

1001

Idso, S.B., and B.A. Kimball. 1991. Downward regulation of photosynthesis and growth at high CO2 levels - no evidence for either phenomenon in 3-year study of sour orange trees. *Plant Physiology 96(3):990-992.*

Numerous photosynthesis and growth measurements of sour orange (Citrus aurantium L.) trees maintained in ambient air and air enriched with an extra 300 microliters per liter of CO2 have revealed the CO2-enriched trees to have consistently sequestered approximately 2.8 times more carbon than the control trees over a period of three full years. Under field conditions in the natural environment, plants may not experience the downward regulation of photosynthetic capacity typically observed in long-term CO2 enrichment experiments with plants growing in pots.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COTTON, ELEVATED LEVELS, EXPOSURE, INHIBITION, PLANTS

1002

Idso, S.B., and B.A. Kimball. 1991. Effects of 2 and a half years of atmospheric CO2 enrichment on the root density distribution of 3-year-old sour orange trees. *Agricultural and Forest Meteorology 55(3-4):345-349.*

Eight sour orange trees planted directly into the ground at Phoenix, Arizona, as small seedlings in July 1987 have been enclosed by four clear-plastic-wall, open-top chambers since November of that year, half of which have been continuously supplied with a CO2 enriched atmosphere consisting of an extra 300 cm3 CO2 m-3 of air. Extensive soil coring of the trees' root zones conducted in July 1990 indicated that two and a half years of growth under these conditions produced a fine root biomass enhancement of 175% in the CO2 enriched trees. This growth enhancement is of the same order of magnitude as our previously reported results for net photosynthesis and trunk and branch volumes for these trees.

1003

Idso, S.B., and B.A. Kimball. 1992. Aboveground inventory of sour orange trees exposed to different atmospheric co2 concentrations for 3 full years. *Agricultural and Forest Meteorology 60(1-2):145-151.*

Sour orange trees have been grown from the seedling stage out- of-doors at Pheonix, Arizona in clear-plastic-wall, open-top enclosures for 3.5 years. For the last 3 years of this period, half of the trees have been continuously exposed to air enriched with an extra 300 cm3 of CO2 m-3 of air. Inventories of all aboveground plant parts conducted at the conclusions of the second and third years of the study reveal that the total number of branches per tree, the total number of leaves per tree, and the total trunk plus branch volume per tree can all be adequately inferred from measurements of trunk cross- sectional area. They also reveal a sustained beneficial impact of atmospheric CO2 enrichment. After 3 full years of differential CO2 exposure, the CO2-enriched trees had nearly 100% more branches, 75% more leaves, approximately 160% more trunk and branch volume, and 190% more trunk, branch and fruit rind volume than the ambient-treatment trees.

KEYWORDS: ENRICHMENT

1004

Idso, S.B., and B.A. Kimball. 1992. Effects of atmospheric co2 enrichment on photosynthesis, respiration, and growth of sour orange trees. *Plant Physiology 99(1):341-343.*

Numerous net photosynthetic and dark respiratory measurements were made over a period of 4 years on leaves of 24 sour orange (Citrus aurantium) trees; 8 of them growing in ambient air at a mean CO2 concentration of 400 microliters per liter, and 16 growing in air enriched with CO2 to concentrations approaching 1000 microliters per liter. Over this CO2 concentration range, net photosynthesis increased linearly with CO2 by more than 200%, whereas dark respiration decreased linearly to only 20% of its initial value. These results, together with those of a comprehensive fine-root biomass determination and two independent above-ground trunk and branch volume inventories, suggest that a doubling of the air's current mean CO2 concentration of 360 microliters per liter would enhance the growth of the trees by a factor of 3.8.

KEYWORDS: CARBON DIOXIDE, YIELD

1005

Idso, S.B., and B.A. Kimball. 1992. Seasonal fine-root biomass development of sour orange trees grown in atmospheres of ambient and elevated co2 concentration. *Plant, Cell and Environment 15(3):337-341.*

Sour orange trees have been grown from the seedling stage out- of-doors at Phoenix, Arizona, USA, in open-top enclosures with clear plastic walls for 3.5 years. For the last 3 years of this period, half of the trees have been continuously exposed to air enriched with CO2 to 300-mu-mol mol-1 above the ambient concentration. At 2-month intervals over the last 12 months, we have determined the fine-root biomass in the top 0.4 m of the soil profile beneath the trees. Results from both treatments define a single relationship between fine-root biomass and trunk cross-sectional area. The data also show the CO2-enriched trees to have approximately 2.3 times more fine-root biomass in this soil layer than the trees grown in ambient air.

KEYWORDS: ENRICHMENT, GLOBAL CARBON-CYCLE, STORAGE

1006

Idso, S.B., and B.A. Kimball. 1993. Effects of atmospheric co2 enrichment on net photosynthesis and dark respiration rates of 3 australian tree species. *Journal of Plant Physiology 141(2):166-171.*

Net photosynthesis and dark respiration rates of leaves of three Australian tree species exposed to a range of atmospheric CO2 concentrations were measured throughout the summer of 1991. For all three species - the Australian bottle tree (Brachychiton populneum (Schott.) R. Br.) and two eucalyptus (Eucalyptus microtheca F. Muell. and E. polyanthemus Schauer) - dark respiration dropped by approximately 50 % for a 360 to 720 muL/L doubling of the air's CO2 concentration, while net photosynthesis rose by a factor of two. These results were not significantly different from results obtained previously for the common sour orange tree (Citrus aurantium L.).

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, ELEVATED CO2, SOUR ORANGE TREES, TERM

1007

Idso, S.B., and B.A. Kimball. 1993. Tree growth in carbon-dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric co2. *Global Biogeochemical Cycles 7(3):537-555.*

In the longest carbon dioxide enrichment experiment ever conducted, well-watered and adequately fertilized sour orange tree seedlings were planted directly into the ground at Phoenix, Arizona, in July 1987 and continuously exposed, from mid-November of that year, to either ambient air or air enriched, with an extra 300 ppmv of CO2 in clear-plastic-wall open-top enclosures. Only 18 months later, the CO2-enriched trees had grown 2.8 times larger than the ambient-treated trees; and they have maintained that productivity differential to the present day. This tremendous growth advantage is due to two major factors: a CO2-induced increase in daytime net photosynthesis and a CO2-induced reduction in nighttime dark respiration. Measurements of these physiological processes in another experiment have shown three Australlian tree species to respond similarly; while an independent study of the atmosphere's seasonal CO2 cycle suggests that all earth's trees, in the mean, probably share this same response. A brief review of the plant science literature outlines how such a large growth response to atmospheric CO2 enrichment might possibly be maintained in light of resource limitations existing in nature. Finally, it is noted that a CO2 "fertilization effect" of this magnitude should substantially slow the rate at which anthropogenic carbon dioxide would otherwise accumulate in the atmosphere, possibly putting an acceptable upper limit on the level to which the CO2 content of the air may ultimately rise.

KEYWORDS: BUSH PLANT- RESPONSE, ELEVATED CO2, LYCOPERSICON-ESCULENTUM MILL, PHOTOSYNTHETIC ACCLIMATION, PINUS-RADIATA, RADIATA D-DON, ROOT RESTRICTION, SOUR ORANGE TREES, STOMATAL CONDUCTANCE, WATER-USE

1008

Idso, S.B., and B.A. Kimball. 1994. Effects of atmospheric co2 enrichment on biomass accumulation and distribution in eldarica pine trees. *Journal of Experimental Botany 45(280):1669-1672.*

Eight Eldarica pine tree (Pinus eldarica L.) seedlings planted directly into the ground at Phoenix, Arizona within four clear- plastic-wall open-top enclosures were grown for a period of 2 years at mean atmospheric CO2 concentrations of 408, 554, 680, and 812 mu L L(-1). Biomass accumulations in needles, branches and boles were all linear functions of CO2 over this concentration range. For a 75% increase in ambient CO2, i.e. for an increase from 400-700 mu L L(-1), the trees experienced a 3.42-fold increase in total above-ground biomass; while for a CO2 concentration doubling from 400-800 mu L L(-1), they experienced a 4.23-fold increase. Bore biomass responded similarly. Needle biomass, however, increased by a smaller amount (2.84-fold and 3.45-fold, respectively, for 400-700 and 400-800 mu L L(-1) increases in CO2); while branch biomass was increased considerably more (by 4.73-fold and 5.97-fold for corresponding increases in CO2).

KEYWORDS: CARBON DIOXIDE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SOUR ORANGE TREES

1009

Idso, S.B., and B.A. Kimball. 1994. Effects of atmospheric co2 enrichment on regrowth of sour orange trees (citrus-aurantium rutaceae) after coppicing. *American Journal of Botany 81(7):843-846.*

Sixteen sour orange tree (Citrus aurantium L.) seedlings were grown out-of-doors at Phoenix, Arizona, in eight clear-plastic- wall open-top enclosures maintained at four different atmospheric CO2 concentrations for a period of 2 years. Over the last year of this period, the trees were coppiced five times. The amount of dry matter harvested at each of these cuttings was a linear function of the atmospheric CO2 concentration to which the trees were exposed. For a 75% increase in atmospheric CO2 from 400 to 700 microliter per liter (mu L liter(-1)), total aboveground biomass rose, in the mean, by a factor of 3.19; while for a 400 to 800 mu L liter(- 1) doubling of the air's CO2 content, it rose by a factor of 3.92. The relative summer (mean air temperature of 32.8 C) response to CO2 was about 20% greater than the relative winter (mean air temperature of 16.4 C) response.

KEYWORDS: AIR, CARBON DIOXIDE, CROP RESPONSES, GROWTH, PAST 2 CENTURIES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS

1010

Idso, S.B., and B.A. Kimball. 1995. Effects of atmospheric CO2 enrichment on the growth of a desert succulent: Agave vilmoriniana Berger. *Journal of Arid Environments 31(4):377-382.*

Small well-watered 'plantlets' of Agave vilmoriniana Berger collected from the flower stalk of a single parent plant were grown out-of-doors at Phoenix, Arizona in clear-plastic-wall open-top enclosures exposed to ambient air and air enriched with CO2 to 300 mu l. l(-1) above ambient. Analysis of 12 harvests of three plantings conducted over a period of 4 years revealed a temperature-dependent CO2-induced growth enhancement for this desert succulent. The linear function used to describe the relationship was indistinguishable from a similar relationship previously derived for 16 non-CAM plants. (C)1995 Academic Press Limited

KEYWORDS: CROP RESPONSES, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRODUCTIVITY, SEEDLINGS

1011

Idso, S.B., and B.A. Kimball. 1997. Effects of long-term atmospheric CO2 enrichment on the growth and fruit production of sour orange trees. *Global Change Biology 3(2):89-96.*

In July of 1987, we planted eight 30-cm-tall sour orange tree seedlings in a field of Avondale loam at Phoenix, Arizona and enclosed them in pairs in clear-plastic-wall open-top chambers. Since 18 November of that year, we have continuously pumped ambient air of approximate to 400 ppmv [CO2] through two of these enclosures, while through the other two we have continuously pumped air of approximate to 700 ppmv [CO2]. By the end of the second year of the study, the trunk plus branch volume of the [CO2]-enriched trees was approximate to 2.75 times greater than that of the ambient-treatment trees. Three years later, this factor had dropped to approximate to 2.0; but the decline in the [CO2]-enriched/ambient-treatment ratio of trunk plus branch volume was nearly perfectly offset by the relative fruit production advantage enjoyed by the [CO2]- enriched trees over that period. In Years 6, 7 and 8, however, there was a moderate drop in total productivity enhancement. This decline may be a delayed acclimation response, or it could be due to enhanced self-shading in the [CO2]-enriched trees or to the fact that, starting early in Year 6, many branches of the [CO2]-enriched trees grew all the way to the walls of their enclosures, so that many blossoms and young fruit were destroyed by intermittent physical trauma produced by the action of wind against the taut plastic in that year and in all succeeding years. Hence, we will have to maintain our experiment for several more years for this lateral growth obstruction to occur to the same degree in the ambient-air chambers as it has in the [CO2]-enriched chambers, in order to determine the long-term equilibrium effects of atmospheric [CO2] enrichment in a spatially confined environment.

KEYWORDS: BRANCH BAG, CARBON DIOXIDE, ELEVATED CO2, EXPOSURE, FIELD, FOLIAR GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, SCIRPUS- OLNEYI, TUSSOCK TUNDRA

1012

Idso, S.B., B.A. Kimball, D.E. Akin, and J. Kridler. 1993. A general relationship between co2-induced reductions in stomatal conductance and concomitant increases in foliage temperature. *Environmental and Experimental Botany 33(3):443-446.*

Simultaneous measurements of the temperatures and stomatal conductances of leaves of sour orange trees growing in normal and CO2-enriched air, together with similar data for water hyacinths and cotton, suggest that a plant's foliage temperature response to atmospheric CO2-enrichment is directly proportional to its degree of stomatal closure, i.e. that plants that experience a greater stomatal closure in response to atmospheric CO2 enrichment experience a greater warming of their foliage. The data also suggest that this primary relationship may be modified by CO2-induced changes in leaf chlorophyll content that may have implications for global climate change.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CROP YIELD, GROWTH, PHOTOSYNTHETIC ACCLIMATION, WATER-USE

1013

Idso, S.B., B.A. Kimball, and S.G. Allen. 1991. CO2 enrichment of sour orange trees - 2.5 years into a long- term experiment. *Plant, Cell and Environment 14(3):351-353.*

Eight sour orange trees have been grown from seedling stage in the field at Phoenix, Arizona, U.S.A., in four identically-vented, open-top, clear-plastic-wall chambers for close to 2.5 years. Half of the chambers have been maintained at ambient atmospheric CO2 concentrations over this period, while half of them have been maintained at 300 ppm (300-mu-mol CO2 per mol air) above ambient. Initially, the trees in each treatment were essentially identical; but in less than 2 years, the trunks of the CO2-enriched trees had become twice as large as their ambient-treatment counterparts. After 2 full years of growth, the enriched trees had 79% more leaves, 56% more primary branches with 172% more volume, 70% more secondary branches with 190% more volume, and 240% more tertiary branches with 855% more volume. In addition, the CO2-enriched trees also had fourth-, fifth- and sixth-order branches, while the ambient- treatment trees had no branches above third order. Total trunk plus branch volume of the CO2-enriched trees was 2.79 times that of the ambient-treatment trees after 2 full years of growth.

KEYWORDS: CARBON DIOXIDE

1014

Idso, S.B., B.A. Kimball, and S.G. Allen. 1991. Net photosynthesis of sour orange trees maintained in atmospheres of ambient and elevated CO2 concentration. *Agricultural and Forest Meteorology 54(1):95-101.*

Eight sour orange trees planted directly into the ground at Phoenix, Arizona, as small seedlings in July 1987 have been enclosed by four clear-plastic-wall, open-top chambers since November of that year. Half of the trees have been continuously supplied with a CO2-enriched atmosphere consisting of an extra 300 cm3 of CO2 per m3 of air. Data from a comprehensive inventory of all above-ground plant parts at the conclusion of two full years of growth under these conditions have revealed that the net effect of the CO2-enriched air was to more than double the normal production of biomass over that time interval. Here we report net photosynthesis measurements made throughout the last summer of the period, which suggest that the primary impetus for this large growth response was an equivalent enhancement of the net photosynthetic rates of the CO2-enriched trees.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT

1015

Idso, S.B., B.A. Kimball, and D.L. Hendrix. 1993. Air-temperature modifies the size-enhancing effects of atmospheric co2 enrichment on sour orange tree leaves. *Environmental and Experimental Botany 33(2):293-299.*

Every other month for a period of 2 years, leaf area and dry weight measurements were made on the foliage of sour orange trees growing in ambient air and in air enriched with an extra 300 mul/l CO2. Leaf starch content measurements were made at approximate 2-month intervals for a period of 1 year. The data demonstrated that all three plant parameters were significantly increased by atmospheric CO2 enrichment, except in the coldest portion of the year. A plot of the ratio of CO2-enriched leaf dry weight to ambient-treatment leaf dry weight against the mean air temperature of the preceding month revealed this relationship with temperature to be linear. The relationship shows atmospheric CO2 enrichment to have a negligible effect on leaf dry weight at a mean air temperature of approximately 5- degrees-C. At a mean air temperature of 35-degrees-C, however, it shows individual CO2-enriched leaves of our experiment to weigh 40% more than their ambient-treatment counterparts. This phenomenon helps to explain the vastly different effects of atmospheric CO2 enrichment that have been reported for a number of diverse ecosystems.

KEYWORDS: CARBON, COMMUNITIES, ELEVATED CO2, ENVIRONMENT, ESTUARINE MARSH, GROWTH-RESPONSE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRODUCTIVITY, TUSSOCK TUNDRA

1016

Idso, S.B., B.A. Kimball, and D.L. Hendrix. 1996. Effects of atmospheric CO2 enrichment on chlorophyll and nitrogen concentrations of sour orange tree leaves. *Environmental and Experimental Botany 36(3):323-331.*

Since 18 November 1987, eight sour orange (Citrus aurantium L.) trees have been maintained under well watered and fertilized conditions within four clear-plastic-wall open-top enclosures, two of which have been continuously supplied with ambient air of approximately 400 mu l 1(-1) CO2 and two of which have been supplied with air enriched to approximately 700 mu l 1(-1) CO2. At weekly intervals throughout years 4-7 of this long-term experiment, we measured chlorophyll a contents of 60 leaves on each of the trees with a hand-held chlorophyl meter that was specifically calibrated for our study. At bi-monthly intervals, we also measured the areas, dry weights and nitrogen contents of 68 leaves from each tree. Expressed on a per-unit-leaf-area basis, leaves from the CO2-enriched trees contained 4.8% less chlorophyll and nitrogen than leaves from the trees exposed to ambient air. Because of their greater leaf numbers, however, the CO2-enriched trees contained 75% more total chlorophyll and nitrogen than thr ambient-treatment trees; the total productivity of the CO2-enriched trees was 175% greater. Consequently, although per-unit-leaf-area chlorophyll and nitrogen contents were slightly lowered by atmospheric CO2 enrichment in our experiment, their use efficiencies were greatly enhanced.

KEYWORDS: EXTRACTABLE CHLOROPHYLL, GROWTH, LEAF GREENNESS, METER, PHOTOSYNTHESIS, TEMPERATURE, WHEAT

1017

Idso, S.B., B.A. Kimball, G.W. Wall, R.L. Garcia, R. Lamorte, P.J. Pinter, J.R. Mauney, G.R. Hendrey, K. Lewin, and J. Nagy. 1994. Effects of free-air co2 enrichment on the light response curve of net photosynthesis in cotton leaves. *Agricultural and Forest Meteorology 70(1-4):183-188.*

Daytime measurements of leaf CO2 exchange rates in a free-air CO2 enrichment (FACE) experiment reveal that at photosynthetically active radiation (PAR) flux rates in excess of 1000 mumol m-2 s-1, cotton leaves exposed to an atmospheric CO2 concentration of approximately 500 mumol mol-1 exhibit net photosynthetic rates about 30% greater than those for leaves of similar plants growing in ambient air. As PAR flux rates drop below this value, the stimulatory effect of elevated CO2 rises, suggesting that the relative benefits of atmospheric CO2 enrichment will be greater for shaded cotton leaves that for those exposed to full sunlight.

KEYWORDS: CARBON DIOXIDE, GROWTH, QUANTUM YIELD, TRANSPIRATION

1018

Idso, S.B., G.W. Wall, and B.A. Kimball. 1993. Interactive effects of atmospheric co2 enrichment and light- intensity reductions on net photosynthesis of sour orange tree leaves. *Environmental and Experimental Botany 33(3):367-375.*

In a tong-term study of the effects of a 300 mul l-1 enrichment of the air's CO2 content on the growth of sour orange trees, a comprehensive set of net photosynthesis and light intensity data was obtained. From these measurements we derived single- leaf light response curves, which together with complementary leaf area index data allowed us to derive full-canopy light response curves. The results showed our 85% enhancement of the air's CO2 content to more than double canopy net photosynthesis at full sunlight. Our analysis demonstrated that the positive direct effect of atmospheric CO2 enrichment on net photosynthesis more than compensated for the negative self- shading effect produced by the CO2-induced proliferation of leaf area.

KEYWORDS: AMBIENT, CARBON DIOXIDE, GROWTH, PLANTS, QUANTUM YIELD, RESPIRATION, RESPONSES, TRANSPIRATION

1019

Igamberdiev, A.U., and I.V. Zabrovskaya. 1994. The effect of light, carbon nutrition, and salinity on the oxidative-metabolism of wolffia-arrhiza. *Russian Journal of Plant Physiology 41(2):208-214.*

The effects of varying conditions of carbon nutrition (sucrose and an inorganic source of carbon in the growth medium), light, and salinity on oxidative metabolism were studied in Wolffia arrhiza (L.) Hork. ex Wimmer. In cells grown on 1% sucrose, the level of the cyanide-resistant (CO2)-C-14 evolution from 1,4-C- 14-succinate as a respiratory substrate was considerably higher than in autotrophically grown plants. When the medium was enriched in inorganic carbon (CO2 or bicarbonate), the rate of metabolization of glucose and other respiratory substrates diminished, and total protein and chlorophyll content decreased. Light incubation enhanced glucose metabolization two- to threefold, whereas succinate transformation was increased by a factor of 1.5 to 2, with a concomitant rise in the electron flow via the cyanide-resistant pathway. Inhibition of the photorespiratory metabolism with alpha-hydroxypyridine- 2-methanesulfonate slowed down glucose and succinate metabolism. NaCl activated glycolate metabolism in autotrophically grown plants and did not influence the rates of glucose and succinate transformation. In contrast, under photoheterotrophic (mixothrophic) growth conditions on sucrose, NaCl added to the cultivation medium led to a considerably higher (three- to fourfold) (CO2)-C-14 evolution from 1,4-C-14- succinate and 1-C-14-glucose. The authors conclude that the adaptation of Wolffia plants to different environmental conditions is accompanied by changes in the metabolic fluxes via cyanide-resistant oxidase, along the glycolate pathway, and other oxidative pathways. These changes conform to the alterations in enzyme activities participating in the oxidative metabolism.

KEYWORDS: CYANIDE, DEHYDROGENASE, PLANTS

1020

Igamberdiev, A.U., G.Q. Zhou, G. Malmberg, and P. Gardestrom. 1997. Respiration of barley protoplasts before and after illumination. *Physiologia Plantarum 99(1):15-22.*

Respiratory O-2 consumption was investigated in dark-adapted barley (Hordeum vulgare L. cv. Gunilla) protoplasts and after illumination for 10 min at high and very low CO2 in the presence of respiratory and photorespiratory inhibitors. In dark-adapted protoplasts no difference was observed between inhibitor treatments in high and very low CO2. The respiratory rate increased somewhat after illumination and a difference in responce to inhibitors was in some cases observed between high and very low CO2. Thus, the operation of the mitochondrial electron transport chain is affected following a period of active photosynthesis. In all situations tested, oligomycin inhibited respiratiory O-2 uptake indicating that respiration of mitochondria in protoplasts is not strictly ADP limited. Antimycin A inhibited respiration more in dark-adapted protoplasts than after illumination whereas SHAM gave the opposite response. Rotenone inhibited respiration both in dark adapted protoplasts (about 30%) and after illumination where the inhibition was much greater in very low CO2 (50%) than in high CO2 (10%). After iilumination in very low CO2, SHAM + rotenone inhibited respiration almost completely (70%). Photorespiratory inhibitors had very small effect on O-2 consumption in darkness. After illumination the effect of aminoacetonitrile (AAN) was also very low whereas a-hydroxypyridine-2-methane sulphonate (HPMS) in photorespiratory conditions inhibited O-2 uptake much stronger (35%). The addition of glyoxylate enhanced respiration in the presence of HPMS up to the

control level suggesting that alternative pathways of glyoxylate conversion might be operating. The differences in inhibitor responses may reflect fine mechanisms for the regulation of energetic balance in the plant cell which consists of switching from electron transport coupled to ATP production to non-coupled transport. Photorespiratory flux is also very flexible, and the suppression of glycine decarboxylation can induce bypass reactions of glyoxylate metabolism.

KEYWORDS: ALTERNATIVE OXIDASE ACTIVITY, CARBOHYDRATE STATUS, CELLS, CHLOROPLASTS, LEAVES, MESOPHYLL PROTOPLASTS, PATHWAY, PEA, PHOTOSYNTHETIC METABOLISM, PLANT-MITOCHONDRIA

1021

Imai, K., and M. Okamotosato. 1991. Effects of temperature on CO2 dependence of gas exchanges in C3 and C4 crop plants. *Japanese Journal of Crop Science 60(1):139-145.*

The effects of elevated CO2 in the atmosphere and the accompanied temperature rise predicted for the future on gas exchanges of two summer C3 (rice, soybean) and two C4 (Japanese millet, finger millet) crop plants were examined. Plants were grown in artificially illuminated growth cabinets under 350 and 500-mu-mol mol-1 ambient CO2 (C(a)) and were measured for rates of CO2 exchange (CER) and transpiration (E) of leaves at 23, 28 and 33-degrees-C in terms of C(a) (0-500-mu-mol mol-1). The responses of CER to C(a) were slightly lower in plants grown in high C(a) than those in normal C(a) and were largely influenced by temperature. The promotive effect of elevating C(a) on CER was larger at higher temperatures, especially in C4 crop plants. With the rise of C(a), the E in C4 crop plants decreased more than in C3 crop plants and it was correlated with the decrease in stomatal conductance to CO2 transfer. The water use efficiency (WUE) of leaves increased with the rise in C(a) but the effect of temperature on WUE was unclear. It is concluded that, whthin limits, under high C(a), C4 crop plants expand their photosynthetic capacity in an environment of high temperature.

1022

Ineichen, K., V. Wiemken, and A. Wiemken. 1995. Shoots, roots and ectomycorrhiza formation of pine-seedlings at elevated atmospheric carbon-dioxide. *Plant, Cell and Environment 18(6):703-707.*

The effect of elevated atmospheric CO2 concentration on the growth of shoots, roots, mycorrhizas and extraradical mycorrhizal mycelia of pine (Pinus silvestris L.) was examined, Two and a half-month-old seedlings were inoculated axenically with the mycorrhizal fungus Pisolithus tinctorius (Pers,) by a method allowing rapid mycorrhiza formation in Petri dishes, The plants were then cultivated for 3 months in growth chambers with daily concentrations of 350 and 600 mu mol mol(-1) CO2 during the day, Whereas plants harvested after 1 and 2 months did not differ appreciably between ambient and increased CO2 concentrations, after 3 months they developed a considerably higher root biomass (+57%) at elevated CO2, but did not increase significantly in root length, The mycorrhizal fungus Pisolithus tinctorius, which depended entirely on the plant assimilates in the model system, grew much faster at increased CO2: 3 times more mycorrhizal root clusters were formed and the extraradical mycelium produced had twice the biomass at elevated as at ambient CO2. No difference in shoot biomass was found between the two treatments after 91d, However, since the total water consumption of seedlings was similar in the two treatments, the water use efficiency was appreciably higher for the seedlings at increased CO2 because of the higher below- ground biomass.

KEYWORDS: AMBIENT, CO2 CONCENTRATION, ENRICHMENT, GROWTH, PLANTS, TREES

1023

Ineson, P., M.F. Cotrufo, R. Bol, D.D. Harkness, and H. Blum. 1996. Quantification of soil carbon inputs under elevated CO2:C-3 plants in a C-4 soil. *Plant and Soil 187(2):345-350.*

The objective of this investigation was to quantify the differences in soil carbon stores after exposure of birch seedlings (Betula pendula Roth.) over one growing season to ambient and elevated carbon dioxide concentrations. One-year- old seedlings of birch were transplanted to pots containing 'C- 4 soil' derived from beneath a maize crop, and placed in ambient (350 mu L L-1) and elevated (600 mu L L-1) plots in a free-air carbon dioxide enrichment (FACE) experiment. After 186 days the plants and soils were destructively sampled, and analysed for differences in root and stem biomass, total plant tissue and soil C contents and delta(13)C values. The trees showed a significant increase (+50%) in root biomass, but stem and leaf biomasses were not significantly affected by treatment. C isotope analyses of leaves and fine roots showed that the isotopic signal from the ambient and elevated CO2 supply was sufficiently distinct from that of the 'C-4 soil' to enable quantification of net root C input to the soil under both ambient and elevated CO2. After 186 days, the pots under ambient conditions contained 3.5 g of C as intact root material, and had gained an additional 0.6 g C added to the soil through root exudation/turnover; comparable figures for the pots under elevated CO2 were 5.9 g C and 1.5 g C, respectively. These data confirm the importance of soils as an enhanced sink for C under elevated atmospheric CO2 concentrations. We propose the use of 'C-4 soils' in elevated CO2 experiments as an important technique for the quantification of root net C inputs under both ambient and elevated CO2 treatments.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, DIOXIDE, ENRICHMENT, RESPONSES, ROOTS, SYSTEM

1024

Ineson, P., P.A. Coward, and U.A. Hartwig. 1998. Soil gas fluxes of N2O, CH4 and CO2 beneath Lolium perenne under elevated CO2: The Swiss free air carbon dioxide enrichment experiment. *Plant and Soil 198(1):89-95.*

Fluxes of nitrous oxide, methane and carbon dioxide were measured from soils under ambient (350 mu L L-1) and enhanced (600 mu L L-1) carbon dioxide partial pressures (pCO(2)) at the 'Free Air Carbon Dioxide Enrichment' (FACE) experiment, Eidgenossische Technische Hochschule (ETH), Eschikon, Switzerland in July 1995, using a GC housed in a mobile laboratory. Measurements were made in plots of Lolium perenne maintained under high N input. During the data collection period N fertiliser was applied at a rate of 14 g m(-2) of N. Elevated pCO(2) appeared to result in an increased (27%) output of N2O, thought to be the consequence of enhanced root-derived available soil C, acting as an energy source for denitrification. The climate, agricultural practices and soils at the FACE experiment combined to give rise to some of the largest N2O emissions recorded for any terrestrial ecosystem. The amount of CO2-C being lost from the control plot was higher (10%) than for the enhanced CO2 plot, and is the reverse of that predicted. The control plot oxidised consistently more CH4 than the enhanced plot, oxidising 25.5 +/- 0.8 mu g m(-2) hr(- 1) of CH4 for the control plot, with an average of 8.5 +/- 0.4 mu g m(-2) hr(-1) of CH4 for the enhanced CO2 plot. This suggests that elevated pCO(2) may lead to a feedback whereby less CH4 is removed from the atmosphere. Despite the limited nature of the current study (in time and space), the observations made here on the interactions of elevated pCO(2) and soil trace gas release suggest that significant interactions are occurring. The feedbacks involved could have importance at the global scale.

KEYWORDS: ATMOSPHERIC CO2, DENITRIFICATION, STIMULATION

1025

Ingestad, T., O. Hellgren, H. Hesseldahl, and A.B.L. Ingestad. 1996. Methods and applications to control the uptake rate of carbon. *Physiologia Plantarum 98(3):667-676.*

Methods to control carbon and nutrient uptake at different availability of carbon were tested on plants of birch (Betula pendula Roth.) and tomato (Lycopersicon esculentum Mill. cv. Solentos). The present paper accounts for the methods and the possibility to maintain steady-state, i.e., a long-term and stable physiological state of acclimated plants. Steady-state comprises, by definition, equality between constant relative growth rates, and relative uptake rates of carbon and nutrients. Two methods were tested. The first, not previously applied, method (a), was based on a constant relative addition rate of carbon, R(AC). In the second method (b), a constant concentration of CO2 in the air, c(a), was used to attain non- limiting conditions. The methods are analogous to those used by us to control plant nutrition, and the generality of fluxes to quantify supply as well as uptake and growth was verified. Thus, different R(AC) resulted suited in clear-cut responses, from strong reduction to non-limitation of uptake and growth, whereas different c(a) levels in the range 100 to 700 ppm had comparatively small effects, with an unclear causality. Non- limiting conditions were achieved at c(a) greater than or equal to 200 ppm. Effects reported in the literature have been based upon the control of c(a), similarly to method (b), whereas results comparable to those obtained with method (a) are lacking. Transpiration rate increased rapidly at c(a) < 200 ppm CO2, and at low R(AC) levels, less than or equal to 0.1 day(- 1), wilting tendencies were observed. Elevated c(a) 500 or 700 ppm, did not increase the relative growth rate (R(G)) but reduced transpiration and increased both nitrogen productivity (growth rate per unit of nitrogen in the plant) and transpiration productivity (growth rate per unit of water transpired by the plant). Obviously, effects of c(a) may be due to changed transpiration rate rather than to changed quantitative availability of CO2. Relative uptake (R(OC)) and growth (R(G)) rates were closely equal to the R(AC) applied (R(AC) approximate to R(UC) approximate to R(G)); i.e., the purely mathematical conditions defining steady-state were fulfilled. This unambiguous and straightforward test of reliability confirms that experimental artefacts did not produce uncontrolled or unintended effects, so that the new technique allows an accurate control of CO2 uptake and plant growth. The results add to previous databases and reference systems, where limiting conditions grade and classify plant performance as deviations from maximum growth. Evidently, methodology in experimentation and in evaluation of plant responses, can be based upon unifying concepts and general theories.

KEYWORDS: BIRCH SEEDLINGS, GROWTH, NITROGEN STRESS, PLANT NUTRITION

1026

Ingvardsen, C., and B. Veierskov. 1994. Response of young barley plants to co2 enrichment. *Journal of Experimental Botany 45(279):1373-1378.*

Barley (Hordeum vulgare L. cv. Digger) was grown for 22 d in enclosed chambers with a CO2 enrichment of 35, 155, 400 or 675 mu mol CO2 mol(-1). CO2 enrichment increased photosynthetic capacity in the plants grown at either of the two highest levels of pCO(2). A CO2 enrichment of 675 mu mol CO2 caused a significant increment of shoot dry weight, whereas no changes were observed in fresh weight, chlorophyll or protein levels. At a light intensity of 860 mu mol m(-2) s(-1) CO2 enrichment caused photosynthetic capacity to increase by 250%, whereas no effect was observed at 80 mu mol m(-2) s(-1). Over time, photosynthesis decreased by 70% independent of CO2. A time-dependent increase in the level of extractable fructose was observed whereas total extractable carbohydrate only changed slightly.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, LEAVES, PHOTOSYNTHESIS, PHYSIOLOGY, RESPIRATION, WHEAT, YIELD

1027

Innes, J.L. 1994. Climatic sensitivity of temperature forests. *Environmental Pollution 83(1-2):237-243.*

Climatic change and associated global changes are of major interest to foresters, both in terms of forest ecology and of future forest production. Predicting the likely effects of global change on forests is extremely difficult due to the critical lack of information on regional changes in meteorological factors relevant to forests. However, existing models of forest production and forest distribution fail to take adequate account of what is already known. Climate and carbon dioxide concentrations have shown substantial changes over the last 100 years. Although the rate of change is likely to increase, recent proposed and implemented control strategies, together with better climatic models, are tending to suggest that the rate of change will be less than initially thought. This means that past changes may provide an increasingly useful source of information. In particular, information on the impact on forests of both long-term climate change and short-term climatic events is rapidly increasing. Such information should be built into future forest response models.

KEYWORDS: CO2, EMISSIONS, FERTILIZATION, GERMANY, GROWTH, INCREASE, MOUNTAINS, NITROGEN, PRODUCTIVITY, RESPONSES

1028

Inoue, Y., B.A. Kimball, J.R. Mauney, R.D. Jackson, P.J. Pinter, and R.J. Reginato. 1990. Stomatal behavior and relationship between photosynthesis and transpiration in field-grown cotton as affected by CO2 enrichment. *Japanese Journal of Crop Science 59(3):510-517.*

1029

Insam, H., E. Baath, M. Berreck, A. Frostegard, M.H. Gerzabek, A. Kraft, F. Schinner, P. Schweiger, and G. Tschuggnall. 1999. Responses of the soil microbiota to elevated CO2 in an artificial tropical ecosystem. *Journal of Microbiological Methods 36(1-2):45-54.*

Plants in artificial tropical ecosystems were grown under ambient (340 mu l l(-1)) and elevated (610 mu l l(-1)) atmospheric CO2 for 530 d under low-nutrient conditions on a substrate free of organic C. At the end of the experiment a number of soil chemical and microbiological variables were determined. Although we found no changes in total soil organic matter under elevated CO2, we did find that after physical fractionation the amount of organic C in the supernatant (< 0.2 mu m) and the amount of water extractable organic C (WEOC) was lower under elevated CO2. The extractable optical density (OD) indicated a higher degree of humification for the elevated than for the ambient CO2 samples (P = 0.032). Microbial biomass C was not significantly altered under high CO2, but total bacterial counts were significantly higher. The microbial biomass C-to-N ratio was also higher at elevated (15.0) than at ambient CO2 (10.0). The number of mycorrhizal spores was lower at high CO2, but ergosterol contents and fungal hyphal lengths were not significantly affected. Changes were found neither in community level physiological profiles (CLPPs) nor in the structural attributes (phospholipid fatty acids, PLFAs) of the microbial community. Overall, the effects on the soil microbiota were small, perhaps as a result of the low nutrient supply and low organic matter content of the soil used in our study. The few significant results showing changes in specific, though relatively minor, organic matter pools may point to possible long-term changes of the more major pools. Furthermore, the data suggest increased competition between plants and microbes for N at high CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, BOUTELOUA-GRACILIS, COMMUNITIES, COTTON, DECOMPOSITION, ENRICHMENT, NITROGEN, ORGANIC-MATTER, ROOT

1030

Inubushi, K., W.G. Cheng, and K. Chander. 1999. Carbon dynamics in submerged soil microcosms as influenced by elevated CO2 and temperature. *Soil Science and Plant Nutrition 45(4):863-872.*

A 45-d incubation experiment was conducted under controlled laboratory conditions to study the interactive effects of elevated CO2 and temperature on the dynamics of microbial biomass C and organic C in hooded paddy soil microcosms amended or unamended with rice straw. The microcosms with the two treatments were transferred separately to four growth chambers to incubate them under 16 h/8 h light and dark conditions. Two of the growth chambers set at 25 and 35 degrees C provided a continuous how of elevated CO2 (equivalent to 800 mu L L-1). Similarly the other two growth chambers were run under near ambient CO2 (400 mu L L-1) conditions at each of the two temperatures. The amounts of soluble carbon, microbial biomass C, chlorophyll-type compounds, and organic C in the surface (0- 1 cm) and sub-surface (below 1 cm) soil layers were measured at 15, 30, and 45 d after incubation. The amount of soluble carbon in the straw-amended soil gradually decreased throughout the incubation period, while no significant differences were detected among the four different conditions. The interactive effects of both elevated CO2 and temperature were found to be positive in terms of the size of the microbial biomass in surface soil, although no significant differences were detected in the subsurface. However, the amount of total soil organic C was larger in the soils incubated at a lower temperature. The amounts of chlorophyll-type compounds doubled in the surface soil when the soils were incubated under elevated CO2 conditions, indicating that the higher incubation concentration of CO2 promoted the growth of algae in surface soil.

KEYWORDS: ATMOSPHERIC CO2, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER

1031

Ioslovich, I., I. Seginer, P.O. Gutman, and M. Borshchevsky. 1995. Suboptimal co2 enrichment of greenhouses. *Journal of Agricultural Engineering Research 60(2):117-136.*

Greenhouse CO2 enrichment in warm climates is restricted by the need to ventilate, leading some growers to intermittent enrichment, where enrichment and ventilation alternate several times an hour. This strategy relies on the heat and CO2 capacity of the system, characterized by a heating time constant of the order of 10 min, during which period ventilation may be suspended. It is shown that, for slowly changing weather, the optimal CO2 enrichment is basically not intermittent (bang-bang control), but rather quasi steady state (smoothly varying singular control). As the disturbance (weather) frequency increases, the quasi steady-state (QSS) solution becomes less and less optimal. Nevertheless, due to the difficulties involved in implementing a truly optimal control (the need for accurate weather forecast and high control fluxes), the sub-optimal QSS control may be a better choice. We chose to try a controller which aims to follow the QSS temperature and CO2 setpoints at all disturbance frequencies. The performance of this controller for high disturbance frequencies is a few per cent lower than the truly optimal solution, but over the whole season this effect may not be significant. On the other hand, the controller is likely to be more robust. Implementation of the QSS solution requires simulaneous ventilation and enrichment, properly balanced.

KEYWORDS: GROWTH, INTERMITTENT

1032

Islam, K.R., C.L. Mulchi, and A.A. Ali. 1999. Tropospheric carbon dioxide or ozone enrichments and moisture effects on soil organic carbon quality. *Journal of Environmental Quality 28(5):1629-1636.*

Carbon, as an active component of organic matter, has considerable effects on soil quality and productivity. The objective of this study was to examine the effect of climate change variables on soil organic C (C-T) quality in an agroecosystem. Wheat (Triticum aestivum L.) and soybean [Glycine max (L.) Merr] plants were grown in 3 m in diam, open- top field chambers and exposed to charcoal-filtered (CF) air at 350 mu L CO2 L-1; CF air + 150 mu L CO2 L-1; nonfiltered (NF) air + 35 nL O-3 L-1; and NF air + 35 nL O-3 L-1 + 150 mu L CO2 L-1 at two soil moisture levels from 1994 to 1996. The 150 mu L CO2 L-1 addition was 18 h d(-1) and the 35 nL O-3 L-l was 7 h d(-1) from April until late October. In response to treatments, the CT contents did not change significantly; however, particulate, oxidizable, dissolved, humic (C-HA) and fulvic (C- FA) acid, and carbohydrate C pools increased in soils under CO2 enrichment and well-watered conditions but decreased under O-3 stress compared with soils under CF ambient air quality. Tropospheric CO2 enrichment and well-watered condition increased, and O-3, stress decreased the log optical density slope for both C-HA and C-FA fractions more than CF ambient air and restricted moisture treatment. Also, the E-465/E-665 ratios of both C-HA and C-FA fractions were higher for the CO2 enrichment and smaller for the O-3 stress compared With CF ambient air quality, Results suggest that tropospheric CO2 enrichment and well-watered conditions may favor an accumulation of low molecular weight and more aliphatic quality of C and O-3 stress favor high molecular weight and more aromatic quality of C.

KEYWORDS: ALLOCATION, DECOMPOSITION, FERTILIZATION, HUMIC SUBSTANCES, INCREASING ATMOSPHERIC CO2, LEAF LITTER, LITTER QUALITY, MATTER DYNAMICS, O-3, WATER

1033

Islam, M.S., T. Matsui, and Y. Yoshida. 1995. Effect of preharvest carbon dioxide enrichment on the postharvest quality of tomatoes. *Journal of the Japanese Society for Horticultural Science 64(3):649-655.*

The effect of preharvest application of elevated CO2 throughout the fruit growing period on organic acid, sugar content, acid invertase activity (beta-fructofuranoside fructohydrolase, EC 3.2.1.26), and color quality in tomato (Lycopersicon esculentum Mill. cv. Momotaro) fruit during storage at 20 degrees C was determined. The CO2-enriched tomato fruits contained significantly lower concentrations of citric, malic and oxalic acids, but had significantly higher reducing sugars and acid invertase activity at harvest and during storage. The concentration of these acids decreased with storage, whereas the activity of acid invertase and reducing sugar contents increased in the treated fruits; they were relatively constant in the control fruits. Furthermore, the elevated CO2 resulted in a deeper red color during storage.

KEYWORDS: ACCUMULATION, FLAVOR, FRUITS, INVERTASE, STARCH, SUGAR

1034

Islam, M.S., T. Matsui, and Y. Yoshida. 1996. Effect of carbon dioxide enrichment on physico-chemical and enzymatic changes in tomato fruits at various stages of maturity. *Scientia Horticulturae 65(2-3):137-149.*

The influence of CO2 enrichment on fruit growth, firmness and colour, together with its effect on the concentrations of ascorbic acid, organic acids and sugars, and the activities of sucrose synthase (SS) (UDP glucose: D-fructose 2- glucosyltransferase, E. C. 2, 4, 1, 13) and sucrose phosphate synthase (SPS) (UDP glucose: D-fructose-6-phosphate 2-glucosyltransferase, E. C. 2. 4. 1. 14) were determined at various stages of maturity in fruits of tomato (Lycopersicon esculentum Mill. cv. Momotaro), CO2 enriched tomatoes had lower amounts of citric, malic and oxalic acids, and higher amounts of ascorbic acid, fructose, glucose and sucrose synthase activity than the control. Elevated CO2 enhanced fruit growth and colouring during development. Citric acid was the primary organic acid followed by malic and oxalic acids. The concentration of organic acids (mg g(-1) fresh weight) and of ascorbic acid (mg 100g(-1) fresh weight) increased with the maturity of fruits; their maximum concentrations were found at the pink stage of ripening, but declined slightly at the red stage. The amount of reducing sugars (mg g(-1) fresh weight) increased with the advancement of maturity, with fructose being the predominant sugar. The decrease in SS activity was accompanied by an increase in the concentrations of reducing sugars. There were no significant differences in fruit firmness, sucrose concentration and SPS activity between the treatments. The SPS activity did not change, but remained relatively constant throughout fruit development. The results also suggest that SS levels correlated positively with sucrose concentration but negatively with the concentration of reducing sugars.

KEYWORDS: CO2, ENZYMES, GREENHOUSES, INVERTASE, MUSKMELON FRUIT, RESPONSES, SINK METABOLISM, SUCROSE PHOSPHATE SYNTHASE, SUGAR ACCUMULATION

1035

Israel, A.A., and P.S. Nobel. 1994. Activities of carboxylating enzymes in the cam species opuntia- ficus-indica grown under current and elevated co2 concentrations. *Photosynthesis Research 40(3):223-229.*

Responses of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPCase) to an elevated atmospheric CO2 concentration were determined along with net CO2 uptake rates for the Crassulacean acid metabolism species Opuntia ficus-indica growing in open-top chambers. During the spring 13 months after planting, total daily net CO2 uptake of basal and first-order daughter cladodes was 28% higher at 720 than at 360 mu l CO2 1(-1). The enhancement, caused mainly by higher CO2 assimilation during the early part of the night, was also observed during late summer (5 months after planting) and the following winter. The activities of Rubisco and PEPCase measured in vitro were both lower at the elevated CO2 concentration, particularly under the more favorable growth conditions in the spring and late summer. Enzyme activity in second-order daughter cladodes increased with cladode age, becoming maximal at 6 to 10 days. The effect of elevated CO2 on Rubisco and PEPCase activity declined with decreasing irradiance, especially for Rubisco. Throughout the 13-month observation period, O. ficus-indica thus showed increased CO2 uptake when the atmospheric CO2 concentration was doubled despite lower activities of both carboxylating enzymes.

KEYWORDS: ACCLIMATION, AGAVE-VILMORINIANA, ATMOSPHERIC CO2, CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, PHOTOSYNTHESIS, PLANTS, PRODUCTIVITY, RESPONSES, SHORT- TERM

1036

Israel, D.W., T.W. Rufty, and J.D. Cure. 1990. Nitrogen and phosphorus nutritional interactions in a CO2 enriched environment. *Journal of Plant Nutrition 13(11):1419-1433.*

Nonnodulated soybean plants (Glycine max. [L.] Merr. 'Lee') were supplied with nutrient solutions containing growth limiting concentrations of N or P to examine effects on N- and P-uptake efficiencies (mg nutrient accumulated/gdw root) and utilization efficiencies in dry matter production (gdw2/mg nutrient). Nutritional treatments were imposed in aerial environments containing either 350 or 700-mu-L/L atmospheric CO2 to determine whether the nutrient interactions were modified when growth rates were altered. Nutrient-stress treatments decreased growth and N- and P-uptake and utilization efficiencies at 27 days after transplanting (DAT) and seed yield at maturity (98 DAT). Atmospheric CO2 enrichment increased growth and N- and P-utilization efficiencies at 27 DAT and seed yield in all nutritional treatments and did not affect N- and P-uptake efficiencies at 27 DAT. Parameter responses to nutrient stress at 27 DAT were not altered by atmospheric CO2 enrichment and vice versa. Nutrient-stress treatments lowered the relative seed yield response to atmospheric CO2 enrichment. Decreased total-N uptake by P- stressed plants was associated with both decreased root growth and N-uptake efficiency of the roots. Nitrogen-utilization efficiency was also decreased by P-stress. This response was associated with decreased plant growth as total-N uptake and plant growth were decreased to the same extent by P stress resulting in unaltered tissue N concentrations. In contrast, decreased total P-uptake by N-stressed plants was associated with a restriction in root growth as P-uptake efficiency of the roots was unaltered. This response was coupled with an increased root-to-shoot dry weight ratio; thus shoot and wholeplant growth were decreased to a much greater extent than total-P uptake which resulted in elevated P concentrations in the tissue. Therefore, P-utilization efficiency was markedly reduced by N stress.

KEYWORDS: AMMONIUM, ELEVATED CARBON-DIOXIDE, GROWTH, NITRATE, PLANTS, RESPONSES, SEED YIELD, TRANSPORT

1037

Isutsa, D.K., M.P. Pritts, and K.W. Mudge. 1994. Rapid propagation of blueberry plants using ex-vitro rooting and controlled acclimatization of micropropagules. *Hortscience 29(10):1124-1126.*

A protocol is presented that enables a propagator to produce field-sized blueberry transplants within 6 months of obtaining microshoots from tissue culture. The protocol involves subjecting microshoots to ex vitro rooting in a fog chamber under 100 mumol.m-2.s-1 photosynthetic photon flux for 7 weeks, transferring plants to a fog tunnel for 2 weeks, then to a greenhouse for 7 more weeks. Plant survival and rooting of cultivars Berkeley (Vaccinium corymbosum L.) and Northsky (Vaccinium angustifolium xcorymbosum) were near 100% under these conditions. Plantlets in fog chambers receiving 100 mumol.m-2.s-1 grew rapidly, while those at lower irradiance levels grew more slowly, and supplemental CO, enhanced growth only at 50 mumol.m-2.s-1. Growth rates slowed when plants were moved into the fog tunnel; but by the end of 16 weeks, plants that were under high irradiance in the fog chamber had root systems that were 15 to 30 times larger than plants under low irradiance. Within 6 months, these plants were 30 to 60 cm tall and suitable for field planting.

KEYWORDS: CO2, CULTURE, ENRICHMENT, GROWTH, HIGHBUSH BLUEBERRY, INVITRO, LIGHT, LOWBUSH BLUEBERRY

1038

Ito, J., S. Hasegawa, K. Fujita, S. Ogasawara, and T. Fujiwara. 1999. Effect of CO2 enrichment on fruit growth and quality in Japanese pear (Pyrus serotina reheder cv. Kosui). *Soil Science and Plant Nutrition 45(2):385-393.*

Six year-old Japanese pear (Pyrus serotina Reheder cv. Kosui) trees

grafted on P. serotina cv. Nihonyamanashi were grown in containers filled with Granite Regosol under glasshouse conditions. At different stages of fruit growth, pear trees were exposed to an elevated CO2 concentration (130 Pa CO2) along with a control (35 Pa CO2). For one group of plants, CO2 enrichment was applied for 79 d from 52 d after full bloom (DAB) to fruit maturity (long-term CO2 enrichment) and for another group the same treatment was applied for 35 d from 96 DAB to fruit maturity (short-term CO2 enrichment). The effects of the elevated CO2 concentration on vegetative growth, mineral contents, and fruit production and quality were examined. Long- term CO2 enrichment enhanced vegetative growth, without any significant effect on the mineral contents in either flower bud or fruit except for a remarkable increase in the K content. Long-term CO2 enrichment increased the fruit size and fresh weight, but had no significant effect on the fruit quality. On the other hand, the short-term CO2 enrichment did not induce any significant change in the fruit size but increased the fruit sugar concentration. Along with the reduction of the sorbitol concentration in fruit, the fructose and sucrose concentrations increased and these changes occurred earlier at elevated CO2 than at ambient CO2 concentrations. From these results, we concluded that the effect of CO2 enrichment on fruit growth varies depending upon the growth stages of fruit: during the initial and fruitlet stages when fruit expansion occurs, CO2 enrichment increases the fruit size, whereas, during maturation when fruit expansion has slowed down and sugar accumulation in fruit is active, it increases the fruit sugar concentration.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, INVERTASE, METABOLISM, PASTURE, PHOTOSYNTHESIS, PLANTS, SORBITOL-RELATED ENZYMES, SOUR ORANGE TREES

1039

Iverson, L.R., and A.M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs 68(4):465-485.*

Projected climate warming will potentially have profound effects on the earth's biota, including a large redistribution of tree species. We developed models to evaluate potential shifts for 80 individual tree species in the eastern United States. First, environmental factors associated with current ranges of tree species were assessed using geographic information systems (GIS) in conjunction with regression tree analysis (RTA). The method was then extended to better understand the potential of species to survive and/or migrate under a changed climate. We collected, summarized, and analyzed data for climate, soils, land use, elevation, and species assemblages for >2100 counties east of the 100th meridian. Forest Inventory Analysis (FIA) data for >100000 forested plots in the East provided the tree species range and abundance information for the trees. RTA was used to devise prediction rules from current species-environment relationships, which were then used to replicate the current distribution as well as predict the future potential distributions under two scenarios of climate change with twofold increases in the level of atmospheric CO2. Validation measures prove the utility of the RTA modeling approach for mapping current tree importance values across large areas, leading to increased confidence in the predictions of potential future species distributions. With our analysis of potential effects, we show that roughly 30 species could expand their range and/or weighted importance at least 10%, while an additional 30 species could decrease by at least 10%, following equilibrium after a changed climate. Depending on the global change scenario used, 4-9 species would potentially move out of the United States to the north. Nearly half of the species assessed (36 out of 80) showed the potential for the ecological optima to shift at least 100 km to the north, including seven that could move >250 km. Given these potential future distributions, actual species redistributions will be controlled by migration rates possible through fragmented landscapes.

KEYWORDS: BALANCE, CLASSIFICATION, CONTINENTAL-SCALE, DECISION-TREE, FORESTS, MODEL, PINE, RESPONSES, TEMPERATURE, VEGETATION

1040

Iverson, L.R., A. Prasad, and M.W. Schwartz. 1999. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with Pinus virginiana. *Ecological Modelling 115(1):77-93.*

We are using a deterministic regression tree analysis model (DISTRIB) and a stochastic migration model (SHIFT) to examine potential distributions of similar to 66 individual species of eastern US trees under a 2 x CO2 climate change scenario. This process is demonstrated for Virginia pine (Pinus virginiana). USDA Forest Service Forest Inventory and Analysis data for more than 100 000 plots and nearly 3 million trees east of the 100th meridian were analyzed and aggregated to the county level to provide species importance values for each of more than 2100 counties. County-level data also were compiled on climate, soils, land use, elevation, and spatial pattern. Regression tree analysis (RTA) was used to devise prediction rules from current species-environment relationships, which were then used to replicate the current distribution and predict the potential future distributions under two scenarios of climate change (2 x CO2). RTA allows different variables to control importance value predictions at different regions, e.g. at the northern versus southern range limits of a species. RTA outputs represent the potential 'environmental envelope' shifts required by species, while the migration model predicts the more realistic shifts based on colonization probabilities from varying species abundances within a fragmented landscape. The model shows severely limited migration in regions of high forest fragmentation, particularly when the species is low in abundance near the range boundary. These tools are providing mechanisms for evaluating the relationships among various environmental and landscape factors associated with tree- species importance and potential migration in a changing global climate.

KEYWORDS: BALANCE, FORESTS, MIGRATION, RANGE, RESPONSES, VEGETATION

1041

Iwasaki, I., N. Kurano, and S. Miyachi. 1996. Effects of high-CO2 stress on photosystem II in a green alga, Chlorococcum littorale, which has a tolerance to high CO2. *Journal of Photochemistry and Photobiology B-Biology 36(3):327-332.*

A green alga, Chlorococcum littorale, is known to have a tolerance to high CO2 conditions. By a sudden change from stir to high CO2, PSII activity of C. littorale decreased temporarily and then recovered, while PSI activity showed the opposite change (Pesheva et al., Plant Cell Physiol, 35 (1994) 379-387). To investigate the efficiency of energy captured by open PSII reaction centers, the quenching of chlorophyll fluorescence of intact cells of C. littorale was analyzed. The data obtained are compared with those obtained with cells of Stichococcus bacillaris which has little tolerance to high CO2. Activities of photosynthetic oxygen evolution of the intact cells and DCIP photoreduction with the crude membrane fraction of C. littorale decreased within 1-2 days, and after about 4 days both activities recovered and/or were elevated to higher levels than those in the air conditions. During this temporal decrease in these activities, the effective quantum yield of PSII also lowered to about 50% of that in air. The values of F- v/F-m transiently decreased indicating photoinhibition in PSII. Such fluorescence quenching parameters recovered after about 4 days. On the other hand, the activities of PSII and other photosynthetic characteristics did not recover in S. bacillaris.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, FLUOROMETER, LIGHT, PH, PHOTOSYNTHESIS

1042

Izrael, Y.A., S.M. Semenov, I.M. Kunina, and T.V. Zamaraeva. 1994. Modification of direct effect of carbon-dioxide on higher- plants due to tropospheric ozone impact. *Doklady Akademii Nauk 338(5):711-713.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, GROWTH

1043

Jablonski, L.M. 1997. Responses of vegetative and reproductive traits to elevated CO2 and nitrogen in Raphanus varieties. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(4):533-545.*

The relationships between the responses to elevated CO2 of the vegetative and reproductive phase were investigated in radish, used as a test system. The hypothesis that an increase in nonfoliar vegetative storage capacity promotes reproductive output was tested. Three cultivars of Raphanus sarivus and the wild, Raphanus raphanistrum, differing in root to shoot ratios, were grown under two levels of CO2 and two levels of nitrogen fertilization. Varieties possessed different strategies of carbon storage and showed distinct responses to CO2 at each vegetative harvest time. Vegetative sinks of hypocotyls, petioles, and young blades were enhanced by CO2. Nitrogen promoted vegetative shoot growth, but did not enhance the reproductive response to CO2. By the end of the reproductive phase, varieties did not differ in total biomass. Reproductive response to CO2 may have been limited by the lack of an effect on the timing of flowering. Correlations in CO2 enhancement ratios were examined in 12 traits of each phase. Only vegetative total leaf area correlated with reproductive mass. Foliar starch correlated with decreased abortion. Enhancements in vegetative biomass did not correlate with any reproductive response. Detailed studies of the reproductive phase are needed to understand the whole-plant response to elevated CO2.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, GROWTH, LEAVES, NITRATE, NUTRITION, PHOTOSYNTHESIS, PRODUCTIVITY, RAPHANISTRUM, WILD RADISH

1044

Jach, M.E., and R. Ceulemans. 1999. Effects of elevated atmospheric CO2 on phenology, growth and crown structure of Scots pine (Pinus sylvestris) seedlings after two years of exposure in the field. *Tree Physiology 19(4-5):289-300.*

Three-year-old Scots pine (Pinus sylvestris L.) seedlings were grown for two years in the ground in open-top chambers supplied with either an ambient or elevated (ambient + 400 mu mol mol(- 1)) CO2 concentration. Phenological observations and measurements of height and stem diameter growth, absolute and relative growth rates, starch and soluble carbohydrate concentrations of the needles, and crown structure and needle properties were made at frequent intervals throughout the two growing seasons. Elevated CO2 significantly advanced the date of bud burst in both years. The increase in total needle area in response to elevated CO2 was accounted for by longer shoots and an increase in individual needle area in the first year, and by an increase in the number and length of shoots in the second year. Stem diameter and tree height were enhanced more by the elevated CO2 treatment in the first year than in the second, indicating a decreased effect of CO2 on growth over time. This was confirmed by a study of absolute and relative growth rates of leader shoots. During the first growing season of CO2 enrichment, mean weekly relative growth rates over the growing season (RGR(m)) were significantly enhanced. During the second year, RGR(m) in ambient CO2 closely matched that in elevated CO2.

KEYWORDS: ABIES L KARST, BIOMASS ALLOCATION, CARBON-DIOXIDE ENRICHMENT, FROST DAMAGE, MINERAL NUTRITION, PHOTOSYNTHESIS, PLANT-RESPONSES, SEASONAL-CHANGES, SPRUCE PICEA-SITCHENSIS, WATER-STRESS

1045

Jackson, R.B., Y. Luo, Z.G. Cardon, O.E. Sala, C.B. Field, and H.A. Mooney. 1995. Photosynthesis, growth and density for the dominant species in a CO2-enriched grassland. *Journal of Biogeography 22(2-3):221-225.*

Although increased atmospheric CO2 frequently increases short- term photosynthetic rates, longer-term photosynthetic responses are more variable. Plant size, reproduction and ecosystem carbon gain are determined, in part, by such photosynthetic responses. Here we examine photosynthetic regulation for the dominant species in a grassland exposed to elevated CO2 and examine whether the observed photosynthetic responses contribute to changes in growth, reproduction and plant density in the same grassland. Avena barbata in the field showed little evidence of photosynthetic downregulation with elevated CO2 at the end of the growing season (differences between treatments <10%). Glasshouse studies also showed little evidence for downregulation of photosynthesis measured at various light and intercellular CO2. concentrations. Although specific leaf mass (leaf mass per unit leaf area) for Avena increased 20% in the field with elevated CO2, leaf nitrogen concentrations decreased 25%, resulting in an 11% reduction in leaf N on a leaf-area basis. For the relatively wet 1993 growing season, Avena barbata increased its size and reproduction approximately 30% in elevated CO2, with a 21% decrease in population density. For the relatively dry 1994 season Avena density was almost doubled in elevated CO2, but increases in individual size and reproduction with CO2 were small (6-18%). The primary effect of CO2 in the drier year appears to have been greater Avena survival, rather than increased individual size.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEM RESPONSES, ELEVATED CO2 CONCENTRATIONS, EXPOSURE, PLANT

1046

Jackson, R.B., and H.L. Reynolds. 1996. Nitrate and ammonium uptake for single- and mixed-species communities grown at elevated CO2. *Oecologia 105(1):74-80.*

Sustained increases in plant production in elevated CO2 depend on adequate belowground resources. Mechanisms for acquiring additional soil resources include increased root allocation and changes in root morphology or physiology. CO2 research to date has focused almost exclusively on changes in biomass and allocation. We examined physiological changes in nitrate and ammonium uptake in elevated CO2, hypothesizing that uptake rates would increase with the amount of available CO2. We combined our physiological estimates of nitrogen uptake with measurements of root biomass to assess whole root-system rates of nitrogen uptake. Surprisingly, physiological rates of ammonium uptake were unchanged with CO2, and rates of nitrate uptake actually decreased significantly ($P<0.005$). Root biomass increased 23% in elevated CO2 ($P<0.005$), but almost all of this increase came in fertilized replicates. Rates of root-system nitrogen uptake in elevated CO2 increased for ammonium in nutrient-rich soil ($P<0.05$) and were unchanged for nitrate ($P>0.80$). Root-system rates of nitrogen uptake were more strongly correlated with physiological uptake rates than with root biomass in unamended soil, but the reverse was true in fertilized replicates. We discuss nitrogen uptake and changes in root biomass in the context of root nutrient concentrations (which were generally

unchanged with CO2) and standing pools of belowground plant nitrogen. In research to date, there appears to be a fairly general increase in root biomass with elevated CO2, and little evidence of up-regulation in root physiology.

KEYWORDS: ANNUAL GRASSLAND, ATMOSPHERE, CARBON DIOXIDE, ECOSYSTEMS, ENRICHMENT, NITROGEN, PLANT, PRODUCTIVITY, RESPONSES, SOIL

1047

Jackson, R.B., O.E. Sala, C.B. Field, and H.A. Mooney. 1994. Co2 alters water-use, carbon gain, and yield for the dominant species in a natural grassland. *Oecologia 98(3-4):257-262.*

Global atmospheric CO2 is increasing at a rate of 1.5-2 ppm per year and is predicted to double by the end of the next century. Understanding how terrestrial ecosystems will respond in this changing environment is an important goal of current research. Here we present results from a field study of elevated CO2 in a California annual grassland. Elevated CO2 led to lower leaf- level stomatal conductance and transpiration (approximately 50%) and higher mid-day leaf water potentials (30-35%) in the most abundant species of the grassland, Avena barbata Brot. Higher CO2 concentrations also resulted in greater midday photosynthetic rates (70% on average). The effects of CO2 on stomatal conductance and leaf water potential decreased towards the end of the growing season, when Avena began to show signs of senescence. Water-use efficiency was approximately doubled in elevated CO2, as estimated by instantaneous gas-exchange measurements and seasonal carbon isotope discrimination. Increases in CO2 and photosynthesis resulted in more seeds per plant (30%) and taller and heavier plants (27% and 41%, respectively). Elevated CO2 also reduced seed N concentrations (9%).

KEYWORDS: ANNUALS, ELEVATED CO2, ENRICHMENT, GROWTH, PLANTS, RESPONSES, SEEDLINGS, TREES

1048

Jackson, R.B., O.E. Sala, J.M. Paruelo, and H.A. Mooney. 1998. Ecosystem water fluxes for two grasslands in elevated CO2: a modeling analysis. *Oecologia 113(4):537-546.*

The need to combine data from CO2 field experiments with climate data remains urgent, particularly because each CO2 experiment cannot run for decades to centuries. Furthermore, predictions for a given biome need to take into account differences in productivity and leaf area index (LAI) independent of CO2-derived changes. In this study, we use long-term weather records and field data from the Jasper Ridge CO2 experiment in Pale Alto, California, to model the effects of CO2 and climate variability on ecosystem water fluxes. The sandstone and serpentine grasslands at Jasper Ridge provide a range of primary productivity and LAI, with the sandstone as the more productive system. Modeled soil water availability agreed well with published observations of time-domain reflectometry in the CO2 experiment. Simulated water fluxes based on 10-year weather data (January 1985-December 1994) showed that the sandstone grassland had a much greater proportion of water movement through plants than did the serpentine; transpiration accounted for approximately 30% of annual fluxes in the sandstone and only 10% in the serpentine. Although simulated physiological and biomass changes were similar in both grasslands, the consequences of elevated CO2 were greater for the sandstone water budget. Elevated CO2 increased soil drainage by 20% in the sandstone, despite an approximately one-fifth increase in plant biomass; in the serpentine, drainage increased by <10% and soil evaporation was unchanged for the same simulated biomass change. Phenological changes, simulated by a 15-day lengthening of the growing season, had minimal impacts on the water budget. Annual variation in the timing and amount of rainfall was important for water fluxes in both grasslands. Elevated CO2 increased sandstone drainage > 50 mm in seven of ten years, but the relative increase in drainage varied from 10% to 300% depending on the year. Early-season transpiration in the sandstone decreased between 26% and 41%, with elevated CO2 resulting in a simulated water savings of 54-76 mm. Even in years when precipitation was similar (e.g., 505 and 479 mm in years 3 and 4), the effect of CO2 varied dramatically. The response of grassland water budgets to CO2 depends on the productivity and structure of the grassland, the amount and timing of rainfall, and CO2-induced changes in physiology. In systems with low LAT, large physiological changes may not necessarily alter total ecosystem water budgets dramatically.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CANOPY, EXCHANGE, GROWTH, LEAF, NITROGEN, PHOTOSYNTHESIS, PLANT, RESPONSES, TRANSPIRATION

1049

Jacob, J., and B.G. Drake. 1993. Long-term co2 enrichment effects on the rubisco content and activity in 2 field-grown C3 plants. *Plant Physiology 102(1):46.*

1050

Jacob, J., C. Greitner, and B.G. Drake. 1995. Acclimation of photosynthesis in relation to rubisco and nonstructural carbohydrate contents and in-situ carboxylase activity in scirpus-olneyi grown at elevated co2 in the field. *Plant, Cell and Environment 18(8):875-884.*

Stands of Scirpus olneyi, a native saltmarsh sedge with C-3 photosynthesis, had been exposed to normal ambient and elevated atmospheric CO2 concentrations (C-a) in their native habitat since 1987, The objective of this investigation was to characterize the acclimation of photosynthesis of Scirpus olneyi stems, the photosynthesizing organs of this species, to long-term elevated C-a treatment in relation to the concentrations of Rubisco and non-structural carbohydrates, Measurements were made on intact stems in the field under existing natural conditions and in the laboratory under controlled conditions on stems excised in the field early in the morning, Plants grown at elevated C-a had a significantly higher (30-59%) net CO2 assimilation rate (A) than those grown at ambient C-a when measurements were performed on excised stems at the respective growth C-a. However, when measurements were made at normal ambient C-a, A was smaller (45-53%) in plants grown at elevated C-a than in those grown at ambient C-a. The reductions in A at normal ambient C-a, carboxylation efficiency and in situ carboxylase activity were caused by a decreased Rubisco concentration (30-58%) in plants grown at elevated C-a; these plants also contained less soluble protein (39-52%). The Rubisco content was 43 to 58% of soluble protein, and this relationship was not significantly altered by the growth CO2 concentrations. The Rubisco activation state increased slightly, but the in situ carboxylase activity decreased substantially in plants grown at elevated C-a. When measurements were made on intact stems in the field, the elevated C-a treatment caused a greater stimulation of A (100%) and a smaller reduction in carboxylation efficiency (which was not statistically significant) than when measurements were made on excised stems in the laboratory. The possible reasons for this are discussed. Plants grown at elevated C-a contained more non-structural carbohydrates (25-53%) than those grown at ambient C-a. Plants grown at elevated C-a appear to have sufficient sink capacity to utilize the additional carbohydrates formed during photosynthesis. Overall, our results are in agreement with the hypothesis that elevated C-a leads to an increased carbohydrate concentration and the ensuing acclimation of the photosynthetic apparatus in C-3 plants results in a reduction in the protein complement, especially Rubisco, which reduces the photosynthetic capacity in plants grown at elevated C-a, relative to plants grown at normal ambient C-a. Nevertheless, when compared at their respective growth C-a, Scirpus olneyi plants grown at

elevated C-a in their native habitat maintained a substantially higher rate of photosynthesis than those grown at normal ambient C-a even after 8 years of growth at elevated C-a.

KEYWORDS: ACTIVATION, C-3, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, HIGH ATMOSPHERIC CO2, LEAVES, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SUNFLOWER

1051

Jacoby, G.C., and R.D. DArrigo. 1997. Tree rings, carbon dioxide, and climatic change. *Proceedings of the National Academy of Sciences of the United States of America 94(16):8350-8353.*

Tree rings have been used in various applications to reconstruct past climates as well as to assess the effects of recent climatic and environmental change on tree growth, In this paper we briefly review two wags that tree rings provide information about climate change and CO2: (i) in determining whether recent: warming during the period of instrumental observations is unusual relative to prior centuries to millennia, and thus might be related to increasing greenhouse gases; and (ii) in evaluating whether enhanced radial growth has taken place in recent decades that appears to be unexplained by climate and might instead be due to increasing atmospheric CO2 or other nutrient fertilization, It is found that a number of tree-ring studies from temperature-sensitive settings indicate unusual recent warming, although there are also exceptions al. certain sires, The present tree-ring evidence for a possible CO2 fertilization effect under natural environmental conditions appears to be very limited.

KEYWORDS: AMERICA, ATMOSPHERIC CO2, ENHANCEMENT, GROWTH, TRENDS

1052

Jager, H.J., U. Hertstein, and A. Fangmeier. 1999. The European Stress Physiology and Climate Experiment - project 1. wheat (ESPACE-wheat): introduction, aims and methodology. *European Journal of Agronomy 10(3-4):155-162.*

The response of crops to CO2 enrichment represents an issue of major concern both for scientists and for policymakers. In a concerted programme funded by the Commission of the European Communities, a Europe-wide experimental and modeling study was carried out to investigate the effects of increasing atmospheric CO2 concentrations, and of environmental stresses such as ozone or water/nutrient shortage, under different climatic conditions on wheat (Triticum aestivum L.). This contribution describes the experimental network and the standard protocol set-up for the assessments which served to improve and to validate process-orientated wheat growth simulation models. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: AIR CO-2 ENRICHMENT, ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, O-3, OZONE, RESPONSES, TEMPERATURE, YIELD

1053

Jalil, A., and R.M. Carlson. 1993. Potassium uptake by marianna plum under limited oxygen and elevated carbon-dioxide levels in the root atmosphere. *Journal of Plant Nutrition 16(4):723-737.*

Potassium (K) uptake rates were determined for Marianna 2624 rootstocks with 'French' prune scions using th nutrient solution depletion technique. The nutrient solutions were bubbled with factorial combinations of nitrogen (N2), oxygen (O2), and carbon dioxide (CO2) to create treatment root atmospheres with O2 ranging from 0.01 to 0.10 m3/m3 and CO2 ranging from 0 to 0.05 m3/m3. The K+ uptake rate was more susceptible to 02 deprivation than to elevated CO2 in the root atmosphere. Decreasing 02 levels from 0.10 M3/M3 decreased K+ uptake in a hyperbolic fashion to no net uptake at 0.01 M3/M3 02. Increasing root atmosphere CO2 from 0 to 0.05 M3/M3 had a small depressing effect on net K+ influx from 60 muM K+ solutions at 0.10 and 0.05 M3/M3 02, but no effect when 02 was 0.025 or 0.01 M3/M3. Elevating CO2 decreased Km for the net K+ influx rate at 0.10 and 0.05 M3/M3 02. Increased pH buffering from higher HCO3 concentration at the plasma membrane surface was suggested to explain the CO2 effect on Km.

KEYWORDS: GROWTH, WHEAT SEEDLINGS

1054

Jansen, D.M. 1990. Potential rice yields in future weather conditions in different parts of asia. *Netherlands Journal of Agricultural Science 38(4):661-680.*

Future climate change is expected to vary between regions, with possible different effects on crop growth. Various sites in Asia were selected to represent major rice growing environments. Historic weather data of these sites were adapted to possible changes in temperature and in CO2 level, to mimic climate change. Potential rice yields at present, and for the years 2020 and 2100 were calculated with a crop growth simulation model. Simulated yields rose in low and middle temperature change scenarios, but decreased in the high temperature scenario. Effects were stronger in the year 2100, when also regional differences became clear: more than elsewhere, yields were affected by high temperatures between 10 and 35-degrees-N. Water use efficiency decreased in the high temperature scenario irrespective of CO2 scenario, and increased otherwise.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITROGEN, ORYZA SATIVA L, PHOTOSYNTHESIS, TEMPERATURE

1055

Janssens, I.A., M. Crookshanks, G. Taylor, and R. Ceulemans. 1998. Elevated atmospheric CO2 increases fine root production, respiration, rhizosphere respiration and soil CO2 efflux in Scots pine seedlings. *Global Change Biology 4(8):871-878.*

In this study, we investigated the impact of elevated atmospheric CO2 (ambient + 350 mu mol mol(-1)) on fine root production and respiration in Scots pine (Pinus sylvestris L.) seedlings. After six months exposure to elevated CO2, root production measured by root in-growth bags, showed significant increases in mean total root length and biomass, which were more than 100% greater compared to the ambient treatment. This increased root length may have lead to a more intensive soil exploration. Chemical analysis of the roofs showed that the roots in the elevated treatment accumulated more starch and had a lower C/N-ratio. Specific root respiration rates were significantly higher in the elevated treatment and this was probably attributed to increased nitrogen concentrations in the roots. Rhizospheric respiration and soil CO2 efflux were also enhanced in the elevated treatment. These results clearly indicate that under elevated atmospheric CO2 root production and development in Scots pine seedlings is altered and respiratory carbon losses through the root system are increased.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ENRICHMENT, COMPENSATORY RESPONSES, GROWTH, LOBLOLLY-PINE, NITROGEN, PLANTAGO-MAJOR, PONDEROSA PINE, TEMPERATURE, TREES

1056

Jarvis, A.J., T.A. Mansfield, and W.J. Davies. 1999. Stomatal behaviour, photosynthesis and transpiration under rising CO2. *Plant, Cell and Environment 22(6):639-648.*

The literature reports enormous variation between species in the extent of stomatal responses to rising CO2. This paper attempts to provide a framework within which some of this diversity can be explained. We describe the role of stomata in the short-term response of leaf gas exchange to increases in ambient CO2 concentration by developing the recently proposed stomatal model of Jarvis gr Davies (1998). In this model stomatal conductance is correlated with the functioning of the photosynthetic system so that the effects of increases in CO2 on stomata are experienced through changes in the rate of photosynthesis in a simple and mechanistically transparent way This model also allows us to consider the effects of evaporative demand and soil moisture availability on stomatal responses to photosynthesis and therefore provides a means of considering these additional sources of variation. We emphasize that the relationship between the rate of photosynthesis and the internal CO2 concentration and also drought will have important effects on the relative gains to be achieved under rising CO2.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CONDUCTANCE, ELEVATED CO2, EMPIRICAL-MODEL, LEAF GAS- EXCHANGE, PARTIAL-PRESSURE, RESPONSES, WATER-VAPOR

1057

Jarvis, P.G. 1995. The role of temperate trees and forests in CO2 fixation. *Vegetatio 121(1-2):157-174.*

The global flask network data indicate that the temperate and boreal forests of the northern hemisphere are a significant sink for anthropogenic CO2. Bowen ratio and eddy covariance technology have been used to measure the net CO2 exchange of deciduous and coniferous forest. Some results from an earlier study on spruce with the Bowen ratio technique are presented. New technology that has been developed to measure fluxes continuously by forest stands is described and data are presented to show the net exchange flux of CO2 by temperate forests. These data support the hypothesis that temperate and boreal forests are significant sinks for carbon dioxide. An extensive programme of experimental impact studies is being carried out by a network of 12 laboratories in Europe funded by the European Commission. Parallel studies are in progress in North America and elsewhere. These studies indicate that doubling the atmospheric CO2 concentration results in increases in tree biomass of 30-40%. Interactions with nutrition are particularly significant. If nitrogen is added at a commensurate rate, the overall effect is that trees grow larger more quickly in elevated CO2 than in ambient air but they are essentially very similar in structure and physiology. However, if nutrients are in short supply, developmental and physiological changes occur. Then elevated CO2 causes changes in dry mass allocation to roots, in phenology of bud burst and set, in photosynthesis, in respiration, and in tree water relations. These changes are exaggerated in low nutrition situations. Process-based models have been developed to scale- up from leaf and tree to the stand scale. These models contain explicit description of processes affected by CO2, and are parameterised using the data collected in the impact studies. It is concluded that forests in the temperate and boreal region can effectively contribute to the removal of anthropogenic CO2 from the atmosphere and that tree growth and production of long-lived wood products should be encouraged as a major contribution towards off-setting the greenhouse effect caused by the burning of fossil fuels.

KEYWORDS: ATMOSPHERE-BIOSPHERE EXCHANGE, CARBON, ENRICHMENT, EVAPOTRANSPIRATION, MAESTRO, SINKS, SITKA SPRUCE, STANDS, STORAGE, WEATHER

1058

Jauhiainen, J., and J. Silvola. 1999. Photosynthesis of Sphagnum fuscum at long-term raised CO2 concentrations. *Annales Botanici Fennici 36(1):11-19.*

Rate of net photosynthesis in Sphagnum fuscum (Schimp.) Klinggr. was measured during long-term (50-122 days), and subsequently during short-term (1/2 h), exposure to 350, 700, 1000 or 2000 ppm CO2 concentrations. Raised CO2 concentrations caused a general increase in the rate of net photosynthesis, increasing the rate of photosynthesis at light saturation and causing a given rate of net CO2 exchange to be reached at lower light fluxes. The relative increase in the rate of net photosynthesis by increasing radiation fluxes was independent of the CO2 treatment. The rates of net photosynthesis at enhanced CO2 concentrations gradually decreased compared to rates found with the 350 ppm treatment and this acclimation was also noticed during short-term exposure to all four CO2 concentrations. At 2000 ppm of CO2, the depression of net photosynthesis at high water contents, found at lower CO2 concentrations, was removed. Observed rates of net photosynthesis indicated that water-use efficiency of Sphagna was not coupled with constant long-term CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, EXPOSURE, MOSS HYLOCOMIUM-SPLENDENS, NORTHERN PEATLANDS, PEAT MOSSES, WATER-CONTENT

1059

Jauhiainen, J., J. Silvola, K. Tolonen, and H. Vasander. 1997. Response of Sphagnum fuscum to water levels and CO2 concentration. *Journal of Bryology 19:391-400.*

Sphagnum fuscum samples collected from an ombrotrophic bog were grown in a greenhouse at six water levels (0,5. 10, 15, 25 and 30 cm) below the capitulam level and in four concentrations of CO2 (350, 700, 1000 and 2000 ppm). The cores of S, fuscum were treated for 87 days and length increment was measured by the plastic strip method and by innate time markers, Water content of the shoot, dry mass of the capitulum, dry mass per unit length of stem and production of dry mass were measured at the end of the experiment. The water content, capitulum dry mass, dry mass per unit length of stem, length increment and dry mass production differed markedly for S. fuscum grown in different water levels. With lower water levels, the water content of the shoot decreased and the dry mass of both the capitulum and unit length of stem increased. The total length increment was highest when the water level was at or near the capitulum level (0-10 cm). No clear trend in dry mass production on an areal basis could be found due to uncoupled responses in length increment and stem dry mass at the experimental water levels. Neither capitulum dry mass nor dry mass per unit length of stem showed distinct trends in S. fuscum grown at different ambient CO2 concentrations. Some increase in length increment and in dry mass production was detected at CO2 concentrations above 350 ppm, but this effect appeared only at high water levels. It is suggested that the low response in length increment and production to CO2 concentration resulted in part from insufficient moisture for photosynthesis at the lower water levels. Also, the possibility of increased nonstructural production is discussed.

KEYWORDS: DECAY, ELEVATED CO2, ENVIRONMENT, FOREST, GROWTH, HABITAT, PEAT MOSSES, PHOTOSYNTHESIS, SOUTHERN FINLAND, SWEDISH RAISED BOG

1060

Jauhiainen, J., H. Vasander, and J. Silvola. 1994. Response of sphagnum-fuscum to n deposition and increased co2. *Journal of Bryology 18:83-96.*

The length increment and production of Sphagnum fuscum with enhanced nitrogen deposition (0, 10, 30 and 100 kg N ha(-1) yr(-1)) and CO2 concentration (350, 700, 1000 and 2000 ppm) were measured. The experiment was carried out in the glasshouse, where S. fuscum was grown with the water table maintained at 10 cm below the moss surface for 120 d. For length growth, 10 kg N ha(-1) yr(-1): and for biomass production, 30 kg N ha(-1) yr(-1) were found to be the optimal loads. A load of 100 kg N ha(-1) yr(-1) inhibited elongation and biomass production almost completely. An increased CO2 concentration reduced length increment slightly, but it did not have a significant effect on biomass production. However, above ambient CO2 concentrations increased capitulum density and stem dry mass per unit length. In addition, increased CO2 concentration accelerated relative growth in Sphagnum carpets when these also received additional nitrogen. The study highlights the high degree of spatial variability that occurs within Sphagnum fuscum. Differences in growth and biomass production between samples, not found in natural conditions, emerged during the experiment. On the basis of our results, the present nitrogen deposition load in Southern Finland (ca 6-10 kg N ha(-1) yr(-1)) is quite suitable for the growth and production of S. fuscum. If N deposition increased substantially, differences in the vitality of the species might be expected.

KEYWORDS: ATMOSPHERIC NITROGEN, BALANCE, CARBON DIOXIDE, GROWTH, MOSSES, PHOTOSYNTHESIS, RAISED BOG, SOUTHERN FINLAND, TEMPERATURE, TUSSOCK TUNDRA

1061

Jauhiainen, J., H. Vasander, and J. Silvola. 1998. Nutrient concentration in Sphagna at increased N-deposition rates and raised atmospheric CO2 concentrations. *Plant Ecology 138(2):149-160.*

Sphagnum fuscum, S. magellanicum, S. angustifolium and S. warnstorfii were treated with N deposition rates (0, 10, 30 and 100 kg ha(-1) a(-1)) and with four atmospheric CO2 concentrations (350, 700, 1000 and 2000 ppm) in greenhouse for 71-120 days. Thereafter, concentrations of total N, P, K, Ca and Mg in the capitulae of the Sphagna were determined. The response of each species to N deposition was related to ecological differences. With increasing N deposition treatments, moss N concentrations increased and higher N:P- ratios were found, the increase being especially clear at the highest N load. Sphagnum fuscum, which occupies ombrotrophic habitats, was the most affected by the increased nitrogen load and as a consequence the other elements were decreased. Oligotrophic S. magellanicum, wide nutrient status tolerant S. angustifolium and meso-eutrophic S. warnstorfii tolerated better increased N deposition, though there were increased concentrations of Ca and Mg in S. warnstorfii and Mg in S. magellanicum. Nitrogen and P concentrations decreased with raised CO2 concentrations, except for S. magellanicum. This seems to be the first time this kind of response in nutrient concentrations to enhanced CO2 concentration has been shown to exist in bryophytes. The concentration of K clearly decreased in S. fuscum as did the concentration of Mg in the other Sphagna with increasing CO2. Sphagnum angustifolium and S. magellanicum, which are the less specialized species, were the least affected by the CO2 treatments.

KEYWORDS: ELEMENT CONCENTRATIONS, ELEVATED CARBON-DIOXIDE, GROWTH, MIRE WATER, NITRATE REDUCTASE, NITROGEN, PEAT BOGS, PHOTOSYNTHESIS, RESPONSES, WATER CHEMISTRY

1062

Jenkinson, D.S., D.E. Adams, and A. Wild. 1991. Model estimates of CO2 emissions from soil in response to global warming. *Nature 351(6324):304-306.*

ONE effect of global warming will be to accelerate the decomposition of soil organic matter, thereby releasing CO2 to the atmosphere, which will further enhance the warming trend 1- 7. Such a feedback mechanism could be quantitatively important, because CO2 is thought to be responsible for approximately 55% of the increase in radiative forcing arising from anthropogenic emissions of gases to the atmosphere 8, and there is about twice as much carbon in the top metre of soil as in the atmosphere 9. Here we use the Rothamsted model for the turnover of organic matter in soil 3 to calculate the amount of CO2 that would be released from the world stock of soil organic matter if temperatures increase as predicted, the annual return of plant debris to the soil being held constant. If world temperatures rise by 0.03-degrees-C yr-1 (the increase considered as most likely by the Intergovernmental Panel on Climate Change 8), we estimate that the additional release of CO2 from soil organic matter over the next 60 years will be 61 x 10(15) gC. This is approximately 19% of the CO2 that will be released by combustion of fossil fuel during the next 60 years if present use of fuel continues unabated.

KEYWORDS: C-14-LABELED RYEGRASS, DECOMPOSITION, FIELD, PLANT- MATERIAL, STRAW, TERRESTRIAL CARBON STORAGE

1063

Jiang, G.M., and G.H. Lin. 1997. Changes of photosynthetic capacity of some plant species under very high CO2 concentrations in Biosphere 2. *Chinese Science Bulletin 42(10):859-864.*

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, RESPONSES

1064

Jiang, W.B., A. Lers, E. Lomaniec, and N. Aharoni. 1999. Senescence-related serine protease in parsley. *Phytochemistry 50(3):377-382.*

During leaf senescence protein degradation is enhanced. In order to obtain information on the enzymes involved in this process, a study was initiated to identify and characterize proteases whose activity is elevated in artificially senescing parsley leaves. A 70-kDa serine protease (EC 3.4.21) was identified by an activity gel assay. This protease activity, which is low in young leaves, was found to increase considerably in parallel to the advance of senescence and the reduction in the protein content of the leaves. A high correlation between the progress of senescence and the increase in the activity of the 70 kDa serine protease was demonstrated. Treatments with CO2 or gibberellic acid, which retard senescence, reduced the protease's activity, whereas acceleration of senescence with ethylene enhanced it.

KEYWORDS: CYSTEINE, INDUCTION, PLANTS

1065

Jiao, J., P. Goodwin, and B. Grodzinski. 1999. Inhibition of photosynthesis and export in geranium grown at two CO2 levels and infected with Xanthomonas campestris pv. Pelargonii. *Plant, Cell and Environment 22(1):15-25.*

The effects of CO2 enrichment on growth of Xanthomonas campestris pv. pelargonii and the impact of infection on the photosynthesis and export of attached, intact, 'source' leaves of geranium (Pelargonium x domesticum, 'Scarlet Orbit Improved') are reported. Two experiments were performed, one with plants without flower buds, and another with plants which were flowering. Measurements were made on healthy and diseased leaves at the CO2 levels (35 Pa or 90 Pa) at which the plants were grown. There were no losses of chlorophyll, or any signs of visible chlorosis or necrosis due to infection. Lower numbers of bacteria were

found in leaves at high CO2, suggesting growth at elevated CO2 created a less favourable condition in the leaf for bacterial growth. Although high CO2 lowered the bacterial number in infected leaves, reductions in photosynthesis and export were greater than at ambient CO2. The capacity of infected source leaves to export photoassimilates at rates observed in the controls was reduced in both light and darkness. In summary, the severity of infection on source leaf function by the bacteria was increased, rather than reduced by CO2 enrichment, underscoring the need for further assessment of plant diseases and bacterial virulence in plants growing under varying CO2 levels.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, C-3, CARBOXYLASE, ELEVATED CO2, LEAF, LEAVES, PLANTS, STEADY-STATE PHOTOSYNTHESIS, TRANSLOCATION

1066

Jiao, J.R., and B. Grodzinski. 1998. Environmental influences on photosynthesis and carbon export in greenhouse roses during development of the flowering shoot. *Journal of the American Society for Horticultural Science 123(6):1081-1088.*

Photosynthesis and concurrent export rates of expanded leaves on the flowering shoot of Rosa hybrida L. 'Samantha' were measured at three stages of shoot and flower bud development. At 35 and 90 Pa CO2 photosynthesis and concurrent export rates of the upper expanded leaves were greater at Stage 3 (i.e., when petal color of the flower bud was visible) than at the two earlier stages of shoot and flower development. The optimum for leaf photosynthesis and concurrent export at ambient CO2 and saturating irradiance were approximate to 25 degrees C. Export was more sensitive to increased temperature than was carbon fixation. For example, at 40 degrees C photosynthesis was 40% lower while the export rate during photosynthesis was reduced by 80 %. Increasing the photon fluence flux rate from 200 to 1000 mu mol.m(-2).s(-1) PAR increased the photosynthetic rate and the concurrent export rate at 35 and 90 Pa CO2, but the increase in export was proportionally greater than that of photosynthesis. At 35 Pa CO2, the rate of C export during photosynthesis increased from 31 to 59% of the concurrent C fixation rate. At 90 Pa CO2, export during photosynthesis increased from 38 to 62% of the photosynthesis rate. The importance of irradiance on translocation processes was further demonstrated by comparing the disappearance of label during the feed period and during an extended night period. Plants grown at each CO2 level exported about three times as much of the C- 14 fixed during a 2-hour feed period in the light as during a subsequent 15-hour dark chase period. The nighttime export and respiration rates of leaves which had been exposed to elevated CO2 levels during the feed were higher than those rates observed at ambient CO2. However, at the end of the chase period, the leaves of plants which had been exposed to CO2 enrichment during the feed also retained more C-14 than did the leaves of the plants which were at ambient CO2. Thus, although more C-14 was fixed and exported under high CO2, the same proportion of labelled assimilates were exported, respired, and retained in the dark as at ambient CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CO2-ENRICHMENT, LEAF AGE, LEAVES, NET CO-2 EXCHANGE, PLANTS, TEMPERATURE, TOMATO, TRANSLOCATION

1067

Jiao, J., M.J. Tsujita, and B. Grodzinski. 1991. Influence of radiation and CO2 enrichment on whole plant net CO2 exchange in roses. *Canadian Journal of Plant Science 71(1):245-252.*

At three stages of flowering shoot development, varying the irradiance and CO2 levels had a similar effect on the whole- plant net CO2 exchange rate (NCER) of Samantha rose plants. At 22-degrees-C, the NCER was saturated at 1000-mu-mol m-2 s-1 photosynthetically active radiation (PAR). The duration of the light period was also important in determining daily carbon (C) gain. When roses were exposed to a constant daily radiant energy dose of 17.6-mu-mol m-2 provided either as a 12-h irradiation interval at 410-mu-mol m-2 s-1 PAR or 24 h of irradiation at 204-mu-mol m-2 s-1 PAR, the plants exposed to 24 h of continuous irradiation at the lower photon flux density retained 80% more C. Under saturating irradiance, the net photosynthetic rate at an enriched (1000-mu-L L-1) CO2 level was almost double that at ambient (350-mu-L L-1) CO2. However, plants grown at ambient and enriched CO2 levels had similar whole-plant NCERs when compared at the same assay CO2 level. Under CO2 enrichment the flower stem was longer and thicker but the flower bud size at harvest was not significantly different to that of roses grown at the ambient CO2 level.

KEYWORDS: CARBON DIOXIDE, CO2, GROWTH, PHOTOSYNTHESIS

1068

Jiao, J., M.J. Tsujita, and B. Grodzinski. 1991. Influence of temperature on net CO2 exchange in roses. *Canadian Journal of Plant Science 71(1):235-243.*

The effect of temperature on net CO2 exchange of source and sink tissues of the flowering shoots and of whole plants was examined using single-stemmed Samantha roses. At all stages of shoot development, the optimal temperature range for whole-plant carbon (C) gain at saturating irradiance and ambient CO2 level was between 20-degrees and 25-degrees-C, narrower than the temperature range for optimal leaf net photosynthesis. Dark respiration increased more dramatically than photosynthesis with temperatures between 15 and 35-degrees-C. At 25-degrees-C, C loss due to respiration from the flower bud at colour bud stage accounted for 45% of the C loss of the flowering shoot. At low irradiance levels (e.g. 200-mu-mol m-2 s-1) whole-plant net photosynthesis was greater at 16-degrees than at 22-degrees-C because of a greater reduction in respiration. Lowering the night temperature from 27 to 17- degrees-C also increased daily C gain due to a reduction in the C lost at night. Whole-plant net photosynthesis of plants grown and measured at enriched (1000 +/- 100-mu-L L-1) CO2 was greater than that of plants grown and measured at ambient (350 +/- 50-mu-L L-1) level at temperatures between 15-degrees and 35-degrees-C. Furthermore, the optimal temperatures for whole- plant net photosynthesis in CO2 enrichment was higher than at ambient CO2 level.

KEYWORDS: AGE, CARBON, LEAF, PHOTOSYNTHESIS, PLANTS, TRANSPORT

1069

Jifon, J.L., A.L. Friend, and P.C. Berrang. 1995. Species mixture and soil-resource availability affect the root- growth response of tree seedlings to elevated atmospheric co21. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(5):824-832.*

The effects of CO2 enrichment on root proliferation of loblolly pine (Pinus taeda L.) and sweetgum (Liquidambar styraciflua L.) seedlings were studied under varied water and nitrogen (N) regimes and in competitive interaction. Seedlings of each species were grown from seed as monocultures or as 50:50 pine- sweetgum mixtures in 22-L pots filled with forest soil. Seedlings were exposed to either ambient (400 ppm) or CO2- enriched (ambient plus 400 ppm) air for 32 weeks in continuously stirred tank reactors. Detailed sampling of very fine roots (<0.5 mm diam.) showed a general increase (up to 2- fold) in root length density (RLD, cm . cm(-3)) with elevated CO2; however, the effects of CO2 on RLD differed according to species, culture type, water, and N availability. In monoculture, low water with low N conditions produced the largest RLD responses to elevated CO2: 75% increase for sweetgum

and 31% increase for pine. In mixed culture, by contrast, the largest RLD responses to CO2 were observed under high water, high N regimes: pine showed a 110% increase and sweetgum a 96% increase. The total RLD of the standing crop in mixture under elevated CO2, high water, and high N was 2.6 cm . cm(-3) compared with 1.6 cm . cm(-3) in ambient CO2, with sweetgum accounting for >75% of the total RLD in both cases. These findings suggest that resource-rich rather than resource- poor soil environments could be the circumstances under which belowground interference from sweetgum would intensify in pine-sweetgum mixtures with rising atmospheric CO2.

KEYWORDS: CARBON DIOXIDE, COMPETITION, ECOSYSTEMS, ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE SEEDLINGS, PATTERNS, PLANTS, QUANTIFICATION, TAEDA SEEDLINGS

1070

Jitla, D.S., G.S. Rogers, S.P. Seneweera, A.S. Basra, R.J. Oldfield, and J.P. Conroy. 1997. Accelerated early growth of rice at elevated CO2 - Is it related to developmental changes in the shoot apex? *Plant Physiology 115(1):15-22.*

The influence of elevated CO2 on the development of the shoot apex and on subsequent vegetative growth and grain yield was investigated using rice (Oryza sativa L. cv Jarrah) grown in flooded soil at either 350 or 700 mu L CO2 L-1. At 8 d after planting (DAP), elevated CO2 increased the height and diameter of the apical dome and lengths of leaf primordia and tiller buds but had no effect on their numbers. By 16 DAP, there were five tiller buds in the apex at 700 mu L CO2 L-1 compared with only three tiller buds at 350 mu L CO2 L-1. These changes in development of the shoot apex at high CO2 were forerunners to faster development of the vegetative shoot at elevated CO2 between 11 and 26 DAP as evidenced by increases in the relative growth rates of the shoot and tillers. Accelerated development at high CO2 was responsible for the 42% increase in tiller number at the maximum tillering stage and the 57% enhancement of grain yield at the final harvest. The link between high CO2 effects on development during the first 15 DAP and final tiller number and grain yield was demonstrated by delaying exposure of plants to high CO2 for 15 d. The delay totally inhibited the tillering response to high CO2, and the increase in grain yield of 20% arose from a greater number of grains per panicle. Consequently, it can be concluded that accelerated development in the shoot apex early in development is crucial for obtaining maximum increases in grain yield at elevated atmospheric CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CELL, ELONGATION, LEAF, LEAVES, PLANTS, PROTEINS, YIELD

1071

John-McKay, M.E., and B. Colman. 1997. Variation in the occurrence of external carbonic anhydrase among strains of the marine diatom Phaeodactylum tricornutum (Bacillariophyceae). *Journal of Phycology 33(6):988-990.*

Eleven different strains of Phaeodactylum tricornutum Bohlin were obtained from three culture collections and were examined for the presence of external and internal carbonic anhydrase (CA). Cells of all strains, grown in standing culture at alkaline pH and low dissolved inorganic carbon had internal CA, but only eight were found to have external CA. External CA activity was reduced when cultures were bubbled with air and was completely repressed when they were grown on 5% CO2. Expression of external CA activity appears to be regulated by CO2 concentration in the growth medium, but within one species, there appears to be a variation in occurrence of external CA and consequently in the mode of inorganic carbon acquisition.

KEYWORDS: ACCUMULATION, CHLORELLA-SACCHAROPHILA, CO2, CYANOBACTERIA, DISSOLVED INORGANIC CARBON, HIGHER-PLANTS, MICROALGAE, PHYTOPLANKTON

1072

Johnsen, K.H. 1993. Growth and ecophysiological responses of black spruce seedlings to elevated co2 under varied water and nutrient additions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(6):1033-1042.*

Two controlled-environment studies examined growth and ecophysiological responses of black spruce (Picea mariana (Mill.) B.S.P.) seedlings to elevated CO2 under varied water and nutrient additions. Growth analyses were conducted followed by measurements of gas exchange, xylem pressure potential and foliar N concentrations. Growth under elevated CO2 (700 ppm) increased final seedling dry weights by 20-48% compared with seedling growth under ambient CO2 (350 ppm). Percent increases in seedling dry weight were greater under drought versus well- watered conditions and higher versus lower nutrient additions. Seedlings grown under elevated CO2 displayed higher water use efficiency than seedlings grown under ambient CO2. This was apparent based upon instantaneous gas exchange as well as xylem potential pressure measurements. Elevated CO2-induced stimulation of relative growth rate was greatest shortly after seedling emergence and decreased with increased seedling size. Acclimation of net photosynthesis was observed and was reversible. Analyses using allometric principles indicate net photosynthetic acclimation resulted from: (i) growth-induced nutrient dilution; (ii) a decrease in foliar N levels not owing to dilution; and (iii) a decrease in net photosynthetic activity.

KEYWORDS: ANATOMY, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PHYSIOLOGY, PINUS-TAEDA SEEDLINGS, ROOT, SHOOT

1073

Johnsen, K.H. 1994. Growth and ecophysiological responses of black spruce seedlings to elevated co2 under varied water and nutrient additions (vol 23, pg 1033, 1993). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 24(3):646.*

1074

Johnsen, K.H., and J.E. Major. 1998. Black spruce family growth performance under ambient and elevated atmospheric CO2. *New Forests 15(3):271-281.*

Seedlings from 20 families of black spruce (Picea mariana (Mill.) B.S.P.), representing a large range in field productivity, were subjected to a greenhouse retrospective test under ambient (409 ppm - year 1, 384 ppm - year 2) and high (686 ppm - year 1, 711 ppm - year 2) atmospheric CO2 environments. After one and two growth cycles, seedling height and diameter growth significantly increased under elevated CO2. At the end of the experiment, seedlings grown under high CO2 had a mean above-ground dry weight of 48.77 g as compared to 26.36 g for seedlings grown under ambient atmospheric CO2. Families were a significant source of variation for all growth parameters. Although the family x CO2 environment interaction was not a statistically significant source of variation in the analysis of variance, the correlation between greenhouse and IS-year field height growth was weaker ($r = 0.29$, $p = 0.2177$) under elevated CO2 compared to ambient CO2 ($r = 0.51$, $p = 0.0223$) following the first growth cycle. However, following the second growth cycle, greenhouse-field correlations were similar between the two CO2 environments (ambient CO2: $r = 0.55$, p

= 0.0115; elevated CO2: r = 0.56, p = 0.0101). Thus, with this set of families, growth performance ranking after two years appears relatively stable under ambient and elevated CO2.

KEYWORDS: EARLY SELECTION, FULL-SIB FAMILIES, GAS-EXCHANGE, PHENOLOGY, RESPONSES, SEEDLINGS, TREES, WATER-STRESS

1075

Johnsen, K.H., and J.R. Seiler. 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce .1. Seedling responses to varied atmospheric CO2 concentrations and photoperiods. *Tree Physiology 16(3):367-373.*

We conducted a greenhouse experiment to determine: (1) if diverse provenances of black spruce (Picea mariana (Mill.) B.S.P.) respond similarly in growth, phenology and physiology to an approximately 300 ppm increase in atmospheric CO2 concentration, and (2) the influence of photoperiod on both provenance and provenance x CO2 interaction effects. Seedlings from provenances that originated from the Yukon (63 degrees 34' N, 135 degrees 55' W), British Columbia (58 degrees 47' N, 123 degrees 38' W), Alberta (52 degrees 22' N, 115 degrees 15' W), Newfoundland (50 degrees 54' N, 56 degrees 06' W) and Ontario (48 degrees 59' N, 80 degrees 38' W and 45 degrees 10' N, 77 degrees 10' W) were subjected to growth analysis in greenhouse growth chambers supplied with 712 +/- 93 (SD) ppm CO2 (elevated) or 394 +/- 59 ppm CO2 (ambient). Seedlings from Provenances 7000 and 6901 were also subjected to an extended photoperiod treatment and periodically measured for shoot and root gas exchange. In response to a natural photoperiod, southern provenances grew more, broke and set bud later, and partitioned more biomass to shoot versus root than northern provenances. These differences among provenances were influenced by the extended photoperiod treatment but not by the elevated CO2 treatment. Averaged across all provenances, elevated CO2 increased seedling final weights by 55%; however, the elevated CO2 treatment had no effect on the provenance differences in any measured trait. We conclude that the large differences in physiology, phenology and growth among these diverse provenances of black spruce were expressed similarly in both ambient and elevated atmospheric CO2 concentrations.

KEYWORDS: ELEVATED CO2, FAMILIES, LOBLOLLY-PINE

1076

Johnson, B.G., B.A. Hale, and D.P. Ormrod. 1996. Carbon dioxide and ozone effects on growth of a legume-grass mixture. *Journal of Environmental Quality 25(4):908-916.*

Atmospheric carbon dioxide (CO2) and photochemical ozone (O-3) have been increasing in the biosphere and will continue to do so with further industrialization and burning of fossil fuels, The purpose of this study was to examine the interaction of CO2 and O-3 on plant growth and aboveground competition using a forage mixture of alfalfa (Medicago sativa L.) and timothy (Phleum pratense L.). Mixtures were grown at two CO2 levels (350 and 700 mu L/L) in controlled environment chambers and exposed to four weekly O-3 episodes of 8-h duration with peak daily concentrations of 0.03, 0.08, 0.13, or 0.18 mu L/L on Days (d) 21, 28, 35, and 42 after seeding. Roots of individual plants were in separate containers, The plants were harvested 2 d after the fmal O-3 exposure. Total dry biomass of alfalfa and timothy was 50 and 40%, respectively, greater at 700 than at 350 mu L CO2/L with low O-3. Increasing peak O-3 concentration decreased alfalfa shoot dry biomass at 700 mu L CO2/L but not at 350 mu L/L and decreased root dry biomass at both CO2 levels. In timothy, intermediate O-3 levels reduced shoot growth but the highest level of O-3 resulted in more shoot growth in the mixture at both CO2 levels. Partitioning of dry matter to alfalfa roots was strongly retarded by increasing O- 3, particularly in the CO2-enriched environment, while timothy root growth vias unaffected by O-3. The enhancement of timothy shoot biomass is, the mixture by exposure to the highest level of O-3 at either CO2 level could not be fully explained by changes in competition between timothy and alfalfa in relation to differential O-3 tolerance.

KEYWORDS: AIR- POLLUTANTS, CLOVER, FORAGE, PASTURE, PLANTS, QUALITY, YIELD

1077

Johnson, D.W. 1999. Simulated nitrogen cycling response to elevated CO2 in Pinus taeda and mixed deciduous forests. *Tree Physiology 19(4-5):321-327.*

Interactions between elevated CO2 and N cycling Introduction were explored with a nutrient cycling model (NuCM, Johnson et ai. 1993, 1995) for a Pinus taeda L, site at Duke University, North Carolina, and a mixed deciduous site at Walker Branch, Tennessee. The simulations tested whether N limitation would prevent growth increases in response to elevated CO2, and whether growth responses to CO2 in N-limited systems could be facilitated by increasing the biomass/N ratio (reducing N concentration) or increasing litter N mineralization, or both. Nitrogen limitation precluded additional growth when target growth rates and litterfall were increased (simulating potential response to elevated CO2) at the Duke University site. At the Walker Branch site, increasing target growth and litterfall caused a 7% increase in growth. Reducing foliar N concentrations reduced growth because of N limitation created by reduced litter quality (C:N ratio), reduced decomposition and increased N accumulation on the forest floor. These effects were most pronounced at the Duke University site, because the forest floor N turnover rate was lower than at the Walker Branch site. Reducing wood N concentration allowed prolonged increases in growth because of greater biomass/N; however, N uptake was reduced, allowing greater N immobilization on the forest floor and in soil. Increased N mineralization caused increased growth at the Duke University site, but not at the Walker Branch site. These simulations pose the counterintuitive hypothesis that increased biogeochemical cycling of N (as a result of increased litterfall N) causes reduced growth in an N-limited system because of increased accumulations of N on the forest floor and in soil. Translocation of N from senescing leaves before litterfall mitigates this response by allowing the trees to retain a greater proportion of N taken up rather than recycle it back to the forest floor and soil where it can be immobilized. Eliminating N translocation at Walker Branch changed the direction as well as the magnitude of the responses in three of the four scenarios simulated. Because the NuCM model does not currently allow translocation in coniferous species, the effects of translocation on N cycling in the Duke University simulations are not known.

KEYWORDS: CARBON DIOXIDE, CYCLES, DEPOSITION, ECOSYSTEMS, FEEDBACK, MODEL, STORAGE

1078

Johnson, D.W., and J.T. Ball. 1990. Environmental-pollution and impacts on soils and forests nutrition in north-america. *Water, Air, and Soil Pollution 54:3-20.*

The effects of acid deposition, excess N deposition, and elevated CO2 on forest soils and nutrition in North America are reviewed. While there remains the possibility that acid deposition and excess N deposition are contributing to declines in red spruce, sugar maple, and southern pines, clear-cut cause and effects are still not evident. Climate is clearly a major factor in red spruce decline in the northeastern U.S., but air pollution may contribute. There is some evidence that soil solution Al may be approaching deleterious levels in southeastern red spruce forests. Lack of proper management may be a major factor in the sugar maple and southern pine declines, but once again, air pollution as a potential

contributor cannot be ignored. Nutrient budget analyses and discoveries of soils base cation depletion in certain sites suggest that base cation status is declining in forests of the southeastern U.S., but thus far, base cation deficiences are uncommon. Recent research has revealed that there are more cases of N-saturated forests in North America than was previously suspected. These systems are characterized by high rates of soil N mineralization, high atmospheric N inputs, low uptakes, or some combination of these factors. Soil leaching and Al mobilization in such systems is often dominated by nitrate. However, the geographical extent of these types of systems is limited, and the traditional view that most forest ecosystems are N limited remains valid, especially where forest management is intensive. The limited information available on tree response to CO2 suggests N-deficient plants often grow faster with elevated CO2, whereas P-deficient plants often do not. Research is needed to 1) determine if the differences in response between N- and P-deficient plants is common, 2) the responses of plants deficient in other nutrients to elevated CO2, and 3) the interactions of CO2 increase, nutrient deficiencies, climate change.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHMENT, DECIDUOUS FOREST, EASTERN UNITED STATES, ELEVATED CO2, LOBLOLLY-PINE, NITROGEN MINERALIZATION, PINUS-RADIATA SEEDLINGS, RED SPRUCE, SIMULATED ACID-RAIN

1079

Johnson, D.W., J.T. Ball, and R.F. Walker. 1997. Effects of CO2 and nitrogen fertilization on vegetation and soil nutrient content in juvenile ponderosa pine. *Plant and Soil 190(1):29-40.*

This paper summarizes the data on nutrient uptake and soil responses in opentop chambers planted with ponderosa pine (Pinus ponderosa Laws.) treated with both N and CO2. Based upon the literature, we hypothesized that 1) elevated CO2 would cause increased growth and yield of biomass per unit uptake of N even if N is limiting, and 2) elevated CO2 would cause increased biomass yield per unit uptake of other nutrients only by growth dilution and only if they are non-limiting. Hypothesis 1 was supported only in part: there were greater yields of biomass per unit N uptake in the first two years of growth but not in the third year. Hypothesis 2 was supported in many cases: elevated CO2 caused growth dilution (decreased concentrations but not decreased uptake) of P, S, and Mg. Effects of elevated CO2 on K, Ca, and B concentrations were smaller and mostly non-significant. There was no evidence that N responded in a unique manner to elevated CO2, despite its unique role in rubisco. Simple growth dilution seemed to explain nutrient responses in almost all cases. There were significant declines in soil exchangeable K+, Ca2+, Mg2+ and extractable P over time which were attributed to disturbance effects associated with plowing. The only statistically significant treatment effects on soils were negative effects of elevated CO2 on mineralizeable N and extractable P, and positive effects of both N fertilization and CO2 on exchangeable Al3+. Soil exchangeable K+, Ca2+, and Mg2+ pools remained much higher than vegetation pools, but extractable P pools were lower than vegetation pools in the third year of growth. There were also large losses of both native soil N and fertilizer N over time. These soil N losses could account for the observed losses in exchangeable K+, Ca2+, Mg2+ if N was nitrified and leached as NO3-.

KEYWORDS: CARBON DIOXIDE, DEFICIENCY, ELEVATED ATMOSPHERIC CO2, ENHANCEMENT, ENRICHMENT, FEEDBACK, FOREST, GROWTH-RESPONSES, PHOSPHORUS, SPRUCE SEEDLINGS

1080

Johnson, D.W., T. Ball, and R.F. Walker. 1995. Effects of elevated co2 and nitrogen on nutrient-uptake in ponderosa pine-seedlings. *Plant and Soil 169:535-545.*

This paper reports on the results of a controlled-environment study on the effects of CO2 (370, 525, and 700 mu mol mel(-1)) and N [0, 200, and 400 mu g N g soil(-1) as (NH4)SO4] on ponderosa pine (Pinus ponderosa) seedlings. Based upon a review of the literature, we hypothesized that N limitations would not prevent a growth response to elevated CO2. The hypothesis was not supported under conditions of extreme N deficiency (no fertilizer added to a very poor soil), but was supported when N limitations were less severe but still suboptimal (lower rate of fertilization), The growth increases in N-fertilized seedlings occurred mainly between 36 and 58 weeks without any additional N uptake. Thus, it appeared that elevated CO2 allowed more efficient use of internal N reserves in the previously-fertilized seedlings, whereas internal N reserves in the unfertilized seedlings were insufficient to allow this response, Uptake rates of other nutrients were generally proportional to growth. Nitrogen treatment caused reductions in soil exchangeable K+, Ca2+, and Mg2+ (presumably because of nitrification and NO3- leaching) but increases in extractable P (presumably due to stimulation of phosphatase activity). The results of this and other seedling studies show that elevated CO2 causes a reduction in tissue N concentration, even under N- rich conditions. The unique response of N is consistent with the hypothesis that the efficiency of Rubisco increases with elevated CO2. These results collectively have significant implications for the response of mature, N-deficient forests to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ECOSYSTEMS, ENRICHMENT, FOREST, GLOBAL CARBON-CYCLE, GROWTH-RESPONSES, LIMITATIONS, SOIL, SPRUCE SEEDLINGS

1081

Johnson, D., D. Geisinger, R. Walker, J. Newman, J. Vose, K. Elliot, and T. Ball. 1994. Soil pco(2), soil respiration, and root activity in co2-fumigated and nitrogen-fertilized ponderosa pine. *Plant and Soil 165(1):129-138.*

The purpose of this paper is to describe the effects of CO2 and N treatments on soil pCO(2), calculated CO2 efflux, root biomass and soil carbon in open-top chambers planted with Pinus ponderosa seedlings. Based upon the literature, it was hypothesized that both elevated CO2 and N would cause increased foot biomass which would in turn cause increases in both total soil CO2 efflux and microbial respiration. This hypothesis was only supported in part: both CO2 and N treatments caused significant increases in root biomass, soil pCO(2), and calculated CO2 efflux, but there were no differences in soil microbial respiration measured in the laboratory. Both correlative and quantitative comparisons of CO2 efflux rates indicated that microbial respiration contributes little to total soil CO2 efflux in the field. Measurements of soil pCO(2) and calculated CO2 efflux provided inexpensive, non-invasive, and relatively sensitive indices of belowground response to CO2 and N treatments.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CO2 EVOLUTION, ECOSYSTEMS, PLANTATIONS, RESPONSES

1082

Johnson, D.W., R.B. Thomas, K.L. Griffin, D.T. Tissue, J.T. Ball, B.R. Strain, and R.F. Walker. 1998. Effects of carbon dioxide and nitrogen on growth and nitrogen uptake in ponderosa and loblolly pine. *Journal of Environmental Quality 27(2):414-425.*

The purpose of this paper is to summarize the results of a series of greenhouse and open-top chamber studies on the effects of N and elevated atmospheric CO2 on ponderosa and loblolly pine (Pinus ponderosa Laws, and P. taeda L.) to evaluate common patterns of

response. Growth response to elevated CO2 ranged from zero to more than 1000%, depending largely upon N status, In both species, growth response to CO2 was greater under moderate N deficiency than under extreme N deficiency or N sufficiency/excess. Elevated CO2 generally caused lowered tissue N concentrations in many (but not all) cases, which in turn resulted in smaller increases in N uptake than in biomass. Growth response to N ranged from -50 (in ponderosa pine) to more than 1000%, depending upon the N status of the control medium. Growth response to N was enhanced by elevated CO2 when N was in the extreme deficiency range but not when N was in the moderate deficiency range. In two separate studies, ponderosa pine responded negatively to high N inputs, and in each case this response was mitigated by elevated CO2. Collectively, these results show that (i) N deficiency is a continuum rather than a step function, (ii) responses to elevated CO2 vary across this continuum of N deficiency, and (iii) elevated CO2 greatly enhances growth response to N additions when N is initially in the extremely deficient range.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, ECOSYSTEMS, ELEVATED CO2, FOREST, LEAF LITTER, LITTER QUALITY, NUTRIENT STATUS, RESPONSES, SOIL N, SPRUCE SEEDLINGS

1083

Johnson, D.W., R.F. Walker, and J.T. Ball. 1995. Combined effects of nitrogen and elevated CO2 on soils from controlled environment studies. *Water, Air, and Soil Pollution 85(3):1551-1556.*

This paper describes the effects of elevated CO2 and N fertilization on soils planted with ponderosa pine (Pinus Ponderosa) seedlings in short-term greenhouse studies. The high degree of homogeneity in the soils used allowed sensitive evaluation of soil changes in response to treatments. Elevated CO2 had no detectable effect upon soil N availability, but both CO2 and N fertilization caused significant changes in soil available (NH4F/HCl-extractable) P. Some of these changes could be accounted for by plant uptake, some were apparently due to differences in P immobilization (biotic or abiotic). N fertilization caused reductions in exchangeable K, Ca and Mg which could not be accounted for by plant uptake and were probably due to increased leaching. None of the reductions in soil available nutrients observed were of sufficient magnitude to cause nutrient deficiencies over the approximate 1-year duration of these studies.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, RESPONSES

1084

Johnson, D.W., R.F. Walker, and J.T. Ball. 1995. Lessons from lysimeters - soil n release from disturbance compromises controlled environment study. *Ecological Applications 5(2):395-400.*

A controlled environment study of the effects of carbon dioxide (CO2) and nitrogen (N) on growth of ponderosa pine seedlings produced results contradictory to those obtained in the field with the same species, soil, and treatments. In the controlled environment study, there was a significant negative growth response to N fertilization, whereas in the field there was a significant positive response to N. The difference was due to high rates of native N mineralization after soil disturbance during potting. This was evident from soil solution NO3- concentrations that peaked at approximate to 5000 mu mol/L in the unfertilized pots and 20 000 mu mol/L in the fertilized pots. These concentrations are orders of magnitude greater than those typically observed in the field. The effects of soil disturbance on N mineralization and nitrification need to be carefully considered before initiating controlled environment studies. The results of this study show that excessive N mineralization caused by soil disturbance can seriously compromise the results of controlled environment studies

KEYWORDS: ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, FOREST

1085

Johnson, H.B., H.W. Polley, and H.S. Mayeux. 1993. Increasing co2 and plant-plant interactions - effects on natural vegetation. *Vegetatio 104:157-170.*

Plant species and functional groups of species show marked differences in photosynthesis and growth in relation to rising atmospheric CO2 concentrations through the range of the 30 % increase of the recent past and the 100 % increase since the last glaciation. A large shift was found in the compositional mix of 26 species of C3's and 17 species of C4's grown from a native soil seed bank in a competitive mode along a CO2 gradient that approximated the CO2 increase of the past 150 years and before. The biomass of C3's increased from near zero to 50 % of the total while that of the C4's was reduced 25 % as CO2 levels approached current ambient. The proposition that acclimation to rising CO2 will largely negate the fertilization effect of higher CO2 levels on C3's is not supported. No signs of photosynthetic acclimation were evident for Avena sativa, Prosopis glandulosa, and Schizachyrium scoparium plants grown in subambient CO2. The effects of changing CO2 levels on vegetation since the last glaciation are thought to have been at least as great, if not greater, than those which should be expected for a doubling of current CO2 levels. Atmospheric CO2 concentrations below 200 ppm are thought to have been instrumental in the rise of the C4 grasslands of North America and other extensive C4 grasslands and savannas of the world. Dramatic invasion of these areas by woody C3 species are accompanying the historical increase in atmospheric CO2 concentration now in progress.

KEYWORDS: C-3, CARBON-DIOXIDE CONCENTRATION, CLIMATE CHANGE, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, ESTUARINE MARSH, GROWTH, OLD- FIELD PERENNIALS, PHOTOSYNTHESIS, TUSSOCK TUNDRA

1086

Johnson, L.C., G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, E.R. Rastetter, J.A. Laundre, and G.L. Murray. 1996. Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia 108(4):737-748.*

We examined the importance of temperature (7 degrees C or 15 degrees C) and soil moisture regime (saturated or field capacity) on the carbon (C) balance of arctic tussock tundra microcosms (intact blocks of soil and vege tation) in growth chambers over an 81-day simulated growing season. We measured gaseous CO2 exchanges, methane (CH4) emissions, and dissolved C losses on intact blocks of tussock (Eriophorum vaginatum) and in tertussock (moss-dominated). We hypothesized that under increased temperature and/or enhanced drainage, C losses from ecosystem respiration (CO2 respired by plants and heterotrophs) would exceed gains from gross photosynthesis causing tussock tundra to become a net source of C to the atmosphere. The field capacity moisture regime caused a decrease in net CO2 storage (NEP) in tussock tundra microcosms. This resulted from a stimulation of ecosystem respiration (probably mostly microbial) with enhanced drainage, rather than a decrease in gross photosynthesis. Elevated temperature alone had no effect on NEP because CO2 losses from increased ecosystem respiration at elevated temperature were compensated by increased CO2 uptake (gross photosynthesis). Although CO2 losses from ecosystem respiration were primarily limited by drainage, CH4 emissions, in contrast, were dependent on temperature. Furthermore, substantial dissolved C losses, especially organic C, and important microhabitat differences must be considered in estimating C balance for the tussock tundra system. As much as similar to 20% of total C fixed in photosynthesis was lost as dissolved organic C. Tussocks

stored similar to 2x more C and emitted 5x more methane than intertussocks. In spite of the limitations of this microcosm experiment, this study has further elucidated the critical role of soil moisture regime and dissolved C losses in regulating net C balance of arctic tussock tundra.

KEYWORDS: ALASKAN TUNDRA, ARCTIC TUNDRA, ATMOSPHERIC CO2, CLIMATIC CHANGE, DIOXIDE, GREENHOUSE, METHANE, RESPONSES, TERRESTRIAL ECOSYSTEMS, WATER-TABLE

1087

Johnson, R.H., and D.E. Lincoln. 1991. Sagebrush carbon allocation patterns and grasshopper nutrition - the influence of CO2 enrichment and soil mineral limitation. *Oecologia 87(1):127-134.*

Artemisia tridentata seedlings were grown under carbon dioxide concentrations of 350 and 650-mu-l l-1 and two levels of soil nutrition. In the high nutrient treatment, increasing CO2 led to a doubling of shoot mass, whereas nutrient limitation completely constrained the response to elevated CO2. Root biomass was unaffected by any treatment. Plant root/shoot ratios declined under carbon dioxide enrichment but increased under low nutrient availability, thus the ratio was apparently controlled by changes in carbon allocation to shoot mass alone. Growth under CO2 enrichment increased the starch concentrations of leaves grown under both nutrient regimes, while increased CO2 and low nutrient availability acted in concert to reduce leaf nitrogen concentration and water content. Carbon dioxide enrichment and soil nutrient limitation both acted to increase the balance of leaf storage carbohydrate versus nitrogen (C/N). The two treatment effects were significantly interactive in that nutrient limitation slightly reduced the C/N balance among the high-CO2 plants. Leaf volatile terpene concentration increased only in the nutrient limited plants and did not follow the overall increase in leaf C/N ratio. Grasshopper consumption was significantly greater on host leaves grown under CO2 enrichment but was reduced on leaves grown under low nutrient availability. An overall negative relationship of consumption versus leaf volatile concentration suggests that terpenes may have been one of several important leaf characteristics limiting consumption of the low nutrient hosts. Digestibility of host leaves grown under the high CO2 treatment was significantly increased and was related to high leaf starch content. Grasshopper growth efficiency (ECI) was significantly reduced by the nutrient limitation treatment but co-varied with leaf water content.

KEYWORDS: DIOXIDE ATMOSPHERES, ELEVATED CO2, GROWTH, INSECT HERBIVORE, LEPIDOPTERA, LIMITING CONDITIONS, NITROGEN, NOCTUIDAE, PLANT-TISSUE, VOLATILE LEAF TERPENES

1088

Johnston, K.M., and O.J. Schmitz. 1997. Wildlife and climate change: Assessing the sensitivity of selected species to simulated doubling of atmospheric CO2. *Global Change Biology 3(6):531-544.*

We explored, using computer simulations, the sensitivity of four mammal species (elk, Cervus canadensis; white-tailed deer, Odocoileus virginianus; Columbian ground squirrel, Spermophilus columbianus; and chipmunk, Tamias striatus) within the continental USA to the effect of anticipated levels of global climate change brought about by a doubling of atmospheric CO2. Sensitivity to the direct effects of climate change were evaluated using a climate-space approach to delineate the range of thermal conditions tolerable by each species. Sensitivity to indirect effects were evaluated by quantifying the association of each species to the current vegetation distribution within the continental USA and using this association to assess whether wildlife species distributions might shift in response to vegetation shifts under climate change. Results indicate that altered thermal conditions alone should have little or no effect on the wildlife species' distributions as physiological tolerance to heat load would allow them to survive. Analyses of the effects of vegetation change indicate that deer and chipmunks should retain their current distributions and possibly expand westward in the USA. For Elk and ground squirrels, there is a possibility that their current distributions would shrink and there is little possibility that each species would spread to new regions. This work emphasizes that the distributions of the four mammalian species are likely to be influenced more by vegetation changes than by thermal conditions. Future efforts to understand the effects of global change on wildlife species should focus on animal-habitat and climate-vegetation linkages.

KEYWORDS: CONSTRAINTS, ECOLOGY, MODELS, SCALE, VEGETATION, WHITE-TAILED DEER

1089

Joles, D.W., A.C. Cameron, A. Shirazi, P.D. Petracek, and R.M. Beaudry. 1994. Modified-atmosphere packaging of heritage red raspberry fruit - respiratory response to reduced oxygen, enhanced carbon- dioxide, and temperature. *Journal of the American Society for Horticultural Science 119(3):540-545.*

'Heritage' raspberries (Rubus idaeus L.) were sealed in low- density polyethylene packages and stored at 0, 10, and 20C during Fall 1990 and 1991 to study respiratory responses under modified atmospheres. A range of steady-state O2 and CO2 partial pressures were achieved by varying fruit weight in packages of a specific surface area and film thickness. Film permeability to O2 and CO2 was measured and combined with surface area and film thickness to estimate total package permeability. Rates of O2 uptake and CO2 production and respiratory quotient (RQ) were calculated using steady-state O2 and CO2 partial pressures, total package permeability, and fruit weight. The O2 uptake rate decreased with decreasing O2 partial pressure over the range of partial pressure studied. The Michaelis-Menten equation was used to model O2 uptake as a function of O2 partial pressure and temperature. The apparent K(m) (K1/2) remained constant (5.6 kPa O2) with temperature, while Q10 was estimated to be 1.9. RQ was modeled as a function of O2 partial pressure and temperature. Headspace ethanol increased at RQs >1.3 to 1.5. Based on RQ, ethanol production, and flavor, we recommend that raspberries be stored at O2 levels above 4 kPa at 0C, 6 kPa at 10C, and 8 kPa at 20C. Steady-state CO2 partial pressures of 3 to 17 kPa had little or no effect on O2 uptake or headspace ethanol partial pressures at 20C.

KEYWORDS: BLUEBERRY, CO2, FRESH PRODUCE, QUALITY, STORAGE

1090

Jones, C.G., and S.E. Hartley. 1999. A protein competition model of phenolic allocation. *Oikos 86(1):27-44.*

We present a Protein Competition Model (PCM) for predicting total phenolic allocation and concentration in leaves of terrestrial higher plants. In contrast to predictions based on the carbon composition of end products, the PCM is based on metabolic origins of pathway constituents, alternative fates of pathway precursors, and biochemical regulatory mechanisms. Protein and phenolic synthesis compete for the common, limiting resource phenylalanine, so protein and phenolic allocation are inversely correlated. Phenolic allocation can be predicted from the effects of development, inherent growth rate and environment on leaf functions that create competing demands for proteins or phenolics. We present the model general principles. We predict phenolic concentrations as leaves develop; in inherently fast versus slow growing species; and in response to the environment (nitrogen, light, phosphorus, heat shock, herbivore and pathogen injury, and carbon dioxide). Because

predictions generally fit observed patterns, we argue that, for phenylalanine-derived phenolics, the mechanistically distinctive PCM complements the Growth Differentiation and Resource Availability Hypotheses, and is a viable, testable alternative to the Carbon Nutrient Balance Hypothesis.

KEYWORDS: CARBON NUTRIENT BALANCE, CHEMICAL-COMPOSITION, DELAYED INDUCIBLE RESISTANCE, ELEVATED ATMOSPHERIC CO2, MINERAL NUTRITION, PHENYLALANINE AMMONIA-LYASE, PHENYLPROPANOID METABOLISM, PLANT-GROWTH RATE, RESOURCE AVAILABILITY HYPOTHESIS, SECONDARY METABOLISM

1091

Jones, M.B., J.C. Brown, A. Raschi, and F. Miglietta. 1995. The effects on arbutus-unedo L of long-term exposure to elevated co2. *Global Change Biology 1(4):295-302.*

Arbutus unedo is a sclerophyllous evergreen, characteristic of Mediterranean coastal scrub vegetation. In Italy, trees of A. unedo have been found close to natural CO2 vents where the mean atmospheric carbon dioxide concentration is about 2200 mu mol mol(-1). Comparisons were made between trees growing in elevated and ambient CO2 concentrations to test for evidence of adaptation to long-term exposure to elevated CO2. Leaves formed at elevated CO2 have a lower stomatal density and stomatal index and higher specific leaf area than those formed at ambient CO2, but there was no change in carbon to nitrogen ratios of the leaf tissue. Stomatal conductance was lower at elevated CO2 during rapid growth in the spring. In mid-summer, under drought stress, stomatal closure of all leaves occurred and in the autumn, when stress was relieved, the conductance of leaves at both elevated and ambient CO2 increased. In the spring, the stomatal conductance of the new flush of leaves at ambient CO2 was higher than the leaves at elevated CO2, increasing instantaneous water use efficiency at elevated CO2. Chlorophyll fluorescence measurements suggested that elevated CO2 provided some protection against photoinhibition in mid- summer. Analysis of A/C-i curves showed that there was no evidence of either upward or downward regulation of photosynthesis at elevated CO2. It is therefore anticipated that A. unedo will have higher growth rates as the ambient CO2 concentrations increase.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ENRICHMENT, GAS-EXCHANGE, INCREASE, LEAVES, PHOTOSYNTHESIS, PLANTS, STOMATAL DENSITY, TREES

1092

Jones, M.B., and M. Jongen. 1996. Sensitivity of temperate grassland species to elevated atmospheric CO2 and the interaction with temperature and water stress. *Agricultural and Food Science in Finland 5(3):271-283.*

The annual cycle of growth of many temperate grasses is limited by low temperatures during the winter and spring and water stress during the summer. Climate change, induced by increase in the concentration of greenhouse gases in the atmosphere, can affect the growth and community structure of temperature grasslands in two ways. The first is directly through changes in atmospheric concentration of CO2 and the second is indirectly through changes in temperature and rainfall. At higher latitudes, where growth is largely temperature limited, it is probable that the direct effects of enhanced CO2 will be less than at low latitudes. However, interactions with increasing temperature and water stress are complex. Temperate grasslands range from intensively managed monocultures of sown species to species-rich natural and semi-natural communities whose local distributions are controlled by variations in soil type and drainage. The different species can show marked differences in their responses to increasing CO2 concentrations, rising temperatures and water stress. This will probably result in major alterations in the community structure of temperate grasslands in the future. In addition to impacts on primary productivity and community structure, a long-term effect of elevated CO2 on grasslands is likely to be a significant increase in soil carbon storage. However, this may be counteracted by increases in temperature.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, PLANT, RESPONSES, STOMATAL CONTROL, USE EFFICIENCY

1093

Jones, M.B., M. Jongen, and T. Doyle. 1996. Effects of elevated carbon dioxide concentrations on agricultural grassland production. *Agricultural and Forest Meteorology 79(4):243-252.*

Open-top chambers have been used on a field-grown perennial ryegrass (Lolium perenne) sward to investigate the long-term responses to elevated CO2 concentrations. A concentration of 2 x ambient CO2 increased annual harvestable yield by about 20%, but the proportional stimulation was not constant throughout the growing season nor from one season to the next. Other effects of elevated CO2 were an increase in carbon/nitrogen ratio of tissues and a decrease in specific leaf area and canopy conductance. There was no effect of CO2 on the digestibility of the harvested grass. It is likely that climate change during the next century will lead to significant increases in agricultural grassland production in northern Europe. Production will be stimulated by a direct fertiliser effect due to the increasing CO2 concentration of the atmosphere.

KEYWORDS: CANOPIES, CO2 CONCENTRATION, FIELD, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, RESPONSES

1094

Jones, M.H., J.T. Fahnestock, D.A. Walker, M.D. Walker, and J.M. Welker. 1998. Carbon dioxide fluxes in moist and dry arctic tundra during season: Responses to increases in summer temperature and winter snow accumulation. *Arctic and Alpine Research 30(4):373-380.*

Climate-induced environmental changes are likely to have pronounced impacts on CO2 flux patterns in arctic ecosystems. We initiated a long-term experiment in 1994 in moist tussock and dry heath tundra in arctic Alaska in which we increased summer air temperature (ca. 2 degrees C) and increased winter snow accumulation (shortening the growing season approximately 4 wk). During the 1996 snow-free season, we measured ecosystem CO2 flux weekly in order to quantify net carbon gain or loss from these systems. Over the duration of the snow-free season, both dry heath and moist tussock tundra exhibited a net loss of carbon to the atmosphere, ranging from 12 to 81 g C m(-2) depending upon experimental treatment. Elevated summer temperatures accelerated net CO2 loss rates over ambient temperatures in both deep and ambient snow treatments, and increased the total amount of carbon emitted during the snow- free season by 26 to 38% in ambient snow plots and by 112 to 326% in deep snow plots. Increased snow accumulation had less impact on CO2 flux than did warming, and snow effects on total carbon loss were not consistent between the two temperature regimes. Ecosystem respiration exceeded assimilation on most sampling dates throughout the season. These data, coupled with winter carbon losses recently demonstrated in the same ecosystems, indicate that the moist and dry arctic ecosystems we examined are currently net sources of atmospheric carbon on an annual basis, and that anticipated global warming may increase carbon losses from these systems.

KEYWORDS: ALASKA, BALANCE, CLIMATE CHANGE, CO2, ECOSYSTEMS, EFFLUX, SOILS, STORAGE, TUSSOCK TUNDRA,

USA

1095

Jones, M.H., S.E. Macdonald, and G.H.R. Henry. 1999. Sex- and habitat-specific responses of a high arctic willow, Salix arctica, to experimental climate change. *Oikos 87(1):129-138.*

Dioecious plant species and those occupying diverse habitats may present special analytical problems to researchers examining effects of climate change. Here we report the results from two complementary studies designed to determine the importance of sex and habitat on gas exchange and growth of male and female individuals of a dioecious, circumpolar willow, Salix arctica, in the Canadian High Arctic. In field studies, male and female willows from dry and wet habitats were subjected to passively enhanced summer temperature (similar to 1.3 degrees C) using small open-top chambers over three years. Peak season gas exchange varied significantly by willow sex and habitat. Overall net assimilation was higher in the dry habitat than in the wet, and higher in females than in males. In the dry habitat, net assimilation of females was enhanced by experimental warming, but decreased in males. In the wet habitat, net assimilation of females was substantially depressed by experimental warming, while males showed an inconsistent response. Development and growth of male and female catkins were enhanced by elevated temperature more than leaf fascicles, but leaf fascicle development and growth varied more between the two habitats, particularly in males. In a controlled environment study, male and female willows from these same wet and dry habitats were grown in a 2x2 factorial experiment including 1 x or 2 x ambient [CO2] and 5 or 12 degrees C. The sexes responded very differently to the experimental treatments, but we found no effect of original habitat. Net assimilation in males was affected by the interaction of temperature and CO2, but in females by CO2 only. Our results demonstrate (a) significant intraspecific and intersexual differences in arctic willow physiology and growth, (b) that these differences are affected by environmental conditions expected to accompany global climate change, and (c) that sex- and habitat-specific responses should be explicitly accounted for in studies of dioecious species.

KEYWORDS: DWARF WILLOW, ELEVATED CO2, GAS-EXCHANGE, GROWTH, PHYSIOLOGY, PLANT SILENE LATIFOLIA, WATER RELATIONS

1096

Jones, P., L.M. Collins, and K.T. Ingram. 1995. Open-top chambers for field studies of crop response to elevated co2 and temperature. *Transactions of the Asae 38(4):1195-1201.*

A new design for Open Top Chambers (OTCs) is described. In addition to providing CO2 controls as do several other existing OTCs, the system is designed to provide elevated temperature control. To provide a more natural vertical microclimate profile, the newly designed system pulls air down through the chamber and out the bottom rather than injecting air at the bottom and venting it out the top of the chamber. A prototype was constructed and performance tests were conducted. Over a 24-h test period with a CO2 concentration setpoint of 660 ppm, individual measurements of concentration taken every 5 min averaged 660.5 ppm with a standard deviation of 26.6 ppm. Temperature controls were rested over 24-h periods for two different setpoints-ambient +4 degrees C and ambient +6 degrees C. For the two test periods the average chamber temperature measurements were 3.98 degrees and 5.99 degrees C above ambient, respectively. Twenty chambers based on the prototype design were constructed and installed at the International Rice Research Institute, Los Banos, Philippines. As intended, the chambers are currently being used to conduct research on rice crop response to elevated CO2 and temperature.

KEYWORDS: CARBON DIOXIDE, CO2, DESIGN, ENVIRONMENT, EXPOSURE, PLANTS

1097

Jones, T.H., L.J. Thompson, J.H. Lawton, T.M. Bezemer, R.D. Bardgett, T.M. Blackburn, K.D. Bruce, P.F. Cannon, G.S. Hall, S.E. Hartley, G. Howson, C.G. Jones, C. Kampichler, E. Kandeler, and D.A. Ritchie. 1998. Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science 280(5362):441-443.*

In model terrestrial ecosystems maintained for three plant generations at elevated concentrations of atmospheric carbon dioxide, increases in photosynthetically fixed carbon were allocated below ground, raising concentrations of dissolved organic carbon in soil. These effects were then transmitted up the decomposer food chain. Soil microbial biomass was unaffected, but the composition of soil fungal species changed, with increases in rates of cellulose decomposition. There were also changes in the abundance and species composition of Collembola, fungal-feeding arthropods. These results have implications for long-term feedback processes in soil ecosystems that are subject to rising global atmospheric carbon dioxide concentrations.

KEYWORDS: COLLEMBOLA, COLONIZATION, COMMUNITIES, DECOMPOSITION, ELEVATED CO2, FUNGI, PLANT-RESPONSES, PREFERENCES, RHIZOSPHERE, SOIL

1098

Jongen, M., P. Fay, and M.B. Jones. 1996. Effects of elevated carbon dioxide and arbuscular mycorrhizal infection on Trifolium repens. *New Phytologist 132(3):413-423.*

Trifolium repens L. cv. aran was grown for 58 d at ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2, with and without the arbuscular mycorrhizal fungus Glomus mosseae (Nicol. & Gerd.) Gerd. St Trappe cv. YV. Plant biomass, mycorrhizal infection, non-structural carbohydrates, C, N and P content were examined. Elevated CO2 (a) significantly increased above- and below-ground biomass, (b) decreased specific leaf area and specific root length, (c) decreased tissue %N and increased the C:N ratio, and (d) significantly increased total non-structural carbohydrates. Inoculating T. repens with Glomus mosseae (a) significantly increased above- and below-ground biomass, (b) increased the total root length and total leaf area, and (c) significantly decreased tissue %P. Evidence of an increased influence of mycorhiza on the P nutrition of T. repens at elevated CO2 was found in the 22% increase in leaf total P (P less than or equal to 0.05) of mycorrhizal plants grown at elevated CO2 compared with nonmycorrhizal plants. No significant interactions were found between CO2 and mycorrhiza treatments. The proportion of T. repens root length colonized by Glomus mosseae was not affected by CO2 concentration. The percentage mycorrhizal infection was 29% at ambient CO2 and 35% at elevated CO2. However, exposure to elevated CO2 significantly increased the total mycorrhizal root length from 3.4 to 6.1 m per plant. The results show little evidence that the role of arbuscular mycorrhiza in the growth and nutrition of T. repens would increase if atmospheric CO2 were to increase as predicted.

KEYWORDS: ATMOSPHERIC CO2, DYNAMICS, GROWTH, INSECT HERBIVORE, NITROGEN, PHOSPHATE, PHOTOSYNTHESIS, PLANTS, SUBTERRANEUM L, WHITE CLOVER

1099

Jongen, M., and M.B. Jones. 1998. Effects of elevated carbon dioxide on plant biomass production and competition in a simulated neutral grassland community. *Annals of Botany 82(1):111-123.*

Using open-top chambers, four prominent species (Lolium perenne, Cynosurus cristatus, Holcus lanatus and Agrostis capillaris) of Irish neutral grasslands were grown at ambient and elevated (700 mu mol mol(-1)) atmospheric CO2 for a period of 8 months. The effects of interspecific competition on plant responses to CO2 enrichment were investigated by growing the species in a four-species mixture. The results indicate that the species differ in their ability to respond to elevated CO2. CO2-enrichment had the largest effect on the biomass production of H. lanatus, but substantial stimulations in biomass production were also found for the other three species. The CO2-stimulation of biomass production for H. lanatus was accompanied by increased tillering. In addition, reductions in specific leaf area were found for all species. Exposure to elevated CO2 increased the community biomass of the four- species mixture. This increase can be mainly attributed to a significant increase in the biomass of H. lanatus at elevated CO2. No statistically-significant changes in species composition of community biomass were found. However, H. lanatus did increase its share of community biomass at each of the harvests, with the other three species, mainly L. perenne, suffering losses in their shares at elevated CO2. The results show that: (1) the species varied in their response to elevated CO2; and (2) species composition in natural plant communities is likely to change at elevated CO2, but these changes may occur rather slowly. Much longer periods of exposure to elevated atmospheric CO2 may be required to permit detection of significant changes in species composition. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, DRY-MATTER, GROWTH, HOLCUS- LANATUS, LOLIUM-PERENNE, PASTURE TURVES, SEASONAL-CHANGES, TRIFOLIUM- REPENS, WHITE CLOVER

1100

Jongen, M., M.B. Jones, T. Hebeisen, H. Blum, and G. Hendrey. 1995. The effects of elevated co2 concentrations on the root-growth of lolium-perenne and trifolium-repens grown in a face system. *Global Change Biology 1(5):361-371.*

Lolium perenne and Trifolium repens were grown in a Free Air CO2 Enrichment (FACE) system at elevated (600 mu mol mol(-1)) and ambient (340 mu mol mol(-1)) carbon dioxide concentrations during a whole growing season. Using a root ingrowth bag technique the extent to which CO2 enrichment influenced the growth of L. perenne and T. repens roots under two contrasting nutrient regimes was examined. Root ingrowth bags were inserted for a fixed time into the soil in order to trap roots. It was also possible to follow the mortality of roots in bags inserted for different time intervals. Root ingrowth of both L. perenne and T. repens increased under elevated CO2 conditions. In L. perenne, root ingrowth decreased with increasing nutrient fertilizer level, but for T. repens the root ingrowth was not affected by the nutrient application rate. Besides biomass measurements, root length estimates were made for T. repens. These showed an increase under elevated CO2 concentrations. Root decomposition appeared to decrease under elevated CO2 concentrations. A possible explanation for this effect is the observed changes in tissue composition, such as the increase in the carbon:nitrogen ratio in roots of L. perenne at elevated CO2 concentrations.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CO2- ENRICHMENT, DRY-MATTER, INSECT HERBIVORE, NITROGEN, PHOSPHORUS, PLANT, RESPONSES

1101

Jordan, D.N., S.F. Zitzer, G.R. Hendrey, K.F. Lewin, J. Nagy, R.S. Nowak, S.D. Smith, J.S. Coleman, and J.R. Seeman. 1999. Biotic, abiotic and performance aspects of the Nevada Desert Free-Air CO2 Enrichment (FACE) Facility. *Global Change Biology 5(6):659-668.*

Arid and semiarid climates comprise roughly 40% of the earth's terrestrial surface. Deserts are predicted to be extremely responsive to global change because they are stressful environments where small absolute changes in water availability or use represent large proportional changes. Water and carbon dioxide fluxes are inherently coupled in plant growth. No documented global change has been more substantial or more rapid than the increase in atmospheric CO2. Free Air CO2 Enrichment (FACE) technology permits manipulation of CO2 in intact communities without altering factors such as light intensity or quality, humidity or wind. The Nevada Desert FACE Facility (NDFF) consists of three 491 m(2) plots in the Mojave Desert receiving 550 mu L L-1 CO2, and six ambient plots to assess both CO2 and fan effects. The shrub community was characterized as a Larrea-Ambrosia-Lycium species complex. Data are reported through 12 months of operation.

KEYWORDS: DIOXIDE, FIELD, WINTER ANNUALS

1102

Julkunentiitto, R., J. Tahvanainen, and J. Silvola. 1993. Increased co2 and nutrient status changes affect phytomass and the production of plant defensive secondary chemicals in salix- myrsinifolia (salisb). *Oecologia 95(4):495-498.*

The effect of CO2 enrichment (700 and 1050 ppm) on phytomass, soluble sugars, leaf nitrogen and secondary chemicals of three Salix myrsinifolia clones was studied in plants cultivated at very poor (sand seedlings) and moderate (peat seedlings) nutrient availability and under low illumination. The total shoot phytomass production of sand seedlings was less than 10% of that of the peat seedlings. Carbon dioxide increased the total shoot phytomass of peat seedlings. When the ambient carbon supply was doubled (to 700 ppm) the growth of sand seedlings was slightly enhanced but 1050 ppm CO2 gave growth figures similar to those at the control CO2 level. Leaf nitrogen content and total soluble sugar contents were significantly higher in peat seedlings than in sand seedlings. Leaf nitrogen showed a decreasing trend in relation to CO2 increase. On the other hand, CO2 did not have any clear-cut effect on total sugars. At the control CO2 level the content of salicortin, which is a dynamic phenolic, was higher in the peat seedlings than in the sand seedlings, but salicin showed the opposite trend. CO2 enrichment considerably decreased these phenolics in the peat seedlings. At the control CO2 level, the content of more static phenolics, such as proanthocyanidins, was higher in sand seedlings. An increased carbon supply considerably increased static phenolics in the peat seedlings. Willow defence against generalist herbivores is moderately decreased by enhancement of atmospheric carbon dioxide.

KEYWORDS: ALLOCATION, BALANCE, PERFORMANCE, PHENOLIC CONSTITUENTS, WILLOWS

1103

Kainulainen, P., J.K. Holopainen, and T. Holopainen. 1998. The influence of elevated CO2 and O-3 concentrations on Scots pine needles: changes in starch and secondary metabolites over three exposure years. *Oecologia 114(4):455-460.*

Scots pine (Pinus sylvestris L.) trees, aged about 20 years old, growing on a natural pine heath were exposed to two concentrations of CO2 (ambient CO2 and double-ambient CO2) and two O-3 regimes (ambient O-3 and double-ambient O-3) and their combination in open-top chambers during growing seasons 1994, 1995 and 1996. Concentrations of foliar starch and secondary compounds are reported in this paper. Starch concentrations remained unaffected by elevated CO2 and/or O-3 concentrations during the first 2 study years. But in the autumn of the last study year, a significantly higher concentration of starch was found in current-year needles of trees exposed to elevated CO2 compared with ambient air. There were large differences in concentrations of starch and

secondary compounds between individual trees. Elevated concentrations of CO2 and/or O-3 did not have any significant effects on the concentrations of foliar total monoterpenes, total resin acids or total phenolics. Significantly higher concentrations of monoterpenes and resin acids and mostly lower concentrations of starch were found in trees growing without chambers than in those growing in open-top chambers, while there were no differences in concentrations of total phenolics between trees growing without or in chambers. The results suggest that elevated concentrations of CO2 might increase foliar starch concentrations in Scots pine, while secondary metabolites remain unaffected. Realistically elevated O-3 concentrations do not have clear effects on carbon allocation to starch and secondary compounds even after 3 exposure years.

KEYWORDS: ACID-RAIN, CARBON NUTRIENT BALANCE, DIOXIDE, GROWTH, L KARST, NORWAY SPRUCE, OZONE, SEEDLINGS, SPRUCE PICEA-ABIES, SYLVESTRIS L

1104

Kajfezbogataj, L., and A. Hocevar. 1994. Assessment of climate-change effects on productivity of beech stand in slovenia using simulation methods. *Agricultural and Forest Meteorology 72(1-2):47-56.*

On the basis of observed climatic trends in Slovenia obtained from 142 years of meteorological observation in Ljubljana (Slovenia) 15 climatic scenarios for the next 60 years are constructed regarding temperature rise and various levels of increasing CO2 concentration. Yearly gross primary production of 80 year old beech stand (Fagus sylvatica) is simulated in daily scale by the PERUN 3 model for healthy trees assuming no water stress. The influence of increased CO2 concentration on physiological processes is assessed over enhanced maximal photosynthesis, lower compensation point and increased stomatal resistance. Results of the simulation, giving decreased primary production of beech stand under the mentioned assumption, are discussed.

KEYWORDS: CARBON DIOXIDE

1105

Kaji, H., M. Ueno, T. Ikebe, and Y. Osajima. 1993. Effects of low o-2 and elevated co2 concentrations on the quality of matsutake [tricholoma-matsutake (s ito et imai) sing] during storage. *Bioscience Biotechnology and Biochemistry 57(3):363-366.*

Matsutake [Tricholoma matsutake (S. ITO et IMAI) SING.] was stored under conditions of low O2 and elevated CO2 concentrations. The storage conditions were as follows: with an O2 concentration of 2.5+/-0.5%, the CO2 concentrations were 5%, 10%, 15%, and 20%, and relative humidity (RH) was about 100%; with an O2 concentration of 2.0+/-0.5%, the CO2 concentrations were 0%, 5%, 10%, and 15%, and RH was about 100%; the storage temperature was 1.0+/-0.1-degrees-C. The fruit was also stored in air and under 100% N2 as controls. Quality factors such as 'neto' (slimy microbial flora which develop on the moist surface of the fruiting body), weight loss, whiteness, firmness, and off-odor were measured. The development of neto and browning (loss of whiteness) of the inner stipe were suppressed for more than 14 days, except with storage under 100% N2. Storage in air and under 0% or a high concentration (> 10%) of CO2 caused an early development of off-odor, compared to storage under 5% and 10% CO2. In air, the development of mold was observed after 14 days. Under a low O2 concentration and 5% to 10% CO2, the quality factors of matsutake were most retained, and the fruit was still acceptable after 14 days of storage. A weight decrease of the fruit was recognized as the CO2 concentration was increased.

KEYWORDS: MUSHROOMS

1106

Kalina, J., and R. Ceulemans. 1997. Clonal differences in the response of dark and light reactions of photosynthesis to elevated atmospheric CO2 in poplar. *Photosynthetica 33(1):51-61.*

Two hybrid poplar (Populus) clones (i.e., fast growing clone Beaupre and slow growing clone Robusta) were grown for two years from cuttings at close spacings in open top chambers (OTCs) under ambient (AC) and elevated [EC = AC + 350 mu mol(CO2) mol(-1)] CO2 treatments, For clone Beaupre no down- regulation of photosynthesis was observed. Two years of growing under EC resulted in an increase in quantum yield of photosystem 2 (PS2), steady state irradiance saturated rate of net photosynthesis (P-Nmax), chlorophyll (Chl) content, and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPC) activity for this clone. We suppose that under nonlimiting conditions of nitrogen and phosphorus content the response to EC was by building up light-harvesting complexes of PS2 and increasing photochemical efficiency of PS2, Due to a high rate of the primary reactions of photosynthesis and a high RuBPCO activity the end product of the response to EC was an increase in P-Nmax and a larger saccharides content, The Robusta clone showed a depression in the primary reactions of photosynthesis under EC, We found a decrease in quantum yield of PS2, Chl and phosphorus contents, and in RuBPCO activity. However, an increase in P-Nmax, saccharides content and Chi a/b ratio was observed. We speculate (1) that the phosphorus deficiency in combination with an increase in CO2 concentrations may lead to a potential damage of the assimilation apparatus of the primary reactions of photosynthesis and to a decrease in photochemical efficiency of PS2; (2) that the primary target of "down-regulation" takes place at PS2 for irradiances above 150 mu mol m(-2) s(-1).

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GROWTH, PHOTOSYSTEM, PLANTS, POPULUS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, TOBACCO

1107

Kampichler, C., E. Kandeler, R.D. Bardgett, T.H. Jones, and L.J. Thompson. 1998. Impact of elevated atmospheric CO2 concentration on soil microbial biomass and activity in a complex, weedy field model ecosystem. *Global Change Biology 4(3):335-346.*

Although soil organisms play an essential role in the cycling of elements in terrestrial ecosystems, little is known of the impact of increasing atmospheric CO2 concentrations on soil microbial processes. We determined microbial biomass and activity in the soil of multitrophic model ecosystems housed in the Ecotron (NERC Centre for Population Biology, Ascot, UK) under two atmospheric CO2 concentrations (ambient vs. ambient + 200 ppm). The model communities consist of four annual plant species which naturally co-occur in weedy fields and disturbed ground throughout southern England, together with their herbivores, parasitoids and soil biota. At the end of two experimental runs lasting 9 and 4.5 months, respectively, root dry weight and quality showed contradictory responses to elevated CO2 concentrations, probably as a consequence of the different time-periods (and hence number of plant generations) in the two experiments. Despite significant root responses no differences in microbial biomass could be detected. Effects of CO2 concentration on microbial activity were also negligible. Specific enzymes (protease and xylanase) showed a significant decrease in activity in one of the experimental runs. This could be related to the higher C:N ratio of root tissue. We compare the results with data from the literature and conclude that the response of complex communities cannot be predicted on the basis of oversimplified experimental set-ups.

KEYWORDS: CARBON DIOXIDE, DECOMPOSITION, ENRICHMENT, LEAF LITTERS, LITTER QUALITY, NITROGEN-CONTENT, NUTRIENT-UPTAKE, PLANT GROWTH, RESPONSES, TALLGRASS PRAIRIE

1108

Kandeler, E., D. Tscherko, R.D. Bardgett, P.J. Hobbs, C. Kampichler, and T.H. Jones. 1998. The response of soil microorganisms and roots to elevated CO2 and temperature in a terrestrial model ecosystem. *Plant and Soil 202(2):251-262.*

We investigate the response of soil microorganisms to atmospheric CO2 and temperature change within model terrestrial ecosystems in the Ecotron. The model communities consisted of four plant species (Cardamine hirsuta, Poa annua, Senecio vulgaris, Spergula arvensis), four herbivorous insect species (two aphids, a leaf-miner, and a whitefly) and their parasitoids, snails, earthworms, woodlice, soil-dwelling Collembola (springtails), nematodes and soil microorganisms (bacteria, fungi, mycorrhizae and Protista). In two successive experiments, the effects of elevated temperature (ambient plus 2 degrees C) at both ambient and elevated CO2 conditions (ambient plus 200 ppm) were investigated. A 40:60 sand:Surrey loam mixture with relatively low nutrient levels was used. Each experiment ran for 9 months and soil microbial biomass (C-mic and N-mic), soil microbial community (fungal and bacterial phospholipid fatty acids), basal respiration, and enzymes involved in the carbon cycling (xylanase, trehalase) were measured at depths of 0-2, 0-10 and 10-20 cm. In addition, root biomass and tissue C:N ratio were determined to provide information on the amount and quality of substrates for microbial growth. Elevated temperature under both ambient and elevated CO2 did not show consistent treatment effects. Elevation of air temperature at ambient CO2 induced an increase in C-mic of the 0-10 cm layer, while at elevated CO2 total phospholipid fatty acids (PLFA) increased after the third generation. The metabolic quotient qCO(2) decreased at elevated temperature in the ambient CO2 run. Xylanase and trehalase skewed no changes in both runs. Root biomass and C:N ratio were not influenced by elevated temperature in ambient CO2. In elevated CO2, however, elevated temperature reduced root biomass in the 0-10 cm and 30-40 cm layers and increased N content of roots in the deeper layers. The different response of root biomass and C:N ratio to elevated temperature may be caused by differences in the dynamics of root decomposition and/or in allocation patterns to coarse or fine roots (i.e. storage vs. resource capture functions). Overall, our data suggests that in soils of low nutrient availability, the effects of climate change on the soil microbial community and processes are likely to be minimal and largely unpredicatable.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ENRICHMENT, GRASSLAND, MANAGEMENT, MICROBIAL BIOMASS, NINHYDRIN-REACTIVE NITROGEN, RESPIRATION, SYSTEMS, TALLGRASS PRAIRIE

1109

Kanechi, M., M. Ochi, M. Abe, N. Inagaki, and S. Maekawa. 1998. The effects of carbon dioxide enrichment, natural ventilation, and light intensity on growth, photosynthesis, and transpiration of cauliflower plantlets cultured in vitro photoautotrophically and photomixotrophically. *Journal of the American Society for Horticultural Science 123(2):176-181.*

The effects of natural ventilation and CO2 enrichment during the rooting stage on the growth and the rates of photosynthesis and transpiration of in vitro cauliflower (Brassica oleracea L.) plantlets were investigated. In vitro plantlets were established in airtight or ventilated vessels with or without CO2 supplied (approximate to 1200.mu g L-1) through gas permeable films attached to the vessel's cap for 15 days before transplanting ex vitro. Leaves generated in vitro in ventilated vessels had a higher photosynthetic rate than those produced in airtight vessels, which lead to greater leaf expansion and shoot and root dry matter accumulation during in vitro culture and acclimatization. Enhanced photosynthesis in leaves of ventilated plantlets was positively correlated with chlorophyll content. Increasing photosynthetically active radiation from 70 to 200 mu mol.m(-1)-s(-1) enhanced the growth of in vitro plantlets under ventilated conditions but it depressed photosynthesis of the leaves grown photomixotrophically with sugar and CO2 enrichment which might be due to the feedback inhibition caused by marked accumulations of sucrose and starch. Higher CO2 levels during in vitro culture enhanced photosynthesis under photoautotrophic conditions, but inhibited it under photomixotrophic conditions. Fifteen days after transplanting ex vitro, high photosynthetic ability and stomatal resistance to transpiratory water loss of ventilated plantlets in vitro had important contributions to rooting and acclimatization. Our findings show that the ventilated culture is effective for accelerating photoautotrophic growth of plantlets by increasing photosynthesis, suggesting that, especially for plantlets growing in vitro without sugar, CO2 enrichment may be necessary to enhance photosynthetic ability.

KEYWORDS: ACCLIMATIZATION, GREENHOUSE, INVITRO, MERISTEM CULTURE, MICROPROPAGATION, SUCROSE, ULTRASTRUCTURE, WATER-LOSS

1110

Kano, A., Y. Fukazawa, M. Aono, and K. Ohkawa. 1992. Effect of age of cuttings, propagation media, and cutting methods on rooting of stephanotis-floribunda brongn. *Journal of the Japanese Society for Horticultural Science 61(3):619-624.*

The effects of cutting methods, cutting media, and age of cutting on rooting capacity of Stephanotis floribunda Brongn. were investigated to improve propagation efficiency. The effects of CO2 enrichment and a new acclimatization technique for cutting were also tested. 1. Cuttings made from older shoots showed a higher rooting percentage than those made from younger ones. 2. Rockwool mats were found to be useful as a cutting medium for S. floribunda. 3. Cuttings with differentiated leaf buds showed higher rooting percentage than those without buds. 4. Rooting was stimulated by placing cuttings in a closed frame, especially when CO2 concentration was high. 5. An acclimatization technique using a computer controlled fan was developed to decrease water stress during the acclimatization period.

1111

Karban, R., and J.S. Thaler. 1999. Plant phase change and resistance to herbivory. *Ecology 80(2):510-517.*

All plants pass through a series of predictable developmental stages during their lives, called phase changes. The phase change from juvenile to adult leaves is known to be associated with changes in resistance against plant pathogens and herbivores in several species. Virtually nothing is known about changes in resistance associated with the transition from embryonic tissue to autotrophic tissue in seedlings. We studied the consequences of transitions from cotyledons to juvenile true leaves to adult true leaves in cotton seedlings (Gossypium hirsutum) for their resistance to spider mites (Tetranychus urticae). Mite populations grew much more rapidly on cotyledons than on true leaves. However, there was no detectable difference in the population growth of mites on juvenile vs. adult true leaves. We suggest that population growth of mites is positively affected by the high rates of photosynthesis of cotyledons relative to true leaves, or by some process or attribute correlated with photosynthesis. Conditions that caused increased rates of photosynthesis (exposure to light and elevated concentrations of CO2) caused mite populations to increase. Greater mite population growth on

cotyledons was not associated with stored reserves in the cotyledons, as the mites did poorly on cotyledons kept in the dark. This study indicates that phase changes can have profound effects on plant resistance to herbivores. Because the seedling stage is so vulnerable to herbivory and so critical to understanding plant population dynamics, a broader consideration of phase changes associated with seedlings is warranted.

KEYWORDS: AGE, CARBON DIOXIDE, COTTON, LEAF ABSCISSION, MATURATION, MITES, PHOTOSYNTHESIS, TREE

1112

Karnosky, D.F., B. Mankovska, K. Percy, R.E. Dickson, G.K. Podila, J. Sober, A. Noormets, G. Hendrey, M.D. Coleman, M. Kubiske, K.S. Pregitzer, and J.G. Isebrands. 1999. Effects of tropospheric O-3 on trembling aspen and interaction with CO2: Results from an O-3-gradient and a face experiment. *Water, Air, and Soil Pollution 116(1-2):311-322.*

Over the years, a series of trembling aspen (Populus tremuloides Michx.) clones differing in O-3 sensitivity have been identified from OTC studies. Three clones (216 and 271[(O- 3 tolerant] and 259 [O-3 sensitive]) have been characterized for O-3 sensitivity by growth and biomass responses, foliar symptoms, gas exchange, chlorophyll content, epicuticular wax characteristics, and antioxidant production. In this study we compared the responses of these same clones exposed to O-3 under field conditions along a natural O-3 gradient and in a Free-Air CO2 and O-3 Enrichment (FACE) facility. In addition, we examined how elevated CO2 affected O-3 symptom development. Visible O-3 symptoms were consistently seen (5 out of 6 years) at two of the three sites along the O-3 gradient and where daily one-hour maximum concentrations were in the range of 96 to 125 ppb. Clonal differences in O-3 sensitivity were consistent with our OTC rankings. Elevated CO2 (200 ppm over ambient and applied during daylight hours during the growing season) reduced visible foliar symptoms for all three clones from 31 to 96% as determined by symptom development in elevated O-3 versus elevated O-3 + CO2 treatments. Degradation of the epicuticular wax surface of all three clones was found at the two elevated O-3 gradient sites. This degradation was quantified by a coefficient of occlusion which was a measure of stomatal occlusion by epicuticular waxes. Statistically significant increases in stomatal occlusion compared to controls were found for all three clones and for all treatments including elevated CO2, elevated O-3, and elevated CO2 + O-3. Our results provide additional evidence that current ambient O- 3 levels in the Great Lakes region are causing adverse effects on trembling aspen. Whether or not elevated CO2 in the future will alleviate some of these adverse effects, as occurred with visible symptoms but not with epicuticular wax degradation, is unknown.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLONES, GROWTH, NATURAL-SELECTION, OZONE TOLERANCE, PHOTOSYNTHESIS, PHYSIOLOGY, POPULUS-TREMULOIDES, SENSITIVITY

1113

Karnosky, D.F., G.K. Podila, Z. Gagnon, P. Pechter, A. Akkapeddi, Y. Sheng, D.E. Riemenschneider, M.D. Coleman, R.E. Dickson, and J.G. Isebrands. 1998. Genetic control of responses to interacting tropospheric ozone and CO2 in Populus tremuloides. *Chemosphere 36(4-5):807-812.*

We exposed trembling aspen (Populus tremuloides Michx.) clones differing in tropospheric ozone (O-3) tolerance in various open-top chamber studies for three growing seasons, and examined the effects of O-3, CO2, and O-3 + CO2 on growth and physiological processes. Ozone in the range of 80 ppm hr (Sum 00) per growing season decreased height, diameter, and stem and leaf biomass slightly in a tolerant clone but severely in a sensitive clone. Elevated CO2 (150 ppm over ambient) did not compensate for the O-3 effects. Antioxidant enzyme analysis showed elevated SOD levels in the tolerant clone but not in the sensitive clone following O-3 exposure. Northern blot analysis indicated that the chloroplastic and cytosolic Cu/Zn SOD's were significantly increased in response to O-3 in the tolerant but not the sensitive clone. Currently, we are conducting molecular analysis to determine the functional significance of SOD's in regulating O-3 tolerance in aspen. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ALLOCATION, ASPEN CLONES, ATMOSPHERIC CO2, BIOMASS, EXPOSURES, FIELD, GROWTH, NATURAL-SELECTION, PRODUCTIVITY, SENSITIVITY

1114

Karowe, D.N., D.H. Seimens, and T. Mitchell-Olds. 1997. Species-specific response of glucosinolate content to elevated atmospheric CO2. *Journal of Chemical Ecology 23(11):2569-2582.*

The carbon/nutrient balance hypothesis has recently been interpreted to predict that plants grown under elevated CO2 environments will allocate excess carbon to defense, resulting in an increase in carbon-based secondary compounds. A related prediction is that, because plant growth will be increasingly nitrogen-limited under elevated CO2 environments, plants will allocate less nitrogen to defense, resulting in decreased levels of nitrogen-containing secondary compounds. We present the first evidence of decreased investment in nitrogen- containing secondary compounds for a plant grown under elevated CO2. We also present evidence that plant response is species specific and is not correlated with changes in leaf nitrogen content or leaf carbon-nitrogen ratio. When three crucifers were grown at 724 +/- 8 ppm CO2, total foliar glucosinolate content decreased significantly for mustard, but not for radish or turnip. Glucosinolate content of the second and fourth young est mustard leaves decreased by 45% and 31%, respectively. In contrast, no significant change in total glucosinolate content was observed in turnip or radish leaves, despite significant decreases in leaf nitrogen content. Total glucosinolate content differed significantly among leaves of different age; however, the trend differed among species. For both mustard and turnip, glucosinolate content was significantly higher in older leaves, while the opposite was true for radish. No significant CO2 x leaf age interaction was observed, suggesting that intraplant patterns of allocation to defense will not change for these species. Changes in nitrogen allocation strategy are likely to be species-specific as plants experience increasing atmospheric CO2 levels. The ecological consequences of CO2-induced changes in plant defensive investment remain to be investigated.

KEYWORDS: ALLELOCHEMICALS, CARBON-DIOXIDE ATMOSPHERES, CRUCIFERAE, DIAMONDBACK MOTH, GROWTH, HERBIVORY, IDENTIFICATION, MUSTARD, NUTRIENT BALANCE, PLUTELLA-XYLOSTELLA

1115

Kartschall, T., S. Grossman, P.J. Pinter, R.L. Garcia, B.A. Kimball, G.W. Wall, D.J. Hunsaker, and R.L. LaMorte. 1995. A simulation of phenology, growth, carbon dioxide exchange and yields under ambient atmosphere and free-air carbon dioxide enrichment (FACE) Maricopa, Arizona, for wheat. *Journal of Biogeography 22(4-5):611-622.*

The impact of increased atmospheric CO2 concentration on the growth and productivity of field grown wheat has been evaluated. Meteorological and soil information from this study were used to validate a model (DEMETER) for simulation of vegetation response to climate change scenarios. The model simulations of phenology, carbon exchange rate, growth and yield for the treatment conditions of the experiment show a reasonable accordance with the experimental data.

KEYWORDS: LEAVES, MODEL

1116

Karunaratne, C., G.A. Moore, R. Jones, and R. Ryan. 1997. Phosphine and its effect on some common insects in cut flowers. *Postharvest Biology and Technology 10(3):255-262.*

The most effective fumigant for insect disinfestation of cut flowers is currently methyl bromide, which will soon be unavailable in several countries. The toxicity of an alternative fumigant, phosphine (2% PH3 and 98% N-2), was tested at 24 degrees C on adult greenhouse thrips (Heliothrips haemorrhoidalis), adult aphids (Myzus persicae) and lightbrown apple moth larvae (LBAM; Epiphyas postvittana). These are commonly found as insect pests on many cut flower crops. Thrips were exposed to phosphine concentrations ranging from 20-600 mu l/l for 1 or 2 h. All thrips were killed within 18 h of exposure after a treatment of 300 mu l/l phosphine for 2 h. Adult aphids and fifth instar LBAM larvae were more resistant to phosphine, and trials were therefore conducted using higher phosphine concentrations (> 500 mu l/l) combined with atmospheric (0.035%) or elevated (33%) CO2. The most effective treatment for aphids was 1000 mu l/l phosphine +33% CO2 for 4 h, which killed all insects within 36 h of exposure. Under atmospheric CO2 levels, 92% of aphids were killed within 36 h after exposure to 1000 mu l/l phosphine for 6 h, with 100% kill attained after exposure to 5000-8000 mu l/l phosphine for 6 h. Elevated CO2 levels did not improve the efficacy of phosphine on LBAM larvae. The optimal treatment was 2000-2500 mu l/l phosphine for 4 or 6 h, which killed 96 or 100% of the larvae, respectively. Under atmospheric CO2 levels, 4000 mu l/l phosphine killed 74% of LBAM larvae after 4 h. and 94% after 6 h exposure. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, TOXIC ACTION

1117

Kasurinen, A., H.S. Helmisaari, and T. Holopainen. 1999. The influence of elevated CO2 and O-3 on fine roots and mycorrhizas of naturally growing young Scots pine trees during three exposure years. *Global Change Biology 5(7):771-780.*

Young Scots pine trees naturally established at a pine heath were exposed to two concentrations of CO2 (ambient and doubled ambient) and two O-3 regimes (ambient and doubled ambient) and their combination in open-top field chambers during growing seasons 1994, 1995 and 1996 (late May to 15 September). Filtered ozone treatment and chamberless control trees were also included in the treatment comparisons. Root in-growth cores were inserted to the undisturbed soil below the branch projection of each tree at the beginning of the fumigation period in 1994 and were harvested at the end of the fumigation periods in 1995 and 1996. Root biomasses were determined from different soil layers in the ingrowth cores, and the infection levels of different mycorrhizal types were calculated. Elevated O-3 and CO2 did not have significant effects on the biomass production of Scots pine coarse (diameter >2 mm) or fine roots (diameter <2 mm) and roots of grasses and dwarf shrubs. Elevated O-3 caused a transient stimulation, observable in 1995, in the proportion of tuber-like mycorrhizas, total mycorrhizas and total short roots but this stimulation disappeared during the last study year. Elevated CO2 did not enhance carbon allocation to root,growth or mycorrhiza formation, although a diminishing trend in the mycorrhiza formation was observed. In the combination treatment increased CO2 inhibited the transient stimulating effect of ozone, and a significant increase of old mycorrhizas was observed. Our conclusion is that doubled CO2 is not able to increase carbon allocation to growth of fine roots or mycorrhizas in nutrient poor forest sites and realistically elevated ozone does not cause a measurable limitation to roots within a period of three exposure years.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, COLONIZATION, ENRICHMENT, FIELD, GROWTH, LOBLOLLY-PINE, PHOTOSYNTHESIS, RESPONSES, SOIL, TROPOSPHERIC OZONE

1118

Kaufman, Y.J., and M.D. Chou. 1993. Model simulations of the competing climatic effects of so2 and co2. *Journal of Climate 6(7):1241-1252.*

Sulfur dioxide-derived cloud condensation nuclei are expected to enhance the planetary albedo, thereby cooling the planet. This effect might counteract the global warming expected from enhanced greenhouse gases. A detailed treatment of the relationship between fossil fuel burning and the SO2 effect on cloud albedo is implemented in a two-dimensional model for assessing the climate impact. Although there are large gaps in our knowledge of the atmospheric sources and sinks of sulfate aerosol, it is possible to reach some general conclusions. Using a conservative approach, results show that the cooling induced by the SO2 emission can presently counteract 50% of the CO2 greenhouse warming. Since 1980, a strong warming trend has been predicted by the model, 0.15-degrees-C, during the 1980- 1990 period alone. The model predicts that by the year 2060 the SO2 cooling reduces climate warming by 0.5-degrees-C or 25% for the Intergovernmental Panel on Climate Change (IPCC) business as usual (BAU) scenario and 0.2-degrees-C or 20% for scenario D (for a slow pace of fossil fuel burning). The hypothesis is examined that the different responses between the Northern Hemisphere (NH) and the Southern Hemisphere (SH) can be used to validate the presence of the SO2-induced cooling. Despite the fact that most of the SO2-induced cooling takes place in the Northern Hemispheric continents, the model-predicted difference in the temperature response between the NH and the SH of -0.2- degrees-C in 1980 is expected to remain about the same at least until 2060. This result is a combined effect of the much faster response of the continents than the oceans and of the larger forcing due to CO2 than due to the SO2. The climatic response to a complete filtering of SO2 from the emission products in order to reduce acid rain is also examined. The result is a warming surge of 0.4-degrees-C in the first few years after the elimination of the SO2 emission.

KEYWORDS: AEROSOLS, ATMOSPHERIC SULFUR, EFFECTIVE PARTICLE RADIUS, FEEDBACK PROCESSES, GLOBAL CLOUD ALBEDO, OPTICAL- THICKNESS, PARAMETERIZATIONS, POLLUTION, SENSITIVITY, SOLAR-RADIATION MEASUREMENTS

1119

Ke, D.Y., E. Yahia, M. Mateos, and A.A. Kader. 1994. Ethanolic fermentation of bartlett pears as influenced by ripening stage and atmospheric composition. *Journal of the American Society for Horticultural Science 119(5):976-982.*

Changes in fermentation volatiles and enzymes were studied in preclimacteric and postclimacteric 'Bartlett' pears (Pyrus communis L.) kept in air, 0.25% O2, 20% O2 + 80% CO2, or 0.25% O2 + 80% CO2 at 20C for 1, 2, or 3 days. All three atmospheres resulted in accumulation of acetaldehyde, ethanol, and ethyl acetate. The postctimacteric pears had higher activity of pyruvate decarboxylase (PDC) and higher concentrations of fermentation volatiles than those of the preclimacteric fruit. For the preclimacteric pears, the 0.25% O2 treatment dramatically increased alcohol dehydrogenase (ADH) activity, which was largely due to the enhancement of one ADH isozyme. Exposure to 20% O2 + 80% CO2 slightly increased ADH activity, but the combination of 0.25% O2 + 80% Co2 resulted in lower ADH activity than 0.25% O2 alone. For the postclimacteric pears, the three atmospheres resulted in higher PDC and ADH activities than those of air control fruit. Ethanolic fermentation in 'Bartlett' pears could be induced by low O2 and/or high CO2 via 1) increased amounts of PDC and ADH;

2) PDC and ADH activation caused by decreased cytoplasmic pH; or 3) PDC and ADH activation or more rapid fermentation due to increased concentrations of their substrates (pyruvate, acetaldehyde, or NADH).

KEYWORDS: ALCOHOL-DEHYDROGENASE, ANAEROBIC NITROGEN, CARBON-DIOXIDE ATMOSPHERES, FRUIT TOLERANCE, INDUCTION, LOW-OXYGEN ATMOSPHERES, POST-HARVEST QUALITY, PYRUVATE DECARBOXYLASE, SHORT- TERM, STORAGE

1120

Ke, D.Y., L.L. Zhou, and A.A. Kader. 1994. Mode of oxygen and carbon-dioxide action on strawberry ester biosynthesis. *Journal of the American Society for Horticultural Science 119(5):971-975.*

'Chandler' strawberries (Fragaria ananassa Duck.) were kept in air, 0.25% O2, 21% O2 + 50% CO2, or 0.25 O2 + 50% CO2 (balance N2) at 5C for 1 to 7 days to study the effects of controlled atmospheres (CAs) on volatiles and fermentation enzymes. Concentrations of acetaldehyde, ethanol, ethyl acetate, and ethyl butyrate were greatly increased, while concentrations of isopropyl acetate, propyl acetate, and butyl acetate were reduced by the three CA treatments compared to those of air-control fruit. The CA treatments enhanced activities of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) but slightly decreased activity of alcohol acetyltransferase (AAT). The results indicate that the enhanced PDC and ADH activities by CA treatments cause ethanol accumulation, which in turn drives the biosynthesis of ethyl esters. The increased ethanol concentration also competes with other alcohols for carboxyl groups for esterification reactions. The reduced AAT activity and limited availability of carboxyl groups due to ethanol competition decrease production of other acetate esters.

KEYWORDS: ATMOSPHERES, CO2, DECAY, FRUIT, QUALITY, SHORT-TERM EXPOSURE, STORAGE, VOLATILES

1121

Keeling, R.F. 1995. The atmospheric oxygen cycle - the oxygen isotopes of atmospheric co2 and o-2 and the o-2/n-2 ratio. *Reviews of Geophysics 33:1253-1262.*

KEYWORDS: DIOXIDE, ENRICHMENT, FRACTIONATION, GLOBAL CARBON-CYCLE, ICE, LEAF WATER, LEAVES, PLANTS, RESPIRATION, SEA

1122

Keith, H., R.J. Raison, and K.L. Jacobsen. 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. *Plant and Soil 196(1):81-99.*

Pools and annual fluxes of carbon (C) were estimated for a mature Eucalyptus pauciflora (snowgum) forest with and without phosphorus (P) fertilizer addition to determine the effect of soil P availability on allocation of C in the stand. Aboveground biomass was estimated from allometric equations relating stem and branch diameters of individual trees to their biomass. Biomass production was calculated from annual increments in tree diameters and measurements of litterfall. Maintenance and construction respiration were calculated for each component using equations given by Ryan (1991a). Total belowground C flux was estimated from measurements of annual soil CO2 efflux less the C content of annual litterfall (assuming forest floor and soil C were at approximate steady state for the year that soil CO2 efflux was measured). The total C content of the standing biomass of the unfertilized stand was 138 t ha(-1), with approximately 80% aboveground and 20% belowground. Forest floor C was 8.5 t ha(-1). Soil C content (0-1 m) was 369 t ha(-1) representing 70% of the total C pool in the ecosystem. Total gross annual C flux aboveground (biomass increment plus litterfall plus respiration) was 11.9 t ha(-1) and gross flux belowground (coarse root increment plus fine root production plus root respiration) was 5.1 t ha(-1). Total annual soil efflux was 7.1 t ha(-1), of which 2.5 t ha(- 1) (35%) was contributed by litter decomposition. The short- term effect of changing the availability of P compared with C on allocation to aboveground versus belowground processes was estimated by comparing fertilized and unfertilized stands during the year after treatment. In the P-fertilized stand annual wood biomass increment increased by 30%, there was no evidence of change in canopy biomass, and belowground C allocation decreased by 19% relative to the unfertilized stand. Total annual C flux was 16.97 and 16.75 t ha(-1) yr(-1) and the ratio of below-to aboveground C allocation was 0.43 and 0.35 in the unfertilized and P-fertilized stands, respectively. Therefore, the major response of the forest stand to increased soil P availability appeared to be a shift in C allocation; with little change in total productivity. These results emphasise that both growth rate and allocation need to be estimated to predict changes in fluxes and storage of C in forests that may occur in response to disturbance or climate change.

KEYWORDS: BIOMASS, CLIMATE CHANGE, DIOXIDE EVOLUTION, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO2, FINE ROOTS, LITTER, NET PRIMARY PRODUCTION, PINE PLANTATIONS, RESPIRATION

1123

Keller, T., J. Guiot, and L. Tessier. 1997. Climatic effect of atmospheric CO2 doubling on radial tree growth in south eastern France. *Journal of Biogeography 24(6):857-864.*

The climatic effect of a doubling of atmospheric CO2 on radial growth of trees was studied in ten populations of three species in south eastern France using an Atmospheric General Circulation Model (AGCM) predicting a 3 degrees C increase of mean temperature and a light rise of precipitation. Results are based on empirical growth climate models, involving an Artificial Neural Network (ANN) technique. Only two of the studied populations, on the boundaries of their ecological area, are sensitive to the climatic variations. One is the larch (Larix decidua Mill.) population located at 2300m on elevation (near the timberline) which shows a radial growth increase. The other is the most southern French Scots pine (Pinus sylvestris L.) population which reacts with a severe growth rate reduction.

1124

Kellogg, E.A., E.J. Farnsworth, E.T. Russo, and F. Bazzaz. 1999. Growth responses of C-4 grasses of contrasting origin to elevated CO2. *Annals of Botany 84(3):279-288.*

Nine grass species representing three independent origins of the C-4 photosynthetic pathway were grown at ambient (350 ppm) and elevated (700 ppm) CO2 and were harvested after flowering. Setaria and Arundinella are both members of the subfamily Panicoideae, and represent a single origin of the pathway. Aristida and Stipagrostis are sister genera in the subfamily Aristidoideae (formerly classified in subfamily Arundinoideae), and represent a second origin. Sporobolus, a member of the subfamily Chloridoideae, represents the third. By investigating two genera each within Panicoideae and Aristidoideae, we test the hypothesis that genera sharing the same origin of C-4 respond similarly. To explore variation among congeneric species, five species of Setaria were also examined to test the hypothesis that congeneric species have similar responses. Plant height and numbers of tillers, branches and inflorescences were measured, both over time and at final harvest. Biomass of roots, shoots, and inflorescences was also measured. Members of the Aristidoideae were generally significantly larger in

elevated CO2, as indicated by measurements of biomass and plant height, whereas representatives of the Panicoideae varied considerably in their response. The two subfamilies differed significantly in their responses to elevated CO2 and this effect outweighed any effect of CO2 alone. Sporobolus, though equally distantly related to Panicoideae and Aristidoideae, had a CO2 response similar to that of some panicoid species. Even within the genus Setaria, some species were significantly smaller at elevated than at ambient CO2, whereas others were larger. This may reflect diversity in internal regulation rather than acclimation or changes in source-sink allocation of carbon. The variation complicates any prediction of responses of C-4 plants to future atmospheric change. Comparison of closely related species, however, may well lead to intriguing new insights into how regulatory pathways of CO2 assimilation are modified during evolution. (C) 1999 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FAMILY POACEAE, GAS-EXCHANGE, GENE-EXPRESSION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEQUENCE DATA, STRESS

1125

Kellomaki, S., T. Karjalainen, and H. Vaisanen. 1997. More timber from boreal forests under changing climate? *Forest Ecology and Management 94(1-3):195-208.*

The effects of increases in temperature, precipitation and atmospheric CO2 concentration on timber yields from stands of Scots pine (Pinus sylvestris L.) in southern Finland (61 degrees N) are addressed. The assessment is based on simulations using a process-based model in which temperature, precipitation, and atmospheric CO2 are among the main drivers linking the dynamics of the tree stands directly and indirectly with the changing climate. These factors control photosynthesis, respiration, transpiration and the uptake of nitrogen and water, with consequent effects on the growth and development of tree stands. The timing of thinnings and the length of the rotation were related to the dynamics of the tree stand in compliance with the thinning rules applied in practical forestry. The simulations indicated that an increase in precipitation of 9 mm per decade alone did not affect timber yields. However, a temperature increase of 0.4 degrees C per decade, and the combination of temperature and precipitation increases would increase timber yields by 10% during one rotation. An elevation in the concentration of atmospheric CO2 by 33 mu mol mol(-1) per decade alone would increase removals of timber by 20%, and a combination of increases in temperature, precipitation and CO2 concentration would increase removals by 30%. A rise in precipitation did not have any effect on the length of the rotation, but the other combinations shortened the rotation; by 9 years in the case of elevating temperature, by 17 years in the case of elevating atmospheric CO2 concentration, and by 23 years in the case of the combined elevation of temperature, precipitation, and CO2 concentration due to more rapid tree growth and development. These changes can be expected to affect the supply of timber and also the profitability of forestry. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, CARBON, ELEVATED CO2, GAS-EXCHANGE, MATTER, PHOTOSYNTHESIS, SCOTS PINE, SIMULATION, SOIL MOISTURE, TEMPERATURE

1126

Kellomaki, S., and H. Vaisanen. 1997. Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecological Modelling 97(1-2):121-140.*

This paper summarizes a forest ecosystem model developed for assessing the effects of climate change on the functioning and structure of boreal coniferous forests under the assumption that temperature and precipitation are the basic dimensions of the niche occupied by any one tree species. Special attention is paid to specifying weather patterns to a level representing the time constant of different physiological and ecological processes relevant to the regeneration, growth and death of trees. The long-term dynamics of the forest ecosystem have been coupled with climatic factors at the level of mechanisms, e.g., photosynthesis and respiration, in terms of the energy flow through the ecosystem. Furthermore, hydrological and nutrient cycles couple the dynamics of the forest ecosystem with climate change through soil processes representing the thermal and hydraulic properties of the soil and the decomposition of litter and humus with the mineralization of nutrients. Simulations for southern Finland (62 degrees N) and northern Finland (66 degrees N) indicated that a transient increase in temperature by 4 degrees C over a period of 100 years could substantially increase soil temperature and reduce soil moisture in forest ecosystems dominated by Scots pine. At the same time, the temperature increase could enhance photosynthetic production and consequent stemwood growth in southern Finland by about 8% and in northern Finland by about 19%. Given the current temperature but elevating CO2 concentration, the increase in photosynthesis in southern Finland could be about 23% and in northern Finland about 21%, but the concurrent elevation in temperature and CO2 concentration increased photosynthesis by about 32% in southern Finland and by about 40% in northern Finland. Transpiration decreased by as much as 10-20% under the changing climate with the consequence that water-use efficiency increased by as much as 25-45%, the higher values representing southern Finland. (C) 1997 Elsevier Science B.V.

KEYWORDS: ELEVATED CO2, GAS-EXCHANGE, HABITAT, IRRADIANCE, NITROGEN, PHOTOSYNTHESIS, REGENERATION, RESPIRATION, SCOTS PINE, SIMULATION

1127

Kellomaki, S., H. Vaisanen, and T. Kolstrom. 1997. Model computations on the effects of elevating temperature and atmospheric CO2 on the regeneration of Scots pine at the timber line in Finland. *Climatic Change 37(4):683-708.*

Based on model computations, the regeneration of Scots pine (Pinus sylvestris L.) was studied at the northern timber line in Finland (70 degrees N) in relation to elevating temperature and atmospheric CO2. If a transient increase of 4 degrees C was assumed during the next 100 years, the length of growing season increased from the current 110-120 days to 150-160 days. This was associated with ca. 5 degrees C increase in the soil temperature over June-August with larger variability in temperature and deeper freezing of the soil due to the reduced depth and duration of the snow cover, At the same time, the moisture content of the surface soil decreased ca. 10% and was more variable, due to less infiltration of water into the soil as a consequence of the enhanced evapotranspiration and deeper freezing of the soil. The temperature elevation alone, or combined with elevating CO2, increased flowering and the subsequent seed crop of Scots pine with a decrease in the frequency of zero crops. In both cases, temperature elevation substantially increased the success of regeneration in terms of the number of seedlings produced after each seed crop. The increasing number of mature seeds was mainly responsible for the enhanced regeneration, but increasing soil temperature also increased the success of regeneration. The soil moisture was seldom limited for seed germination. In terms of the density of seedling stands, and the height and diameter growth of the seedlings, the establishment of a seedling stand was substantially improved under the combined elevation of temperature and CO2 in such a way that the temperature increased the number of mature seeds and enhanced germination of seeds and CO2 increased seedling growth. Even under the changing climatic conditions, however, the growth of the seedling stands was slow, which indicated that the northward advance of the timber line would probably be very slow, even though regeneration was no longer a limiting factor.

KEYWORDS: CHANGING CLIMATE, FORESTS, HABITAT, NITROGEN, PHOTOSYNTHESIS, SIMULATION, SOIL MOISTURE, TREES, WATER

1128

Kellomaki, S., and K.Y. Wang. 1996. Photosynthetic responses to needle water potentials in Scots pine after a four-year exposure to elevated CO2 and temperature. *Tree Physiology 16(9):765-772.*

Effects of needle water potential (psi(1)) on gas exchange of Scots pine (Pinus sylvestris L.) grown for 4 years in open-top chambers with elevated temperature (ET), elevated CO2 (EC) or a combination of elevated temperature and CO2 (EC + ET) were examined at a high photon flux density (PPFD), saturated leaf to air water vapor pressure deficit (VPD) and optimal temperature (T). We used the Farquhar model of photosynthesis to estimate the separate effects of psi 1 and the treatments on maximum carboxylation efficiency (V-c,V-max), ribulose-1,5- bisphosphate regeneration capacity (J), rate of respiration in the light (R(d)), intercellular partial pressure of CO2 (Ci) and stomatal conductance (G(s)). Depression of CO2 assimilation rate at low psi(1) was the result of both stomatal and non- stomatal limitations on photosynthetic processes; however, stomatal limitations dominated during short-term water stress (psi(1)<-1.2 MPa), whereas nonstomatal limitations dominated during severe water stress. Among the nonstomatal components, the decrease in J contributed more to the decline in photosynthesis than the decrease in Long-term elevation of CO2 and temperature led to differences in the maximum values of the parameters, the threshold values of psi(1) and the sensitivity of the parameters to decreasing psi(1). The CO2 treatment decreased the maximum values of V-c,V-max J and R(d) but significantly increased the sensitivity of V-c,V-max J and Rd to decreasing psi(1) ($P < 0.05$). The effects of the ET and EC + ET treatments on V-c,V-max J and R(d) were opposite to the effects of the EC treatment on these parameters. The values of G(s), which were measured simultaneously with maximum net rate of assimilation (A(max)), declined in a curvilinear fashion as psi(1) decreased. Both the EC + ET and ET treatments significantly decreased the sensitivity of G(s) to decreasing psi(1-). We conclude that, in the future, acclimation to increased atmospheric CO2 and temperature could increase the tolerance of Scots pine to water stress.

KEYWORDS: COTTON, DROUGHT, GAS-EXCHANGE, IRRADIANCE, LEAVES, STOMATAL CONDUCTANCE, STRESS

1129

Kellomaki, S., and K.Y. Wang. 1997. Effects of elevated O-3 and CO2 concentrations on photosynthesis and stomatal conductance in Scots pine. *Plant, Cell and Environment 20(8):995-1006.*

Naturally regenerated Scots pines (Pinus sylvestris L.), aged 28-30 years old, were grown in open-top chambers and subjected in situ to three ozone (O-3) regimes, two concentrations of CO2, and a combination of O-3 and CO2 treatments from 15 April to 15 September for two growing seasons (1994 and 1995), The gas exchanges of current-year and 1-year-old shoots were measured, along with the nitrogen content of needles, In order to investigate the factors underlying modifications in photosynthesis, five parameters linked to photosynthetic performance and three to stomatal conductance were determined, Elevated O-3 concentrations led to a significant decline in the CO2 compensation point (I*), maximum RuP2-saturated rate of carboxylation (V-emax), maximum rate of electron transport (J(max)) maximum stomatal conductance (g(smax)) and sensitivity of stomatal conductance to changes in leaf-to-air vapour pressure difference (partial derivative g(s)/partial derivative D-v) in both shoot-age classes, However, the effect of elevated O-3 concentrations on the respiration rate in light (R-d) was dependent on shoot age, Elevated CO2 (700 mu mol mol(-1)) significantly decreased J(max) and g(smax) but increased R-d in 1-year-old shoots and the partial derivative(s)/partial derivative D-v in both shoot-age classes, The interactive effects of O-3 and CO2 on some key parameters (e.g. V-emax and J(max)) were significant. This may be closely related to regulation of the maximum stomatal conductance and stomatal sensitivity induced by elevated CO2. As a consequence, the injury induced by O-3 was reduced through decreased ozone uptake in 1-year-old shoots, but not in the current-year shoots, Compared to ambient O-3 concentration, reduced O-3 concentrations (charcoal-filtered air) did not lead to significant changes in any of the measured parameters, Compared to the control treatment, calculations showed that elevated O-3 concentrations decreased the apparent quantum yield by 35% and by 18%, and the maximum rate of photosynthesis by 21% and by 29% in the current-year and 1-year-old shoots, respectively, Changes in the nitrogen content of needles resulting from the various treatments were associated with modifications in photosynthetic components.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, GAS-EXCHANGE, L KARST, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PICEA-ABIES L, SOURCE-SINK RELATIONS

1130

Kellomaki, S., and K.Y. Wang. 1997. Effects of elevated O-3 and CO2 on chlorophyll fluorescence and gas exchange in Scots pine during the third growing season. *Environmental Pollution 97(1-2):17-27.*

Naturally regenerated, 30-year-old Scots pines (Pinus Sylvestris L.) were grown in open-top chambers and exposed in situ to doubled ambient O-3, doubled ambient CO2 and a combination of elevated O-3 and CO2 from 15 April to 15 September for three growing seasons (1994-1996). To examine the effects of O-3 and/or CO2 on photosynthesis, chlorophyll a fluorescence and gas exchange were measured simultaneously. Doubled ambient O-3 significantly decreased the rates of photosynthesis at all levels of photon flux density. This was related mainly to a significant decrease in the photochemical efficiency of photosystem II (PS II) and the rate of whole electron transport, rather than to a decrease in stomatal conductance. When measurements were made at doubled ambient concentration of CO2 (700 mu mol mol(-1)), doubled ambient CO2 treatment did not lend to a significant change in the intrinsic capacity of photosynthesis, as manifested by no changes in PS II, the rate of electron transport, the maximal rate of photosynthesis and the apparent quantum yield of CO2 assimilation. However, elevated CO2 increased the sensitivity of stomatal conductance to light and decreased maximal stomatal conductance. When O-3 and CO2 were combined, the O-3-induced decrease in photosynthesis rate was reduced significantly by a high concentration of CO2. This may be partly related to the decrease in stomatal conductance induced by the high concentration of CO2. The complete mechanism behind this interaction is, however, still unclear. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ABIES L KARST, CARBON DIOXIDE, ELECTRON-TRANSPORT, LIGHT-RESPONSE CURVES, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PHOTOSYSTEM-II ACTIVITY, SOURCE-SINK RELATIONS

1131

Kellomaki, S., and K.Y. Wang. 1997. Effects of long-term CO2 and temperature elevation on crown nitrogen distribution and daily photosynthetic performance of Scots pine. *Forest Ecology and Management 99(3):309-326.*

Single Scots pines (Pinus sylvestris L.), aged 20-25 years, were grown in open-top chambers and exposed to elevated temperature (Elev. T), elevated CO2 (Elev. C) and a combination of elevated CO2 and temperature (Elev. C + T) for 3 years. The vertical distribution of needle

nitrogen concentration was measured simultaneously with gas exchange of attached shoots. Based on the measurements, the dependencies on needle nitrogen concentrations of four photosynthetic parameters, i.e., RuP2 (ribulose 1,5-bisphosphate)-saturated rate of carboxylation (V-cmax), maximum potential electron transport (J(max)), the rate of respiration in the light (R-d) and light-use-efficiency factor (delta), were determined. Using a crown multilayer model, the performance of daily crown photosynthesis in Scots pine was predicted. Compared to the control treatment, the mean concentration of nitrogen in the foliage decreased by 20% and by 17% for trees grown under Elev. C and under Elev. C + T, respectively, but increased by 4% for trees grown under Elev. T. However, the total content of foliage nitrogen per unit ground area increased by 25% for trees grown under Elev. C, by 19% for trees grown under Elev. C + T and by 6% for trees grown under Elev. T; these were due to the increase in the total needle area index. Regressions showed that the foliage grown under Elev. C and Elev. C + T had steeper slopes representing the responses of V-cmax, and R-d and delta to leaf nitrogen concentrations, while Elev. C + T and Elev. T had steeper slopes representing the response of J(max) to needle nitrogen concentrations. Predictions showed that, on a typical sunny day, the daily total of crown photosynthesis increased 22% and 27%, separately for Elev. C and Elev. C + T, and by only 9% for Elev. T alone. Furthermore, the increased daily crown photosynthesis, resulting from treatments involving elevated CO2, can be attributed mainly to an increase in the ambient CO2 concentration and the needle area index, while modification of the intrinsic photosynthetic capacity had only a marginal effect. Based on the current pattern of crown nitrogen allocation, the prediction showed also that the relationship between daily crown photosynthesis and crown nitrogen content was strongly dependent on the daily incident PAR and air temperature. The CO2-elevated treatments led to an increase in the sensitivity of daily crown photosynthesis to changes in crown nitrogen content, daily incident PAR and temperature, while the temperature-elevated treatment had the opposite effect on the sensitivity. (C) 1997 Elsevier Science B.V.

KEYWORDS: ACCLIMATION, CANOPY PHOTOSYNTHESIS, CARBON GAIN, ENRICHMENT, EUCALYPTUS-GRANDIS, GAS-EXCHANGE, GROWTH, LEAF NITROGEN, MINERAL NUTRITION, SPATIAL DISTRIBUTIONS

1132

Kellomaki, S., and K.Y. Wang. 1997. Photosynthetic responses of Scots pine to elevated CO2 and nitrogen supply: Results of a branch-in-bag experiment. *Tree Physiology 17(4):231-240.*

Naturally seeded Scots pine (Pinus sylvestris L.) trees, age 25-30 years, were subjected to two soil-nitrogen-supply regimes and to elevated atmospheric CO2 concentrations by the branch- in-bag method from April 15 to September 15 for two or three years. Gas exchange in detached shoots was measured in a diffuse radiation field. Seven parameters associated with photosynthetic performance and two describing stomatal conductance were determined to assess the effects of treatments on photosynthetic components. An elevated concentration of CO2 did not lead to a significant downward regulation in maximum carboxylation rate (V-cmax) or maximum electron transport rate (J(max)), but it significantly decreased light-saturated stomatal conductance (g(sat)) and increased minimum stomatal conductance (g(min)). Light-saturated rates of CO2 assimilation were higher (24-31 %) in shoots grown and measured at elevated CO2 concentration than in shoots grown and measured ured at ambient CO2 concentration, regardless of treatment time or nitrogen-supply regime. High soil-nitrogen supply significantly increased photosynthetic capacity, corresponding to significant increases in V-cmax and J(max). However, the combined elevated CO2 + high nitrogen-supply treatment did not enhance the photosynthetic response above that observed in the elevated CO2 treatment alone.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, GROWTH, QUANTUM YIELD, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TERM

1133

Kellomaki, S., and K.Y. Wang. 1998. Daily and seasonal CO2 exchange in Scots pine grown under elevated O-3 and CO2: experiment and simulation. *Plant Ecology 136(2):229-248.*

Starting in early spring of 1994, naturally regenerated, 30- year-old Scots pine (Pinus sylvestris L.) trees were grown in open-top chambers and exposed in situ to doubled ambient O-3, doubled ambient CO2 and a combination of O-3 and CO2 from 15 April to 15 September. To investigate daily and seasonal responses of CO2 exchange to elevated O-3 and CO2, the CO2 exchange of shoots was measured continuously by an automatic system for measuring gas exchange during the course of one year (from 1 Januray to 31 December 1996). A process-based model of shoot photosynthesis was constructed to quantify modifications in the intrinsic capacity of photosynthesis and stomatal conductance by simulating the daily CO2 exchange data from the field. Results showed that on most days of the year the model simulated well the daily course of shoot photosynthesis. Elevated O-3 significantly decreased photosynthetic capacity and stomatal conductance during the whole photosynthetic period. Elevated O-3 also led to a delay in onset of photosynthetic recovery in early spring and an increase in the sensitivity of photosynthesis to environmental stress conditions. The combination of elevated O-3 and CO2 had an effect on photosynthesis and stomatal conductance similar to that of elevated O-3 alone, but significantly reduced the O-3 induced depression of photosynthesis. Elevated CO2 significantly increased the photosynthetic capacity of Scots pine during the main growing season but slightly decreased it in early spring and late autumn. The model calculation showed that, compared to the control treatment, elevated O-3 alone and the combination of elevated O-3 and CO2 decreased the annual total of net photosynthesis per unit leaf area by 55% and 38%, respectively. Elevated CO2 increased the annual total of net photosynthesis by 13%.

KEYWORDS: 4-YEAR EXPOSURE, ABIES L KARST, AIR-POLLUTANTS, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, MIDDAY STOMATAL CLOSURE, NET PHOTOSYNTHESIS, OZONE POLLUTION, PHOTOSYNTHETIC RESPONSES, SOLAR RADIATION

1134

Kellomaki, S., and K.Y. Wang. 1998. Growth, respiration and nitrogen content in needles of Scots pine exposed to elevated ozone and carbon dioxide in the field. *Environmental Pollution 101(2):263-274.*

Single Scots pine (Pinus sylvestris L.) trees, aged 30 years, were grown in open-top chambers and exposed to two atmospheric concentrations of ozone (O-3; ambient and elevation) and carbon dioxide (CO2) as single variables or in combination for 3 years (1994-96). Needle growth, respiration and nitrogen content were measured simultaneously over the period of needle expansion. Compared to ambient treatment (33 nmol mol(-1) O-3 and 350 mu mol mol(-1) CO2) doubled ambient O-3 (69 nmol mol(-1)) significantly reduced the specific growth rates (SGRs) of the needles in the early stage of needle expansion and needle nitrogen concentration (N-1) in the late stage, but increased apparent respiration rates (ARRs) in the late stage. Doubled ambient CO2 (about 650 mu mol mol(-1)) significantly increased maximum SGR but reduced ARR and N-1 in the late stage of needle expansion. The changes in ARR induced by the different treatments may be associated with treatment-induced changes in needle growth, metabolic activities and turnover of nitrogenous compounds. When ARR was partitioned into its two functional components, growth and maintenance respiration, the results

showed that neither doubled ambient O-3 nor doubled ambient CO2 influenced the growth respiration coefficients (R-g). However, doubled ambient O-3 significantly increased the maintenance respiration coefficients (R-m) regardless of the needle development stage, while doubled ambient CO2 significantly reduced R-m only in the late stage of needle expansion. The increase in R-m under doubled ambient O-3 conditions appeared to be related to an increase in metabolic activities, whereas the decrease in R-m under doubled ambient CO2 conditions may be attributed to the reduced N-1 and turnover rate of nitrogenous compounds per unit. The combination of elevated O-3 and CO2 had very similar effects on growth, respiration and N-1 to doubled ambient O-3 alone, but the interactive mechanism of the two gases is still not clear.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, GAS-EXCHANGE, L KARST, MAINTENANCE RESPIRATION, NONSTRUCTURAL CARBOHYDRATE CONTENT, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PICEA-ABIES L, PLANT RESPIRATION

1135

Kellomaki, S., and K.Y. Wang. 1998. Sap flow in Scots pines growing under conditions of year-round carbon dioxide enrichment and temperature elevation. *Plant, Cell and Environment 21(10):969-981.*

Starting in 1996, individual trees of Scots pine (Pinus sylvestris L.) aged 30 years were grown in closed-top chambers and exposed to normal ambient conditions (CON), elevated CO2 (Elev. C), elevated temperature (Elev. T) and a combination of elevated CO2 and temperature (Elev. C + T). Using the constant- power heat balance method, sap flow was monitored simultaneously in a total of 16 trees, four for each treatment, over a 32 d period (after the completion of needle expansion and branch elongation in 1997). An overall variation in diurnal sap flow totals (F-t) was evident during the period of measurement (days 167-198, 1997) regardless of the treatments, with a range from 0.15 to 2.82 kg tree(-1) d(-1). Elev. C reduced F-t by 4.1-13.7% compared with CON on most days (P varies from 0.042 to 0.108), but slightly increased it on some days (P greater than or equal to 0.131), depending on the weather conditions. Although the decrease in F-t caused by Elev. C was statistically significant on only a few days (P < 0.042), the cumulative F-t, for the 32 d decreased by 14.4% (P = 0.047), indicating that Elev. C may have an important influence on seasonal water use of the Scots pine. Analysis of the diurnal courses of sap flow combined with corresponding weather factors indicated that the CO2-induced decrease in F-t could be largely attributed to an increase in stomatal sensitivity to vapour pressure deficit (VPD), whereas the CO2- induced increase in F-t related to an increase in stomatal sensitivity to low light levels. Elev. T increased F-t by 11.2- 35.6% throughout the measuring period and the cumulative F-t for the 32 d by 32.5% (P = 0.019), which could be largely attributed to the temperature-induced increase in current-year needle area and decrease in stomatal sensitivity to high levels of VPD. There were no significant interactive effects of CO2 and temperature on sap flow, so that Elev. C + T had approximately the same F-t as Elev. T and similar diurnal patterns of sap flow, suggesting that the temperature factor played a dominant role in the case of Elev. C + T.

KEYWORDS: 4-YEAR EXPOSURE, ATMOSPHERIC CO2, CLIMATE CHANGE, CO2- ENRICHMENT, GROWTH, PHOTOSYNTHETIC RESPONSES, SOIL MOISTURE, STOMATAL CONDUCTANCE, TRANSPIRATION RESPONSES, WATER-USE EFFICIENCY

1136

Kellomaki, S., and K.Y. Wang. 1999. Short-term environmental controls of heat and water vapour fluxes above a boreal coniferous forest: model computations compared with measurements by eddy correlation. *Ecological Modelling 124(2-3):145-173.*

Eddy correlation and stern how measurements were coupled with detailed microclimate and soil measurements made in a boreal Scots pine forest in the late growing season of 1998 to determine sensible and latent heat fluxes from the soil and the canopy separately. A 'resistance/energy' model is constructed and parametrized in order to reproduce the dynamics of water and heat exchange between the soil, the canopy and the atmosphere as a part of a larger forest ecosystem model (FinnFor; Kellomaki and Vaisanen, 1997). Unique features of the present model are that (1) energy flux equations are expressed in terms of conceptual resistances and their solutions are obtained by closing two surface energy budget equations defined separately for canopy and soil surface; (2) the forest canopy is divided into shaded and sunlit fractions in the radiation transfer submodel and the canopy resistance submodels; (3) a numerical integrating solutions are derived separately for net radiation absorption in the canopy, bulk canopy resistance and the bulk aerodynamic resistances of the forest; and (4) iterative determinations of canopy water potential based on a classical one-dimensional water how model enable the model to represent explicitly the interaction between the above-ground and the below-ground water dynamics. The model is validated against 19-day flux measurements. In general, the total system sensible heat flux (H), total system latent heat flux (lambda E), canopy latent heat flux (lambda E-c), and soil surface heat flux (G(s)) computed by the model matched well with the measured data. Based on 1/2 h flux measurements, daily lambda E varied from 0.50-7.38 MW m(-2), H from 0.64-8.3 MW m(-2): and lambda E-c from 0.30-6.93 MW m(-2). The Bowen ratio (H/lambda E) ranged from -4.5 to 9.8, but 82% of the values for the Bowen ratio were within 0.5-2.5. The model computations showed that daily lambda E-c and H-c accounted for 21-64% and 43-66% of the daily total system flux, respectively. Daily soil latent heat (lambda E,) and soil sensible heat (H-s) fluxes accounted for 0.02-4.5% and 0.05-7.6%, respectively, and the daily energy storage within the canopy (S-c) and G(s) accounted for 0.1-7.2% and 0.8-5.6%, respectively. Plotting of 1/2 h flux data against a single environmental factor indicated that a 68% change in lambda E-c and a 72% change in H-c can be explained by a change in canopy radiation absorption (R-nc) at the 5% probability level. The high correlation between the canopy fluxes and R-nc could be related to the moderate weather conditions and high soil water content during the selected days, whereas lambda E- s, H-s, S-c and G(s) give no significant correlation with R-n. As expected. lambda E-c was strongly dependent on canopy resistance (r(cs)), but less impact on aerodynamic resistances during most of the measuring time. The proportion of energy partitioning in H and lambda E exhibited a clear diurnal trend and was mainly controlled by the system total resistance and the vapour pressure deficit, but less related to changes in soil water content.

KEYWORDS: 4-YEAR EXPOSURE, DOUGLAS-FIR, ELEVATED CO2, ENERGY- TRANSPORT, PINUS-PINASTER AIT, SAP FLOW, SCOTS PINE, SPARSE CROPS, STOMATAL CONDUCTANCE, SURFACE-TEMPERATURE

1137

Kelly, D.W., P.R. Hicklenton, and E.G. Reekie. 1991. Photosynthetic response of geranium to elevated co2 as affected by leaf age and time of co2 exposure. *Canadian Journal of Botany-Revue Canadienne De Botanique 69(11):2482-2488.*

Geranium plants were grown from seed in chambers maintained at 350 or 1000-mu-L.L-1 CO2. Photopsynthesis as affected by leaf age and by leaf position was determined. Elevated CO2 enhanced photosynthesis to the greatest extent in middle-aged leaves; very young leaves exhibited little enhancement, and net photosynthesis in the oldest leaves was depressed by elevated CO2. Temporary increases in net photosynthesis (relative to leaves developed at high CO2) resulted when young leaves grown at 350-mu-L.L-1 CO2 were switched to 1000-mu-L.L-1 CO2.

Leaves switched later in development exhibited permanent enhancement. Middle-aged leaves exhibited a temporary depression followed by permanent enhancement. Leaves developed at high CO2 and switched to low CO2 did not exhibit any photosynthetic depression relative to plants grown continuously at low CO2. Similarly, leaves developed at low CO2 switched to high CO2 for various lengths of time, and returned to low CO2 showed no photosynthetic depression. Leaves developed at low CO2 and switched to high CO2 exhibited increases in specific leaf weight and leaf thickness. The increase in leaf thickness was proportional to length of time spent at high CO2. High CO2 depressed the rate at which stomata developed but did not affect final stomatal density. Results suggest that photosynthesis at low CO2 was limited by CO2 regardless of developmental environment, whereas photosynthesis at high CO2 was limited by the developmental characteristics of the leaf. Further, both biochemical and structural modifications appear to be involved in this response. Because of the very different responses of young versus old leaves, future studies should be careful to consider leaf age in assessing response to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXCHANGE, LEAVES, LONG-TERM EXPOSURE, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, SOYBEAN PHYSIOLOGY, STARCH

1138

Kemp, P.R., D.G. Waldecker, C.E. Owensby, J.F. Reynolds, and R.A. Virginia. 1994. Effects of elevated co2 and nitrogen-fertilization pretreatments on decomposition on tallgrass prairie leaf-litter. *Plant and Soil 165(1):115-127.*

Standing dead and green foliage litter was collected in early November 1990 from Andropogon gerardii (C-4), Sorghastrum nutans (C-4), and Poa pratensis (C-3) plants that were grown in large open-top chambers under ambient or twice ambient CO2 and with or without nitrogen fertilization (45 kg N ha(-1)). The litter was placed in mesh bags on the soil surface of pristine prairie adjacent to the growth treatment plots and allowed to decay under natural conditions. Litter bags were retrieved at fixed intervals and litter was analyzed for mass loss, carbon chemistry, and total Kjeldahl nitrogen and phosphorus. The results indicate that growth treatments had a relatively minor effect on the initial chemical composition of the litter and its subsequent rate of decay or chemical composition. This suggests that a large indirect effect of CO2 on surface litter decomposition in the tallgrass prairie would not occur by way of changes in chemistry of leaf litter However, there was a large difference in characteristics of leaf Litter decomposition among the species. Paa leaf fitter had a different initial chemistry and decayed more rapidly than C-4 grasses. We conclude that an indirect effect of CO2 on decomposition and nutrient cycling could occur if CO2 induces changes in the relative aboveground biomass of the prairie species.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO2, CHIHUAHUAN DESERT, DETRITUS, ECOSYSTEMS, LIGNIN CONTENT, PHOSPHORUS DYNAMICS, PINE NEEDLE LITTER, PLANTS, RESPONSES

1139

Kennedy, A.D. 1995. Antarctic terrestrial ecosystem response to global environmental-change. *Annual Review of Ecology and Systematics 26:683-704.*

Geographical isolation and climatic constraints are responsible for the low biodiversity and structural simplicity of the antarctic terrestrial ecosystem Under projected scenarios of global change, both limiting factors may be released. Alien species immigration is likely to be facilitated as modified ocean and atmospheric circulation introduce exotic water- and air-borne propagules from neighboring continents. Elevated temperature, UV radiation, CO2, and precipitation will combine additively and synergistically to favor new trajectories of community development. It can be predicted that existing patterns of colonization, recruitment, succession, phenology and mortality will be perturbed with concomitant effects for ecosystem function through changes in biomass, trophodynamics, nutrient cycling, and resource partitioning. Soil propagule banks will play an important role through founder effects. Uniquely in Antarctica, many of the short-term consequences of global change will depend on the ecophysiological relationships of cryptogamic plants. However, in the long term, climatic warming will favor an increase in phanerogamic biomass since these species are currently excluded by the low cumulative degree-days > 0 degrees C. It has been suggested that antarctic communities may be particularly vulnerable to global change: Their slow rate of development and restricted gene flow limit response to new conditions. However, vulnerability must be defined with respect to both the direction and rate of change and it is likely that some perturbations will enhance the complexity and productivity of the biota, with negative feedback to the global carbon cycle. The chapter concludes with a discussion of institutional issues surrounding this topic.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATIC CHANGE, COLD TOLERANCE, CONTINENTAL ANTARCTICA, CRYPTOPYGUS-ANTARCTICUS, ICE CORES, OZONE DEPLETION, PHOTOSYNTHETIC RESPONSE, TUSSOCK TUNDRA

1140

Kennedy, A.D. 1995. Simulated climate-change - are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations. *Global Change Biology 1(1):29-42.*

This paper considers the use of passive greenhouse apparatus in field experiments investigating the biological consequences of climate change. The litreature contains many accounts of such experiments claiming relevance of greenhouse treatment effects to global change scenarios. However, inadequacies in microclimate monitoring, together with incomplete understanding of greenhouse modes of action, cast doubt upon such claims. Here, treatment effects upon temperature (magnitude, range, variation, rates of change), moisture (humidity, precipitation, soil water content), light (intensity, spectral distribution), gas composition, snow cover, and wind speed are reviewed in the context of Intergovernmental Panel on Climate Change (IPCC) predictions. It is revealed that greenhouses modify each of these potentially limiting factors in a complex and interactive manner, but that the relationship between this modification and forecast conditions of climate change is poor. Interpretation of biological responses, and their extrapolation to predictive models, is thus unreliable. In order that future greenhouse experiments may overcome criticisms of artefact and lack of rigour, two amendments to methodology are proposed: (1) objective-orientated design of greenhouse apparatus (2) multiple controls addressing individual environmental factors. The importance of a priori testing of microclimate treatment effects is stressed.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, CO2, ERIOPHORUM VAGINATUM, GROWTH, PLANTS, RESPONSES, SENSITIVITY, TEMPERATURE, ULTRAVIOLET-RADIATION, VEGETATION

1141

Kennedy, A.D. 1995. Temperature effects of passive greenhouse apparatus in high- latitude climate-change experiments. *Functional Ecology 9(2):340-350.*

1. Passive greenhouse apparatus is commonly used to investigate the in situ biological response of terrestrial communities to global warming. 2. Although close conformity of greenhouse treatment effects to general circulation model (GCM) scenarios is widely claimed, no proof of such

a relationship has yet been published. 3. Here, the relationship between passive greenhouse thermal environment and future climate conditions is considered using temperature data collected from within and without greenhouses deployed in the maritime Antarctic. It is revealed that in terms of thermal extremes, diel and annual variation, and overall distribution across the temperature spectrum, such apparatus achieves only poor simulation of GCM forecasts. 4. During summer, greenhouses induce an amplified daily range of temperatures, elevated maxima and accelerated rates of change. 5. During spring and autumn, diel temperature variation continues inside the greenhouses while snow cover protects the controls. 6. During winter, an inverse treatment effect occurs, in which the relative depth of snow cover causes lower temperatures in greenhouses than in controls. 7. These treatment effects differ significantly from GCM climate predictions. Changes recorded in the composition, structure and function of greenhouse biota may thus be artefacts of the methodology. 8. Thorough a priori testing of greenhouse treatment effects is recommended for future climate change studies that are to be conducted in environments subject to seasonal snowfall, solar elevation and day length.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, COLD TOLERANCE, DESIGN, ECOSYSTEMS, ELEVATED CO2, ERIOPHORUM VAGINATUM, GROWTH, HABITATS, POLAR, RESPONSES

1142

Kerbel, E.L., A.A. Kader, and R.J. Romani. 1990. Respiratory and glycolytic response of suspension-cultured passe-crassane pear fruit cells to elevated CO2 concentrations. *Journal of the American Society for Horticultural Science 115(1):111-114.*

1143

Kerslake, J.E., S.J. Woodin, and S.E. Hartley. 1998. Effects of carbon dioxide and nitrogen enrichment on a plant- insect interaction: the quality of Calluna vulgaris as a host for Operophtera brumata. *New Phytologist 140(1):43-53.*

Calluna vulgaris L. (Hull) is not one of the usual hosts of the winter moth, Operophtera brumata L., but outbreaks have caused extensive damage to heather moorland in Scotland in recent years. This study investigated the potential role of environmental change in such outbreaks by rearing O. brumata larvae on C. vulgaris plants grown in open-top chambers for 20 months with enriched CO2 (600 ppm) and nitrogen supply (average 52.5 kg N ha(-1) yr(-1)) in factorial combination. This prolonged exposure to elevated CO2 caused no change in shoot growth, photosynthesis or foliar C:N ratio of C, vulgaris, even with increased N supply, indicating that the absence of response was not due to N limitation. Increased N supply itself resulted in increased shoot growth and a decrease in tissue C:N ratio. Phenolic content did not change in response to either CO2 or N enrichment, contrary to the predictions of the carbon/nutrient balance hypothesis. In line with the absence of plant response, there was no effect of CO2 on the development of Operophtera brumata on C, vulgaris, and so continued increase in atmospheric CO2 concentration is unlikely to affect directly O. brumata outbreaks on heather moorland. Operophtera brumata showed increased larval development, growth rate and pupal weight on N-treated plants, correlated both to the decrease in foliar C:N ratio, and to the increase in shoot extension which was predictive of survivorship. Thus, increased atmospheric N deposition, or increased rates of mineralization in a warmer environment, might increase the severity of O. brumata outbreaks on C. vulgaris. Since the combination of high N availability and disturbance of heather canopy by herbivory is known to result in increased dominance of grasses, it is suggested that this could lead to further degradation of moorland in upland Britain.

KEYWORDS: AVAILABILITY, DECIDUOUS TREES, ELEVATED ATMOSPHERIC CO2, GROWTH, HEATHER MOORLAND, HERBIVORE INTERACTIONS, L HULL, LARVAL EMERGENCE, NUTRIENT BALANCE HYPOTHESIS, SOIL NUTRIENT

1144

Kerstiens, G. 1995. Cuticular water permeance of european trees and shrubs grown in polluted and unpolluted atmospheres, and its relation to stomatal response to humidity in beech (fagus-sylvatica L). *New Phytologist 129(3):495-503.*

Cuticular water permeance (P) of astomatous adaxial surfaces of intact leaves was determined in Acer pseudoplatanus L., Betula pubescens Ehrh., Corylus avellana L., Fagus sylvatica L. and Prunus avium L. Water evaporating from the stomata-bearing abaxial leaf surface could not reach the moisture analyzer and the values of P presented here are therefore free from errors that often arise from unintentional inclusion of residual stomatal transpiration. Plants were exposed from before bud-break for several months to 20-50 ppb SO2 (Fagus), a combination of 50-60 ppb SO2 and 50-60 ppb NO2 (Betula), 300- 400 ppb NO (Acer, Corylus, Fagus), regular ozone episodes of up to 120 ppb (Fagus, Prunus), or an elevated level of CO2 (600 ppm for 2 yr; Acer, Fagus). Permeances were in the range 0.6- 2.9 x 10(-5) m s-1 and were unaffected by most treatments. In Prunus, P increased slightly but significantly in the NO treatment. In Corylus and Fagus, P was sometimes found to be reduced by fumigation with NO, but not always. Betula leaves grown under elevated SO2 and NO2 showed higher values of P only if they were visibly damaged. Minimum conductances (g(min) estimated from water loss rates of both sides of detached hypostomatous leaves were higher than P, and were more strongly affected by treatments. In these cases, the most probable explanation is some damage to stomatal function resulting in a reduced ability to close after leaf excision. Effects of growing conditions and time of year on P were found, which allowed a hypothetical interaction between P and stomatal sensitivity to air humidity to be tested in beech. No unambiguous indication of such a relationship was found.

KEYWORDS: AIR-POLLUTION, CARBON DIOXIDE, FUMIGATION, LEAVES, OZONE, PERMEABILITY, PLANT CUTICLES, STRESS, SYSTEM, TRANSPIRATION

1145

Kerstiens, G. 1997. Why is increasing shade-tolerance of trees correlated with increasing stimulation of growth by elevated CO2? *Plant Physiology 114(3):371.*

1146

Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO2 in trees. *Physiologia Plantarum 102(3):472-480.*

Evidence from 10 studies comparing angiosperm trees and 5 studies comparing conifers or differing shade-tolerance was analysed. The number of intraphyletic comparisons in which the more shade-tolerant species showed the greater relative increase of biomass in elevated CO2 was significantly higher than would be expected by chance alone. It is suggested that more shade-tolerant species are inherently better disposed. in terms of plant architecture and partitioning of biomass and nitrogen, to utilise resources (light, water, nutrients) that are potentially limiting in elevated CO2 and that these traitu are responsible for the interaction between shade-tolerance and CO2 concentration. Compared with less shade-tolerant angiosperm trees, more shade-tolerant angiosperm species generally have a lower lear area ratio in ambient CO2 and show a smaller relative reduction in elevated CO2. Furthermore, leaf nitrogen content is usually lower in more shads-tolerant angiosperm species and tends to be more strongly reduced by

elevated CO2 in those species. Within angiosperm trees, more shade-tolerant species showed a stronger stimulation of net leaf photosynthetic I ate in most experiments, but this trend was not significant.

KEYWORDS: ATMOSPHERIC CO2, C-3 PHOTOSYNTHETIC SYSTEM, CARBON-DIOXIDE ENRICHMENT, FAGUS-SYLVATICA L, GROWTH-RESPONSES, LEAF GAS- EXCHANGE, LOW-LIGHT, NITROGEN-AVAILABILITY, RAIN-FOREST TREES, SUCCESSIONAL STATUS

1147

Kerstiens, G., and C.V. Hawes. 1994. Response of growth and carbon allocation to elevated co2 in young cherry (prunus-avium L) saplings in relation to root environment. *New Phytologist 128(4):607-614.*

The hypothesis that inadequate rooting volume may reduce the growth stimulation by elevated CO2 in potted tree seedlings and saplings was tested experimentally and by surveying the literature. One-year-old cherry saplings were grown for one season in naturally lit growth chambers in eight combinations of CO2 concentration (ambient; ambient + 250 ppm) and root environment (four types). The latter included (1) moderately restrictive pot volume (4 l) in combination with two levels of fertilizer addition (1a, 1b); (2) 10 l pots with total fertilizer content per pot as in treatment 1a, and (3) 20 l pots with five plants sharing five times the space and nutrient resources of treatment 1a. Plants were harvested in April, May, June, August and September. The overall mean effect of high CO2 plant dry mass by the end of the season was +24%. Interactive effects of root environments and CO2 concentrations on dry mass were not significant at the 5% level, but repeated measurements of basal stem diameter of individual plants indicated a significant impact of root environment on the response to CO2. Overall growth enhancement by elevated CO2 did not differ significantly between harvests, but it tended to increase during the season in those root environments which restricted growth in ambient CO2 most strongly (1a and 3). The hypothesis was rejected for this experiment. Leaf area and stem height were not affected by any treatment. The variation of carbon allocation to roots and shoots with plant size was very similar in all treatments. Plants grew faster in elevated CO2 very early in the season, and this resulted in small but significant differences between seasonal patterns of biomass partitioning in ambient and elevated CO2. A survey of 33 studies on growth responses of 47 tree species to elevated CO2 (600-800 ppm) showed that the relative change in biomass was not related to the ratio of plant biomass and pot volume found in either ambient or elevated CO2. We conclude that there is no evidence that inadequate pot volume had a negative impact on the stimulation of growth of tree species in elevated CO2.

KEYWORDS: DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS

1148

Kerstiens, G., J. Townend, J. Heath, and T.A. Mansfield. 1995. Effects of water and nutrient availability on physiological- responses of woody species to elevated co2. *Forestry 68(4):303-315.*

The growth responses to elevated CO2 found in experiments are highly variable and depend on other experimental parameters such as irrigation, fertilization, light regime, etc. As yet, the strength or even the sign of most interactions is all but impossible to predict from first principles. Experiments in ambient and CO2-enriched ambient air (+250 p.p.m.) have been conducted in specially adapted greenhouses (Solardomes) at Lancaster University for the past four seasons on Sitka spruce (Picea sitchensis (Bong.) Carr.), wild cherry (Prunus avium L.), beech (Fagus sylvatica L.) and pedunculate oak (Quercus robur L.). These experiments are reviewed together with other published studies on interactive effects of elevated CO2 and water and nutrient supply on physiological processes, in particular gas exchange, in tree species. It is often assumed that drought tolerance will increase in elevated CO2 because of a suppression of stomatal conductance and an increase in instantaneous water use efficiency. There is, however, some evidence that such effects could be more than offset in beech by CO2-induced increases in leaf area. It is tentatively suggested that in beech, drought tolerance could already have been reduced by the increase in atmospheric CO2 over the last century.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR-STYRACIFLUA, LOBLOLLY-PINE SEEDLINGS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, TAEDA SEEDLINGS

1149

Keutgen, N., K. Chen, and F. Lenz. 1997. Responses of strawberry leaf photosynthesis, chlorophyll fluorescence and macronutrient contents to elevated CO2. *Journal of Plant Physiology 150(4):395-400.*

Gas exchange, chlorophyll fluorescence parameters, and macronutrient contents were investigated in young (< 3 weeks), medium (4 - 6 weeks) and old (7 - 9 weeks) strawberry leaves growing at 300, 450, 600, 750, and 300 ppm CO2. An increase of the CO2 level to 600 ppm promoted leaf net photosynthesis, but a further rise led to a decrease of net CO2 assimilation. The reduction of net photosynthetic rate was less distinct in young leaves exposed to CO2 levels above 600 ppm for less than 3 weeks, indicating that the reduction might depend on the period of exposition or leaf age. Transpiration and stomatal conductance were significantly affected by leaf age, but not by CO2 concentrations. Medium leaves were characterised by a higher transpiration rate and stomatal conductance than young and old ones. In leaves growing at high CO2 levels Chl a and b contents as well as the a/b ratio decreased. The contents of N, P, K, Ca and Mg were lower in leaves growing at high CO2 concentrations than in those at low ones. An elevated CO2 level above 750 ppm led to a general macronutrient deficiency and was accompanied by a distinct decrease of optimal quantum yield, due to a rise of basal fluorescence, and an increase of non- photochemical energy dissipation in old leaves.

KEYWORDS: BIOCHEMISTRY, GAS-EXCHANGE, GROWTH, LEAVES, STEADY-STATE PHOTOSYNTHESIS, TOMATO PLANTS

1150

KhavariNejad, R.A. 1996. Growth of tomato plants under carbon dioxide enrichment. *Photosynthetica 32(3):471-474.*

Under short-term CO2 enrichment (1200 cm(3) m(-3)) Of 4-weeks old tomato plants (Lycopersicon esculentum Mill., Eurocross BB, F-1-hybrid) net assimilation rate increased by about 58 %, leaf area increased slightly, fresh matters were not much influenced, but dry matters (except for roots) increased. Stomatal opening in tomato plants was enhanced under CO2 enrichment and the enhancement decreased with time.

KEYWORDS: CO2-ENRICHED ATMOSPHERES

1151

Kickert, R.N., G. Tonella, A. Simonov, and S.V. Krupa. 1999. Predictive modeling of effects under global change. *Environmental Pollution 100(1-3):87-132.*

The status of computer simulation models from around the world for evaluating the possible ecological, environmental, and societal consequences of global change is presented in this paper. In addition, a

brief synopsis of the state of the science of these impacts is included. Issues considered include future changes in climate and patterns of land use for societal needs, Models dis cussed relate to vegetation (e.g, crop), soil, bio-geochemistry, water, and wildlife responses to conventional, forecasted changes in temperature and precipitation. Also described are models of these responses, alone and interactively, to increased CO2, other air pollutants and UV-B radiation, as the state of the science allows. Further, models of land-use change are included. Additionally, global multiple sector models of environment, natural resources, human population dynamics, economics, energy, and political relations are reviewed for integrated impact assessment. To the extent available, information on computer software and hardware requirements is presented for the various models. The paper concludes with comments about using these technologies as they relate to ecological risk assessment for policy decision analysis. Such an effort is hampered by considerable uncertainties with the output of existing models, because of the uncertainties associated with input data and the definitions of their dose-response relationships. The concluding suggestions point the direction for new developments in modeling and analyses that are needed for the 21st century.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOSPHERE-MODEL, CLIMATE-CHANGE SCENARIOS, ELEVATED CO2, FOREST ECOSYSTEM PROCESSES, GENERIC PLANT SIMULATOR, LAND-USE CHANGE, OF-THE- ART, ORGANIC-MATTER DYNAMICS, SOLLING SPRUCE SITE

1152

Kicklighter, D.W., M. Bruno, S. Donges, G. Esser, M. Heimann, J. Helfrich, F. Ift, F. Joos, J. Kaduk, G.H. Kohlmaier, A.D. McGuire, J.M. Melillo, R. Meyer, B. Moore, A. Nadler, I.C. Prentice, W. Sauf, A.L. Schloss, S. Sitch, U. Wittenberg, and G. Wurth. 1999. A first-order analysis of the potential role of CO2 fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus Series B-Chemical and Physical Meteorology 51(2):343-366.*

We compared the simulated responses of net primary production, heterotrophic respiration, net ecosystem production and carbon storage in natural terrestrial ecosystems to historical (1765 to 1990) and projected (1990 to 2300) changes of atmospheric CO2 concentration of four terrestrial biosphere models: the Bern model, the Frankfurt Biosphere Model (FBM), the High- Resolution Biosphere Model (HRBM) and the Terrestrial Ecosystem Model (TEM). The results of the model intercomparison suggest that CO2 fertilization of natural terrestrial vegetation has the potential to account for a large fraction of the so-called "missing carbon sink" of 2.0 Pg C in 1990. Estimates of this potential are reduced when the models incorporate the concept that CO2 fertilization can be limited by nutrient availability. Although the model estimates differ on the potential size (126 to 461 Pg C) of the future terrestrial sink caused by CO2 fertilization, the results of the four models suggest that natural terrestrial ecosystems will have a limited capacity to act as a sink of atmospheric CO2 in the future as a result of physiological constraints and nutrient constraints on NPP. All the spatially explicit models estimate a carbon sink in both tropical and northern temperate regions, but the strength of these sinks varies over time. Differences in the simulated response of terrestrial ecosystems to CO2 fertilization among the models in this intercomparison study reflect the fact that the models have highlighted different aspects of the effect of CO2 fertilization on carbon dynamics of natural terrestrial ecosystems including feedback mechanisms. As interactions with nitrogen fertilization, climate change and forest regrowth may play an important role in simulating the response of terrestrial ecosystems to CO2 fertilization, these factors should be included in future analyses. Improvements in spatially explicit data sets, whole-ecosystem experiments and the availability of net carbon exchange measurements across the globe will also help to improve future evaluations of the role of CO2 fertilization on terrestrial carbon storage.

KEYWORDS: ATMOSPHERIC CARBON, CLIMATE CHANGE, DIOXIDE ENRICHMENT, EDDY-COVARIANCE, LAND-USE CHANGE, NET PRIMARY PRODUCTION, NITROGEN DEPOSITION, RAIN-FOREST, TROPICAL DEFORESTATION, WATER-VAPOR

1153

Kim, H.Y., T. Horie, H. Nakagawa, and K. Wada. 1996. Effects of elevated CO2 concentration and high temperature on growth and yield of rice. *Japanese Journal of Crop Science 65(4):634-643.*

Phenological development, biomass production and the related growth characteristics of rice (cv Akihikari) in canopy were measured over the entire growth period under different CO2 concentrations and air temperature regimes in temperature gradient chambers (TGCs), in order to clarify the effects of anticipated global climate change on rice production. The TGC is a plastic tunnel with the dimensions of 26m in length, 2. 05m in width and 1.7m in height in which air was ventilated at varying rates to created a 4 degrees C temperature gradient along its longitudinal axis. Two TGCs were used for this experiment;one was kept at ambient CO2 (congruent to 350 mu LL(-1)) concentration and the other at 690 mu LL(-1) throughout the entire growth period. CO2 x temperature treatmets were applied to potted rice plants displaced in TGC at the density of 20 hills m(-2) in 1991, and on transplanted plants on soil bed in TGC at 25 hills m(-2) in 1992. In both years, a sufficient amount of nutrition was applied in split. The nearly doubled CO2 concentration (690 mu LL(-1)) accelerated phenological development of rice toward heading with more pronounced effects at higher temperatures. The number of days to heading of elevated CO2 plants at 30 degrees C was 11% less than that of ambient CO2 plants. The elevated CO2 concentration remarkably promoted both total and productive tiller numbers, whereas it gave a negligibly small effect on plant height. Also, the elevated CO2 concentration gave minor effects on leaf area index except at the initial growth stage, coinciding with the previous workers' results. The elevated CO2 concentration markedly promoted crop dry matter production, on which temperature appeared to give negligibly small effects. The relative enhancement rate by the doubled CO2 on crop dry weight at maturity was estimated to be 24% as average over the entire temperature range (26 similar to 30 degrees C) in both years. The insensitive temperature response in the enhancement rate was contrary to previous workers' results. This is considered to be due to previous workers' results being based on largely isolated plants where radiation might less limit the growth than in the present experiment in the canopy condition.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ORYZA-SATIVA

1154

Kim, H.Y., T. Horie, H. Nakagawa, and K. Wada. 1996. Effects of elevated CO2 concentration and high temperature on growth and yield of rice .2. The effect on yield and its components of Ahihikari rice. *Japanese Journal of Crop Science 65(4):644-651.*

Yield and its component organs of rice (cv. Akihikari) were examined for populations grown under two different CO2 concentrations (350 and 690 mu LL(-1)) x four temperature regimes in temperature gradient chambers (TGCs) in two cropping seasons of 1991 and 1992. The temperature treatments ranged 27.2 similar to 31.1 degrees C in 1991 and 26.0 similar to 29.3 degrees C in 1992 on average over the entire growth period. The relative yield increases by nearly doubling the CO2 concentration under the lowest temperature conditions were 40% and 22% in 1991 and 1992, respectively. These yield increases were mainly attributable to the increased spikelet number per unit area by elevated CO2, whereas the CO2 effects on ripening percentage and weight of single grain mass were relatively small. The difference in the CO2

enhancement rate in the spikelet number and hence in the yield between the two years was considered to reflect the difference in the nitrogen (N) application rate, as total amounts of N applied were 24 g m(-2) in 1991 and 12 g m(-2) in 1992. With the increase in temperature, yields at ambient and elevated CO2 concentrations decreased drastically with a more pronounced reduction with elevated CO2, resulting in no CO2 enrichment effect on rice yield at higher temperatures. The yield decline at higher temperatures was primarily due to an increase in the number of sterile spikelets and slightly due to the increase in imperfectly ripened grains. The spikelet sterility was most closely related to the daily maximum temperature averaged over the flowering period.

KEYWORDS: CARBON DIOXIDE, ORYZA-SATIVA

1155

Kimball, B.A., R.L. LaMorte, P.J. Pinter, G.W. Wall, D.J. Hunsaker, F.J. Adamsen, S.W. Leavitt, T.L. Thompson, A.D. Matthias, and T.J. Brooks. 1999. Free-air CO2 enrichment and soil nitrogen effects on energy balance and evapotranspiration of wheat. *Water Resources Research 35(4):1179-1190.*

In order to determine the likely effects of the increasing atmospheric CO, concentration on future evapotranspiration, ET, plots of field-grown wheat were exposed to concentrations of 550 mu mol/mol CO2 (or 200 mu mol/mol above current ambient levels of about 360 mu mol/mol) using a free-air CO2 enrichment (FACE) facility. Data were collected for four growing seasons at ample water and fertilizer (high N) and for two seasons when soil nitrogen was limited (low N). Measurements were made of net radiation, R-n; soil heat flux; air and soil temperatures; canopy temperature, T-s; and wind speed. Sensible heat flux was calculated from the wind and temperature measurements. ET, that is, latent heat flux, was determined as a residual in the energy balance. The FACE treatment increased daytime T-s about 0.6 degrees and 1.1 degrees C at high and low N, respectively. Daily total R-n was reduced by 1.3% at both levels of N. Daily ET was consistently lower in the FACE plots, by about 6.7% and 19.5% for high and low N, respectively.

KEYWORDS: 1989 FACE EXPERIMENT, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, COTTON, DOWNWIND EVOLUTION, LOCAL ADVECTION, RADIATIVE SURFACE-TEMPERATURE, SAP FLOW, SCALAR FLUXES, WATER-USE

1156

Kimball, B.A., R.L. Lamorte, R.S. Seay, P.J. Pinter, R.R. Rokey, D.J. Hunsaker, W.A. Dugas, M.L. Heuer, J.R. Mauney, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effects of free-air co2 enrichment on energy-balance and evapotranspiration of cotton. *Agricultural and Forest Meteorology 70(1-4):259-278.*

The effects of free-air CO2 enrichment (FACE) at 550 mumol mol- 1 on the energy balance and evapotranspiration, ET, of cotton (Gossypium hirsutum L.) were investigated. Latent heat flux, lambdaET, was calculated as the residual in an energy balance approach from determinations of net radiation, R(n), minus surface soil heat flux, G0, minus sensible heat flux, H. R(n) was directly measured. G0 was determined from measurements with soil heat flux plates at 10 mm depth, corrected for temperature changes in the soil above. H was determined from measurements of air temperature with aspirated psychrometers, of foliage temperature with IR thermometers, and of wind speed with cup anemometers. Under ambient CO2 (control) conditions (about 370 mumol mol-1), the lambdaET from the energy balance approach agreed fairly well with values from several other methods, including the Bowen ratio method, lending credence to the technique. However, the results had an uncertainty of the order of 20% associated with the R(n) measurements. Therefore, an apparent increase in ET of about 13% in the FACE plots was judged insignificant. The conclusion that any effects of CO2 enrichment to 550 mumol mol-1 on the ET of cotton were too small to be detected was consistent with the results of other investigators who determined ET in the same experiment using stem flow gauges and the soil water balance.

KEYWORDS: CARBON DIOXIDE, CROP YIELD, EVAPORATION, INCREASING ATMOSPHERIC CO2, LATENT-HEAT, RADIATIVE SURFACE-TEMPERATURE, WATER-USE, WHEAT CANOPY

1157

Kimball, B.A., and J.R. Mauney. 1993. Response of cotton to varying co2, irrigation, and nitrogen - yield and growth. *Agronomy Journal 85(3):706-712.*

The CO2 concentration of the atmosphere is increasing and is expected to double sometime near the middle of the next century. To determine the effects of such a CO2 increase on cotton (Gossypium hirsutum L.) growth and productivity, a series of experiments from 1983 through 1987 were conducted with open-top CO2-enriched field chambers at ample as well as limiting levels of water and N at Phoenix, AZ. Comparisons with open-field plots showed that there was a significant chamber effect, amounting to a 30% average increase in growth inside, but under dry conditions in 1985, the situation was reversed. No significant effects of CO2 on harvest index, root-shoot ratio, or lint percentage were found, so the primary effect of elevated CO2 was to produce plants that were larger. Comparing the results of 500 and 650 mumol mol-1 CO2 treatments, the increments of growth from ambient (about 350 mumol mol-1) to 500 mumol mol-1 were not significantly different from increments from 500 to 650 mumol mol-1. No statistically significant interactions were detected between CO2 level and either irrigation or nitrogen level, even when these variables were sufficiently low enough to limit growth. However, under well-maintained water stress conditions, the growth response to CO2 tended to be somewhat larger than under normal irrigation levels. Averaging over all the data available from these experiments, seed cotton yield (lint plus seed) and above- ground biomass were increased by 60 and 63%, respectively, by CO2 enrichment to 650 mumol mol-1.

KEYWORDS: CARBON DIOXIDE, CHAMBERS, ELEVATED LEVELS, ENRICHMENT, FIELD, PLANT GROWTH, POPULATIONS, SOIL, STRESS, WATER-USE

1158

Kimball, B.A., J.R. Mauney, F.S. Nakayama, and S.B. Idso. 1993. Effects of elevated co2 and climate variables on plants. *Journal of Soil and Water Conservation 48(1):9-14.*

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TEMPERATURE, YIELD

1159

Kimball, B.A., J.R. Mauney, F.S. Nakayama, and S.B. Idso. 1993. Effects of increasing atmospheric co2 on vegetation. *Vegetatio 104:65-75.*

The increasing atmospheric CO2 concentration probably will have significant direct effects on vegetation whether predicted changes in climate occur or not. Averaging over many prior greenhouse and growth chamber studies, plant growth and yield have typically increased more than 30%, with a doubling of CO2 concentration. Such a doubling also causes stomatal conductance to decrease about 37 which typically increases leaf temperatures more than 1-degrees-C, and which may decrease evapotranspiration, although increases in leaf area counteract the latter effect. Interactions between CO2 and climate variables also appear important. In one study the growth increase from near-doubled

CO2 ranged from minus 60% at 12- degrees-C to 0% at 19-degrees-C to plus 130% at 34-degrees-C, suggesting that if the climate warms, the average growth response to doubled CO2 could be consistently higher than the 30% mentioned above. Even when growing in nutrient-poor soil, the growth response to elevated CO2 has been large, in contrast to nutrient solution studies which showed little response. Several studies have suggested that under water-stress, the CO2 growth stimulation is as large or larger than under wellwatered conditions. Therefore, the direct CO2 effect will compensate somewhat, if not completely, for a hotter drier climate. And if any climate change is small, then plant growth and crop yields will probably be significantly higher in the future high-CO2 world.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TEMPERATURE, YIELD

1160

Kimball, B.A., P.J. Pinter, R.L. Garcia, R.L. LaMorte, G.W. Wall, D.J. Hunsaker, G. Wechsung, F. Wechsung, and T. Kartschall. 1995. Productivity and water use of wheat under free-air CO2 enrichment. *Global Change Biology 1(6):429-442.*

A free-air CO2 enrichment (FACE) experiment was conducted at Maricopa, Arizona, on wheat from December 1992 through May 1993. The FACE apparatus maintained the CO2 concentration, [CO2], at 550 mu mol mol(-1) across four replicate 25-m- diameter circular plots under natural conditions in an open field. Four matching Control plots at ambient [CO2] (about 370 mu mol mol(-1)) were also installed in the field. In addition to the two levels of [CO2], there were ample (Wet) and limiting (Dry) levels of water supplied through a subsurface drip irrigation system in a strip, split-plot design. Measurements were made of net radiation, R(n); soil heat flux, G(o); soil temperature; foliage or surface temperature; air dry and wet bulb temperatures; and wind speed. Sensible heat flux, H, was calculated from the wind and temperature measurements. Latent heat nux, lambda ET, and evapotranspiration, ET, were determined as the residual in the energy balance. The FACE treatment reduced daily total R(n) by an average 4%. Daily FACE sensible heat flux, H, was higher in the FACE plots. Daily latent heat flux, lambda ET, and evapotranspiration, ET, were consistently lower in the FACE plots than in the Control plots for most of the growing season, about 8% on the average. Net canopy photosynthesis was stimulated by an average 19 and 44% in the Wet and Dry plots, respectively, by elevated [CO2] for most of the growing season. No significant acclimation or down regulation was observed. There was little above-ground growth response to elevated [CO2] early in the season when temperatures were cool. Then, as temperatures warmed into spring, the FACE plants grew about 20% more than the Control plants at ambient [CO2], as shown by above-ground biomass accumulation. Root biomass accumulation was also stimulated about 20%. In May the FACE plants matured and senesced about a week earlier than the Controls in the Wet plots. The FACE plants averaged 0.6 degrees C warmer than the Controls from February through April in the well-watered plots, and we speculate that this temperature rise contributed to the earlier maturity. Because of the acceleration of senescence, there was a shortening of the duration of grain filling, and consequently, there was a narrowing of the final biomass and yield differences. The 20% mid-season growth advantage of FACE shrunk to about an 8% yield advantage in the Wet plots, while the yield differences between FACE and Control remained at about 20% in the Dry plots.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COTTON, CROP YIELD, GROWTH, TEMPERATURE

1161

King, A.W., W.R. Emanuel, S.D. Wullschleger, and W.M. Post. 1995. In search of the missing carbon sink - a model of terrestrial biospheric response to land-use change and atmospheric co2. *Tellus Series B-Chemical and Physical Meteorology 47(4):501-519.*

Estimates of the net exchange of carbon between the terrestrial biosphere and the atmosphere may be too large because the models of carbon release from changes in land use do not allow for enhanced carbon assimilation by the terrestrial biosphere in response to increasing atmospheric CO2. We address this deficiency with a model of terrestrial biosphere that includes both ecosystem response to land-use perturbation and vegetation response to atmospheric CO2. Model inputs specify the areas affected by land-use change since 1700. The carbon dynamics of the affected areas are described by an area distribution function for vegetation carbon density and a compartment model of carbon in vegetation, litter, and soil. Vegetation growth is modeled as the difference between net primary production (NPP) and mortality. NPP, the net flux of carbon from atmosphere to vegetation, is a logistic function of vegetation carbon density. The response of NPP to atmospheric CO2 is modeled with three response functions: a logarithmic, a rectangular- hyperbolic, and a response function derived from a biochemical model of C-3 photosynthesis. The response functions are parameterized by ecosystem type with data from CO2 exposure experiments. Elevated CO2 affects the NPP of both undisturbed and recovering ecosystems. We use the model to test the hypothesis that the CO2 enhancement of terrestrial NPP explains the historical missing carbon sink of the the global carbon cycle budget. Our estimates of the biosphere's CO2 enhanced carbon flux are much smaller than the reconstructed missing carbon sink. We conclude that our model results do not support the hypothesis.

KEYWORDS: CLIMATIC CHANGE, CYCLE, DEPOSITION, ECOSYSTEMS, GLOBAL CLIMATE, PLANTS, STORAGE, TROPICAL DEFORESTATION

1162

King, A.W., W.M. Post, and S.D. Wullschleger. 1997. The potential response of terrestrial carbon storage to changes in climate and atmospheric CO2. *Climatic Change 35(2):199-227.*

We use a georeferenced model of ecosystem carbon dynamics to explore the sensitivity of global terrestrial carbon storage to changes in atmospheric CO2 and climate. We model changes in ecosystem carbon density, but we do not model shifts in vegetation type. A model of annual NPP is coupled with a model of carbon allocation in vegetation and a model of decomposition and soil carbon dynamics. NPP is a function of climate and atmospheric CO2 concentration. The CO2 response is derived from a biochemical model of photosynthesis. With no change in climate, a doubling of atmospheric CO2 from 280 ppm to 560 ppm enhances equilibrium global NPP by 16.9%; equilibrium global terrestrial ecosystem carbon (TEC) increases by 14.9%. Simulations with no change in atmospheric CO2 concentration but changes in climate from five atmospheric general circulation models yield increases in global NPP of 10.0-14.8%. The changes in NPP are very nearly balanced by changes in decomposition, and the resulting changes in TEC range from an increase of 1.1% to a decrease of 1.1%. These results are similar to those from analyses using bioclimatic biome models that simulate shifts in ecosystem distribution but do not model changes in carbon density within vegetation types. With changes in both climate and a doubling of atmospheric CO2, our model generates increases in NPP of 30.2-36.5%. The increases in NPP and litter inputs to the soil more than compensate for any climate stimulation of decomposition and lead to increases in global TEC of 15.4-18.2%.

KEYWORDS: BIOSPHERE, CYCLE, MODEL, PHYSIOLOGY, SENSITIVITY, SIMULATION, SOIL, TEMPERATURE, TURNOVER, VEGETATION

1163

King, D.A. 1995. Equilibrium-analysis of a decomposition and yield model applied to pinus-radiata plantations on sites of contrasting fertility. *Ecological Modelling 83(3):349-358.*

Recent models of growth and nutrient cycling relate forest productivity to canopy photosynthesis, as influenced by the effect of nutrient cycling on foliar nitrogen concentration. A useful approach for analysing the impact of elevated CO2 or altered nitrogen inputs on production is to consider model solutions where recycling leaves, fine roots, litter and soil organic pools of intermediate turnover time are in equilibrium, while tree stems and recalcitrant humus are accumulating or releasing carbon and nitrogen. This equilibrium analysis, employed by the Generic Decomposition and Yield (G'DAY) model, was applied to Pinus radiata plantations growing on an infertile site in Australia and a fertile site in New Zealand. Predicted productivities and foliar nitrogen concentrations were substantially lower than observed for the young (12-year- old) stands, particularly for the fertile site. The model predictions were closer to values expected for older stands late in the commercial rotation cycle when reduced wood production rates reduce the net nitrogen requirements for growth. These results underscore the importance of the net release of nitrogen from soil organic matter early in the life of a stand and suggest that care should be taken in using equilibrium analyses to estimate the impacts of elevated [CO2] on forest production.

KEYWORDS: BIOMASS, FERTILIZATION, FOREST, GROWTH, NEW-ZEALAND, NITROGEN, NUTRIENT, PRODUCTIVITY, STAND DEVELOPMENT, WATER

1164

King, J.S., R.B. Thomas, and B.R. Strain. 1996. Growth and carbon accumulation in root systems of Pinus taeda and Pinus ponderosa seedlings as affected by varying CO2, temperature and nitrogen. *Tree Physiology 16(7):635-642.*

It has been hypothesized that increasing atmospheric CO2 concentration enhances accumulation of carbon in fine roots, thereby altering soil carbon dynamics and nutrient cycling. To evaluate possible changes to belowground pools of carbon and nitrogen in response to elevated CO2, an early and a late successional species of pine (Pinus taeda L. and Pinus ponderosa Dougl. ex Laws, respectively) were grown from seed for 160 days in a 35 or 70 Pa CO2 partial pressure at low or high temperature (30-year weekly mean and 30 year weekly mean + 5 degrees C) and a soil solution nitrogen concentration of 1 or 5 mM NH4NO3 at the Duke University Phytotron. Seedlings were harvested at monthly intervals and growth parameters of the primary root, secondary root and tap root fractions evaluated. Total root biomass of P. ponderosa showed a positive CO2 response (105% increase) (P = 0.0001) as a result of significant increases in all root fractions in the elevated CO2 treatment, but all other main effects and interactions were insignificant. In I? taeda, there were significant interactions between CO2 and temperature (P = 0.04) and CO2 and nitrogen (P = 0.04) for total root biomass. An allometric analysis indicated that modulation of the secondary root fraction was the main response of the trees to altered environmental conditions. In P. ponderosa, there was an increase in the secondary root fraction relative to the primary and tap root fractions under conditions of low temperature. In P. taeda, there was a shift in carbon accumulation to the secondary roots relative to the primary roots under low temperature and low nitrogen. Neither species exhibited shifts in carbon accumulation in response to elevated CO2. We conclude that both species have the potential to increase be lowground biomass substantially in response to rising atmospheric CO2 concentration, and this response is sensitive to temperature and nitrogen in P. taeda. Both species displayed small shifts in belowground carbon accumulation in response to altered temperature and nitrogen that may have substantial ecosystem consequences over time.

KEYWORDS: ECOSYSTEMS

1165

King, J.S., R.B. Thomas, and B.R. Strain. 1997. Morphology and tissue quality of seedling root systems of Pinus taeda and Pinus ponderosa as affected by varying CO2, temperature, and nitrogen. *Plant and Soil 195(1):107-119.*

Rising atmospheric carbon dioxide, nitrogen deposition and warmer temperatures may alter the quantity and quality of plant-derived organic matter available to soil biota, potentially altering rates of belowground herbivory and decomposition. Our objective was to simulate future growth conditions for an early successional (loblolly) and late successional (ponderosa) species of pine to determine if the physical and chemical properties of the root systems would change. Seedlings were grown for 160 days in greenhouses at the Duke University Phytotron at 35 or 70 Pa CO2 partial pressure, ambient or ambient +5 degrees C temperature, and 1 or 5 mMNH(4)O(3). Roots from harvested seedlings were analyzed for changes in surface area, specific root length, mass, total nonstructural carbohydrates (TNC), and concentrations of macro-nutrients. Surface area increased in both species under elevated CO2, due primarily to increases in root length, and this response was greatest (+138%) in loblolly pine at high temperature. Specific root length decreased in loblolly pine at elevated CO2 but increases in mass more than compensated for this, resulting in net increases in total length. TNC was unaffected and nutrient concentrations decreased only slightly at elevated CO2, possibly from anatomical changes to the root tissues. We conclude that future growth conditions will enhance soil exploration by some species of pine, but root carbohydrate levels and nutrient concentrations will not be greatly affected, leaving rates of root herbivory and decomposition unaltered.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AVAILABILITY, ELEVATED CO2, ENRICHMENT, GROWTH, LOBLOLLY-PINE, PLANTS, RESPONSES, SOIL BIOTA, WATER

1166

King, S.P., M.R. Badger, and R.T. Furbank. 1998. CO2 refixation characteristics of developing canola seeds and silique wall. *Australian Journal of Plant Physiology 25(3):377-386.*

The potential for developing canola (Brassica napus L.) seeds and the interior silique (pod) wall to refix respired CO2 has been investigated. From ribulose-1,5-bisphosphate carboxylase- oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPC) activities, seeds were estimated to have a greater CO2, fixation capacity than silique wall endocarp during oil filling. The major component of seed fixation capacity was embryo Rubisco, which had a total activity of 6.3 nmol min(-1) embryo(-1) (3.7 mu mol min(-1) mg chlorophyll(-1)) at 28 days after anthesis (DAA) with smaller contributions from seed coat and embryo PEPC. Rubisco activities were probably maximal in vivo because of high silique cavity CO2 concentrations (0.8 to 2.5%). Seed chlorophyll content rapidly increased over 10-fold from 20 to 30 DAA and, with 20% of incident light transmitted through the silique wall, embryos demonstrated appreciable photosynthetic electron transport rates and most energy produced appeared to be used for Rubisco-catalysed CO2 fixation. Endocarp refixation capacity was less than seeds because chlorophyll content was not enriched and PEPC activities were relatively small. These data indicate that developing seeds and also endocarp refix respired CO2 and that embryo chlorophyll plays a critical role in this refixation.

KEYWORDS: ACCUMULATION, BRASSICA-CAMPESTRIS L, CHLOROPHYLL FLUORESCENCE, EMBRYOS, FIXATION, INVIVO, NAPUS, OILSEED RAPE, PISUM SATIVUM L, POD WALL

1167

Kinney, K.K., and R.L. Lindroth. 1997. Responses of three deciduous tree species to atmospheric CO2 and soil NO3- availability. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 27(1):1-10.*

This research evaluated the direct and interactive effects of atmospheric CO2 and soil NO3- availability on growth and biomass partitioning of quaking aspen (Populus tremuloides Michx.), red oak (Quercus rubra L.), and sugar maple (Acer saccharum Marsh.). In the split split plot experimental design, NO3- availability (low and high) and tree species were nested in two levels of atmospheric CO2 (ambient, 355 mu L/L; elevated, 650 mu L/L). Seedlings were grown for 57 days in environmental control rooms. Increased CO2 and NO3- availability positively and (mostly) independently influenced total growth and relative growth rates. Moderate to weak interactions between CO2 and NO3- for several growth parameters (e.g., leaf production, shoot length, root collar diameter) in some species indicated an enhanced response to CO2 enrichment under conditions of high NO3- availability. Interactive effects were most pronounced in aspen. Seedling growth and allocation responses to CO2 and NO3- were frequently species specific and associated with successional status. For example, proportional increases in growth in response to elevated CO2 were greatest for sugar maple and least for quaking aspen, whereas the converse was hue with respect to response to high NO3- availability. This research indicates that the impact of enriched CO2 atmospheres on forest communities will be influenced by both nutrient availability and unique species characteristics.

KEYWORDS: CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO2, FORESTS, NITROGEN, NUTRIENTS, PLANTS, SEEDLINGS

1168

Kinney, K.K., R.L. Lindroth, S.M. Jung, and E.V. Nordheim. 1997. Effects of CO2 and NO3- availability on deciduous trees: Phytochemistry and insect performance. *Ecology 78(1):215-230.*

Increasing concentrations of atmospheric CO2 will interact with other environmental factors to influence the physiology and ecology of trees. This research evaluated how plant phytochemical responses to enriched atmospheric CO2 are affected by the availability of soil nitrate (NO3-) and how these chemical changes, in turn, alter the performance of a tree-feeding folivore. Seedlings of three deciduous tree species-quaking aspen (Populus tremuloides), red oak (Quercus rubra), and sugar maple (Acer saccharum)-were grown in ambient (355 mu L/L) or elevated (650 mu L/L) CO2 in combination with low (1.25 mmol/L) or high (7.5 mmol/L) soil NO3- availability. After 60 d, foliage was analysed for changes in nutrients and allelochemicals likely to be influenced by the availability of CO2 and NO3-. Penultimate gypsy moth larvae (Lymantria dispar) were reared on foliage (aspen and maple) to determine how performance would be affected by host chemical changes. Using the framework of carbon-nutrient balance (CNB) theory, we tested three hypotheses regarding the impact of CO2 and NO3- availability on plant chemistry and insect performance: (1) nitrogen-based compounds will decrease, and carbon-based compounds will increase in response to elevated CO2 and/or low NO3-; (2) aspen will exhibit the greatest change in C:N ratios, and maple the least; and (3) phytochemical changes will influence gypsy moth performance, with larvae fed aspen being affected more than those fed maple. Concentrations of nitrogen and soluble protein decreased, whereas concentrations of starch, condensed tannins, and ellagitannins increased, in response to elevated CO2 and/or low NO3-. Responses of simple carbohydrates and phenolic glycosides were variable, however, suggesting that foliar accumulations of "dynamic metabolites" do not follow the predictions of CNB theory as well as do those of stable end products. With respect to Hypothesis 2, we found that absolute (net) changes in foliar C:N ratios were greatest for aspen and least for oak, whereas relative (proportional) changes were greatest for maple and least for aspen. Thus, Hypothesis 2 was only partially supported by the data. Considering Hypothesis 3, we found that elevated CO2 treatments had little effect on gypsy moth development time, growth rate, or larval mass. Larvae reared on aspen foliage grown under elevated CO2 exhibited increased consumption but decreased conversion efficiencies. Gypsy moth responses to NO3- were strongly host specific: the highest consumption and food digestibility occurred in larvae on high-NO3- aspen, whereas the fastest growth rates occurred in larvae on high-NO3- maple. In short, our results again only partially supported the predicted pattern, They indicate, however, that the magnitude of insect response elicited by resource-mediated shifts in host chemistry will depend on how levels of compounds with specific importance to insect fitness (e.g., phenolic glycosides in aspen) are affected. Overall, we observed relatively few true interactions (i.e,, nonadditive) between carbon and nitrogen availability vis a vis foliar chemistry and insect performance. Tree species, however, frequently interacted with CO2 and/or NO3- availability to affect both sets of parameters. These results suggest that the effects of elevated atmospheric CO2 on terrestrial plant communities will not be homogeneous, but will depend on species composition and soil nutrient availability.

KEYWORDS: ATMOSPHERIC CO2, CARBON NUTRIENT BALANCE, CHEMISTRY, ELEVATED CO2, GROWTH, MINERAL NUTRITION, NITROGEN, PAPER BIRCH, PLANTS, RESPONSES

1169

Kinsman, E.A., C. Lewis, M.S. Davies, J.E. Young, D. Francis, I.D. Thomas, K.H. Chorlton, and H.J. Ougham. 1996. Effects of temperature and elevated CO2 on cell division in shoot meristems: Differential responses of two natural populations of Dactylis glomerata L. *Plant, Cell and Environment 19(6):775-780.*

The aim was to establish whether temperature and/or elevated [CO2] (similar to 700 mu mol mol(-1)) affects the cell doubling time (cdt) in the different zones of the shoot apex of two natural populations of Dactylis glomerata originating in Portugal (38 degrees 53' N) and in Sweden (63 degrees 09' N). In the Portuguese population at ambient [CO2], only the pith rib meristem (PRM) exhibited a significant shortening of cdts from 10 to 30 degrees C, Elevated [CO2] resulted in a significant shortening of cdt, particularly in the PRM where cdt was reduced 4 . 8- and 6 . 1-fold at 10 and 20 degrees C, respectively, but only 2-fold at 30 degrees C, In the Swedish population at ambient [CO2], there were no consistent temperature-dependent alterations to cdt and this population was less responsive to elevated [CO2] than the Portuguese population, Nevertheless, elevated [CO2] resulted in a significant shortening of the cdt for some of the zones; the maximum reduction occurred in the PRM at 30 degrees C. We concluded that in the shoot apex of the Portuguese population, and most notably in the PRM, 10 and 20 degrees C were non- optimal temperatures for cell division, whilst the Swedish population was relatively buffered against temperature change, Elevated [CO2] resulted in substantially greater reductions in cdts in the shoot meristem of the Portuguese population than in that of the Swedish population.

KEYWORDS: PLANTS

1170

Kinsman, E.A., C. Lewis, M.S. Davies, J.E. Young, D. Francis, B. Vilhar, and H.J. Ougham. 1997. Elevated CO2 stimulates cells to divide in grass meristems: a differential effect in two natural populations of Dactylis glomerata. *Plant, Cell and Environment 20(10):1309-1316.*

In this study, we tested the hypothesis that elevated [CO2] shortens the cell cycle in meristems of Dactylis glomerata, more in a Portuguese population (38 degrees 53'N) than in a Swedish population (63 degrees

09'N). In the shoot meristem, the cell cycle shortened to about the same extent (approximate to 26%) in both populations exposed to the elevated [CO2] treatment, In the root meristem, the cell cycle shortened by 17% in the Portuguese and by 8% in the Swedish population, However, the proportion of rapidly cycling cells increased in the Portuguese much more than in the Swedish population in both meristems, In the root meristem, there was a 1.86-fold increase in the Portuguese compared with a 1.31-fold increase in the Swedish, In the shoot meristem, the increases were 1.5-3-fold for the Portuguese and 1.2-fold for the Swedish, The data are consistent in showing that a major response to the elevated [CO2] treatment was an increase in the proportion of cells that were cycling and that this was more marked for the Portuguese population, A more general response to the elevated [CO2] treatment was a shortening of the cell cycle regardless of population.

KEYWORDS: ALTITUDES, CYCLE, DIVISION, GROWTH, PLANTS, RATES, SHOOT APEX, SINAPIS, TEMPERATURE, TRANSITION

1171

Kirdmanee, C., Y. Kitaya, and T. Kozai. 1995. Effects of co2 enrichment and supporting material in-vitro on photoautotrophic growth of eucalyptus plantlets in-vitro and ex-vitro. *In Vitro Cellular & Developmental Biology-Plant 31(3):144-149.*

Eucalyptus camaldulensis shoots were cultured photoautotrophically in vitro for 6 wk with four different types of supporting materials (agar matrix, Gelrite matrix, plastic net, or vermiculite) under CO2-nonenriched or CO2- enriched conditions. Plantlets from each treatment in vitro were then grown ex vitro in a greenhouse for 4 wk. The growth and net photosynthetic rate of plantlets in, vitro, as well as subsequent growth, survival percentage, transpiration rate, and net photosynthetic rate of plantlets ex vitro were evaluated. CO2 enrichment significantly increased growth (total dry weight and number of primary roots) and net photosynthetic rate of plantlets in vitro, as well as the growth and survival percentage of plantlets ex vitro regardless of the type of supporting materials. The growth in vitro was greatest in the vermiculite, followed by the plastic net, Gelrite matrix, and agar matrix (in descending order) under either the CO2- nonenriched or CO2-enriched conditions. The growth and survival percentage of plantlets ex vitro were highest in the vermiculite under the CO2-enriched condition. The extensive root system produced in vitro was necessary for growth and survival of plantlets ex vitro.

KEYWORDS: ACCLIMATIZATION, ASPARAGUS, CULTURE, INVITRO, LIGHT, RASPBERRY

1172

Kirkham, M.B., H. He, T.P. Bolger, D.J. Lawlor, and E.T. Kanemasu. 1991. Leaf photosynthesis and water-use of big bluestem under elevated carbon-dioxide. *Crop Science 31(6):1589-1594.*

With the atmospheric concentration of CO2 increasing, it is important to know how this will affect crop growth. The objective of the study was to determine the effect of elevated CO2 on big bluestem (Andropogon gerardii Vitman) growing in a tallgrass prairie on a Tully silty clay loam (fine, mixed, mesic Pachic Argiustoll) kept at a high water level (field capacity) or a low water level (half field capacity). Sixteen cylindrical plastic chambers were placed on the prairie to maintain the two levels of CO2 (mean +/- SD: 337 +/- 32 Ind 658 +/- 81-mu-mol mol-1) over a full growing season. Soil-water content was measured weekly with a neutron probe. Photosynthesis, transpiration, stomatal resistance, and intercellular CO2 concentration were determined with a portable leaf Photosynthetic system. Canopy temperature was monitored with an infrared thermometer. Elevated (doubled) CO2 reduced transpiration rate of big bluestem by 25 and 35% under the high- and low-water treatments, respectively. Under both watering regimes, stomatal resistance was greater by almost- equal-to 1.6 s cm-1 with doubled CO2 than with ambient CO2. Plants grown with doubled CO2 at high- and low-water levels had warmer canopy temperatures (average 1.15 and 0.70-degrees-C warmer, respectively) than plants grown at ambient CO2. Carbon- dioxide concentration did not affect the rate of photosynthesis, even though intercellular CO2 concentration was increased under high CO2. Elevated CO2 did not increase the height of plants grown at the high water level, but it did increase the height at the low water level by an average of 9 cm.

KEYWORDS: ATMOSPHERIC CO2, CROP YIELD, ENRICHMENT, RESPONSES

1173

Kirschbaum, M.U.F. 1994. The sensitivity of C-3 photosynthesis to increasing co2 concentration - a theoretical-analysis of its dependence on temperature and background co2 concentration. *Plant, Cell and Environment 17(6):747-754.*

The atmospheric CO2 concentration has increased from the pre-industrial concentration of about 280 mu mol mol(-1) to its present concentration of over 350 mu mol mol(-1), and continues to increase. As the rate of photosynthesis in C-3 plants is strongly dependent on CO2 concentration, this should have a marked effect on photosynthesis, and hence on plant growth and productivity. The magnitude of photosynthetic responses can be calculated based on the well-developed theory of photosynthetic response to intercellular CO2 concentration. A simple biochemically based model of photosynthesis was coupled to a model of stomatal conductance to calculate photosynthetic responses to ambient CO2 concentration. In the combined model, photosynthesis was much more responsive to CO2 at high than at low temperatures. At 350 mu mol mol(-1), photosynthesis at 35 degrees C reached 51% of the rate that would have been possible with non-limiting CO2, whereas at 5 degrees C, 77% of the CO2 non-limited rate was attained. Relative CO2 sensitivity also became smaller at elevated CO2, as CO2 concentration increased towards saturation. As photosynthesis was far from being saturated at the current ambient CO2 concentration, considerable further gains in photosynthesis were predicted through continuing increases in CO2 concentration. The strong interaction with temperature also leads to photosynthesis in different global regions experiencing very different sensitivities to increasing CO2 concentrations.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CONDUCTANCE, ELEVATED CO2, ENVIRONMENTS, GROWTH, HUMIDITY, MODELS, RESPONSES

1174

Kirschbaum, M.U.F. 1999. Modelling forest growth and carbon storage in response to increasing CO2 and temperature. *Tellus Series B-Chemical and Physical Meteorology 51(5):871-888.*

The response of plant growth to increasing climate change remains one of the unresolved issues in understanding the future of the terrestrial biosphere. It was investigated here by using the comprehensive forest growth model CenW 1.0.5 which integrates routines for the fluxes of carbon and water, interception of radiation and the cycling of nutrients. It was run with water and/or nutrient limitations on a background of naturally observed climate at Canberra, Australia. It was parameterised for Pinus radiata, the commercially most important plantation species in Australia. The simulations showed that under water-limited conditions, forest growth was highly sensitive to doubling CO2, with growth increases of over 50% on average and even greater increases in dry years. In contrast, when water supply was adequate, but nutrients were limiting, growth increases were smaller, with an initial increase of about 15% during the first year after CO2 was doubled. This growth increase diminished further over subsequent years so that after 20 years, there

was virtually no remaining effect. This diminishing response was due to developing nutrient limitations caused by extra carbon input which immobilised nutrients in the soil. When both water and nutrients were adequate, growth was increased by about 15-20% with no decrease over time. Increasing ambient temperature had a positive effect on growth under nutrient limited conditions by stimulating nitrogen mineralisation rates, but had very little effect when nutrients were non-limiting. Responses were qualitatively similar when conditions were changed gradually. In response to increasing CO2 by 2 mu mol mol(-1) yr(-1) over 50 years, growth was increased by only 1% under nutrient- limited condition but by 16% under water-limited conditions. When temperature and CO2 were both changed to emulate conditions between 1950 and 2030, growth was enhanced between 5-15% over the 80-year period due to the effect of CO2 on photosynthesis and water economy especially under water-limited conditions, and due to the effect of increasing temperature in mineralising greater amounts of nutrients. These results show that there is not one universally applicable biological growth response to increasing temperature and CO2, but that they interact in complex ways with a number of other growth limiting factors. Any response factor of plants to CO2 can only be quantified if the important interacting factors can be independently characterised for different situations.

KEYWORDS: ATMOSPHERIC CO2, C STORAGE, CLIMATE CHANGE, DIOXIDE, ELEVATED CO2, LIMITED CONDITIONS, LONG-TERM, NET PRIMARY, RESPIRATION, TERRESTRIAL ECOSYSTEMS

1175

Kirschbaum, M.U.F. 2000. Will changes in soil organic carbon act as a positive or negative feedback on global warming? *Biogeochemistry 48(1):21-51.*

The world's soils contain about 1500 Gt of organic carbon to a depth of 1m and a further 900 Gt from 1-2m. A change of total soil organic carbon by just 10% would thus be equivalent to all the anthropogenic CO2 emitted over 30 years. Warming is likely to increase both the rate of decomposition and net primary production (NPP), with a fraction of NPP forming new organic carbon. Evidence from various sources can be used to assess whether NPP or the rate of decomposition has the greater temperature sensitivity, and, hence, whether warming is likely to lead to an increase or decrease in soil organic carbon. Evidence is reviewed from laboratory-based incubations, field measurements of organic carbon storage, carbon isotope ratios and soil respiration with either naturally varying temperatures or after experimentally increasing soil temperatures. Estimates of terrestrial carbon stored at the Last Glacial Maximum are also reviewed. The review concludes that the temperature dependence of organic matter decomposition can be best described as: d(T) = exp[3.36 (T - 40)/(T + 31.79)] where d(T) is the normalised decomposition rate at temperature T (in degrees C). In this equation, decomposition rate is normalised to '1' at 40 degrees C. The review concludes by simulating the likely changes in soil organic carbon with warming. In summary, it appears likely that warming will have the effect of reducing soil organic carbon by stimulating decomposition rates more than NPP. However, increasing CO2 is likely to simultaneously have the effect of increasing soil organic carbon through increases in NPP. Any changes are also likely to be very slow. The net effect of changes in soil organic carbon on atmospheric CO2 loading over the next decades to centuries is, therefore, likely to be small.

KEYWORDS: ATMOSPHERIC CO2, BOREAL FOREST, CLIMATE CHANGE, LAND-USE, LAST GLACIAL MAXIMUM, MATTER DYNAMICS, NITROGEN MINERALIZATION, SPRUCE-FIR FOREST, TEMPERATURE-DEPENDENCE, TRACE GAS FLUXES

1176

Kirschbaum, M.U.F., D.A. King, H.N. Comins, R.E. McMurtrie, B.E. Medlyn, S. Pongracic, D. Murty, H. Keith, R.J. Raison, P.K. Khanna, and D.W. Sheriff. 1994. Modeling forest response to increasing co2 concentration under nutrient-limited conditions. *Plant, Cell and Environment 17(10):1081-1099.*

The growth rates of woody plants depend on both the rate of photosynthetic carbon gain and the availability of essential nutrients. Instantaneous carbon gain is known to increase in response to increasing atmospheric CO2 concentration, but it is uncertain whether this will translate into increased growth in the longer term under nutrient-limited conditions. An analytical model to address this question was developed by Comins and McMurtrie (1993, Ecological Applications 3, 666- 681). Their model was further tested and analysed. Manipulation of various assumptions in the model revealed its key assumptions and allowed a more confident prediction of expected growth responses to CO2 enrichment under nutrient-limited conditions. The analysis indicated that conclusions about the CO2 sensitivity of production were strongly influenced by assumptions about the relationship between foliar and heartwood nitrogen concentrations. With heartwood nitrogen concentration proportional to foliar nitrogen concentration, the model predicted a strong response of plant productivity to increasing CO2 concentration, whereas with heartwood nitrogen concentration set constant, the model predicted only a very slight growth response to changing CO2 concentration. On the other hand, predictions were only slightly affected by: (1) assumptions about the extent of nitrogen retranslocation out of senescing roots and foliage or wood during heartwood formation; (2) the effects of nitrogen status on specific Leaf area or (3) leaf longevity; (4) carbon allocation between different plant parts; or (5) changes in the N:C ratio of organic matter sequestered in the passive pool of soil organic matter. Modification of the effect of foliar nitrogen concentration on the light utilization coefficient had only a small effect on the CO2 sensitivity for pines. However, this conclusion was strongly dependent on the chosen relationship between single- leaf photosynthesis and leaf nitrogen concentration. Overall, the analysis suggested that trees growing under nitrogen- limited conditions can respond to increasing atmospheric CO2 concentration with considerable increases in growth.

KEYWORDS: CARBON DIOXIDE, DARK RESPIRATION, ELEVATED CO2, INTERNAL NITROGEN CONCENTRATION, LEAF LIFE-SPAN, ORGANIC-MATTER, PHOTOSYNTHETIC ACCLIMATION, PINUS-RADIATA FOLIAGE, PLANT- COMMUNITIES, SHOOT RATIOS

1177

Kirschbaum, M.U.F., B.E. Medlyn, D.A. King, S. Pongracic, D. Murty, H. Keith, P.K. Khanna, P. Snowdon, and R.J. Raison. 1998. Modelling forest-growth response to increasing CO2 concentration in relation to various factors affecting nutrient supply. *Global Change Biology 4(1):23-41.*

It is well recognized that photosynthesis of C3 plants is highly responsive to CO2 concentration. However, in natural ecosystems, plants are subject to a range of feedback effects that can interact with increased photosynthetic carbon gain in different ways so that it is not clear to what extent increased photosynthesis will translate into increased growth. To assess the probable growth response of nutrient-limited forests to increasing CO2 concentration, we use a previously developed modelling framework and apply it under conditions where the supply of nutrients is affected by a range of different factors. Our analysis indicates that forest growth is likely to be highly stimulated by increasing CO2 concentration in forests with high fertility, in forests with nitrogen fixing plants, in those subject to fire or where nitrogen in wood is effectively removed from the biologically active cycle either through physical removal of stems in harvesting or through continued stem growth over long time periods. Forest growth is likely to be stimulated by CO2 concentration in both phosphorus-and sulphur-

limited forests provided nutrients in heartwood of trees are removed from the active nutrient cycle. Without this removal from the cycling system, however, sulphur-limited forests should show little response to increasing CO2. In phosphorus-limited forests without phosphorus removal, the response to increasing CO2 depends further on the equilibration state of the large pool of unavailable secondary phosphorus. Considered over periods of centuries during which the secondary pool has equilibrated, growth of phosphorus-limited forests is likely to be only weakly stimulated by increasing CO2 concentration. However, over shorter periods, increasing CO2 concentration should lead to a substantial increase in productivity. In general, it can be concluded that systems that are more open with respect to nutrient gains and losses are likely to be more responsive to increasing CO2 concentration than systems where the amount of available nutrients is less variable. In more open systems, operation at a lower internal nutrient concentration as a result of increasing atmospheric CO2 concentration can lead to reduced nutrient losses per unit carbon gain. Our analysis shows that the effect of increasing CO2 on forest growth can differ substantially between forests due to interactions with a range of factors that affect nutrient supply. The response of a particular forest to increasing CO2 concentration can only be predicted if the main factors controlling nutrient supply and growth in that forest are understood and incorporated into an assessment.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, DYNAMICS, ECOSYSTEM PROCESSES, ELEVATED CO2, ENRICHMENT, LONG-TERM RESPONSE, SEEDLINGS, SPRUCE, TEMPERATURE

1178

Kitao, M., T.T. Lei, and T. Koike. 1997. Comparison of photosynthetic responses to manganese toxicity of deciduous bread-leaved trees in northern Japan. *Environmental Pollution 97(1-2):113-118.*

The effects of manganese (Mn) toxicity on photosynthesis of four tree species in northern Japan representing different successional traits were examined. The four species are: Betula ermanii (Be) and Alnus hirsuta (Ah) representing two early successional species, Ulmus davidiana var. japonica (Ud) as the mid-successional species, and Acer mono (Am) as the late successional species. Seedlings were grown hydroponically in a solution containing nutrients and Mn of four concentrations (1, 10, 50, 100 mg litre(-1)) for 50 days. Gas exchange measurements indicate that in all species, Mn accumulation in leaves resulted in the decline of light-saturated net photosynthetic rate at ambient CO2 pressure (35 Pa, Pn(amb)) and at saturating (5%) CO2 pressure (Pn(sat)), and of carboxylation efficiency but has little effect on the maximum efficiency of photochemistry. Sensitivity to elevated levels of Mn differed among species where the decline of Pn(amb) was much more modest in the two early successional species of Be and Ah than the mid-and late successional species of Ud and Am. The same trends were observed in both Pn(sat) and carboxylation efficiency. Based on these results, we suggest that early successional species (Betula ermanii and Alnus hirsuta) have greater tolerance for excess Mn in leaves than mid-and late successional species. (C) 1997 Elsevier Science Ltd.

KEYWORDS: C-3 PLANTS, CARBOXYLASE, CHLOROPHYLL, COWPEA VIGNA-UNGUICULATA, GROWTH, LIGHT, PHYSIOLOGY, TEMPERATURE, TOBACCO, TOLERANCE

1179

Kitaya, Y., G.H. Niu, T. Kozai, and M. Ohashi. 1998. Photosynthetic photon flux, photoperiod, and CO2 concentration affect growth and morphology of lettuce plug transplants. *Hortscience 33(6):988-991.*

Lettuce (Lactuca sativa L. cv. Summer-green) plug transplants were grown for 3 weeks under 16 combinations of four levels (100, 150, 200, and 300 mu mol.m(-2).s(-1)) of photosynthetic photon flux (PPF), two photoperiods (16 and 24 h), and two levels of CO2 (400 and 800 mu mol.mol(-1)) in growth chambers maintained at an air temperature of 20 +/- 2 OC. As PPF increased, dry mass (DM), percent DM, and leaf number increased, while ratio of shoot to root dry mass (S/R), ratio of leaf length to leaf width (LL/LW), specific leaf area, and hypocotyl length decreased. At the same PPF, DM was increased by 25% to 100% and 10% to 100% with extended photoperiod and elevated CO2 concentration, respectively. Dry mass, percent DM, and leaf number increased linearly with daily light integral (DLI, the product of PPF and photoperiod), while S/R, specific leaf area, LL/LW and hypocotyl length decreased as DLI increased under each CO2 concentration. Hypocotyl length was influenced by PPF and photoperiod, but not by CO2 concentration. Leaf morphology, which can be reflected by LL/LW, was substantially influenced by PPF at 100 to 200 mu mol.m(-2).s(-1), but not at 200 to 300 mu mol.m(-2).s(-1). At the same DLI, the longer photoperiod promoted growth under the low CO2 concentration, but not under the high CO2 concentrat ion. Longer photoperiod and/or higher CO2 conce ntration compensated for a low PPF.

KEYWORDS: GREENHOUSE, LIGHT, PLANTS, QUALITY, TOMATO

1180

Kleemola, J., J. Peltonen, and P. Peltonensainio. 1994. Apical development and growth of barley under different co2 and nitrogen regimes. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 173(2):79-92.*

Increases in atmospheric carbon dioxide (CO2) concentration have stimulated interest in the response of agricultural crops to elevated levels of CO2. Several studies have addressed the response of C3 cereals to CO2, but the interactive effect of nutrient supply and CO2 on apical development and spikelet set and survival has not been investigated thoroughly. Hence, an experiment was conducted in the greenhouse to evaluate the effect of high (700 mumol CO2mol-1 air) and low (400 mumol mol- 1) levels of atmospheric CO2 on apical development, spikelet set and abortion, and pre- and post-anthesis growth in spring barley (Hordeum vulgare L.) grown under high N (0.3 g N pot-1 before sowing +0.11 g N pot-1 week-1) and low N (0.3 g N pot-1) regimes. The plants were grown in 5 L pots. Development of spike was hastened due to CO2 enrichment, and the C+ plants pollinated few days earlier than the C- plants. Carbon dioxide enrichment had no effect on date of ripening. Development of spike slowed following application of extra N, and plants pollinated 10 days later and matured 2 weeks later when compared with plants under low N. Carbon dioxide enrichment did not affect the number of spikelets at anthesis. Excess N decreased spikelet abortion and the increased maximum number of spikelets under both [CO2]. Barley plants did not tiller when grown in low [CO2] and low N. Increased endogenous IAA concentration in those plants, recorded three days before tillers appeared in other treatments, may have contributed to this. Carbon dioxide enrichment increased the C concentration of plants, but decreased the N concentration under high N regime. Both the C and N concentration of plants were increased under high N regime. Carbon dioxide enrichment increased the total dry matter of mature plants by 9% under high N regime and by 21% under low N regime. Under high [CO2] increased kernel number on tiller spikes, and increased kernel weight both on main stem and on tiller spikes resulted in a 23% increase in kernel yield under low N regime and 76% increase in kernel yield under high N regime. The rate of N application influenced growth and yield components to a greater extent than CO2 enrichment. At maturity, plant dry matter, kernel weight, the number of kernels per spike, and the number of spikes per plant were higher under high N regime than under low N regime. Long days (16 h), low light intensity (280 mumol m-2s-1), and at constant temperature of 20-degrees-C high [CO2] increased kernel weight and the number of kernels on tiller spikes under high and low N application rate, but did not increase the number of kernels on main stem spike, or the number of tillers or tiller spikes per plant.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GRAIN-YIELD, PHYSIOLOGY, SPRING WHEAT, TEMPERATURE, YIELD COMPONENTS

1181

Klieber, A., B. Ratanachinakorn, and D.H. Simons. 1996. Effects of low oxygen and high carbon dioxide on tomato cultivar 'Bermuda' fruit physiology and composition. *Scientia Horticulturae 65(4):251-261.*

Breaker stage tomatoes (Lycopersicon esculentum Mill., cultivar 'Bermuda') were treated in air, 0.5% or 1.0% oxygen (O-2) in nitrogen (N-2) or 80% carbon dioxide (CO2) in air for 1, 3, 5 or 7 days at 22 degrees C, A 1 day low O-2 treatment delayed ripening after treatment by 1-2 days compared to a ripening period of 4 days for the control; elevated CO2 for 1 day had no effect on ripening after treatment, Low O-2 increased production of ethanol and acetaldehyde compared to the control and high CO2. Fruit treated for 3 or more days in low O-2 or high CO2 showed skin injury and blotchy ripening. Disease incidence increased with treatment time, but could be controlled in 1 day treatments by reducing relative humidity to about 70%, Firmness, total soluble solids, titratable acidity and pH of pericarp and gel of 1 day treated fruit were not different from the control.

KEYWORDS: ACETALDEHYDE, ATMOSPHERE, ETHANOL, EXPOSURES, NITROGEN, QUALITY, STORAGE

1182

Klironomos, J.N., M.C. Rillig, and M.F. Allen. 1996. Below-ground microbial and microfaunal responses to Artemisia tridentata grown under elevated atmospheric CO2. *Functional Ecology 10(4):527-534.*

1. Soil microbes are fed primarily by root-derived substrates, fulfil functions such as mineralization, immobilization, decomposition, pathogeneity and improvement of plant nutrition, and form the basis of the below-ground food web. Hitherto, belowground processes have generally been monitored using a 'black-box' approach, thereby ignoring effects of global change at a finer level of resolution. We describe shifts in the activity between microbial functional groups associated with roots of Artemisia tridentata, and the influence of this change on higher trophic levels, 2. We tested the hypothesis that elevated atmospheric CO2 causes the soil community to change qualitatively. We measured the responses of several soil microbe and soil microfaunal parameters to a double-ambient CO2 concentration and nutrient additions. The soil community, as measured by those parameters, showed great changes in response to the treatments. There was a very strong interaction between elevated CO2 and the nutrient addition. 3. Under low nutrient conditions, total microbial biomass did not change under elevated atmospheric CO2, but doubled under conditions of elevated CO2 and added nutrients. As we increased the resolution of our analysis, however, results shifted. Under low nutrient conditions, mycorrhizal fungi responded positively to elevated CO2, whereas with added soil nutrients they responded negatively to the same elevated CO2 concentration. Bacteria and non-mycorrhizal fungi did not respond under the former conditions but more than doubled in biomass under conditions of elevated CO2 and added nutrients. Soil fauna was also affected by the treatments. Overall, elevated CO2 shifted carbon flow in the plant-soil system to a more mutualistic-closed, mycorrhizal-dominated system, whereas the combination of elevated CO2 and nutrient addition shifted carbon flow to a more opportunistic-open, saprobe/pathogen-dominated one. 4. This indicates that elevated atmospheric CO2 may lead to far less predictable feedback patterns than previously thought and that qualitative shifts in the soil community may be far more important than mere changes in total C sink strength.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, COLLEMBOLA, COLONIZATION, ENRICHMENT, FEEDBACK, NATURAL ECOSYSTEMS, RHIZOSPHERE, ROOTS, SOIL

1183

Klironomos, J.N., M.C. Rillig, M.F. Allen, D.R. Zak, M. Kubiske, and K.S. Pregitzer. 1997. Soil fungal-arthropod responses to Populus tremuloides grown under enriched atmospheric CO2 under field conditions. *Global Change Biology 3(6):473-478.*

We investigated the influence of elevated CO2 and soil N availability on the growth of arbuscular mycorrhizal and non- mycorrhizal fungi, and on the number of mycophagous soil microarthropods associated with the roots of Populus tremuloides. CO2 concentration did not significantly affect percentage infection of Populus roots by mycorrhizal or non-mycorrhizal fungi. However, the extra-radical hyphal network was altered both qualitatively and quantitatively, and there was a strong interaction between CO2 and soil N availability. Under N-poor soil. conditions, elevated CO2 stimulated hyphal length by arbuscular mycorrhizal fungi, but depressed growth by non-mycorrhizal fungi. There was no CO2 effect at high N availability. High N availability stimulated growth by opportunistic saprobic/pathogenic fungi. Soil mites were not affected by any treatment, but collembolan numbers were positively correlated with the increase in non-mycorrhizal fungi. Results indicate a strong interaction between CO2 concentration and soil N availability on mycorrhizal functioning and on fungal-based soil food webs.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, CLIMATE CHANGE, COLONIZATION, ECOSYSTEMS, ELEVATED CO2, NITROGEN, PLANT, RHIZOSPHERE, ROOTS

1184

Klironomos, J.N., M.C. Rillig, M.F. Allen, D.R. Zak, K.S. Pregitzer, and M.E. Kubiske. 1997. Increased levels of airborne fungal spores in response to Populus tremuloides grown under elevated atmospheric CO2. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(10):1670-1673.*

Soil fungi are important components of terrestrial ecosystems. They function as decomposers, pathogens, parasites, and mutualistic symbionts. Their main mode of dispersal is to liberate spores into the atmosphere. In this study we tested the hypothesis that a higher atmospheric CO2 concentration will induce greater sporulation in common soil fungi, leading to higher concentrations of fungal propagules in the atmosphere. In our field experiment, the concentration of airborne fungal propagules, mostly spores, increased fourfold under twice- ambient CO2 concentrations. Analysis of decomposing leaf litter (likely the main source of airborne fungal propagules) indicated that the fungi produced fivefold more spores under elevated CO2. Our results provide evidence that elevations in atmospheric CO2 concentration can directly affect microbial function, which may have important implications for litter decay, fungal dispersal, and human respiratory health.

KEYWORDS: CARBON DIOXIDE, DIAGNOSIS, NITROGEN

1185

Klironomos, J.N., M. Ursic, M. Rillig, and M.F. Allen. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to Artemisia tridentata grown under elevated atmospheric CO2. *New Phytologist 138(4):599-605.*

Arbuscular mycorrhizal (AM) fungi form mutualistic symbioses with the root systems of most plant species. These mutualisms regulate nutrient exchange in the plant-soil interface and might influence the way in

which plants respond to increasing atmospheric CO2. In other experiments, mycorrhizal responses to elevated CO2 have been variable, so in this study we test the hypothesis that different genera of AM fungi differ in their response, and in turn alter the plant's response, to elevated CO2. Four species from three genera of AM fungi were tested. Artemisia tridentata Nutt. seedlings were inoculated with either Glomus intraradices Schenck & Smith, Glomus etunicatum Becker & Gerdemann, Acaulospora sp. or Scutellospora calospora (Nicol. & Gerd.) Walker & Sanders and grown at either ambient CO2 (350 ppm) or elevated CO2 (700 ppm). Several significant inter-specific responses were detected. Elevated CO2 caused percent arbuscular and hyphal colonization to increase for the two Glomus species, but not for Acaulospora sp. or S. calospora. Vesicular colonization was not affected by elevated CO2 for any fungal species. In the extra-radical phase, the two Glomus species produced a significantly higher number of spores in response to elevated CO2, whereas Acaulospora sp. and S. calospora developed significantly higher hyphal lengths. These data show that AM fungal taxa differ in their growth allocation strategies and in their responses to elevated CO2, and that mycorrhizal diversity should not be overlooked in global change research.

KEYWORDS: BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, DIVERSITY, ECOLOGY, ENRICHMENT, GRASSLAND, MORPHOLOGY, PATTERNS, PLANT

1186

Kloppenburg, W.D., B.G. Wolthers, F. Stellaard, H. Elzinga, T. Tepper, P.E. deJong, and R.M. Huisman. 1997. Determination of urea kinetics by isotope dilution with [C- 13]urea and gas chromatography isotope ratio mass spectrometry (GC-IRMS) analysis. *Clinical Science 93(1):73-80.*

1. Stable urea isotopes can be used to study urea kinetics in humans, The use of stable urea isotopes far studying urea kinetic parameters in humans on a large scale is hampered by the high costs of the labelled material, We devised a urea dilution for measurement of the distribution volume, production rate and clearance of urea in healthy subjects and renal failure patients using the inexpensive single labelled [C- 13]urea isotope with subsequent analysis by headspace chromatography-isotope ratio MS (GC-IRMS) of the [C-13]urea enrichment, 2. The method involves measurement of the molar percentage excess of [C-13]urea in plasma samples taken over a 4 h period after an intravenous bolus injection of [C-13]urea, During the sample processing procedure, the plasma samples together with calibration samples containing a known molar percentage excess of [C-13]urea are acidified with phosphoric acid to remove endogenous CO2, and are subsequently incubated with urease to convert the urea present in the plasma samples into CO2. The C-13 enrichment of the generated CO2 is analysed by means of GC-IRMS, This method allows measurement of the molar percentage excess of [C-13]urea to an accuracy of 0.02%. 3. Reproducibility studies showed that the sample processing procedure [within-run coefficient of variation (CV) <2.8% and between-run CV <8.8%] and the GC-IRMS analysis (within-day CV <1.3% and between-day CV <1.3%) could be repeated with good reproducibility, 4. In clinical urea kinetic studies in a healthy subject and in a renal failure patient without residual renal function, reproducible values of the distribution volume, production rate and clearance of urea were determined using minimal amounts of [C-13]urea (25-50 mg). 5. because only low [C-13]urea enrichments are needed in this urea dilution method using GC-IRMS analysis, the costs of urea kinetic studies are reduced considerably, especially in patients with renal failure.

KEYWORDS: HEMODIALYSIS, MODEL

1187

Knapp, A.K., M. Cocke, E.P. Hamerlynck, and C.E. Owensby. 1994. Effect of elevated co2 on stomatal density and distribution in a C-4 grass and a C-3 forb under field conditions. *Annals of Botany 74(6):595-599.*

Two common tallgrass prairie species, Andropogon gerardii, the dominant C-4 grass in this North American grassland, and Salvia pitcheri, a C-3 forb, were exposed to ambient and elevated (twice ambient) CO2 within open-top chambers throughout the 1993 growing season. After full canopy development, stomatal density on abaxial and adaxial surfaces, guard cell length and specific leaf mass (SLM; mg cm(-2) were determined for plants in the chambers as well as in adjacent unchambered plots. Record high rainfall amounts during the 1993 growing season minimized water stress in these plants (leaf xylem pressure potential was usually > -1.5 MPa in A. gerardii) and also minimized differences in water status among treatments. In A. gerardii, stomatal density was significantly higher (190 +/- 7 mm(-2); mean +/- s.e.) in plants grown outside of the chambers compared to plants that developed inside the ambient CO2 chambers (161 +/- 5 mm(-2)). Thus, there was a significant 'chamber effect' on stomatal density. At elevated levels of CO2, stomatal density was even lower (P < 0.05; 121 +/- 5 mm(- 2)). Most stomata were on abaxial leaf surfaces in this grass, but the ratio of adaxial to abaxial stomatal density was greater at elevated levels of CO2. In S. pitcheri, stomatal density was also significantly lower when plants were grown in the open-top chambers (235 +/- 10 mm(-2) outside vs. 140 +/- 6 mm(-2) in the ambient CO2 chamber). However, stomatal density was greater at elevated CO2 (218 +/- 12 mm(-2)) compared to plants from the ambient CO2 chamber. The ratio of stomata on adaxial vs. abaxial surfaces did not vary significantly in this herb. Guard cell lengths were not significantly affected by growth in the chambers or by elevated CO2 for either species. Growth within the chambers resulted in lower SLM in S. pitcheri, but CO2 concentration had no effect. In A. gerardii, SLM was lower at elevated CO2. These results indicate that stomatal and leaf responses to elevated CO2 are species specific, and reinforce the need to assess chamber effects along with treatment effects (CO2) when using open-top chambers.

KEYWORDS: ATMOSPHERIC CO2, DROUGHT, INCREASE, NUMBERS, PATTERNS, PHOTOSYNTHESIS, PLANT WATER RELATIONS, RESPONSES, TALLGRASS PRAIRIE

1188

Knapp, A.K., S.L. Conard, and J.M. Blair. 1998. Determinants of soil CO2 flux from a sub-humid grassland: Effect of fire and fire history. *Ecological Applications 8(3):760-770.*

Soil CO2 flux (J(CO2)) was measured at midday over a 2-yr period in undisturbed tallgrass prairie (Konza Prairie, Kansas, USA) to quantify seasonal and annual budgets, to evaluate temperature and moisture as determinants of soil CO2 flux, and to assess the effect of a common land management tool, spring fire, and fire history on soil respiration. We hypothesized that: (1) maximum rates and annual estimates of soil J(CO2) would be greater in more productive burned sites than in unburned sites, (2) soil J(CO2) would be greater in newly burned sites with a history of fire exclusion than in annually burned sites (consistent with differences in aboveground production), and (3) soil temperature and water availability would be primary abiotic determinants of soil J(CO2) in tallgrass prairie. A preliminary assessment of the effects of large herbivores on soil J(CO2) was included to evaluate the hypothesis that removal of aboveground biomass would reduce soil J(CO2). Results indicated that spring fire increased maximum monthly soil J(CO2) by 20-55% relative to unburned tallgrass prairie, with greatest monthly differences measured in April (fourfold higher in burned sites). In burned sites that differed in fire history, maximum monthly J(CO2) in annually burned prairie was 33% greater than in burned sites with a history of fire exclusion. Soil J(CO2) in these latter sites was still significantly higher than in unburned sites. Soil J(CO2) in sites grazed by bison was reduced by as much as 30% relative to adjacent ungrazed areas. Reduced root biomass and activity in grazed areas, unburned sites,

and sites with a history of fire exclusion suggest that plants play a major role in determining soil J(CO2) in this grassland. Soil temperature at 5 cm was related strongly to midday J(CO2) in both annually burned sites (r(2) = 0.58) and unburned sites (r(2) = 0.71). In contrast, differences in soil moisture among sites, enhanced by comparing irrigated grassland to control areas, increased maximum monthly J(CO2) by only 8%. Thus, soil temperature was the primary abiotic determinant of soil J(CO2) during this study. Maximum monthly estimates of soil J(CO2) in tallgrass prairie ranged from 10.3 mu mol CO2 . m(-2) . s(-1) in unburned sites to 15.1 mu mol . m(-2) . s(-1) in annually burned irrigated sites, whereas annual estimates varied from 4.7 to 7.8 kg CO2/m(2). Over the 2-yr period, spring fire increased estimated annual soil J(CO2) by 38-51% relative to unburned sites, while irrigation increased annual soil J(CO2) by 13%. These estimates for tallgrass prairie are much higher than those reported for most temperate ecosystems but are similar to estimates for tropical forests. Characteristics of undisturbed tallgrass prairie that may lead to high levels of soil J(CO2) include: high above- and belowground productivity; a relatively high proportion of C stored belowground; levels of soil microbial biomass and activity that are among the highest in native ecosystems in the United States; and the lack of a single dominant factor such as temperature, moisture, or nutrient availability, that consistently limits biotic processes during the growing season. The sensitivity of soil J(CO2) in tallgrass prairie to different land use practices (fire and grazing) suggests that it is critical to include these factors in the development of grassland C budgets, as well as in regional models that estimate biogeochemical responses to land use change.

KEYWORDS: ANDROPOGON-GERARDII, CARBON, EARTHWORM POPULATIONS, ELEVATED CO2, NORTH-AMERICA, PANICUM-VIRGATUM, RESPIRATION, TEMPERATE GRASSLAND, UNBURNED TALLGRASS PRAIRIE, WATER RELATIONS

1189

Knapp, A.K., J.T. Fahnestock, and C.E. Owensby. 1994. Elevated atmospheric co2 alters stomatal responses to variable sunlight in a C-4 grass. *Plant, Cell and Environment 17(2):189-195.*

Native tallgrass prairie in NE Kansas was exposed to elevated (twice ambient) or ambient atmospheric CO2 levels in open-top chambers. Within chambers or in adjacent unchambered plots, the dominant C-4 grass, Andropogon gerardii, was subjected to fluctuations in sunlight similar to that produced by clouds or within canopy shading (full sun > 1500 mu mol m(-2) s(-1) versus 350 mu mol m(-2) s(-1) shade) and responses in gas exchange were measured. These field experiments demonstrated that stomatal conductance in A. gerardii achieved new steady state levels more rapidly after abrupt changes in sunlight at elevated CO2 when compared to plants at ambient CO2. This was due primarily to the 50% reduction in stomatal conductance at elevated CO2, but was also a result of more rapid stomatal responses. Time constants describing stomatal responses were significantly reduced (29-33%) at elevated CO2. As a result, water loss was decreased by as much as 57% (6.5% due to more rapid stomatal responses). Concurrent increases in leaf xylem pressure potential during periods of sunlight variability provided additional evidence that more rapid stomatal responses at elevated CO2 enhanced plant water status. CO2-induced alterations in the kinetics of stomatal responses to variable sunlight will likely enhance direct effects of elevated CO2 on plant water relations in all ecosystems.

KEYWORDS: ANDROPOGON-GERARDII, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH FORM, LEAVES, PHOTOSYNTHETIC INDUCTION STATE, SUBALPINE PLANTS, TALLGRASS PRAIRIE, TERM, WATER-USE EFFICIENCY

1190

Knapp, A.K., E.P. Hamerlynck, J.M. Ham, and C.E. Owensby. 1996. Responses in stomatal conductance to elevated CO2 in 12 grassland species that differ in growth form. *Vegetatio 125(1):31-41.*

Responses in stomatal conductance (g(st)) and leaf xylem pressure potential (psi(leaf)) to elevated CO2 (2x ambient) were compared among 12 tallgrass prairie species that differed in growth form and growth rate. Open-top chambers (OTCs, 4.5 m diameter, 4.0 m in height) were used to expose plants to ambient and elevated CO2 concentrations from April through November in undisturbed tallgrass prairie in NE Kansas (USA). In June and August, psi(leaf) was usually higher in all species at elevated CO2 and was lowest in adjacent field plots (without OTCs). During June, when water availability was high, elevated CO2 resulted in decreased g(st) in 10 of the 12 species measured. Greatest decreases in g(st) (ca. 50%) occurred in growth forms with the highest potential growth rates (C-3 and C-4 grasses, and C-3 ruderals). In contrast, no significant decrease in g(st) was measured in the two C-3 shrubs. During a dry period in September, reductions in g(st) at elevated CO2 were measured in only two species (a C-3 ruderal and a C-4 grass) whereas increased g(st) at elevated CO2 was measured in the shrubs and a C-3 forb. These increases in g(st) were attributed to enhanced psi(leaf) in the elevated CO2 plants resulting from increased soil water availability and/or greater root biomass. During a wet period in September, only reductions in g(st) were measured in response to elevated CO2. Thus, there was significant interspecific variability in stomatal responses to CO2 that may be related to growth form or growth rate and plant water relations. The effect of growth in the OTCs, relative to field plants, was usually positive for g(st) and was greatest (> 30%) when water availability was low, but only 6-12% when psi(leaf) was high. The results of this study confirm the importance of considering interactions between indirect effects of high CO2 of plant water relations and direct effects of elevated CO2 on g(st), particularly in ecosystems such as grasslands where water availability often limits productivity. A product of this interaction is that the potential exists for either positive or negative responses in g(st) to be measured at elevated levels of CO2.

KEYWORDS: ANDROPOGON-GERARDII, ATMOSPHERIC CO2, C-4 GRASS, CARBON DIOXIDE, GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, TALLGRASS PRAIRIE, VARIABLE SUNLIGHT, WATER RELATIONS

1191

Knapp, A.K., E.P. Hamerlynck, and C.E. Owensby. 1993. Photosynthetic and water relations responses to elevated co-2 in the C-4 grass andropogon-gerardii. *International Journal of Plant Science 154(4):459-466.*

Undisturbed tallgrass prairie, dominated by the C-4 grass Andropogon gerardii, was exposed to ambient and elevated (double ambient) levels of atmospheric CO2 in large open-top chambers throughout the 1991 and 1992 growing seasons. Responses in leaf xylem pressure potential (psi), net photosynthesis (A), and stomatal conductance (g) were measured in both years for A. gerardii grown within chambers and from adjacent field plots. In 1992, maximum photosynthetic capacity (A(max)), apparent quantum requirement (Q(r)), the photosynthetic light compensation point (LCP), and dark respiration (R(d)) were also measured. Midday psi was significantly higher in plants grown at elevated CO2 in both years, and seasonally averaged psi was 0.48-0.70 MPa lower in 1991 (a dry year) than 1992 (a wet year). In 1991, A and g were significantly higher (regardless of measurement CO2 level) in plants grown at elevated vs. ambient CO2. These increases were measured in well-watered plants insuring that these plants differed only in CO2 growth conditions and previous exposure to low psi. Increased A at elevated CO2 occurred (as much as 7.1 mu mol m(-2) s(-1)) over a broad range of temperatures (17-35 C), but the temperature optimum for A was similar at both 350 and 700 mu L L(-1) CO2. In 1992, no differences in A, A(max), Q(r), LCP, or R(d) were detected when ambient and elevated CO2 plants were compared. In plants collected

from field plots, R(d), LCP, and leaf N were significantly higher than in plants within the chambers indicating that a chamber effect exists for these parameters. In both years, g was significantly reduced (21%-51%) when measured at 700 vs. 350 mu L L(-1) CO2. Peak aboveground biomass was increased at elevated CO2 in 1991 but not in 1992. These data indicate that for C-4 grasses, effects of elevated CO2 may only be detectable in years with significant water stress, a common occurrence in the central North American tallgrass prairies.

KEYWORDS: CARBON-DIOXIDE EFFLUX, CO2, GROWTH, LEAVES, PLANTS, SOIL MOISTURE, STRESS, TALLGRASS PRAIRIE, TERM

1192

Knapp, P.A., and P.T. Soule. 1998. Recent Juniperus occidentalis (western juniper) expansion on a protected site in central Oregon. *Global Change Biology 4(3):347-357.*

The expansion of Juniperus occidentalis (western juniper) has been extensive in the last century, and increases in density and cover have been linked with the indirect effects of domestic livestock grazing (i.e. cessation of periodic fires, increases of nurse-plant sites), and more favourable climatic conditions. In this study, we document changes in vegetation (including J. occidentalis) in central Oregon over a 23-year period and relate these changes to their probable causes. In June 1995 we returned to the Horse Ridge Research Natural Area (HRRNA), a site that has a history of minimal anthropogenic impacts, to replicate a 1972 vegetation survey. Using the canopy-intercept method, line intercept method, and aerial photography analysis to measure herbaceous cover, shrub cover and tree cover, respectively, we found significant changes had occurred in the 23-year period between studies. Relative changes of tree, shrub, and perennial herbaceous cover were 59%, 7%, and -38%, respectively. Relative increases in J. occidentalis density, as measured by the number of clumps and the number of stems, were 37% and 53%, respectively. Mean maximum height of J. occidentalis had increased by 10%. We examined the role of potentially confounding influences (e.g. fire, grazing, pathogens, climatic variability) and found that none of the traditional mechanisms implicated in J. occidentalis expansion adequately explained the observed changes. We suggest that the role of biological inertia of both anthropogenic and natural means may have had a profound effect on the J. occidentalis ecology of HRRNA.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, CLIMATE, DESERT, GROWTH, RESPONSES, VEGETATION CHANGE, WATER-USE EFFICIENCY, YIELD

1193

Knapp, T., and R. Mookerjee. 1996. Population growth and global CO2 emissions - A secular perspective. *Energy Policy 24(1):31-37.*

Considerable scientific effort has been applied to the question of whether worldwide fossil fuel combustion and the resultant emission of CO2 (as well as emissions of other greenhouse gases) will cause a discernible enhancement of the greenhouse effect in the next century, A more precise understanding of the contribution of human activity to potential global warming (vis-ri-vis natural climatic variability) is of critical policy interest, Surprisingly little research has been devoted to establishing the underlying statistical relationship between human activities and CO2 emissions, In this paper, we explore the nature of the relationship between global population growth and CO2 emissions by employing the test of causality developed by Granger on annual data for 1880-1989, as well as more comprehensive error correction and cointegration models, The results suggest a lack of a long-term equilibrium relationship, but imply a short-term dynamic relationship from CO2 to population growth.

KEYWORDS: CARBON DIOXIDE, CLIMATE, MODELS, TEMPERATURES, VARIABLES

1194

Kobayashi, K. 1994. Mapping results of crop growth simulation in a vector-space. *Agricultural and Forest Meteorology 68(1-2):43-61.*

Crop growth models can be used to address the mode-of-action of the global change impacts on crop yield as well as to predict the extent of the yield change. Presented in this paper are the framework to analyze the simulated yield change caused by the variations of many influencing factors and some methods to visualize the yield change. In the framework, the simulated yield change is mapped into an n-dimensional vector space, where n is the number of the simulated cases, e.g. years or locations. Yield changes owing to the individual impacts as well as the impact of simultaneous changes in all the factors are represented by vectors in the n-dimensional space. Contributions of the individual impacts to the simulated yield change and the interrelations between the impacts can be represented by the magnitude and orientation of the vectors. To visualize the vectors, however, the dimension n must be three or less. This is not the case, in general, and hence some methods are needed to reduce the dimension. By combining the influencing factors into three or less groups, the vectors for each group can be visualized in a subspace of dimension three or less. Impacts within each group may be further visualized in the same way. Taking an average is another way to reduce the dimension of the vector space. With it, the n-dimensional space is partitioned into a one-dimensional space for the mean and an (n - 1)-dimensional space for the deviation of the yield change. These methods were applied to an example of the simulated yield changes in soybean and maize owing to climate change (precipitation increase and temperature rise) and elevated CO2 (increases in the radiation use efficiency and the water use efficiency). The analyses revealed the differences between soybean and maize with respect to their responses to the simulated impacts of the climate change and the elevated CO2. These inter-specific differences were related to the differential changes in growth processes. The difference between the two impacts, i.e. the climate change and the CO2 increase, was also addressed. Utilities of the above approach were discussed and compared with the sensitivity analysis. Limitation of this approach was also discussed.

KEYWORDS: ADJUSTMENTS, CARBON, CLIMATE CHANGE, FARMER SCENARIO, MODEL, NITROGEN LIMITATIONS, PRESENT TECHNOLOGY, RADIATION, SOYBEAN YIELD, TEMPERATURE

1195

Kohlmaier, G.H., C. Hager, G. Wurth, M.K.B. Ludeke, P. Ramage, F.W. Badeck, J. Kindermann, and T. Lang. 1995. Effects of the age class distributions of the temperate and boreal forests on the global co2 source-sink function. *Tellus Series B-Chemical and Physical Meteorology 47(1-2):212-231.*

The role of the temperate and boreal forests as a global CO2 source or sink is examined, both for the present time and for the next hundred years. The results of the Forest Resource Assessment for 1990 of the Economic Comission for Europe and the Food and Agricultural Organisation of the United Nations (1992) serve as the main database in this study. Out of the estimated total area of approximately 20 . 10(6) km(2) of forests and wooded lands in tile temperate and boreal zone only approximately fifty percent is documented within the category of exploitable Forests, which are examined in detail here. In this study, a general formalism of the time evolution of an ensemble of forests within an ecological province is developed using the formalism of the Leslie matrix. This matrix can be formulated if the age class dependent mortalities which arise from the disturbances are known. A distinction is made between the natural disturbances by fire, wind throw and insect

infestations and disturbances introduced through harvesting of timber. Through the use of Richards growth function each age class of a given biome is related to the corresponding biomass and annual increment. The data reported on the mean net annual increment and on the mean biomass serve to calibrate the model. The difference of the reported nut annual increment and annual fellings of approximately 550 . 10(6) m(3) roundwood correspond to a sink of 210-330 Mt of carbon per year excluding any changes in the soil balance. it could be shown that the present distribution of forest age classes for the United States, Canada, Europe, or the former Soviet Union does not correspond to a quasi-stationary state, in which biomass is accumulated only due to a stimulated growth under enhanced atmospheric CO2 levels. The present CO, sink function will not persist in the next century, if harvesting rates increase with 0.5% annually or even less. The future state will also be influenced by the effect of the greenhouse climate, the impact of which may range from a stimulating effect on growth. which is calculated by the Frankfurt biosphere model, up to a transitional negative effect through a shift in vegetation zones.

KEYWORDS: BIOMES, BUDGET, CARBON STORAGE, DIOXIDE, FORMER SOVIET-UNION, UNITED-STATES

1196

Koike, T. 1995. Effects of co2 in interaction with temperature and soil fertility on the foliar phenology of alder, birch, and maple seedlings. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):149-157.*

The foliar phenology of potted 1-year-old seedlings of alder (Alnus hirsuta Turcz.), maple (Acer mono Maxim.), and birch (Betula platyphylla Sukatch, var. japonica Hara) was observed from May to September in eight growth environments: factorial combinations of temperatures (light:dark, 30:20 degrees C and 26:16 degrees C), CO2 level (70 and 36 Pa), and nutrient regime (high versus low levels of fertilization). Seedlings grown at high fertility always had more leaves, and under high CO2, shed leaves slightly later than seedlings grown at low fertility. Except for maple, production of newly formed shoots and leaves was accelerated by high CO2. In maple, high CO2 only increased the number of flushes of the leader shoot. Alder and birch accelerated sylleptic shoot and leaf production at high CO2 in fertile conditions. The production of new leaves by alder grown at high CO2 and low fertility was almost the same as that grown under normal CO2 at high fertility. At high CO2, the timing of winter bud formation of monopodial alder and maple was delayed, while that of sympodial birch was almost the same as at ambient CO2.

KEYWORDS: BETULA-PENDULA ROTH, DECIDUOUS TREES, ELEVATED CO2, ENRICHMENT, GROWTH, LEAF, LIQUIDAMBAR-STYRACIFLUA, NORTHEASTERN UNITED-STATES, PINUS-TAEDA SEEDLINGS, WOODY-PLANTS

1197

Koike, T., T.T. Lei, T.C. Maximov, R. Tabuchi, K. Takahashi, and B.I. Ivanov. 1996. Comparison of the photosynthetic capacity of Siberian and Japanese birch seedlings grown in elevated CO2 and temperature. *Tree Physiology 16(3):381-385.*

The effects of increased CO2 and temperature on the photosynthetic capacity of Siberian white birch and Japanese white birch (Betula platyphylla Sukatch. and B. platyphylla Sukatch. var. japonica Hara) were measured. Birch seedlings were raised with a CO2 partial pressure of 36 +/- 0.3 Pa (i.e., ambient) or 70 +/- 0.6 Pa at day/night temperatures of either 30/16 degrees C or 26/12 degrees C. Siberian birch leaves were smaller and thicker than Japanese birch leaves. Water use efficiency and nitrogen use efficiency of Siberian birch grown in the CO2-enriched air were higher than those of Japanese birch. Both species showed a physiological adjustment to the growth CO2 partial pressure. Carboxylation efficiency and quantum yield of both species grown in CO2-enriched air were lower than those of seedlings grown in ambient CO2. The adaptation of Siberian and Japanese birch to elevated CO2 and temperature are discussed in relation to predicted climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, LIMITATIONS, NITROGEN-USE, PLANTS, RESPONSES, TUSSOCK TUNDRA

1198

Kojima, S. 1994. Effects of global climatic warming on the boreal forest. *Journal of Plant Research 107(1085):91-97.*

On the basis of the predictions of the global climatic warming induced by anthropogenic activities, as provided by climatologists, current state of knowledge regarding possible ecological consequences of the warming on the boreal biome was discussed. A 600 to 700 km northward advance of the biome along with the warming was predicted. Such a shift could take place for half a century or so, which would be an unprecedentedly fast rate of progression. This might cause a serious disorder in species composition of the biome, particularly in the boundary regions. As to the carbon sink or source issues, considerable uncertainties and knowledge gaps existed. Elevated temperature and CO2 levels would stimulate photosynthesis to result in an increase of CO2 uptake, while the temperature increase would promote decomposition of organic matter especially that stored in the soils to release CO2 to the atmosphere. Behaviors of northern peat bogs, where ca. 700 Gt of organic matter was thought to be accumulated, would seriously affect the balance. However, overall ecosystematic carbon balance was yet to be fully studied. It was realized that multifunctional approaches needed to be developed so as to integrate pieces of various information into a holistic picture. Need for international collaboration research efforts was also addressed.

KEYWORDS: ALASKAN TUNDRA, ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, CANADA, ELEVATED CO2, GENERAL-CIRCULATION MODEL, INCREASE, SENSITIVITY, TEMPERATURE, TUSSOCK TUNDRA

1199

Kontak, D.J., and R. Kerrich. 1997. An isotopic (C, O, Sr) study of vein gold deposits in the Meguma terrane, Nova Scotia: Implication for source reservoirs. *Economic Geology and the Bulletin of the Society of Economic Geologists 92(2):161-180.*

Vein quartz, carbonate, and tourmaline from 19 Meguma gold deposits in the Meguma terrane of Nova Scotia have been analyzed for stable (delta(18)O, delta(13)C) and radiogenic (Sr-87/Sr-86) isotopes in order to assess the nature and origin of the vein-forming fluids. hs with other mesothermal gold provinces, the Meguma gold deposits are well suited to such a study because carbonate is the next most abundant phase after quartz in these mesothermal lode gold deposits. All vein types have been sampled for quartz and carbonate and, in addition, all compositional and textural varieties of carbonate have been sampled. Vein quartz is of uniform isotopic composition with most delta(18)O values between 10.2 to 17.6 per mil (avg ca. 14 parts per thousand), except for one deposit (West Gore Sb-Au) where values go to 19.4 per mil. There is no systematic variation for quartz within a deposit or position within the Meguma Group stratigraphy. Vein carbonate delta(18)O values range from 11.8 to 27.5 per mil, with most in the 13 to 16 per mil range. The relatively O-18-enriched carbonates reflect exchange with low-temperature fluids based on analyses of quartz-carbo;late pairs that indicate disequilibrium fractionation (Delta(quartz-carbonate) less than or equal to 0); this is best illustrated by the strong negative correlation between delta(18)O(carbonate) and Delta(quartz-carbonate). The

delta(18)O(water) is estimated at 10 +/- 3 per mil for a temperature of vein formation of 350 degrees to 400 degrees C and using the appropriate mineral-water fractionation equations. Whereas delta(water)(18) values partly overlap the field for magmatic fluids, the values are wholly consistent with a metamorphic fluid, and it is considered unlikely that a primary magmatic fluid signature has been substantially modified due to wall-rock influences given that mesothermal gold systems are sites of high fluid/rock ratios. Vein carbonate has delta(13)C values of -13.1 to -25.9 per mil, but a slight negative correlation between delta(13)C(carbonate) and Delta(quartz-carbonate) suggests that the primary values lie in the range -20 to -25 per mil. Thus, the delta(13)C values indicate a reduced, biogenic source for the carbon. Oxidation of the reduced carbon, as indicated by CO2 in fluid inclusions, may have occurred via hydrolysis of graphite or dissolution of carbonate minerals, both of which occur in the wall-rock lithologies of the Meguma Group, the latter of which has the appropriate isotopic composition. The initial Sr-87/Sr-66 of the vein fluid, estimated from the analyses of 52 vein carbonates (17 deposits) and four tourmalines (three deposits), ranges from 0.70118 to 0.72284 and within deposits considerable variation is observed. There is insufficient data to quantify the extent of the low-temperature overprint which has modified the C and O isotope data, although it is likely that some influence is present. Nevertheless, the data cannot be reconciled by a source confined exclusively to the Meguma Group, which suggests, therefore, involvement of another reservoir(s). The isotopic heterogeneity can be explained by variable amounts of contamination of a primary fluid with radiogenic Sr derived from Meguma Group lithologies by interaction along the fluid path or at the site of vein formation concomitant with wall-rock alteration; as discussed above, a dominantly magmatic source is not considered feasible. This fluid source is suggested to be within the structural basement to the Meguma Group, and the Liscomb gneisses are the favored source based on the combined results of the Sr isotope data presented herein and previously published Pb isotope data. Collectively, the data indicate that a primary fluid of metamorphic origin has had its isotopic signature variably modified due to interaction with different reservoirs. The most affected isotopic systems are C and S (based on earlier work on delta(35)S values) which are abundant as graphite carbonate and sulfides in the Meguma wall rock, respectively. The range in Sr-87/Sr-86 values of the fluid also reflects contamination, but this was quite variable. The uniform delta(18)O(water) value for the fluid indicates that this was the least affected isotopic system, except for the later exchange of carbonate at low temperatures.

KEYWORDS: ABITIBI GREENSTONE-BELT, BEAVER-DAM DEPOSIT, CANADIAN CORDILLERA, LISCOMB COMPLEX, NEW-ZEALAND, PLASMA-MASS SPECTROMETRY, SOUTH MOUNTAIN BATHOLITH, SOUTHEASTERN ALASKA, STABLE ISOTOPE, WESTERN-AUSTRALIA

1200

Koricheva, J., S. Larsson, E. Haukioja, and M. Keinanen. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. *Oikos 83(2):212-226.*

Our aim in this study was to determine how well phenotypic variation iri foliar concentrations of carbon-based secondary compounds (CBSCs) in woody plants can be predicted on the basis of two resource-based hypotheses, i.e. the carbon-nutrient balance (CNB) and growth-differentiation balance (GDB) hypotheses. We conducted a meta-analysis of literature data with respect to responses of CBSCs, carbohydrates and nitrogen to six types of environmental manipulations (fertilization with nitrogen or phosphorus, shading, CO2 enrichment, drought stress, ozone exposure): Plant responses to nitrogen fertilization, shading and CO2 enrichment in terms of pooled CBSCs and carbohydrates were consistent with predictions made with the two hypotheses. However, among biosynthetically distinct groups of CBSCs only concentrations of phenylpropanoid-derived compounds changed as predicted; hydrolyzable tannins and terpenoids, in particular, were less responsive. Phosphorus fertilization did not affect concentrations of CBSC or primary metabolites. Plant responses to drought and ozone exposure presumably were driven by plant demands for particular types of compounds (osmolites in the case of drought and antioxidants in the case of ozone exposure) rather than by changes in resource availability. Based on the relative importance of the treatment effects, we propose a hierarchical model of carbon allocation to CBSCs. The model implies that CBSC production is determined by both resource availability and specific demand-side responses. However, these two mechanisms work at different hierarchical levels. The domain of the CNB and GDB hypotheses is at the high hierarchical levels, predicting the total amount of carbon that can be allocated to CBSCs. Predicting altered concentrations of individual CBSCs, i.e. low hierarchy levels, probably demands biosynthetically detailed models which also take into account the history of plant interactions with biotic and abiotic factors.

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, CITRUS RED MITE, DEER CERVUS-ELAPHUS, DELAYED INDUCIBLE RESISTANCE, ELEVATED ATMOSPHERIC CO2, GROWTH-DIFFERENTIATION BALANCE, LIRIODENDRON-TULIPIFERA L, PINUS TAEDA L, ULMUS-AMERICANA SEEDLINGS

1201

Korner, C. 1995. Towards a better experimental basis for upscaling plant- responses to elevated co2 and climate warming. *Plant, Cell and Environment 18(10):1101-1110.*

Few of the most common assumptions used in models of responses of plants and ecosystems to elevated CO2 and climate warming have been tested under realistic life conditions, It is shown that some unexpected discrepancies between predictions and experimental findings exist, suggesting that a better empirical basis is required for predictions, The following ten suggestions may improve our potential to scale up from experimental scales to the real world, (1) Experiments should be timed to account for non-linearity in system responsiveness, asynchrony of responses and developmental differences, (2) By altering mineral nutrient supply, a wide range of CO2 responses can be 'produced', thus requiring realistic soil conditions, (3) Distinctions should be made between 'doubling CO2 supply' and biologically effective degrees of CO2 enrichment. (4) Because of the non-linearity of plant responses to CO2, studies of at least three instead of two CO2 concentrations are necessary to describe future trends adequately, (5) Edge effects, in particular unscreened side light, may lead to allometric anomalies, strongly constraining up-scaling to stand-scale CO2 responses, (6) Variables such as growth, yield, net primary production and C turnover are often confused with carbon pools, carbon sequestration or net ecosystem production, (7) Mono- and interspecific interactions between individuals may lead to completely unpredictable CO2 responses, (8) Experiments with seedlings benefit from the absence of prehistory effects but are likely to be irrelevant for the responses of larger trees which, on the other hand, may be constrained by carryover effects, Tree ring research indicates immediate sensitivity of large trees to environmental changes, supporting their usefulness in short-term CO2-enrichment experiments, (9) In predicting temperature responses, acclimation deserves more attention, (10) The significance of developmental responses is largely under-represented in experimental research, although these responses may overrule many of the other effects of atmospheric change, Results of more realistic experiments which account for these problems will provide a better basis for modelling the future of the biosphere.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, COMPETITION, ECOSYSTEMS, GROWTH, LOLIUM-PERENNE, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, TREES

1202

Korner, C. 1997. From alpine grassland to tropical forests: Biological consequences of elevated atmospheric CO2 (a synthesis of Swiss research) - Introduction. *Acta Oecologica-International Journal of Ecology 18(3):163-164.*

KEYWORDS: RESPONSES

1203

Korner, C. 1998. Tropical forests in a Co-2-rich world. *Climatic Change 39(2-3):297-315.*

Tropical forests resemble, besides their enormous genetic diversity, the single largest biomass carbon pool in the world. Only a 'small' annual increase of this pool could trap the current surplus of atmospheric CO2. The fact that this is not happening already today (after the world has seen a 27% increase in atmospheric CO2 in only 150 years) sets the boundaries of the likely trends to be expected in the future. In contrast to the possibly small overall responses of the tropical forest carbon pool, individual plant responses to CO2 enrichment will be significant. Since species and their genotypes will not respond in identical ways, selective processes will be induced which will lead to new community structures and alterations of numerous plant-plant, plant- animal and plant-microbe interactions. Examples are provided for such subtile CO2 effects, measured both in the greenhouse and in the field. From what is known currently it is concluded that in closed humid tropical forests leaf area index is unlikely to increase, mineral nutrient and water demand may (at least temporarily) become reduced, and leaf tissue quality plus associated consumer behavior will be altered. The big unknown is the behavior of tropical soils and their microflora and fauna. There is a realistic possibility that carbon turnover will be increased in tropical forests in a CO2-enriched world, which would have substantial implications for nutrient cycling.

KEYWORDS: CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSES, INCREASING ATMOSPHERIC CO2, LONG-TERM EXPOSURE, MODEL-ECOSYSTEMS, NUTRIENT LIMITATION, PLANT- COMMUNITIES, TREES, WATER-USE

1204

Korner, C., and J.A. Arnone. 1992. Responses to elevated carbon-dioxide in artificial tropical ecosystems. *Science 257(5077):1672-1675.*

Carbon, nutrient, and water balance as well as key plant and soil processes were simultaneously monitored for humid tropical plant communities treated with CO2-enriched atmospheres. Despite vigorous growth, no significant differences in stand biomass (of both the understory and overstory), leaf area index, nitrogen or water consumption, or leaf stomatal behavior were detected between ambient and elevated CO2 treatments. Major responses under elevated CO2 included massive starch accumulation in the tops of canopies, increased fine-root production, and a doubling of CO2 evolution from the soil. Stimulated rhizosphere activity was accompanied by increased loss of soil carbon and increased mineral nutrient leaching. This study points at the inadequacy of scaling-up from physiological baselines to ecosystems without accounting for interactions among components, and it emphasizes the urgent need for whole-system experimental approaches in global-change research.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, COMMUNITIES, COTTON, ENRICHMENT, GROWTH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, TEMPERATURE, TUSSOCK TUNDRA

1205

Korner, C., and M. Diemer. 1994. Evidence that plants from high-altitudes retain their greater photosynthetic efficiency under elevated co2. *Functional Ecology 8(1):58-68.*

1. Herbaceous plant species native to low and high altitudes in the Alps evolved under CO2 partial pressures (P-a) that differ as much as pre-industrial P-a differs from present day P-a at low altitude (e.g. 21% for a 2000-m difference in altitude). 2. In a previous study we showed that the efficiency of CO2 uptake (ECU) in typical high-altitude species is generally greater than in low-altitude species. Here we investigate whether this difference prevails under longer-term exposure to altered P-a. 3. Alpine and lowland species (mainly Ranunculus glacialis/R. acris and Geum reptans/G. rivale) were grown under various CO2 regimes in full daylight growth chambers at their respective natural growth temperature and photoperiod. When they were grown at twice the present CO2 level only moderate downward adjustment of photosynthesis was observed in both groups of species. The adjustments were not enough to compensate for the effect of increased CO2 supply. These trends prevailed under reciprocally exchanged alpine/lowland partial pressure of CO2 at the same total atmospheric pressure. 4. Irrespective of altitudinal origin, greatest downward adjustment of photosynthesis was found in species with the most pronounced accumulation of non-structural carbohydrate and dilution of leaf nitrogen when grown under elevated CO2 (e.g. in G. rivale). 5. These results suggest that, at least initially, the alpine plant species studied may attain relatively greater carbon gains in a CO2-enriched atmosphere than comparable lowland plant species.

1206

Korner, C., M. Diemer, B. Schappi, P. Niklaus, and J. Arnone. 1997. The responses of alpine grassland to four seasons of CO2 enrichment: a synthesis. *Acta Oecologica-International Journal of Ecology 18(3):165-175.*

Alpine grassland at 2 470 m altitude in the Swiss Central Alps was exposed to elevated CO2 by using open top chambers (16 ambient, 16 elevated CO2). Some plots received mineral fertilizer at a rate of N-deposition commonly measured in low altitude parts of Europe. Here we present a summary of results and data from the final harvest. Above-ground biomass measured after the completion of growth in the fourth season of treatment was not affected by CO2 enrichment as was found by previous biometric estimates, but mean below-ground biomass was slightly stimulated (+ 12%, n.s.). In con trast, net CO2 uptake per unit land area was strongly stimulated by CO2 enrichment al the beginning of the experiment, and during the early part of each season. However, the CO2 stimulation decreased during the later part of each growing season. By year four, also mid- season differences in CO2 uptake per unit land area had disappeared. Neither microbial biomass, soil respiration in the laboratory, nor in situ land-area-based CO2 evolution during the 10 week growing season increased under elevated CO2. The total biomass N-pool and free soil nitrate and ammonium (capture by ion exchange resin bags) remained unaffected, whereas leaf nitrogen concentration was reduced and nonstructural carbohydrate concentration increased under elevated CO2 in forbs. These differences in tissue composition largely disappeared during senescence and litter formation. Despite low CO2 responsiveness at ecosystem level, species responses differed in terms of nitrogen, carbohydrates, tillering and flowering, suggesting the possibility for long- term changes in community structure. Addition of NPK equivalent to 40 kg N ha(-1) a(-1) had massive effects on all plant traits studied, but did not enable stimulated growth under CO2 enrichment. However, when fertilizer and CO2 enrichment were provided jointly, soil microbes were stimulated indicating a co-limitation by carbon and nutrients (most likely nitrogen). Since responses to elevated CO2 were absent in both warm and cold growing seasons, we conclude that this late successional plant community is carbon saturated at current atmospheric CO2 concentrations for reasons not directly

related to nutrient supply and climate. Perhaps, contrary to our expectation, evolutionary adjustments of this "old" ecosystem to the life conditions at high altitudes caused carbon to become a surplus resource today.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FEEDBACK, PLANTS

1207

Korner, C., and F. Miglietta. 1994. Long-term effects of naturally elevated co2 on mediterranean grassland and forest trees. *Oecologia 99(3-4):343-351.*

We investigated the carbon supply status in species-rich mediterranean plant communities growing in a bowl-shaped 1-ha "CO2 spring" area near Sienna, Italy. A geothermic "lime- kiln" has provided these communities, for as long as historical records are available, with pure CO2 that mixes with ambient air at canopy level to daytime means of 500-1000 ppm CO2. Immediately outside the spring area similar plant communities are growing on similar substrate, and in the same climate, but under ca. 355 ppm CO2. We found no evidence that plants in the CO2 spring area grow faster, flower earlier or become larger. However, we found very large differences in tissue quality among the 40 species studied inside and outside the spring area. Depending on weather conditions, the mean concentration of total non-structural carbohydrates (TNC, sugars and starch) in leaves of herbaceous plants was 38-47% higher in the spring area. Fast growing ruderals growing on garden soil inside and outside the spring area show the same response. Among trees, leaves of the deciduous Quercus pubscens contain twice as much TNC inside as outside the vent area, whereas evergreen Q. ilex leaves show no significant difference. TNC levels in branch wood paralleled leaf values. TNC in shade leaves was also higher. Elevated CO2 had no effect on the sugar fraction, therefore differences in TNC are due to starch accumulation. Leaf nitrogen concentration decreases under elevated CO2. These observations suggest that the commonly reported TNC accumulation and N depletion in leaves growing under elevated CO2 are not restricted to the artificial conditions of short-term CO2 enrichment experiments but persist over very long periods. Such an alteration of tissue composition can be expected to occur in other plant communities also if atmospheric CO2 levels continue to rise. Effects on food webs and nutrient cycling are likely.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE CONTENT, CARBON DIOXIDE, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SOUR ORANGE TREES, VEGETATION

1208

Korner, C., S. Pelaezriedl, and A.J.E. Vanbel. 1995. Co2 responsiveness of plants - a possible link to phloem loading. *Plant, Cell and Environment 18(5):595-600.*

Of the many responses of plants to elevated CO2, accumulation of total non-structural carbohydrates (TNC in % dry weight) in leaves is one of the most consistent, Insufficient sink activity or transport capacity may explain this obvious disparity between CO2 assimilation and carbohydrate dissipation and structural investment, If transport capacity contributes to the problem, phloem loading may be the crucial step, It has been hypothesized that symplastic phloem loading is less efficient than apoplastic: phloem loading, and hence plant species using the symplastic pathway and growing under high light and good water supply should accumulate more TNC at any given CO2 level, but particularly under elevated CO2. We tested this hypothesis by carrying out CO2 enrichment experiments with 28 plant species known to belong to groups of contrasting phloem loading type. Under current ambient CO2 symplastic loaders were found to accumulate 36% TNC compared with only 19% in apoplastic loaders (P = 0.0016), CO2 enrichment to 600 mu mol mol(-1) increased TNC in both groups by the same absolute amount, bringing the mean TNC level to 41% in symplastic loaders (compared to 25% in apoplastic loaders), which may be close to TNC saturation (coupled with chloroplast malfunction), Eight tree species, ranked as symplastic loaders by their minor vein companion cell configuration, showed TNC responses more similar to those of apoplastic herbaceous loaders, Similar results are obtained when TNC is expressed on a unit leaf area basis, since mean specific leaf areas of groups were not significantly different, We conclude that phloem loading has a surprisingly strong effect on leaf tissue composition, and thus may translate into alterations of food webs and ecosystem functioning, particularly under high CO2.

KEYWORDS: COTTON, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, RESPONSES, TEMPERATURE

1209

Korner, C., and M. Wurth. 1996. A simple method for testing leaf responses of tall tropical forest trees to elevated CO2. *Oecologia 107(4):421-425.*

The effects of atmospheric CO2 enrichment on mature trees in their natural environment are largely unknown. Here we present a new, and inexpensive technique which can be used in situ to address some key physiological questions related to the CO2 problem. Small, light-weight cups mounted on the lower side of rigid leaves at the top of tall tropical forest trees were supplied with CO2-enriched air derived from a low-technology air mixing device utilizing forest floor CO2 evolution. We present the scientific rationale for such field experiments, technical details, an assessment of potential cup artifacts and first results illustrating effects of elevated CO2 on stomata and carbohydrate accumulation in the canopies of mature trees.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CARBON-DIOXIDE, BRANCH BAG, ENRICHMENT, GROWTH, PLANT, STOMATAL CONDUCTANCE

1210

Korthals, R.L., S.L. Knight, R.R. Crawford, and L.L. Christianson. 1995. Development and testing of a simple carbon-dioxide enrichment controller for growth chambers. *Transactions of the Asae 38(1):207-211.*

Proportional and proportional plus integral (PI) computer algorithms were implemented with a low cost pulse width modulated injection system to control CO2 in a 7.8 m(3) growth chamber. Experimental studies with plants in the growth chamber showed that average CO2 concentrations over 12 h were within 3 and 1 mu mol mol(-1) of set point for the proportional and PI controllers, respectively. The positive offset in CO2 concentration found for the proportional control was attributed to sampled measurements and pulse width modulated CO2 injection, and discussion was presented on how true errors differ from measured error estimates for pulse width modulated injection with long sampling periods relative to injection periods.

1211

Kostkarick, R., and W.J. Manning. 1993. Radish (raphanus-sativus L) - a model for studying plant- responses to air-pollutants and other environmental stresses. *Environmental Pollution 82(2):107-138.*

The use of Raphanus sativus L. as a model crop for studies on plant response to environmental stresses is reviewed with emphasis on the effects of different atmospheric pollutants (O3, SO2, NO2, acidic precipitation) and their combinations. Responses to temperature, light

supply, water stress, and atmospheric CO2 are also studied and discussed. In addition, the references reviewed are evaluated in terms of their experimental protocols on growth conditions and recommendations for optimal ranges of environmental and cultural variables, i.e. light, temperature, nutrient supply are given. Its distinct pattern of biomass partitioning, the small dimensions along with short and easy culture make radish an excellent experimental plant. The fleshy below-ground storage organ, formed by the hypocotyl and upper radicle, acts as the major sink during vegetative development. Abundant assimilate supply due to elevated levels of CO2 along with high irradiation frequently promote hypocotyl growth more than shoot growth, whereas under conditions of stress shoot growth is maintained at the expense of the hypocotyl. This makes the hypocotyl:shoot ratio of radish a very sensitive and suitable indicator for various environmental stresses. Potential weaknesses and short- comings of radish in its role as a model crop, particularly the high variability of injury and growth responses, are discussed along with possible solutions. Future research needs are derived from the summarized results presented and from some disparities among findings within the literature reviewed.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, FOLIAR INJURY, GROWTH-RESPONSE, NITROGEN-DIOXIDE, SIMULATED ACIDIC RAIN, SULFUR- DIOXIDE MIXTURES, VAR RADICULA-PERS, VEGETABLE PLANTS, WINTER CONDITIONS

1212

Kothavala, Z. 1999. The duration and severity of drought over eastern Australia simulated by a coupled ocean-atmosphere GCM with a transient increase in CO2. *Environmental Modelling & Software 14(4):243-252.*

The combined effects of precipitation and temperature simulated by a coupled ocean-atmosphere General Circulation Model that showed an El Nino-like pattern with a transient increase in CO2, was examined for its effects on drought over eastern Australia. The Palmer Drought Severity Index (PDSI) was applied to determine the duration and severity of drought over a 30- year period due to decreased precipitation over the region. Application of the PDSI, using monthly mean temperature and total monthly precipitation to the final 30 years of the transient CO2 simulation revealed more prolonged and more intense periods of drought under enhanced greenhouse conditions when compared to a similar time span of the present-day simulation. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: CIRCULATION, CLIMATE CHANGE, EUROPE, FLOODS, INDEX, MODEL, PRECIPITATION, SPATIAL VARIABILITY

1213

Kottke, I. 1997. Fungal adhesion pad formation and penetration of root cuticle in early stage mycorrhizas of Picea abies and Laccaria amethystea. *Protoplasma 196(1-2):55-64.*

Primary events during the establishment of the fungus-root symbiosis in ectomycorrhizas are still little understood. No attention has been paid so far to the adhesion of hyphae to the root cuticle and penetration of this barrier, although the importance of the cuticle has been shown for pathogen-plant interactions. Early developmental stages of in vitro mycorrhization of Laccaria amethystea on Picea abies after short periods of incubation in growth chambers under elevated CO2 concentrations were studied by light and transmission electron microscopy. No structural changes in mycorrhization related to elevated CO2 were found, but fine roots and mycorrhizas developed faster. Adhesion pad formation was observed at hyphal tips in contact with the root cuticle. The adhesion pad was connected to the outer cell wall layer of the hypha and reacted positively to the Swift reaction for cysteine rich proteins. Although the reaction cannot be considered as totally specific, findings are discussed in respect to hydrophobins, which have recently been found to be expressed during early steps in ectomycorrhizal development. The root cuticle was dissolved and penetrated by fungal tips of the fingerlike branching mycelium attached to the root surface. The findings are compared with well documented pathogenic fungus-plant interactions at the cuticle. The possibility of restriction of hyphal attack to that part of the cuticle covering cell junctions is discussed.

KEYWORDS: A-BINDING SITES, ATTACHMENT, CUTINASE, ECTOMYCORRHIZAS, HARTIG NET, NECTRIA-HAEMATOCOCCA, PHENOLICS, PISOLITHUS-TINCTORIUS, SPORES, SURFACE

1214

Kozai, T., K. Iwabuchi, K. Watanabe, and I. Watanabe. 1991. Photoautotrophic and photomixotrophic growth of strawberry plantlets invitro and changes in nutrient composition of the medium. *Plant Cell Tissue and Organ Culture 25(2):107-115.*

Explants excised from strawberry (Fragaria x ananassa Duch.) plantlets were cultured in vitro for 21 days on half-strength MS (Murashige & Skoog 1962) basal liquid medium with 20 g l-1 sucrose and without sugar in the vessels capped with gas permeable microporous polypropylene film. The experiments were conducted under CO2 nonenriched (350-450-mu-mol mol-1 in the culture room) and CO2 enriched (2,000-mu-mol mol-1 during the photoperiod in the culture room) conditions with a PPF (photosynthetic photon flux) of 200-mu-mol m-2 s-1. The CO2 concentration in the vessels decreased to approximately 200-mu- mol mol-1 during the photoperiod on day 21 under CO2 nonenriched conditions. The fresh and dry weight, net photosynthetic rate (NPR) per plantlet, NPR per g leaf fresh weight, NPR per g leaf dry weight, the number of unfolded leaves, and ion uptake of PO4(3-), NO3-, Ca2+, Mg2+ and K+ on day 21 were the greatest under photoautotrophic (no sugar in the medium) and CO2 enriched conditions. The residual percent of PO4(3-) was 3% on day 21 under photoautotrophic and CO2 enriched conditions.

KEYWORDS: CULTURES, ENRICHMENT

1215

Kozai, T., C. Kubota, and B.R. Jeong. 1997. Environmental control for the large-scale production of plants through in vitro techniques. *Plant Cell Tissue and Organ Culture 51(1):49-56.*

Leafy or chlorophyllous explants of a number of plant species currently micropropagated have been found to have high photosynthetic ability. Their growth and development have been promoted on sugar-free medium rather than on sugar-containing medium, provided that the environmental factors, such as CO2 concentration, light intensity and relative humidity, are controlled for promoting photosynthesis and transpiration of explants/shoots/plantlets in. vitro. Thus, environmental control is essential for promoting photosynthetic growth and development of in vitro plantlets. Several types of sugar-free (photoautotrophic) culture systems for large-scale micropropagation of plants have been developed. Advantages of sugar-free over conventional (heterotrophic or photomixotrophic) micropropagation systems are as follows: growth and development of plantlets in vitro are faster and more uniform, plantlets in vitro have less physiological and morphological disorders, biological contamination in vitro is less, plantlets have a higher percentage of survival during acclimatization ex vitro, and larger culture vessels could be used because of less biological contamination. Hence, production costs could be reduced and plant quality could be improved significantly with photoautotrophic micropropagation. Methods for the measurement and control of in vitro environments and the beneficial effects of environmental control on photosynthetic growth, development, and morphogenesis in large-scale production of

micropropagated plantlets are presented.

KEYWORDS: CO2- ENRICHMENT, CULTURE VESSEL, ELONGATION, INVITRO, LIGHT, PHOTOAUTOTROPHIC GROWTH, PHOTOSYNTHETIC CHARACTERISTICS, REGENERANTS, TRANSPLANTS

1216

Kozai, T., S. Kushihashi, C. Kubota, and K. Fujiwara. 1992. Effect of the difference between photoperiod and dark period temperatures, and photosynthetic photon flux-density on the shoot length and growth of potato plantlets invitro. *Journal of the Japanese Society for Horticultural Science 61(1):93-98.*

Potato plantlets (Solanum tuberosum L. cv. Benimaru) under CO2 enriched and photoautotrophic culture conditions were subjected to three different photo-/dark period temperature combinations (25-degrees/15-degrees-C, 200/20-degrees-C and 15-degrees/25- degrees-C) and two levels of photosynthetic photon flux densities (74 and 147-mu-mol.m-2.sec-1). The shoot length of the plantlets under the same photosytnthetic photon flux density (PPF) was reduced with decreasing the difference between photoperiod and dark period temperatures (it is named DIF, photoperiod temperature minus dark period temperature). No marked differences in the fresh and dry weights per plantlet were observed among the three DIF treatments in each PPF treatment. The higher PPF led to a decrease in the shoot length, an increase in the fresh weight, dry weight and leaf area per plantlet in each DIF treatment. It is suggested that shoot length of plantlets in vitro under CO2 enriched and photoautotrophic culture conditions can be controlled without reducing the weight increments and leaf area per plantlet by regulating the difference between photoperiod and dark period temperatures.

1217

Kozai, T., K. Watanabe, and B.R. Jeong. 1995. Stem elongation and growth of solanum-tuberosum L in-vitro in response to photosynthetic photon flux, photoperiod and difference in photoperiod and dark period temperatures. *Scientia Horticulturae 64(1-2):1-9.*

Stem elongation and growth of potato plantlets under three DIF (difference in photoperiod and dark period temperatures) levels, -9, 0 and +9, combined with two PPF (photosynthetic photon flux) levels, 70 (low) and 140 (high) mu mol m(-2) s(-1) provided by white cool fluorescent lamps, under 16 h day(-1) (long) or 8 h day(-1) (short) photoperiods, were studied. Four nodal cuttings were cultured for 21 days on 0.6 X 10(-4) m(3) MS (Murashige and Skoog, 1962, Physiol. Plant., 15: 473-497) agar (8 kg m(-3)) medium with no added sugar in 3.7 X 10(-3) m(3) polycarbonate boxes. Each box had two 10 mm holes covered with microporous filter to facilitate air exchange (3.6 air exchanges per hour). The average daily temperature in the culture room was set the same at 23 degrees C for all treatments, and CO2 concentration and relative humidity were maintained at 400-500 mu mol mol(-1) and 50-70%, respectively. Stem length was significantly suppressed under 0 or -9 DIF, high PPF and long photoperiod. Stem diameter, leaf area and number of leaves were significantly enhanced by long photoperiod and high PPF, but affected little by DIF level. Specific leaf area was little affected by photoperiod, but decreased under high PPF and under low DIF. Long photoperiod and high PPF led to an increase in the fresh and dry weights maintaining similar percentage dry matter and to enhanced root growth. Under the same amount of integrated PPF, fresh and dry weights of leaf, stem, root and whole plantlet were significantly higher under the long photoperiod and low PPF conditions than under the short photoperiod and high PPF conditions. Because of suppressed root growth under short photoperiod, shoot to root dry weight ratio increased under short photoperiod, but was not affected by DIF. It is suggested that under photoautotrophic conditions a combination of high PPF level, long photoperiod, and zero or negative DIF produces potato plantlets in vitro of short and thick stem with similar number and increased area of leaves, which are desirable for transfer to ex vitro conditions.

KEYWORDS: ALTERNATIONS, CAMPANULA-ISOPHYLLA MORETTI, INITIAL GROWTH, INVITRO, LIGHT-QUALITY, MORPHOLOGY, NIGHT TEMPERATURE, SEEDLINGS

1218

Kramer, G.F., E.H. Lee, R.A. Rowland, and C.L. Mulchi. 1991. Effects of elevated CO2 concentration on the polyamine levels of field-grown soybean at 3 O3 regimes. *Environmental Pollution 73(2):137-152.*

Effects of increased ozone (O3) and carbon dioxide (CO2) on polyamine levels were determined in soybean (Glycine max L. Merr. cv. Clark) grown in open-top field chambers. The chamber treatments consisted of three O3 regimes equal to charcoal filtered (CF), non-filtered (NF), and non-filtered plus 40 nl litre-1 O3 and CO2 treatments equal to 350, 400 and 500-mu-l litre-1 for a total of nine treatments. Leaf samples were taken at three different times during the growing season. Examination of growth and physiological characteristics, such as photosynthesis, stomatal resistance, and shoot weight, revealed that increasing CO2 ameliorated the deleterious effects of increased O3. Results from the initial harvest, at the pre-flowering growth stage (23 days of treatment), showed that increasing O3 at ambient CO2 caused increases in putrescine (Put) and spermidine (Spd) of up to six-fold. These effects were lessened with increased CO2. Elevated CO2 increased polyamines in plants treated with CF air, but had no effect in the presence of ambient or enhanced O3 levels. Leaves harvested during peak flowering (37 days of treatment) showed O3-induced increases in Put and Spd at ambient CO2 concentrations. However, increased CO2 levels inhibited this response by blocking the O3-induced polyamine increase. Leaves harvested during the pod fill stage (57 days of treatment) showed no significant O3 or CO2 effects on polyamine levels. Our results demonstrate that current ambient O3 levels induce the accumulation of Put and Spd early in the growing season and that further increases in O3 could result in even greater polyamine increases. These results are consistent with a possible antiozonant function for polyamines. The ability of increased CO2 to protect soybeans from O3 damage, however, does not appear to involve polyamine accumulation.

KEYWORDS: AIR- POLLUTANTS, ASCORBIC-ACID, INHIBITION, LEAF, LEAVES, NET PHOTOSYNTHESIS, OZONE, PLANTS, STRESS, ZUCCHINI SQUASH

1219

Kramer, K., A. Friend, and I. Leinonen. 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. *Climate Research 7(1):31-41.*

The importance of 3 phenological types of deciduous tree, and the effects of the occurrence of frost damage on growth of mixed-species forests, were evaluated using the models FORGRO and HYBRID, The climate change scenarios used were a doubling of the CO2 concentration (700 mu mol mol(-1)) and an increase in temperature ranging from 0 to 7 degrees C. Both FORGRO and HYBRID are mechanistic models treating eco-physiological processes in detail. FORGRO highlights potential growth in managed forests where all individuals of one species are of the same age and size, whereas HYBRID highlights growth in natural forests, including regeneration and mortality of individual trees that differ in age and size. Furthermore, the importance of inaccurate prediction of phenological events and frost hardiness for growth in mixed-species stands was evaluated by comparing dynamic models to

regression models. The dynamic models predict the timing of phenological events annually and the progression of frost hardiness during dormancy, whereas the regression models represent empirical relationships between the change in the average date of phenological events with a rise in mean winter temperature and the level of frost hardiness at the moment of leaf unfolding. The results of the climate change scenarios indicate for both FORGRO and HYBRID that: (1) the differences in net primary production (NPP) of the 3 phenological types considered are enhanced when grown in a mixed-species stand compared to a monospecies stand; and (2) the effects of frost damage on growth are more prominent in mixed-species stands than in monospecies stands. Regarding the accuracy of the dynamic approach compared to the regression approach for predicting the timing of leaf unfolding and spring frost damage, the dynamic approach for leaf unfolding results in a similar response of NPP to the regression approach, both for the monospecies and the mixed-species situation. The dynamic approach, however, yields larger differences in the NPP between the phenological types because the model predicts a greater advancement of leaf unfolding than does the regression approach. Comparing the regression approach to the dynamic approach with regard to frost hardiness, the regression approach shows a greater frequency of frost damage; because, according to the dynamic approach the minimum level of frost hardiness is attained after the date of leaf unfolding, thus reducing this frequency.

KEYWORDS: PHOTOSYNTHESIS, TRANSPIRATION, TREES

1220

Kramer, K., and G.M.J. Mohren. 1996. Sensitivity of FORGRO to climatic change scenarios: A case study on Betula pubescens, Fagus sylvatica and Quercus robur in the Netherlands. *Climatic Change 34(2):231-237.*

The impacts of the climate change predictions of four general circulation models (GFDL, GISS, OSU and UKMO) on net primary production (NPP) of Betula pubescens, Fagus sylvatica and Quercus robur in The Netherlands were analysed using the process-based model FORGRO. FORGRO is a model suitable to simulate growth of managed mono-species stands. For the GCMs mentioned, both transient and equilibrium 2 x CO2 scenarios of temperature and precipitation change were evaluated and compared with responses under current climate. It was found that the NPP increases in the transient scenarios, but remains the same or declines in the 2 x CO2 scenarios. This is because respiration increases more with rising temperature than photosynthesis. During the transient scenarios this effect gradually increases, while in the 2 x CO2 scenario this effect is operating over the entire simulation period. If water limitation is taken into account, then the NPP of the reference scenario is reduced. In both the transient and 2 x CO2 scenarios this water limitation is annulated, resulting in a stronger response of NPP compared to the situation without water limitation. This enhancement of the response is most pronounced in the transient scenario due to the gradual effect of temperature on respiration. Similar results were obtained with a version of FORGRO in which the photosynthesis module of HYBRID (PGEN) is incorporated, although the response in FORGRO- PGEN is usually higher than that of FORGRO. This is because the response of photosynthesis to CO2 rises with increasing temperature as defined in the PGEN-model, but not according to FORGRO.

KEYWORDS: CONDUCTANCE, GROWTH, MODEL, PHOTOSYNTHESIS, PREDICT

1221

Krapfenbauer, A., and K. Wriessnig. 1995. Anthropogenic environmental-pollution - the share of agriculture. *Bodenkultur 46(3):269-283.*

The increase of environmental pollution is in direct relation to the consumption of fossil coal, gas and oil and the progressive growth of the world population. Since 1950 these issues increased considerably and they will continue to increase in the future. At the moment the population increases by 1.9 %, the consumption of energy between 2 and 3 % and the environmental pollution up to 3.5 % annually. With the progressive growth of the world population and the increase in prosperity in the developed countries the demand for food increased also progressively and therewith the productivity index of the units of arable land, by growing consumption of fertilizers and the installation of irrigation systems. At the same time the pollution of air, water and soil caused by agriculture also grew progressively. But up to date there is still a shortcoming of reliable statistical facts and figures. A higher productivity index of the units of arable land in the different ecoclimatic zones of the earth leads to higher production and consumption by an inevitably higher turnover of plant nutrients and diverse gaseous substances, for example carbon mono- and dioxide, diverse compounds of nitrogen etc. At the same time an excess of the "critical loads" for soil, air and water must be expected. The main items of the emissions produced by an intensified agriculture are, besides carbon mono- and dioxide, methane, nitric and nitrous oxide, ammonia and diverse hydrocarbons. A higher productivity index is consequently related to a higher consumption. This also leads to an intensified turnover of carbon dioxide. There is consequently a progressive input of carbon dioxide resulting from the emissions of burning fossil fuel in the recently produced and consumed biomass. This inevitably leads to a higher level of carbon dioxide in the air. A main source of emissions of methane and ammonia is animal breeding. In Austria at this time from each of the 3,508.000 hectars of land used by agriculture annual emissions of 63 kg methane and 11 kg ammonia are resulting theoretically. The use of organic and inorganic fertilizers, the growing cultivation of legumes and the emissions of nitrogen compounds resulting from burning processes elevate likewise the pool and the annual turnover of nitrogen compounds by production and consumption of biomass. Inevitably related to it is a growing amount of the annual input of nitrogen compounds to the air, the soil and the water. A rough approximation says that at present agriculture contributes to the global anthropogenic pollution of the environment (air, soil and water) 85 % of the ammonia, 81 % of the nitrous oxide, 35 % of nitric mono- and dioxide, 70 % of the methane, 52 % of the carbon monoxide and 21 % of the carbon dioxide. Not considered in the figure for carbon dioxide is the inevitable increase of the level of CO2 in the air by the elevated turnover of biomass. The world population growth in the future leads to an increasing contribution of agriculture to the anthropogenic environmental pollution. For the developed countries this is an obligatory challenge to avoid surplus production. On a global scale there must be a sensible reduction of animal breeding to reduce the high emissions of methane and ammonia from this sector of agriculture. It must also be considered, that by feeding animals with vegetable food stuff, which also could be used for direct nutrition of man, the efficiency of it is lowered by a factor of 1:10. In spite of a growing crisis to maintain the alimentation of the growing world population in many countries the nutrition of man must rapidly be centered on vegetable food stuff rich in protein. At the same time an essential reduction of the environmental pollution resulting from animal breeding could be realized. Beside of it and other reducing issues a continuous growth of the world population, the energy consumption and environmental pollution will make it necessary to observe the development and reactions in the environment by monitoring and phenological observations. The results must be used to counteract finally by looking for adaptation strategies. Considering the realities it must be realized that by all means to mobilize for counteracting the environmental pollution directly, a certain climate change will be inevitable. The consequences will also be an outstanding challenge for the agriculture.

1222

Krapp, A., B. Hofmann, C. Schafer, and M. Stitt. 1993. Regulation of the expression of rbcs and other photosynthetic genes by carbohydrates - a mechanism for the sink regulation of photosynthesis. *Plant Journal 3(6):817-828.*

These experiments were carried out to investigate whether accumulation of carbohydrate leads to decreased expression of genes involved in photosynthesis. Addition of glucose to autotrophic cell suspension cultures of Chenopodium led to a large and reversible decrease of the steady state transcript levels of rbcS, cab and atp-delta within 5 h, but did not decrease 18S rRNA or transcript for two glycolytic enzymes. Run-on transcription in isolated nuclei showed that transcription rate had been decreased. [S-35]Methionine feeding showed that de novo synthesis of Rubisco was inhibited. Decreased rbcS transcript was also found after feeding glucose to detached leaves, and in transgenic plants expressing invertase in the apoplast to inhibit phloem transport, and in leaves on intact tobacco and potato plants which were cold- girdled to decrease export. The decrease of rbcS transcript level occurred within 12 h of cold-girdling. Comparison of carbohydrate content and rbcS transcript level indicated that carbohydrate content per se is not the direct signal for regulation of gene expression. Feeding of transported analogues indicates that metabolism rather than transport of the sugars is required. Over-expression of rbcS was found in low CO2, again indicating metabolic control of expression. ft is proposed that photosynthetic gene expression is inhibited by metabolic factors related to high carbohydrate content, and that this represents a basic mechanism for the 'sink regulation' of photosynthesis.

KEYWORDS: ACCLIMATION, CALVIN CYCLE ENZYMES, CELL-WALL, ELEVATED CO2, INHIBITION, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STARCH, SUCROSE SYNTHESIS, TRANSGENIC TOBACCO PLANTS

1223

Krapp, A., and M. Stitt. 1995. An evaluation of direct and indirect mechanisms for the sink- regulation of photosynthesis in spinach - changes in gas- exchange, carbohydrates, metabolites, enzyme-activities and steady-state transcript levels after cold-girdling source leaves. *Planta 195(3):313-323.*

Mature source leaves of spinach (Spinacia oleracea L.) plants growing hydroponically in a 9 h light (350 mu mol photons.m(- 2).s(-1))/15 h dark cycle at 20 degrees C in a climate chamber were fitted with a cold girdle around the petiole, 2 h into the light period. Samples were taken 1, 3 and 7 h later, and at the end of the photoperiod for the following 4 d. Control samples were taken from ungirdled leaves. in the first 7 h after fitting the cold girdle there was (compared to the control leaves) a two to fivefold accumulation of sucrose, glucose, fructose and starch, a 40-50% increase of hexose-phosphates and ribulose-1,5-bisphosphate, a decrease of glycerate-3-phosphate, a small decrease in sucrose-phosphate synthase activation, an increase of fructose-2,6-bisphosphate, increased activation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), but no significant change in photosynthetic rate or stomatal conductance. Steady-state transcript levels for rbcS (small subunit of Rubisco) and atp-D (D-subunit of the thylakoid ATP synthase) decreased 30%, cab (chlorophyll-a-binding protein) decreased by 15% and agp-S (S-isoenzyme of ADP-glucose pyrophosphorylase) and nra (nitrate reductase) rose twofold. On the following days, levels of carbohydrates continued to rise and the changes of metabolites were maintained. Transcripts for rbcS, cab and atpD declined to 20, 70 and 25% of the control values. From day 3 onward the maximum activity of Rubisco declined. This was accompanied by a further increase of Rubisco activation to over 90% and, from day 4 onwards, an inhibition of photosynthesis which was associated with high internal CO2 concentration (c(i)), high ribulose-1,5-bisphosphate, and low glycerate-3-phosphate. When the cold-girdle was removed on day 5 there was a gradual recovery of photosynthesis and decline of c(i) over the next 2 d. Hexose-phosphates levels and transcripts for rbcS, cab and atp-D completely recovered within 2 d, even though the levels of carbohydrates had not fully recovered. Activity of Rubisco only reverted partly after 2 d, and Rubisco activation state and the ribulose-1,5-bisphosphate/glycerate-3-phosphate ratio were still higher than in control leaves. Transcripts for nra and agp-S were also still higher than in control leaves. It is concluded (i) that a reversible modulation of gene expression in response to the export rate plays a central role in the mid-term feedback "sink" regulation of photosynthesis, and (ii) that feedback regulation of CO2 fixation by changes of P-i are of little importance in spinach under these conditions. Further (iii) the rapid and reciprocal changes in nra and agpS transcripts, compared to rbcS, provide evidence that gene expression could also contribute to the modulation of nitrate assimilation and carbohydrate storage in conditions of decreased sink demand.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CALVIN CYCLE ENZYMES, CHLOROPHYLL CONTENT, ELEVATED CO2, LIGHT ACTIVATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE PHOSPHATE SYNTHASE, TRANSGENIC TOBACCO PLANTS, YEAST- DERIVED INVERTASE

1224

Krauchi, N. 1993. Potential impacts of a climate change on forest ecosystems. *European Journal of Forest Pathology 23(1):28-50.*

Review of literature indicates that many uncertainties and assumptions exist in predicting the impacts of a climate change on forest ecosystems. However, current knowledge is sufficient to encourage any measures that are combating climate change, that is to reduce first and foremost the release of harmful substances to the atmosphere, lithosphere and biosphere.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GREENHOUSE, INCREASE, RADIATION BUDGET, RESPONSES, SENSITIVITY, TREES, VEGETATION

1225

Kriebitzsch, W.U., M. Liesebach, and F. Scholz. 1999. The influence of elevated CO2 on growth parameters of various provenances of European beech (Fagus sylvatica L.) at different irradiance. *Forstwissenschaftliches Centralblatt 118(1):51-65.*

In a greenhouse experiment one year old seedlings of seven provenances of beech (Fagus sylvatica L.) were grown under controlled conditions at two CO2 levels (350 ppm and 650 ppm) and different light intensities (2%, 17% and 100% relative irradiance). The response of the plants eo the various treatments was investigated by means of the leaf development during the growing season. At the end of the vegetation period leaf area and leaf dry weight per single leaf and per plant were measured. At the beginning of the growing period the provenances differed significantly in height and at the end of the vegetation period also in the mean leaf number, leaf area and leaf dry weight per plant. The area per single leaf is - in contrast to leaf dry weight and the specific leaf area - similar among all seven provenances. The light has an effect on all measured leaf parameters. In full light the leaf development started very early. Leaf number, leaf area, and leaf dry weight per single leaf and per plant decrease and specific leaf area increases under low light conditions. In the treatment "elevated CO2 environment and full irradiance" leaf number, leaf area and leaf dry weight per single leaf and per plant increased too. At reduced irradiance a higher CO2 content does not influence the measured leaf parameters. The results show already at this early stage that the climatic factors influencing plant growth and elevated CO2 interact strongly. For an overall view of the plants' reaction to growth conditions, investigations of the gas exchange of the leaves

and anatomical and morphological studies will be added.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, LEAF ANATOMY, LIGHT, RESPONSES, SEEDLINGS, TREES

1226

Kriebitzsch, W.U., M. Liesebach, and F. Scholz. 1999. Interactions between CO2 content and light on growth parameters of various provenances of beech (Fagus sylvatica L.). *Berichte Uber Landwirtschaft 77(1):65-76.*

In a greenhouse experiment one year old seedlings of seven provenances of beech (Fagus sylvatica L.) were grown under controlled conditions at two CO2 levels (350 ppm and 650 ppm) and different light intensities (2%, 17% and 100% relative irradiance). The response of the plants to the various treatments was investigated by means of the leaf development during the growing season. At the end of the vegetation period leaf area and leaf dry weight per single leaf and per plant were measured. At the beginning of the growing period the provenances differed significantly in the mean leaf number, leaf area and leaf dry weight per plant. The area per single leaf is - in Contrast to leaf dry weight and the specific leaf area - similar among all seven provenances. The light has an effect on all measured leaf parameters. In full light the leaf development started very early. Leaf number, leaf area, and leaf dry weight per single leaf and per plant decrease and specific leaf area increases under low light conditions. In the treatment "elevated CO2 environment and full irradiance" leaf number, leaf area and leaf dry weight per single leaf and per plant increased too. At reduced irradiance a higher CO2 content does not influence the measured leaf parameters. The results show already at this early stage that genetic variation is important and the climatic factors influencing plant growth and elevated CO2 interact strongly. For an overall view of the plants' reaction to growth conditions, investigations of the gas exchange of the leaves and anatomical and morphological studies will be added.

KEYWORDS: AMBIENT, AVAILABILITY, ELEVATED CARBON-DIOXIDE, ENRICHMENT, FOREST, NUTRIENTS, RESPONSES, SEEDLINGS, TREES

1227

Krishnan, P., and G. Ramakrishnayya. 1999. Survival of rice during complete submergence: effect of potassium bicarbonate application. *Australian Journal of Plant Physiology 26(8):793-800.*

The effect of potassium bicarbonate application to floodwater on the survival and growth of submergence-tolerant (FR13A) and -intolerant (IR42) rice cultivars during complete submergence was investigated. Potassium bicarbonate, applied at different rates to enhance floodwater carbon dioxide concentrations, increased the floodwater oxygen concentration. The treatment that had CuSO4, added alone to reduce algal growth showed the lowest O-2 concentration at the time of submergence and after 10 d of submergence. Potassium bicarbonate at higher rates tended to maintain the floodwater pH near neutrality while copper sulfate affected pH increase during a 10-day period of complete submergence. Potassium bicarbonate addition led to 100% survival of tolerant FR13A. Potassium bicarbonate, even at 0.01 mol m(-3) enhanced the survival of intolerant IR42 to 69% and at 0.1, 0.5 and 1.0 mol m(-3), the survival was above 85%. Dry weights of submerged plants showed increases in both rice cultivars in floodwater treated with potassium bicarbonate. The dry weight and leaf chlorophyll concentration of both cultivars increased with increasing rates of potassium bicarbonate. Algal chlorophyll concentration of floodwater treated with potassium bicarbonate was comparable to that of the control without copper sulfate. The findings suggest a possibility of environmental manipulation of floodwater by potassium bicarbonate application to enhance the survival and growth of rice cultivars during complete submergence.

KEYWORDS: CO2, FLOODWATER, GROWTH, TOLERANCE

1228

Kronfuss, G., A. Polle, M. Tausz, W.M. Havranek, and G. Wieser. 1998. Effects of ozone and mild drought stress on gas exchange, antioxidants and chloroplast pigments in current-year needles of young Norway spruce [Picea abies (L.) Karst.]. *Trees-Structure and Function 12(8):482-489.*

To investigate the effects of ozone exposure and soil drought, singly and in combination, on gas-exchange, antioxidant contents and pigments in current-year needles of Norway spruce [Picea abies (L.) Karst.] 4-year-old seedlings were fumigated in growth chambers with either charcoal-filtered air or with 100 nl l(-1) ozone for 106 days. After 3 weeks a 20% reduction in gas exchange was observed In ozone-treated seedlings. However, no further decrease occurred in spite of continued ozone exposure. Whole needle ascorbate and apoplastic ascorbate increased until the end of the experiment and contents were 62% and 82%, respectively, higher than in ozone-free controls. This increase in ascorbate might have protected net photosynthesis from Further decline. Ozone pre-treated plants and ozone-free controls were subjected to soil drought for 38 days which caused stomatal narrowing. Thereby ozone uptake was reduced when compared to well watered seedlings. At the end of the experiment drought alone, and even more in combination with ozone, had also caused an increase in ascorbate. Glutathione increased only in drought-stressed seedlings. The redox states of the ascorbate and the glutathione pools were not affected by any treatment. Superoxide dismutase activity declined under both stresses but was most reduced by ozone alone. While chlorophyll and neoxanthin contents remained unchanged, carotenes were significantly decreased upon drought. The combination of O-3 and drought induced increased lutein contents, an increased pool size of the xanthophyll cycle as well as an increased epoxidation status of the xanthophyll cycle. These results suggest that spruce needles seem To be able to acclimate to ozone stress but also to drought stress by increasing their ascorbate pools and protecting pigments.

KEYWORDS: ELEVATED CO2, ENHANCED OZONE, EXPOSURE, FAGUS-SYLVATICA L, GROWTH-RESPONSES, LARIX-DECIDUA MILL, PHOTOSYNTHESIS, RED SPRUCE, SEEDLINGS, WATER DEFICIT

1229

Krug, H., and H.P. Liebig. 1995. Models for planning and control of transplant production in climate controlled greenhouses .2. Production control. *Gartenbauwissenschaft 60(1):22-28.*

A model has been developed to control transplant growth. It is based on growth curves, derived under varied greenhouse climates (global irradiances, artificial light, air and soil heating, CO2-concentration), and corresponding growth rates, which were related to the intensities of the climatic factors by a regression function. The best fit for the growth rates was obtained by splitting the raising period in an exponential phase, described by a constant Relative Growth Rate, and a linear phase, described by the Mean Growth Rate. As the frequency distribution shows, 81% of the 186 sets from October to March hit the 4 +/- 0.2 g data of the growth function in +/- 2 days. Simulations for the most extremes out of 36 years weather conditions for 5 dates from October to February show the deviations from the estimated curves based on long term normals, the potentials of climate control by decreasing or increasing set points of air temperature, CO2 concentration, and artificial light as well as the effects of the starting point for control. Aspects of application and completion as well as the necessity of timing

by CO2 enrichment and artificial lighting are discussed.

1230

Kruger, E.L., J.C. Volin, and R.L. Lindroth. 1998. Influences of atmospheric CO2 enrichment on the responses of sugar maple and trembling aspen to defoliation. *New Phytologist 140(1):85-94.*

Impacts of defoliation on the growth and physiology of sugar maple (Acev saccharum Marsh.) and trembling aspen (Populus tremuloides Michx.) were examined in ambient and CO2-enriched atmospheres. Saplings were grown for 70 d in controlled environments, wherein CO2 mole fractions averaged either 356 mu mol mol(-1) or 645 mu mol mol(-1), under a PPF of 500 mu mol m(-2) s(-1). On day 49 of the study, 50 % of the leaf area was removed from a subset of each species in both CO2 environments. Relative growth rate (RGR) and its physiological and morphological determinants were monitored before and after defoliation. For non-defoliated saplings of both species, a slight stimulation of RGR (c. 5 %) in elevated CO2 led to a modest increase (9-11 %) in final sapling weight. In the case of maple, the minimal growth response corresponded with minor CO2 effects on specific leaf area (SLA) and leaf weight ratio (LWR), and an apparent CO2-induced down-regulation of photosynthetic metabolism. For aspen, the CO2 stimulation of photosynthesis was largely offset by a decrease in SLA. Responses to defoliation differed markedly between species and CO2 environments. Defoliation decreased maple RGR in ambient CO2, whereas the opposite occurred in elevated CO2. The latter led to complete recovery of plant weight (compensation), and was attributed to a defoliation-induced increase in carbon allocation to new leaves, along with a reversal of photosynthetic CO2 acclimation in that foliage. In both environments, aspen RGR increased after defoliation, facilitating almost full compensation. Defoliation increased light penetration into the aspen canopy, and it was estimated that the resultant stimulation of photosynthesis in lower leaves would have more than offset the concomitant decrease in LWR. CO2 enrichment might substantially enhance the ability of certain tree species to recover from herbivory. Moreover, responses to elevated CO2 might be largest in the presence of stresses, such as herbivory, that decrease plant source:sink ratios.

KEYWORDS: CARBON DIOXIDE, DECIDUOUS TREES, ELEVATED CO2, GAS-EXCHANGE, INSECT PERFORMANCE, NO3 AVAILABILITY, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RELATIVE GROWTH-RATE, SEEDLINGS

1231

Kruijt, B., C. Barton, A. Rey, and P.G. Jarvis. 1999. The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO2 concentration and climate. *Hydrology and Earth System Sciences 3(1):55-69.*

The 3-dimensional forest model MAESTRO was used to simulate daily and annual photosynthesis and transpiration fluxes of forest stands and the sensitivity of these flutes to potential changes in atmospheric CO2 concentration ([CO2]), temperature, water stress and phenology. The effects of possible feed-backs from increased leaf area and limitations to leaf nutrition were simulated by imposing changes in leaf area and nitrogen content. Two different tree species were considered: Picea sitchensis (Bong.) Carr., a conifer with long needle longevity and large leaf area, and Betula pendula Roth., a broad-leaved deciduous species with an open canopy and small leaf area. Canopy photosynthetic production in trees was predicted to increase with atmospheric [CO2] and length of the growing season and to decrease with increased water stress. Associated increases in leaf area increased production further only in the B. pendula canopy, where the original leaf area was relatively small. Assumed limitations in N uptake affected B. pendula more than P. sitchensis. The effect of increased temperature was shown to depend on leaf area and nitrogen content. The different sensitivities of the two species were related to their very different canopy structure. increased [CO2] reduced transpiration, but larger leaf area, early leaf growth, and higher temperature all led to increased water use. These effects were limited by feedbacks from soil water stress. The simulations suggest that, with the projected climate change, there is some increase in stand annual 'water use efficiency', but that actual water losses to the atmosphere may not always decrease.

KEYWORDS: ELEVATED CO2, ENRICHMENT, FOREST ECOSYSTEMS, GAS-EXCHANGE, GROWTH-RESPONSE, LEAF, MODEL, PLANT GROWTH, SPRUCE PICEA-SITCHENSIS, TEMPERATURE

1232

Krupa, S.V. 1997. Global climate change: Processes and products - An overview. *Environmental Monitoring and Assessment 46(1-2):73-88.*

Our knowledge of global climate change has many uncertainties. Whether global air temperature will increase, by how much, and when, are subject to debate, but there is little doubt that tropospheric concentrations of several trace gases are increasing. While possible increases in the average air temperature is a product of these changes, the increases in the trace gases alone will have an effect on agriculture. Increases in the ambient concentrations of carbon dioxide are expected to have a positive net effect on crop production. In contrast, any increases in the penetration of surface-level ultraviolet-B (280-320 nm) radiation, and known increases in surface ozone concentrations, are considered to have adverse effects on certain crops. Our present knowledge of the joint effects on crops of elevated levels of carbon dioxide, ultraviolet-B radiation and ozone, and possible alterations in air temperature and precipitation patterns, is virtually zero. Therefore, any predictions of the effects of global climate change on agriculture are subject to significant uncertainties. In contrast, coupling of climate change (only temperature and precipitation) models to crop production has led to a number of future scenarios. In spite of their present limitations, results from these efforts can be useful in planning for future agriculture.

KEYWORDS: CO2, DEPLETION, EXPOSURES, RESPONSES, SOLAR ULTRAVIOLET-RADIATION, STRATOSPHERIC OZONE, SURFACE, TROPOSPHERIC OZONE, UV-B RADIATION, VEGETATION

1233

Krupa, S.V., and R.N. Kickert. 1993. The greenhouse-effect - the impacts of carbon-dioxide (co2), ultraviolet-b (uv-b) radiation and ozone (o3) on vegetation (crops). *Vegetatio 104:223-238.*

Man's influence on the 'greenhouse effect,' the heating of the atmosphere due to increasing concentrations of tropospheric trace gases, is of much international concern. Among the climatic variables, elevated levels of carbon dioxide (CO2), ultraviolet-B (UV-B) radiation and ozone (O3) are known to have a direct effect on vegetation. Our current knowledge of these effects is mainly based on studies involving single stress mode. Thus, the joint effects of CO2, UV-B and O3 on vegetation are poorly understood. Nevertheless, based on the literature analysis of plant response to individual stress factors, it can be concluded that sorghum, pea, bean, potato, oat, lettuce, cucumber, rice and tomato are among the crop species potentially sensitive to the joint effects of the aforementioned three variables. Similar information for tree species is essentially lacking. At least with some climatic variables such as O3, present modeling efforts of cause-effect relationships have proven to be controversial. While at a regional geographic scale ambient CO2 concentrations appear to be relatively homogeneous, ambient concentrations of O3 exhibit significant temporal and spatial variability. Because of the protective action of O3 against UV-B, similar but inverse

temporal and spatial variability is expected in the surface levels of UV-B. Thus, future experimental designs should consider these exposure dynamics and modeling cause-effect relationships should be directed to stochastic processes.

KEYWORDS: ATMOSPHERIC CO2, EXPOSURE, FIELD, PROTECT VEGETATION, RESPONSES, STRATOSPHERIC OZONE, SURFACE, TROPOSPHERIC OZONE, UNITED-STATES, YIELD

1234

Krupa, S.V., and A.H. Legge. 1995. Air-quality and its possible impacts on the terrestrial ecosystems of the north-american great-plains - an overview. *Environmental Pollution 88(1):1-11.*

Over the past several decades, numerous studies have been conducted on the impacts of air pollutants (air quality) on terrestrial ecosystems (crops and forests). Although ambient air is always composed of pollutant mixtures, in determining the relative air quality and its ecosystem impacts at a given geographic location and time, a predominant number of studies have shown that at the present time surface level O-3 is the most important phytotoxic air pollutant. Within the North American Great Plains, the precursors; for surface-level O-3 are mainly anthropogenic NOx and VOCs (volatile organic compounds). Texas and Alberta ta are the top regions of such emissions in the United States and Canada, respectively. This appears to be due mainly to the prevalence of natural gas and/or oil industry in the two regions and the consequent urbanization. Nevertheless, the total emissions of NOx and VOCs within the North American Great Plains represent only about 25- 36% of the corresponding total emissions within the contiguous United States and the whole of Canada. Within the Great Plains many major crop and tree species are known to be sensitive to O-3. This sensitivity assessment, however, is based mainly on our knowledge from univariate (O-3 only) exposure-plant response studies. In the context of global climate change, in almost all similar univariate studies, elevated CO2, concentrations have produced increases in plant biomass (both crop and tree species). The question remains as to whether this stimulation will offset any adverse effects of elevated surface O-3 concentrations. Future research must address this important issue both for the Great Plains and for all other geographic locations, taking into consideration spatial and temporal variabilities in the ambient concentrations of the two trace gases.

KEYWORDS: B RADIATION, OZONE

1235

Kubiske, M.E., and K.S. Pregitzer. 1996. Effects of elevated CO2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology 16(3):351-358.*

Photosynthetic light response curves (A/PPFD), leaf N concentration and content, and relative leaf absorbance (alpha(r)) were measured in 1-year-old seedlings of shade- intolerant Betula papyrifera Marsh., moderately shade-tolerant Quercus rubra L. and shade-tolerant Acer rubrum L. Seedlings were grown in full sun or 26% of full sun (shade) and in ambient (350 ppm) or elevated (714 ppm) CO2 for 80 days. In the shade treatments, 80% of the daily PPFD on cloud-free days was provided by two 30-min sun patches at midday. In e. rubra and A. rubrum, leaf N concentration and a, were significantly higher in seedlings in the shade treatments than in the sun treatments, and leaf N concentration was lower in seedlings in the ambient CO2 treatments than in the elevated CO2 treatments. Changes in a, and leaf N content suggest that reapportionment of leaf N into light harvesting machinery in response to shade and elevated CO2 tended to increase with increasing shade tolerance of the plant. Shifts induced by elevated CO2 in the A/PPFD relationship in sun plants were largest in B. papyrifera and least in A. rubrum: the reverse was true for shade plants. Elevated CO2 resulted in increased light-saturated A in every species x light treatment combination, except in shaded B. papyrifera. The light compensation point (T) decreased in response to shade in all species, and in response to elevated CO2 in A. rubrum and e. rubra. Acer rubrum had the greatest increases in apparent quantum yield (phi) in response to shade and elevated CO2. To illustrate the effects of shifts in A, r and phi on daily C gain, daily integrated C balance was calculated for individual sun and shade leaves. Ignoring possible stomatal effects, estimated daily (24 h) leaf C balance was 218 to 442% higher in the elevated CO2 treatments than in the ambient CO2 treatments in both sun and shade seedlings of e. rubra and A. rubrum. These results suggest that the ability of species to acclimate photosynthetically to elevated CO:! may, in part, be related to their ability to adapt to low irradiance. Such a relationship has implications for altered C balance and nitrogen use efficiency of understory seedlings.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, PHASEOLUS-VULGARIS L, PLANT-PLANT INTERACTIONS, SEEDLINGS, SUCCESSIONAL STATUS, TROPICAL TREES, WATER-STRESS

1236

Kubiske, M.E., and K.S. Pregitzer. 1997. Ecophysiological responses to simulated canopy gaps of two tree species of contrasting shade tolerance in elevated CO2. *Functional Ecology 11(1):24-32.*

1. One-year-old seedlings of shade tolerant Acer rubrum and intolerant Betula papyrifera were grown in ambient and twice ambient (elevated) CO2, and in full sun and 80% shade for 90 days. The shaded seedlings received 30-min sun patches twice during the course of the day, Gas exchange and tissue-wafer relations were measured at midday in the sun plants and following 20 min of exposure to full sun in the shade plants to determine the effect of elevated CO2 on constraints to sun- patch utilization in these species. 2. Elevated CO2 had the largest stimulation of photosynthesis in B. papyrifera sun plants and A. rubrum shade plants, 3. Higher photosynthesis per unit leaf area in sun plants than in shade plants of B. papyrifera was largely owing to differences in leaf morphology, Acer rubrum exhibited sun/shade differences in photosynthesis per unit leaf mass consistent with biochemical acclimation to shade. 4. Betula papyrifera exhibited CO2 responses that would facilitate tolerance to leaf water deficits in large sun patches, including osmotic adjustment and higher transpiration and stomatal conductance at a given leaf-water potential, whereas A. rubrum exhibited large increases in photosynthetic nitrogen-use efficiency. 5. Results suggest that species of contrasting successional ranks respond differently to elevated CO2, in ways that are consistent with the habitats in which they typically occur.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, COOCCURRING BIRCH, GROWTH-RESPONSE, LEAF GAS- EXCHANGE, LIGHT CONDITIONS, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER RELATIONS

1237

Kubiske, M.E., K.S. Pregitzer, C.J. Mikan, D.R. Zak, J.L. Maziasz, and J.A. Teeri. 1997. Populus tremuloides photosynthesis and crown architecture in response to elevated CO2 and soil N availability. *Oecologia 110(3):328-336.*

We tested the hypothesis that elevated CO2 would stimulate proportionally higher photosynthesis in the lower crown of Populus trees due to less N retranslocation, compared to tree crowns in ambient CO2. Such a response could increase belowground C allocation, particularly in trees with an indeterminate growth pattern such as Populus tremuloides. Rooted cuttings of P. tremuloides were grown in ambient and twice ambient (elevated) CO2 and in low and high soil N

availability (89 +/- 7 and 333 +/- 16 ng N g(-1) day(-1) net mineralization, respectively) for 95 days using open-top chambers and open-bottom root boxes. Elevated CO2 resulted in significantly higher maximum leaf photosynthesis (A(max)) at both soil N levels. A(max) was higher at high N than at low N soil in elevated, but not ambient CO2. Photosynthetic N use efficiency was higher at elevated than ambient CO2 in both soil types. Elevated CO2 resulted in proportionally higher whole leaf A in the lower three-quarters to one-half of the crown for both soil types. At elevated CO2 and high N availability, lower crown leaves had significantly lower ratios of carboxylation capacity to electron transport capacity (V-cmax/J(max)) than at ambient CO2 and/or low N availability. From the top to the bottom of the tree crowns, V-cmax/J(max) increased in ambient CO2, but it decreased in elevated CO2 indicating a greater relative investment of N into light harvesting for the lower crown. Only the mid-crown leaves at both N levels exhibited photosynthetic down regulation to elevated CO2. Stem biomass segments (consisting of three nodes and internodes) were compared to the total A(leaf) for each segment. This analysis indicated that increased A(leaf) at elevated CO2 did not result in a proportional increase in local stem segment mass, suggest ing that C allocation to sinks other than the local stem segment increased disproportionally. Since C allocated to roots in young Populus trees is primarily assimilated by leaves in the lower crown, the results of this study suggest a mechanism by which C allocation to roots in young trees may increase in elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON GAIN, ECOSYSTEMS, GAS-EXCHANGE, LEAF AGE, NITROGEN, NODAL REGION, PLANTS, POPLAR POPULUS, SHOOT GROWTH

1238

Kubiske, M.E., K.S. Pregitzer, D.R. Zak, and C.J. Mikan. 1998. Growth and C allocation of Populus tremuloides genotypes in response to atmospheric CO2 and soil N availability. *New Phytologist 140(2):251-260.*

We grew cuttings of two early (mid Oct.) and two late (early Nov.) leaf-fall Populus tremuloides Michx. genotypes (referred to as genotype pairs) for c. 150 d in open-top chambers to understand how twice-ambient (elevated) CO2 and soil N availability would affect growth and C allocation. For the study, we selected genotypes differing in leaf area duration to find out if late-season photosynthesis influenced C allocation to roots. Both elevated CO2 and high soil N availability significantly increased estimated whole-tree photosynthesis, but they did so in different ways. Elevated CO2 stimulated leaf-level photosynthesis rates, whereas high soil N availability resulted in greater total plant leaf area. The early leaf-fall genotype pair had significantly higher photosynthesis rates per unit leaf area than the late leaf-fall genotype pair and elevated CO2 enhanced this difference. The early leaf-fall genotype pair had less leaf area than the late leaf-fall genotype pair, and their rate of leaf area development decreased earlier in the season. Across both genotype pairs, high soil N availability significantly increased fine root length production and mortality by increasing both the amount of root length present, and by decreasing the life span of individual roots. Elevated CO2 resulted in significantly increased fine root production and mortality in high N but not low N soil and did not affect fine root life span. The early leaf-fall genotype pair had significantly greater fine root length production than the late leaf-fall genotype pair across all CO2 and N treatments. These differences in belowground C allocations are consistent with the hypothesis that belowground C and N cycling is strongly influenced by soil N availability and will increase under elevated atmospheric CO2. In addition, this study reinforces the need for better understanding of the variation in tree responses to elevated CO2, within and among species.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FINE ROOTS, GAS-EXCHANGE, LEAF, NITROGEN STRESS, PHYSIOLOGY, PLANT, ROOT-GROWTH

1239

Kubo, Y., O. Hirata, A. Inaba, and R. Nakamura. 1996. Respiration and ethylene production in fruits and vegetables held in carbon dioxide-enriched atmospheres - Effects of temperature and carbon dioxide concentration. *Journal of the Japanese Society for Horticultural Science 65(2):403-408.*

The rates of respiration and ethylene production in various fruits and vegetables held in 0.60% CO2 at 25 degrees C or 60% CO2 at 5-25 degrees C were determined by an automated microcomputer system. In peaches, apples, tomatoes, and broccoli, dose-dependent decreases of O-2 uptake and C2H4 production were observed during treatment with various concentrations of CO2 at 25 degrees C. Oxygen uptake in bananas was inhibited at 10% CO2 and higher, whereas C2H4 production increased as the ambient CO2 concentration was elevated. CO2 concentration had little or no effect on O-2 uptake in satsuma mandarin. Oxygen uptake in lettuce at 20% CO2 and below was similar to that under air, whereas induction of C2H4 production and an enhanced O-2 uptake were observed in lettuce held in 40% CO2 and higher. Inhibition of O-2 uptake and C2H4 production in peaches by 60% CO2 declined as the temperature was lowered to the range of 5-25 degrees C. In broccoli held in 60% CO2, the inhibition of O-2 uptake was temperature-dependent, but C2H4 production was suppressed to trace level at all temperatures. The induction of C2H4 production and enhancement of O-2 uptake in lettuce by 60% CO2 occurred distinctly at 25 degrees C, slightly at 15 degrees C, but not at 10 degrees C and 5 degrees C.

KEYWORDS: CO2, CROPS, STORAGE

1240

Kubo, Y., A. Inaba, and R. Nakamura. 1990. Respiration and C2H4 production in various harvested crops held in CO2-enriched atmospheres. *Journal of the American Society for Horticultural Science 115(6):975-978.*

1241

Kubo, Y., K. Sakota, A. Inaba, and R. Nakamura. 1996. Effects of high carbon dioxide exposure on ethylene biosynthesis in peach and tomato fruits. *Journal of the Japanese Society for Horticultural Science 65(2):409-415.*

Ethylene production, oxygen uptake, the activities of 1-aminocyclopropane-1-carboxylic acid (ACC) synthase and ACC oxidase in vivo and the contents of ACC and 1- (malonylamino)cyclopropane-1-carboxylic acid (MACC) were determined in peach and tomato fruits held in carbon dioxide- enriched atmosphere. Ethylene production in peaches decreased to a trace level with 60% carbon dioxide and in tomatoes to 50% of the initial level. The ethylene production rates in both fruits reverted to the initial level when the fruits were transferred back to air. Oxygen uptake in both fruits was markedly inhibited during carbon dioxide exposure. In vivo activities of ACC oxidase and ACC synthase in both fruits were also inhibited during carbon dioxide exposure. ACC content in peaches held in carbon dioxide-enriched atmosphere decreased but it increased in tomatoes. The level of MACC in peaches was constant during carbon dioxide treatment, whereas that in tomatoes slightly increased. These results indicate that inhibition in ethylene production by carbon dioxide may be mediated mainly by reduced conversion of ACC to ethylene in tomatoes, whereas in peaches, the inhibition is attributed to both reduced conversion of S-adenosylmethionine to ACC and ACC to ethylene.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ASSAY, ATMOSPHERES, CO2, CONVERSION, CROPS, IDENTIFICATION, RESPIRATION, VEGETABLES

1242

Kubo, Y., H. Tsuji, A. Inaba, and R. Nakamura. 1993. Effects of elevated co2 concentrations on the ripening in banana fruit by exogenous C2h4. *Journal of the Japanese Society for Horticultural Science 62(2):451-455.*

Green bananas were treated with 0 to 60% CO2 and 1 to 100 PPM C2H4 to study their interaction on the ripening process. 1. The CO2 treatment did not block completely the initiation of ripening of banana by exogenous C2H4. When the concentration of applied C2H4 was kept constant and the CO2 concentration high, the appearance of the yellow pigment in the peel was delayed. 2. The combination of various concentrations of CO2 and C2H4 on the respiratory climacterics in green banana, monitored with an automated microcomputer system, revealed that the onset of the climacteric rise of bananas under any CO2 concentration combined with 1 PPM C2H4 commenced simultaneously with fruits which were kept under air and 1 PPM C2H4. However, the progress of the climacteric rise was slower and the peaks were lower at high CO2 concentration than they were at low CO2 concentrations. With 60% CO2 and 100 PPM C2H4, the fruit color remained green until the end of the gas treatment, in spite of the slow respiratory rise and ripening of the flesh. Our results suggest that the elevated CO2 concentration has no effect on the initiation-time of banana ripening induced.by exogenous C2H4 but lowers the progress rate of ripening.

KEYWORDS: ATMOSPHERES, CROPS, ETHYLENE, RESPIRATION, VEGETABLES

1243

Kuehny, J.S., M.M. Peet, P.V. Nelson, and D.H. Willits. 1991. Nutrient dilution by starch in CO2-enriched chrysanthemum. *Journal of Experimental Botany 42(239):711-716.*

Increasing growth irradiance and CO2 generally decreases foliar nutrient concentration on a dry weight basis and increases foliar starch concentration. However, the extent to which starch concentrations 'dilute' foliar nutrient concentrations when the latter are expressed on a dry weight basis is not known. To determine the importance of differential starch accumulation in calculating nutrient concentrations on a dry weight basis, leaf nutrient and starch concentrations were measured in Chrysanthemum x morifolium 'Fiesta' (Ramat.) cuttings grown at three irradiance levels and two CO2 levels for eight weeks in both winter and spring. On a dry weight basis, foliar concentrations of most nutrients were lower in both seasons as a result of the elevated CO2 and irradiance levels, and total dry weights were higher. Per cent starch was greater at the high CO, level in both seasons but was only greater at higher irradiances in the winter experiment. When starch was subtracted from the leaf dry weights, the differences between CO2 and irradiance treatments disappeared with respect to N, P, K, Ca, Mg, S, and B but not for Fe, Mn, Zn, and Cu.

KEYWORDS: ACCLIMATION, CARBOHYDRATE, CARBON-DIOXIDE CONCENTRATION, GREENHOUSES, GROWTH, HIGH CO2, LIGHT-INTENSITY, MORIFOLIUM RAMAT, PHYSIOLOGY

1244

Kuhn, M., C. Niewohner, M. Isenbeck-Schroter, and H.D. Schulz. 1998. Determination of major and minor constituents in anoxic thermal brines of deep sandstone aquifers in Northern Germany. *Water Research 32(2):265-274.*

The common process of low energy geothermal exploitation is the doublet of production- and reinjection borehole. The quality of water reinjected into a elastic reservoir is essential for the reliability of an injection well. In order to estimate precipitation reactions it is necessary to obtain extensive reliable analysis data of the water for the use of thermodynamic modelling. For thermal anoxic brines, the analysis of major and especially minor ion content is difficult because of matrix effects and possible iron precipitation. A selection of analysing methods were applied to two anoxic thermal brines of deep sandstone aquifers of Northern Germany. Detection limits and measured data of the major constituents are presented of Na+, K+, NH4+, Ca2+, Mg2+, Ba2+, Sr2+, Fe- total, Mn2+, SiO44-, B(OH)(3), Zn2+, Pb2+, Cd2+, F-, Cl-, Br-, I-, SO42-, SO32-, S2-, PO43-, NO3-, NO2- and DOC. The measurements were done with ICP-OES, ionselective electrodes, photometry, polarography, titration methods, ion chromatography and TOC-analyzer. Except for SO(4)(2-)and Cl-, the anion analysis was done on-site, since the high iron content in the anoxic water requires acidification in order to prevent iron hydroxide precipitation. The minor constituents Zn2+, Pb2+, Cu2+, Cd2+, Cr3+, Sc3+, Co2+, Y3+, La3+, Ce3+, Al3+, were enriched by trace matrix separation using the cation exchange resin Chelex((R))100. The element concentrations in the acidic eluates of the Chelex((R))100 columns were measured using ICP- MS. The pH dependency of the exchange equilibrium at pH values of 4, 5 and 6 (buffered and unbuffered) as well as the relation to the salt content between 35 and 250 gl(-1) total dissolved solids of Na-K-Ca-Mg-Cl-SO4 were evaluated by sensitivity analysis.

KEYWORDS: CHELEX-100 RESIN, ELEMENTS, HEAVY-METALS, PRE-CONCENTRATION EFFICIENCY, SEAWATER, SPECTROMETRY

1245

Kull, O., A. Sober, M.D. Coleman, R.E. Dickson, J.G. Isebrands, Z. Gagnon, and D.F. Karnosky. 1996. Photosynthetic responses of aspen clones to simultaneous exposures of ozone and CO2. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(4):639-648.*

Current projections indicate steady increases in both trophospheric ozone and carbon dioxide well into the next century with concurrent increases in plant stress. Because information about effects of these interacting stresses on forest trees is limited, we have conducted ozone and carbon dioxide experiments using ozone-tolerant and ozone-sensitive trembling aspen (Populus tremuloides Michx.) clones (clones 216 and 259, respectively). Aspen plants were grown either in pots (square-wave study) or in the ground (episodic study) in open- top chambers. Plants in the square-wave study were exposed for a single growing season to charcoal-filtered air (CF) or to CF plus elevated carbon dioxide (CO2), ozone (O-3), or O-3 plus CO2 (O-3 + CO2). Plants in the episodic study were exposed for three growing seasons to CF, twice simulated ambient (2x) O-3 (2x O-3), or 2x O-3 plus CO2 (2x O-3 + CO2). Photosynthetic measurements were made either in the open-top chambers at treatment CO2 concentrations or in controlled-environment cuvettes with various CO2 concentrations, producing assimilation versus intercellular CO2 concentration (A/C-i) curves. Ozone decreased photosynthetic rate and stomatal conductance and accelerated leaf senescence. Elevated CO2 increased photosynthetic rate and decreased stomatal conductance when measured at treatment CO2 concentrations, and exacerbated the negative effect of O-3 on photosynthesis. For example, for clone 259, photosynthesis decreased 9% for the O-3 treatment compared with the CF treatment, but decreased 24% for the O-3 + CO2 treatment compared with the CO2 treatment. Similar decreases for clone 216 of 2% and 6% for O-3 and O-3 + CO2, respectively, were not significant. A/C-i curves showed that O-3 decreased carboxylation efficiency and maximum photosynthetic rate and that photosynthetic inhibition in response to O-3 was greater with

elevated CO2. The simultaneous declines in all factors of photosynthetic gas exchange measurements suggest that the equilibrium between stomatal conductance, carboxylation, and light harvesting systems was not disrupted by O-3 and O-3 x CO2 interactions. Carbon dioxide did not ameliorate the detrimental effects of O-3 on the leaf photosynthetic apparatus. In fact, the O-3-tolerant clone appeared more sensitive to O-3 with elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, BISPHOSPHATE CARBOXYLASE OXYGENASE, CARBON DIOXIDE, DIFFERENTIAL RESPONSE, GAS-EXCHANGE, LOBLOLLY-PINE, NET PHOTOSYNTHESIS, PHASEOLUS-VULGARIS, POPULUS-TREMULOIDES MICHX, STOMATAL CONDUCTANCE

1246

Kunz, R.P., R.E. Schulze, and R.J. Scholes. 1995. An approach to modelling spatial changes of plant carbon:nitrogen ratios in southern Africa in relation to anticipated global climate change. *Journal of Biogeography 22(2-3):401-408.*

The carbon to nitrogen (C:N) ratio is the main factor determining the forage quality of a plant, with a low C:N ratio indicating relatively good plant digestibility and a high C:N ratio inferring relatively poor forage quality. Global atmospheric composition and climate change effects on plant carbon to nitrogen ratios are thus likely to be important when predicting possible second-order impacts of the enhanced greenhouse effect on rangeland forage quality and the resultant feeding habits of foraging animals and herbivorous insects. Equations relating the assimilation of total carbon and nitrogen rates to monthly air temperature, the ambient CO2 level and soil fertility were used together with detailed spatial climatic and soil databases to simulate regional patterns of C:N ratios over southern Africa. Carbon to nitrogen ratios were estimated for both the present climate and for a possible future climate scenario defined by a general 2 degrees C mean daily temperature increase over southern Africa (but with latitudinal, seasonal and diurnal adjustments made), an increase in atmospheric CO2 concentration from 360 to 560 ppmv, but with no changes in precipitation patterns. When C:N differences between future and present climates are examined, results indicate both relative increases and decreases over southern Africa in a regional context, ranging from - 8 to + 8%. Areas where the C:N ratios decreased indicate that for the future climate scenario which was assumed the relative increase in assimilated nitrogen would be greater than that for carbon. Similarly, areas where the C:N ratios increased indicate that the relative increase in assimilated carbon would be greater than that for nitrogen. In this study, regions sensitive to climate change effects on C:N ratios in southern Africa have therefore been identified and with that, those areas where the consumption of plant matter may be expected to increase or decrease as a result of anticipated global climate change.

1247

Kurets, V.K., S.N. Drozdov, and E.G. Popov. 1999. Intraspecies diversity in the response of net photosynthesis in cucumber plants to elevated concentrations of atmospheric carbon dioxide. *Russian Journal of Plant Physiology 46(2):159-162.*

Relationships between net photosynthesis of intact cucumber plants (Cucumis sativus L., cvs. Alma-Atinskii 1, Teplichnyi rannii 65, and Syurpriz 66) and irradiance, air and soil temperatures, and ambient CO2 concentration were simulated by the multiway factorial method. Analysis of the models demonstrated marked cultivar-specific differences in plant responses to environmental conditions, in terms of both the potential highest values and conditions for their expression. This allowed us to conclude that the models of relationships between CO2 exchange in intact plants and environmental conditions can be used for the assessment of biological diversity at the intraspecies level.

1248

Kurooka, H., S. Fukunaga, E. Yuda, S. Nakagawa, and S. Horiuchi. 1990. Effect of carbon-dioxide enrichment on vine growth and berry quality of kyoho grapes. *Journal of the Japanese Society for Horticultural Science 59(3):463-470.*

Although ambient temperature is kept adequate, grape cultivation under covered facilities during winter months in Japan gives rise to low yields of poor quality berries because of low light intensities. This investigation was conducted in leaf chamber, using Vitis labruscana Bailey cv. Kyoho, to determine the influence of leaf age, light intensity, and CO2 concentrations on photosynthesis. The effects of CO2 enrichment on vine growth and fruit quality were also investigated in growth chambers. 1. The rate of photosynthesis per unit leaf area (Pn) between May 28 and September 19 rapidly increased with leaf growth, reaching a maximum of 18.9 mg CO2/dm2/hr, 37 days after the unfolding of a leaf. Pn then gradually decreased with leaf age. In young leaves, higher CO2 concentrations and stronger light intensities resulted in a significant increase in Pn. Older leaves exhibited a similar enhancement of Pn upon exposure to high light intensity. Pn was saturated at 828 ppm CO2. 2. Administration of 1,000 to 1,100 ppm CO2 to vines for an 8 hr/day at a late stage of berry development until harvest had no effect on berry size but resulted in an increase in sugar and anthocyanin contents but a decrease in organic acid content. Dry weight of newly developed roots doubled as a result of CO2 enrichment. 3. Application of CO2 under a long-day photoperiod at an early stage of berry development to a week before veraison markedly promoted shoot elongation. Furthermore, CO2 enrichment gave a 36% increase in both berry and cluster weights and also a higher sugar-acid ratio at harvest.

KEYWORDS: CO2- ENRICHMENT, COTTON, PHOTOSYNTHETIC RATE, RESPONSES, TOMATOES, YIELD

1249

Kurschner, W.M., I. Stulen, and P.J.C. Kuiper. 1997. PREDICTIONS for plant and vegetation responses to global change (elevated CO2) within a palaeo-ecophysiological perspective. *Plant Physiology 114(3):21002.*

1250

Kurschner, W.M., I. Stulen, F. Wagner, and P.J.C. Kuiper. 1998. Comparison of palaeobotanical observations with experimental data on the leaf anatomy of durmast oak [Quercus petraea (Fagaceae)] in response to environmental change. *Annals of Botany 81(5):657-664.*

To test whether stomatal density measurements on oak leaf remains are reliable tools for assessing palaeoatmospheric carbon dioxide concentration [CO2], under changing Late Miocene palaeoenvironmental conditions, young seedings of oak (Quercus petraea, Liebl.) were grown at elevated vs. ambient atmospheric [CO2] and at high humidity combined with an increased air temperature. The leaf anatomy of the young oaks was compared with that of fossil leaves of the same species. In the experiments, stomatal density and stomatal index were significantly decreased at elevated [CO2] in comparison to ambient [CO2]. Elevated [CO2] induced leaf cell expansion and reduced the intercellular air space by 35%. Leaf cell size or length were also stimulated at high air humidity and temperature. Regardless of a temperate or subtropical palaeoclimate, leaf cell size in fossil oak was not enhanced, since neither epidermal cell density nor length of the stomatal apparatus changed. The absence of these effects may be attributed to the phenological response of trees to climatic changes that

balanced temporal changes in environmental variables to maintain leaf growth under optimal and stable conditions. Quercus petraea, which evolved under recurring depletions in the palaeoatmospheric [CO2], may possess sufficient phenotypic plasticity to alter stomatal frequency in hypostomatous leaves allowing high maximum stomatal conductance and high assimilation rates during these phases of low [CO2]. (C) 1998 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FOSSIL LEAVES, GROWTH, POPLAR CLONES, STOMATAL DENSITY, TREE, WOODY-PLANTS

1251

Kurschner, W.M., F. Wagner, E.H. Visscher, and H. Visscher. 1997. Predicting the response of leaf stomatal frequency to a future CO2-enriched atmosphere: constraints from historical observations. *Geologische Rundschau 86(2):512-517.*

The majority of the water flux from the earth's land surface to the atmosphere passes through the tiny pores (stomata) in the leaves of land plants. The maximum conductance to diffusion of the leaves, determined by the number and geometry of stomata, has a profound effect on the terrestrial water and energy balance. Among tree species, there is ever increasing evidence that anthropogenic increase in atmospheric CO2 concentrations results in a decrease in stomatal frequency. The rate of historical CO2 responsiveness of individual tree species can be used to calibrate empirical models of non-linear (sigmoid) stomatal frequency response to CO2 increase. Modelled response curves for European tree birches (Betula pendula, Betula pubescens) and Durmast oak (Quercus petraea) predict different response limits to CO2 increase (similar to 350 and similar to 400 ppmv, respectively), indicating that non-linear stomatal frequency responses may vary from one tree species to another. Information on a wider selection of species is needed, but the models suggest that the maximum effect of anthropogenic CO2 increase on stomatal frequency has already been reached. Further research is required to establish the effect of rapidly declining response rates on future stomatal conductance of the ecologically contrasting trees of boreal, temperate, subtropical and tropical forests.

KEYWORDS: CARBON DIOXIDE, CLIMATE, DENSITY RECORD, ELEVATED CO2, ENRICHMENT, FOSSIL LEAVES, INCREASE, OAK LEAVES, PAST 2 CENTURIES, PLANT-RESPONSES

1252

Kurz, C., U. Schmieden, P. Strobel, and A. Wild. 1998. The combined effect of CO2, ozone, and drought on the radical scavenging system of young oak trees (Quercus petraea) - A phytothron study. *Chemosphere 36(4-5):783-788.*

In order to study the combined effects of CO2, ozone, and drought, we simulated in a controlled environment the climatic conditions of a German oak stand with high ozone (daytime: 80 ppb, control: 20 ppb) during one vegetative period under a regime of low and high CO2 concentration (370 vs 720 ppm) and drought (4 weeks < -800 hPa). To investigate the effects of CO2, ozone and drought on the radical scavenging system, we monitored the level of glutathione, ascorbate, and a- tocopherol. However, it is important that, under the regime of elevated CO2, the antioxidative behaviour of glutathione and ascorbate appears to be masked by their function as storage molecules for sulfur or carbon. (C)1998 Elsevier Science Ltd.

KEYWORDS: AIR- POLLUTANTS, ANTIOXIDATIVE SYSTEMS, ASCORBIC-ACID, HEALTHY, MOUNTAIN SITES, NORWAY SPRUCE, PINE, PLANT-RESPONSES, SEEDLINGS, SPRUCE NEEDLES

1253

Kutik, J., L. Natr, H.H. DemmersDerks, and D.W. Lawlor. 1995. Chloroplast ultrastructure of sugar beet (Beta vulgaris L) cultivated in normal and elevated CO2 concentrations with two contrasted nitrogen supplies. *Journal of Experimental Botany 46(293):1797-1802.*

Sugar beet (Beta vulgaris L., cultivar Celt) plants were grown under simulated field conditions in pots and supplied with adequate or deficient nitrogen (HN and LN, respectively) combined with two CO2 concentrations, ambient (c. 350 mu mol mol(-1) CO2-AC), or elevated CO2 (c. 600 mu mol mol(-1) CO2- HC). Chloroplast structure in mesophyll palisade cells of mature leaves (leaf number 19 in HN and 9 in LN), sampled at midday on 16 August 1993 was studied by transmission elec- tron microscopy and quantified stereologically. The ultrastructure of palisade parenchyma chloroplasts was affected by the elevated CO2 concentration and strikingly affected by nitrogen supply. Chloroplast diameter (cross-sectional length) was slightly, but not significantly, greater in HC than AC treatments within an N treatment, but was smaller in LN than HN; chloroplast cross-sectional area also increased with HC in both N treatments, but only significantly so in LN. Elevated CO2 reduced the proportion of total thylakoids (significant at 5% and 0.1% in HN and LN, respectively) due to decreased granal thylakoids, but the proportion of inter-granal (stromal) thylakoid membranes was not affected compared to chloroplasts from plants grown with ambient CO2. Chloroplast stroma increased as a proportion of chloroplast volume with elevated compared to ambient CO2 with HN but not LN. Starch inclusions were not significantly different with elevated compared to ambient CO2 at HN, but the proportion of starch increased considerably at elevated compared to ambient CO2 at LN, indicating an over-production of assimilates. Plastoglobuli in chloroplasts increased with deficient N, but decreased with elevated CO2. Larger chloroplasts with a greater proportion of stroma, but a smaller proportion of granal thylakoids, suggest increased CO, assimilating capacity and decreased light harvesting/PSII capacity with elevated CO2.

KEYWORDS: LEAF, LEAVES, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, WHEAT

1254

Kwa, S.H., Y.C. Wee, and P.P. Kumar. 1995. Ammonium and nitrate uptake and nitrate reductase activity of photoautotrophic callus cultures of the fern Platycerium coronarium (Koenig) DESV. *In Vitro Cellular & Developmental Biology-Plant 31(4):211-214.*

The uptake of nitrate and ammonium by callus of Platycerium coronarium from the culture medium was examined. Nitrate reductase activity of photoautotrophic callus cultures under CO2 enrichment was significantly lower compared to the cultures without CO2 enrichment, but higher than that of heterotrophic callus cultured on medium with 2% (wt/vol) sucrose. When sucrose concentration of the heterotrophic culture was lowered to 0.2%, nitrate reductase activity increased. The level of nitrate reductase activity increased by about 25% in the heterotrophic callus with an increase in 2,4-D from 2 mu M to 10 mu M, despite a decline in fresh weight gain. However, photoautotrophic cultures with 1% CO2 enrichment showed 20% decline in nitrate reductase activity and 45% decline in fresh weight gain with a similar increase in 2,4-D level. The rate of uptake of nitrate from the culture medium was unrelated to the level of nitrate reductase activity in the callus. For photoautotrophic callus under CO2 enrichment, the presence of 1% (vol/vol) CO2 generally resulted in the highest rate of nitrate uptake. The rate of uptake of ammonium was higher for callus cultured on 2 mu M 2,4-D compared to that on 10 mu M 2,4-D.

KEYWORDS: CO2, GROWTH, ROOTS

1255

Kwa, S.H., Y.C. Wee, and P.P. Kumar. 1997. Ribulose-1,5-bisphosphate carboxylase and phosphoenolpyruvate carboxylase activities of photoautotrophic callus of Platycerium coronarium (Koenig ex OF Muell.) Desv. under CO2 enrichment. *Plant Cell Tissue and Organ Culture 50(2):75-82.*

The in vitro activities of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and phosphoenolpyruvate carboxylase (PEPC) were measured in cell-free extracts of Platycerium coronarium callus cultured for up to 42 days under photoautotrophic conditions with CO2 enrichment. With an increase in CO2 in the culture environment to 10% (v/v) at low light, the apparent photoautotrophic fixation of CO2 by Rubisco declined, whereas the non-photoautotrophic CO2 fixation by PEPC activity was enhanced. Hence, photosynthesis appears to play a lesser role in providing carbon skeletons and energy with prolonged culture in a CO2-enriched environment. Instead, the anaplerotic supply of C-skeletons by PEPC may be important under such a situation. Short-term (HCO3-)-C-14 fixation experiments indicated that photoautotrophic callus cultured for 3 weeks with 10% CO2 enrichment assimilated less (CO2)-C-14 than the control (0.03% CO2). Analyses of C-14-metabolites indicated that about 50% of the total soluble (CO2)-C-14 fixed was in the organic acid fraction and 35% in the amino acid fraction. Despite the changes in the in vitro Rubisco/PEPC activity-ratio, no significant change in the C-14 distribution pattern was apparent in response to increasing sucrose or CO2 concentrations. The suppression of Rubisco activity and total chlorophyll content in high sucrose or elevated CO2 concentrations suggests an inhibition of the capacity for photoautotrophic callus growth under these conditions.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CELLS, CHLOROPHYLL SYNTHESIS, ELEVATED CO2, ESTABLISHMENT, EXPRESSION, PHOTOSYNTHESIS, SUCROSE SUPPRESSION, SUSPENSION-CULTURE

1256

Kwa, S.H., Y.C. Wee, T.M. Lim, and P.P. Kumar. 1995. Establishment and physiological analyses of photoautotrophic callus-cultures of the fern platycerium-coronarium (koenig) desv under co2 enrichment. *Journal of Experimental Botany 46(291):1535-1542.*

Gametophyte-derived callus cultures of Platycerium coronarium could be maintained under photoautotrophic conditions on Murashige and Skoog medium supplemented with 2 mu M 2,4- dichlorophenoxyacetic acid (2,4-D) and with CO2 enrichment. Progressive reduction of sucrose from the medium resulted in a reduction in growth, but an increase in total chlorophyll content. When subculturing was delayed beyond 2 weeks, callus cells differentiated into gametophytes on the medium with less than or equal to 0.2% sucrose and no CO2 enrichment. Enriching the photoautotrophic cultures on 2 mu M 2,4-D with 1% CO2 resulted in about 1.7-fold increase in fresh weight within 42 d. Total chlorophyll content was generally higher with 1% CO2 enrichment than with 10%. F-v/F-m ratio was higher for callus on low levels of sucrose (less than or equal to 0.5%) than that on sucrose greater than or equal to 1.0%. An increase in autofluorescence of chloroplasts, but not the size, was observed with decreasing sucrose levels in the medium. Autofluorescence decreased with increase in CO2 from 0.03%. Our data are in agreement with the view that long-term exposure to high levels of CO2 can cause a decrease in photosynthetic capacity.

KEYWORDS: CELLS, CHLOROPHYLL SYNTHESIS, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, SUCROSE SUPPRESSION

1257

Kytoviita, M.M., J. Pelloux, V. Fontaine, B. Botton, and P. Dizengremel. 1999. Elevated CO2 does not ameliorate effects of ozone on carbon allocation in Pinus halepensis and Betula pendula in symbiosis with Paxillus involutus. *Physiologia Plantarum 106(4):370-377.*

The effect of 700 mu mol CO2 mol(-1), 200 mmol ozone mol(-1) and a combination of the two on carbon allocation was examined in Pinus halepensis co-cultured with Betula pendula in symbiosis with the ectomycorrhizal fungus Paxillus involutus, The results show that under low nutrient and ozone levels, elevated CO2 has no effect on the growth of B. pendula or P. halepensis seedlings nor on net carbon partitioning between plant parts. Elevated CO2 did not enhance the growth of the fungus in symbiosis with the birch, On the other hand, ozone had a strong negative effect on the growth of the birch, which corresponded with the significantly reduced growth rates of the fungus. Exposure to elevated CO2 did not ameliorate the negative effects of ozone on birch; in contrast, it acted as an additional stress factor. Neither ozone nor CO2 had significant effects on biomass accumulation in the pine seedlings, Ozone stimulated the spread of mycorrhizal infection from the birch seedlings to neighbouring pines and had no statistically significant effects on phosphoenolpyruvate carboxylase (PEPC) or ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity in the pine needles or on PEPC activity in pine roots.

KEYWORDS: ATMOSPHERIC CO2, ECTOMYCORRHIZAL COLONIZATION, GAS-EXCHANGE, JUVENILE PONDEROSA PINE, MYCORRHIZAL COLONIZATION, NORWAY SPRUCE, PHOSPHOENOLPYRUVATE CARBOXYLASE ACTIVITY, PICEA-ABIES L, SPRUCE NEEDLES, TAEDA L SEEDLINGS

1258

Laforge, F., C. Lussier, Y. Desjardins, and A. Gosselin. 1991. Effect of light-intensity and CO2 enrichment during invitro rooting on subsequent growth of plantlets of strawberry, raspberry and asparagus in acclimatization. *Scientia Horticulturae 47(3-4):259-269.*

Growth of plantlets of asparagus (Asparagus officinalis L.), raspberry (Rubus idaeus L.) and strawberry (Fragaria X ananassa Duch.), treated during the in vitro rooting stage under three photosynthetic photon flux densities (PPFD) (80, 125 and 250- mu-mol s-1 m-2) (17.5, 26.9 and 53.8 W m-2 (PAR), respectively) and three CO2 enrichment levels (CDE) (330, 1650 and 3000-mu- mol mol-1), was monitored during the acclimatization stage. For the three species, generic differences were observed in the plant response to treatments. A significant residual growth enhancement was caused by CDE. High PPFD in vitro increased the dry weight of strawberry and fresh weight of asparagus in acclimatization. Raspberry leaf dry weight was increased by 262% in acclimatization after in vitro treatment with high CDE. This enhanced the performance of micropropagated plantlets in acclimatization and reduced by 2 weeks the acclimatization period with raspberry. Our results suggest that in vitro leaves may be a source of nutritional reserves for leaves initiated ex vitro, but do not exclude a morphogenetic effect of CO2 during the in vitro rooting stage.

KEYWORDS: ANATOMY, EXVITRO, SEEDLINGS, SOIL

1259

Laisk, A., and G.E. Edwards. 1997. CO2 and temperature-dependent induction in C-4 photosynthesis: an approach to the hierarchy of rate-limiting processes. *Australian Journal of Plant Physiology 24(4):505-516.*

Rate-limiting processes for C-4 photosynthesis were examined in Sorghum bicolor, an NADP-ME type species, and Amaranthus cruentus, an NAD-ME type C-4 species, by studying the kinetics of transient changes in photosynthetic rates following rapid changes in CO2 or temperature. Primary responses (faster than 15 s) to increasing CO2 or

temperature are considered direct effects on the turnover rate of the C-4 cycle, whereas medium transient changes (2-3 min) are considered due to build-up of C-4 cycle intermediates, and the slowest transient changes (20- 30 min) are thought to be related to end product synthesis. Reciprocal plot of carboxylation rates versus cell wall (dissolved) CO2 concentration (C-w) gives an apparent K-m (CO2) of 8 mu M and a V-m of 200 mu mol m(-2) s(-1) for PEP carboxylase, which is about 4 times higher than the maximum rate of photosynthesis. Under strictly limiting CO2, the rate of PEP carboxylation in C-4 photosynthesis is independent of temperature (20-35 degrees C), suggesting a physical rather than a biochemical limitation. It is suggested that the rates of C-3 and C-4 cycles are coordinated through the pool sizes of the C-4 cycle, which are in equilibrium with the pool of 3- phosphoglyceric acid. At low CO2, the C-4 pools decrease and are slowly regenerated at elevated CO2, restricting the CO2 response of C-4 photosynthesis.

KEYWORDS: CARBON ASSIMILATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, MATHEMATICAL-MODEL, NADP+-MALATE DEHYDROGENASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PYRUVATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, ZEA MAYS L

1260

Laitat, E., and H. Boussard. 1995. Comparative response on gas exchange of Picea spp exposed to increased atmospheric CO2 in open top chambers at two test sites. *Journal of Biogeography 22(2-3):241-248.*

We took comparative measurements of gas exchange response curves of two species of spruce (Picea abies (L.) Karst and Picea sitchensis (Bong.) Carr.) exposed to high levels of atmospheric carbon dioxide (CO2) in two test stations: Vielsalm (Belgium) and Glendevon (United Kingdom). The photosynthetic response of these two species to variations in concentrations of intercellular CO2 and to variations in light intensity were measured in situ using an integrated transportable differential CO2 and water vapour exchange measuring system. The response curves were adjusted by the Mitscherlich function. The statistical analysis of our measurements and adjustments reveal similarities in the reaction of Picea abies and Picea sitchensis to a doubling of the present level of atmospheric CO2. Regarding the photosynthesis response curves to intercellular CO2 variation, we noted a decrease in the maximum photosynthesis rate and the carboxylation rate accompanied by an increased compensation point. Regarding the photosynthesis response curves to the light variation, we found that dark respiration and photochemical efficiency remained unchanged, and the maximum photosynthesis rate was slightly higher in an atmosphere enriched in CO2. These experimental contexts would seem to indicate that the current and forecast levels of CO2 are not ecological factors limiting primary productivity, and that the increase in atmospheric CO2 interacts with other environmental factors.

KEYWORDS: CARBON DIOXIDE, PHOTOSYNTHESIS

1261

Lake, J.C., and L. Hughes. 1999. Nectar production and floral characteristics of Tropaeolum majus L. grown in ambient and elevated carbon dioxide. *Annals of Botany 84(4):535-541.*

Tropaeolum majus (nasturtiums) were grown from seed in growth cabinets, under 380 and 750 ppmv CO2. Elevated CO2 significantly increased nectar secretion rate, both in flowers milked of nectar daily and in once sampled, 3-d-old flowers. Elevated CO2 did not affect time to flowering, total number of flowers produced, pollen to ovule ratio, or the total or individual concentrations of nectar amino acids. The dry weight and longevity of individual flowers was also unchanged. Nectar sugar content was unchanged by elevated CO2 in a subset of flowers used to assess the 3-d-old nectar volume. This subset did not show the same increase in nectar volume under elevated CO2 as the full set, resulting in the concentration of sugars remaining unchanged. Overall, the quantity rather than the quality of the nectar changed under elevated CO2 while flower characteristics remained constant, implying that the identity of pollinators may remain the same while foraging behaviour (e.g. number of visits per plant, distance travelled) may change in the future. (C) 1999 Annals of Botany Company.

KEYWORDS: AMINO-ACIDS, BUTTERFLIES, CO2 LEVELS, FLOWER CONSTANCY, LONG, NITROGEN, PHENOLOGY, PLANT, REPRODUCTION, RESPONSES

1262

Lal, M., K.K. Singh, L.S. Rathore, G. Srinivasan, and S.A. Saseendran. 1998. Vulnerability of rice and wheat yields in NW India to future changes in climate. *Agricultural and Forest Meteorology 89(2):101-114.*

Agricultural sector is one of the sensitive areas which would be influenced by the projected global warming and associated climate change. In spite of the uncertainties about the precise magnitude of climate change on regional scales, an assessment of the possible impacts of changes in key climatic elements on our agricultural resources is important for formulating response strategies. In this study, vulnerability of wheat and rice crops in northwest India to the projected climate change is examined. CERES wheat and rice models adopted for the study were validated for their ability to reproduce yields at the selected NW Indian stations. The sensitivity experiments with these models showed higher yields for both wheat and rice (28% and 15% respectively for a doubling of CO2) under elevated CO2 levels. A 3 degrees C (2 degrees C) rise in air temperature nearly cancels out the positive effect of elevated CO2 on the wheat (rice) yields. While the wheat crops are found to be sensitive to increase in maximum temperature, the rice crops are vulnerable to increase in minimum temperature. The combined effect of enhanced CO2 and imposed thermal stress on the wheat (rice) crop is 21% (4%) increase in yield for the irrigation schedule presently practised in the region. While the adverse impacts of likely water shortage on wheat crops would be minimised to a certain extent under elevated CO2 levels, they would largely be maintained for the rice crops resulting in about 20% net decline in rice yields. In general, acute water shortage conditions combined with the thermal stress should adversely affect both the wheat and more severely the rice productivity in NW India even under the positive effects of elevated CO2 in the future. (C) 1998 Elsevier Science B.V.

KEYWORDS: AEROSOLS, GREENHOUSE GASES, SIMULATION, TEMPERATURE

1263

Lal, M., K.K. Singh, G. Srinivasan, L.S. Rathore, D. Naidu, and C.N. Tripathi. 1999. Growth and yield responses of soybean in Madhya Pradesh, India to climate variability and change. *Agricultural and Forest Meteorology 93(1):53-70.*

This study is aimed at assessing the impact of thermal and moisture stresses associated with observed intraseasonal and interannual variability in key climatic elements on the nature and extent of losses in growth and yield of soybean crop in central India through the use of CROPGRO model. The crops are found to be more sensitive to higher cumulative heat units during cropping season. The yields respond substantially to temporal variations in rainfall (associated with observed swings in the continuity of monsoon). Prolonged dry spells at critical life stages of the soybean crop are found to adversely affect crop development and growth and hence the yields at selected sites. We have also examined the plausible effects of future climate change on soybean

yields in the selected region based on simulations carried out for doubled atmospheric CO2 level and with modified weather variables using the available seasonal projections for the future. Our findings on the response of elevated CO2 concentrations in the atmosphere suggest higher yields (50% increase) for soybean crop for a doubling of CO2. However, a 3 degrees C rise in surface air temperature almost cancels out the positive effects of elevated CO2 on the yield. Soybean crops at selected site are more vulnerable to increases in maximum temperature than in minimum temperature. The combined effect of doubled CO2 and anticipated thermal stress (likely by middle of the next century) on soybean crop is about 36% increase in yield at the selected sites. A decline in daily rainfall amount by 10% restricts this yield gain to about 32%. Deficient rainfall with uneven distribution during the monsoon season could be a critical factor for the soybean productivity even under the positive effects of elevated CO2 in the future. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, CO2, GRAIN LEGUMES, GREENHOUSE GASES, INCREASE, SENSITIVITY, SIMULATION, SULFATE AEROSOLS, TEMPERATURE, TRANSPIRATION

1264

Lal, M., P.H. Whetton, A.B. Pittock, and B. Chakraborty. 1998. Simulation of present-day climate over the Indian subcontinent by general circulation models. *Terrestrial Atmospheric and Oceanic Sciences 9(1):69-96.*

There continues to be some improvement in the ability of general circulation models to simulate the present-day climate on large scales although further improvements in the model resolution and parameterization of physical processes are still needed for the realistic simulation of regional climates. Quantitative assessment of the magnitude of climate change on a regional scale and its implications are essential for understanding, planning and management of resources at national/regional levels. In developing countries like India, where the economy is largely regulated by variability in summer monsoon rainfall, the consideration of measures for reducing the impacts of global change should begin as soon as possible, particularly with regard to floods and droughts, cyclone disaster preparedness, hydrological planning in semi-arid regions and coastal zone management issues. With this in view, we examine here the skill of a range of global climate models in simulating the regional climatology of the Indian subcontinent. This is a necessary first step in preparing climate change scenarios for the region. The simulation of the current broad scale patterns of mean sea level pressure, temperature and precipitation over the northern hemisphere and over the Indian subcontinent in particular are assessed for a broad range of global climate modelling experiments. The experiments included both slab ocean and coupled ocean experiments. Five experiments are identified as having a fairly realistic simulation and may be considered acceptable for use in regional climate change assessments. All of these are of relatively high resolution and use a Q-flux correction (in the slab ocean experiments) or a flux correction (in the coupled ocean experiments). A further four experiments, with somewhat poorer regional climate simulations, are acceptable but only to a moderate degree of confidence. However, some six experiments have such marked deficiencies in their simulation of present- day regional climatology that we consider them unacceptable for regional climate change assessment.

KEYWORDS: CARBON DIOXIDE, CO2, GCM, IMPACT, OCEAN-ATMOSPHERE MODEL, SENSITIVITY, SPATIAL VARIABILITY, TEMPERATURE

1265

Lal, R. 1997. Residue management, conservation tillage and soil restoration for mitigating greenhouse effect by CO2-enrichment. *Soil & Tillage Research 43(1-2):81-107.*

This manuscript reviews the potential impact of residue management, conservation tillage and soil restoration on carbon sequestration in world soils. The greenhouse effect is among four principal ecological issues of global concern that include: (i) adequacy of land resources to meet needs of present and future generations; (ii) role of world soils and agricultural practices in the 'greenhouse' effect; (iii) potential of crop residue management, restoration of degraded soils, and conservation tillage in carbon sequestration in soil; and (iv) minimizing risks of soil degradation by enhancing soil resilience and soil quality. Annual increase in CO, concentration in the atmosphere is 3.2 x 10(15) g, and there exists a potential to mitigate this effect through C sequestration in soils. Just as world soils are an important active pool of organic carbon and play a major role in the global carbon cycle, crop residue is a major renewable resource which also has an important impact on the global carbon cycle. I have estimated the annual production of crop residue to be about 3.4 billion Mg in the world. If 15% of C contained in the residue can be converted to passive soil organic carbon (SOC) fraction, it may lead to C sequestration at the rate of 0.2 x 10(15) g/yr. Similarly restoring presently degraded soils, estimated at about 2.0 billion ha, and increasing SOC content by 0.01%/yr may lead C sequestration at the rate of 3.0 Pg C/yr. Conservation tillage is an important tool for crop residue management, restoration of degraded soil, and for enhancing C sequestration in soil. Conservation tillage, any tillage system that maintains at least 30% of the soil surface covered by residue, was practised in 1995 on about 40 x 10(6) ha or 35.5% of planted area in USA. It is projected that by the year 2020, conservation tillage may be adopted on 75% of cropland in USA (140 x 10(6) ha), 50% in other developed countries (225 x 10(6) ha), and 25% in developing countries (172 x 10(6) ha). The projected conversion of conventional to conservation tillage may lead to a global C sequestration by 2020 at a low estimate of 1.5 x 10(15) g, and at a high estimate of 4.9 x 10(15) g of C. These potentials of C sequestration can be realized through adoption of regional, national and global soil policy that stipulate appropriate use of world soil resources. (C) 1997 Elsevier Science B.V.

KEYWORDS: C-13 NATURAL ABUNDANCE, CONTINUOUS CULTIVATION, LONG-TERM TRENDS, NO-TILLAGE, ORGANIC-MATTER TURNOVER, PARTICLE-SIZE FRACTIONS, PHYSICAL-PROPERTIES, REDUCED TILLAGE, SOUTHERN QUEENSLAND, WATER-STABLE AGGREGATION

1266

Lambers, H. 1993. Rising co2, secondary plant-metabolism, plant-herbivore interactions and litter decomposition - theoretical considerations. *Vegetatio 104:263-271.*

A brief account is given of the ecological significance of quantitatively important secondary plant compounds, mainly those of a phenolic nature, in herbivory and decomposition. Phenolic compounds accumulate to a greater extent in slow- growing species than in fast-growing ones, particularly when soil conditions (nutrients, water) restrict growth. Two hypotheses to explain the increased concentration of phenolics when soil conditions are unfavorable are presented. The first hypothesis (the 'carbon supply model of secondary plant metabolism') considers the increased levels of non-structural carbohydrates as the major trigger. The second hypothesis (the 'amino acid diversion model of secondary plant metabolism') states that increased accumulation of phenolics stems from a decreased use of a common precursor (phenylalanine or tyrosine) for protein synthesis. Current experimental evidence, though still fairly limited, supports the second hypothesis, but further testing is required before the first model can be rejected. So far, there is very little evidence for a direct effect of atmospheric CO2 on the concentration of secondary compounds in higher plants. However, there are likely to be indirect effects, due to a stronger limitation by the nitrogen supply in plants whose growth has been promoted by atmospheric CO2. It is concluded that it is very likely that phenolic compounds accumulate to a greater extent in plants exposed to elevated

CO2, due to a greater limitation of nutrients, rather than as a direct effect of elevated CO2.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, CHEMICAL DEFENSE, ELEVATED CO2, ESTUARINE MARSH, GROWTH, INSECT HERBIVORE, LEAF LITTER, NITROGEN, NUTRIENT BALANCE, PHENOLICS

1267

Lambers, H., I. Stulen, and A. vanderWerf. 1996. Carbon use in root respiration as affected by elevated atmospheric CO-2. *Plant and Soil 187(2):251-263.*

The use of fossil fuel is predicted to cause an increase of the atmospheric CO2 concentration, which will affect the global pattern of temperature and precipitation. It is therefore essential to incorporate effects of temperature and water supply on the carbon requirement for root respiration of plants to predict effects of elevated [CO2] on the carbon budget of natural and managed systems. There is insufficient information to support the contentention that an increase in the concentration of CO2 in the atmosphere will enhance the CO2 concentration in the soil to an extent that is likely to affect root respiration. Moreover, there is no convincing evidence for a direct effect of elevated atmospheric [CO2] on the rate of root respiration per unit root mass or the fraction of carbon required for root respiration. However, there are likely to be indirect effects of elevated [CO2] on the carbon requirement of plants in natural systems. Firstly, it is very likely that the carbon requirement of root respiration relative to that fixed in photosynthesis will increase when elevated [CO2] induces a decrease in nutrient status of the plants. Although earlier papers have emphasized that elevated [CO2] favours investment of biomass in roots relative to that in leaves, these are in fact indirect effects. The increase in root weight ratio is due to the more rapid depletion of nutrients in the root environment as a consequence of enhanced growth. This will decrease the specific rate of root respiration, but increase the carbon requirement as a fraction of the carbon fixed in photosynthesis. It is likely that these effects will be minor in systems where the nutrient supply is very high, e.g, in many managed arable systems, and increase with decreasing soil fertility, i.e. in many natural systems. Secondly, a decrease in rainfall in some parts of the world may cause a shortage in water supply which favours the carbon partitioning to roots. Water stress is likely to reduce rates of root respiration per unit root mass, but enhance the fraction of total assimilates required for root respiration, due to greater allocation of biomass to roots. Increased temperatures are unlikely to affect the specific rate of root respiration in all species. Broadly generalized, the effect of temperature on biomass allocation is that the relative investment of biomass in roots is lowest at a certain optimum temperature and increases at both higher and lower temperatures. The root respiration of some species acclimates to growth temperature, so that the effect of global temperature rise is entirely accounted for by the effect of temperature on biomass allocation. The specific rate of root respiration of other species will increase with global warming. In response to global warming the carbon requirement of roots is likely to decrease in temperate regions, when temperatures are suboptimal for the roots' capacity to acquire water. Here global warming will induce a smaller biomass allocation to the roots. Conversely, the carbon requirements are more likely to increase in mediterranean environments, where temperatures are often supraoptimal and a rise in temperature will induce greater allocation of biomass to the roots.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, DRYING SOIL, FERTILIZER APPLICATION, GROWTH, MOWN GRASSLAND, NITROGEN, PLANTAGO-MAJOR, SHOOT, TEMPERATURE

1268

Lambers, H., R. VandenBoogaard, E.J. Veneklaas, and R. Villar. 1995. Effects of global environmental change on carbon partitioning in vegetative plants of Triticum aestivum and closely related Aegilops species. *Global Change Biology 1(6):397-406.*

The use of fossil fuel is predicted to cause an increase of the atmospheric CO2 concentration, which will affect the global pattern of temperature and precipitation. It is therefore essential to incorporate effects of temperature and water supply on carbon partitioning of plants to predict effects of elevated [CO2] on growth and yield of Triticum aestivum. Although earlier papers have emphasized that elevated [CO2] favours investment of biomass in roots relative to that in leaves, it has now become clear that these are indirect effects, due to the more rapid depletion of nutrients in the root environment as a consequence of enhanced growth. Broadly generalized, the effect of temperature on biomass allocation in the vegetative stage is that the relative investment of biomass in roots is lowest at a certain optimum temperature and increases at both higher and lower temperatures. This is found not only when the temperature of the entire plant is varied, but also when only root temperature is changed whilst shoot temperature is kept constant. Effects of temperature on the allocation pattern can be explained largely by the effect of root temperature on the roots' capacity to transport water. Effects of a shortage in water supply on carbon partitioning are unambiguous: roots receive relatively more carbon. The pattern of biomass allocation in the vegetative stage and variation in water-use efficiency are prime factors determining a plant's potential for early growth and yield in different environments. In a comparison of a range of T. aestivum cultivars, a high water-use efficiency at the plant level correlates positively with a large investment in both leaf and root biomass, a low stomatal conductance and a large investment in photosynthetic capacity. We also present evidence that a lower investment of biomass in roots is not only associated with lower respiratory costs for root growth, but also with lower specific costs for ion uptake. We suggest the combination of a number of traits in future wheat cultivars, i.e. a high investment of biomass in leaves, which have a low stomatal conductance and a high photosynthetic capacity, and a low investment of biomass in roots, which have low respiratory costs. Such cultivars are considered highly appropriate in a future world, especially in the dryer regions. Although variation for the desired traits already exists among wheat cultivars, it is much larger among wild Aegilops species, which can readily be crossed with T. aestivum. Such wild relatives may be exploited to develop new wheat cultivars well-adapted to changed climatic conditions.

KEYWORDS: ABSCISIC- ACID, ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, GROWTH, MAIZE PLANTS, NITROGEN, ROOT TEMPERATURE, SHOOT, WATER DEFICIT, WHEAT

1269

Lamhamedi, M.S., and P.Y. Bernier. 1994. Ecophysiology and field performance of black spruce (picea- mariana) - a review. *Annales Des Sciences Forestieres 51(6):529-551.*

This paper presents a literature review of black spruce (Picea mariana [Mill] BSP) ecophysiology concerning the response of net photosynthesis and stomata to changes in environmental factors. Current knowledge on root growth, mineral nutrition and response to high temperature, CO2 enrichment and climate change, frosts, water stress and flooding are also covered. The review ends with an overview of stand establishment and field performance of planted seedlings. The authors highlight the need for research on the long-term effects of multiple stresses, such as climate change and air pollution on the black spruce ecosystem.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CONTAINER SEEDLINGS, FROST HARDINESS, JACK PINE-SEEDLINGS, NORTHERN CONIFERS, PLANTED WHITE-PINE, ROOT-GROWTH CAPACITY, SOIL TEMPERATURE, WATER RELATIONS

1270

Landolt, W., and I. Pfenninger. 1997. The effect of elevated CO2 and soil type on non-structural carbohydrates in beech leaves and Norway spruce needles growing in model ecosystems. *Acta Oecologica-International Journal of Ecology 18(3):351-359.*

Young beech and Norway spruce trees from two Swiss provenances were both planted in an acidic and calcareous soil in 16 open- top chambers. Half of the plants were exposed to elevated CO2 (ambient, ambient + 200 mu l l(-1), 24 hrs/day, 365 days/year) and enhanced nitrogen deposition (2.5, 25 kg ha(-1) yr(-1)) throughout a single growing season. Leaf and needle samples from all 64 trees were collected (2 provenances x 2 soil types x 4 treatments x 4 replications) at the end of July and September. These were analysed for starch, soluble carbohydrates and total non-structural carbohydrates (TNC). Increased starch and TNC levels were found in plants under elevated CO2 and those growing on the acidic soil. These effects were not consistent in both species or on both sampling dates. Soluble carbohydrates were only effected significantly by sail type. So far no interactions have been found between CO2, N or soil type on any date and in any fraction. It is concluded that soil type should be considered when discussing the effects of elevated CO2 on starch, soluble carbohydrate or TNC contents in beech and spruce trees.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECLINE, GROWTH, NITROGEN, NUTRITION, PLANTS, SOURCE-SINK RELATIONS

1271

Landsberg, J., and M.S. Smith. 1992. A functional scheme for predicting the outbreak potential of herbivorous insects under global atmospheric change. *Australian Journal of Botany 40(4-5):565-577.*

There are many possible ways in which changes in the global atmosphere could influence the outbreak potential of herbivorous insects; we clarify these by developing a scheme for analysing insect populations in terms of functional attributes that are both important in population regulation and responsive to global change. This analysis shows that elevated CO2 is not likely to have a major influence on probability of insect outbreak, except possibly in systems in which nitrogen-based defensive compounds are produced by plants in response to herbivory. Systems that will have high potential to outbreak, if climatic conditions become more favourable for plant growth and responses are not constrained by other resources, include those in which both herbivorous insects and host plants have highly flexible growth patterns and activity cues. Global changes that increase environmental stress on host plants are most likely to favour sap-feeding insects. Critical enemy (predator or parasitoid) control of the dormant phase of herbivorous insects may be very important in preventing or allowing outbreaks, but is often poorly understood.

KEYWORDS: CARBON DIOXIDE, DEFOLIATION, FOLIAGE, GROWTH, MOTH, POPULATION-DYNAMICS, TREES

1272

Lange, D.L., and A.A. Kader. 1997. Changes in alternative pathway and mitochondrial respiration in avocado in response to elevated carbon dioxide levels. *Journal of the American Society for Horticultural Science 122(2):245-252.*

Partially ripened avocado [Persea americana (Mill.) cv, Hass] fruit harvested in either June or Aug, 1994 were kept at 10 degrees C in air (21% O-2), 20% CO2 (17% O-2, balance N-2), or 40% CO2 (13% O-2, balance N-2) for 7 to 12 days and then were transferred to air at 10 degrees C for 2 to 3 days, Mitochondrial respiration was stimulated in response to elevated CO, treatments at 10 degrees C. A shift to alternative pathway (Alt) respiration occurred on day 4 in experiments using avocados from both harvest dates, with a return to initial levels in only the 20% CO2-treated fruit (June- harvested fruit after return to air), Elevated CO2 at 20 degrees C decreased the in vitro O-2 consumption of isolated mitochondria compared to mitochondria kept in air, The Alt pathway contributed less to the total O-2 uptake of CO2-treated mitochondria compared to mitochondria kept in air, The respiratory control ratios of the CO2-treated fruit and mitochondria were higher and lower, respectively, than the air controls. Induction of 33 to 37 kD proteins (corresponding to the size of the alternative oxidase proteins) occurred in avocados after 4 days in 40% CO2. These results indicate that elevated CO2 has various effects depending on concentration, duration and temperature of exposure, and mitochondrial function of avocado fruit, such as increased and altered respiratory oxidation and up-regulation of alternative oxidase proteins.

KEYWORDS: CYANIDE-RESISTANT RESPIRATION, ETHYLENE, HIGHER-PLANT MITOCHONDRIA, METABOLISM, OXIDASE, SELF-RESTORATION, SENSITIVE METHOD, TOBACCO

1273

Lange, D.L., and A.A. Kader. 1997. Effects of elevated carbon dioxide on key mitochondrial respiratory enzymes in 'Hass' avocado fruit and fruit disks. *Journal of the American Society for Horticultural Science 122(2):238-244.*

Preclimacteric avocado [Persea americana (Mill.) cv, Hass] fruit or fruit disks as well as fruit harvested in either June (midseason) or August (late season) and partially ripened were kept in air (21% O-2 + 78% N-2), 20% CO2 + 17% O-2 (63% N-2), or 40% CO2 + 13% O-2 (47% N-2) at either 10 or 20 degrees C. Ethylene production by preclimacteric fruit completely inhibited during CO2 exposure, whereas there was only partial inhibition of ethylene production when partially ripened fruit were exposed, Compared to the fruit stored in air, O-2 uptake of fruit stored in 20% CO2 was decreased by 20%, whereas the fruit stored in 40% CO2 showed 25% more O-2 uptake than air- stored fruit, Fruit subjected to a storage regime of 40% CO2 at 10 degrees C followed by 2 d in air had the best visual quality, In general, climacteric fruit treated with 20% CO2 at 10 degrees C showed increased pyruvate dehydrogenase (PDH) activity and decreased cytochrome oxidase (CytOx) activity, Fruit stored in 40% CO2 had reduced CytOx activity compared to air-stored fruit, and PDH activity was variable depending on the harvest season of the fruit, Our results show that the effect of elevated CO2 on a given enzyme depends on concentration of CO2, duration of exposure, physiological state of the fruit, and type of tissue exposed.

KEYWORDS: ATMOSPHERES, ETHYLENE, METABOLISM, OXYGEN, PEAR FRUIT, QUALITY

1274

Lange, D.L., and A.A. Kader. 1997. Elevated carbon dioxide exposure alters intracellular pH and energy charge in avocado fruit tissue. *Journal of the American Society for Horticultural Science 122(2):253-257.*

Changes in cytosolic and vacuolar pH, ATP, ADP, and the ATP : ADP ratio were measured in whole fruit or mesocarp disks of avocado [Persea americana (Mill.) cv, Hass] during brief exposures to elevated CO2. Intact climacteric fruit exposed to air (21% O-2), 20% CO2(17% O-2, balance N-2), or 40% CO2 (13% O-2, balance N-2) had cytosolic pH values of 7.0, 6.6, and 6.4, respectively, while mesocarp disks had cytosolic pH values of 6.9, 6.7, and 6.4, respectively. The beta-ATP levels of intact climacteric fruit exposed to 20% CO2 or 40% CO2 for 2 h were reduced by 25% or 43%, respectively, relative to air-exposed fruit. HPLC analysis of nucleotide phosphates from preclimacteric

avocados revealed that ATP levels and the ATP : ADP ratio increased in 40% compared to the air-stored fruit. However, 1 day after transfer to air, the effects of elevated CO2 had dissipated. These modifications in cellular state could alter the activity of respiratory enzymes in fruit exposed to elevated CO2 atmospheres.

KEYWORDS: CELLS, CO2, RESPIRATION, VACUOLAR PH

1275

Lange, O.L., T.G.A. Green, H. Reichenberger, and A. Meyer. 1996. Photosynthetic depression at high thallus water contents in lichens: Concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal Peltigera species. *Botanica Acta 109(1):43-50.*

Lichens, being poikilohydric, have varying thallus water contents (WC) and show a complex interaction between net photosynthesis (NP) and WC. NP can be depressed at low WC (desiccation effects) and, in some species, also at high WC. In the latter case the depression is normally ascribed to increased CO2 diffusion resistances through water blockage. Recently, an earlier explanation, that the depression at high WC is due to recycling of CO2 from increased dark respiration processes (DR), has been given renewed prominence. The two explanations were distinguished by the concurrent use of gas exchange and chlorophyll fluorescence techniques to investigate NP:WC relationships in the lichens Peltigero leucophlebia (green algal) and P. neckeri (cyanobacterial). Both species had a distinct optimal WC for NP with depressed values at low and high WC. The maximal quantum yield for both CO2 fixation (initial slope of light response curves of NP) and photosystem II (fluorescence signals of dark-adapted thalli) was depressed only at low WC and remained high at optimal and greater WC. In contrast, the relative electron transport rate (ETR, derived from fluorescence signals of thalli in the light) tracked NP and was depressed at low and high WC. The depression of both NP and ETR at high WC (not that at low WC) could be prevented by using elevated external CO2 concentrations. A single, linear relationship was found between all values of gross photosynthesis (NP + DR) and ETR regardless of external CO2 concentration or WC. Our results show that, for these lichens, the depression in NP at high WC is a real fall in photosynthetic rate of the photobionts and is not due to recycling of CO2. The removal of the depression in NP and ETR at high WC by using elevated external CO2 levels allows us to conclude that an additional CO2 diffusion resistance is present.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CHLOROPHYLL FLUORESCENCE, CO2 EXCHANGE, ELECTRON-TRANSPORT, RESISTANCES

1276

Lange, O.L., S.C. Hahn, G. Muller, A. Meyer, and J.D. Tenhunen. 1996. Upland tundra in the foothills of the Brooks Range, Alaska: Influence of light, water content and temperature on CO2 exchange of characteristic lichen species. *Flora 191(1):67-83.*

In a previous publication we described diel courses of CO2 exchange and microclimate conditions for characteristic Lichens in their natural habitat within upland tundra communities of northern Alaska. The influence of individual environmental factors on net photosynthesis (NP) of Cetraria cucullata, Dactylina arctica, Masonhalea richardsonii, Peltigera aphthosa, Peltigera malacea, Stereocaulon alpinum, and Thamnolia vermicularis was analyzed in the present study. CO2 exchange measurements were conducted in the laboratory, and clear response characteristics with respect to light, water content (WC), temperature, and external CO2 concentration were established under controlled conditions. In addition, dependencies of NP on these factors were extracted from field data. These measurements show a high scatter in data points, however, they represent the range of actual performance of the lichens under natural conditions. In general both, field and laboratory data sets, agree well with respect to absolute rates of photosynthetic capacity as well as response characteristics. The combined information from both sources enable us to identify and describe those physiological features which are relevant for photosynthetic production of the lichens at this tundra site. There were large differences in maximal rates of NP attained under natural ambient CO2 which were expressed more strongly under conditions of CO2 saturation. Photosynthetic capacity of the cyanobacterial P. malacea is ten times higher than that of the green algal M. richardsonii. In the field, actual photosynthesis often seemed to be depressed due to photoinhibition. Photosynthetic carbon gain occurred even with thallus temperatures of -10 degrees C, while the temperature optimum of NP was between 11 and 22 degrees C. Most of the species responded to supra-optimal degrees of WC with a pronounced depression in NP. Elevated ambient CO2 concentration prevented this decrease in NP, indicating that it was caused by increased resistance of the thallus to CO2 diffusion. Depression of NP at high thallus WC regularly occurred under natural conditions, impairing primary production. Response characteristic of the lichens to experimental increase in ambient CO2 is highly dependent on thallus hydration. At optimal WC some species are already saturated by natural ambient CO2 at least at lower light intensities. Possible future increase in natural ambient CO2 concentration will impact lichen NP in particular when the thalli are highly water saturated.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CAROTENOID COMPOSITION, CONTINENTAL ANTARCTIC CRYPTOGAMS, GREEN-ALGAL LICHENS, MOISTURE, PATTERNS, PHOTOINHIBITION, PHOTOSYNTHESIS, PHYSIOLOGICAL INVESTIGATIONS, USNEA-SPHACELATA

1277

Laporte, M.M., J.A. Galagan, J.A. Shapiro, M.R. Boersig, C.K. Shewmaker, and T.D. Sharkey. 1997. Sucrose-phosphate synthase activity and yield analysis of tomato plants transformed with maize sucrose-phosphate synthase. *Planta 203(2):253-259.*

Sucrose synthesis is a major element of the interactions between photosynthesis and plant growth and development. Tomato (Lycopersicon esculentum Mill. cv. UC82B) plants transformed with maize sucrose-phosphate synthase (SPS; EC 2.3.1.14) expressed from either a ribulose-1,5-bisphosphate carboxylase- oxygenase (Rubisco) small subunit promoter (SSU) or the cauliflower mosaic virus 35S promoter (35S) were used to study effects of increased sucrose synthesis rates on plant growth. The plants were grown in growth chambers, field plots, and open-top chambers. The 35S plants had a 2 to 3-fold increase in young-leaf SPS activity, a 10 to 20-fold increase in young-root SPS activity and no increase in young-fruit SPS activity. The leaf SPS activity in;one of the 35S lines fell to control levels by two months of age. The SSU plants had a 4 to 5-fold increase in leaf SPS activity and no significant increase in root or young-fruit SPS activity. One 35S line, which maintained high leaf SPS activity throughout development, yielded 70-80% more than controls at both normal and elevated CO2 in open-top chambers in the field and 20-30% more than controls in two additional field trials. The other 35S line and the two SSU lines either yielded less or did not differ from controls under several growth conditions. Since only one of four transformed lines showed an increase in yield, we can not yet conclude that increased leaf SPS activity leads to increased yield. However, increased leaf SPS activity appears to result in increased fruit sugar content since all three lines with increased leaf SPS usually also had increased fruit sugars.

KEYWORDS: CARBON DIOXIDE, CO2, EXPRESSION, GENES, LEAVES, MECHANISM, PHOTOSYNTHESIS, TEMPERATURE, TRANSGENIC PLANTS

1278

Larigauderie, A., J.F. Reynolds, and B.R. Strain. 1994. Root response to co2 enrichment and nitrogen supply in loblolly-pine. *Plant and Soil 165(1):21-32.*

This paper examines how elevated CO2 and nitrogen (N) supply affect plant characteristics of loblolly pine (Pinus taeda L.) with an emphasis on root morphology. Seedlings were grown in greenhouses from seeds during one growing season at two atmospheric CO2 concentrations (375 and 710 mu L L(-1)) and two N levels (High and Low). Root morphological characteristics were determined using a scanner and an image analysis program on a Macintosh computer. In the high N treatment, elevated CO2 increased total plant dry weight by 80% and did not modify root to shoot (R/S) dry weight ratio, and leaf and plant N concentration at the end of the growing season. In the low N treatment, elevated CO2 increased total dry weight by 60%. Plant and leaf N concentration declined and R/S ratio tended to increase. Nitrogen uptake rate on both a root length and a root dry weight basis was greater at elevated CO2 in the high N treatment and lower in the low N treatment. We argue that N stress resulting from short exposures to nutrients might help explain the lower N concentrations observed at high CO2 in other experiments; Nitrogen and CO2 levels modified root morphology. High N increased the number of secondary lateral roots per length of first order lateral root and high CO2 increased the length of secondary lateral roots per length of first order lateral root. Number and length of first order lateral roots were not modified by either treatment. Specific root length of main axis, and to a lower degree, of first order laterals, declined at high CO2, especially at high N. Basal stem diameter and first order root diameters increased at high CO2, especially at high N. Elevated CO2 increased the proportion of upper lateral roots within the root system.

KEYWORDS: CARBOHYDRATE, CARBON-DIOXIDE ENRICHMENT, GROWTH, NUTRITION, PLANTS, SEEDLINGS

1279

Larsen, M., and C.B. Watkins. 1995. Firmness and concentrations of acetaldehyde, ethyl-acetate and ethanol in strawberries stored in controlled and modified atmospheres. *Postharvest Biology and Technology 5(1-2):39-50.*

'Pajaro' strawberries (Fragaria x ananassa Duch.) were stored at 0 degrees C in a range of controlled atmosphere (CA) conditions with CO2 concentrations up to 24%, O-2 concentrations down to 1%, or a combination of 10% CO2 and 2% O-2 Elevated CO2 concentrations resulted in firmer fruit, while low O-2 did not affect texture. Off-flavours developed after 3 days of storage at 20% CO2, but decreased when fruit was subsequently held for 24 h at 20 degrees C. However, off- flavours were persistent after CA storage for 7 days or more. Off-flavours were related to increases in ethyl acetate and ethanol concentrations but not to acetaldehyde. Beneficial atmospheres of close to 10% CO2 and 2% O-2 resulted in a firmer texture and delayed ripening with no off-flavour development. However, fruit quality was poor when similar atmospheres were developed in modified atmosphere (MA)-producing polythene bags. Rapid imposition of CA resulted in better quality fruit than when MAs around the fruit were developed gradually.

KEYWORDS: DECAY, FRUIT, LIFE, QUALITY, STORAGE

1280

Larson, D.L. 1994. Potential effects of anthropogenic greenhouse gases on avian habitats and populations in the northern great-plains. *American Midland Naturalist 131(2):330-346.*

Biotic response to the buildup of greenhouse gases in Earth's atmosphere is considerably more complex than an adjustment to changing temperature and precipitation. The fertilization effect CO2 has on some plants, the impact UVB radiation has on health and productivity of organisms, and the resulting changes in competitive balance and trophic structure must also be considered. The intent of this paper is to review direct and indirect effects of anthropogenic greenhouse gases on wildlife, and to explore possible effects on populations of birds and their habitats in the northern Great Plains. Many of the potential effects of increasing greenhouse gases, such as declining plant nutritional value, changes in timing of insect emergence, and fewer and saltier wetlands, foreshadow a decline in avian populations on the Great Plains. However, other possible effects such as increased drought resistance and water use efficiency of vegetation, longer growing seasons, and greater overall plant biomass promise at least some mitigation. Effects of multiple simultaneous perturbations such as can be expected under doubled CO2 scenarios will require substantial basic research to clarify.

KEYWORDS: ACTIVE ULTRAVIOLET-RADIATION, ALPINE LIFE ZONE, ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE CHANGE, ECOSYSTEM RESPONSES, ELEVATED CO2, LATITUDINAL GRADIENT, LESSER SNOW GEESE, PRAIRIE WETLANDS

1281

Lasceve, G., H. Gautier, J. Jappe, and A. Vavasseur. 1993. Modulation of the blue-light response of stomata of commelina-communis by co2. *Physiologia Plantarum 88(3):453-459.*

Effects of CO2 on stomatal movements of Commelina communis L. were studied with plants, epidermal strips and guard cell protoplasts. With plants, the stomatal response induced by a blue light pulse was studied for different ambient CO2 concentration ranging from CO2-deprived air to 100 Pa in darkness or under red light. It was observed that the blue light response could be obtained not only under a red light background but also in darkness and CO2-free air, the two responses being quite similar. With epidermal strips, the effect of CO2 on ferricyanide reductase activity at the guard cell plasmalemma was studied by transmission electron microscopy. In the presence of ferric ions, reduced ferricyanide gives an electron dense precipitate of Prussian Blue. In darkness and air, no precipitate was observed. In darkness and CO2-free air as well as under light and normal air, a precipitate was found along the plasmalemma of the guard cells, indicating a ferricyanide reductase activity. With guard cell protoplasts suspended in a medium either in equilibrium with air or in a CO2-free medium the H+ extrusion induced by a blue light pulse added to a red light background was measured. A low CO2 content was obtained by adding photosynthetic algae to the suspension of guard cell protoplasts. In a CO2-free medium the rate of H+ extrusion was enhanced. The results are discussed on the basis of a possible competition for reducing power between CO2 fixation and a putative blue light dependent redox chain located on the plasma membrane.

KEYWORDS: EXTRUSION, FERRICYANIDE, GUARD-CELL PROTOPLASTS, MESOPHYLL, METABOLISM, PLASMA-MEMBRANE, REDOX SYSTEM, REDUCTION, TRANSPORT, VICIA-FABA

1282

Lashof, D.A., B.J. DeAngelo, S.R. Saleska, and J. Harte. 1997. Terrestrial ecosystem feedbacks to global climate change. *Annual Review of Energy and the Environment 22:75-118.*

Anthropogenic greenhouse gases are expected to induce changes in global climate that can alter ecosystems in ways that, in turn, may further affect climate. Such climate-ecosystem interactions can generate either positive or negative feedbacks to the climate system, thereby

either enhancing or diminishing the magnitude of global climate change. Important terrestrial feedback mechanisms include CO2 fertilization (negative feedbacks), carbon storage in vegetation and soils (positive and negative feedbacks), vegetation albedo (positive feedbacks), and peatland methane emissions (positive and negative feedbacks). While the processes involved are complex, not readily quantifiable, and demonstrate both positive and negative feedback potential, we conclude that the combined effect of the feedback mechanisms reviewed here will likely amplify climate change relative to current projections that have not yet adequately incorporated these mechanisms.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ICE-CORE RECORD, LAST GLACIAL MAXIMUM, METHANE EMISSIONS, PLANT-RESPONSES, STOMATAL-RESISTANCE, TRACE GAS FLUXES, TROPICAL DEFORESTATION

1283

Lau, O.L. 1998. Effect of growing season, harvest maturity, waxing, low O-2 and elevated CO2 on flesh browning disorders in 'Braeburn' apples. *Postharvest Biology and Technology 14(2):131-141.*

British Columbia-grown 'Braeburn' apples (Malus x domestica Borkh.) stored for 6 months in air at 0 degrees C were, on average, 70 N in flesh firmness and had 0.48% titratable acidity. Fruit held in 1.2 or 1.5% O-2 + 1.0 or 1.2% CO2 controlled atmosphere (CA) storage were 8 N firmer, 20% higher in titratable acidity, and had significantly less core browning and superficial scald than fruit held in air for the same period. However, CA-stored fruit were highly susceptible to Braeburn browning disorder (BBD) and internal cavities (IC) after cool growing seasons [1993, 1995, and 1996; < 1300 degree-days > 10 degrees C (DD10) accumulated between May 1 and harvest]. Susceptibility of fruit to BED and IC was greatest in late-harvested fruit (starch index > 2.5 on a 0-9 scale) stored in 3.0% CO2 and 1.5% O-2. Storage at 1.7, 2.0, 3.0 and 4.0 degrees C did not decrease BED or IC incidence and tended to increase core browning (1996) and flesh softening (1994 and 1996) compared with fruit kept at 0 degrees C. Coating fruit with Shellac wax, but not Carnauba wax, increased BBD in air- stored fruit. Following a cool growing season it is recommended that 'Braeburn' apples be harvested at starch index values between 2.5 and 3.0 and stored in air storage at 0 degrees C to avoid the risks of scald, BED and IC. The fruit may be stored in <1.0% CO2 (preferably close to 0.1%) and > 1.5% O-2 after warm seasons (>1300 DD10). (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, GOLDEN DELICIOUS APPLES, LOW OXYGEN, QUALITY, STORAGE PROCEDURES

1284

Lauber, W., and C. Korner. 1997. In situ stomatal responses to long-term CO2 enrichment in calcareous grassland plants. *Acta Oecologica-International Journal of Ecology 18(3):221-229.*

A calcareous grassland community growing under full season CO? enrichment at low altitude in the Swiss Jura mountains was investigated for diurnal and seasonal variations of leaf diffusive conductance. A new CO2 enrichment method (Screen aided CO2 control, SACC) permitted irt situ leaf porometry under natural climatic conditions without disturbance of plants. At 600 ppm CO2, leaf conductance in the dominant species, Bromus erectus (a species so far not showing a growth response to elevated CO2) was reduced to half the values measured in controls. Tn contrast, leaf conductance in Carex flacca, a species of low cover (the only species so far exhibiting a dramatic growth stimulation by CO2 fertilization) remained almost unaffected by elevated CO2. Sanguisorba minor; Plantago media, and Cirsium acaule showed intermediate responses. Trifolium montanum, studied only on a single day, showed a reduction like Bromus. Differences between treatments were largest under humid conditions and disappeared during dry periods. In none of the species studied did stomatal density or stomatal index differ between treatments. A parallel investigation of whole ecosystem evapotranspiration indicated only small (< 10%) and non significant CO2 responses, suggesting that both aerodynamic effects at the canopy level and a great interspecific variation of leaf level responses overshadow the clear CO2 response of Bromus stomata. The different stomatal responses to CO2 enrichment are likely to alter species specific water consumption, and may thus affect community structure in the long run.

KEYWORDS: ACCLIMATION, C-4 GRASS, CARBON DIOXIDE, CONDUCTANCE, DENSITY, ELEVATED ATMOSPHERIC CO2, EXPOSURE, GAS-EXCHANGE, LEAVES, PHOTOSYNTHETIC CAPACITY

1285

Laurila, H.A. 1995. Modelling the effects of elevated CO2 and temperature on Swedish and German spring wheat varieties with CERES-wheat and AFRC-wheat crop models. *Journal of Biogeography 22(4-5):591-595.*

A study validating the CERES-wheat and the AFRC-wheat crop models was performed on Swedish (cv. Polkka) and German (cv. Nandu) spring wheat (Triticum aestivum L.) varieties under northern long day conditions. Validation consisted of the calibration of the phenological submodels in both crop models for Finnish conditions. Calibration results were used in simulating the effects of elevated CO2 and temperature on the yields and biomass production and the phenological development of the Swedish and the German varieties. The Swedish variety is currently commonly-cultivated in Finland. Based on the validation work, the CERES-wheat and the AFRC-wheat models will be used in the climate change Geographical Information System (GIS) for Finnish national scale crop potential estimations: different climate change scenarios for cereals will simulate the future Finnish growing conditions currently prevailing in Denmark and northern Germany.

KEYWORDS: CARBON DIOXIDE, WINTER-WHEAT

1286

Lavelle, P., D. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O.W. Heal, and S. Dhillion. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. *European Journal of Soil Biology 33(4):159-193.*

In this review the interactions between plant, animal and microbial components of the soil biota are represented by a model which allocates a pivotal functional role to the large, abundant invertebrates which ingest or manipulate both organic and mineral material, forming long-lasting microstructures. These invertebrates are designated soil ecosystem engineers and it is argued using data on numerical and biomass densities, geographical distribution and known functional roles, that earthworms and termites are the most important engineers in terrestrial ecosystems. Evidence is presented that they may exert influence on the diversity and activity of biota in subordinate trophic levels, for example litter transformers, micropredators and microfloras mediating fundamental nutrient transformations. Links between the activity and diversity of engineers and the physical properties of soils, including structural heterogeneity, stability, distribution of organic matter and infiltration and retention of water are also described. In considering the probable effects of global change on engineers, it is hypothesized that living plants affect both the abundance and diversity of engineers, through the quantity and quality of litter and other effects. Changes in their communities will therefore affect engineers. Expected changes in

temperature will expand the latitudinal distribution of termites and favour humivorous termites and endogeic earthworm species that feed in the soil. In some regions, however, these changes will not occur since local fauna may not include representatives of these groups. Although elevated CO2 may impact engineers through effects on plant growth (notably an increase in C/N ratio), land use intensification, particularly physical disturbance of forests, is of more immediate concern as changes in the functional group balance within engineers communities can be demonstrated. In addition, exotic species of earthworms may colonize disturbed land, with adverse effects on soil structure. Disturbance affects termites by reducing diversity (especially of soil-feeding forms) and some species may reach crop pest status, owing to changes in the availability of organic matter.

KEYWORDS: ELEVATED ATMOSPHERIC CO2, FUNGUS-GROWING TERMITES, MBALMAYO FOREST RESERVE, MILLSONIA-ANOMALA, MOUND-BUILDING TERMITES, NO-TILLAGE AGROECOSYSTEMS, ORGANIC-MATTER, PONTOSCOLEX-CORETHRURUS GLOSSOSCOLECIDAE, SOUTHERN GUINEA SAVANNA, TROPICAL GEOPHAGOUS EARTHWORM

1287

Lavigne, C., A. Mignot, and J. Stocklin. 1999. Genetic variation in the response of pollen germination to nutrient availability and elevated atmospheric CO2 concentrations in Epilobium angustifolium. *International Journal of Plant Science 160(1):109-115.*

It is expected that global climatic changes could lead to shifts in the genotypic composition of species that exhibit genetic variation in the response of fitness-related traits to an increase of atmospheric CO2. In plants that reproduce sexually, fitness can be described both by a female and a male component. Whereas the existence of genetic variation in the response to elevated CO2 of traits related to female fitness has been the focus of recent studies, studies on the response of the male component of fitness are still missing. Here, we report on the effects of elevated atmospheric CO2 and nutrient availability on che pollen quality of five full-sib families of Epilobium angustifolium. We did not detect an effect of the treatments on the in vitro pollen tube growth. However, we observed significant variation among families for pollen germination probabilities and a significant family x CO2 x nutrient interaction on this trait. This indicates that, in combination with nutrients increased CO2 could exert a selection pressure resulting in changes in the genetic structure of populations and in their mean response to CO2. It seems important that this evolution is included in models simulating the consequences of climate change on plant communities.

KEYWORDS: ARABIDOPSIS-THALIANA, CARBON DIOXIDE, COMPETITIVE ABILITY, CUCURBITA-PEPO CUCURBITACEAE, ERYTHRONIUM-GRANDIFLORUM, GAMETOPHYTIC SELECTION, GROWTH-RESPONSE, MIMULUS-GUTTATUS, RAPHANUS-RAPHANISTRUM, WILD RADISH

1288

Lavigne, M.B. 1996. Comparing stem respiration and growth of jack pine provenances from northern and southern locations. *Tree Physiology 16(10):847-852.*

Stem respiration rates of 31-year-old jack pine (Pinus banksiana Lamb.) trees from northern and southern provenances growing in a common garden were compared. At 15 degrees C, the seasonal course of stem respiration rate of northern provenances was not statistically different from that of southern provenances. A relationship existed between maintenance respiration rate and stem growth rate. Because relationships between sapwood relative growth rate and annual growth and maintenance respiration rates were similar for northern and southern provenances, no clinal differences in stem respiration rates were observed.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, MATURE LEAVES, PERENNE CV S23, REQUIREMENTS, RESPONSES, SELECTION, SIMULATED SWARDS

1289

Lavola, A., and R. Julkunentiitto. 1994. The effect of elevated carbon-dioxide and fertilization on primary and secondary metabolites in birch, betula-pendula (roth). *Oecologia 99(3-4):315-321.*

Seedlings of European white birch (Betula pendula Roth) were grown in growth chambers for one growth season under four carbon dioxide regimes (350, 700, 1050 and 1400 pm) and at three fertilization levels (0, 100 and 500 kg ha(-1) monthly). The soluble carbohydrates and secondary phenolics in the leaves and stems were analysed. It was found that fertilizer addition reduced the amounts of glucose and fructose while sucrose remained almost unaffected. The sugar content of leaves increased at 700 ppm and 1050 ppm of CO2 and decreased at the highest CO2 concentration (1400 ppm). The amounts of proanthocyanidins and flavonoids in leaves decreased with fertilization addition and increased with CO2 enrichment. The production of simple phenolic glucosides varied according to the fertilization and CO2 treatments. The triterpenoid content of stems seemed to increase with fertilization and CO2 addition. Our results indicate that the production of phytochemicals in the birch seedlings is very sensitive to both fertilization and CO2 addition, which is in agreement with earlier studies, and thus provide some support for the hypothesis of carbon allocation to plant defence when there is an excess of carbon and nutrient. The considerable variation in the production of secondary components may indicate that the synthesis of these defensive metabolites can be regulated by a plant to certain extent, depending on the ability of the plant to acclimate to changes in the physical environment.

KEYWORDS: ALASKA PAPER BIRCH, ALLOCATION, ATMOSPHERIC CO2, CHLOROPHYLL CONTENT, CO2-ENRICHMENT, GROWTH, NITROGEN- FERTILIZATION, NUTRIENT BALANCE, PLANTS, SALIX-MYRSINIFOLIA

1290

Lawler, I.R., W.J. Foley, I.E. Woodrow, and S.J. Cork. 1997. The effects of elevated CO2 atmospheres on the nutritional quality of Eucalyptus foliage and its interaction with soil nutrient and light availability. *Oecologia 109(1):59-68.*

Seedlings of Eucalyptus tereticornis (Smith) were grown under two levels of availability each of CO2 (352 and 793 mu mol mol(-1)), soil nutrients (1/24 and 1/4 Hoagland's solution) and light (full and 30% sunlight). Low soil nutrient availability or high light increased the C:N ratio of leaves, leading to lower leaf nitrogen concentrations, higher leaf specific weights and higher levels of both total phenolics and condensed tannins. These results were consistent with other studies of the effect of environmental resource availability on foliage composition. Similar results were observed when the C:N ratio of leaves was increased under elevated CO2. The changes in leaf chemistry induced by the treatments affected the performance of 4th-instar larvae of Chrysophtharta flaveola (Chapuis) fed on the leaves. Increased C:N ratios of leaves reduced digestive efficiencies and pupal body sizes and increased mortality. Below a threshold nitrogen concentration of approximately 1% dry mass, severe reductions in the performance of larvae were recorded. Such changes may have significant consequences for herbivores of Eucalyptus, particularly in view of projected increases in atmospheric CO2.

KEYWORDS: ALLELOCHEMICALS, CARBON ALLOCATION, CHRYSOMELIDAE, COLEOPTERA, DIETARY FIBER, NITROGEN, PAROPSIS-ATOMARIA OLIVIER, PLANTS, POLYSACCHARIDES, RESPONSES

1291

Lawlor, D.W., and R.A.C. Mitchell. 1991. The effects of increasing CO2 on crop photosynthesis and productivity - a review of field studies. *Plant, Cell and Environment 14(8):807-818.*

Only a small proportion of elevated CO2 studies on crops have taken place in the field. They generally confirm results obtained in controlled environments: CO2 increases photosynthesis, dry matter production and yield, substantially in C3 species, but less in C4, it decreases stomatal conductance and transpiration in C3 and C4 species and greatly improves water-use efficiency in all plants. The increased productivity of crops with CO2 enrichment is also related to the greater leaf area produced. Stimulation of yield is due more to an increase in the number of yield-forming structures than in their size. There is little evidence of a consistent effect of CO2 on partitioning of dry matter between organs or on their chemical composition, except for tubers. Work has concentrated on a few crops (largely soybean) and more is needed on crops for which there are few data (e.g. rice). Field studies on the effects of elevated CO2 in combination with temperature, water and nutrition are essential; they should be related to the development and improvement of mechanistic crop models, and designed to test their predictions.

KEYWORDS: AGAVE-VILMORINIANA, AIR- TEMPERATURE, ATMOSPHERIC CO2, CO2-ENRICHED ATMOSPHERE, ELEVATED CARBON-DIOXIDE, LEAF-AREA, PLANT GROWTH, SOYBEAN PHYSIOLOGY, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1292

Lawlor, D.W., R.A.C. Mitchell, J. Franklin, V.J. Mitchell, S.P. Driscoll, and E. Delgado. 1993. Facility for studying the effects of elevated carbon-dioxide concentration and increased temperature on crops. *Plant, Cell and Environment 16(5):603-608.*

The requirements for the experimental study of the effects of global climate change conditions on plants are outlined. A semi-controlled plant growth facility is described which allows the study of elevated CO2 and temperature, and their interaction on the growth of plants under radiation and temperature conditions similar to the field. During an experiment on winter wheat (cv. Mercia), which ran from December 1990 through to August 1991, the facility maintained mean daytime CO2 concentrations of 363 and 692 cm3 m-3 for targets of 350 and 700 cm3 m-3 respectively. Temperatures were set to follow outside ambient or outside ambient +4-degrees-C, and hourly means were within 0.5-degrees-C of the target for 92% of the time for target temperatures greater than 6-degrees- C. Total photosynthetically active radiation incident on the crop (solar radiation supplemented by artifical light with natural photoperiod) was 2% greater than the total measured outside over the same period.

KEYWORDS: CO2, FIELD, PRODUCTIVITY, SOURCE-SINK RELATIONS, WHEAT, YIELD

1293

Lawton, J.H., S. Naeem, R.M. Woodfin, V.K. Brown, A. Gange, H.J.C. Godfray, P.A. Heads, S. Lawler, D. Magda, C.D. Thomas, L.J. Thompson, and S. Young. 1993. The ecotron - a controlled environmental facility for the investigation of population and ecosystem processes. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 341(1296):181-194.*

This paper reports on aspects of the design and philosophy of the Ecotron, an integrated series of 16 controlled environmental chambers at the NERC Centre for Population Biology. The Ecotron serves as an experimental means for analysing population and community dynamics and ecosystem processes under controlled physical conditions. Within the chambers, terrestrial experimental communities are assembled into foodwebs of desired complexity from a pool of species selected for their preadaptations to the physical conditions of the Ecotron. These species include decomposers (earthworms, snails, microarthropods and microbes), primary producers (16 species of plants), primary consumers (four species of herbivorous arthropods), and secondary consumers (four species of parasitoids). The design of the Ecotron is unique in several aspects with respect to its blend of biology and technology. It supports small, dynamic communities of up to 30 plant and metazoan species, thereby making it among the more biologically complex controlled environmental systems currently in use. Its architecture permits replication and variation of spatial scale in experimental design. Its artificial climate simulates natural environmental conditions within chambers allowing experimental control over light, water, temperature, humidity, and in the near future CO2 and uv-B radiation. Sensors monitor both macro- and micro-environmental conditions of a number of physical factors within the chambers. Preliminary experiments show the Ecotron to be an excellent facility for long-term population and community-level experiments. We discuss the results of one of these early experiments and briefly consider ongoing and future experiments.

KEYWORDS: CLIMATE CHANGE, COMPETITION, DECIDUOUS WOODLAND, ELEVATED CO2, FIELD, HERBACEOUS VEGETATION, HOST-PARASITOID ASSOCIATIONS, PATCHY ENVIRONMENTS, PERSISTENCE, TREE LEAF LITTER

1294

Leadley, P.W., and B.G. Drake. 1993. Open top chambers for exposing plant canopies to elevated co2 concentration and for measuring net gas-exchange. *Vegetatio 104:3-15.*

Open top chamber design and function are reviewed. All of the chambers described maintain CO2 concentrations measured at a central location within +/- 30 ppm of a desired target when averaged over the growing season, but the spatial and temporal range within any chamber may be closer to 100 ppm. Compared with unchambered companion plots, open top chambers modify the microenvironment in the following ways: temperatures are increased up to 3-degrees-C depending on the chamber design and location of the measurement; light intensity is typically diminished by as much as 20%; wind velocity is lower and constant; and relative humidity is higher. The chamber environment may significantly alter plant growth when compared with unchambered controls, but the chamber effect on growth has not been clearly attributed to a single or even a few environmental factors. A method for modifying an open top chamber for tracking gas exchange between natural vegetation and the ambient air is described. This modification consists of the addition of a top with exit chimney to reduce dilution of chamber CO2 by external ambient air, is quickly made and permits estimation of the effects of elevated CO2 and water vapor exchange. The relatively simple design and construction of open top chambers make them the most likely method to be used in the near future for long-term elevated CO2 exposure of small trees, crops and grassland ecosystems. Improvements in the basic geometry to improve control of temperature, reduce the variation of CO2 concentrations, and increase the turbulence and wind speed in the canopy boundary layer are desirable objectives. Similarly, modifications for measuring water vapor and carbon dioxide gas exchange will extend the usefulness of open top chambers to include non-destructive monitoring of the responses of ecosystems to rising atmospheric CO2.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, COMMUNITIES, ESTUARINE MARSH, FIELD CHAMBERS, GROWTH, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION

1295

Leadley, P.W., P. Niklaus, R. Stocker, and C. Korner. 1997. Screen-aided CO2 control (SACC): a middle ground between FACE and open-top chambers. *Acta Oecologica-International Journal of Ecology 18(3):207-219.*

We have developed a novel CO2 exposure system for natural vegetation that is a middle ground between Free Air CO2 Enrichment (FACE) and traditional open-top chambers (OTC). Screen-Aided CO2 Control (SACC) technology uses much less CO2 per experiment and per replicate than FACE and is superior to OTCs in terms of its effects on microclimate. A SACC unit consists of a thin metal frame, a clear plastic "screen", and a pipe at the base of the screen through which CO2 enriched jets of air are directed into the unit. There is a gap between the ground and the bottom of the pipe and the screen is relatively short in comparison to the maximum height of the vegetation. Our SACC units are hexagonal and enclose a ground area of 1.27 m(2). SACC works in the following way: 1) the screen breaks the wind and creates turbulent mixing within the unit, 2) the mixing of the outside air with the CO2 enriched jets of air,generates relatively uniform CO2 concentrations within the screened-in vegetation, and 3) a fully automated system monitors CO2 concentrations and adjusts CO2 injection rates for each unit every ca. IO minutes to maintain preset CO2 concentrations. Twenty-four hour means of CO2 concentrations in the middle of a unit are typically maintained within 1 mu l l(- 1) of their set points. Spatial variation and short-term fluctuations in CO2 concentration are similar to those in OTCs and FACE. CO2 consumption at our site is 5 kg CO2 day(-1) replicate(-1) for a total of ca. 30 tons per year for 20 elevated CO2 SACC units. Compared to OTCs, SACC units have reduced temperature peaks at full sunlight, minimal effects on solar radiation, reduced rainfall interception by chamber walls, and freer access of small animals to experimental plots. We believe that SACC is the best method for exposing short stature vegetation to elevated CO2 when financial constraints do not allow for a properly replicated FACE experiment.

KEYWORDS: ENRICHMENT, ENVIRONMENT, FIELD

1296

Leadley, P.W., P.A. Niklaus, R. Stocker, and C. Korner. 1999. A field study of the effects of elevated CO2 on plant biomass and community structure in a calcareous grassland. *Oecologia 118(1):39-49.*

The effects of elevated CO2 on plant biomass and community structure have been studied for four seasons in a calcareous grassland in northwest Switzerland. This highly diverse, semi- natural plant community is dominated by the perennial grass Bromus erectus and is mown twice a year to maintain species composition. Plots of 1.3 m(2) were exposed to ambient or elevated CO2 concentrations (n = 8) using a novel CO2 exposure technique, screen-aided CO2 control (SACC) starting in March 1994. In the 1st year of treatment, the annual harvested biomass (sum of aboveground biomass from mowings in June and October) was not significantly affected by elevated CO2. However, biomass increased significantly at elevated CO2 in the 2nd (+20%, P = 0.05), 3rd (+21%, P = 0.02) and 4th years (+29%, P = 0.02). There were no detectable differences in root biomass in the top 8 cm of soil between CO2 treatments on eight out of nine sampling dates. There were significant differences in CO2 responsiveness between functional groups (legumes, non- leguminous forbs, graminoids) in the 2nd (P = 0.07) and 3rd (P < 0.001) years of the study. The order of CO2 responsiveness among functional groups changed substantially from the 2nd to the 3rd year; for example, non-leguminous forbs had the smallest relative response in the 2nd year and the largest in the 3rd year. By the 3rd year of CO2 exposure, large species- specific differences in CO2 response had developed. For five important species or genera the order of responsiveness was Lotus corniculatus (+271%), Carex flacca (+249%), Bromus erectus (+ 33%), Sanguisorba minor (no significant CO2 effect), and six Trifolium species (a negative response that was not significant). The positive CO2 responses in Bromus and Carex were most closely related to increases in tiller number. Species richness was not affected by CO2 treatment, but species evenness increased under elevated CO2 (modified Hill ratio; P = 0.03) in June of the 3rd year, resulting in a marginally significant increase in species diversity (Simpson's index; P = 0.09). This and other experiments with calcareous grassland plants show that elevated atmospheric CO2 concentrations can substantially alter the structure of calcareous grassland communities and may increase plant community biomass.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON, CHALK GRASSLAND, ECOSYSTEMS, ENRICHMENT, GROWTH, LEAF, LEVEL RESPONSES, ROOT

1297

Leadley, P.W., and J.F. Reynolds. 1992. Long-term response of an arctic sedge to climate change - a simulation study. *Ecological Applications 2(4):323-340.*

It appears that polar regions of the Ear-th will bear the brunt of global temperature increases. Because of the ecological importance of the sedge Eriophorum vaginatum in the arctic and the large amount ot data available on its growth and physiology, we chose this species as a test case to model the potential long-term response of arctic plants to global climate change. Our simulation model utilizes a mechanistic framework and includes the effects of light, temperature, season length, nitrogen availability, and CO2 concentration on E. vaginatum growth dynamics. The model was parameterized based on a series of published studies of the growth responses of E. vaginatum to nutrients and validated using (1) field studies on the growth responses of E. vaginatum to temperature and shading, and (2) the effects of elevated CO2 and temperature on E. vaginatum photosynthesis. The effect of a 50-yr period of climate change on peak biomass (overwintering biomass plus seasonal production) in E. vaginatum was explored. We use climate change here to refer to linear increases over a 50-yr period in temperature (from 8-degrees to 13-degrees-C), season length (from 100 to 120 d), and atmospheric CO2 (from 340 to 680 muL/L). Similarly, a wide range of nitrogen availabilities (from 9 to 18 g.m 2.vr-1) was also examined because of its importance in productivity. The model predicts that a simultaneous increase in the direct effects of temperature, season length, and CO2, with no change in nitrogen availability, will result in a slight decrease in peak biomass. A simulated long-term doubling of nitrogen availability results in an almost-equal-to 70% increase in peak biomass, whereas with concurrent changes in climate and nitrogen availability, the model predicts a slight decline in peak biomass compared to increases in nitrogen alone. In essence, the model predicts that climate change will have substantial effects on E. vaginatum only indirectly through changes in nitrogen availability. Simulated peak biomass responds linearly up to a doubling of current nitrogen availabilities. Therefore, at low- to-moderate increases in nitrogen availability, the predicted response of E. vaginatum to climate change is linearly (and almost exclusively) dependent on our ability to predict the effects of climate change on nitrogen cycling. At nitrogen availabilities > 2 x current availabilities, the relationship flattens out very rapidly because the plant becomes limited by carbon uptake. Thus, if nitrogen availabilities more than double in the future, E. vaginatum may shift from being a nutrient-limited to a carbon-limited system and, consequently, increased season length and elevated CO2 concentrations may play an important role in controlling E. vaginatum productivity.

KEYWORDS: ACCUMULATION, ALASKAN TUSSOCK TUNDRA,

BIOMASS, CARBON DIOXIDE, ERIOPHORUM VAGINATUM, GROWTH, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, VEGETATION TYPES

1298

Leadley, P.W., and J. Stocklin. 1996. Effects of elevated CO2 on model calcareous grasslands: Community, species, and genotype level responses. *Global Change Biology 2(4):389-397.*

We investigated the responses of model calcareous grassland communities to three CO2 concentrations: 330, 500, and 660 mu L L(-1). The communities were composed of six species, Bromus erectus Hudson, Festuca ovina L., Prunella vulgaris L., Prunella grandiflora (L.) Scholler, Hieracium pilosella L., and Trifolium repens L., that are native to the calcareous grasslands of Europe. Genotypic variation in CO2 response was studied in Bromus erectus and Festuca ovina. Plants were harvested after c. 126 days of growth. We found that: 1 At the community level, there were marginally significant (0.1 greater than or equal to P > 0.05) increases in leaf and litter dry weight with increasing CO2 concentration. 2 There were significant differences between species in CO2 response, including both negative and positive responses. Prunella vulgaris had a significant negative response; Hieracium pilosella and Festuca ovina had significant positive responses; Prunella grandiflora had a marginally significant positive response; and Bromus erectus and Trifolium repens did not have significant responses. 3 There was significant variation among genotypes in the response to elevated CO2 in Bromus erectus, but not in Festuca ovina. Based on the observed species- and genotype-level variation in CO2 response of calcareous grassland plants in this and other studies, we speculate that increasing atmospheric CO2 concentrations will alter community structure in calcareous grasslands.

KEYWORDS: AMBIENT, ENRICHMENT, GROWTH, NITROGEN, NUTRIENTS, PLANTAGO, TEMPERATURE

1299

Leavitt, S.W., E.A. Paul, A. Galadima, F.S. Nakayama, S.R. Danzer, H. Johnson, and B.A. Kimball. 1996. Carbon isotopes and carbon turnover in cotton and wheat FACE experiments. *Plant and Soil 187(2):147-155.*

The Maricopa cotton and wheat FACE (free-air CO2 enrichment) experiments offer propitious opportunity to quantify carbon turnover. The commercial CO2 (delta(13)C approximate to-37 parts per thousand) used to elevate CO2 concentration in field plots provided a strongly C-12-depleted tracer. Soil CO2 and delta(13)C of soil organic carbon (SOC) in CO2-enriched and Control plots were measured between the final cotton FACE project (October 1991) and the end of the second wheat experiment (June 1994). The initial C-13-depletion in SOC of cotton FACE plots (measured by the difference in delta(13)C between FACE and Control plots) persisted at the same level (1.9 parts per thousand) 1.5 years after the experiment ended. A similar depletion was observed in soil CO2 evolved in the same plots, indicating ongoing decomposition of the new SOC. The SOC delta(13)C of wheat plots before and after two growing seasons showed increasing C-13-depletion in FACE relative to Control. Isotopic mass balance was consistent with 5-6% new carbon input from the two wheat crops. This is lower than the 12-13% calculated for FACE cotton and perhaps a consequence of the larger root system of cotton or the 3-year duration of the cotton experiments versus 2 years for the wheat.

KEYWORDS: DIOXIDE, DYNAMICS, NATURAL C-13 ABUNDANCE, SOIL ORGANIC MATTER

1300

Leavitt, S.W., E.A. Paul, B.A. Kimball, G.R. Hendrey, J.R. Mauney, R. Rauschkolb, H. Rogers, K.F. Lewin, J. Nagy, P.J. Pinter, and H.B. Johnson. 1994. Carbon-isotope dynamics of free-air co2-enriched cotton and soils. *Agricultural and Forest Meteorology 70(1-4):87-101.*

A role for soils as global carbon sink or source under increasing atmospheric CO2 concentrations has been speculative. Free-air carbon dioxide enrichment (FACE) experiments with cotton, conducted from 1989 to 1991 at the Maricopa Agricultural Center in Arizona, maintained circular plots at 550 mumol mol-1 CO2 with tank CO2 while adjacent ambient control plots averaged about 370 mumol mol-1 CO2. This provided an exceptional test for entry of carbon into soils because the petrochemically derived tank CO2 used to enrich the air above the FACE plots was depleted in both radiocarbon (C-14 content was 0% modern carbon (pmC)) and C-13 (delta13 C almost- equal-to -36 parts per thousand) relative to background air, thus serving as a potent isotopic tracer. Flask air samples, and plant and soil samples were collected in conjunction with the 1991 experiment. Most of the isotopic analyses on the plants were performed on the holecellulose component. Soil organic carbon was obtained by first removing carbonate with HCl, floating off plant fragments with a NaCl solution, and picking out remaining plant fragments under magnification. The delta C-13 of the air above the FACE plots was approximately - 15 to - 19 parts per thousand, i.e. much more C-13 depleted than the background air of approximately -7.5parts per thousand. The delta C-13 values of plants and soils in the FACE plots were 10-12 parts per thousand and 2 parts per thousand C-13-depleted, respectively, compared with their control counterparts. The C-14 content of the FACE cotton plants was approximately 40 pmC lower than that of the control cotton, but the C-14 results from soils were conflicting and therefore not as revealing as the delta C-13 of soils. Soil stable-carbon isotope patterns were consistent, and mass balance calculations indicate that about 10% of the present organic carbon content in the FACE soil derived from the 3 year FACE experiment. At a minimum, this is an important quantitative measure of carbon turnover, but the presence of C- 13-depleted carbon, even in the recalcitrant 6 N HCl resistant soil organic fraction (average age 2200 years before present (BP)), suggests that at least some portion of this 10% is an actual increase in carbon accumulation. Similar isotopic studies on FACE experiments in different ecosystems could permit more definitive assessment of carbon turnover rates and perhaps provide insight into the extent to which soil organic matter can accommodate the 'missing' carbon in the global carbon cycle.

KEYWORDS: ABUNDANCE, FLUXES, ROOT

1301

LeCain, D.R., and J.A. Morgan. 1998. Growth, gas exchange, leaf nitrogen and carbohydrate concentrations in NAD-ME and NADP-ME C-4 grasses grown in elevated CO2. *Physiologia Plantarum 102(2):297-306.*

Plants with the C-4 photosynthetic pathway have predominantly one of three decarboxylation enzymes in their bundle sheath cells. Within the grass family (Poaceae) bundle sheath leakiness to CO2 is purported to be lowest in the nicotinamide adenine dinucleotide phosphate-malic enzyme (NADP-ME, EC 1.1.1.40) group, highest in the NAD-ME (EC 1.1.1.39) group and intermediate in the phosphoenolpyruvate carboxykinase (PCK, EC 4.1.1.32) group. We investigated the hypothesis that growth and photosynthesis of NAD-ME C-4 grasses would respond more to elevated CO2 treatment than NADP-ME grasses. Plants were frown in 8-1 pots in growth chambers with ample water and fertilizer for 39 days at a continuous CO2 concentration of either 350 or 700 mu l 1(-1). NAD-ME species included Bouteloua gracilis Lag. ex Steud (Blue grama), Buchloe dactyloides (Nutt.) Engelm. (Buffalo grass) and Panicum virgatum L. (Switchgrass) and the NADP-ME species were Andropogon gerardii Vittman (Big bluestem), Schizachyrium scoparium (Michx.) Nash (Little bluestem), and Sorghastrum mutans (L.) Nash

(Indian grass). Contrary to our hypothesis, growth of the NADP-ME grasses was generally greater under elevated CO2 (significant for A. gerardii and S. mutans), while none of the NAD-ME grasses had a significant growth response. Increased leaf total non- structural carbohydrate (TNC) was associated with greater growth responses of NADP-ME grasses. Decreased leaf nitrogen in NADP-ME species grown at elevated CO2 was found to be an artifact of TNC dilution. Assimilation (A) vs intercellular CO2 (C-i) curves revealed that leaf photosynthesis was not saturated at 350 mu l 1(-1) CO2, in any of these C-4 grasses. Assimilation of elevated CO2-grown A. gerardii was higher than in plants grown in ambient CO2. In contrast, B. gracilis grown in elevated CO2 displayed lower A, a trait more commonly reported in C-3 plants. Photosynthetic acclimation is B. gracilis was not related to leaf TNC or nitrogen concentrations, but A:C-i curves suggest a reduction in activity of both phosphoenolpyruvate (PEP) carboxylase (EC 4.1.1.31) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39). Some adaptation of stomatal functioning was also seen in B. gracilis and A. gerardii leaves grown in elevated CO2. Our study shows that C-4 grasses have the capacity for increased growth and photosynthesis under elevated CO2 even when water and nutrients are non-limiting. While it was the NADP-ME species which had significant responses in the present study, we have previously reported significant growth increases in elevated CO2 for B. gracilis.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, BOUTELOUA-GRACILIS C-4, CARBON DIOXIDE, ENRICHMENT, PASCOPYRUM-SMITHII C-3, PHOTOSYNTHESIS, PLANTS, RESPONSES, TEMPERATURE

1302

Lechowicz, M.J., and T. Koike. 1995. Phenology and seasonality of woody-plants - an unappreciated element in global change research. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):147-148.*

KEYWORDS: BUDBURST, CO2, FROST DAMAGE, INCREASE, TEMPERATE TREES

1303

Ledergerber, S., P.W. Leadley, J. Stocklin, and B. Baur. 1998. Feeding behaviour of juvenile snails (Helix pomatia) to four plant species grown at elevated atmospheric CO2. *Acta Oecologica-International Journal of Ecology 19(1):89-95.*

The feeding behaviour of juveniles of the land snail Helix pomatia was examined in model plant communities consisting of Trifolium repens, Hieracium pilosella, Bromus erectus and Prunella vulgaris that are common species in extensively managed calcareous grasslands in the Swiss Jura mountains. The plant communities were grown either at ambient (350 ppm) or elevated (600 ppm) CO2 concentrations. Leaves of T. repens and P. vulgaris grown in elevated atmospheric CO2 had a lower specific leaf area, and leaves of T. repens had lower percentage N on a dry weight basis than leaves grown under ambient CO2 concentration. Snails fed on all four plant species, but showed a overwhelming preference for T. repens (percentages of total biomass consumed were 91.9 % at 350 ppm and 97.6 % at 600 ppm). The species-specific feeding intensity of juvenile H. pomatia did not differ between the two treatments. The total dry weight of T. repens consumed by the snails was marginally greater (P = 0.06) at elevated CO2, but there were no significant differences in leaf N or leaf area eaten. These findings are similar to numerous other studies showing that invertebrates increase their consumption of plant material to balance reductions in plant N concentrations at elevated CO2 treatments. Helix pomatia that fed on plants grown at elevated CO2 atmosphere showed a larger increase in relative wet weight than those that fed on plants from ambient CO2 conditions. However, the weight gain of H. pomatia was poorly correlated with amount of plant tissue consumed, so we suggest that the effect of CO2 on weight gain in H. pomatia was due to a change in the quality of T. repens leaves. (C) Elsevier, Paris.

KEYWORDS: HERBIVORY, PAPER BIRCH, PERFORMANCE, QUALITY, RESPONSES

1304

Ledergerber, S., G.H. Thommen, and B. Baur. 1997. Grazing damage to plants and gastropod and grasshopper densities in a CO2-enrichment experiment on calcareous grassland. *Acta Oecologica-International Journal of Ecology 18(3):255-261.*

Plant-herbivore interactions may change as atmospheric CO2 concentrations continue to rise. We examined the effects of elevated atmospheric CO2 and CO2-exposure chambers on the grazing damage to plants, and on the abundances of potential herbivores (terrestrial gastropods and grasshoppers) in a calcareous grassland in the Jura mountains of Switzerland (village of Nenzlingen). Individuals of most plant species examined showed slight grazing damage. However, plots with CO2 enrichment and plots with ambient atmosphere did not differ in the extent of grazing damage. Similarly, plots with CO2 enrichment and plots with ambient atmosphere did not differ in either gastropod or grasshopper density. Experimental plots with and without chambers did not differ in the number of gastropods. However, the densities of gastropods and grasshoppers and extent of grazing damage to plants were generally lower in the experimental area than in the grassland outside the experimental field.

KEYWORDS: ATMOSPHERES, CO2, INSECT HERBIVORE INTERACTIONS

1305

Lee, E.H., R.C. Pausch, R.A. Rowland, C.L. Mulchi, and B.F.T. Rudorff. 1997. Responses of field-grown soybean (cv. Essex) to elevated SO2 under two atmospheric CO2 concentrations. *Environmental and Experimental Botany 37(2-3):85-93.*

The objective of this research was to determine the effects of elevated concentrations of carbon dioxide (CO2) and sulfur dioxide (SO2) on field-grown soybean. Soybeans (Glycine max L. Merr. cv. 'Essex') were grown a full-season in open-top field chambers exposed to either ambient (350 mu l L-1) or elevated CO2 (500 mu l L-1) levels under two levels of SO2 (0.00 and 0.12 mu l L-1). Enriched CO2, with or without SO2 treatments, significantly increased net photosynthesis rates, leaf area index (LAI; in R4 growth stage) and leaf dry weight, but did not significantly affect stomatal resistance, transpiration rates, leaf area, plant height, total biomass or grain yield. Elevated SO2 treatments significantly decreased photosynthesis and LAI during pod fill stages, but did not significantly affect stomatal resistance, transpiration, total biomass, plant height or grain yield. Sulfur dioxide inhibited growth and development (i.e., LAI) during canopy coverage before any effects on photosynthesis were detected. The interactive effects of CO2 and SO2 treatments on the gas exchange parameters were significant during pod fill, where high SO2 reduced photosynthesis at ambient CO2 but not under elevated CO2. Leaf area index values were likewise reduced by SO2 exposure under ambient CO2 during late flowering and pod fill stages. Thus, enriched CO2 under high SO2 exposure partially compensated for the negative impact of SO2 stress on PS and LAI during the pod fill stages. (C) 1997 Elsevier Science B.V.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, FUMIGATION, GLYCINE-MAX, PHOTOSYNTHESIS, PLANTS, SPRUCE TREES, SULFUR-DIOXIDE

1306

Lee, H.S.J., and P.G. Jarvis. 1995. Trees differ from crops and from each other in their responses to increases in CO2 concentration. *Journal of Biogeography 22(2-3):323-330.*

Length of exposure, degree of maturity and type of tissue all affect the results obtained in response to elevated CO2 treatment of trees. Seedlings are most responsive and, in many cases, the first few weeks or months of exposure may set the pattern for future growth. Measurements of leaf photosynthesis and respiration are not good predictors for incorporation of carbon into tissue. Seasonal changes in non-structural carbohydrates, emissions of isoprenes from leaves and exudation from roots can 'waste' photosynthate. However, these are difficult or impossible to quantify. Currently, the only generalization that can be made is that growth will be accelerated but the magnitude of this depends on tissue type, nutrition and environmental conditions. The implications of this for a future elevated atmospheric CO2 world are complex. Interactions and competition between species should be incorporated into long-term studies. These studies must, themselves, be incorporated into appropriate models which take into account regional soils and climates for use in prediction of the effects of global climate change on trees and forests.

KEYWORDS: ALLOCATION, ELEVATED CARBON-DIOXIDE, ENHANCEMENT, ENRICHMENT, GROWTH, NUTRIENTS, NUTRITION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS

1307

Lee, H.Y., W.S. Chow, and Y.N. Hong. 1999. Photoinactivation of photosystem II in leaves of Capsicum annuum. *Physiologia Plantarum 105(2):377-384.*

Leaf discs of Capsicum annuum L. were illuminated in air enriched with 1% CO2 in the absence or presence of lincomycin, an inhibitor of chloroplast-encoded protein synthesis. The loss of functional photosystem (PS) II complexes with increase in cumulative light dose (photon exposure), assessed by the O-2 yield per single-turnover flash, was greater in leaves of plants grown in low light than those in high light; it was also exacerbated in the presence of lincomycin. A single exponential decay can describe the relationship between the loss of functional PSII and increase in cumulative photon exposure. From this relationship we obtained both the maximum quantum yield of photoinactivation of PSII at limiting photon exposures and the coefficient k, interpreted as the probability of photoinactivation of PSII per unit photon exposure. Parallel measurements of chlorophyll fluorescence after light treatment showed that 1/F-o--1/F-m was linearly correlated with the functionality of PSII, where F-o and F-m are the chlorophyll fluorescence yields corresponding to open and closed PSII reaction centers, respectively. Using 1/F-o--I/F-m as a convenient indicator of PSII functionality, it was found that PSII is present in excess; only after tbe loss of about 40% functional PSII complexes did PSII begin to limit photosynthetic capacity in capsicum leaves.

KEYWORDS: ANTENNA SIZE, COEFFICIENTS, FLUORESCENCE, GROWTH IRRADIANCE, LEAF-DISKS, LIGHT, PHOTOINHIBITION, PHOTOSYNTHETIC APPARATUS, RATE-CONSTANT, YIELD

1308

Lee, J.J., D.L. Phillips, and R.F. Dodson. 1996. Sensitivity of the US corn belt to climate change and elevated CO2 .2. Soil erosion and organic carbon. *Agricultural Systems 52(4):503-521.*

Climate models indicate that increasing atmospheric concentrations of carbon dioxide and other greenhouse gases could alter climate globally. The EPIC (Erosion/Productivity Impact Calculator) model was used to examine the sensitivity of soil erosion (wind, water) and soil organic carbon (SOC) (15 cm and 1 m depth) across the US corn belt to changes in temperature (+2 degrees C), precipitation (+/-10%, +/-20%), wind speed (+/-10%, +/-20%), and atmospheric CO2 concentration (350, 625 ppmv). One-hundred-year simulations were run for each of 100 sites under 36 climate/CO2 regimes. The 100-year regionally aggregated mean water erosion rates increased linearly with precipitation, whereas the wind erosion rates decreased and total erosion rates increased by 15-18%. Total erosion increased with increased temperature. Increasing CO2 from 350 to 625 ppmv (with temperature increased by 2 degrees C and mean wind speed held constant) had no effect on water erosion, despite increases in annual total and peak runoff; this was attributed to increased vegetation cover. Wind erosion decreased by 4-11% under increased CO2. Wind erosion was very sensitive to mean wind speed, increasing four-fold and decreasing 10-fold for a 20% increase or decrease in mean wind speed, respectively. This was attributed to a threshold effect. SOC to 1 m decreased 4.8 Mg-C ha(-1) from an initial value of 18.1 Mg-C ha(-1) during the 100-year baseline simulation. About 50% of this loss (2.3 Mg-C ha(-1)) was due to transport off- site by soil erosion. SOC in the top 15 cm decreased 0.8 Mg-C ha(-1) from an initial value of 4.9 Mg-C ha(-1). Increased temperature and precipitation accelerated these losses of SOC, whereas increased CO2 slowed the losses. Copyright (C) 1996 Published by Elsevier Science Ltd

KEYWORDS: MODEL, YIELD

1309

Lee, X.H., J.D. Fuentes, R.M. Staebler, and H.H. Neumann. 1999. Long-term observation of the atmospheric exchange of CO2 with a temperate deciduous forest in southern Ontario, Canada. *Journal of Geophysical Research-Atmospheres 104(D13):15975-15984.*

This paper reports the results of the analysis of eddy covariance CO2 data obtained at a successional forest of maple and aspen at Camp Borden in southern Ontario, Canada, between July 1995 and December 1997. Main findings are (1) The Michaelis-Menton model explains >50-65% of the observed variance of the daytime net ecosystem carbon exchange (NEE) during the growing season; leaf wetness appears to be an important variable contributing to the remaining variance. (2) The whole-ecosystem respiration rate as a function of the 5-cm soil temperature shows a seasonal "hysteresis" (higher rate in the later part of the year), suggesting a nonnegligible contribution by deep soil/roots and the influence of litter age. (3) There is evidence of photosynthetic activities immediately after the spring snowmelt/soil warming, but the. daily NEE did not switch sign till about 40 days later; our best estimates of the annual net carbon uptake by the ecosystem net ecosystem production (NEP) are -1,0, -1.2, and -2.8 t C ha(-1) yr(-1) for the periods July 19, 1995, to July 18, 1996, January 1 to December 31, 1996, and January 1 to December 31, 1997, respectively, with an uncertainty of +/-0.4 t C ha(-1) yr(-1). (4) The higher NEP value in 1997 than in 1996 was caused by lower growing season soil temperature, cooler spring and fall transitional periods, and higher photon flux in 1997; possible enhancement in canopy photosynthetic capacity may also have played a role. In addition, three main sources of uncertainties, data gap, fetch, and mass flow, are discussed, it is suggested that collective use of the methods available for assessing the whole-ecosystem respiration (friction velocity threshold, mass flow theory, and dark respiration from the forest light response) may increase the confidence level of NEP estimates.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CLIMATE, EDDY-CORRELATION, FLUXES, RAIN-FOREST, SENSITIVITY, SOIL RESPIRATION, USE EFFICIENCY, VEGETATION, WATER-VAPOR EXCHANGE

1310

Leech, R.M., and J.L. Marrison. 1996. Immunofluorescent

quantitation of chloroplast proteins. *Plant Journal 10(6):1169-1175.*

Using scanning light microscopy software to detect and measure immunofluorescence in leaf sections Rubisco concentration in situ in chloroplasts has been accurately determined throughout development. The fluorescence measurements were calibrated by comparison with values for Rubisco accumulation obtained from rocket immunoelectrophoresis profiles of soluble protein from isolated cells and from chloroplasts using a purified sample of Rubisco as the standard. It has been shown that in situ immunofluorescence can be used for cytoquantitation of proteins within individual chloroplasts to a sensitivity of 1fg and also for the comparison of the protein levels in adjacent chloroplasts and cells. Several important applications of this new technique are discussed.

KEYWORDS: CELLS, DIVISION, DNA, ELEVATED CO2, GROWN WHEAT LEAVES, TEMPERATURE

1311

Leemans, R. 1992. Modeling ecological and agricultural impacts of global change on a global scale. *Journal of Scientific & Industrial Research 51(8-9):709-724.*

The changing composition of the atmosphere could lead to significant changes in regional and continental climate. The methodology to develop consistent climate-change scenarios and to link them to different impact-models is discussed. Results of both static and dynamic models are presented and the advantages and disadvantages of the different approaches are addressed. Examples are drawn from different impact studies on large-scale vegetation patterns, forest dynamics and agricultural systems. General conclusions of these studies are that vegetation and agricultural zones will shift on global, continental and regional scales, but that large uncertainties still exist in the timing, actual response and rate of change of the current zones. Despite these uncertainties, the direction of these models indicates future developments and could be used for policy purposes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC CHANGE, CO2, CONSEQUENCES, DYNAMICS, FORESTS, GROWTH, PHOTOSYNTHESIS, SENSITIVITY, VEGETATION

1312

Leemans, R., A. vanAmstel, C. Battjes, E. Kreileman, and S. Toet. 1996. The land cover and carbon cycle consequences of large-scale utilizations of biomass as an energy source. *Global Environmental Change-Human and Policy Dimensions 6(4):335-357.*

The use of modern biomass for energy generation has been considered in many studies as a possible measure for reducing or stabilizing global carbon dioxide (CO2) emissions. In this paper we assess the impacts of large-scale global utilization of biomass on regional and grid scale land cover, greenhouse gas emissions, and carbon cycle. We have implemented in the global environmental change model IMAGE the LESS biomass intensive scenario, which was developed for the Second Assessment Report of IPCC. This scenario illustrates the potential for reducing energy related emission by different sets of fuel mixes and a higher energy efficiency. Our analysis especially covers different consequences involved with such modern biomass scenarios. We emphasize influences of CO2 concentrations and climate change on biomass crop yield, land use, competition between food and biomass crops, and the different interregional trade patterns for modern biomass based energy. Our simulations show that the original LESS scenario is rather optimistic on the land requirements for large-scale biomass plantations. Our simulations show that 797 Mha is required while the original LESS scenario is based on 550 Mha. Such expansion of agricultural land will influence deforestation patterns and have significant consequences for environmental issues, such as biodiversity. Altering modern biomass requirements and the locations where they are grown in the scenario shows that the outcome is sensitive for regional emissions and feedbacks in the C cycle and that competition between food and modern biomass can be significant, We conclude that the cultivation of targe quantities of modern biomass is feasible, but that its effectiveness to reduce emissions of greenhouse gases has to he evaluated in combination with many other environmental land use and soclo-economic factors. Copyright (C) 1996 Elsevier Science Ltd

KEYWORDS: CROPS, EMISSIONS, GLOBAL CHANGE, MODEL, SCENARIOS, SEQUESTRATION

1313

Leishman, M.R., L. Hughes, K. French, D. Armstrong, and M. Westoby. 1992. Seed and seedling biology in relation to modeling vegetation dynamics under global climate change. *Australian Journal of Botany 40(4-5):599-613.*

The distribution of many plant species will change with global climate change, depending on their ability to disperse into, and establish in, new communities. Past migrations of species under climate change have been an order of magnitude slower than the rate of predicted climate change for the next century. The limited evidence available suggests that chance long distance dispersal events will be critically important in determining migration rates. We examine the JABOWA-derived gap replacement models and vital attributes/FATE models and ask: what do we need to know about dispersal and establishment to make improved projections of vegetation dynamics under climate change using these models? The minimal modifications of these models required to incorporate directional migration of species are described. To predict establishment success of species, we suggest that a more fundamental understanding is needed of how establishment ability under different conditions relates to seed and seedling attributes and how this may be affected by elevated CO2. Finally, we examine whether plant functional types based on vegetative attributes (used to model the response of adult plants) are correlated with functional types based on seed and seedling attributes. Available evidence suggests that the two sets of attributes are not strongly correlated; consequently, models of vegetation dynamics will need to incorporate seed biology explicitly.

KEYWORDS: CO2, COMPUTER-MODEL, DISPERSAL, ESTABLISHMENT, GROWTH, PATTERNS, RAIN-FOREST, SUCCESSION MODEL, TEMPERATURES, WOODY-PLANTS

1314

Lenssen, G.M., J. Lamers, M. Stroetenga, and J. Rozema. 1993. Interactive effects of atmospheric co2 enrichment, salinity and flooding on growth of C-3 (elymus-athericus) and C-4 (spartina- anglica) salt-marsh species. *Vegetatio 104:379-388.*

The growth response of Dutch salt marsh species (C3 and C4) to atmospheric CO2 enrichment was investigated. Tillers of the C3 species Elymus athericus were grown in combinations of 380 and 720 mul l-1 CO2 and low (0) and high (300 mM NaCl) soil salinity. CO2 enrichment increased dry matter production and leaf area development while both parameters were reduced at high salinity. The relative growth response to CO2 enrichment was higher under saline conditions. Growth increase at elevated CO2 was higher after 34 than 71 days. A lower response to CO2 enrichment after 71 days was associated with a decreased specific leaf area (SLA). In two other experiments the effect of CO2 (380 and 720 mul l-1) on growth of the C4 species Spartina anglica was studied. In the first experiment total plant dry weight was reduced by 20% at elevated CO2. SLA also decreased at high CO2. The effect of elevated CO2 was also studied in combination with soil salinity (50 and 400 mM NaCl) and flooding. Again plant weight was reduced (10%) at elevated

CO2, except under the combined treatment high salinity/non- flooded. But these effects were not significant. High salinity reduced total plant weight while flooding had no effect. Causes of the salinity-dependent effect of CO2 enrichment on growth and consequences of elevated CO2 for competition between C3 and C4 species are discussed.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPLASTS, GAS-EXCHANGE, IRRADIANCE, LEAVES, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, RESPONSES, SEEDLINGS, WATER-STRESS

1315

Lenssen, G.M., W.E. Vanduin, P. Jak, and J. Rozema. 1995. The response of aster-tripolium and puccinellia-maritima to atmospheric carbon-dioxide enrichment and their interactions with flooding and salinity. *Aquatic Botany 50(2):181-192.*

The effects of 380 and 720 mumol mol-1 atmospheric CO2 on growth, dry matter allocation, net leaf photosynthesis and stomatal conductance of the C3 salt marsh species Aster tripolium L. and Puccinellia maritima (Hudson) Parl. were studied. Plants were grown in pots under combinations of low (50-250 mM NaCl) or high (450-550 mM NaCl) salinity and non- flooded or flooded salt marsh soil. High salinity reduced growth of both species, while flooding increased biomass production of A. tripolium. Root weight of A. tripolium and total plant weight of P. maritima was increased by atmospheric CO2 enrichment when the soil was flooded. Under non-flooded conditions, the effect of elevated CO2 on growth was small (P. maritima) or absent (A. tripolium). The relative increase in total plant weight of both species by elevated CO2 was higher under saline conditions. Dry matter allocation between root, stem and leaf, as reflected in leaf weight ratio and shoot to root ratio, was not changed by elevated CO2, while specific leaf area was slightly decreased by CO2 enrichment. Elevated CO2 stimulated net leaf photosynthesis of both species, while stomatal conductance decreased. These effects were not changed by salinity or flooding treatment.

KEYWORDS: C-3, COMMUNITIES, ELEVATED CO2, ELYMUS-ATHERICUS, ENVIRONMENT, ESTUARINE MARSH, GROWTH, HALOPHYTES, NITROGEN, PHOSPHORUS

1316

Leonardos, E.D., and B. Grodzinski. 1997. Photosynthesis, export and carbon partitioning in source leaves of C-3, C-3-C-4 intermediate and C-4 Panicum species at ambient and elevated CO2 levels. *Plant Physiology 114(3):221.*

1317

Leonardos, E.D., M.J. Tsujita, and B. Grodzinski. 1994. Net carbon-dioxide exchange-rates and predicted growth-patterns in alstroemeria-jacqueline at varying irradiances, carbon- dioxide concentrations, and air temperatures. *Journal of the American Society for Horticultural Science 119(6):1265-1275.*

The influence of irradiance, CO2 concentration, and air temperature on leaf and whole-plant net C exchange rate (NCER) of Alstroemeria 'Jacqueline' was studied. At ambient CO2, leaf net photosynthesis was maximum at irradiances above 600 mu mol.m(-2).s(-1) photosynthetically active radiation (PAR), while whole-plant NCER required 1200 mu mol.m(-2).s(-1) PAR to be saturated. Leaf and whole-plant NCERs were doubled under CO2 enrichment of 1500 to 2000 mu l CO2/liter. Leaf and whole-plant NCERs declined as temperature increased from 20 to 35C. Whereas the optimum temperature range for leaf net photosynthesis was 17 to 23C, whole-plant NCER, even at high light and high CO2, declined above 12C. Dark respiration of leaves and whole plants increased with a Q(10) of approximate to 2 at 15 to 35C. In an analysis of day effects, irradiance, CO2 concentration, and temperature contributed 58%, 23%, and 14%, respectively, to the total variation in NCER explained by a second-order polynomial model (R(2)=0.85). Interactions among the factors accounted for 4% of the variation in day C assimilation. The potential whole- plant growth rates during varying greenhouse day and night temperature regimes were predicted for short- and long-day scenarios. The data are discussed with the view of designing experiments to test the importance of C gain in supporting flowering and high yield during routine harvest of Alstroemeria plants under commercial greenhouse conditions.

KEYWORDS: CO2 EXCHANGE, PHOTOPERIOD, PLANT, REGINA

1318

LeThiec, D., and M. Dixon. 1996. Acclimation of photosynthesis in Norway spruce and red oak grown in open-top chambers and subjected to natural drought and to elevated CO2. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 26(1):87-94.*

Eight-year-old Norway spruce (Picea abies (L.) Karst.) and 6- year-old red oak (Quercus rubra L.) trees planted directly into the soil were enclosed in open-top chambers and exposed to either 350 or 700 mu mol . mol(-1) of CO2 for three growing seasons. During the third year a natural drought was allowed to develop, reducing the predawn leaf water potential to between - 0.80 and -1.15 MPa. Intensive gas-exchange measurements were performed before, during, and after the drought. CO2 response curves revealed mesophyll limitation to photosynthesis in drought-stressed trees grown in elevated levels of CO2. The water-use efficiency was greater for trees grown at elevated CO2, but less so during drought in red oak and the same between treatments for drought-stressed spruce. Diurnal measurements showed that enhancement of assimilation rates of trees grown at 700 mu mol . mol(-1) depended upon the time of day that measurements were made. There was an acclimation to increased CO2 in both species that could not be explained by leaf area differences, available soil for roots, nutrient limitation, or starch accumulation.

KEYWORDS: ASSIMILATION, EFFICIENCY, ENHANCEMENT, ENRICHMENT, GAS-EXCHANGE, IRRADIANCE, LEAVES, SEEDLINGS, WATER-STRESS

1319

Lethiec, D., M. Dixon, P. Loosveldt, and J.P. Garrec. 1995. Seasonal and annual variations of phosphorus, calcium, potassium and manganese contents in different cross-sections of picea-abies (L) karst needles and quercus-rubra L leaves exposed to elevated co2. *Trees-Structure and Function 10(2):55-62.*

Norway spruce and red oak trees were planted directly into the soil and enclosed in open-top chambers. For 2 years the trees were exposed to both ambient and elevated CO2 concentrations (700 mu mol mol(-1)) and during this time variations in nutrient concentrations were studied. CO2-treated plants had decreases in global leaf concentrations of nitrogen, potassium, calcium and manganese for both species. When different areas of the foliage were analysed however, the response showed much variability between the respective sites and between species. Furthermore the nutrient concentrations changed differently as the plant material aged and this change showed inter-treatment differences. These results show how it may be important to analyse plant material of different ages and at different cell sites when studying nutrient levels.

1320

Leung, L.R., and S.J. Ghan. 1999. Pacific northwest climate sensitivity simulated by a regional climate model driven by a GCM. Part II: 2xCO(2) simulations. *Journal of Climate 12(7):2031-2053.*

Global climate change due to increasing concentrations of greenhouse gases has stimulated numerous studies and discussions about its possible impacts on water resources. Climate scenarios generated by climate models at spatial resolutions ranging from about 50 km to 400 km may not provide enough spatial specificity for use in impact assessment. In Parts I and II of this paper. the spatial specificity issue is addressed by examining what information on mesoscale and small- scale spatial features can be gained by using a regional climate model with a subgrid parameterization of orographic precipitation and land surface cover, driven by a general circulation model. Numerical experiments have been performed to simulate the present-day climatology and the climate conditions corresponding to a doubling of atmospheric CO2 concentration. This paper describes and contrasts the large-scale and mesoscale features of the greenhouse warming climate signals simulated by the general circulation modal and regional climate model over the Pacific Northwest. Results indicate that changes in the large-scale circulation exhibit strong seasonal variability. There is an average warming of about 2 degrees C, and precipitation generally increases over the Pacific Northwest and decreases over California. The precipitation signal over the Pacific Northwest is only statistically significant during spring, when both the change in the large- scale circulation and increase in water vapor enhance the moisture convergence toward the north Pacific coast. The combined effects of surface temperature and precipitation changes are such that snow cover is reduced by up to 50% on average, causing large changes in the seasonal runoff. This paper also describes the high spatial resolution (1.5 km) climate signals simulated by the regional climate model. Reductions in snow cover of 50%-90% are found in areas near the snow line of the control simulation. Analyses of the variations of the climate signals with surface elevation ranging from sea level to 4000 m over two mountain ranges in the Pacific Northwest show that because of changes in the alitude of the freezing level, strong elevation dependency is found in the surface temperature, rainfall. snowfall, snow cover, and runoff signals.

KEYWORDS: ATMOSPHERIC CO2, WATER-RESOURCES

1321

Leverenz, J.W. 1995. Shade shoot structure of conifers and the photosynthetic response to light at 2 co2 partial pressures. *Functional Ecology 9(3):413-421.*

1. The response of net photosynthesis to irradiance was measured for shade-adapted shoots of different conifer species. Shoots were illuminated unidirectionally or in a light integrating sphere to study the effects of shoot structure. 2. Shoot structure was quantified as R(max) the ratio of the shoot-silhouette area to the leaf-silhouette area. 3. The initial slopes and the convexities (rate of bending) of the light response curves were strongly affected by R(max) during unilateral illumination. There was also a strong positive effect of R(max) on the maximum efficiency of net photosynthesis and a strong negative effect of R(max) on the light compensation point. 4. Increasing atmospheric CO2 partial pressure (C-a) from 35 to 70 Pa did not affect the convexity of the light response curves nor rates of dark respiration. 5. Increasing C-a affected the initial slope, the light compensation point, the maximum rate of photosynthesis and the efficiency of net photosynthesis. 6. Except for the maximum rate of net photosynthesis, the responses to C-a were controlled by shoot structure. 7. Studies of the effect of atmospheric CO2 on photosynthesis and growth in conifers need to consider variations in shoot structure.

KEYWORDS: AREA, CURVE, ELEVATED CO2, GROWTH, MODELS, SCOTS PINE, SEEDLINGS, STANDS, TEMPERATURES

1322

Levis, S., J.A. Foley, and D. Pollard. 1999. Potential high-latitude vegetation feedbacks on CO2-induced climate change. *Geophysical Research Letters 26(6):747-750.*

We use a fully coupled climate-vegetation model to examine the potential effects of changes in vegetation cover on simulations of CO2-induced climate change. We find that vegetation feedbacks, acting mainly through changes in surface albedo, enhance greenhouse warming in the northern high latitudes during spring and summer months. In spring and summer, land surfaces north of 45 degrees N are warmed by 3.3 and 1.7 degrees C by a doubling of CO2 alone; vegetation feedbacks produce an additional warming of between 1.1-1.6 and 0.4-0.5 degrees C, respectively. In winter, however, vegetation feedbacks appear to oppose the 5.6 degrees C radiative warming, particularly over Eurasia. These results demonstrate that vegetation feedbacks are potentially significant and must be included in assessments of anthropogenic climate change.

KEYWORDS: BALANCE, BOREAL FOREST, DOUBLED ATMOSPHERIC CO2, GLOBAL CLIMATE, MODEL, SURFACE ALBEDO

1323

Lewin, K.F., G.R. Hendrey, J. Nagy, and R.L. Lamorte. 1994. Design and application of a free-air carbon-dioxide enrichment facility. *Agricultural and Forest Meteorology 70(1-4):15-29.*

Growth chambers and other enclosures used in plant physiology and growth studies tend to introduce chamber effects that alter the microclimate around the plants compared with the natural environment. A free-air (chamberless) carbon dioxide enrichment (FACE) system has been developed by Brookhaven National Laboratory (BNL) to provide controlled fumigation conditions while minimizing the potential to impose a discernible chamber effect. This system is capable of exposing large numbers of field-grown plants to elevated levels of atmospheric carbon dioxide (CO2) from seedling emergence until physiologic maturity. A FACE User Facility was established at the Maricopa Agricultural Center, University of Arizona, for continuous enrichment of CO2 at a set point of 550 mumol mol-1 during daylight hours throughout the cotton crop growing seasons of 1989-1991. The facility consisted of four circular BNL FACE arrays and associated equipment placed in a commercial cotton plantation. FACE array diameters of 23, 25, and 27 m were tested. The FACE facility included the ability to operate the experimental plots under two watering regimes using an automated, sub-surface irrigation system. CO2 was stored in a 48 000 kg receiver and vaporized with a heat exchanger that used water at ambient temperature as the energy source. The 1 min average CO2 concentration was held to within +/- 20% of the set point more than 98% of the time that the arrays were operating during all three seasons. In 1991, the long term average CO2 concentration measured at 63 points throughout the volume of a 20 m diameter experimental plot (ground to canopy top) centered within a 25 m diameter FACE array was 568 mumol mol-1. All of the FACE arrays operated for more than 99% of the planned experimental period in 1991. These 3 years of operation have demonstrated that the BNL FACE technology can be used as a basis for a large scale facility devoted to studying the fate of carbon in the terrestrial environment.

1324

Lewis, C.E., G. Peratoner, A.J. Cairns, D.R. Causton, and C.H. Foyer. 1999. Acclimation of the summer annual species, Lolium temulentum, to CO2 enrichment. *Planta 210(1):104-114.*

Lolium temulentum L. Ba 3081 was grown hydroponically in air (350 mu mol mol(-1) CO2) and elevated CO2 (700 mu mol mol(-1) CO2) at two irradiances (150 and 500 mu mol m(-2) s(-1)) for 35 days at which point the plants were harvested. Elevated CO2 did not modify relative growth rate or biomass at either irradiance. Foliar carbon-to-nitrogen ratios were decreased at elevated CO2 and plants had a greater number of shorter tillers, particularly at the lower growth irradiance. Both light-limited and light-saturated rates of photosynthesis were stimulated. The amount of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) protein was increased at elevated CO2, but maximum extractable Rubisco activities were not significantly increased. A pronounced decrease in the Rubisco activation stale was found with CO2 enrichment, particularly at the higher growth irradiance. Elevated-CO2-induced changes in leaf carbohydrate composition were small in comparison to those caused by changes in irradiance. No CO2-dependent effects on fructan biosynthesis were observed. Leaf respiration rates were increased by 68% in plants grown with CO2 enrichment and low light. We conclude that high CO2 will only result in increased biomass if total light input favourably increases the photosynthesis-to-respiration ratio. At low irradiances, biomass is more limited by increased rates of respiration than by CO2-induced enhancement of photosynthesis.

KEYWORDS: AMBIENT CO2, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, EXCISED LEAVES, FRUCTAN BIOSYNTHESIS, NITRATE REDUCTASE, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, PLANT-GROWTH ANALYSIS

1325

Lewis, J.D., K.L. Griffin, R.B. Thomas, and B.R. Strain. 1994. Phosphorus supply affects the photosynthetic capacity of loblolly-pine grown in elevated carbon-dioxide. *Tree Physiology 14(11):1229-1244.*

Effects of phosphorus supply and mycorrhizal status on the response of photosynthetic capacity to elevated CO2 were investigated in loblolly pine (Pinus taeda L.) seedlings. Seedlings were grown in greenhouses maintained at either 35.5 or 71.0 Pa CO2 in a full factorial experiment with or without mycorrhizal inoculum (Pisolithus tinctorius (Pers.) Coker & Couch) and with an adequate or a limiting supply of phosphorus. Assimilation versus internal CO2 partial pressure (C(i)) curves were used to estimate maximum Rubisco activity (V(c,max)), electron transport mediated ribulose 1,5-bisphosphate regeneration capacity (J(max)), phosphate regeneration capacity (PiRC) and daytime respiration rates (R(d)). Nonmycorrhizal seedlings grown with limiting phosphorus had significantly reduced V(c,max) and PiRC compared to seedlings in other treatments. Elevated CO2 increased photosynthetic capacity in nonmycorrhizal seedlings in the low phosphorus treatment by increasing PiRC, whereas it induced phosphorus limitation in mycorrhizal seedlings in the low phosphorus treatment and did not affect the photosynthetic capacity of seedlings in the high phosphorus treatment. Despite the variety of effects on photosynthetic capacity, seedlings in the elevated CO2 treatments had higher net assimilation rates than seedlings in the ambient CO2 treatments. We conclude that phosphorus supply affects photosynthetic capacity during long-term exposure to elevated CO2 through effects on Rubisco activity and ribulose 1,5-bisphosphate regeneration rates.

1326

Lewis, J.D., D. Olszyk, and D.T. Tingey. 1999. Seasonal patterns of photosynthetic light response in Douglas- fir seedlings subjected to elevated atmospheric CO2 and temperature. *Tree Physiology 19(4-5):243-252.*

Increases in atmospheric CO2 concentration and temperature are predicted to increase the light response of photosynthesis by increasing light-saturated photosynthetic rates and apparent quantum yields. We examined the interactive effects of elevated atmospheric CO2 concentration and temperature on the light response of photosynthesis in Douglas-fir (Pseudotsuga menziesii (Mirb.) France) seedlings. Seedlings were grown in sunlit chambers controlled to track either ambient (similar to 400 ppm) CO2 or ambient + 200 ppm CO2, at ambient temperature or ambient +4 degrees C. Photosynthetic light response curves were measured over an 18-month period beginning 32 months after treatments were initiated. Light-response curves were measured at the growth CO2 concentration, and were used to calculate the light-saturated rate of photosynthesis, light compensation point, quantum yield and respiration rate. Elevated CO2 increased apparent quantum yields during two of five measurement periods, but did not significantly affect light- saturated net photosynthetic rates, light compensation points or respiration rates. Elevated temperature increased all parameters. There were no significant interactions between CO2 concentration and temperature. We conclude that down-regulation of photosynthesis occurred in the elevated CO2 treatments such that carbon uptake at a given irradiance was similar across CO2 treatments. In contrast, increasing temperature may substantially increase carbon uptake rates in Douglas-fir, assuming other environmental factors do not limit photosynthesis; however, it is not clear whether the increased carbon uptake will increase growth rates or be offset by increased carbon efflux through respiration.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, COMPENSATORY RESPONSES, DECIDUOUS FOREST, DIFFERENT IRRADIANCE LEVELS, GAS-EXCHANGE, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, LOBLOLLY-PINE, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1327

Lewis, J.D., and B.R. Strain. 1996. The role of mycorrhizas in the response of Pinus taeda seedlings to elevated CO2. *New Phytologist 133(3):431-443.*

The effects of mycorrhizal status, phosphorus supply and CO2 partial pressure on production and allocation of biomass in seedlings from two populations of Pinus taeda L. were examined. Seedlings from a North Carolina and a Florida population were grown in sterile soil in a full-factorial experiment with one of two phosphorus treatments (low P, high P) and at one of two CO2 partial pressures (35.5, 71.0 Pa). One half of the seedlings were inoculated with Pisolithus tinctorius (Pers.) Coker & Couch hyphae and spores. Seedlings were harvested 60, 90 and 120 d after emergence. Elevated CO2 significantly increased total seedling dry mass in all treatments at all three harvests. Phosphorus limitation reduced seedling growth, and mycorrhizas increased seedling growth in seedlings limited by phosphorus supply. Generally, however, there were no interactions between CO2, phosphorus supply and mycorrhizal status on dry mass of seedlings. Mycorrhizas probably did not affect the response of dry mass to elevated CO2 because phosphorus limitation did not reduce response of dry mass to elevated CO2. Phosphorus-limited seedlings responded to elevated CO2 as a result of increased phosphorus uptake, resulting from increased total root dry mass, and increased phosphorus use efficiency. Although mycorrhizal colonization did not affect the response of biomass to elevated CO2, it significantly reduced the response of needle area. As a result, specific leaf area (leaf area per unit plant biomass) was lower in mycorrhizal seedlings grown in elevated CO2 than in mycorrhizal seedlings grown in ambient CO2. Because there were no effects on relative growth rate or seedling dry mass, reductions in specific leaf area suggest that elevated CO2 reduced the relative cost of the symbiosis.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, FUNGUS PISOLITHUS-TINCTORIUS, LIQUIDAMBAR- STYRACIFLUA, LONG-TERM EXPOSURE, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC ACCLIMATION,

RADIATA D-DON, TRIFOLIUM-SUBTERRANEUM L, UNITED-STATES

1328

Lewis, J.D., R.B. Thomas, and B.R. Strain. 1994. Effect of elevated co2 on mycorrhizal colonization of loblolly- pine (pinus-taeda L) seedlings. *Plant and Soil 165(1):81-88.*

Interactive effects of elevated atmospheric CO2 and phosphorus supply on mycorrhizal colonization rates were investigated using loblolly pine (Pinus taeda L.) seedlings from Florida and coastal North Carolina. Seedlings from both populations were grown in greenhouses maintained at either 35.5 Pa or 71.0 Pa CO2. In both CO2 treatments, seedlings were grown in a full factorial experiment with or without mycorrhizal inoculum and with an adequate or a limiting supply of phosphorus. Seedlings were harvested 60, 90 and 120 days after emergence and at each harvest root subsamples were examined to determine the percent of fine roots that were mycorrhizal. Additionally, root carbohydrate and nutrient levels were measured at each harvest. Root starch, sugar and total non-structural carbohydrate (TNC) concentrations were increased by growth in elevated CO2 and decreased by mycorrhizal colonization. Phosphorus stress decreased root starch concentrations, increased root sugar concentrations and did not significantly affect TNC concentrations. However, despite significant effects on root carbohydrate levels, there were generally no significant treatment effects on mycorrhizal colonization. Additionally, at all harvests, root starch and sugar concentrations were not correlated with percent of fine roots that were mycorrhizal. These results suggest that although elevated CO2 may significantly increase root carbohydrate levels, the increases may not affect the percent of fine roots that are mycorrhizal.

KEYWORDS: GROWTH, INCREASES, INFECTION, NUTRIENT, PHOSPHORUS, PLANTS, QUERCUS-ALBA, SOIL

1329

Lewis, J.D., D.T. Tissue, and B.R. Strain. 1996. Seasonal response of photosynthesis to elevated CO2 in loblolly pine (Pinus taeda L) over two growing seasons. *Global Change Biology 2(2):103-114.*

Trees growing in natural systems undergo seasonal changes in environmental factors that generate seasonal differences in net photosynthetic rates. To examine how seasonal changes in the environment affect the response of net photosynthetic rates to elevated CO2, we grew Pinus taeda L. seedlings for three growing seasons in open-top chambers continuously maintained at either ambient or ambient + 30 Pa CO2. Seedlings were grown in the ground, under natural conditions of light, temperature and nutrient and water availability. Photosynthetic capacity was measured bimonthly using net photosynthetic rate vs. intercellular CO2 partial pressure (A-C-i) curves. Maximum Rubisco activity (Vc(max) and ribulose 1,5-bisphosphate regeneration capacity mediated by electron transport (J(max)) and phosphate regeneration (PiRC) were calculated from A-C-i curves using a biochemically based model. Rubisco activity, activation state and content, and leaf carbohydrate, chlorophyll and nitrogen concentrations were measured concurrently with photosynthesis measurements. This paper presents results from the second and third years of treatment. Mean leaf nitrogen concentrations ranged from 13.7 to 23.8 mg g(-1), indicating that seedlings were not nitrogen deficient. Relative to ambient CO2 seedlings, elevated CO2 increased light-saturated net photosynthetic rates 60-110% during the summer, but < 30% during the winter. A relatively strong correlation between leaf temperature and the relative response of net photosynthetic rates to elevated CO2 suggests a strong effect of leaf temperature. During the third growing season, elevated CO2 reduced Rubisco activity 30% relative to ambient CO2 seedlings, nearly completely balancing Rubisco and RuBP- regeneration regulation of photosynthesis. However, reductions in Rubisco activity did not eliminate the seasonal pattern in the relative response of net photosynthetic rates to elevated CO2. These results indicate that seasonal differences in the relative response of net photosynthetic rates to elevated CO2 are likely to occur in natural systems.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, PHASEOLUS-VULGARIS L, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SCIRPUS- OLNEYI, TUSSOCK TUNDRA

1330

Leymarie, J., G. Lasceve, and A. Vavasseur. 1998. Interaction of stomatal responses to ABA and CO2 in Arabidopsis thaliana. *Australian Journal of Plant Physiology 25(7):785-791.*

Stomatal responses to ABA and CO2 were investigated in Arabidopsis thaliana (L.) Heynh. wild-type and ABA insensitive mutants (abi1-1, abi2-1, abi1-1 abi2-1) at the whole plant and at the isolated epidermis levels. In wild-type plants, feeding roots with ABA (1-50 mu M) triggered a rapid drop in leaf conductance which levelled off during the following photoperiods, and strongly inhibited the increase in conductance induced by light. The rapid response was strongly inhibited in abi1-1, abi2-1 and abi1-1 abi2-1 double mutants, but a residual long-term decrease in leaf conductance was still observed. In wild-type plants, exogenous ABA strongly enhanced the response to CO2 removal. Conversely, in the absence of CO2 the effect of ABA was drastically reduced in epidermal strip experiments. These results reveal a strong interaction between sensing of ABA and CO2 in stomata of A. thaliana. Despite an initially wide stomatal aperture in abi-1, abi-2 and double mutant plants, their stomatal responses to light and CO2 removal were half those of wild-type plants. Moreover these responses were totally independent of the presence of ABA, suggesting that ABI1 and ABI2 are either directly involved in the interaction between the two signalling pathways or, alternatively located upstream of this point of interaction.

KEYWORDS: ABSCISIC- ACID, CALCIUM, CARBON DIOXIDE, GUARD-CELLS, MUTANTS, MUTATIONS, PROTEIN PHOSPHATASE, SIGNAL-TRANSDUCTION, SLOW ANION CHANNELS, WATER-STRESS

1331

Leymarie, J., G. Lasceve, and A. Vavasseur. 1999. Elevated CO2 enhances stomatal responses to osmotic stress and abscisic acid in Arabidopsis thaliana. *Plant, Cell and Environment 22(3):301-308.*

Carbon dioxide and abscisic acid (ABA) are two major signals triggering stomatal closure. Their putative interaction in stomatal regulation was investigated in well-watered air-grown or double CO2-grown Arabidopsis thaliana plants, using gas exchange and epidermal strip experiments. With plants grown in normal air, a doubling of the CO2 concentration resulted in a rapid and transient drop in leaf conductance followed by recovery to the pre-treatment level after about two photoperiods. Despite the fact that plants placed in air or in double CO2 for 2 d exhibited similar levels of leaf conductance, their stomatal responses to an osmotic stress (0.16-0.24 MPa) were different. The decrease in leaf conductance in response to the osmotic stress was strongly enhanced at elevated CO2, Similarly, the drop in leaf conductance triggered by 1 mu M ABA applied at the root level was stronger at double CO2. Identical experiments were performed with plants fully grown at double CO2, Levels of leaf conductance and carbon assimilation rate measured at double CO2 were similar for air-grown and elevated CO2-grown plants. An enhanced response to ABA was still observed at high CO2 in pre- conditioned plants. It is concluded that: (i) in the absence of stress, elevated CO2 slightly affects leaf conductance in A. thaliana; (ii) there is a strong interaction in stomatal responses to

CO2 and ABA which is not modified by growth at elevated CO2.

KEYWORDS: ANION CHANNELS, ATMOSPHERIC CO2, CARBOHYDRATE ACCUMULATION, CARBON DIOXIDE, CYTOSOLIC CA-2, GUARD-CELLS, SHORT- TERM, VICIA-FABA, WATER-USE EFFICIENCY

1332

Li, A., G.M. Berntson, D.L. Godbold, and F.A. Bazzaz. 1998. The dynamics of root production and loss in Betula papyrifera seedlings in response to elevated CO2 and an aluminium pulse. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde 161(1):17-21.*

Seedlings of Betula papyrifera were grown in sand/nutrient solution cultures in rhizotrone growth containers under elevated (700 ppm) or ambient (375 ppm) atmospheric CO2 concentrations for approximately 10 weeks. Thirty seven days after the begin of the experiment the plants were exposed to a 10 day pulse of 400 or 1200 mu M Al. Elevated atmospheric CO2 increased both root production and loss. Exposure to Al reduced root production and slightly reduced root loss. The reduced root production due to Al was amplified after the pulse had receded, resulting in a significantly lower net and gross root production at the end of the experiment. There were no clear CO2 x Al interactions.

KEYWORDS: CARBON, GROWTH, MALATE, PLANTS, RESISTANCE, RHIZOSPHERE

1333

Li, A.G., A. Trent, G.W. Wall, B.A. Kimball, Y.S. Hou, P.J. Pinter, R.L. Garcia, D.V. Hunsaker, and R.L. Lamorte. 1997. Free-air CO2 enrichment effects on rate and duration of apical development of spring wheat. *Crop Science 37(3):789-796.*

Rates and durations of individual phases of wheat (Triticum aestivum L.) apical development are among the most important factors that determine yield components. Because atmospheric CO2 has been increasing steadily, it is important to evaluate the effects of elevated CO2 on wheat development. This study was conducted to determine rates and durations of leaf, spikelet, and floret primordium initiation in a Free-Air Carbon Dioxide Enrichment (FACE) system. Spring wheat (cv. Yecora Roja) was planted at the University of Arizona Maricopa Agricultural Center. The two CO2 concentrations were 550 (elevated) and 370 (ambient) mu mol mol(-1) CO2. Individual plant samples were collected every 3 to 4 d. We dissected the main stem (MS), coleoptile tiller (T0), primary tillers (T1, T2, and T3) and secondary tillers (T00, T01, T02, T10, T11, and T12) and counted primordia. Apex primordium data were fitted to a four-piece linear-spline segmented regression model with the SAS proc NLIN. No influence of elevated CO2 (550 mu mol mol(- 1)) on leaf primordium initiation of MS was detected. Nevertheless, CO2 enrichment significantly increased rates of spikelet primordium initiation of MS, T1, T2, T10, and T11, and diminished the durations of spikelet development phase of MS, T1, T2, T3, T10, and T11. Within the floret phase, CO2 enrichment significantly increased rates of floret primordium initiation of MS, T0, T1, T2, and T3, and diminished the time to the completion of floret primordium initiation of MS, T0, T1, T3, and T11. The information from this study will be utilized to predict wheat apical development and grain production in the elevated atmospheric CO2 environments of the future.

KEYWORDS: EAR DEVELOPMENT, FIELD, GROWTH, INFLORESCENCE DEVELOPMENT, PHOTOPERIOD, PRIMORDIUM INITIATION, SPIKELET NUMBER, TEMPERATURE, WINTER-WHEAT, YIELD

1334

Li, A.G., G.W. Wall, A. Trent, and Y.S. Hou. 1999. Free-air CO2 enrichment effects on apex dimensional growth of spring wheat. *Crop Science 39(4):1083-1088.*

Although primordium initiation in wheat (Triticum aestivum L,) has been extensively researched, a complete description of the growth dynamics of the apex at elevated CO2 concentrations is lacking. This study determined the rates of main stem and tiller apical elongation and widening in plants grown under two levels of CO2 concentration. Spring wheat was grown at the University of Arizona's Maricopa Agricultural Center at elevated (550 mu mol mol(-1)) or ambient (370 mu mol mol(-1)) CO2 concentrations. Individual plant samples were collected at different developmental stages and dissected. After dissection, the Lengths and widths of the spires of the main stem (MS), coleoptile tiller (T0), primary tillers (T1, T2, and T3), and secondary tillers (T00, T01, T02, T10, T11, and T12) were measured with a stage micrometer. Apex dimensions were fitted to an exponential model, Elevated CO2 increased the apex lengths of T2 at the double ridge stage, and of T3 and T10 at the double ridge and the terminal spikelet stages, and the apex widths of T2 at double ridge stage, and of T2, T3, T10, and T11 at the flag leaf appearance stage. Combining these results with a parallel study, the longer apices did not have more spikelet primordia, but wider apices had more floret primordia, Elevated CO2 changed apex elongation or widening patterns within a plant by enhancing elongation or widening rates of the MS, and later formed tillers. Earlier-formed tillers were less responsive to elevated CO2 levels. This information will be used in modeling wheat apical development and grain production in the elevated atmospheric CO2 environments of the future.

KEYWORDS: APICAL DEVELOPMENT, NITROGEN, SHOOT APEX, TEMPERATURE

1335

Li, C.S., S. Frolking, and R. Harriss. 1994. Modeling carbon biogeochemistry in agricultural soils. *Global Biogeochemical Cycles 8(3):237-254.*

An existing model of C and N dynamics in soils was supplemented with a plant growth submodel and cropping practice routines (fertilization, irrigation, tillage, crop rotation, and manure amendments) to study the biogeochemistry of soil carbon in arable lands. The new model was validated against field results for short-term (1-9 years) decomposition experiments, the seasonal pattern of soil CO2 respiration, and long-term (100 years) soil carbon storage dynamics. A series of sensitivity runs investigated the impact of varying agricultural practices on soil organic carbon (SOC) sequestration. The tests were simulated for corn (maize) plots over a range of soil and climate conditions typical of the United States, The largest carbon sequestration occurred with manure additions; the results were very sensitive to soil texture (more clay led to greater sequestration). Increased N fertilization generally enhanced carbon sequestration, but the results were sensitive to soil texture, initial soil carbon content, and annual precipitation. Reduced tillage also generally (but not always) increased SOC content, though the results were very sensitive to soil texture, initial SOC content, and annual precipitation. A series of long-term simulations investigated the SOC equilibrium for various agricultural practices, soil and climate conditions, and crop rotations. Equilibrium SOC content increased with decreasing temperatures, increasing clay content, enhanced N fertilization, manure amendments, and crops with higher residue yield. Time to equilibrium appears to be one hundred to several hundred years. In all cases, equilibration time was longer for increasing SOC content than for decreasing SOC content. Efforts to enhance carbon sequestration in agricultural soils would do well to focus on those specific areas and agricultural practices with the greatest potential for increasing soil carbon content.

KEYWORDS: CORN, CROPLAND, DRIVEN, NITROUS-OXIDE

EVOLUTION, ORGANIC-CARBON, PLANTS, RAINFALL EVENTS, ROOT RESPIRATION, TILLAGE

1336

Li, J.H., P. Dijkstra, C.R. Hinkle, R.M. Wheeler, and B.G. Drake. 1999. Photosynthetic acclimation to elevated atmospheric CO2 concentration in the Florida scrub-oak species Quercus geminata and Quercus myrtifolia growing in their native environment. *Tree Physiology 19(4-5):229-234.*

Long-term effects of elevated CO2 concentration (ambient plus 350 mu mol mol(-1)) on leaf photosynthetic acclimation of two species of a scrub-oak community, Quercus myrtifolia Willd. and Quercus geminata Small, were studied. Plants of both species were grown in open-top chambers in their natural habitat at Kennedy Space Center, Florida, USA. Compared to ambient CO2, elevated CO2 stimulated photosynthetic rates by 73 and 51% for Q. geminata and Q. myrtifolia, respectively. Maximum rate of carboxylation (V-cmax) was significantly reduced by elevated CO2 in Q. myrtifolia (28%) but not in Q. geminata. Maximum rate of potential electron transport (J(max)) was not significantly reduced by elevated CO2 in either species. In response to elevated CO2, specific leaf area decreased in Q, myrtifolia (22%), but not in Q. geminata. Elevated CO:! caused a significant accumulation of sugars (54%) and starch (264%) in Q, myrtifolia leaves, but not in Q. geminata leaves. Total Rubisco activity in Q. myrtifolia leaves was reduced 40% by elevated CO2, whereas no significant reduction occurred in Q, geminata leaves. Although both species share a common habitat, they exhibited marked differences in photosynthetic acclimation to elevated CO2 concentration.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LEAVES, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1337

Li, J.H., J. Gale, A. Novoplansky, S. Barak, and M. Volokita. 1999. Response of tomato plants to saline water as affected by carbon dioxide supplementation. II. Physiological responses. *Journal of Horticultural Science & Biotechnology 74(2):238-242.*

Photosynthesis of tomato plants (Lycopersicon esculentum (L.) Mill. cv. F144) was studied under conditions of CO2 supplementation and salinity. The purpose of the study was to elucidate the mechanisms underlying the effects of salinity on the acclimation of tomato plants to CO2 supplementation. Plants were grown under either low (355 mu mol mol(-1)) or elevated (1200 +/- 50 mu mol mol(-1)) CO2 and were irrigated with low concentrations of mixed salts. The highest salinity level (E.C. 7 dS m(-1)) was that used to produce quality tomatoes in the Negev highlands, in Israel. During early development (three weeks after planting), the net photosynthetic rate of the leaves was much higher under elevated CO2, and other than a slight decrease in quantum yield efficiency as measured by fluorescence (Delta F/F-m'), no signs of acclimation to high levels of CO2 were apparent. Clear acclimation to high CO2 concentration was evident ten weeks after planting when the net photosynthetic rate, photosynthetic capacity, and carboxylation efficiency of leaves of non-salinized plants were strongly suppressed under elevated CO2. This was accompanied by reductions in carboxylation efficiency, Rubisco activity and PSII quantum yield, and an increased accumulation of leaf soluble sugars. The reduction in photosynthetic capacity in the high CO2 plants was less in plants grown at the highest salinity level. This was correlated with an increase in the PSII quantum yield parameters (F-v/F-m) and Delta F/F-m') but not with Rubisco activity which was affected by the Cat treatments only. These results explain the effects of high CO2 on yields in tomatoes grown at high levels of salt (Li ct al., 1999).

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, EXPRESSION, GAS-EXCHANGE, GENES, GROWTH, MECHANISM, PHOTOSYNTHETIC ACCLIMATION, STRESS

1338

Li, J.H., M. Sagi, J. Gale, M. Volokita, and A. Novoplansky. 1999. Response of tomato plants to saline water as affected by carbon dioxide supplementation. I. Growth, yield and fruit quality. *Journal of Horticultural Science & Biotechnology 74(2):232-237.*

Tomato plants (Lycopersicon esculentum (L.) Mill. cv. F144) were irrigated with low concentrations of mixed salts; the highest level (E.C. 7 dS m(-1)) simulated conditions used to produce quality tomatoes in the Negev highlands. CO2 enrichment (to 1200 mu mol mol(-1), given during the daytime) increased plant growth at the early stage of development. However, later growth enhancement was maintained only when combined with salt stress. In the absence of CO2 supplementation, overall growth decreased with salt (7 dS m(-1)) to 58% and fresh biomass yields to 53% of the controls. However, under elevated CO2 concentrations total plant dry biomass was not reduced by salt stress. CO2 enrichment of plants grown with 7 dS m(-1) salt increased total fresh fruit yields by 48% and maintained fruit quality in terms of total soluble salts, glucose and acidity. Fruit ripening was about 10 d earlier under CO2 enrichment, regardless of salinity treatment. It is suggested that a combined utilization of brackish water and CO2 supplementation may enable the production of high-quality fruits without incurring all the inevitable loss in yields associated with salt treatment.

KEYWORDS: CO2- ENRICHMENT, WHEAT

1339

Li, Q.L., and D.T. Canvin. 1997. Oxygen photoreduction and its effect on CO2 accumulation and assimilation in air-grown cells of Synechococcus UTEX 625. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(2):274-283.*

Mass spectrometric measurements of O-16(2), O-18(2), and (CO2)- C-13 were used to measure the rates of gross O-2 evolution, O-2 uptake, and CO2 assimilation in relation to light intensity, temperature, pH, and O-2 concentration by air-grown cells of the cyanobacterium Synechococcus UTEX 625. CO2 fixation and O-2 photoreduction increased with increased light intensity and, although CO2 fixation was saturated at 250 mu mol . m(-2). s(- 1), O-2 photoreduction was not saturated until about 550 mu mol . m(-2). s(-1). At high light intensity addition of inorganic carbon to the cells stimulated O-2 photoreduction 2-fold when CO2 fixation was allowed and 5-fold when CO2 fixation was inhibited with iodoacetamide. The ability of O-2 to act as an acceptor of photosynthetically generated reducing power was dependent upon the O-2 concentration, and the substrate concentration required for half maximum rate (K-1/2(O-2)) was 53.2 +/- 4.2 mu M (mean +/- SD, n = 3). The Q(10) for oxygen photoreduction was about 2. A certain amount (10%) of O-2 appeared to be required for maximum photosynthesis, as photosynthesis was inhibited under anaerobic conditions, especially at high light intensity. The point of inhibition is unknown but it seemed unlikely to be on CO2 transport or the concentration of intracellular dissolved inorganic carbon (C- i), as the rate of initial CO2 transport was enhanced and the intracellular C-i pool increased in size under anaerobic conditions.

KEYWORDS: ACTIVE-TRANSPORT, CHLAMYDOMONAS-REINHARDTII, CHLOROPHYLL-A FLUORESCENCE, CYANOBACTERIUM, ELECTRON FLOW, INORGANIC CARBON, LEOPOLIENSIS, O-2 PHOTOREDUCTION, PHOTOSYNTHESIS, REDUCTION

1340

Li, W., and W.J. Campbell. 1996. Response of rubisco activase protein levels in two species following grown at elevated CO2. *Plant Physiology 111(2):347.*

1341

Liakatas, A., D. Roussopoulos, and W.J. Whittington. 1998. Controlled-temperature effects on cotton yield and fibre properties. *Journal of Agricultural Science 130:463-471.*

Temperature effects on cotton yield and fibre properties of three cotton cultivars were determined. Plants were grown in pots maintained in growth rooms at varying day and night temperatures representing seasonally constant or varying (C) or daily varying (V) regimes. Yield and fibre characters responded to variation of daily mean and amplitude of temperature. Mean temperature reduction improved yield components, but fibre length, uniformity, strength and micronaire were increased by high, particularly high day, temperatures. A large daily temperature amplitude produced an intermediate number of flowers and the lowest retention percentage. Fruiting and yield were increased by reduction in temperature down to the threshold mean temperature of 22 degrees C. However, V-regimes with a low minimum temperature acted as a further drop (below 22 degrees C) of temperature and adversely affected these characters, An adverse effect of low minimum temperature combined with a moderate day temperature was observed also on lint percentage and fibre properties. Varietal differences were more pronounced for highly heritable characters such as fibre properties, for which significant interactions between varieties and temperature also occurred. Differences in reproductive development were not sufficient to be of much practical importance.

KEYWORDS: ELEVATED CO2, LEAVES, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS

1342

Liang, N.S., and K. Maruyama. 1995. Interactive effects of CO2 enrichment and drought stress on gas exchange and water-use efficiency in Alnus firma. *Environmental and Experimental Botany 35(3):353-361.*

Independent and interactive effects of atmospheric CO2 enrichment and drought stress on leaf conductance, photosynthetic performance, transpiration and water-use efficiency in 2-year-old Alnus firma, a common pioneer tree species, were assessed. Measurements were conducted in a controlled environment laboratory at three CO2 concentrations [350 (ambient), 600 and 900 (enrichment) mu mol mol(-1)] and combined with five water regimes [leaf water potential of higher than -0.3 (well-watered), -0.5 and -0.8 (moderate drought), -1.0 and lower than -1.2 (serious drought stress) MPa]. Under well-watered conditions, rates of net photosynthesis significantly (P<0.01) increased with increasing CO2 concentrations; leaf conductance significantly decreased. With drought stress established, leaf conductance, photosynthesis and transpiration decreased. However, leaf water-use efficiency increased with drought stress, with potential transpiration affected sooner than potential photosynthesis. The combined effects of COP enrichment and drought stress on water-use efficiency were significant in that the result of net photosynthesis was stimulated while transpiration in CO2 enriched plants resembled that of unenriched plants under conditions of drought stress. The results presented here suggest that if a doubling of atmospheric COP concentration occurs by the mid-21st Century, then the photosynthetic rate of A. firma in drought-affected regions may be expected to increase. A reduction in total water use, however, is not indicated.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, GROWTH, LIQUIDAMBAR- STYRACIFLUA, MODEL, PHOSPHORUS DEFICIENCY, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RESPONSES, WHEAT

1343

Liang, N., K. Maruyama, and Y. Huang. 1995. Interactions of elevated co2 and drought stress in gas-exchange and water-use efficiency in 3 temperate deciduous tree species. *Photosynthetica 31(4):529-539.*

The effect of CO2 increase on gas exchange and water-use efficiency (WUE) in three temperate deciduous species (Fagus crenata, Ginkgo biloba and Alnus firma) under gradually- developing drought-stress was assessed. Seedlings were grown within transparent open-top cabinets and maintained for 4 months at mean CO2 concentrations of either 350 (ambient; C- 350) Or 700 mu mol mol(-1) (elevated; C-700) and combined with five water regimes [leaf water potential, Psi(w), higher than - 0.3 (well-watered), -0.5 and -0.8 (moderate drought), -1.0 and fewer than -1.2 MPa (serious drought-stress)]. Increase in CO2 concentration induced a 60 % average increase in net photosynthetic rate (P-N) under well-watered conditions. The effect of C-700 became more pronounced with drought stress established, with an 80 % average increase in P-N at Psi(w), as low as -0.8 MPa; leaf conductance to water vapour transfer (g(s)) and transpiration rate (E), however, were significantly decreased. Consequently, WUE increased under drought, through drought stress affected potential E sooner than potential P-N. The interaction of CO2 x drought stress on WUE was significant in that P-N was stimulated while E in C-700 enriched plants resembled that of C-350 plants under drought. Hence if a doubling of atmospheric CO2 concentration occurs by the mid 21(st) century, then greater P-N in F. crenata, G. biloba and A. firma may be expected and the drought susceptibility of these species will be substantially enhanced.

KEYWORDS: ATMOSPHERE, CARBON DIOXIDE, ENRICHMENT, GROWTH, LIMITED CONDITIONS, PHOTOSYNTHESIS, PLANTS, RESPONSES, WHEAT, YIELD

1344

Liang, N., K. Maruyama, and Y. Huang. 1996. Effects of CO2 concentration on the photosynthetic and carboxylation efficiencies of Fagus crenata and Quercus crispula. *Photosynthetica 32(3):355-365.*

To determine the effects of limited and elevated CO2 concentrations on leaf photosynthesis which may suggest the effects of global CO2 level increase and global warming on forest structure, the photosynthetic and carboxylation efficiencies were investigated in two representative co-occurring tree species in the cool-temperate natural forests in central Japan, Fagus crenata and Quercus crispula. Measurements were performed for four-year-old seedlings in CO2-air mixtures of 175, 350, 700 and 900 mu mol mol(-1), respectively, with photosynthetic irradiance (I) decreasing gradually from 1200 mu mol m(-2) s(-1) to darkness, and at 25 +/- 0.2 degrees C leaf temperature and 1.8 +/- 0.2 kPa leaf to air vapour pressure deficit. The CO2 concentrations strongly stimulated net photosynthetic rate, P-N (p<0.001), and the photosynthetic efficiency, alpha, for both F. crenata and Q. crispula. Carboxylation efficiency of Q. crispula was dependent on I, with a significantly higher efficiency of CO2 utilization at an I of 1200 than of 500 mu mol m(-2) s(-1). A decrease in I from 1200 to 500 mu mol m(-2) s(-1), however, did not prevent a curvilinear increase in P-N at increased CO2 concentrations. In contrast, F. crenata seedlings showed less difference in PN between low-I and high-I environments. Nonetheless, F. crenata showed a greater CO2 response, with alpha increased by 25 % from 350 to 700 mu mol(CO2) mol(-1). alpha of Q. crispula, however, increased by less than 20 % as CO2 concentration increased from 350 to 700 mu mol mol(-1). The higher P-N at high CO2 concentration under low I was attributed to the CO2 concentration

accompanied by a significant decrease in compensation irradiance. These results suggest that the continuous increase in global CO2 concentrations will directly result in an increase in photosynthetic efficiencies of both F. crenata and Q. crispula. The competitive relationship between the two species will change if a doubling of atmospheric CO2 concentration occurs;by the mid of the 21(st) century, with F. crenata benefiting more from CO2 fertilization than Q. crispula.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, IRRADIANCE, LIGHT-INTENSITY, LIQUIDAMBAR-STYRACIFLUA, LONG-TERM ELEVATION, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1345

Lim, L.Y., Y.C. Hew, S.C. Wong, and C.S. Hew. 1992. Effects of light-intensity, sugar and co-2 concentrations on growth and mineral uptake of dendrobium plantlets. *Journal of Horticultural Science 67(5):601-611.*

The effects of light intensity, sugar and CO2 concentrations on nitrate and ammonium uptake, growth and photosynthetic activity of dendrobium plantlets grown on agar medium were studied. There was a preferential uptake of ammonium over nitrate. Uptake of nitrate was relatively low and increased with increase in light intensity or when the culture medium was supplemented with sugar. Ammonium uptake was also affected by light. However, the rates of ammonium and nitrate uptake were sluggish. The fresh weight of plantlets increased with the presence of sugar in the media but the relative growth rate decreased. CO2 enrichment did not increase ion uptake or growth. The nutrition of plantlets in culture was mainly heterotrophic, as indicated by the changes in titratable acidity, delta-C-13 values and (CO2)-C-14 fixation.

KEYWORDS: CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ELEVATED CO2, INVITRO, NITRATE UPTAKE, PHOTOSYNTHESIS, SHORT- TERM

1346

Lin, E.D., Y.F. Liu, and Y. Li. 1997. Agricultural C cycle and greenhouse gas emission in China. *Nutrient Cycling in Agroecosystems 49(1-3):295-299.*

This paper assesses the production, consumption and store of organic carbon in the agricultural system, including all products from agriculture, of China. An estimation showed that about 90% of carbon uptake by agricultural systems would be emitted or returned to the atmosphere by several types from 1990 to 2000, others remain in durable agricultural products and soil. Even though the fixation rate is getting lower, generally speaking Chinese agriculture is a "sink" but not a "source" in respect to the atmospheric CO2 and CH4 concentrations in both the current period and that after few decades. China's Soil stores 12% of the whole soil carbon in the World. Considering the different global warming potentials (GWP), an approach to the country budgets of CO2 and CH4 has been presented based on the measurements in rice paddies and in the Tibet and Inner Mongolia grasslands.

KEYWORDS: CLIMATE

1347

Lin, G.H., J. Adams, B. Farnsworth, Y.D. Wei, B.D.V. Marino, and J.A. Berry. 1999. Ecosystem carbon exchange in two terrestrial ecosystem mesocosms under changing atmospheric CO2 concentrations. *Oecologia 119(1):97-108.*

The ecosystem-level carbon uptake and respiration were measured under different CO2 concentrations in the tropical rainforest and the coastal desert of Biosphere 2, a large enclosed facility. When the mesocosms were sealed and subjected to step- wise changes in atmospheric CO2 between daily means of 450 and 900 mu mol mol(-1), net ecosystem exchange (NEE) of CO2 was derived using the diurnal changes in atmospheric CO2 concentrations. The step-wise CO2 treatment was effectively replicated as indicated by the high repeatability of NEE measurements under similar CO2 concentrations over a 12-week period. In the rainforest mesocosm, daily NEE was increased significantly by the high CO2 treatments because of much higher enhancement of canopy CO2 assimilation relative to the increase in the nighttime ecosystem respiration under high CO2. Furthermore, the response of daytime NEE to increasing atmospheric CO2, in this mesocosm was not linear, with a saturation concentration of 750 mu mol mol(-1). In the desert mesocosm, a combination of a reduction in ecosystem respiration and a small increase in canopy CO2 assimilation in the high CO2 treatments also enhanced daily NEE. Although soil respiration was not affected by the short-term change in atmospheric CO2 in either mesocosm, plant dark respiration was increased significantly by the high CO2 treatments in the rainforest mesocosm while the opposite was found in the desert mesocosm. The high CO2 treatments increased the ecosystem light compensation points in both mesocosms. High CO2 significantly increased ecosystem radiation use efficiency in the rainforest mesocosm, but had a much smaller effect in the desert mesocosm. The desert mesocosm showed much lower absolute response in NEE to atmospheric CO2 than the rainforest mesocosm, probably because of the presence of C-4 plants. This study illustrates the importance of large-scale experimental research in the study of complex global change issues.

KEYWORDS: AMAZONIA, DIOXIDE, ELEVATED CO2, FLUXES, GROWTH, RESPONSES, SYSTEM, TROPICAL RAIN-FOREST, WATER

1348

Lin, G.H., J.R. Ehleringer, P.T. Rygiewicz, M.G. Johnson, and D.T. Tingey. 1999. Elevated CO2 and temperature impacts on different components of soil CO2 efflux in Douglas-fir terracosms. *Global Change Biology 5(2):157-168.*

Although numerous studies indicate that increasing atmospheric CO2 or temperature data are available on the responses of three major components of soil respiration [i.e. rhizosphere respiration (root and root exudates), litter decomposition, and oxidation of soil organic matter] to different CO2 and temperature conditions. In this study, we applied a dual stable isotope approach to investigate the impact of elevated CO2 and elevated temperature on these components of soil CO2 efflux in Douglas-fir terracosms. We measured both soil CO2 efflux rates and the C-13 and O-18 isotopic compositions of soil CO2 efflux in 12 sun-lit and environmentally controlled terracosms with 4- year-old Douglas fir seedlings and reconstructed forest soils under two CO2 concentrations (ambient and 200 ppmv above ambient) and two air temperature regimes (ambient and 4 degrees C above ambient). The stable isotope data were used to estimate the relative contributions of different components to the overall soil CO2 efflux. In most cases, litter decomposition was the dominant component of soil CO2 efflux in this system, followed by rhizosphere respiration and soil organic matter oxidation. Both elevated atmospheric CO2 concentration and elevated temperature stimulated rhizosphere respiration and litter decomposition. The oxidation of soil organic matter was stimulated only by increasing temperature. Release of newly fixed carbon as root respiration was the most responsive to elevated CO2, while soil organic matter decomposition was most responsive to increasing temperature. Although some assumptions associated with this new method need to be further validated, application of this dual-isotope approach can provide new insights into the responses of soil carbon dynamics in forest ecosystems to future climate changes.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE,

DECOMPOSITION, PONDEROSA PINE, RESPIRATION, RESPONSES, RHIZOSPHERE, TRACE GAS FLUXES, TURNOVER, VEGETATION

1349

Lin, G.H., B.D.V. Marino, Y.D. Wei, J. Adams, F. Tubiello, and J.A. Berry. 1998. An experimental and modeling study of responses in ecosystems carbon exchanges to increasing CO2 concentrations using a tropical rainforest mesocosm. *Australian Journal of Plant Physiology 25(5):547-556.*

The ecosystem carbon exchanges in the enclosed rainforest of Biosphere 2, an enclosed apparatus comprised of large synthetic ecosystems, were measured and modeled during the winter of 1995-1996 under different atmospheric CO2 concentrations. On eight separate days, this mesocosm was exposed to various levels of CO2 ranging from about 380 to 820 mu mol mol(-1) daily mean and then sealed 24 hours for continuous measurements of ecosystem CO2 fluxes. Our results indicated that net ecosystem carbon exchange in the mesocosm was enhanced by increasing CO2 over the short periods studied (2-7 weeks), but, as expected from physiological studies, the response is not linear. The main effect of shortterm CO2 change was the enhancement of canopy CO2 assimilation, while soil respiration was not affected by the atmospheric CO2 concentration. The whole ecosystem radiation use efficiency was significantly higher under higher CO2. The results of direct measurements were predicted well by a simple canopy model (the 'big-leaf' model) that incorporates current physiological understanding of the biochemistry of leaf photosynthesis. Validation of this model with a range of CO2 and light levels indicates that it can be used with confidence to predict the responses of natural ecosystems to global climate change. Response of ecosystem processes to elevated CO2 with relaxation time longer than a few weeks could not be resolved in this study, but longer-term closure experiments are planned to examine these processes.

KEYWORDS: ACCLIMATION, AMAZONIA, ASSIMILATION, BIOSPHERE, DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, RAIN-FOREST

1350

Lin, W.H., K.Z. Bai, and T.Y. Kuang. 1999. Effects of elevated CO2 and high temperature on single leaf and canopy photosynthesis of rice. *Acta Botanica Sinica 41(6):624-628.*

The increase of atmospheric CO2 concentration is indisputable. In such condition, photosynthetic response of leaf is relatively well studied, while the comparison of that between single leaf and whole canopy is less emphasized. The stimulation of elevated CO2 on canopy photosynthesis may be different from that on single leaf level. In this study, leaf and canopy photosynthesis of rice (Oryza sativa L.) were studied throughout the growing season. High CO2 and temperature had. a synergetic stimulation on single leaf photosynthetic rate until grain filling. Photosynthesis of leaf was stimulated by high CO2, although the stimulation was decreased by higher temperature at grain filling stage. On the other hand, the simulation of elevated CO2 on canopy photosynthesis leveled off with time. Stimulation at canopy level disappeared by grain filling stage in both temperature treatments. Green leaf area index was not significantly affected by CO2 at maturity, but greater in plants grown at higher temperature. Leaf nitrogen content decreased with the increase of CO2 concentration although it was not statistically significant at maturity. Canopy respiration rate increased at flowering stage indicating higher carbon loss: Shading effect caused bu leaf development reached maximum at flowering stage. The CO2 stimulation on photosynthesis was greater in single leaf than in canopy, Since enhanced CO2 significantly increased biomass of rice stems and panicles, increase in canopy respiration caused diminishment of CO2 stimulation in canopy net photosynthesis. Leaf nitrogen in the canopy level decreased with CO2 concentration and may eventually hasten CO2 stimulation on canopy photosynthesis. Early senescence of canopy leaves in high CO2 is also a possible cause.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, TRANSPIRATION

1351

Lin, W.H., and D.L. Wang. 1998. Effects of elevated CO2 on growth and carbon partitioning in rice. *Chinese Science Bulletin 43(23):1982-1986.*

Rice (Oryza sativa cv. Jindao 1187) was grown in open-top chambers which contained ambient and enriched CO2. CO2 elevation stimulated rice tillering during early vegetative stage. However, panicle dry weight per plant did not change at maturity stage. Root biomass was enhanced by high CO2. Root/shoot ratio was increased under high CO2 at maturity, indicating more carbon allocation to the below-bround part in rice under high CO2.

KEYWORDS: ACCLIMATION, DIOXIDE, INSITU, YIELD

1352

Lin, W.H., L.H. Ziska, O.S. Namuco, and K. Bai. 1997. The interaction of high temperature and elevated CO2 on photosynthetic acclimation of single leaves of rice in situ. *Physiologia Plantarum 99(1):178-184.*

Rice (Oryza sativa L. cv. IR72) was grown at three different CO2 concentrations (ambient, ambient + 200 mu mol mol(-1), ambient + 300 mu mol mol(-1)) at two different growth temperatures (ambient, ambient + 4 degrees C) from sowing to maturity to determine longterm photosynthetic acclimation to elevated CO2 with and without increasing temperature. Single leaves of rice showed a cooperative enhancement of photosynthetic rate with elevated CO2 and temperature during tillering, relative to the elevated CO2 condition alone. However, after flowering, the degree of photosynthetic stimulation by elevated CO2 was reduced for the ambient + 4 degrees C treatment, This increasing insensitivity to CO2 appeared to be accompanied by a reduction in ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity and/or concentration as evidenced by the reduction in the assimilation (A) to internal CO2, C-1) response curve. The reproductive response (e.g. percent filled grains, panicle weight) was reduced at the higher growth temperature and presumably reflects a greater increase in floral sterility. Results indicate that while CO2 and temperature could act synergistically at the biochemical level, the direct effect of temperature on floral development with a subsequent reduction in carbon utilization may change sink strength so as to limit photosynthetic stimulation by elevated CO2, concentration.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, LEAF-AREA, RESPONSES

1353

Lincoln, D.E. 1993. The influence of plant carbon-dioxide and nutrient supply on susceptibility to insect herbivores. *Vegetatio 104:273-280.*

The carbon/nutrient ratio of plants has been hypothesized to be a significant regulator of plant susceptibility of leaf-eating insects. As rising atmospheric carbon dioxide stimulates photosynthesis, host plant carbon supply is increased and the accompanying higher levels of carbohydrates, especially starch, apparently 'dilute' the protein content of the leaf. When host plant nitrogen supply is limited, plant responses include increased carbohydrate accumulation, reduced leaf protein content, but also increased carbon-based defensive chemicals. No

change, however, has been observed in the concentration of leaf defensive allelochemicals with elevated carbon dioxide during host plant growth. Insect responses to carbon-fertilized leaves include increased consumption with little change in growth, or alternatively, little change in consumption with decreased growth, as well as enhanced leaf digestibility, reduced nitrogen use efficiency, and reduced fecundity. The effects of plant carbon and nutrient supply on herbivores appear to result, at least in part, from independent processes affecting secondary metabolism.

KEYWORDS: ALLOCATION, CHEMICAL DEFENSE, ELEVATED CO2, ENRICHED CO2 ATMOSPHERES, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, LIMITATION, NITROGEN-CONTENT, NOCTUIDAE

1354

Lincoln, D.E., E.D. Fajer, and R.H. Johnson. 1993. Plant insect herbivore interactions in elevated co2 environments. *Trends in Ecology and Evolution 8(2):64-68.*

The increasing concentration of CO2 in the atmosphere is expected to lead to global changes in the physical environment of terrestrial organisms. We are beginning to understand how these changes are transmitted into pervasive effects on the interactions between plants and their leaf-feeding insect herbivores. An elevated CO2 atmosphere often stimulates plant carbon assimilation and growth and alters carbon allocation patterns. This, in turn, determines the quality of plants as resources for herbivorous insects. These 'quality' factors include: the concentrations of water, nitrogen and allelochemicals in host-plant leaves, and the toughness and starch and fiber content of leaf tissue. Because these parameters change in plants grown in enriched CO2 environments, the doubled CO2 levels anticipated for the next century will alter the dynamics of plant-insect herbivore interactions because herbivore consumption, growth and fitness are affected by the typically lower quality of plants grown under these conditions.

KEYWORDS: ALLOCATION, CARBON-DIOXIDE ATMOSPHERES, COTTON, ENRICHMENT, GROWTH, JUNONIA-COENIA, LEPIDOPTERA, NITROGEN, NOCTUIDAE, QUERCUS-ALBA

1355

Lindhout, P., and G. Pet. 1990. Effects of CO2 enrichment on young plant-growth of 96 genotypes of tomato (Lycopersicon esculentum). *Euphytica 51(2):191-196.*

The early growth of 96 genotypes of tomato was studied at 320 ppm CO2 and at 750 ppm CO2 in separate climate rooms. Plants were harvested at 40 and 55 days after sowing. Fresh and dry weights were determined. Large differences between genotypes were found for average plant fresh and dry weights and for relative growth rates. The average overall growth enhancement by CO2 enrichment was 2.3. Two genotypes showed significant genotype x CO2 interaction. The consequences of these results for tomato breeding are discussed.

1356

Lindner, M., H. Bugmann, P. Lasch, M. Flechsig, and W. Cramer. 1997. Regional impacts of climatic change on forests in the state of Brandenburg, Germany. *Agricultural and Forest Meteorology 84(1-2):123-135.*

The changes of climate projected for the next century will most likely alter both the environment and the growth of forests, In a regional case study, the two forest gap models FORSKA and FORCLIM were applied to simulate vegetation composition using spatially differentiated site data on a 10 x 10-km grid across the state of Brandenburg, Northeast Germany, Three climate scenarios were used to investigate the possible consequences of a changing climate on the environmental constraints of forest,growth in the state. To test the: plausibility of the forest composition simulated by the two models, their results were compared with a map of potential natural vegetation as well as with each other. The simulation results show that both models respond realistically to the spatial variability of the environment and thus are suitable for regional applications. However, there are a number of quantitative differences between the simulation results of the models. FORSKA's strength is in simulating the ecological effects of the spatial variability of soil water holding capacity and nitrogen availability, whereas FORCLIM realistically portrays the climate-induced distribution limits of trees, e.g. beech (Fagus sylvatica L.). The study suggests that climatic change could have considerable consequences for future competitive relationships between species. According to the two models, the main driving force of vegetation change would be the increased occurrence of drought, which already today determines some distribution limits of tree species in Brandenburg, Under the strongest change of climate investigated in the present study, none of the species currently present on the landscape could grow any more in certain areas of Brandenburg. Conclusions are drawn concerning the importance of regional model applications for testing model performance under a wide variety of environmental conditions as well as for forest planning, Regional analyses of the impacts of climate change on forests may help to develop forest management strategies to cope with the risk of changing environmental conditions.

KEYWORDS: COMMUNITIES, DYNAMICS, ECOSYSTEMS, ELEVATED CO2, MODEL, NORTHERN FORESTS, SIMULATION

1357

Lindner, M., R. Sievanen, and H. Pretzsch. 1997. Improving the simulation of stand structure in a forest gap model. *Forest Ecology and Management 95(2):183-195.*

There is currently great interest in improving the applicability of forest gap models to changing environmental conditions, in order to facilitate the assessment of possible impacts of climatic change on forest ecosystems. Moreover, for the development of mitigation strategies, it is necessary to include forest management options in the models. Both the simulation of transient effects of climatic change and of forest management regimes require a realistic representation of stand structure in gap models, since tree species respond to variations in stand density in characteristic ways, depending on their ecological strategies. In this study, we compared the effect of five different height growth functions that are sensitive to stand density on simulated stand structure of the FORSKA forest gap model. We used long term observation data from a beech thinning trial at Fabrikschleichach, Bavaria, to test the alternative functions. First, we compared simulation results of the original FORSKA model with measured stand development from 1870 to 1990. Whereas simulated stand level variables (e.g. biomass, mean diameter and height) showed good correspondence with observations, individual tree dimensions and simulated stand structure were quite unrealistic. After calibrating parameters of the height growth functions with data from a lightly thinned plot at Fabrikschleichach, we ran the model with data from a heavily thinned plot for validation. All five functions considerably improved the simulation of height/diameter relationships and stand structure. However, there were distinct differences between functions. The best correspondence with measurements was shown by a function which uses the relative radiation intensity in the centre of a tree crown as an indicator of the competition status of the tree. This function is rather simple and needs only two growth parameters, which can be derived for different functional types of species, according to their shade tolerance. With the new, flexible height growth function it should be possible to extend the applicability of gap models to more realistic simulation experiments including forest management and

natural disturbances. To our knowledge, this was the first attempt to employ long term forest observation data for the calibration and validation of a forest gap model. The results suggest that such data could be very useful in model testing and improvement. (C) 1997 Elsevier Science B.V.

KEYWORDS: CO2, CO2-INDUCED CLIMATE CHANGE, DISTURBANCE, DYNAMICS, ECOSYSTEMS, GLOBAL CHANGE, GROWTH, LANDSCAPES, TRANSIENT-RESPONSE, VEGETATION

1358

Lindqvist, K., and R. Lignell. 1997. Intracellular partitioning of (CO2)-C-14 in phytoplankton during a growth season in the northern Baltic. *Marine Ecology-Progress Series 152(1-3):41-50.*

During the phytoplankton succession in the northern Baltic in 1988, the distribution of (CO2)-C-14 assimilated by algae into the main molecular groups [proteins, polysaccharides, lipids and low molar mass compounds (LMC)] after in situ Light (6 h) and Light to dark (20 h from ca 11:00 to 07:00 h) incubations at 2 m depth (just below maximum (CO2)-C-14 fixation) was studied. By early May, the high winter levels of mineral nutrients were depleted from the water column, and in middle May the spring bloom predominated by large dinoflagellates (diatoms subdominant) peaked. The proportion of C-14 lipids was usually ca 15% of total (CO2)-C-14 fixation, but it showed a distinct peak of 40% in middle May. The C-14-Lipid peak probably reflected nutrient stress of the algae, since nutrient (N+P) enrichment decreased this peak by 15 percentage points in 100 l enclosures. During the decline of the spring bloom, the proportion of C-14 proteins increased despite low ambient mineral N concentrations. In summer, the phytoplankton community (mainly small flagellates) consistently exhibited remarkable channelling of (CO2)-C-14 into proteins (50 to 60%), which conformed to the low particulate organic C:N ratios of ca 7 (mol/mol). Summer upwellings, which introduced nutrients into the mixed layer, seemed to be accompanied by the highest proportions of C-14 proteins. The proportion of C-14 polysaccharides was usually ca 20%. After 6 h incubations, this proportion was significantly (on average 10 percentage points) higher than after 20 h, while the inverse was true with C-14 proteins, which reflected continuous nocturnal synthesis of proteins (enzymes) at the expense of polysaccharide storage products. In con elusion, the high proportions of algal C-14 proteins in summer suggest that phytoplankton is usually not physiologically N limited in our study area and provides N- sufficient food for herbivores, hence enabling high efficiency of algal C transfer to higher trophic levels.

KEYWORDS: CARBON INCORPORATION, COMMUNITY, COPEPODS, MARINE-PHYTOPLANKTON, NITROGEN, NUTRIENT LIMITATION, PARTICULATE, PATTERNS, PHOTOSYNTHESIS, SPRING BLOOM

1359

Lindroth, R.L., G.E. Arteel, and K.K. Kinney. 1995. Responses of 3 saturniid species to paper birch grown under enriched co2 atmospheres. *Functional Ecology 9(2):306-311.*

1. Interactions between trees and tree-feeding insects are likely to shift under conditions of enriched atmospheric CO2 owing to changes in foliar chemical composition. This study addressed the effects of CO2-mediated changes in leaf chemistry on performance of three silkmoth (Saturniidae) species: cecropia (Hyalophora cecropia), luna (Actias luna) and polyphemus (Antheraea polyphemus polyphemus). 2. Growth under elevated CO2 atmospheres decreased nitrogen concentrations (23%) but tripled starch and doubled condensed tannin concentrations, resulting in a marked increase in foliar carbon:nitrogen ratio. 3. Survival of first stadium larvae was marginally reduced when reared on high CO2 leaves. 4. Development rates were prolonged, growth rates tended to decline, consumption increased and food processing efficiencies decreased for fourth stadium larvae reared on high CO2 leaves. The magnitude of responses varied among species. 5. Overall performance of these saturniid species, at least when feeding on birch, is predicted to decline under atmospheric CO2 conditions anticipated for the next century.

KEYWORDS: NITROGEN

1360

Lindroth, R.L., S.M. Jung, and A.M. Feuker. 1993. Detoxication activity in the gypsy-moth - effects of host co2 and no3-availability. *Journal of Chemical Ecology 19(2):357-367.*

We investigated the effects of host species and resource (carbon dioxide, nitrate) availability on activity of detoxication enzymes in the gypsy moth, Lymantria dispar. Larvae were fed foliage from quaking aspen or sugar maple grown under ambient or elevated atmospheric CO2, with low or high soil NO3- availability. Enzyme solutions were prepared from larval midguts and assayed for activity of cytochrome P-450 monooxygenase, esterase, glutathione transferase, and carbonyl reductase enzymes. Activity of each enzyme system was influenced by larval host species, CO2 or NO3- availability, or an interaction of factors. Activity of all but glutathione transferases was highest in larvae reared on aspen. Elevated atmospheric CO2 promoted all but transferase activity in larvae reared on aspen, but had little if any impact on enzyme activities of larvae reared on maple. High NO3- availability enhanced activity of most enzyme systems in gypsy moths fed high CO2 foliage, but the effect was less consistent for insects fed ambient CO2 foliage. This research shows that gypsy moths respond biochemically not only to interspecific differences in host chemistry, but also to resource-mediated, intraspecific changes in host chemistry. Such responses are likely to be important for the dynamics of plant-insect interactions as they occur now and as they will be altered by global atmospheric changes in the future.

KEYWORDS: ALLELOCHEMICALS, CHEMISTRY, DETOXIFICATION ENZYME-ACTIVITY, INDUCTION, LEPIDOPTERA, MICROSOMAL OXIDASES, NOCTUIDAE, PLANT, RESPONSES, SPODOPTERA-ERIDANIA

1361

Lindroth, R.L., and K.K. Kinney. 1998. Consequences of enriched atmospheric CO2 and defoliation for foliar chemistry and gypsy moth performance. *Journal of Chemical Ecology 24(10):1677-1695.*

Elevated concentrations of atmospheric CO2 are likely to interact with other factors affecting plant physiology to alter plant chemical profiles and plant-herbivore interactions. We evaluated the independent and interactive effects of enriched CO2 and artificial defoliation on foliar chemistry of quaking aspen (Populus tremuloides) and sugar maple (Acer saccharum), and the consequences of such changes for short-term performance of the gypsy moth (Lymantria dispar). We grew aspen and maple seedlings in ambient (similar to 360 ppm) and enriched (650 ppm) CO2 environments at the University of Wisconsin Biotron. Seven weeks after budbreak, trees in half of the rooms were subjected to 50% defoliation. Afterwards, foliage was collected for chemical analyses, and feeding trials were conducted with fourth-stadium gypsy moths. Enriched CO2 altered foliar levels of water, nitrogen, carbohydrates, and phenolics, and responses generally differed between the two tree species. Defoliation induced chemical changes only in aspen. We found no significant interactions between CO2 and defoliation for levels of carbon- based defenses (phenolic glycosides and tannins). CO2 treatment altered the performance of larvae fed aspen, but not maple, whereas defoliation had little effect on performance of insects. In general, results from this experimental system do not support the hypothesis that induction of carbon-based chemical defenses, and

attendant effects on insects, will be stronger in a CO2-enriched world.

KEYWORDS: ALLOCATION PATTERNS, CARBON NUTRIENT BALANCE, DECIDUOUS TREES, DIETARY NITROGEN, ELEVATED CO2, FOREST TENT CATERPILLARS, INSECT PERFORMANCE, NO3 AVAILABILITY, PHYTOCHEMISTRY, PLANTS

1362

Lindroth, R.L., K.K. Kinney, and C.L. Platz. 1993. Responses of deciduous trees to elevated atmospheric co2 - productivity, phytochemistry, and insect performance. *Ecology 74(3):763-777.*

Although rising levels of atmospheric carbon dioxide are expected to directly affect forest ecosystems, little is known of how specific ecological interactions will be modified. This research evaluated the effects of enriched CO2 on the productivity and phytochemistry of forest trees and performance of associated insects. Our experimental system consisted of three tree species (quaking aspen [Populus tremuloides], red oak [Quercus rubra], sugar maple [Acer saccharum]) that span a range from fast to slow growing, and two species of leaf- feeding insects (gypsy moth [Lymantria dispar] and forest tent caterpillar [Malacosoma disstria]). Carbon-nutrient balance theory provided a framework for tests of three hypotheses; in response to enriched CO2: (1) relative increases in tree growth rates will be greatest for aspen and least for maple, (2) relative decreases in protein and increases in carbon-based compounds will be greatest for aspen and least for maple, and (3) relative reductions in performance will be greatest for insects fed aspen and least for insects fed maple. We grew 1- yr-old seedlings for 60 d under ambient (385 +/- 5 muL/L) or elevated (642 +/- 2 muL/L) CO2 regimes at the University of Wisconsin Biotron. After 50 d, we conducted feeding trials with penultimate-instar gypsy moth and forest tent caterpillars. After 60 d, a second set of trees was harvested and partitioned into root, stem, and leaf tissues. We subsequently analyzed leaf material for a variety of compounds known to affect performance of insect herbivores. In terms of actual dry-matter production, aspen responded the most to enriched CO2 atmospheres whereas maple responded the least. Proportional growth increases (relative to ambient plants), however, were highest for oak and least for maple. Effects of elevated CO2 on biomass allocation patterns differed among the three species; root-to-shoot ratios increased in aspen, decreased in oak, and did not change in maple. Enriched CO2 altered concentrations of primary and secondary metabolites in leaves, but the magnitude and direction of effects were species-specific. Aspen showed the largest change in storage carbon compounds (starch), whereas maple experienced the largest change in defensive carbon compounds (condensed and hydrolyzable tannins). Consumption rates of insects fed high-CO2 aspen increased dramatically, but growth rates declined. The two species of insects differed in response to oak and maple grown under enriched CO2. Gypsy moths grew better on high-CO2 Oak, whereas forest tent caterpillars were unaffected; tent caterpillars tended to grow less on high-CO2 maple, whereas gypsy moths were unaffected. Changes in insect performance parameters were related to changes in foliar chemistry. Responses of plants and insects agreed with some, but not all, of the predictions of carbon-nutrient balance theory. This study illustrates that tree productivity and chemistry, and the performance of associated insects, will change under CO2 atmospheres predicted for the next century. Changes in higher level ecological processes, such as community structure and nutrient cycling, are also implicated.

KEYWORDS: BIRCH BETULA, CARBON-DIOXIDE CONCENTRATION, CHEMICAL DEFENSE, GROWTH-RESPONSES, MINERAL NUTRITION, NUTRIENT BALANCE, PHENOLIC GLYCOSIDES, PHOTOSYNTHETIC ACCLIMATION, QUAKING ASPEN, SECONDARY METABOLITES

1363

Lindroth, R.L., S. Roth, E.L. Kruger, J.C. Volin, and P.A. Koss. 1997. CO2-mediated changes in aspen chemistry: Effects on gypsy moth performance and susceptibility to virus. *Global Change Biology 3(3):279-289.*

We investigated the effects of long-term CO2 enrichment on foliar chemistry of quaking aspen (Populus tremuloides) and the consequences of chemical changes for performance of the gypsy moth (Lymantria dispar) and susceptibility of the gypsy moth to a nucleopolyhedrosis virus (NPV). Foliage was collected from outdoor open-top chambers and fed to insects in a quarantine rearing facility. Under enriched CO2, levels of leaf nitrogen declined marginally, levels of starch and phenolic glycosides did not change, and levels of condensed tannins increased. Long-term bioassays revealed reduced growth (especially females), prolonged development and increased consumption in larvae fed high-CO2 foliage but no significant differences in final pupal weights or female fecundity. Short-term bioassays showed weaker, and sex-specific, effects of CO2 treatment on larval performance. Correlation analyses revealed strong, negative associations between insect performance and phenolic glycoside concentrations, independent of CO2 treatment. Larval susceptibility to NPV did not differ between CO2 treatments, suggesting that effects of this natural enemy on gypsy moths are buffered from CO2-induced changes in foliar chemistry. Our results emphasize that the impact of enriched CO2 on plant- insect interactions will be determined Rot only by how concentrations of plant compounds are altered, but also by the relevance of particular compounds for insect fitness. This work also underscores the need for studies of genetic variation in plant responses to enriched CO2 and long-term population-level responses of insects to CO2-induced changes in host quality.

KEYWORDS: CARBON NUTRIENT BALANCE, CATERPILLARS, DEFENSE, ELEVATED ATMOSPHERIC CO2, FOOD-CONSUMPTION, HERBIVORE, INSECT PERFORMANCE, PAPER BIRCH, PHYTOCHEMISTRY, PLANTS

1364

Linker, R., I. Seginer, and P.O. Gutman. 1998. Optimal CO2 control in a greenhouse modeled with neural networks. *Computers and Electronics in Agriculture 19(3):289-310.*

CO, enrichment in warm climates requires a delicate balance between the need to ventilate and the desire to enrich. Model- based optimization can achieve this balance, but requires reliable models of the greenhouse environment and of the crop response. This study assumes that the crop response is known, and focuses on the greenhouse model. Neural network greenhouse models were trained using data collected over two summer months in a small greenhouse. The models were reduced to minimum size, by predicting separately the temperature and CO2 concentration, and by eliminating any unessential input. The resulting models not only fit the data well, they also seem qualitatively correct, and produce reasonable optimization results. Using these models, the effect of evaporative cooling on extending the enrichment duration is demonstrated.

KEYWORDS: ENRICHMENT

1365

Lippert, M., K.H. Haberle, K. Steiner, H.D. Payer, and K.E. Rehfuess. 1996. Interactive effects of elevated CO2 and O-3 on photosynthesis and biomass production of clonal 5-year-old Norway spruce [Picea abies (L) Karst] under different nitrogen nutrition and irrigation treatments. *Trees-Structure and Function 10(6):382-392.*

To study the: single and combined effects of elevated carbon dioxide (CO2), ozone (O-3), nitrogen nutrition, and water supply on photosynthetic gas exchange and biomass accumulation of Norway

spruce, a four-factorial experiment was conducted in closed environmental chambers. Each factor was applied at two levels: (i) ambient and elevated (ambient + 200 mu l l(-1)) CO2, (ii) 20 and 80 nl l(-1) O-3. (iii) low and high nitrogen fertilization, and (iv) a well watered and a drought treatment. Neither elevated O-3 nor CO2 significantly changed stomatal conductances of spruce needles. Adverse effects of elevated O-3 on photosynthetic parameters such as net assimilation rate and carboxylation efficiency occurred only when tile plants were well watered and in a good nutritional status, After 6 weeks enhanced atmospheric CO2 resulted in increased net assimilation rates provided that nutrition was well balanced and plants were well watered, Acclimation processes became apparent and are interpreted as a consequence of sink regulation. While O-3 effects were apparent only in biomass of 1-year-old plant material. elevated CO2-resulted in higher biomass of the buds expanding during the exposure and increased root biomass significantly. Above- and below-ground biomass were strongly influenced by the water and nutrition treatments.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE-OXYGENASE, GAS-EXCHANGE, GROWTH, LOW OZONE CONCENTRATIONS, PLANTS, SEEDLINGS, WATER-STRESS

1366

Lippert, M., K. Steiner, T. Pfirrmann, and H.D. Payer. 1997. Assessing the impact of elevated O-3 and CO2 on gas exchange characteristics of differently K supplied clonal Norway spruce trees during exposure and the following season. *Trees-Structure and Function 11(5):306-315.*

Well-supplied and K-deficient 4-year-old clonal Norway spruce trees were exposed to combinations of two levels of ozone (20 and 80 nl 1(-1) O-3) and carbon dioxide (350 and 750 mu 1 1(-1) CO2) to study the effects of possible future climate factors on gas exchange characteristics. The fumigation was performed in environmental chambers for a complete growing season. After the exposure, plants were cultivated outdoors to investigate possible recovery and delayed effects. During the exposure 1- year-old needles responded to the 80 nl 1(-1) O-3 treatment by a sharp but transient decrease of both apparent carboxylation efficiency (CE) and maximum photosynthetic capacity (A(2500)). Elevated CO2 also reduced CE and A(2500). The effect became stronger in the course of the exposure and was accompanied by decreases of N and P as well as chlorophyll contents. In case of K deficiency, the acclimation response of current-year needles was even more pronounced reflecting lower sink capacities for carbon metabolites. The joint application of elevated O-3 and CO2 resulted in the lowest values of gas exchange parameters and chlorophyll contents. At the beginning of the growing season after the exposure and under outdoor conditions, all these treatment effects disappeared in the needles which had developed during the fumigation. In the course of the development of the new flush, however, the well- supplied 1-year-old needles which had been treated with 80 nl 1(-1) O-3 and 350 mu 1 1(-1) CO2 in the year before, exhibited a sharp decline of CE and A(2500). Simultaneously, chlorotic mottle and bands developed. These delayed symptoms are discussed in the context of the previously published "memory" effect for O-3 (Sandermann et al. 1989). Additionally, evidence is presented that shoot development is altered in plants which had been exposed to elevated O-3.

KEYWORDS: AIR-POLLUTION, ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, L KARST, OZONE, PHOTOSYNTHETIC ACCLIMATION, PICEA-ABIES L, RED SPRUCE, WATER-STRESS

1367

Liu, S.Y., and R.O. Teskey. 1995. Responses of foliar gas-exchange to long-term elevated co2 concentrations in mature loblolly-pine trees. *Tree Physiology 15(6):351-359.*

Branches of field-grown mature loblolly pine (Pinus taeda L.) trees were exposed for 2 years (1992 and 1993) to ambient or elevated CO2 concentrations (ambient + 165 mu mol mol(-1) or ambient + 330 mu mol mol(-1) CO2). Exposure to elevated CO2 concentrations enhanced rates of net photosynthesis (P-n) by 53-111% compared to P-n of foliage exposed to ambient CO2. At the same CO2 measurement concentration, the ratio of intercellular to atmospheric CO2 concentration (C-i/C-a) and stomatal conductance to water vapor did not differ among foliage grown in an ambient or enriched CO2 concentration. Analysis of the relationship between P-n and C-i indicated no significant change in carboxylation efficiency of ribulose-1,5- bisphosphate carboxylase/oxygenase during growth in elevated CO2 concentrations. Based on estimates derived from P-n/C-i curves, there were no apparent treatment differences in dark respiration, CO2 compensation point or P-n at the mean C-i. In 1992, foliage in the three CO2 treatments yielded similar estimates of CO2-saturated P-n (P-max), whereas in 1993, estimates of P-max were higher far branches grown in elevated CO2 than in ambient CO2. We conclude that field-grown loblolly pine trees do not exhibit downward acclimation of leaf-level photosynthesis in their long-term response to elevated CO2 concentrations.

KEYWORDS: ATMOSPHERIC CO2, BRANCH BAG, CARBON DIOXIDE, GROWTH, LEAF-AREA, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, STOMATAL CONDUCTANCE, WATER-STRESS

1368

Liu, Y.T., T.M. Karnauchow, K.F. Jarrell, D.L. Balkwill, G.R. Drake, D. Ringelberg, R. Clarno, and D.R. Boone. 1997. Description of two new thermophilic Desulfotomaculum spp., Desulfotomaculum putei sp. nov, from a deep terrestrial subsurface, and Desulfotomaculum luciae sp. nov, from a hot spring. *International Journal of Systematic Bacteriology 47(3):615-621.*

Six strains of thermophilic, endospore-forming, sulfate- reducing bacteria were enriched and isolated from 2.7 km below the earth's surface in the Taylorsville Triassic Basin in Virginia, The cells of these strains were motile rods that were 1 to 1.1 mu m in diameter and 2 to 5 mu m long. The cells grew by oxidizing H-2, formate, methanol (weakly), lactate (incompletely, to acetate and CO2), or pyruvate (incompletely) while reducing sulfate to sulfide; acetate did not serve as a catabolic substrate, Thiosulfate or sulfite could replace sulfate as an electron acceptor, The results of a phylogenetic analysis of the 16S rRNA gene indicated that these strains belong to the genus Desulfotomaculum, but are distinct from previously described Desulfotomaculum species, Thus, we propose a new species, Desulfotomaculum putei, for them, with strain TH-11 (= SMCC W459) as the type strain, The results of our phylogenetic analysis also indicated that strain SLTT, which was isolated from a hot spring and has been described previously (T. M. Karnauchow, S. F. Koval, and K. F. Jarrell, Syst. Appl. Microbiol, 15:296-310, 1992), is also a member of the genus Desulfotomaculum and is distinct from other species in this genus, We therefore propose the new species Desulfotomaculum luciae for this organism; strain SLT (= SMCC W644) is the type strain of D. luciae.

KEYWORDS: 2,4-DICHLOROPHENOL, GEN-NOV, GROWTH, SEDIMENTS, SEQUENCE, SULFATE-REDUCING BACTERIUM, TEMPERATURE, WATER

1369

Livingston, N.J., D. Whitehead, F.M. Kelliher, Y.P. Wang, J.C. Grace, A.S. Walcroft, J.N. Byers, T.M. McSeveny, and P. Millard. 1998. Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young Pinus radiata D. Don tree.

Plant, Cell and Environment 21(8):795-803.

The three dimensional distribution of intercepted radiation, intercellular CO2 concentration (C-i) and late summer needle nitrogen (N) concentration were determined at the tips of all 54 branches in a 6.2-m-tall Pinus radiata D, Don tree growing in a New Zealand plantation. Measurements included above- and below-canopy irradiance, leaf stable carbon isotopic composition (delta(13)C) and tree canopy architecture. The radiation absorption component of the model, MAESTRO, was tested on site and then used to determine the branch tip distribution of intercepted radiation. We hypothesized that in branch tip needles: (i) the allocation of nitrogen and other nutrients would be closely associated with the distribution of intercepted radiation, reflecting carbon gain optimization theory, and (ii) C-i would predominantly reflect changes in photosynthetic rate (A) rather than stomatal conductance (g(s)), indicating that the increase in A for a given increase in N concentration was larger than the corresponding increase in g(s). Needle nitrogen concentration was poorly related to intercepted radiation, regardless of the period over which the latter was calculated. At a given height, there was a large azimuthal variation in intercepted radiation but N concentration was remarkably uniform around the tree canopy, There was, however, a linear and positive correspondence between N concentration and delta(13)C and needle height above ground (r(2) = 0.73 and 0.68, respectively). The very strong linear correspondence between N concentration and C-i (r(2) = 0.71) was interpreted, using gas exchange measurements, as supporting our second hypothesis. Recognizing the strong apical control in P. radiata and possible effects of leaf nitrogen storage in an evergreen species, we propose that the tree leader must have constituted a very strong carbon sink throughout the growing season, and that the proximity of branch tip needles to the leader affected their photosynthetic capacity and nutrient concentration, independent of intercepted radiation. This implies an integrated internal determination of resource allocation within the tree and challenges the current convention that resources are optimally distributed according to the profile of intercepted radiation.

KEYWORDS: C-3 PLANTS, CANOPY, DIOXIDE, DISCRIMINATION, ELEVATED CO2, FOLIAR NITROGEN, LEAF NITROGEN, LEAVES, PHOTOSYNTHESIS, USE EFFICIENCY

1370

Lloyd, J. 1999. The CO2 dependence of photosynthesis, plant growth responses to elevated CO2 concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO2 concentrations and increased nitrogen deposition at a global scale. *Functional Ecology 13(4):439-459.*

1. Appropriate rates of carbon acquisition by temperate and boreal forests are re-evaluatted, Based on continental-scale forestry data it is suggested that the productivity of temperate and boreal forests has been overestimated previously. 2, Using these values, a model of the integrated response of ecosystems to carbon dioxide concentration and soil nitrogen availability is presented. The model does not assume constant C/N ratios in plant or soil and considers effects of increases in atmospheric CO2 concentrations and nitrogen deposition separately or together. 3, For temperate-zone forests a co- occurrence of a CO2 increase and nitrogen deposition doubles the increase in net primary productivity and carbon sequestration that would be the case for nitrogen deposition occurring on its own. Considered separately, the effect of the atmospheric CO2 increase is less than even moderate rates of anthropogenic N deposition for temperate or boreal forests. By contrast, for tropical forests, the atmospheric CO2 increase is sufficient to induce large rates of carbon accumulation in plants and soil. 4, Application of the model at the global scale suggests large localized sinks for CO2 in either tropical rain forests or in forested or grassland areas of Europe and North America where appreciable N deposition occurs. Overall, the model suggests a terrestrial sink owing to CO2 fertilization and N deposition of about 0.2 Pmol C per year. About half of this is in the mid-latitudes of the northern hemisphere and about half in the tropics.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON DIOXIDE, CYCLE, DIFFERENT CLIMATES, ECOSYSTEMS, MODEL, ORGANIC-MATTER, TERRESTRIAL BIOSPHERE, TROPICAL FORESTS

1371

Lloyd, J. 1999. Current perspectives on the terrestrial carbon cycle. *Tellus Series B-Chemical and Physical Meteorology 51(2):336-342.*

Over the last 5 or so years, there have been significant advances in the understanding of the current role of the terrestrial biosphere in the global carbon cycle, especially in terms of how pools and fluxes are affected by variations in climate (including interannual variability as well as longer-term climate change), increases in atmospheric CO, concentrations and changed rates of atmospheric nitrogen deposition. At the same time, significant advances have been made in terms of both direct. measurement of ecosystem productivity and in an understanding of the key underlying mechanisms modulating carbon fluxes from terrestrial systems. A brief synopsis of these advances is the subject of this paper.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, ECOSYSTEMS, ELEVATED CO2, EUROPEAN FORESTS, MYCORRHIZAL COLONIZATION, NET PRIMARY PRODUCTION, NITROGEN, PHOSPHORUS, PLANT GROWTH, TROPICAL RAIN-FOREST

1372

Lloyd, J., and G.D. Farquhar. 1996. The CO2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO2 concentrations and their interaction with soil nutrient status .1. General principles and forest ecosystems. *Functional Ecology 10(1):4-32.*

KEYWORDS: AMBIENT PARTIAL-PRESSURE, CARBON-DIOXIDE ENRICHMENT, MAINTENANCE RESPIRATION, NET PRIMARY PRODUCTION, NITRATE ASSIMILATION, NITROGEN NUTRITION, PHOSPHORUS-NUTRITION, ROOT RESPIRATION, SIEB EX SPRENG, TREE GROWTH

1373

Loaiza, J., and M. Cantwell. 1997. Postharvest physiology and quality of cilantro (Coriandrum sativum L). *Hortscience 32(1):104-107.*

Respiration rates of freshly harvested cilantro were moderately high (CO2 at 15 to 20 mu L . g(-1). h(-1)) and ethylene production rates were low (<0.2 nL . g(-1). h(-1)) at 5 degrees C and were typical of green leafy tissues. Cilantro stored in darkness at a range of temperatures in air or controlled atmospheres was evaluated periodically for visual quality, decay, aroma, off-odor, color, and chlorophyll content. Cilantro stored in air at 0 degrees C had good visual quality for 18 to 22 days, while at 5 and 7.5 degrees C good quality was maintained for about 14 and 7 days, respectively. An atmosphere of air plus 5% or 9% CO2 extended the shelf-life of cilantro stored at 7.5 degrees C to about 14 days. Quality of cilantro stored in 3% O(2)plus CO2 was similar to that stored in air plus CO2. Atmospheres enriched with 9% to 10% CO2 caused dark lesions after 18 days; 20% CO2 caused severe injury after 7 days. Although visual quality could be maintained for up to 22 days, typical cilantro aroma decreased notably after 14 days, regardless of storage conditions.

KEYWORDS: ETHYLENE, LEAVES, STORAGE, VEGETABLES

1374

Loats, K.V., and J. Rebbeck. 1999. Interactive effects of ozone and elevated carbon dioxide on the growth and physiology of black cherry, green ash, and yellow- poplar seedlings. *Environmental Pollution 106(2):237-248.*

Potted seedlings of black cherry (Prunus serotina Ehrh.) (BC), green ash (Fraxinus pennsylvanica Marsh.) (GA), and yellow- poplar (Liriodendron tulipifera L.) (YP) were exposed to one of the four treatments: (1) charcoal-filtered air (CF) at ambient CO2 (control); (2) twice ambient O-3 (2XO(3)); (3) twice ambient CO2 (650 mu l l(-1)) plus CF air (2xCO(2)); or (4) twice ambient CO2 (650 yl l(-1)) plus twice ambient O-3 (2XCO(2)+2XO(3)) The treatments were duplicated in eight continuously stirred tank reactors for 10 weeks. Gas exchange was measured during the last 3 weeks of treatment and all seedlings were destructively harvested after 10 weeks. Significant interactive effects of O-3 and CO2 on the gas exchange of all three species were limited. The effects of elevated CO2 and O-3, singly and combined, on light-saturated net photosynthesis (A(max)) and stomatal conductance (g(s)) were inconsistent across species. In all three species, elevated O-3 had no effect on g(s). Elevated CO2 significantly increased A(max) in GA and YP foliage, and decreased g(s) in YP foliage. Maximum carbon exchange rates and quantum efficiencies derived from light-response curves increased, while compensation irradiance and dark respiration decreased in all three species when exposed to 2xCO(2). Elevated O-3 affected few of these parameters but any change that was observed was opposite to that fi-om exposure to 2xCO(2)-air. Interactive effects of CO2 and O-3 On light-response parameters were limited. Carboxylation efficiencies, derived from CO2-response curves (A/C-i curves) decreased only in YP foliage exposed to 2xCO(2)-air. In general, growth was significantly stimulated by 2xCO(2) in all three species; though there were few significant growth responses following exposure to 2xO(3) or the combination of 2xCO(2) plus 2xO(3). Results indicate that responses to interacting stressors such as O-3 and CO2 are species specific. (C) 1999 Published by Elsevier Science Ltd. All rights reserved.

KEYWORDS: ABIES L KARST, ACER- SACCHARUM MARSH, ATMOSPHERIC CO2, ENVIRONMENT ALTERS RESPONSE, GAS-EXCHANGE, HYBRID POPULUS L, LIRIODENDRON-TULIPIFERA L, NET PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TROPOSPHERIC OZONE

1375

Lockwood, J.G. 1999. Is potential evapotranspiration and its relationship with actual evapotranspiration sensitive to elevated atmospheric CO2 levels? *Climatic Change 41(2):193-212.*

The possibility is examined that potential evapotranspiration values may be sensitive to changes in atmospheric carbon dioxide content. Enhanced levels of atmospheric CO2 increase water use efficiency of vegetation by improving growth rates and suppressing transpiration per unit leaf area. Highly cultivated crops without water or nutrient constraints are able to show the greatest growth improvements. In many natural or semi-natural ecosystems, under enhanced atmospheric CO2 concentrations, limits on the availability of soil nutrients severely constrains the possibility of improvements in growth and significant increases in leaf area index that could compensate for a decrease in transpiration per unit leaf area. Thus, in many natural or semi-natural ecosystems, which often form water gathering grounds in river basins, enhanced levels of CO2 will suppress transpiration and perhaps increase the proporation of precipitation that forms runoff or ground water. In low vegetation covers, such as grassland, the rates of transpiration and also evaporation from canopies that are wet after rainfall (interception loss) are very similar. In these canopies, evapotranspiration is unlikely to be significantly increased by small increases in leaf area index. It is suggested that the suppression of potential evapotranspiration by enhanced CO2 levels will be small, but that actual transpiration from tall, slow growing vegetation covers may be significantly suppressed. Thus for some vegetation covers the relationship between actual and potential evapotranspiration may be sensitive to CO2 levels. If this is so, it could be of importance to many water balance calculations. The suppression of evapotranspiration by enhanced CO2 levels will be most noticeable in dry climates where interception loss is insignificant and largely masked in very wet climates where a large proportion of evapotranspiration consists of interception loss.

KEYWORDS: CARBON DIOXIDE, EVAPORATION, GLOBAL CLIMATE MODEL, INCREASES, PINE CANOPY, RESPONSES, STOMATAL-RESISTANCE, TEMPERATURE, TRANSPIRATION, VEGETATION

1376

Loehle, C. 1995. Anomalous responses of plants to co2 enrichment. *Oikos 73(2):181-187.*

A number of unexplained responses of plants to CO2 enrichment have been observed. These anomalies can be explained on the basis of growth analysis of whole plants. Some plants may fail to respond to enrichment because they are long-lived and have conservative growth responses or come from impoverished habitats. Apparent (but not real) acclimation to CO2 enrichment might be observed if only part of the growth curve over the life of a perennial is studied. The apparent increased efficiency of nitrogen use may merely be an increase in storage of nonstructural carbohydrate. A model analysis of these effects is presented. Discrepancies among species in relative responses of different plant parts are argued to be largely a function of where the plant typically stores nonstructural carbohydrates, which itself is a function of plant growth stage. Thus, a closer consideration of plant growth strategies and growth partitioning is needed to properly interpret results of CO2 enrichment studies.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, HABITAT TEMPLET, LIFE-HISTORY STRATEGIES, MINERAL NUTRITION, NITROGEN CONCENTRATION, ROOT, SHOOT RATIOS

1377

Loiseau, P., and J.F. Soussana. 1999. Elevated [CO2], temperature increase and N supply effects on the accumulation of below-ground carbon in a temperate grassland ecosystem. *Plant and Soil 212(2):123-134.*

The effects of elevated [CO2] (700 mu l l(-1) [CO2]) and temperature increase (+3 degrees C) on carbon accumulation in a grassland soil were studied at two N-fertiliser supplies (160 and 530 kgN ha(-1) year(-1)) in a long-term experiment (2.5 years) on well established ryegrass swards (Lolium perenne L.,) supplied with the same amounts of irrigation water. For all experimental treatments, the C:N ratio of the top soil organic matter fractions increased with their particle size. Elevated CO2 concentration increased the C:N ratios of the below-ground phytomass and of the macro-organic matter. A supplemental fertiliser N or a 3 degrees C increase in elevated [CO2] reduced it. At the last sampling date, elevated [CO2] did not affect the C:N ratio of the soil organic matter fractions, but increased significantly the accumulation of roots and of macro- organic matter above 200 mu m (MOM). An increased N-fertiliser supply stimulated the accumulation of the non harvested plant phytomass and of the OM between 2 and 50 mu m, without positive effect on the macro-organic matter > 200 mu m. Elevated [CO2] increased C accumulation in the OM fractions above 50 mu m by +2.1 tC ha(-1), on average, whereas increasing the fertiliser N supply led to an average supplemental accumulation of +0.8 tC ha(-1). There was no significant effect of a 3 degrees C temperature increase under elevated [CO2] on C accumulation in the OM fractions above 50 mu m.

KEYWORDS: ATMOSPHERIC CO2, BALANCE, COTTON, DECOMPOSITION, DIOXIDE, ENRICHMENT, MICROBIAL BIOMASS, NITROGEN, SOIL CARBON, SWARD

1378

Loiseau, P., and J.F. Soussana. 1999. Elevated [CO2], temperature increase and N supply effects on the turnover of below-ground carbon in a temperate grassland ecosystem. *Plant and Soil 210(2):233-247.*

The effects of elevated [CO2] (700 mu l l(-1) CO2) and temperature increase (+3 degrees C) on carbon turnover in grassland soils were studied during 2.5 years at two N fertiliser supplies (160 and 530 kg N ha(-1) y(-1)) in an experiment with well-established ryegrass swards (Lolium perenne) supplied with the same amounts of irrigation water. During the growing season, swards from the control climate (350 mu l l(-1) [CO2] at outdoor air temperature) were pulse labelled by the addition of (CO2)-C-13. The elevated [CO2] treatments were continuously labelled by the addition of fossil-fuel derived CO2 (C-13 of -40 to -50 parts per thousand). Prior to the start of the experimental treatments, the carbon accumulated in the plant parts and in the soil macro-organic matter ('old' C) was at -32 parts per thousand. During the experiment, the carbon fixed in the plant material ('new' C) was at -14 and -54 parts per thousand in the ambient and elevated [CO2] treatments, respectively. During the experiment, the C-13 isotopic mass balance method was used to calculate, for the top soil (0-15 cm), the carbon turnover in the stubble and roots and in the soil macro-organic matter above 200 mu (MOM). Elevated [CO2] stimulated the turnover of organic carbon in the roots and stubble and in the MOM at N+, but not at N-. At the high N supply, the mean replacement time of 'old' C by 'new' C declined in elevated, compared to ambient [CO2], from 18 to 7 months for the roots and stubble and from 25 to 17 months for the MOM. This resulted from increased rates of 'new' C accumulation and of 'old' C decay. By contrast, at the low N supply, despite an increase in the rate of accumulation of 'new' C, the soil C pools did not turnover faster in elevated [CO2], as the rate of 'old' C decomposition was reduced. A 3 degrees C temperature increase in elevated [CO2] decreased the input of fresh C to the roots and stubble and enhanced significantly the exponential rate for the 'old' C decomposition in the roots and stubble. An increased fertiliser N supply reduced the carbon turnover in the roots and stubble and in the MOM, in ambient but not in elevated [CO2]. The respective roles for carbon turnover in the coarse soil OM fractions, of the C:N ratio of the litter, of the inorganic N availability and of a possible priming effect between C- substrates are discussed.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE ENRICHMENT, GLOBAL CHANGE, LITTER QUALITY, NATURAL C-13 ABUNDANCE, ROOT-GROWTH, SOIL ORGANIC MATTER, TALLGRASS PRAIRIE, TERM DECOMPOSITION, WATER-USE

1379

Long, S.P., N.R. Baker, and C.A. Raines. 1993. Analyzing the responses of photosynthetic co2 assimilation to long-term elevation of atmospheric co2 concentration. *Vegetatio 104:33-45.*

Understanding how photosynthetic capacity acclimatises when plants are grown in an atmosphere of rising CO2 concentrations will be vital to the development of mechanistic models of the response of plant productivity to global environmental change. A limitation to the study of acclimatisation is the small amount of material that may be destructively harvested from long-term studies of the effects of elevation of CO2 concentration. Technological developments in the measurement of gas exchange, fluorescence and absorption spectroscopy, coupled with theoretical developments in the interpretation of measured values now allow detailed analyses of limitations to photosynthesis in vivo. The use of leaf chambers with Ulbricht integrating spheres allows separation of change in the maximum efficiency of energy transduction in the assimilation of CO2 from changes in tissue absorptance. Analysis of the response of CO2 assimilation to intercellular CO2 concentration allows quantitative determination of the limitation imposed by stomata, carboxylation efficiency, and the rate of regeneration of ribulose 1:5 bisphosphate. Chlorophyll fluorescence provides a rapid method for detecting photoinhibition in heterogeneously illuminated leaves within canopies in the field. Modulated fluorescence and absorption spectroscopy allow parallel measurements of the efficiency of light utilisation in electron transport through photosystems I and II in situ.

KEYWORDS: ABSORBANCE CHANGES, ACCLIMATION, APPARATUS, CHLOROPHYLL FLUORESCENCE, LEAVES, LIGHT, PHOTOINHIBITION, QUANTUM YIELD, RISING CO2, STOMATAL CONDUCTANCE

1380

Long, S.P., and B.G. Drake. 1991. Effect of the long-term elevation of CO2 concentration in the field on the quantum yield of photosynthesis of the C3 sedge, Scirpus olneyi. *Plant Physiology 96(1):221-226.*

CO2 concentration was elevated throughout 3 years around stands of the C3 sedge Scirpus olneyi on a tidal marsh of the Chesapeake Bay. The hypothesis that tissues developed in an elevated CO2 atmosphere will show an acclimatory decrease in photosynthetic capacity under light-limiting conditions was examined. The absorbed light quantum yield of CO2 uptake (phi- abs and the efficiency of photosystem II photochemistry were determined for plants which had developed in open top chambers with CO2 concentrations in air of 680 micromoles per mole, and of 351 micromoles per mole as controls. An Ulbricht sphere cuvette incorporated into an open gas exchange system was used to determine phi-abs and a portable chlorophyll fluorimeter was used to estimate the photochemical efficiency of photosystem II. When measured in an atmosphere with 10 millimoles per mole O2 to suppress photorespiration, shoots showed a phi-abs of 0.093 +/- 0.003, with no statistically significant difference between shoots grown in elevated or control CO2 concentrations. Efficiency of photosystem II photochemistry was also unchanged by development in an elevated CO2 atmosphere. Shoots grown and measured in 680 micromoles per mole of CO2 in air showed a phi- abs of 0.078 +/- 0.004 compared with O.065 +/- 0.003 for leaves grown and measured in 351 micromoles per mole CO2 in air; a highly significant increase. In accordance with the change in phi-abs, the light compensation point of photosynthesis decreased from 51 +/- 3 to 31 +/- 3 micromoles per square meter per second for stems grown and measured in 351 and 680 micromoles per mole of CO2 in air, respectively. The results suggest that even after 3 years of growth in elevated CO2, there is no evidence of acclimation in capacity for photosynthesis under light-limited conditions which would counteract the stimulation of photosynthetic CO2 uptake otherwise expected through decreased photorespiration.

KEYWORDS: C-4 PLANTS, CHAMBER, CHLOROPHYLL FLUORESCENCE, LEAVES, MARSH

1381

Long, S.P., and P.R. Hutchin. 1991. Primary production in grasslands and coniferous forests with climate change - an overview. *Ecological Applications 1(2):139-156.*

In energy terms primary production is the driving step of the global carbon cycle. To predict the interaction of ecosystems with the "greenhouse" effect, it is necessary to understand how primary production, consumption, and decomposition will respond to climate change. Most estimates of primary production have been made by extrapolation from measured standing crops. For grasslands we show this approach to be seriously in error. Even where detailed studies of

turnover and belowground production have been undertaken, errors are invariably high, severely limiting the value of models based on correlation of climate with measured production. Detailed information is available on the responses of individual plant processes to individual climatic variables at the leaf, plant, and stand level, giving potential for a more mechanistic approach in modelling. This approach is limited by lack of information on multivariate interactions and on some key physiological processes, and by uncertainties in scaling up to populations and communities. Despite this, some important insights to possible community responses, particularly those of C3 and C4 types, may be gained from knowledge of responses at the plant level and below. This review outlines the expected character of climate change in grasslands and coniferous forests. Knowledge of the responses of different physiological processes underlying production to individual aspects of climate change is considered, and its implications for higher levels of organization are discussed. Although feasible, mechanistic models of production compound the errors associated with individual process responses with uncertainties surrounding interaction and scaling up, and result in very large errors in any prediction of response to climate change. We conclude that there is insufficient information to predict accurately the response of primary production to climate change. The key processes for which information is inadequate and the parameters that have meaning at different scales need to be identified. Of particular promise is the approach of predicting production from light interception and conversion efficiency.

KEYWORDS: C-4 PHOTOSYNTHESIS, CARBONIC-ANHYDRASE, CHLOROPHYLL FLUORESCENCE, COLD-ACCLIMATED SEEDLINGS, DARK RESPIRATION, ELEVATED CO2 CONCENTRATIONS, FREEZING TEMPERATURES, HIGH LIGHT LEVELS, NITROGEN-USE EFFICIENCY, PINE PINUS-SYLVESTRIS

1382

Lootens, P., and J. Heursel. 1998. Irradiance, temperature, and carbon dioxide enrichment affect photosynthesis in Phalaenopsis hybrids. *Hortscience 33(7):1183-1185.*

The short-term effects of photosynthetic photon flux (PPF), day/night temperatures and CO2 concentration on CO2 exchange were determined for two Phalaenopsis hybrids. At 20 degrees C, the saturating PPF for photosynthesis was 180 mu mol.m(-2).s(- 1). At this PPF and ambient CO2 level (380 mu L.L-1), a day/night temperature of 20/15 degrees C resulted in the largest daily CO2 uptake. Higher night temperatures probably increased the respiration rate and lowered daily CO2 uptake in comparison with 20/15 degrees C. An increase in the CO2 concentration from 380 to 950 mu L.L-1 increased daily CO2 uptake by 82%.

KEYWORDS: CO2, CRASSULACEAN ACID METABOLISM, ENERGY-DISSIPATION, FLUORESCENCE, LEAVES, LIGHT, PHOTOCHEMICAL EFFICIENCY, REDUCTION STATE, RESPONSES, SHORT- TERM

1383

Lord, D., S. Morissette, and J. Allaire. 1993. Influence of light-intensity, nocturnal air-temperature and carbon-dioxide levels on greenhouse black spruce seedlings (picea-marianna). *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(1):101-110.*

Growth of containerized black spruce seedlings grown in greenhouses was studied in relation to factors known to influence plant growth. Artificial light intensity (3.80 and 72.04 mumol.m-2.s-1) and night air temperature (5, 10, 12.5, 15, and 20-degrees-C) were considered in a first experiment and artificial light intensity (4.24 and 59.57 mumol.m-2.s-1) and CO2 air concentration (ambient and 1000 muL.L-1) in a second one. Higher light intensity and CO2 enrichment increased dry biomass of seedlings as well as growth in height and stem diameter. Both factors similarly enhanced the last two parameters since height/diameter ratios showed little variation among treatments. Reducing night air temperature down to 10- degrees-C did not significantly influence height growth nor biomass increase when high intensity light was provided. Lower light intensity raised the threshold to 12.5-degrees-C. Shoot height, diameter, and dry biomass as well as the number of branches and buds per millimeter were strongly reduced by a 5- degrees-C night air temperature. High intensity light enhanced growth of containerized black spruce seedlings more than CO2 enrichment or a 5-degrees-C night air temperature. When used simultaneously, these growth enhancing factors had a synergistic effect during most of the treatment period; thereafter, the effect became partially additive. The relative growth rate peaked at the onset of exponential shoot growth and decreased after this point. However, the enhancing factors were still efficient since absolute growth differences between seedlings grown under the most-favorable conditions and controls kept increasing, The faster growing pace imposed by these growth enhancing conditions during the treatment period was maintained over the entire first growing season.

KEYWORDS: CO2- ENRICHMENT, DRY-MATTER PRODUCTION, GROWTH, PHOTOPERIOD

1384

Loretan, P.A., C.K. Bonsi, D.G. Mortley, R.M. Wheeler, C.L. Mackowiak, W.A. Hill, C.E. Morris, A.A. Trotman, and P.P. David. 1994. Effects of several environmental-factors on sweet-potato growth. *Life Sciences and Space Research XXV (3) 14(11):277-280.*

Effects of relative humidity, light intensity and photoperiod on growth of 'Ga Jet' and 'TI-155' sweetpotato cultivars, using the nutrient film technique (NFT), have been reported. In this study, the effect of ambient temperature regimes (constant 28 degrees C and diurnal 28:22 degrees C day:night) and different CO2 levels (ambient, 400,1 000, and 10 000 mu L/L - 400, 1 000 and 10 000 ppm) on growth of one or both of these cultivars in NFT are reported. For a 24-h photoperiod, no storage roots were produced for either cultivar in NFT when sweetpotato plants were grown at a constant temperature of 28 degrees C. For the same photoperiod, when a 28:22 degrees C diurnal temperature variation was used, there were still no storage roots for 'TI- 155' but the cv. 'Ga Jet' produced 537 g/plant of storage roots. For both a 12-h and 24-h photoperiod,'Ga Jet' storage root fresh and dry weight tended to be higher with a 28:22 degrees C diurnal temperature variation than with a constant 28 degrees C temperature regime. Preliminary results with both 'Ga Jet' and 'TI-155' cultivars indicate a distinctive diurnal stomatal response for sweetpotato grown in NFT under an ambient CO2 level. The stomatal conductance values observed for 'Ga Jet' at elevated CO2 levels indicated that the difference between the light- and dark-period conductance rates persisted at 400, 1 000, and 10 000 mu L/L.

KEYWORDS: POTATO

1385

Louche-Tessandier, D., G. Samson, C. Hernandez-Sebastia, P. Chagvardieff, and Y. Desjardins. 1999. Importance of light and CO2 on the effects of endomycorrhizal colonization on growth and photosynthesis of potato plantlets (Solanum tuberosum) in an in vitro tripartite system. *New Phytologist 142(3):539-550.*

A factorial analysis was conducted to investigate the effects of different levels of photosynthetic photon flux (PPF) and CO2 concentration on the interactions between the vesicular- arbuscular endomycorrhizal fungus Glomus intraradices and potato plantlets (Solanum tuberosum) cultured in an in vitro tripartite system. We observed that CO2 enrichment from 350 to 10000 ppm stimulated root colonization by the fungus, and that

this stimulation was more pronounced under high PPF (300 mu mol m(-2) s(-1)) than low PPF (60 mu mol m(-2) s(-1)). Consistent with these observations, the effects of G. intraradices on dry matter production in potato plantlets were strongly dependent on the CO2 and PPF levels during cultivation. There was no significant effect of the mycorrhizal fungus on dry matter production at 350 ppm of CO2 However, under the high CO, concentration, mycorrhiza had opposite effects on dry matter production depending on the PPF: a decrease (-21%) and a stimulation (+25%) of dry matter production after 2 wk of growth under low and high PPF, respectively, were observed in presence of G. intraradices relative to plantlets grown in its absence. Furthermore, in mycorrhizal plantlets grown under high levels of both PPF and CO2 the chlorophyll and carotenoid contents as well as the quantum yields of photosynthetic electron transport and the photochemical quenching qP of the chlorophyll-a fluorescence measured near the PPF during growth were all higher than in non-infected plantlets. Our results therefore indicate that mycorrhizal G. intraradices can alleviate the down regulation of photosynthesis related to sink limitation, and its effect on dry matter production is strongly dependent on the levels of CO2 and PPF during growth which determine the balance between the photosynthetic carbon uptake by the plantlets and the carbon cost by the fungus.

KEYWORDS: ARBUSCULAR MYCORRHIZAE, CHLOROPHYLL FLUORESCENCE, CULTURE, ELEVATED CO2, INFECTION, MYCORRHIZAL FUNGAL INOCULUM, PHOTOSYSTEM, PRENUCLEAR MINITUBERS, QUANTUM YIELD, RESPIRATION

1386

Lovelock, C.E., D. Kyllo, M. Popp, H. Isopp, A. Virgo, and K. Winter. 1997. Symbiotic vesicular-arbuscular mycorrhizae influence maximum rates of photosynthesis in tropical tree seedlings grown under elevated CO2. *Australian Journal of Plant Physiology 24(2):185-194.*

To investigate the importance of phosphorus and carbohydrate concentrations in influencing photosynthetic capacity of tropical forest tree seedlings under elevated CO2, we grew seedlings of Beilschmiedia pendula (Sw.) Hemsl. (Lauraceae) under elevated CO2 concentrations either with or without vesicular-arbuscular (VA) mycorrhizae. VA-mycorrhizae increased phosphorus concentrations in all plant organs (leaves, stems and roots). Maximum rates of photosynthesis (A(max)) measured under saturating levels of CO2 and light were correlated with leaf phosphorus concentrations. VA-mycorrhizae also increased leaf carbohydrate concentrations, particularly under elevated CO2, but levels were low and within the range observed in naturally occurring forest species. Root carbohydrate concentrations were reduced in VA-mycorrhizal plants relative to non-mycorrhizal plants. These results indicate an important role for VA-mycorrhizae in controlling photosynthetic rates and sink strength in tropical trees, and thus in determining their response to future increases in atmospheric CO2 concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, INFECTION, MINERAL NUTRITION, PHOSPHORUS, PLANTS, RAIN-FOREST TREES, RESPONSES, SOIL, TRANSLOCATION

1387

Lovelock, C.E., D. Kyllo, and K. Winter. 1996. Growth responses to vesicular-arbuscular mycorrhizae and elevated CO2 in seedlings of a tropical tree, Beilschmiedia pendula (vol 10, pg 662, 1996). *Functional Ecology 10(6):784.*

1388

Lovelock, C.E., D. Kyllo, and K. Winter. 1996. Growth responses to vesicular-arbuscular mycorrhizae and elevated CO2 in seedlings of a tropical tree, Beilschmiedia pendula. *Functional Ecology 10(5):662-667.*

1. Vesicular-arbuscular (VA) mycorrhizae increased relative growth rates (RGR) of the shade-tolerant tropical tree species Beilschmiedia pendula at both ambient and doubled CO2 concentrations. 2. RGR was correlated with the net assimilation rate (NAR) of plants. Within this general correlation, in plants with similar RGR, NAR was decreased in VA-mycorrhizal plants compared with non-mycorrhizal plants. As RGR is the product of NAR and the leaf area ratio (LAR, the ratio of leaf area to plant mass), increases in RGR in VA-mycorrhizal plants were the results of increased LAR. Thus, VA-mycorrhizae increased growth rates of B. pendula by altering the morphology of the seedlings. 3. Under elevated CO2 the amount of fungus within roots increased in VA-mycorrhizal plants compared with those grown under ambient CO2 and this was associated with a greater post-inoculation depression in leaf growth. Post- inoculation depressions in leaf growth and the lower NAR (in plants with similar RGR) of VA-mycorrhizal plants indicate there is increased carbon transfer to soils under elevated CO2.

KEYWORDS: ASSOCIATIONS, ATMOSPHERIC CO2, CARBON, DEMAND, ECOSYSTEMS, FOREST, INFECTION, PLANTAGO-MAJOR, RESPIRATION

1389

Lovelock, C.E., J. Posada, and K. Winter. 1999. Effects of elevated CO2 and defoliation on compensatory growth and photosynthesis of seedlings in a tropical tree, Copaifera aromatica. *Biotropica 31(2):279-287.*

After defoliation by herbivores, some plants exhibit enhanced rates of photosynthesis and growth that enable them to compensate for lost tissue, thus maintaining their fitness relative to competing, undefoliated plants. Our aim was to determine whether compensatory photosynthesis and growth would be altered by increasing concentrations of atmospheric CO2. Defoliation of developing leaflets on seedlings of a tropical tree, Copaifera aromatica, caused increases in photosynthesis under ambient CO2, but not under elevated CO2. An enhancement in the development of buds in the leaf axils followed defoliation at ambient levels of CO2. In contrast, under elevated CO2, enhanced development of buds occurred in undefoliated plants with no further enhancement in bud development due to exposure to elevated CO2. Growth of leaf area after defoliation was increased, particularly under elevated CO2. Despite this increase, defoliated plants grown under elevated CO2 were further from compensating for tissue lost during defoliation after 5-1/2 weeks than those grown under ambient CO2 concentrations.

KEYWORDS: ACCLIMATION, CAPACITY, CARBON DIOXIDE, FITNESS, FOREST, PATTERNS, PLANT, RESPONSES, SIMULATED HERBIVORY, STRESS

1390

Lovelock, C.E., A. Virgo, M. Popp, and K. Winter. 1999. Effects of elevated CO2 concentrations on photosynthesis, growth and reproduction of branches of the tropical canopy tree species, Luehea seemannii Tr. & Planch. *Plant, Cell and Environment 22(1):49-59.*

Mature trees have already experienced substantial increases in CO2 concentrations during their lifetimes, and will experience continuing increases in the future. Small open-top chambers were used to enclose branchlets that were at a height of between 20 and 25 m in the canopy of the tree species Luehea seemannii Tr. & Planch. in a tropical forest in Panama. Elevated concentrations of CO2 increased the rate of photosynthetic carbon fixation and decreased stomatal conductance of leaves, but did not influence the growth of leaf area per chamber, the production of flower buds and fruit nor the concentration of

nonstructural carbohydrates within leaves. The production of flower buds was highly correlated with the leaf area produced in the second flush of leaves, indicating that the branchlets of mature trees of Luehea seemannii are autonomous to a considerable extent. Elevated levels of CO2 did increase the concentration of nonstructural carbohydrates in woody stem tissue. Elevated CO2 concentration also they increased the ratio of leaf area to total biomass of branchlets, and tended to reduce individual fruit weight. These data suggest that the biomass allocation patterns of mature trees may change under future elevated levels of CO2. Although there were no effects on growth during the experiment, the possibility of increased growth in the season following CO2 enrichment due to increased carbohydrate concentrations in woody tissue cannot be excluded.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FOREST, GAS-EXCHANGE, LEAF, PINUS-TAEDA TREES, RESPONSES, SOIL, WATER-USE

1391

Lovelock, C.E., K. Winter, R. Mersits, and M. Popp. 1998. Responses of communities of tropical tree species to elevated CO2 in a forest clearing. *Oecologia 116(1-2):207-218.*

Communities of ten species of tropical forest tree seedlings from three successional classes were grown at ambient and elevated CO2 in large open-top chambers on the edge of a forest in Panama. Communities grew from 20 cm to approximately 2 m in height in 6 months. No enhancements in plant biomass accumulation occurred under elevated CO2 either in the whole communities or in growth of individual species. Reductions in leaf area index under elevated CO2 were observed, as were decreases in leaf nitrogen concentrations and increases in the C:N ratio of leaf tissue. Species tended to respond individualistically to elevated CO2, but some generalizations of how successional groupings responded could be made. Early and mid-successional species generally showed greater responses to elevated CO2 than late-successional species, particularly with respect to increases in photosynthetic rates and leaf starch concentrations, and reductions in leaf area ratio. Late-successional species showed greater increases in C:N ratios in response to elevated CO2 than did other species. Our results indicate that there may not be an increase in the growth of regenerating tropical forest under elevated CO2, but that there could be changes in soil nutrient availability because of reductions in leaf tissue quality, particularly in late- successional species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DECOMPOSITION RATES, ECOSYSTEMS, ENRICHMENT, GROWTH ENHANCEMENT, LEAF LITTER, ORGANIC-MATTER, PLANT FUNCTIONAL TYPES, RAIN-FOREST, SOIL NUTRIENT

1392

Luan, J.S., Y.Q. Luo, and J.F. Reynolds. 1999. Responses of a loblolly pine ecosystem to CO2 enrichment: a modeling analysis. *Tree Physiology 19(4-5):279-287.*

The development of the Free-Air CO2 Enrichment (FACE) facilities represents a substantial advance in experimental technology for studying ecosystem responses to elevated CO2. A challenge arising from the application of this technology is the utilization of short-term FACE results for predicting long- term ecosystem responses. This modeling study was designed to explore interactions of various processes on ecosystem productivity at elevated CO2 on the decadal scale. We used a forest model (FORDYN) to analyze CO2 responses-particularly soil nitrogen dynamics, carbon production and storage-of a loblolly pine ecosystem in the Duke University Forest. When a 14-year-old stand was exposed to elevated CO2, simulated increases in annual net primary productivity (NPP) were 13, 10 and 7.5% in Years 1, 2 and 10, respectively, compared with values at ambient CO2. Carbon storage increased by 4% in trees and 9.2% in soil in Year 10 in response to elevated CO2. When the ecosystem was exposed to elevated CO2 from the beginning of forest regrowth, annual NPP and carbon storage in trees and soil were increased by 32, 18 and 20%, respectively, compared with values at ambient CO2. In addition, simulation of a 20% increase in mineralization rate led to a slight increase in biomass growth and carbon storage, but the simulated 20% increase in fine root turnover rate considerably increased annual NPP and carbon storage in soil. The modeling results indicated that (1) stimulation of NPP and carbon storage by elevated CO2, is transient and (2) effects of elevated CO2 on ecosystem processes-canopy development, soil nitrogen mineralization and root turnover-have great impacts on ecosystem C dynamics. A detailed understanding of these processes will improve our ability to predict long-term ecosystem responses to CO2 enrichment.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FOREST, GROWTH, NITROGEN, PHOTOSYNTHESIS, SEEDLINGS, TAEDA L, TERRESTRIAL ECOSYSTEMS, TREES

1393

Lucas, W.J., A. Olesinski, R.J. Hull, J.S. Haudenshield, C.M. Deom, R.N. Beachy, and S. Wolf. 1993. Influence of the tobacco mosaic-virus 30-kda movement protein on carbon metabolism and photosynthate partitioning in transgenic tobacco plants. *Planta 190(1):88-96.*

Transgenic tobacco (Nicotiana tabacum L.) plants expressing the 30-kDa movement protein of tobacco mosaic virus (TMV-MP) were employed to investigate the influence of a localized change in mesophyll-bundle sheath plasmodesmal size exclusion limit on photosynthetic performance and on carbon metabolism and allocation. Under conditions of saturating irradiance, tobacco plants expressing the TMV-MP were found to have higher photosynthetic CO2-response curves compared with vector control plants. However, this difference was significant only in the presence of elevated CO2 levels. Photosynthetic measurements made in the greenhouse, under endogenous growth conditions, revealed that there was little difference between TMV-MP- expressing and control tobacco plants. However, analysis of carbon metabolites within source leaves where a TMV-MP-induced increase in plasmodesmal size exclusion limit had recently taken place established that the levels of sucrose, glucose, fructose and starch were considerably elevated above those present in equivalent control leaves. Although expression of the TMV-MP did not alter total plant biomass, it reduced carbon allocation to the lower region of the stem and roots. This difference in biomass distribution was clearly evident in the lower root-to-shoot ratios for the TMV-MP transgenic plants. Microinjection (dye-coupling) studies established that the TMV- MP-associated reduction in photosynthate delivery (allocation) to the roots was not due to a direct effect on root cortical plasmodesmata. Rather, this change appeared to result from an alteration in phloem transport from young source leaves in which the TMV-MP had yet to exert its influence over plasmodesmal size exclusion limits. These results are discussed in terms of the rate-limiting steps involved in sucrose movement into the phloem.

KEYWORDS: BUNDLE SHEATH-CELLS, C-4 PLANTS, COMMELINA-BENGHALENSIS, EXCLUSION LIMIT, LEAVES, MINOR VEINS, PLASMODESMATAL FREQUENCY, ROOT, SHOOT, SYMPLASTIC CONNECTIONS

1394

Ludeke, M.K.B., S. Donges, R.D. Otto, J. Kindermann, F.W. Badeck, P. Ramge, U. Jakel, and G.H. Kohlmaier. 1995. Responses in npp and carbon stores of the northern biomes to a co2-induced climatic-change, as evaluated by the frankfurt biosphere model (fbm). *Tellus Series B-Chemical and Physical Meteorology 47(1-2):191-205.*

To assess the role of the boreal and temperate forests and the tundra ecosystems in a future CO2-induced climate change, the Frankfurt biosphere model(FBM) was applied to the 3xCO(2) climate as calculated by the GCM of the MPI fur Meteorologie in Hamburg. The FBM predicts on a 1 degrees x1 degrees spatial grid the seasonal and perannual course of leaf biomass and feeder roots, woody biomass, soil carbon and soil water in response to the seasonal course of light, precipitation and temperature. The phenology is controlled by the flux balance of carbon gains and losses, thus being dependent on the driving climate and the state of vegetation. Two equilibrium runs based on the 3xCO(2) climate were performed: (1) Considering the pure climate effect (with no direct CO2 fertilization) we obtained a 22% decrease of the net primary production (NPP) due to enhanced autotrophic respiration and increased water limitation. Together with the effect on the soils this results in a 170 Gt carbon source. (2) Considering a CO2-induced enhancement of the maximum photosynthesis the pure climate effect is more than compensated and we predict a NPP increase of 9% and a total carbon sink of 50 Ct C. This effect may even be an underestimate if one takes into consideration a shift in the optimum temperature for photosynthesis under enhanced levels of atmospheric CO2 as proposed by Long and Drake.

KEYWORDS: CO2, ECOSYSTEMS, EXCHANGE, FORESTS, GRASSLANDS, NET PRIMARY PRODUCTION, STORAGE, TEMPERATURE, VEGETATION

1395

Ludewig, F., U. Sonnewald, F. Kauder, D. Heineke, M. Geiger, M. Stitt, B.T. Muller-Rober, B. Gillissen, C. Kuhn, and W.B. Frommer. 1998. The role of transient starch in acclimation to elevated atmospheric CO2. *Febs Letters 429(2):147-151.*

Although increased concentrations of CO2 stimulate photosynthesis, this stimulation is often lost during prolonged exposure to elevated carbon dioxide, leading to an attenuation of the potential gain in yield. Under these conditions, a wide variety of species accumulates non-structural carbohydrates in leaves, It has been proposed that starch accumulation directly inhibits photosynthesis, that the rate of sucrose and starch synthesis limits photosynthesis, or that accumulation of sugars triggers changes in gene expression resulting in loser activities of Rubisco and inhibition of photosynthesis. To distinguish these explanations, transgenic plants unable to accumulate transient starch due to leaf mesophyll-specific antisense expression of AGP B were grown at ambient and elevated carbon dioxide. There was a positive correlation between the capacity for starch synthesis and the rate of photosynthesis at elevated CO2 concentrations, showing that the capability to synthesize leaf starch is essential for photosynthesis in elevated carbon dioxide, The results show that in elevated carbon dioxide, photosynthesis is restricted by the rate of end product synthesis, Accumulation of starch is not responsible for inhibition of photosynthesis, Although transgenic plants contained increased levels of hexoses, transcripts of photosynthetic genes were not downregulated and Rubisco activity was not decreased arguing against a role of sugar sensing in acclimation to high CO2, (C) 1998 Federation of European Biochemical Societies.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CARBON DIOXIDE, CLONING, EXPRESSION, GENES, INHIBITION, LEADS, PHOTOSYNTHESIS, SUCROSE, TOMATO PLANTS

1396

Lukewille, A., and R.F. Wright. 1997. Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biology 3(1):13-21.*

Boreal forest ecosystems are sensitive to global warming, caused by increasing emissions of CO2 and other greenhouse gases. Assessment of the biological response to future climate change is based mainly on large-scale models. Whole-ecosystem experiments provide one of the few available tools by which ecosystem response can be measured and with which global models can be evaluated. Boreal ecosystem response to global change may be manifest by alterations in nitrogen (N) dynamics, as N is often the growth limiting nutrient. The CLIMEX (Climate Change Experiment) project entails catchment-scale manipulations of CO2 (to 560 ppmv) and temperature (by + 3 to + 5 degrees C) to whole forest ecosystems in southern Norway. Soil temperature is increased at 400-m(2) EGIL catchment by means of electric cables placed on the soil surface. Soil warming at EGIL catchment caused an increase in nitrate and ammonium concentrations in runoff in the first year of treatment. We hypothesize that higher temperature increased N release by mineralization. Whether these responses are only transient will be shown by additional years' treatment.

KEYWORDS: ARCTIC TUNDRA, CARBON DIOXIDE, CO2, ECOSYSTEMS, MINERALIZATION, RESPONSES, SINK, WHOLE-CATCHMENT

1397

Lund, C.P., W.J. Riley, L.L. Pierce, and C.B. Field. 1999. The effects of chamber pressurization on soil-surface CO2 flux and the implications for NEE measurements under elevated CO2. *Global Change Biology 5(3):269-281.*

Soil and ecosystem trace gas fluxes are commonly measured using the dynamic chamber technique. Although the chamber pressure anomalies associated with this method are known to be a source of error, their effects have not been fully characterized. In this study, we use results from soil gas-exchange experiments and a soil CO2 transport model to characterize the effects of chamber pressure on soil CO2 efflux in an annual California grassland. For greater than ambient chamber pressures, experimental data show that soil-surface CO2 flux decreases as a nonlinear function of increasing chamber pressure; this decrease is larger for drier soils. In dry soil, a gauge pressure of 0.5 Pa reduced the measured soil CO2 efflux by roughly 70% relative to the control measurement at ambient pressure. Results from the soil CO2 transport model show that pressurizing the flux chamber above ambient pressure effectively flushes CO2 from the soil by generating a downward now of air through the soil air-filled pore space. This advective flow of air reduces the CO2 concentration gradient across the soil-atmosphere interface, resulting in a smaller diffusive flux into the chamber head space. Simulations also show that the reduction in diffusive flux is a function of chamber pressure, soil moisture, soil texture, the depth distribution of soil CO2 generation, and chamber diameter. These results highlight the need for caution in the interpretation of dynamic chamber trace gas flux measurements. A portion of the frequently observed increase in net ecosystem carbon uptake under elevated CO2 may be an artifact resulting from the impact of chamber pressurization on soil CO2 efflux.

KEYWORDS: ATMOSPHERIC CO2, CARBON, CLEAR-CUT, EFFLUX, EVOLUTION, FOREST SOILS, GAS-EXCHANGE, PRAIRIE, ROOT RESPIRATION, WATER-VAPOR

1398

Luo, Y., J.L. Chen, J.F. Reynolds, C.B. Field, and H.A. Mooney. 1997. Disproportional increases in photosynthesis and plant biomass in a Californian grassland exposed to elevated CO2: a simulation analysis. *Functional Ecology 11(6):696-704.*

1. Elevated CO2 concentrations often lead to increased photosynthetic carbon uptake in plants, but this does nor necessarily result in a proportional increase in plant biomass. We examined this paradox for grasslands in northern California that have been exposed to elevated

CO2 since 1992. We evaluated the effects of physiological adjustments on plant growth and carbon balance of the dominant species, Avena barbata, using a plant growth model. 2. Without physiological adjustments, an observed 70% increase in leaf photosynthesis in elevated CO2 was predicted to increase plant biomass by 97% whereas experimental measurements suggested 5 and 13% decreases in 1992 and 1993, respectively, and a 40% increase in 1994. 3. Simulations with an increase in carbon allocation to roots by 29%, or leaf death rate by 80%, or non-structural carbohydrate storage by 60%, or leaf mass per unit area by 25% each predicted an approximately 40% increase in plant biomass in 1994 under elevated CO2. It follows that greater suppression of the biomass responses to elevated CO2, in 1992 and 1993 resulted from variable combinations of these physiological adjustments. 4. This modelling study concludes that (a) an increase in carbon loss or (b) a decrease in carbon-use efficiency or (c) an increase in carbon allocation to root growth will result in an increase in biomass growth that is less than that in leaf photosynthesis under elevated CO2. Alternatively, if carbon loss is reduced (e.g, depressed respiration) and/or carbon allocation to leaf growth is increased, biomass growth may be stimulated more than leaf photosynthesis by atmospheric CO2 concentration. Moreover, this modelling exercise suggests that physiological adjustments may have substantial effects on ecosystem carbon processes by varying ecosystem carbon influx, litterfall and Litter quality.

KEYWORDS: CANOPY, CARBON BALANCE, ECOSYSTEMS, ENRICHMENT, GROWTH, NUTRIENT, RESPIRATION, RESPONSES

1399

Luo, Y., C.B. Field, and H.A. Mooney. 1994. Predicting responses of photosynthesis and root fraction to elevated [co2](a) - interactions among carbon, nitrogen, and growth. *Plant, Cell and Environment 17(11):1195-1204.*

At elevated atmospheric CO2 concentrations ([CO2](a)), photosynthetic capacity (A(max)) and root fraction (eta(R), the ratio of root to plant dry mass) increased in some studies and decreased in others. Here, we have explored possible causes of this, focusing on the relative magnitudes of the effects of elevated [CO2](a) on specific leaf (n(m)) and plant (n(p)) nitrogen concentrations, leaf mass per unit area (h), and plant nitrogen productivity (alpha). In our survey of 39 studies with 35 species, we found that elevated [CO2](a) led to decreased n(m) and n(p) in all the studies and to increased h and alpha in most of the studies. The magnitudes of these changes varied with species and with experimental conditions. Based on a model that integrated [CO2](a)-induced changes in leaf nitrogen into a biochemically based model of leaf photosynthesis, we predicted that, to a first approximation, photosynthesis will be upregulated (A(max) will increase) when growth at increased [CO2](a) leads to increases in h that are larger than decreases in n(m). Photosynthesis will be downregulated (A(max) will decrease) when increases in h are smaller than decreases in n(m). The model suggests that photosynthetic capacity increases at elevated [CO2](a) only when additional leaf mesophyll more than compensates the effects of nitrogen dilution. We considered two kinds of regulatory paradigms that could lead to varying responses of eta(R) to elevated [CO2](a), and compared the predictions of each with the data. A simple static model based on the functional balance concept predicts that eta(R) should increase when neither n(p) nor h is very responsive to elevated [CO2](a). The quantitative and qualitative agreement of the predictions with data from the literature, however, is poor. A model that predicts eta(R) from the relative sensitivities of photosynthesis and relative growth rate to elevated [CO2](a) corresponds much more closely to the observations. In general, root fraction increases if the response of photosynthesis to [CO2](a) is greater than that of relative growth rate.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, C-3 PLANTS, COOCCURRING BIRCH, DIOXIDE CONCENTRATION, LEAF NITROGEN, MINERAL NUTRITION, N2 FIXATION, SHOOT RATIO, VULGARIS L, WHITE CLOVER

1400

Luo, Y., C.B. Field, and H.A. Mooney. 1997. Adapting GePSi (generic plant simulator) for modeling studies in the Jasper Ridge CO2 project. *Ecological Modelling 94(1):81-88.*

In order to conduct modeling studies on the effects of elevated atmospheric carbon dioxide concentration ([CO2]) on plant and ecosystem processes at the Jasper Ridge grassland in northern California, the generic plant simulator (GePSi) (Chen: J.-L. and Reynolds, J.F., 1997. Ecol. Model., 94: 53-66), is modified to simulate grass dynamics. This modification was attempted by the authors of this paper, who had no prior experience with the model. Prior to this project, GePSi, which is implemented in the object-oriented programming (OOP) language, C++, had only been used to model trees and woody shrubs. This exercise addressed several of the concepts presented in this volume concerning the purported benefits of genericness, modularity, and OOP in plant modeling. The objective of this paper is to briefly summarize the extent to which these benefits were realized and some of the problems encountered. Our evaluation is presented in terms of: (1) design considerations, including the importance of how the modules in GePSi were defined; and (2) the implementation phase, which critiques the use of OOP for facilitating the transfer of the model. This study suggests that generic, modular models such as GePSi will facilitate the interactions of model developers and users and reduce duplication of effort in model development. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON, ELEVATED CO2, ENRICHMENT, GROWTH, LOBLOLLY-PINE, NITROGEN, PHOTOSYNTHETIC CAPACITY, PREDICTING RESPONSES, SEEDLINGS

1401

Luo, Y.H., and B.R. Strain. 1992. Leaf water status in velvetleaf under long-term interactions of water-stress, atmospheric humidity, and carbon-dioxide. *Journal of Plant Physiology 139(5):600-604.*

Well watered and water-stressed Abutilon theophrastic, were grown with relative humidity of 45% or 85% at 30-degrees-C and CO2 concentrations of 350 or 650-mu-mol mol-1. Elevated leaf water potentials of the water-stressed plants grown in both high and low humidities were caused by CO2 enrichment. Elevated water content (kg m-2 leaf area) caused by CO2 enrichment, higher water content at a given water potential, and notably lower rate in desiccation from detached leaves all occurred only in the plants grown in low humidity. These results may be related to enhanced dehydration resistance of the plants that experienced long-term low humidity.

KEYWORDS: CO2- ENRICHMENT, DROUGHT, EXCHANGE, PLANTS, RESPONSES, SOIL

1402

Luo, Y.Q., R.B. Jackson, C.B. Field, and H.A. Mooney. 1996. Elevated CO2 increases belowground respiration in California grasslands. *Oecologia 108(1):130-137.*

This study was designed to identify potential effects of elevated CO2 on belowground respiration (the sum of root and heterotrophic respiration) in field and microcosm ecosystems and on the annual carbon budget. We made three sets of respiration measurements in two CO2 treatments, i.e., (1) monthly in the sandstone grassland and in microcosms from November 1993 to June 1994; (2) at the annual peak of live biomass (March and April) in the serpentine and sandstone grasslands in 1993 and 1994; and (3) at peak biomass in the microcosms with monocultures of seven species in 1993. To help understand ecosystem carbon cycling,

we also made supplementary measurements of belowground respiration monthly in sandstone and serpentine grasslands located within 500 m of the CO2 experiment site. The seasonal average respiration rate in the sandstone grassland was 2.12 mu mol m(-2) s(-1) in elevated CO2, which was 32% higher than the 1.49 mu mol m(-2) s(-1) measured in ambient CO2 (P = 0.007). Studies of seven individual species in the microcosms indicated that respiration was positively correlated with plant biomass and increased, on average, by 70% with CO2. Monthly measurements revealed a strong seasonality in belowground respiration, being low (0-0.5 mu mol CO2 m(-2) s(-1) in the two grasslands adjacent to the CO2 site) in the summer dry season and high (2-4 mu mol CO2 m(- 1) s(-1) in the sandstone grassland and 2-7 mu mol CO2 m(-1) s(-1) in the microcosms) during the growing season from the onset of fall rains in November to early spring in April and May. Estimated annual carbon effluxes from the soil were 323 and 440 g C m(-2) year(-1) for the sandstone grasslands in ambient and elevated CO2. That CO2-stimulated increase in annual soil carbon efflux is more than twice as big as the increase in aboveground net primary productivity (NPPa) and approximately 60% of NPPa in this grassland in the current CO2 environment. The results of this study suggest that below- ground respiration can dissipate most of the increase in photosynthesis stimulated by elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON, ENRICHMENT, FLUX, FOREST, NITROGEN, PONDEROSA PINE, SOIL RESPIRATION, TEMPERATURE, TUSSOCK TUNDRA

1403

Luo, Y.Q., and H.A. Mooney. 1995. Long-term CO2 stimulation of carbon influx into global terrestrial ecosystems: Issues and approaches. *Journal of Biogeography 22(4-5):797-803.*

Estimating the additional amount of global photosynthetic carbon influx into terrestrial ecosystems (P-G) becomes possible with a leaf-level factor (L) developed by Luo & Mooney only when an increase in atmospheric CO2 concentration (C-a) is small. Applying the L factor to study long-term stimulation of P-G with a large increase in C-a needs understanding of adjustments in leaf properties, canopy structure and ecosystem nitrogen availability, which could, potentially, feedback to photosynthetic carbon influx. Leaf photosynthetic properties vary greatly with elevated CO2 among species. Aggregation over a group of species, however, shows a small change, suggesting that globally averaged changes in leaf properties may be trivial. Canopy adjustment in elevated CO2 is largely unknown whereas indirect measurements suggest faster development of foliar canopy in elevated than ambient CO2. Biogeochemical feedback of nitrogen on global carbon influx is involved with two general issues: CO2 effects on ecosystem nitrogen availability and interactive effects of nitrogen and CO2 on photosynthesis. Although nitrogen itself strongly influences photosynthesis, regulation of CO2 effects on photosynthesis by nitrogen is still inconclusive. Ecosystem nitrogen availability is determined by a balance of several nitrogen fluxes, including plant uptake. mineralization, deposition, fixation, denitrification, volatilization and leaching. Elevated CO2 stimulates more plant biomass growth, demanding more nitrogen uptake. Mineralization increased in two studies, decreased in one and was unchanged in one. CO2 stimulation of nitrogen fixation increases nitrogen availability in ecosystems, potentially to match increased photosynthetic potential in the long term. Effects of volatilization, denitrification and leaching are yet to be assessed. Overall, intact ecosystem studies of canopy structure and nitrogen dynamics in elevated CO2 are particularly needed for our quantifying long-term stimulation of global photosynthetic carbon influx.

KEYWORDS: ATMOSPHERIC CARBON, CLIMATE CHANGE, DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, NITROGEN STRESS, PHOTOSYNTHESIS, PLANTS, SEEDLINGS

1404

Luo, Y.Q., and P.S. Nobel. 1993. Growth-characteristics of newly initiated cladodes of opuntia- ficus-indica as affected by shading, drought and elevated co2. *Physiologia Plantarum 87(4):467-474.*

Biomass accumulation and area expansion of newly initiated cladodes of Opuntia ficus-indica were studied to help understand the high productivity of this Crassulacena acid metabolism species. In a glasshouse, both dry weight and area increased more and more rapidly for about 30 days and then increased linearly with time up to 63 days. The relative growth rate averaged 0.12 day-1, comparable to values for productive C3 and C, plants. New cladodes initiated on basal cladodes with 2-fold higher initial dry weight grew twice as fast. Drought reduced biomass accumulation and area expansion of new cladodes by 62 and 52%, respectively. A 70% reduction in irradiation decreased biomass accumulation of new cladodes by 17% and their thickness by 11%. In a growth chamber containing 720 mumol CO2 (mol air)-1, biomass of newly initiated cladodes was 7% higher, area was 8% less, specific mass was 16% higher and less carbohydrate was translocated from basal cladodes than for 360 mumol CO2 mol-1. The large capacity for storage of carbohydrate and water in basal cladodes of O. ficus-indica apparently buffered environmental stresses, thereby reducing their effects on growth of daughter cladodes.

KEYWORDS: ACID METABOLISM PLANT, WATER RELATIONS

1405

Luo, Y.Q., J. Reynolds, Y.P. Wang, and D. Wolfe. 1999. A search for predictive understanding of plant responses to elevated [CO2]. *Global Change Biology 5(2):143-156.*

This paper reviews two decades of effort by the scientific community in a search for predictive understanding of plant responses to elevated [CO2]. To evaluate the progress of research in leaf photosynthesis, plant respiration, root nutrient uptake, and carbon partitioning, we divided scientific activities into four phases: (I) initial assessments derived from our existing knowledge base to provide frameworks for experimental studies; (II) experimental tests of the initial assessments; (III) in cases where assessments were invalidated, synthesis of experimental results to stimulate alternative hypotheses and further experimentation; and (IV) formation of new knowledge. This paper suggests that photosynthetic research may have gone through all four phases, considering that (a) variable responses of photosynthesis to [CO2] are generally explainable, (b) extrapolation of leaf-level studies to the global scale has been examined, and (c) molecular studies are under way. Investigation of plant respiratory responses to [CO2] has reached the third phase: experimental results have been accumulated, and mechanistic approaches are being developed to examine alternative hypotheses in search for new concepts and/or new quantitative frameworks to understand respiratory responses to elevated [CO2]. The study of nutrient uptake kinetics is still in the second phase: experimental evidence has contradicted some of the initial assessments, and more experimental studies need to be designed before generalizations can be made. It is quite unfortunate that we have not made much progress in understanding mechanisms of carbon partitioning during the past two decades. This is due in part to the fact that some of the holistic theories, such as functional balance and optimality, have not evolved into testable hypotheses to guide experimental studies. This paper urges modelers to play an increasing role in plant-CO2 research by disassembling these existing theories into hypotheses and urges experimentalists to design experiments to examine these holistic concepts.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, GROWTH-RESPONSE, LEAF RESPIRATION, LONG-TERM EXPOSURE, NET PRIMARY PRODUCTION, NITROGEN CONCENTRATION, PHOTOSYNTHETIC ACCLIMATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOURCE-SINK RELATIONS,

1406

Luo, Y.Q., D.A. Sims, and K.L. Griffin. 1998. Nonlinearity of photosynthetic responses to growth in rising atmospheric CO2: an experimental and modelling study. *Global Change Biology 4(2):173-183.*

Nonlinear responses of photosynthesis to the CO2 concentration at which plants were grown (C-g) have been often reported in the literature. This study was designed to develop mechanistic understanding of the nonlinear responses with both experimental and modelling approaches. Soybean (Glycine max) was grown in five levels of C-g (280, 350, 525, 700, 1000 ppm) with either a high or low rate of nitrogen fertilization. When the rate of nitrogen fertilization was high, the photosynthetic rate measured at C-g was highest in plants from the 700 ppm CO2 treatment. When the rate of nitrogen fertilization was low, little variation was observed in the photosynthetic rates of plants from the different treatments measured at their respective C-g. Measurements of CO2-induced changes in mass- based leaf nitrogen concentration (n(m) an index of changes in biochemical processes) and leaf mass per unit area (h, an index of morphological properties) were used in a model and indicate that the nonlinearity of photosynthetic responses to C-g is largely determined by relative changes in photosynthetic sensitivity, biochemical downregulation, and morphological upregulation. In order to further understand the nonlinear responses, we compiled data from the literature on CO2-induced changes in n(m) and h. These compiled data indicate that h generally increases and n(m) usually decreases with increasing C-g, but that the trajectories and magnitudes of the changes in h and n(m) vary with species and growth environments. Integration of these variables (n(m) and h) into a biochemically based model of photosynthesis enabled us to predict diverse responses of photosynthesis to C-g. Thus a general mechanism is suggested for the highly variable, nonlinear responses of photosynthesis to C-g reported in the literature.

KEYWORDS: ACCLIMATION, C-3 PLANTS, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, FIELD, LEAF PHOTOSYNTHESIS, LEAVES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TEMPERATURE

1407

Luo, Y.Q., D.A. Sims, R.B. Thomas, D.T. Tissue, and J.T. Ball. 1996. Sensitivity of leaf photosynthesis to CO2 concentration is an invariant function for C-3 plants: A test with experimental data and global applications. *Global Biogeochemical Cycles 10(2):209-222.*

Rising atmospheric CO2 concentration (C-a) may alter two components (sensitivity and acclimation) of global photosynthetic carbon influx into terrestrial ecosystems (P-G). Most existing global models focus on long-term acclimation We have developed a leaf-level function (L) to quantify short-term increment of P-G associated with sensitivity. The L function is the normalized response of leaf photosynthesis to a small change in C-a and has been suggested to be an invariant function for C-3 plants grown in diverse environments. This paper tests the hypothesis that L is an invariant function. We calculated values of L from 9 sets of experimental data which incorporated photosynthetic responses of 12 plant species to measurement conditions of light and temperature and to growth in different light, temperature, nitrogen, phosphorus, water stress, and CO2 concentration. Absolute rates of leaf photosynthesis differed by more than tenfold due to species differences and environmental variation. However, L values derived from these data sets converged into a narrow range defined by two equations of the L function, confirming that L was insensitive to differences in photosynthetic capacity among species and between plants acclimated to different growth environments. Using the L function, we predict that a yearly increase of 1.5 parts per million (ppm) in C-a will induce an increase in P-G by 0.18 to 0.34 Gt (1 Gt = 10(15) g) C yr(-1) in 1993, provided that (1) P-G = 120 Gt C yr(-1), (2) 85% of P- g is generated by C-3 plant assimilation, and (3) the 1.5-ppm increase in C-a will not induce significant photosynthetic acclimation.

KEYWORDS: ASSIMILATION, CLIMATE CHANGE, CONDUCTANCE, ELEVATED CO2, LEAVES, LIMITATIONS, PARTIAL-PRESSURE, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

1408

Lurie, S. 1993. Modified atmosphere storage of peaches and nectarines to reduce storage disorders. *Journal of Food Quality 16(1):57-65.*

Low density polyethylene or polyolefin films were used to seal pack various varieties of peaches and nectarines. Low density polyethylene film of 40 micron thickness was beneficial in extending storage life of these fruits and decreasing internal flesh breakdown and reddening, while polyolefin film was ineffective. Six fruits per pack generated a higher CO2 and lower O2 modified atmosphere than two or four fruits per pack and gave better quality fruit after storage. The improvement of fruit quality was correlated with elevated CO2 levels rather than with decreased O2 levels.

1409

Luscher, A., G.R. Hendrey, and J. Nosberger. 1998. Long-term responsiveness to free air CO2 enrichment of functional types, species and genotypes of plants from fertile permanent grassland. *Oecologia 113(1):37-45.*

To test inter- and intraspecific variability in the responsiveness to elevated CO2, 9-14 different genotypes of each of 12 perennial species from fertile permanent grassland were grown in Lolium perenne swards under ambient (35 Pa) and elevated (60 Pa) atmospheric partial pressure of CO2 (pCO(2)) for 3 years in a free air carbon dioxide enrichment (FACE) experiment. The plant species were grouped according to their functional types: grasses (L. perenne, L. multiflorum, Arrhenatherum elatius, Dactylis glomerata, Festuca pratensis, Holcus lanatus, Trisetum flavescens), non-legume dicots (Rumex obtusifolius, R. acetosa, Ranunculus friesianus), and legumes (Trifolium repens, T. pratense). Yield (above a cutting height of 4.5 cm) was measured three times per year. The results were as follow. (1) There were highly significant differences in the responsiveness to elevated pCO(2) between the three functional types; legumes showed the strongest and grasses the weakest yield increase at elevated pCO(2). (2) There were differences in the temporal development of responsiveness to elevated pCO(2) among the functional types. The responsiveness of the legumes declined from the first to the second year, while the responsiveness of the non-legume dicots increased over the 3 years. During the growing season, the grasses and the non- legume dicots showed the strongest response to elevated pCO(2) during reproductive growth in the spring. (3) There were no significant genotypic differences in responsiveness to elevated pCO(2). Our results suggest that, due to interspecific differences in the responsiveness to elevated pCO(2), the species proportion within fertile temperate grassland may change if the increase in pCO(2) continues. Due to the temporal differences in the responsiveness to elevated pCO(2) among species, complex effects of elevated pCO(2) on competitive interactions in mixed swards must be expected. The existence of genotypic variability in the responsiveness to elevated pCO(2), on which selection could act, was not found under our experimental conditions.

KEYWORDS: ECOSYSTEM, ELEVATED CARBON-DIOXIDE, ENVIRONMENTS, GROWTH, LOLIUM-PERENNE, N2 FIXATION, NITROGEN, RESPONSES, SWARDS, TEMPERATURE

1410

Luscher, A., and J. Nosberger. 1997. Interspecific and intraspecific variability in the response of grasses and legumes to free air CO2 enrichment. *Acta Oecologica-International Journal of Ecology 18(3):269-275.*

Nine to fourteen genotypes of seven grass and two legume species from permanent grassland were grown at two levels of atmospheric CO2 concentration in gaps of established Lolium perenne swards in a Free Air Carbon dioxide Enrichment (FACE) experiment. Cumulative biomass of individual plants was determined for two growing seasons. In the first year, elevated CO2 increased biomass production in all species. The CO2- induced increase in the biomass of Trifolium repens and I: pratense (159%) was much greater than the increase in the grass species (27%). In the second year the response to elevated CO2 was weaker in gasses (2%, ns) and legumes (73%). However, interspecific differences in the response to CO2 remained significant. Interspecific differences in the response to elevated CO2 occurred between the two functional groups of grasses and legumes, while within these groups no significant interspecific differences were found. In contrast to the interspecific variability in the response to CO2, no significant intraspecific variability in the response to CO2 was detected. Our results suggest that significant interspecific differences in the response to CO2, occur. Intraspecific differences in the response to elevated CO2 were, however, not detected. Thus, it seems unlikely that evolutionary adaptation of the species' response to elevated CO2 will level out the inter specific differences in the response to CO2.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH-RESPONSE, N2 FIXATION, NITROGEN, PHOSPHORUS, PLANTS

1411

Lussenhop, J., A. Treonis, P.S. Curtis, J.A. Teeri, and C.S. Vogel. 1998. Response of soil biota to elevated atmospheric CO2 in poplar model systems. *Oecologia 113(2):247-251.*

We tested the hypotheses that increased belowground allocation of carbon by hybrid poplar saplings grown under elevated atmospheric CO2 would increase mass or turnover of soil biota in bulk but not in rhizosphere soil. Hybrid poplar saplings (Populus x euramericana cv. Eugenei) were grown for 5 months in open-bottom root boxes at the University of Michigan Biological Station in northern, lower Michigan. The experimental design was a randomized-block design with factorial combinations of high or low soil N and ambient (34 Pa) or elevated (69 Pa) CO2 in five blocks. Rhizosphere microbial biomass carbon was 1.7 times greater in high-than in low-N soil, and did not respond to elevated CO2. The density of protozoa did not respond to soil N but increased marginally ($P < 0.06$) under elevated CO2. Only in high-N soil did arbuscular mycorrhizal fungi and microarthropods respond to CO2. In high-N soil, arbuscular mycorrhizal root mass was twice as great, and extramatrical hyphae were 11% longer in elevated than in ambient CO2 treatments. Microarthropod density and activity were determined in situ using minirhizotrons. Microarthropod density did not change in response to elevated CO2, but in high-N soil, microarthropods were more strongly associated with fine roots under elevated than ambient treatments. Overall, in contrast to the hypotheses, the strongest response to elevated atmospheric CO2 was in the rhizosphere where (1) unchanged microbial biomass and greater numbers of protozoa ($P < 0.06$) suggested faster bacterial turnover, (2) arbuscular mycorrhizal root length increased, and (3) the number of microarthropods observed on fine roots rose.

KEYWORDS: ARBUSCULAR MYCORRHIZAL INFECTION, CARBON DIOXIDE, ENRICHMENT, GROWTH, MATTER CONTENTS, MICROBIAL BIOMASS, NITROGEN, POPULATIONS, RHIZOSPHERE, ROOTS

1412

Lutze, J.L., and R.M. Gifford. 1995. Carbon storage and productivity of a carbon dioxide enriched nitrogen limited grass sward after one year's growth. *Journal of Biogeography 22(2-3):227-233.*

Determining the response of nitrogen restricted ecosystems to carbon dioxide enrichment is important in evaluating the role of the terrestrial biosphere in the unidentified sink in global carbon cycle models. Swards of the C3 grass Danthonia richardsonii (Cashmere) were established in large pots filled with a soil of low C and N content. The swards were continuously supplied with N at rates of 2, 6 and 18 g m(-2) yr(-1), and exposed to atmospheric CO2 concentrations of either 357 or 712 mu L L(-1). After 1 year's growth the high CO2 treatments gained 19, 53 and 43% more C than at low CO2 concentrations for the low, medium and high N treatments, respectively. This extra C gain was found in all plant and soil pools at the medium N level. At the low N level no extra C was found in the roots. At the high N level no extra carbon was found in the soil. Leaf area index was not affected by growth at high CO2. The extra C was gained with the same total N investment in green leaf in the two lowest N treatments, and with 30% less N in green leaf at the highest N level. Growth at the high CO2 concentration resulted in all C pools having a higher C:N ratio. Total water use was decreased and water use efficiency increased by growth at the high CO2 concentration. It was noted that if these results were transferable to the held, and if the higher C:N ratios do not reduce longer term productivity by reducing N-mineralization rates, grasslands could form a substantial part of the unidentified C sink. The potential feedback of decreased N availability in the longer term is being investigated in the final 3 years of the experiment.

KEYWORDS: DECOMPOSITION, ELEVATED ATMOSPHERIC CO2, FEEDBACK, LEAF LITTER, PLANTS, ROOT, WEIGHT

1413

Lutze, J.L., and R.M. Gifford. 1998. Acquisition and allocation of carbon and nitrogen by Danthonia richardsonii in response to restricted nitrogen supply and CO2 enrichment. *Plant, Cell and Environment 21(11):1133-1141.*

Dry weight (DW) and nitrogen (N) accumulation and allocation were measured in isolated plants of Danthonia richardsonii (Wallaby Grass) for 37 d following seed imbibition, Plants were grown at approximate to 365 or 735 mu L L-1 CO2 with N supply of 0.05, 0.2 or 0.5 mg N plant(-1) d(-1). Elevated CO2 increased DW accumulation by 28% (low-N) to 103% (high-N), following an initial stimulation of relative growth rate. Net assimilation rate and leaf nitrogen productivity mere increased by elevated CO2, while N concentration was reduced. N uptake per unit root surface area was unaffected by CO2 enrichment, The ratio of leaf area to root surface area was decreased by CO2 enrichment. Allometric analysis revealed a decrease in the shoot-N to root-N ratio at elevated CO2, while the shoot-DW to root-DW ratio was unchanged. Allometric analysis showed leaf area was reduced, while root surface area was unchanged by elevated CO2, indicating a down-regulation of total plant capacity for carbon gain rather than a stimulation of mineral nutrient acquisition capacity Overall, growth in elevated CO2 resulted in changes in plant morphology and nitrogen use, other than those associated simply with changing plant size and non- structural carbohydrate content.

KEYWORDS: AVAILABILITY, DIOXIDE, ELEVATED CO2, GRASS, GROWTH-RESPONSES, NUTRIENT-UPTAKE, PHOTOSYNTHETIC ACCLIMATION, PINE, PLANTS, ROOT-GROWTH

1414

Lutze, J.L., and R.M. Gifford. 1998. Carbon accumulation, distribution and water use of Danthonia richardsonii swards in response to CO2 and nitrogen supply over four years of growth. *Global Change*

Biology 4(8):851-861.

Microcosms of Danthonia richardsonii (Cashmore) accumulated more carbon when grown under CO2 enrichment (719 mu L L-1 cf. 359 mu L L-1) over a four-year period, even when nitrogen availability severely restricted productivity (enhancement ratios for total microcosm C accumulation of 1.21, 1.14 and 1.29 for mineral N supplies of 2.2, 6.7 and 19.8 g N m-2 y-1, respectively). The effect of CO2 enrichment on total system carbon content did not diminish with time. Increased carbon accumulation occurred despite the development over time of a lower leaf area index and less carbon in the green leaf fraction at high CO2. The extra carbon accumulated at high CO2 in the soil, senesced leaf and leaf litter fractions at all N levels, and in root at high-N, while at low-and mid-N less carbon accumulated in the root fraction at high CO2. The rate of leaf turnover was increased under CO2 enrichment, as indicated by increases in the carbon mass ratio of senesced to green leaf lamina. Microcosm evapotranspiration rates were lower at high CO2 when water was in abundant supply, resulting in higher average soil water contents. The higher soil water contents at high CO2 have important implications for microcosm function, and may have contributed significantly to the increased carbon accumulation at high CO2. These results indicate that CO2 enrichment can increase carbon accumulation by a simple soil-plant system, and that any increase in whole system carbon accumulation may not be evident from snapshot measurements of live plant carbon.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CONIFEROUS FORESTS, DIOXIDE, ELEVATED CO2, ENRICHMENT, PLANT, ROOTS, SOIL CARBON, TALLGRASS PRAIRIE

1415

Lutze, J.L., J.S. Roden, C.J. Holly, J. Wolfe, J.J.G. Egerton, and M.C. Ball. 1998. Elevated atmospheric [CO2] promotes frost damage in evergreen tree seedlings. *Plant, Cell and Environment 21(6):631-635.*

Growth under elevated [CO2] promoted spring frost damage in field grown seedlings of snow gum (Eucalyptus pauciflora Sieb, ex Spreng,), one of the most frost tolerant of eucalypts, Freezing began in the leaf midvein, consistent with it being a major site of frost damage under field conditions. The average ice nucleation temperature was higher in leaves grown under elevated [CO2] (- 5.7 degrees C versus - 4.3 degrees C), consistent with the greater incidence of frost damage in these leaves (34% versus 68% of leaves damaged). These results have major implications for agriculture, forestry and vegetation dynamics, as an increase in frost susceptibility may reduce potential gains in productivity from CO2 fertilization and may affect predictions of vegetation change based on increasing temperature.

KEYWORDS: TEMPERATURE

1416

Luxmoore, R.J., P.J. Hanson, J.J. Beauchamp, and J.D. Joslin. 1998. Passive nighttime warming facility for forest ecosystem research. *Tree Physiology 18(8-9):615-623.*

A nighttime warming experiment is proposed. Over the last four decades a significant rise in nighttime mini mum temperature has been determined from analysis of meteorological records from a global distribution of locations. The experiment involves nighttime deployment of infrared (IR) reflecting curtains around four sides of a forest canopy and across the top of the forest to mimic the top-down warming effect of cloud cover. The curtains are deployed with cable and pulley systems mounted on a tower and scaffolding structure built around the selected forest site. The trunk space is not enclosed except as an optional manipulation. The curtains reflect long-wave radiation emitted from the forest and ground back into the forest warming the trees, litter, and soil. Excellent infrared reflection can be obtained with commercially available fabrics that have aluminum foil bonded to one side. A canopy warming of 3 to 5 degrees C is expected on cloudless nights, and on cloudy nights, a warming of 1 to 3 degrees C is anticipated relative to a control plot. The curtains are withdrawn by computer control during the day and also at night during periods with precipitation or excessive wind. Examples of hypothesized ecosystem responses to nighttime warming include: (1) increase in tree maintenance respiration (decreasing carbon reserves and ultimately tree growth), (2) increase in the length of the growing season (increasing growth), (3) increase in soil respiration, (4) increase in litter decomposition, (5) increase in mineralization of N and other nutrients from soil organic matter, (6) increase in nutrient uptake (increasing growth), and (7) increase in N immobilization in litter. Hypothesis 1 has the opposite consequence for tree growth to Hypotheses 2 and 6, and thus opposite consequences for the feedback regulation that vegetation has on net greenhouse gas releases to the atmosphere. If Hypothesis 1 is dominant, warming could lead to more warming from the additional CO2 emissions. Site- specific meteorological, ecophysiological. and phenological measurements are obtained in the warming treatment and in a carefully selected control plot to investigate site-specific hypotheses, Measurements made on both plots for a baseline period and during the period of curtain deployment provide data to test the hypotheses statistically by the "before-after-control-impact" method applicable to unreplicated experiments. The enclosure has a modular design that can be adapted and combined with other forest-scale manipulation experiments such as free air CO2 enrichment and throughfall displacement.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, CO2-ENRICHMENT, GROWTH, IMPACT ASSESSMENT, RESPIRATION, SOIL-NITROGEN MINERALIZATION, SPRUCE, TEMPERATURE-RANGE, UPLAND OAK FOREST

1417

Luxmoore, R.J., S.D. Wullschleger, and P.J. Hanson. 1993. Forest responses to co2 enrichment and climate warming. *Water, Air, and Soil Pollution 70(1-4):309-323.*

Two of the major uncertainties in forecasting future terrestrial sources and SinkS Of CO2 are the CO2-enhanced growth response of forests and soil warming effects on net CO2 efflux from forests. Carbon dioxide enrichment of tree seedlings over time periods less than 1 yr has generally resulted in enhanced rates of photosynthesis, decreased respiration, and increased growth, with minor increases in leaf area and small changes in C allocation. Exposure of woody species to elevated CO2 over several years has shown that high rates of photosynthesis may be sustained, but net C accumulation may not necessarily increase if CO2 release from soil respiration increases. The impact of the 25% rise in atmospheric CO2 with industrialization has been examined in tree ring chronologies from a range of species and locations. In contrast to the seedling tree results, there is no convincing evidence for CO2-enhanced stem growth of mature trees during the last several decades. However, if mature trees show a preferential root growth response to CO2 enrichment, the gain in root mass for an oak-hickory forest in eastern Tennessee is estimated to be only 9% over the last 40 years. Root data bases are inadequate for detecting such an effect. A very small shift in ecosystem nutrients from soil to vegetation could support CO2-enhanced growth. Climate warming and the accompanying increase in mean soil temperature could have a greater effect than CO2 enrichment on terrestrial sources and sinks Of CO2. Soil respiration and N mineralization have been shown to increase with soil temperature. If plant growth increases with increased N availability, and more C is fixed in growth than is released by soil respiration, then a negative feedback on climate warming will occur. If warming results in a net increase in CO2 efflux from forests, then a positive feedback will follow. A 2 to 4-degrees-C increase in soil temperature could increase CO2 efflux from soil by 15 to 32% in eastern deciduous forests. Quantifying C budget

responses of forests to future global change scenarios will be speculative until mature tree responses to CO2 enrichment and the effects of temperature on terrestrial sources and sinks of CO2 can be determined.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, GAS-EXCHANGE, INTERIOR ALASKA, RESPIRATION, ROOT-GROWTH, SEEDLINGS, SOIL-NITROGEN MINERALIZATION, TEMPERATURE, TREES

1418

MacDonald, N.W., D.L. Randlett, and D.R. Zak. 1999. Soil warming and carbon loss from a lake states spodosol. *Soil Science Society of America Journal 63(1):211-218.*

Elevated soil temperatures may increase C loss from soils by accelerating microbial respiration and dissolved organic C leaching. We evaluated the effect of elevated soil temperatures on C losses from a forest Spodosol by incubating soil cores from surface (Oa + A + E) and subsurface (Bhs) horizons at two seasonal temperature regimes. One regime simulated the normal course of soil temperatures in northern lower Michigan, and the other simulated soil temperatures representing an amount of warming that might occur under some global warming theory calculations. We measured the amounts of CO2-C respired and dissolved organic C leached from the soil cores during a 33-wk period. Microbial respiration rates, after adjustment for variation in initial rates, were significantly increased by soil warming and were greater in surface than in subsurface horizons. Warming significantly increased cumulative C respired, with greater losses from surface soils (greater than or equal to 50 mg C g(-1) C) as compared with subsurface soils (less than or equal to 25 mg C g(-1) C). Mean quantities of dissolved organic C leached, ranging from 2.3 to 3.2 mg C g(-1) C, did not differ significantly by soil horizon or temperature regime. Increased microbial respiration in surface soil horizons was the process most responsive to soil warming in the Spodosol samples we examined. Whether this is a short-term effect that would disappear once pools of labile C are exhausted, or represents a long-term response to soil warming, remains uncertain.

KEYWORDS: AIR- POLLUTION GRADIENT, CLIMATE CHANGE, DECIDUOUS FOREST, DISSOLVED ORGANIC-CARBON, MICROBIAL RESPIRATION, NET NITROGEN, NITROGEN MINERALIZATION, NORTHERN HARDWOOD FORESTS, TEMPERATURE, TRACE GAS FLUXES

1419

Mackay, R.M., and M.A.K. Khalil. 1995. Doubled co2 experiments with the global-change-research-center 2-dimensional statistical dynamical climate model. *Journal of Geophysical Research-Atmospheres 100(D10):21127-21135.*

The zonally averaged response of the Global Change Research Center two-dimensional (2-D) statistical dynamical climate model (GCRC 2-D SDCM) to a doubling of atmospheric carbon dioxide (350 parts per million by volume (ppmv) to 700 ppmv) is reported. The model solves the two-dimensional primitive equations in finite difference form (mass continuity, Newton's second law, and the first law of thermodynamics) for the prognostic variables: zonal mean density, zonal mean zonal velocity, zonal mean meridional velocity, and zonal mean temperature on a grid that has 18 nodes in latitude and 9 vertical nodes (plus the surface). The equation of state, p = rho RT, and an assumed hydrostatic atmosphere, Delta p = -rho g Delta z, are used to diagnostically calculate the zonal mean pressure and vertical velocity for each grid node, and the moisture balance equation is used to estimate the precipitation rate. The model includes seasonal variations in solar intensity, including the effects of eccentricity, and has observed land and ocean fractions set for each zone. Seasonally varying values of cloud amounts, relative humidity profiles, ozone, and sea ice are all prescribed in the model. Equator to pole ocean heat transport is simulated in the model by turbulent diffusion. The change in global mean annual surface air temperature due to a doubling of atmospheric CO2 in the 2-D model is 1.61 K, which is close to that simulated by the one- dimensional (1-D) radiative convective model (RCM) which is at the heart of the 2-D model radiation code (1.67 K for the moist adiabatic lapse rate assumption in 1-D RCM). We find that the change in temperature structure of the model atmosphere has many of the characteristics common to General Circulation Models, including amplified warming at the poles and the upper tropical troposphere, and stratospheric cooling. Because of the potential importance of atmospheric circulation feedbacks on climate change, we have also investigated the response of the zonal wind field to a doubling of CO2 and have found distinct patterns of change that are related to the change in temperature structure. In addition, we find that both the global mean kinetic energy and simulated Hadley circulation increase when CO2 is doubled. The increase in mean kinetic energy is a result of the increase in upper level meridional temperature gradients simulated by the model. It is stressed that changes in atmospheric dynamics associated with increased carbon dioxide may also be very important to the final steady state distribution of such greenhouse gases as ozone and water vapor. Hence further research in this regard is warranted.

KEYWORDS: GENERAL-CIRCULATION, IMPACT, PARAMETERIZATION

1420

Mackowiak, C.L., and R.M. Wheeler. 1996. Growth and stomatal behavior of hydroponically cultured potato (Solanum tuberosum L) at elevated and super-elevated CO2. *Journal of Plant Physiology 149(1-2):205-210.*

Potato cultivars Denali and Norland were grown in a controlled environment under low irradiance and CO2 partial pressures of 50, 100, 500, and 1000 Pa. The highest CO2 partial pressures, 500 and 1000 Pa, reduced tuber yield when compared to 100 Pa CO2. Upper canopy stomatal conductance was greatest at the higher CO2 partial pressures (500 and 1000 Pa) for both cultivars, and conductance of Denali was consistently higher than Norland. Stomatal conductance tended to decline sooner with plant age at 50 and 100 Pa CO2 than at 500 and 1000 Pa. Water uptake was also greatest at the higher CO2 partial pressures, which resulted in lowest water-use efficiencies at 500 and 1000 Pa. These observations suggest that stomatal function under very high CO2 partial pressures (500-1000 Pa) does not follow known patterns observed at moderate partial pressures (50-100 Pa). Although there is little concern about CO2 partial pressures reaching extreme levels in the natural environment, this information should be useful for controlled environments or space life support systems (e.g. space vehicles or habitats), where CO2 partial pressures of 500-1000 Pa are common.

KEYWORDS: ALLOCATION, EXCHANGE, INDIVIDUAL TUBERS, LIFE SUPPORT SYSTEMS, PHOTOPERIODS, PHOTOSYNTHATE, SPACE, TEMPERATURE

1421

Madsen, T.V. 1993. Growth and photosynthetic acclimation by ranunculus-aquatilis L in response to inorganic carbon availability. *New Phytologist 125(4):707-715.*

Relative growth rates of Ranunculus aquatilis L. were measured in the laboratory at dissolved inorganic carbon (DIC) concentrations between 0.2 and 5.2 mM at air-equilibrium CO2 (16 mu M) and also at 0.55 mM DIC with elevated CO2 (350 mu M). For plants grown at air-equilibrium CO2, growth was limited by inorganic carbon below 1.6 mM DIC and

the apparent half saturation constant was 0.5 mM. The growth rate at elevated CO2 was 50% higher than the carbon saturated rates obtained at high DIC concentrations and air-equibrium CO2, where HCO3- is dominant. This difference is suggested to be caused by differences in uptake mechanisms for CO2 and HCO3-. Uptake of CO2 is a diffusive process, whereas HCO3- use is an active process which involves uptake/transport systems in the cell membranes. The plants acclimated to the DIC regime for growth by reductions in carboxylation efficiency and bicarbonate affinity, but enhanced photosynthetic capacity at elevated DIC. Within the range of concentrations used, the acclimation to CO2 and HCO3- was quantitatively similar, except for the HCO3- uptake capacity which increased at high DIC and air-equilibrium CO2 but declined at elevated CO2. Dark respiration was unaffected by inorganic carbon per se, but increased with growth rate. Maintenance respiration was constant among treatments. It is concluded that inorganic carbon, apart from being the primary substrate for photosynthesis, has secondary growth regulatory effects which affect the photosynthetic apparatus of the plants.

KEYWORDS: AFFINITY, BICARBONATE, CO2, DIFFERENTIAL ABILITY, ENVIRONMENTAL-FACTORS, FRESH-WATER MACROPHYTES, LIGHT, PH, PLANTS, STREAMS

1422

Madsen, T.V., S.C. Maberly, and G. Bowes. 1996. Photosynthetic acclimation of submersed angiosperms to CO2 and HCO3-. *Aquatic Botany 53(1-2):15-30.*

Photosynthetic acclimation after growth under a factorial combination of three concentrations of CO2 (1, 16 and 910 mu M) and two concentrations of HCO3- (0.2 and 1.5 mM) was measured for Callitriche cophocarpa Sendt., Elodea canadensis L.C. Rich. and Ranunculus peltatus Schrank. Callitriche cophocarpa was restricted to CO2 as a carbon source while the other two species also used HCO3-. None of the species showed C-4-like photosynthesis as evidenced by low activities of phosphoenolpyruvate carboxylase. Carbon exchange characteristics and biochemical capacities were down-regulated in response to increasing inorganic carbon during growth. In all three species, P-max initial slope of net photosynthesis versus [CO2], rubisco activity, protein content and chlorophyll content decreased, and CO2 compensation concentration increased with increased inorganic carbon, In addition, for the two HCO3- users, the rate of HCO3--dependent photosynthesis at zero [CO2] and 1.5 mM HCO3- decreased with inorganic carbon. The response to increased [GO,] was greater than that to increased [HCO3-]. Morphological acclimation to inorganic carbon was evident in all species. The root/shoot ratio increased with increasing [CO2] but was unaffected by [HCO3-]. The specific leaf area declined with carbon availability in Callitriche and Ranunculus, whereas no change was observed in Elodea. There was a significant positive correlation between various carbon exchange characteristics and between these and the chlorophyll content and rubisco activity, suggesting that carbon exchange, light capture and carbon fixation are regulated in parallel in response to carbon availability. The general down-regulation response shown by these aquatic plants to elevated inorganic carbon resembles the response of some terrestrial C-3 species to elevated CO2.

KEYWORDS: AQUATIC MACROPHYTES, BICARBONATE, CARBON DIOXIDE, FRESH-WATER MACROPHYTES, GROWTH, LIGHT, PLANTS

1423

Madsen, T.V., H.B.A. Prins, and G. Bowe. 1997. Will elevated CO2 affect aquatic plants? *Plant Physiology 114(3):21001.*

1424

Madsen, T.V., K. Sandjensen, and S. Beer. 1993. Comparison of photosynthetic performance and carboxylation capacity in a range of aquatic macrophytes of different growth forms. *Aquatic Botany 44(4):373-384.*

Photosynthesis, carbon extraction capacity and ribulose-1,5- biphosphate carboxylase/oxygenase (RUBISCO) activity were determined for 35 species of submerged aquatic macrophytes differing with respect to taxonomy, growth form and habitat. Photosynthetic rates per unit of chlorophyll and dry weight at ambient CO2 concentrations (about 15 muM) as well as carbon extraction capacity increased among plant groups in the order: isoetids, amphibious species, elodeids with no apparent HCO3- use, elodeids with HCO3- use, marine angiosperms and marine macroalgae. Photosynthetic rates at elevated CO2 concentrations (300-350 muM) showed the same pattern but smaller differences among the groups. Only for some of the marine macroalgae did photosynthesis at ambient CO2 approach photosynthesis at elevated CO2. Species with high carbon extraction capacity, presumably based on active HCO3- use, usually had low RUBISCO activity, low chlorophyll content and low surface to volume ratio. The opposite pattern was found among species with low carbon extraction capacity. The low chlorophyll content and high chlorophyll specific photosynthesis of species with high carbon transport capability (i.e. particularly the marine algae), suggest that running costs associated with inorganic carbon assimilation are reduced when a CO2 concentrating system operates.

KEYWORDS: CO2, FRESH-WATER MACROPHYTES, INORGANIC CARBON, MARINE, PLANTS, ROOTS

1425

Maevskaya, S.N., T.F. Andreeva, S.Y. Voevudskaya, and N.N. Cherkanova. 1990. Effect of elevated CO2 concentration on photosynthesis and nitrogen-metabolism of mustard plants. *Soviet Plant Physiology 37(5):687-692.*

We investigated the effect of prolonged (8- to 10-day) influence of elevated atmospheric CO2 content (0.14%) on the photosynthetic rate and nitrogen metabolism in mustard plants (Brassica juncea L.). The photosynthetic rate and intensity of nitrogen metabolism in leaves of mustard plants in the vegetative phase of growth are higher under conditions of elevated atmospheric CO2 concentration than in leaves of plants that developed under conditions of normal CO2 content in the atmosphere. Intensification of nitrogen metabolism occurred mainly due to increase of NR activity. Activity of GS and GO increased to a lesser extent. Significant changes were detected in the rates of synthesis of separate amino acids. Thus, formation of alanine and aspartic acid increased by 84 and 40%, respectively, but the rates of glycine and serine synthesis declined. The excess of amino acids (alanine and aspartic acid) is evacuated from the metabolic pool into vacuoles, with the result that a normal metabolic pool of amino acids is preserved. A state of homeostasis is preserved, protein and chlorophyll synthesis is not disturbed, and growth and biomass accumulation intensify in plants under conditions of elevated CO2 concentration.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, GROWTH, WHEAT

1426

Magan, N., and E.S. Baxter. 1996. Effect of increased CO2 concentration and temperature on the phyllosphere mycoflora of winter wheat flag leaves during ripening. *Annals of Applied Biology 129(2):189-195.*

The impact of elevated carbon dioxide (CO2, 600/700 mu mol mol(-1)) and temperature (+ 4 degrees C) on phyllosphere fungi colonising flag leaves of mini crops of winter wheat cv. Mercia between anthesis and

harvest was determined in a computer- controlled environment facility in 1993 and 1994. In both years the total fungal populations (cm(2) leaf) were found to have increased due to exposure to either elevated CO2 and elevated CO2 + temperature treatments. This was mainly due to significant increases in populations of Cladosporium spp. (C. cladosporioides and C. herbarum) on the flag leaves during ripening. Other phyllosphere component species such as white and pink yeasts were not markedly affected by treatments. The range of fungal species found in such controlled environment chambers was narrower than that commonly found on nag leaves of field grown crops. Common and important colonisers of leaves and ripening ears such as Aureobasidium pullulans, Epicoccum nigrum and Fusarium spp. were seldom isolated.

KEYWORDS: FUNGI, GROWTH, OPEN-AIR FUMIGATION, OZONE, SULFUR-DIOXIDE, YIELD

1427

Maillard, P., E. Deleens, F. Castell, and F.A. Daudet. 1999. Source-sink relationships for carbon and nitrogen during early growth of Juglans regia L. seedlings: analysis at two elevated CO2 concentrations. *Annals of Forest Science 56(1):59-69.*

Assimilation and allocation of carbon (C) and nitrogen (N) were studied in seedlings (Jugalan regia L.) grown for 55 days under controlled conditions (22 degrees C, 12 h, 90 % relative humidity [RH]) using two CO, concentrations (550 and 800 mu L L-1 CO,). C and N decrease in seeds was unaltered by CO2. At the end of seed contribution (day 35), C and N accumulation in seedlings was favoured under 800 mu L L-1 [CO2], resulting in an increase of about +50 % for C and +35 % for N. Growth enhancement was larger in roots than in shoot, resulting in a higher root:shoot ratio (R:S = 0.62) with respect to 550 mu L L-1 CO, (R:S = 0.40) at day 55. These results were due, in order, to: 1) a shoot respiration temporarily depressed by [CO2], 2) a reduction by 46 % of the root + soil respiration, 3) a stimulation by 14 % of the C assimilation and 1) an increased uptake and assimilation of N coming from the rooting medium. An increased use of N originated from the seed was observed in leaves and lateral roots, suggesting optimisation of distribution of stored N pools by seedlings. These changes finally gave rise to an increased C:N ratio for taproot (+27 %), roots (+20 %), stem (+28 %), and leaves (+12 %), suggesting a N dilution in the tissues. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, AUTOTROPHY, DIOXIDE, ENRICHMENT, QUERCUS-ROBUR SEEDLINGS, RESPIRATION, TERM, WALNUT SEEDLINGS, WOODY-PLANTS

1428

Majeau, N., and J.R. Coleman. 1996. Effect of CO2 concentration on carbonic anhydrase and ribulose- 1,5-biphosphate carboxylase/oxygenase expression in pea. *Plant Physiology 112(2):569-574.*

The effect of external CO2 concentration on the expression of carbonic anhydrase (CA) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) was examined in pea (Pisum sativum cv Little Marvel) leaves. Enzyme activities and their transcript levels were reduced in plants grown at 1000 mu L/L CO2 compared with plants grown in ambient air. Growth at 160 mu L/L CO2 also appeared to reduce steady-state transcript levels for rbcS, the gene encoding the small subunit of Rubisco, and for ca, the gene encoding CA; however, rbcS transcripts were reduced to a greater extent at this concentration. Rubisco activity was slightly lower in plants grown at 160 mu L/L CO2, and CA activity was significantly higher than that observed in air-grown plants. Transfer of plants from 1000 mu L/L to air levels of CO2 resulted in a rapid increase in both ca and rbcS transcript abundance in fully expanded leaves, followed by an increase in enzyme activity. Plants transferred from air to high-CO2 concentrations appeared to modulate transcript abundance and enzyme activity less quickly. Foliar carbohydrate levels were also examined in plants grown continuously at high and ambient CO2, and following changes in growth conditions that rapidly altered ca and rbcS transcript abundance and enzyme activities.

KEYWORDS: ACCLIMATION, ANTISENSE RNA, ATMOSPHERIC CO2, CHLAMYDOMONAS-REINHARDTII, ELEVATED CO2, GAS-EXCHANGE, MECHANISM, PHOTOSYNTHESIS, TOMATO PLANTS, TRANSGENIC TOBACCO PLANTS

1429

Makino, A. 1994. Biochemistry of C3-photosynthesis in high co2. *Journal of Plant Research 107(1085):79-84.*

The short-term responses of C3 photosynthesis to high CO2 are described first. Regulation of photosynthesis in the short term is determined by interaction among the capacities of light harvesting, electron transport, ribulose-1, 5-bisphosphate carboxylase (Rubisco) and orthophosphate (Pi) regeneration during starch and sucrose synthesis. Photosynthesis under high CO2 conditions is limited by either electron transport or Pi regeneration capacities, and Rubisco is deactivated to maintain a balance between each step in the photosynthetic pathway. Subsequently, the long-term effects on photosynthesis are discussed. Long-term CO2 enhancement leads to carbohydrate accumulation. Accumulation of carbohydrates is not associated with a Pi-regeneration limitation on photosynthesis, and this limitation is apparently removed during long-term exposure to high CO2. Enhanced CO2 does not affect Rubisco content and electron transport capacity for a given leaf-nitrogen content. In addition, the deactivated Rubisco immediately after exposure to high CO2 does not recover during the subsequent prolonged exposure. Such evidence may indicate that plants do not necessarily have an ideal acclimation response to high CO2 at the biochemical level.

KEYWORDS: C-3 PLANTS, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELECTRON-TRANSPORT, ELEVATED CO2, GAS-EXCHANGE, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE

1430

Makino, A., M. Harada, T. Sato, H. Nakano, and T. Mae. 1997. Growth and N allocation in rice plants under CO2 enrichment. *Plant Physiology 115(1):199-203.*

The effects of CO2 enrichment on growth and N allocation of rice (Oryza sativa L.) were examined. The plants were grown hydroponically in growth chambers with a 14-h photoperiod (1000 mu mol quanta m(-2) s(-1)) and a day/night temperature of 25/20 degrees C. From the 28th to 70th d after germination, the plants were exposed to two CO2 partial pressures, namely 36 and 100 Pa. The CO2 enrichment increased the final biomass, but this was caused by a stimulation of the growth rate during the first week of the exposure to elevated CO2 partial pressures. The disappearance of the initial stimulation of the growth rate was associated with a decreased leaf area ratio. Furthermore, CO2 enrichment decreased the investment of N in the leaf blades, whereas the N allocation into the leaf sheaths and roots increased. Thus, the decrease in leaf N content by CO2 enrichment was not due to dilution of N caused by a relative increase in the plant biomass but was due to the change in N allocation at the whole-plant level. We conclude that the growth responses of rice to CO2 enrichment are mainly controlled by leaf area expansion and N allocation into leaf blades at the whole-plant level.

KEYWORDS: ELEVATED CO2, LEAF-AREA, NITROGEN-USE, PARTIAL-PRESSURE, PHOTOSYNTHESIS, RIBULOSE-1;5-

BISPHOSPHATE CARBOXYLASE-OXYGENASE, TEMPERATURE, TRANSPIRATION, WINTER-WHEAT, YIELD

1431

Makino, A., and T. Mae. 1999. Photosynthesis and plant growth at elevated levels of CO2. *Plant and Cell Physiology 40(10):999-1006.*

In this review, we discuss the effects of elevated CO2 levels on photosynthesis in relation to the whole plant growth in terrestrial higher C-3 plants. Short-term CO2 enrichment stimulates the rate of photosynthesis. Plant mass is also enhanced by CO2 enrichment. However, the effects of long-term CO2 enrichment on photosynthesis are variable. Generally, the prolonged exposure to CO2 enrichment reduces the initial stimulation of photosynthesis in many species, and frequently suppresses photosynthesis. These responses are attributed to secondary responses related to either excess carbohydrate accumulation or decreased N content rather than direct responses to CO2. Accumulation of carbohydrates in leaves may lead to the repression of photosynthetic gene expression and excess starch seems to hinder CO2 diffusion. Therefore, the species which have the sink organs for carbohydrate accumulation do not show the suppression of photosynthesis. The suppression of photosynthesis by CO2 enrichment is always associated with decreases in leaf N and Rubisco contents. These decreases are not due to dilution of N caused by a relative increase in the plant mass but are the result of a decrease in N allocation to leaves at the level of the whole plant, and the decrease in Rubisco content is not selective. Leaf senescence and plant development are also accelerated by CO2 enrichment. However, they are independent of each other in some species. Thus, various responses to CO2 observed at the level of a single leaf result from manifold responses at the level of the whole plant grown under conditions of CO2 enrichment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LONG-TERM EXPOSURE, NITROGEN ALLOCATION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RICE LEAVES, WHEAT LEAVES

1432

Makino, A., H. Nakano, T. Mae, T. Shimada, M. Matsuoka, K. Shimamoto, M.M. Tokutomi, and N. Yamamoto. 1997. Rubisco and N allocation in rice under elevated CO2. Optimization of Rubisco content by antisense rbc S. *Plant Physiology 114(3):1091.*

1433

Makino, A., T. Shimada, S. Takumi, K. Kaneko, M. Matsuoka, K. Shimamoto, H. Nakano, M. MiyaoTokutomi, T. Mae, and N. Yamamoto. 1997. Does decrease in ribulose-1,5-bisphosphate carboxylase by antisense RbcS lead to a higher N-use efficiency of photosynthesis under conditions of saturating CO2 and light in rice plants? *Plant Physiology 114(2):483-491.*

Rice (Oryza sativa L.) plants with decreased ribulose-1,5- bisphosphate carboxylase (Rubisco) were obtained by transformation with the rice rbcS antisense gene under the control of the rice rbcS promoter. The primary transformants were screened for the Rubisco to leaf N ratio, and the transformant with 65% wild-type Rubisco was selected as a plant set with optimal Rubisco content at saturating. CO2 partial pressures for photosynthesis under conditions of high irradiance and 25 degrees C. This optimal Rubisco content was estimated from the amounts and kinetic constants of Rubisco and the gas-exchange data. The R-1 selfed progeny of the selected transformant were grown hydroponically with different N concentrations. Rubisco content in the R-1 population was distributed into two groups: 56 plants had about 65% wild-type Rubisco, whereas 23 plants were very similar to the wild type. Although the plants with decreased Rubisco showed 20% lower rates of light-saturated photosynthesis in normal air (36 Pa CO2), they had 5 to 15% higher rates of photosynthesis in elevated partial pressures of CO2 (100-115 Pa CO2) than the wild-type plants for a given leaf N content. We conclude that the rice plants with 65% wild-type Rubisco show a higher N-use efficiency of photosynthesis under conditions of saturating CO2 and high irradiance.

KEYWORDS: C-3 PLANTS, ELEVATED CO2, GAS-EXCHANGE, INTACT LEAVES, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, RIBULOSE 1;5-BISPHOSPHATE, SMALL-SUBUNIT, SUCROSE SYNTHESIS ENZYMES, TRANSGENIC TOBACCO

1434

Makino, Y., K. Iwasaki, and T. Hirata. 1996. A theoretical model for oxygen consumption in fresh produce under an atmosphere with carbon dioxide. *Journal of Agricultural Engineering Research 65(3):193-203.*

A practical model for fresh produce, which includes the effect of the depression of respiration caused by CO2, is proposed on the basis of the modified Langmuir adsorption theory. The O-2 consumption rates for several kinds of fresh produce under atmospheric conditions with enhanced CO2 were measured and the data was analysed using the proposed model. The rate parameters of the model for estimating respiration of fresh produce were determined, and the model was found to be adaptable for describing the O-2 consumption in terms of the depression by CO2. Mathematical analysis of a modified atmosphere packaging (MAP) system for shredded cabbage and broccoli was carried out using the proposed rate equation and the basic mass balance. The simulated results agreed well with the experimental data. The proposed O-2 consumption model is considered to be useful for the design of MAP systems under the atmospheric condition with CO2 gas. (C) 1996 Silsoe Research Institute

KEYWORDS: CO2, FRUITS, GAS-EXCHANGE, O2, PACKAGE, PRINCIPLES, QUALITY, RESPIRATION, VEGETABLES

1435

Malanson, G.P. 1993. Comment on modeling ecological response to climatic-change. *Climatic Change 23(2):95-109.*

Researchers have developed many computer simulation models to project ecological responses to climatic change. Three general types of models are examined: transfer functions, stand models, and physiological models. Criteria for evaluation are, first, ability to represent observed and theoretical responses to climatic change i.e., geographical migration, individualistic responses, and disequilibrium or inertia, and second, ability to provide useful information on biological diversity and impacts on society. Because of their roots in ecological interactions at the species level, stand models best meet these criteria at present, but physiological models have greater potential, given unlimited computing power.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, COMPUTER-AIDED RECONSTRUCTION, EASTERN NORTH-AMERICA, ELEVATED CO2, FOREST ECOSYSTEM PROCESSES, GRASSLAND ECOSYSTEMS, GREAT-PLAINS, INCREASING CO2, QUATERNARY LANDSCAPE DYNAMICS

1436

Malhi, Y., D.D. Baldocchi, and P.G. Jarvis. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment 22(6):715-740.*

Forest biomes are major reserves for terrestrial carbon, and major components of global primary productivity. The carbon balance of forests is determined by a number of component processes of carbon acquisition and carbon loss, and a small shift in the magnitude of these processes would have a large impact on the global carbon cycle, In this paper, we discuss the climatic influences on the carbon dynamics of boreal, temperate and tropical forests by presenting a new synthesis of micrometeorological, ecophysiological and forestry data, concentrating on three case-study sites. Historical changes in the carbon balance of each biome are also reviewed, and the evidence for a carbon sink in each forest biome and its likely behaviour under future global change are discussed. We conclude that there have been significant advances in determining the carbon balance of forests, but there are still critical uncertainties remaining, particularly in the behaviour of sob carbon stocks.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, DECIDUOUS FOREST, INTERANNUAL CLIMATE VARIABILITY, LAND-USE CHANGE, LAST GLACIAL MAXIMUM, LONG-TERM MEASUREMENTS, NET PRIMARY PRODUCTION, RAIN-FOREST, TERRESTRIAL ECOSYSTEMS, WATER-VAPOR EXCHANGE

1437

Malmstrom, C.M., and C.B. Field. 1997. Virus-induced differences in the response of oat plants to elevated carbon dioxide. *Plant, Cell and Environment 20(2):178-188.*

Disease is an integral element of agricultural and natural systems, but the roles pathogens play in determining ecosystem response to elevated CO2 have rarely been examined. To investigate whether disease can alter the response of plants to CO2, we examined the effects of doubled CO2 (approximate to 700 mu mol mol(-1)) on Avena sativa infected with barley yellow dwarf virus (BYDV), a common pathogen of cereals and grasses. Oats infected with BYDV showed a significantly greater biomass response to CO2 enrichment than did healthy plants. Root mass of diseased plants increased by 37-60% with CO2 enrichment, but was largely unaffected in healthy plants. CO2 enrichment increased midday leaf-level photosynthesis and instantaneous water use efficiency by 34 and 93% in healthy plants and by 48 and 174% in infected plants. Foliar carbohydrates increased with both CO2 enrichment and BYDV infection, but the two factors affected individual peals dissimilarly. CO2 enrichment may alter the epidemiology of BYDV by increasing the persistence of infected plants.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO2, BARLEY YELLOW DWARF, CARBOHYDRATE-COMPOSITION, CO2 CONCENTRATION, GROWTH, METABOLISM, SUGAR-BEET LEAVES, TRANSGENIC TOBACCO PLANTS, WHEAT

1438

Malmstrom, C.M., M.V. Thompson, G.P. Juday, S.O. Los, J.T. Randerson, and C.B. Field. 1997. Interannual variation in global-scale net primary production: Testing model estimates. *Global Biogeochemical Cycles 11(3):367-392.*

Testing estimates of year-to-year variation in global net primary production (NPP) poses some challenges. Large-scale, multiyear records of production are not readily available for natural systems but are for agricultural systems, We use records of agricultural yields at selected sites to test NPP estimates produced by CASA, a global-scale production model driven by both meteorological data and the satellite-derived normalized difference vegetation index (NDVI). We also test estimates produced by the Miami model, which has underlain several analyses of biosphere response to interannual changes in climate. In addition, we test estimates against tree ring data for one boreal site for which data from both coniferous and deciduous species were available. The agricultural tests demonstrate that CASA can reasonably estimate interannual variation in production. The Miami model estimates variation more poorly. However, differences in NDVI-processing algorithms substantially affect CASA's estimates of interannual variation. Of the four versions tested, the FASIR NDVI most closely reproduced yield data and showed the least correlation with changes in equatorial crossing time of the National Oceanic and Atmospheric Administration satellites, One issue raised is the source of the positive trends evident in CASA's NDVI-based estimates of global NPP. The existence of these trends is consistent with potential stimulation of terrestrial production by factors such as CO2 enrichment, N fertilization, or temperature warming, but the magnitude of the global trends seen is significantly greater than suggested by constraints imposed by atmospheric fluxes.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AVHRR DATA, CALIBRATION, DATA SET, DIFFERENCE VEGETATION INDEX, GROSS PRIMARY PRODUCTIVITY, HIGH-RESOLUTION RADIOMETER, SATELLITE DATA, TEMPERATURE, VARIABILITY

1439

Manderscheid, R., J. Bender, H.J. Jager, and H.J. Weigel. 1995. Effects of season long co2 enrichment on cereals .2. Nutrient concentrations and grain quality. *Agriculture Ecosystems & Environment 54(3):175-185.*

Two cultivars each of spring wheat (Triticum aestivum L., cv. Star and cv. Turbo) and spring barley (Hordeum vulgare L., cv. Alexis and cv. Arena) were exposed season-long to ambient (384 p.p.m.) and above ambient CO2 concentrations (551, 718 p.p.m.) in open-top chambers. Plant samples were taken at the booting stage and at maturity. Concentrations (grams per gram dry weight) of macro (Ca, K, Mg, N, P, S) and micronutrients (Fe, Mn, Zn) were measured in stems, leaves, ears and grains, and the amino acid composition of the grain protein was determined. For most nutrients studied the sequence and size of the response of the four cereal plants to the CO, enrichment was cv. Arena < cv. Alexis < cv. Turbo < cv. Star. The CO2 enrichment usually produced a decrease in nutrient concentrations, which was already detectable at the booting stage and was further enhanced until plant maturity. Nutrient concentrations of straw were more affected than those of grains. The decrease in concentration was greatest for N followed by Mg, Ca and K, and the maximum decrease as compared with ambient CO2 amounted to 43%, 35%, 33% and 21% for straw, and 30%, 13%, 28% and - 6% for grains. Concentrations of micronutrients were also found to be partially decreased by about 10-30%. At 718 p.p.m. CO, grain protein concentrations were 96% (cv. Arena), 85% (cv. Alexis), 72% (cv. Turbo) and 70% (cv. Star) of the ambient CO2 value, however, the index of essential amino acids was increased. Overall, the CO2 enrichment did not decrease the nutrient harvest index of all nutrients except of sulphur. Nutrient use efficiency increased by high CO2 levels for cv. Star and cv. Turbo and decreased for cv. Arena.

KEYWORDS: ATMOSPHERIC CO2, CARBOHYDRATE, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, ELEVATED CO2, GROWTH, NITROGEN CONCENTRATIONS, PHYSIOLOGY, RESPONSES, WINTER-WHEAT

1440

Manderscheid, R., J. Bender, U. Schenk, and H.J. Weigel. 1997. Response of biomass and nitrogen yield of white clover to radiation and atmospheric CO2 concentration. *Environmental and Experimental Botany 38(2):131-143.*

The objectives of the present study were to test (i) whether the effect of season-long CO2 enrichment on plant dry matter production of white clover (Trifolium repens cv. Karina) depends on the temperature or can solely be explained by changes in radiation use efficiency, and (ii)

whether the atmospheric CO2 concentration affects the relationship between tissue %N and plant biomass. Plants were grown in pots with adequate nutrient and water supply and were exposed to ambient and above ambient CO2 concentrations (approximately + 80 ppm, + 160 ppm, + 280 ppm) in open-top chambers for two seasons. Nitrogen fertilizer was given only before the experiment started to promote N-2 fixation. Plants were clipped to a height of 5 cm, when the canopy had reached a height of about 20 cm and when the CO2 effect had not been diminished due to self-shading of the leaves. Photon exposure (400-700 nm) measured above the canopy was linearly related to the above ground biomass, the leaf area index and the nitrogen yield (r(2)>0.94). The slopes of the curves depended on the CO2 concentration. Since most of the radiation (>90%) was absorbed by the foliage, the slopes were used to calculate the CO2 effect on the radiation use efficiency of biomass production, which is shown to increase curvilinearly between 380 and 660 ppm CO2 from 2.7 g MJ(-1) to 3.9 g MJ(-1). CO2 enrichment increased above ground biomass by increasing the leaf number, the individual leaf weight and the leaf area; specific leaf weight was not affected. The relative CO2 response varied between harvests; there was a slight but not significant positive relationship with mean daytime temperature. At the beginning of the season, plant nitrogen concentration in the above ground biomass was decreased by CO2 enrichment. However, at later growth stages, when the plants depended solely on N-2 fixation, nitrogen concentration was found to be increased when the nitrogen concentration value was adjusted for the decrease due to the higher biomass of the plants exposed to elevated CO2. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, LOLIUM-PERENNE, OPEN-TOP CHAMBERS, PASTURE TURVES, PERENNIAL RYEGRASS, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, TRIFOLIUM-REPENS L, USE EFFICIENCY

1441

Manderscheid, R., and H.J. Weigel. 1995. Do increasing atmospheric co2 concentrations contribute to yield increases of german crops. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 175(2):73-82.*

The global atmospheric CO2-concentration is increasing and there has been an increase in Germany of about 30 ppm from 340 ppm to 370 ppm CO2 during the last two decades. The hectare yield of many crops has also increased during this time period. The objective of the present study was to estimate whether the past and future change in the atmospheric composition significantly contributes to the increase in hectare yield. Different crop species (beans, Phaseolus vulgaris, cv Pfalzer Juni; spring barley, Hordeum vulgare L., cvs. Alexis and Arena; spring wheat, Triticum aestivum L., cvs. Star and Turbo; maize, Zea mays L., cvs. Bonny and Boss) were grown at ambient (372 ppm) and at slightly elevated CO2-concentrations (459 ppm and 539 ppm) in open-top chambers and the effect of the different CO2-concentrations on the growth and yield of the plants was measured. The past and future CO2-effect was estimated from the slope of a linear CO2-yield curve (percentage increase in yield per ppm CO2, 100 % at 370 ppm) fitted to the data and those from previous studies on wheat and maize. The percentage increase in yield per ppm CO2 is insignificant for beans, of borderline significance for silage maize (0.06 % per ppm), and 0.35 % per ppm and 0.26 % per ppm for barley and wheat, respectively. The CO2-elevation primarily decreases the tiller dieback of the cereals. Considering the increase in CO2 of 30 ppm and in the hectare yield of 25 % (barley) and 28 % (wheat) from 1970 to 1990, the contribution of CO2 to the increase in the agricultural production is estimated to be one fourth up to one half of the increase in hectare yield of spring cereals. Given a recent yearly increase of 2 ppm the future CO2-related increase in hectare yield is estimated to be about 0.5-0.7 % per year.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, PHASEOLUS-VULGARIS, PLANTS, RESPONSES, WHEAT

1442

Manderscheid, R., and H.J. Weigel. 1997. Photosynthetic and growth responses of old and modern spring wheat cultivars to atmospheric CO2 enrichment. *Agriculture Ecosystems & Environment 64(1):65-73.*

Cultivars of spring wheat (Triticum aestivum L.) introduced between 1890 and I988 were cultivated in pots under optimal growth conditions and exposed during the whole growing season to normal (379 p.p.m.) and elevated CO2 concentrations (689 p.p.m.) in open-top chambers. CO2 effects were measured at anthesis on flag leaf composition (chlorophyll and protein) and photosynthetic parameters, and at maturity on plant growth and yield. CO2 enrichment did not affect light saturated rate of photosynthesis measured at 400 p.p.m. CO2 or protein, total chlorophyll and dry weight content per unit leaf area. However, single flag leaf area and fresh weight per leaf area were increased by CO2. This increase was possibly responsible for a significant decrease in the chlorophyll a/b ratio. Under normal atmospheric CO2 concentration, the total above-ground biomass, stem weight and height, and ear number were negatively correlated with the year of cultivar release. Despite no evidence of CO2 acclimation, i.e, changes in flag leaf composition, CO2 enrichment resulted in a greater growth stimulation of the older than the modern cultivars. This was due to a greater CO2 effect on those growth components that were altered during plant breeding of wheat in the past, i.e. stem weight and height, and ear number. The average CO2-related increase in biomass and grain yield amounted to ca 46% and 28% for the three old (1890-1943) and three modem cultivars (1965- 1988), respectively. Differences in yield response to CO2 enrichment between old and modern cultivars could be mainly explained by changes in ear number. (C) 1997 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, COMPONENTS, ELEVATED CO2, IMPROVEMENT, LEAVES, PLANTS, TEMPERATURE, VARIETIES, WINTER-WHEAT, YIELD

1443

Manninen, P., J. Pakarinen, and H. Kallio. 1997. Large-scale supercritical carbon dioxide extraction and supercritical carbon dioxide countercurrent extraction of cloudberry seed oil. *Journal of Agricultural and Food Chemistry 45(7):2533-2538.*

Dried press residue of cloudberry [Rubus chamaemorus (Rosaceae)] was extracted with carbon dioxide at pressures of 90-300 bar and at a temperature of 40 or 60 degrees C using a pilot-scale or a production-scale plant. The yield of the extract at the highest pressure was approximately 15% less than that obtained with Soxhlet extraction using diethyl ether as solvent. The extracts were either solids or viscous oils depending on the amount of neutral lipids, which increased with increasing pressure. No significant differences in the composition of the major constituent fatty acids in any of the extracts were found. The color of the extracts was clearly dependent an the amount of carotenes, which consisted mainly of beta-carotene. The content of carotenes in the extracts did not increase at pressures higher than 150 bar. The amount of tocopherols in the extracts obtained at highest pressure was found to be approximately 3 times less than that at lower pressures. Countercurrent CO2 extraction of the cloudberry oil extracted at 300 bar and 40 degrees C resulted in enrichment of tocopherols in the extracts and a decrease in the amount of carotenes. The concentrations of tocopherols and carotenes in all of the CO2 extracts, the countercurrent extracts, and the raffinates were found to be clearly higher than those in the edible part of fresh cloudberry reported by other authors.

1444

Mansfield, J.L., P.S. Curtis, D.R. Zak, and K.S. Pregitzer. 1999. Genotypic variation for condensed tannin production in trembling aspen (Populs tremuloides, Salicaceae) under elevated CO2 and in high- and low-fertility soil. *American Journal of Botany 86(8):1154-1159.*

The carbon/nutrient balance hypothesis suggests that leaf carbon to nitrogen ratios influence the synthesis of secondary compounds such as condensed tannins. We studied the effects of rising atmospheric carbon dioxide on carbon to nitrogen ratios and tannin production. Six genotypes of Populus tremuloides were grown under elevated and ambient CO2 partial pressure and high- and low-fertility soil in field open-top chambers in northern lower Michigan, USA. During the second year of exposure, leaves were harvested three times (June, August, and September) and analyzed for condensed tannin concentration. The carbon/nutrient balance hypothesis was supported overall, with significantly greater leaf tannin concentration at high CO2 and low soil fertility compared to ambient CO2 and high soil fertility. However, some genotypes increased tannin concentration at elevated compared to ambient CO2, while others showed no CO2 response. performance of lepidopteran leaf miner (Phyllonorycter tremuloidiella) larvae feeding on these plants varied across genotypes, CO2, and fertility treatments. These results suggest that with rising atmospheric CO2, plant secondary compound production may vary within species. This could have consequences for plant-herbivore and plant-microbe interactions and for the evolutionary response of this species to global climate change.

KEYWORDS: ATMOSPHERIC CO2, CARBON NUTRIENT BALANCE, CLONAL VARIATION, FOLIAR CHEMISTRY, FOREST TENT CATERPILLARS, GYPSY MOTHS, INSECT HERBIVORE, PERFORMANCE, RAPHANUS-RAPHANISTRUM, WILD RADISH

1445

Mansfield, T.A. 1998. Stomata and plant water relations: does air pollution create problems? *Environmental Pollution 101(1):1-11.*

Small changes in the gaseous composition of the atmosphere have many different impacts on terrestrial plants. Some of the most important involve changes in stomatal control of leaf conductance. Evolution has provided highly complex mechanisms by which stomata respond to a wide range of environmental factors to balance the conflicting priorities of carbon gain for photosynthesis and water conservation. These mechanisms involve direct responses of the guard cells to aspects of the aerial environment, and hormonal communication within the plant enabling conductance to be adjusted according to soil moisture status. Various aspects of these delicately balanced mechanisms can be disturbed by air pollutants. Impairment of the regulation of plant water use by SO2 and O-3 has been known for some years, but there are still many obstacles to our understanding of the variations in response between species, or even between genotypes of the same species. A surprising outcome of some recent studies is the suggestion that CO2 pollution may disrupt the control of water relations in some species because their stomata do not close sufficiently in CO2- enriched air. It has often been taken for granted that the elevation of atmospheric CO2 would lead to economies in water use by plant canopies, but the underlying assumptions are now being seriously questioned.

KEYWORDS: ABIES L KARST, ABSCISIC- ACID, CARBON DIOXIDE, CYTOSOLIC-FREE CALCIUM, ELEVATED CO2, FAGUS-SYLVATICA L, FOLIAR GAS-EXCHANGE, NORWAY SPRUCE, PICEA-ABIES, SOIL-MOISTURE STRESS

1446

Marek, L.F., and M.H. Spalding. 1991. Changes in photorespiratory enzyme-activity in response to limiting CO2 in Chlamydomonas reinhardtii. *Plant Physiology 97(1):420-425.*

The activity of two photorespiratory enzymes, phosphoglycolate phosphatase (PGPase) and glycolate dehydrogenase (glycolate DH), changes when CO2-enriched wild-type (WT) Chlamydomonas reinhardtii cells are transferred to air levels of CO2. Adaptation to air levels of CO2 by Chlamydomonas involves induction of a CO2-concentrating mechanism (CCM) which increases the internal inorganic carbon concentration and suppresses oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase. PGPase in cell extracts shows a transient increase in activity that reaches a maximum 3 to 5 hours after transfer and then declines to the original level within 48 hours. The decline in PGPase activity begins at about the time that physiological evidence indicates the CCM is approaching maximal activity. Glycolate DH activity in 24 hour air-adapted WT cells is double that seen in CO2-enriched cells. Unlike WT, the high-CO2-requiring mutant, cia-5, does not respond to limiting CO2 conditions: it does not induce any known aspects of the CCM and it does not show changes in PGPase or glycolate DH activities. Other known mutants of the CCM show patterns of PGPase and glycolate DH activity after transfer to limiting CO2 which are different from WT and cia-5 but which are consistent with changes in activity being initiated by the same factor that induces the CCM, although secondary regulation must also be involved.

KEYWORDS: ADAPTATION, CONCENTRATING MECHANISM, DEFICIENT, EXCHANGE, EXCRETION, GLYCOLATE DEHYDROGENASE, MUTANT, PHOTOSYNTHESIS

1447

Marek, M.V., and J. Kalina. 1996. Comparison of two experimental approaches used in the investigations of the long-term effects of elevated CO2 concentration. *Photosynthetica 32(1):129-133.*

Two experimental devices used in the investigations of the long-term effects of elevated CO2 were compared from the point of view of occurrence of downregulation of photosynthesis. The comparison was made on the basis of net photosynthetic rate/internal CO2 concentration (P-N/C-i) response and effective quantum yield of photosystem 2 (PS2), respectively. In branch bags, the needles of Norway spruce showed no down regulation of photosynthetic capacity. However, in open top chambers decreases in maximal P-N (32%), carboxylation efficiency (28%) and potential photochemical efficiency of PS2 (8%), and the quantum yield (up to 50%) were detected.

KEYWORDS: EXPOSURE, PLANTS

1448

Marek, M.V., J. Kalina, and M. Matouskova. 1995. Response of photosynthetic carbon assimilation of norway spruce exposed to long-term elevation of co2 concentration. *Photosynthetica 31(2):209-220.*

Young (12 years old) Norway spruce (Picea abies [L.] Karst.) trees were exposed to ambient CO2 or ambient + 350 mu mol(CO2) mol(-1) continuously over 2 growing seasons in open-top chambers, under field conditions of a mountain stand. Comprehesive analysis of CO2 assimilation was performed after 4 and 22 weeks of the second growing season to evaluate the influence of elevated atmospheric CO2. A combination of gas exchange and a mathematical mo del of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) activity was used. After 4 weeks of exposure no statistically significant stimulation of the radiant energy and CO2 saturated rate of CO2 uptake (P-Nsat) by the elevated CO2 concentration was found. Yet after 24 weeks a statistically significant depression of P-Nsat (38 %) and carboxylation efficiency (32 %) was observed. Depression of photosynthetic activity by elevated CO2 resulted from a decrease in the RuBPCO carboxylation rate. The electron transport rate was also modified similarly to the rate of RuBP formation. An accompanying decrease in nitrogen content of the needles (by 12 %) together with an increase in total saccharides (by 34 %) was observed

after 24 weeks of exposure to enhanced CO2.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERIC CO2, DIOXIDE CONCENTRATION, ENRICHMENT, GAS-EXCHANGE, GROWTH, INHIBITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, TEMPERATURE

1449

Marek, M.V., M. Sprtova, and J. Kalina. 1997. The photosynthetic irradiance-response of Norway spruce exposed to a long-term elevation of CO2 concentration. *Photosynthetica 33(2):259-268.*

During an open-top chamber experiment performed in a mountain stand of young (12-year-old) Norway spruce (Picea abies [L.] Karst.), the trees were exposed to one of two CO2 concentrations (ambient CO2, AC, or AC + 350 mu mol mol(-1) = elevated CO2, EC) continuously over three growing seasons. To evaluate the EC influence, measurements of the relations between the rate of net CO2 uptake (P-N) and incidental photosynthetically active photon flux density (PPFD), as well as the content of photosynthetic pigments and chlorophyll (Chl) a fluorescence were taken in the third growing season. The short-term response to EC was evident mainly on ribulose-1,5- bisphosphate carboxylase/oxygenase kinetics without any significant change to the utilization of radiant energy. The long-term effect of EC was responsible for a decrease in P-N, Content of Chl a + b, F-v/F-m ratio, quantum yield of fluorescence, and photochemical quenching. Changes of stoichiometry between the electron transport, Calvin cycle and the end-product synthesis were confirmed for responses to the longterm import of EC and led to a definition of the photosynthetic acclimation to EC an Norway spruce.

KEYWORDS: ACCLIMATION, ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, ENRICHMENT, GROWTH, INHIBITION, LEAVES, LIGHT-RESPONSE

1450

Margolis, H.A., and M.G. Ryan. 1997. A physiological basis for biosphere-atmosphere interactions in the boreal forest: an overview. *Tree Physiology 17(8-9):491-499.*

Interdisciplinary field experiments for global change research are large, intensive efforts that study the controls on fluxes of carbon, water, trace gases, and energy between terrestrial ecosystems and the atmosphere at a range of spatial scales. Forest ecophysiology can make significant contributions to such efforts by measuring, interpreting, and modeling these fluxes for the individual components of forest ecosystems and then integrating the results into holistic ecosystem process models. The Boreal Ecosystem-Atmosphere Study (BOREAS) was undertaken because of the importance of the boreal forest biome to various global change issues. The study was conducted from 1993 to 1996 at sites in Saskatchewan and Manitoba, Canada. Results have shown that physiological processes of plants in the boreal forest can have large-scale consequences. For example, the composition of tree species strongly influences flux rates, with deciduous species having much higher carbon and water fluxes than coniferous species. Additionally, physiological limitations to transpiration in boreal conifers, even when soil water is abundant, reduces latent heat flux and increases sensible heat flux over large regions. This physiological control of transpiration can increase the depth of the atmospheric boundary layer on warm spring days to a level similar to that found in desert biomes. This special issue features 10 articles that address various aspects of the physiological basis of biosphere-atmosphere interactions in the boreal forest. The articles emphasize the environmental controls on water flux, carbon flux, and ecosystem productivity.

KEYWORDS: CARBON DIOXIDE, CLIMATIC CHANGE, CO2, EASTERN SIBERIA, ECOSYSTEM, EXCHANGE, FIELD EXPERIMENT FIFE, MODELS, RADIATION, REFLECTANCE

1451

Margolis, H.A., and L.P. Vezina. 1990. Atmospheric CO2 enrichment and the development of frost hardiness in containerized black spruce seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 20(9):1392-1398.*

1452

Marilley, L., U.A. Hartwig, and M. Aragno. 1999. Influence of an elevated atmospheric CO2 content on soil and rhizosphere bacterial communities beneath Lolium perenne and Trifolium repens under field conditions. *Microbial Ecology 38(1):39-49.*

The increase in atmospheric CO2 content alters C-3 plant photosynthetic rate, leading to changes in rhizodeposition and other root activities. This may influence the activity, the biomass, and the structure of soil and rhizosphere microbial communities and therefore the nutrient cycling rates and the plant growth. The present paper focuses on bacterial numbers and on community structure. The rhizospheres of two grassland plants, Lolium perenne (ryegrass) and Trifolium repens (white clover), were divided into three fractions: the bulk soil, the rhizospheric soil, and the rhizoplaneendorhizosphere. The elevated atmospheric CO2 content increased the most probable numbers of heterotrophic bacteria in the rhizosphere of L. perenne. However, this effect lasted only at the beginning of the vegetation period for T. repens. Community structure was assessed after isolation of DNA, PCR amplification, and construction of cloned 16S rDNA libraries. Amplified ribosomal DNA restriction analysis (ARDRA) and colony hybridization with an oligonucleotide probe designed to detect Pseudomonas spp. showed under elevated atmospheric CO2 content an increased dominance of pseudomonads in the rhizosphere of L. perenne and a decreased dominance in the rhizosphere of T. repens. This work provides evidence for a CO2-induced alteration in the structure of the rhizosphere bacterial populations, suggesting a possible alteration of the plant-growth-promoting- rhizobacterial (PGPR) effect.

KEYWORDS: 16S RDNA, CARBON DIOXIDE, DIVERSITY, ENRICHMENT, GROWTH, NITROGEN CYCLES, PSEUDOMONAS, RIBOSOMAL-RNA GENES, ROOTS, SYMBIOTIC N-2 FIXATION

1453

Marino, B.D.V., T.R. Mahato, J.W. Druitt, L. Leight, G.H. Lin, R.M. Russell, and F.N. Tubiello. 1999. The agricultural biome of Biosphere 2: Structure, composition and function. *Ecological Engineering 13(1-4):199-234.*

The agricultural mesocosm of Biosphere 2, known as the Intensive Agricultural Biome (IAB), provided food for the inhabitants of the facility during two periods of material closure between 1991 and 1994 (Mission I, September 26, 1991 to September 26, 1993, eight-person crew; Mission II, March 6, 1994 to September 17, 1994, seven-person crew). The design and operation of the mesocosm and preliminary results for food production of the IAB are described for both periods. The overall rate of crop production for the 0.22 ha area (soil depth of 1 m; soil and atmospheric volumes of approximately 2000 m(3) and 38000 m(3), respectively) sustained both crews. Overall production rates in Biosphere 2 exceeded those characteristic of fertile agricultural land in the most efficient agrarian communities, despite comparatively lower light levels, lack of insect pollinators and unusually dense insect pests. Crop yields were markedly higher for Mission II than for Mission I due, in part, to experience and improvements based on the first closure. The health of the Biospherians is briefly discussed in the context of a low-

calorie (1800-2200 kcal day(-1) per person for Mission I and 2200-2400 kcal day(- 1) for Mission II), nutrient-dense diet characteristic of the Biosphere 2 food paradigm. sigh productivity and biodiversity were due to many factors including high resolution climate control, hyper-intensive agricultural practices, selection and planting of food crops adapted to humid, tropical and sub- tropical conditions, nutrient recycling, intensive pest management, and the superambient levels of atmospheric CO2 (concentrations up to 4500 ppmv were reported during the 1991 to 1994 occupations). Radiation use efficiency (RUE) for wheat for both periods and a post-Mission II planting were comparable to RUEs observed in other experimental elevated CO2 settings such as Controlled Ecological Life Support-Systems (CELSS) and Free Air CO2 Enrichment studies (FACE) even though yields were comparatively lower due to low light levels. Integrated management of pests, soil conditions and agricultural practices were key factors in the sustainability of the IAB resulting in minimization of plant loss due to insect herbivory, nematode infestation and reduction in the quality of IAB soils. The use of soils rather than hydroponic systems for the IAB had significant consequences for CO2, N2O and O-2 concentrations in the Biosphere 2 atmosphere and rendered primary regeneration technologies ineffective over the periods of closure. The initial high organic carbon content of the IAB soils prescribed by the designers proved to be the largest single source of CO2 and the largest sink for O-2. The choice of a soil-based compared to a hydroponic-based agricultural system contributed to the accumulation of N2O to levels as high as 300 times current ambient levels (approximately 310 ppbv). The IAB of Biosphere 2 has the potential; with system improvement, to be a high-yielding, self-sustaining agricultural mesocosm suited for a variety of research endeavors.

KEYWORDS: CELSS, CO2, ENVIRONMENT, LIFE-SUPPORT, PERFORMANCE, PLANT GROWTH, PRODUCTIVITY, SOILS, SYSTEMS, WHEAT

1454

Mark, U., and M. Tevini. 1997. Effects of solar ultraviolet-B radiation, temperature and CO2 on growth and physiology of sunflower and maize seedlings. *Plant Ecology 128(1-2):224-234.*

The effects of solar UV-B radiation, in combination with elevated temperature (4 degrees C) and CO2 (680 mu L L-1) concentration, on sunflower and maize seedlings were studied from May to August in 1991 at the research station Quinta de Sao Pedro in Portugal (38.7 degrees N). The ambient solar radiation of Portugal was reduced to levels of Central European latitudes by using the ozone filter technique. This radiation served as control, while the ambient solar radiation of Portugal was to simulate intense UV-B treatment (+30%). All plants were grown up to 18 days in 4 climate controlled growth chambers simulating a daily course of temperature with T-max=28 degrees C or 32 degrees C, resp., and ambient CO2 concentrations (340 mu L L-1); in one chamber the CO2 concentration was twice as high (680 mu L L-1). Under intense UV-B and at 28 degrees C (T-max) all growth parameters (height, leaf area, fresh and dry weight, stem elongation rate, relative growth rate) of sunflower and maize seedlings were reduced down to 35% as compared to controls. An increase in growing temperature by 4 degrees C, alone or in combination with doubled CO2, compensated or even overcompensated the UV-B effect so that the treated plants were comparable to controls. Chlorophyll content, on a leaf area basis, increased under intense UV-B radiation. This increase was compensated by lower leaf areas, resulting in comparable chlorophyll contents. Similar to growth, also the net photosynthetic rates of sunflower and maize seedlings were reduced down to 29% by intense UV-B calculated on a chlorophyll basis. This reduction was compensated by an increased temperature. Doubling of CO2 concentration had effects only on sunflower seedlings in which the photosynthetic rates were higher than in the controls. Dark respiration rates of the seedlings were not influenced by any experimental condition. Transpiration and water use efficiency (wue) were not influenced by intense UV-B. Higher temperatures led to higher transpiration rates and lower water use efficiencies, resp. Doubling of CO2 reduced the transpiration rate drastically while for wue maximum values were recorded.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP PLANTS, DARK RESPIRATION, ENRICHMENT, GAS-EXCHANGE, HIGHER-PLANTS, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC CHARACTERISTICS, PHOTOSYSTEM, WHEAT

1455

Markkola, A.M., A. Ohtonen, U. AhonenJonnarth, and R. Ohtonen. 1996. Scots pine responses to CO2 enrichment .1. Ectomycorrhizal fungi and soil fauna. *Environmental Pollution 94(3):309-316.*

Ectomycorrhizal Scots pine seedlings were grown in unfertilized forest soil at ambient and double (ca 700 ppm) atmospheric concentrations of CO2. The biomass of seedlings and fungal biomass both in the roots and in the soil and the numbers of certain groups of soil animals were measured under summer conditions and after an artificial winter acclimation period No biomass parameter showed any significant change due to CO2 elevation. Increases were found during the winter acclimation period in total and fine root biomasses, fungal biomass in the soil and total fungal biomass both in the roots and in the soil, while the ratio of needle biomass:fungal biomass and the shoot:root ratio decreased. The N concentration in previous- year needles was lower in the double CO2 environment than with ambient CO2. Enchytraeids almost disappeared in the double CO2 environment during winter acclimation, while the numbers of nematodes increased at the same time in both treatments.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, ELEVATED CO2, GAS-EXCHANGE, MYCORRHIZAL COLONIZATION, PLANTS, POLLUTION GRADIENT, ROOTS, SEEDLING GROWTH, SOURCE-SINK RELATIONS

1456

Marks, S., and K. Clay. 1990. Effects of CO2 enrichment, nutrient addition, and fungal endophyte-infection on the growth of 2 grasses. *Oecologia 84(2):207-214.*

1457

Marks, S., and D.E. Lincoln. 1996. Antiherbivore defense mutualism under elevated carbon dioxide levels: A fungal endophyte and grass. *Environmental Entomology 25(3):618-623.*

Previous studies have shown that insects commonly consume more when fed leaf tissue grown under CO2 enrichment, but with few negative effects on growth. However, lepidopteran larvae fed tissue infected with Balansiae fungal endophytes (which produce toxic alkaloids) typically eat less but also suffer negative effects on growth and survival. This study was carried out to understand how these 2 factors may interact to affect larval consumption and growth in fall armyworm, Spodoptera frugiperda (J. E. Smith) (Lepidoptera: Noctuidae). Infected and uninfected ramets of a single genotype of tall fescue, Festuca arundinacea Schreb., were grown under CO2 concentrations of 400 and 700 mu l CO2/liter of air. Relative consumption of leaf tissue by larvae was 32% greater in the high CO2 treatment compared with leaves grown under low CO2 concentrations, but was not influenced by infection. As expected, larvae had significantly decreased relative growth rates when fed infected tissue, with their growth rates somewhat increased under high CO2 levels increased CO2 level and infection both led to significantly reduced efficiency of conversion of ingested food. These 2

factors also interacted so that the lowest efficiency of conversion of ingested food was seen when both infection and an enriched atmospheric CO2 environment were present. As global atmospheric CO2 levels continue to increase, it appears that fungal endophytes will continue to be important in turfgrasses as protection against insect herbivores and may lead to increased fitness for infected plant genotypes.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, INFECTED TALL FESCUE, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, PERENNIAL RYEGRASS, PERFORMANCE, PLANT, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH

1458

Maroco, J.P., G.E. Edwards, and M.S.B. Ku. 1999. Photosynthetic acclimation of maize to growth under elevated levels of carbon dioxide. *Planta 210(1):115-125.*

The effects of elevated CO2 concentrations on the photochemistry, biochemistry and physiology of C-4 photosynthesis were studied in maize (Zea mays L.). Plants were grown at ambient (350 mu L L-1) or ca. 3 times ambient (1100 mu L L-1) CO2 levels under high light conditions in a greenhouse for 30 d. Relative to plants grown at ambient CO2 levels, plants grown under elevated CO2 accumulated ca. 20% more biomass and 23% more leaf area. When measured at the CO2 concentration of growth, mature leaves of high-CO2-grown plants had higher light-saturated rates of photosynthesis (ca. 15%), lower stomatal conductance (71%), higher water-use efficiency (225%) and higher dark respiration rates (100%). High-CO2-grown plants had lower carboxylation efficiencies (23%), measured under limiting CO2, and lower leaf protein contents (22%). Activities of a number of C-3 and C-4 cycle enzymes decreased on a leaf-area basis in the high-CO2-grown plants by 5-30%, with NADP-malate dehydrogenase exhibiting the greatest decrease. In contrast, activities of fructose 1,6- bisphosphatase and ADP-glucose pyrophosphorylase increased significantly under elevated CO2 condition (8% and 36%, respectively). These data show that the C-4 plant maize may benefit from elevated CO2 through acclimation in the capacities of certain photosynthetic enzymes. The increased capacity to synthesize sucrose and starch, and to utilize these endproducts of photosynthesis to produce extra energy by respiration, may contribute to the enhanced growth of maize under elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, C-4, CARBOHYDRATE, ENRICHMENT, GAS-EXCHANGE, GENE-EXPRESSION, HIGH CO2 CONCENTRATIONS, LEAVES, PLANT GROWTH, WATER-USE

1459

Marshall, J.D., and R.A. Monserud. 1996. Homeostatic gas-exchange parameters inferred from C-13/C-12 in tree rings of conifers. *Oecologia 105(1):13-21.*

The CO2 concentration of the atmosphere has increased by almost 30% in the past two centuries, with most of the increase (> 5 Pa) during the past 60 years. Controlled environment studies of crop plants dependent on the C-3 photosynthetic pathway indicate that an increase of this magnitude would enhance net photosynthesis, reduce stomatal conductance, and increase the difference in CO2 concentration across the stomata, i.e., CO2 concentration outside the leaf to that within (c(a)-c(i)). Here we report evidence, based on stable isotope composition of tree rings from three species of field-grown, native conifer trees; that the trees have indeed responded. However, rather than increasing c(a)-c(i), intercellular CO2 concentrations have shifted upward to match the rise in atmospheric concentrations, holding c(a)-c(i) constant. No differences were detected among Douglas-fir (Pseudotsuga menziesii), ponderosa pine (Pinus ponderosa), or western white pine (Pinus monticola). The values of c(a)-c(i) were inferred from stable carbon isotope ratio (delta(13)C) of tree ring holocellulose adjusted for the 0.6- 2.6 parts per thousand difference between holocellulose and whole sapwood. The cellulose extraction removed contaminants deposited in the tree ring after it formed and the adjustment corrected for the enrichment of cellulose relative to whole tissue. The whole sapwood values were then adjusted for published estimates of past atmospheric delta(13)CO(2) and CO2 concentrations. To avoid confounding tree age with CO2, cellulose deposited by saplings in the inner rings of trees when the mature trees were saplings, between 1910-1929 and 1941-1970: thus saplings were compared to saplings. In a separate analysis, the juvenile effect, which describes the tendency for delta(13)C to increase in the first decades of a tree's life, was quantified independent of source CO2 effects. This study provides evidence that conifers have undergone adjustments in the intercellular CO2 concentration that have maintained c(a)-c(i) constant. Based on these results and others, we suggest that c(a)-c(i) which has also been referred to as the intrinsic water-use efficiency, should be considered a homeostatic gas-exchange set point for these conifer species.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CARBON ISOTOPE DISCRIMINATION, DIOXIDE CONCENTRATION, DOUGLAS-FIR, ELEVATED CO2, GROWTH, LEAVES, PARTIAL-PRESSURE, PHOTOSYNTHESIS, WATER-USE EFFICIENCY

1460

Martin, C.A., J.C. Stutz, B.A. Kimball, S.B. Idso, and D.H. Akey. 1995. Growth and topological changes of citrus-limon (L) burm f eureka in response to high-temperatures and elevated atmospheric carbon-dioxide. *Journal of the American Society for Horticultural Science 120(6):1025-1031.*

Growth and topological indices of 'Eureka' lemon were measured after 6 months in well-watered and well-fertilized conditions and factorial combinations of moderate (29/21C day/night) or high (42/32C day/night) temperatures and ambient (350 to 380 mu mol . mol(-1)) or elevated (constant 680 mu mol . mol(-1)) CO2. In high temperatures, plants were smaller and had higher levels of leaf chlorophyll alpha than in moderate temperatures. Moreover, plants in high temperatures and elevated CO2 had about 15% higher levels of leaf chlorophyll alpha than those in high temperatures and ambient CO2. In high temperatures, plant growth in elevated CO2 was about 87% more than in ambient CO2. Thus, high CO2 reduced the negative effect of high temperature on shoot growth, In moderate temperatures, plant growth in elevated CO2 Was only about 21% more than in ambient CO2. Irrespective of temperature treatments, shoot branch architecture in elevated CO2 was more hierarchical than those in ambient CO2. Specific shoot extension, a topological measure of branch frequency, was not affected by elevated CO2 in moderate temperatures, but was increased by elevated CO2 enrichment in high temperatures-an indication of decreased branch frequency and increased apical dominance, In moderate temperatures, plants in elevated CO2 had fibrous root branch patterns that were less hierarchical than at ambient CO2. The lengths of exterior and interior fibrous roots between branch points and the length of second-degree adventitious lateral branches were increased >50% by high temperatures compared with moderate temperatures, Root length between branch points was not affected by CO2 levels.

KEYWORDS: ARCHITECTURAL ANALYSIS, CARBOXYLASE, CO2 CONCENTRATIONS, ENRICHMENT, GAS-EXCHANGE, PHOTOSYNTHESIS, PLANT-ROOT SYSTEMS, PRODUCTIVITY, RESPIRATION, SEEDLINGS

1461

Martin, P. 1992. Exe: a climatically sensitive model to study climate change and co2 enhancement effects on forests. *Australian Journal of Botany 40(4-5):717-735.*

Vegetation plays a significant role in determining the local and regional hydrology of ice-free continental surfaces and the dynamics of the atmosphere above it. Vegetation also influences the global climate directly by affecting atmospheric chemistry. In particular, it partially controls the carbon cycle. In turn, vegetation is influenced by climate and changes in the ambient concentration of CO2. This may have important consequences for agriculture and natural resource exploitation. A formal recognition of atmosphere/biosphere interrelationships is crucial but insufficient. Systematic investigations of the interactions between climate, plant physiology and ecology are badly needed. In this spirit, this paper presents the results of numerical simulations performed with the Energy, water and momentum exchange, and Ecological dynamics (EXE) model at a local scale over periods of 400-800 (simulation) years. EXE constitutes a first attempt to couple a physiologically based water budget and an explicit treatment of ecological dynamics. In principle, EXE could be forced by the output of an atmospheric general circulation model (GCM). Within this context, the paper demonstrates through the examples it analyses that both potential stomatal response to CO2 and the possible range of changes in atmospheric relative humidity are likely major factors in determining the ecosystem response to greenhouse warming. Consequently, they should be considered in future studies of this kind. The paper also provides explanations regarding the movement of ecotones, defined as the transition zones between different vegetation assemblages. Taking the North American forest/prairie boundary as a case study, the analysis of the results shows how, in a greenhouse warmed world, St Paul, MN, might look like North Platte, NE. Finally, building on the previous example by using two different models, this study illustrates that results can be strongly model dependent and encourages extreme caution in their interpretation.

KEYWORDS: AMAZONIAN RAINFOREST, SIMPLE BIOSPHERE MODEL

1462

Martin, P.H., and A.B. Guenther. 1995. Insights into the dynamics of forest succession and non-methane hydrocarbon trace gas emissions. *Journal of Biogeography 22(2-3):493-499.*

Natural biogenic non-methane hydrocarbon (NMHC) emissions significantly influence the concentrations of free hydroxyl and peroxy radicals, carbon monoxide and tropospheric ozone. Present concerns with air pollution and the global carbon balance call for a better understanding of the respective roles of climate dynamics and vegetation succession in determining NMHC emissions. This constitutes the focus of the present paper. The approach consists in coupling the Energy, Water and Momentum Exchange and Ecological Dynamics model, a climatically sensitive, physically based gap phase forest dynamics model, and NMHC trace gas emission algorithms to assess possible changes in NMHC emissions from forests under stationary and changing climatic conditions. In summary, it is possible to follow the temporal evolution of foliar emissions over centuries using a vegetation dynamics model coupled with an NMHC emissions module. Significant changes in isoprene and terpene emissions can take place as vegetation succession occurs under stationary climatic conditions and as climatic perturbations of the type and magnitude foreseen for global change alter the local microclimate. As illustrated by two examples, emissions may decrease or increase depending on the local climate and vegetation. The respective actions of changes in species absolute and relative abundance and changes in temperature interact very non-linearly making changes in emissions difficult to predict. None the less, coupled models of the kind described here may provide useful insights into the direction of such changes.

KEYWORDS: CARBON, CLIMATE, CO2, MODEL

1463

Martinez, I., M.I. Orus, and E. Marco. 1997. Carboxysome structure and function in a mutant of Synechococcus that requires high levels of CO2 for growth. *Plant Physiology and Biochemistry 35(2):137-146.*

The high CO2-requiring mutant N1 of Synechococcus sp. PCC 7942 possesses aberrant carboxysomes and is unable to utilize the internal inorganic carbon pool for photosynthesis. Normal carboxysomal carbonic anhydrase (EC 4.2.1.1) and ribulose 1,5 bisphosphate carboxylase/oxygenase (EC 4.1.1.39) activities were obtained under saturated substrate concentrations, but limiting concentrations of inorganic carbon resulted in a lower Rubisco activity compared to the wild type. The polypeptidic pattern of carboxysome-enriched fractions showed no differences between wild type and mutant N1, suggesting that the putative gene product inactivated in the mutant does not constitute a polypeptide of the carboxysome shell, but could play an important role in the process of carboxysome assembly. Data obtained are discussed in relation to the proposed quantitative model of the inorganic carbon concentrating mechanism of cyanobacteria.

KEYWORDS: CONCENTRATING MECHANISM, CYANOBACTERIA, GENE, INORGANIC CARBON FLUXES, PCC7942, PHOTOSYNTHESIS, REGION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SP STRAIN PCC-7942, THIOBACILLUS-NEAPOLITANUS

1464

Martins, A., A. Casimiro, and M.S. Pais. 1997. Influence of mycorrhization on physiological parameters of micropropagated Castanea sativa Mill. plants. *Mycorrhiza 7(3):161-165.*

Mycorrhizal micropropagated Castanea sativa plants were studied in terms of growth and physiological parameters following in vitro mycorrhization with Pisolithus tinctorius. Mycorrhization enhanced growth of micropropagated chestnut plants, increased their protein content and photosynthetic rates, decreased the respiratory rates and CO2 compensation point, RuBisCO activity was not significantly different in mycorrhizal and control plants, although there was an increase in the amount of RuBisCO in the former. Mycorrhization increased plant biomass and improved plants physiological status, thus enhancing the acclimatization process.

KEYWORDS: CARBON BALANCE, DOUGLAS-FIR, FUNGI, GROWTH, LEAVES, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, SEEDLINGS, WILLOW ECTOMYCORRHIZAS

1465

Martos, J.M.G. 1993. Effect of co2 in storage atmosphere on mill olive fruit physiology. *Grasas Y Aceites 44(2):81-84.*

Olive fruits (Olea europaea) used for oil production were stored at 5-degrees-C and four different atmospheres (%CO2/%O2/%N2: 0/21/78; 5/20/75; 10/19/71 and 20/17/63). At 5- degrees-C the enrichment of the storage atmosphere with greater-than-or-equal-to 5% CO2 concentrations produced a proportional increase of the physiological disorder occurring in stored fruits. This occurrence had a strong relationship with the appearence of fruit decay. Simple refrigeration at 5- degrees-C was sufficient to mantain the same degree of ripening of olive fruits for 60 days. However, a longer period of storage at 5-degrees-C originated a remarkable incidence of chilling injuries in the fruits.

1466

Masle, J. 1992. Will plant performance on soils prone to drought or with

high mechanical impedance to root penetration be improved under elevated atmospheric CO2 concentration? *Australian Journal of Botany 40(4-5):491-500.*

Plants growing on dry soils or on soils with high mechanical resistance to root penetration grow more slowly and exhibit lower stomatal conductance than those growing on moist and loose soils. In most situations in nature where edaphic stresses develop rather slowly (compared to stresses imposed in most pot experiments conducted under controlled conditions), photosynthesis is mainly reduced via stomatal effects rather than via changes in mesophyll capacity for photosynthesis. Elevated CO2 will induce an increase in the internal partial pressure of CO2, despite stomatal conductance being lowered even further. Photosynthesis will therefore be improved, and leaf turgor will be increased. It is widely thought that growth on dry or hard soils is not carbon limited because levels of soluble carbohydrates in the leaves and root cells are increased. It is shown in this paper that growth on soil with high mechanical resistance does respond to elevated CO2. However, this response is smaller than expected from the increase of carbon assimilation rate because: (a) carbon partitioning is altered so that supplementary carbohydrates are preferentially allocated to the roots; (b) leaf growth sensitivity to internal availability of sugars is lower than in plants growing on loose soils. These alterations of 'sink activity' and carbon partitioning are mediated by unknown signalling factor(s) induced in the roots. It is not known whether the root factors acting in droughted plants are of the same nature. In both droughted and impeded plants the interacting effects of these factors and of ambient CO2 levels are likely to result in improved transpiration efficiency. More experiments are needed in this area, however, especially to ascertain the relative contribution of changes in growth patterns versus changes in the patterns of water use. In conclusion, the importance of identifying the nature of the sink limitations induced by root signals is emphasised. It is a fundamental area of research to be developed not only for assessing growth responses to rising CO2 under edaphic stress, but likely also for reconciling conflicting responses of field- grown and pot-grown plants.

KEYWORDS: ABSCISIC- ACID, CARBON DIOXIDE, DRYING SOIL, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC CAPACITY, STOMATAL CONDUCTANCE, WATER-STRESS, WHEAT SEEDLINGS

1467

Masle, J., G.S. Hudson, and M.R. Badger. 1993. Effects of ambient co2 concentration on growth and nitrogen use in tobacco (nicotiana-tabacum) plants transformed with an antisense gene to the small-subunit of ribulose-1,5- bisphosphate carboxylase oxygenase. *Plant Physiology 103(4):1075-1088.*

Growth of the R1 progeny of a tobacco plant (Nicotiana tabacum) transformed with an antisense gene to the small subunit of ribulose-1,5-carboxylase/oxygenase (Rubisco) was analyzed under 330 and 930 mubar of CO2, at an irradiance of 1000 mumol quanta m-2 s-1. Rubisco activity was reduced to 30 to 50% and 13 to 18% of that in the wild type when one and two copies of the antisense gene, respectively, were present in the genome, whereas null plants and wild-type plants had similar phenotypes. At 330 mubar of CO2 all antisense plants were smaller than the wild type. There was no indication that Rubisco is present in excess in the wild type with respect to growth under high light. Raising ambient CO2 pressure to 930 mubar caused plants with one copy of the DNA transferred from plasmid to plant genome to achieve the same size as the wild type at 330 mubar, but plants with two copies remained smaller. Differences in final size were due mostly to early differences in relative rate of leaf area expansion (m2 m-2 d-1) or of biomass accumulation (g g-1 d-1): within less than 2 weeks after germination relative growth rates reached a steady-state value similar for all plants. Plants with greater carboxylation rates were characterized by a higher ratio of leaf carbon to leaf area, and at later stages, they were characterized also by a relatively greater allocation of structural and nonstructural carbon to roots versus leaves. However, these changes per se did not appear to be causing the long-term insensitivity of relative growth rates to variations in carboxylation rate. Nor was this insensitivity due to feedback inhibition of photosynthesis in leaves grown at high partial pressure of CO2 in the air (p(a)) or with high Rubisco activity, even when the amount of starch approached 40% of leaf dry weight. We propose that other intrinsic rate-limiting processes that are independent of carbohydrate supply were involved. Under plentiful nitrogen supply, reduction in the amount of nitrogen invested in Rubisco was more than compensated for by an increase in leaf nitrate. Nitrogen content of organic matter, excluding Rubisco, was unaffected by the antisense gene. In contrast, it was systematically lower at elevated p(a) than at normal p(a). Combined with the positive effects of p(a) on growth, this resulted in the single-dose antisense plants growing as fast at 930 mubar of CO2 as the wild-type plants at 330 mubar of CO2 but at a lower organic nitrogen cost.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, IMPACT, LEAVES, LIGHT, PARTIAL-PRESSURE, PHOTOSYNTHETIC ACCLIMATION, RBCS, RIBULOSE BISPHOSPHATE CARBOXYLASE, WHEAT SEEDLINGS

1468

Matamala, R., and B.G. Drake. 1999. The influence of atmospheric CO2 enrichment on plant-soil nitrogen interactions in a wetland plant community on the Chesapeake Bay. *Plant and Soil 210(1):93-101.*

We investigated plant and soil nitrogen pools and soil processes in monospecific stands of the C-3 sedge Scirpus olneyi and the C-4 grass Spartina patens grown in the field in open top chambers in a brackish marsh on the Chesapeake Bay. Stands of S. olneyi responded to eight years of elevated CO2, by increased rates of net ecosystem gas exchange and a large stimulation of net ecosystem production. We conducted our study in the summer of 1994 and 1995 when soil cores were collected and aboveground biomass was estimated. Nitrogen concentration in elevated CO2 treatments was reduced 15% in stems of S. olneyi and 8% in the upper 10 cm of the soil profile. While total plant nitrogen per unit of land area remained the same between treatments, total soil nitrogen showed a non- significant tendency to decrease in the upper 10 cm of the soil profile in elevated CO2 both years of study. A significant decrease in soil bulk density largely contributed to the observed decrease in soil nitrogen. Exchangeable nitrogen and potential denitrification rates were also reduced in elevated CO2, but net nitrogen mineralization was unchanged by elevated CO2 treatment in S. olneyi both years. Plants and soils in a pure stand of the C-4 grass, S. patens, showed none of these effects of elevated CO2 treatment. Our data provides evidence of changes in nitrogen dynamics of an ecosystem exposed to elevated CO2 for eight years; however due to the variability in these data, we cannot say if or how these changes are likely to impact the effect of rising CO2 on primary production or carbon accumulation in this ecosystem in the future.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, DECOMPOSITION, DENITRIFICATION, ELEVATED CO2, ESTUARINE MARSH, GAS FLUXES, LEAF LITTER, LOLIUM-PERENNE, PHOTOSYNTHESIS, SCIRPUS- OLNEYI

1469

Mathooko, F.M. 1996. Regulation of ethylene biosynthesis in higher plants by carbon dioxide. *Postharvest Biology and Technology 7(1-2):1-26.*

Elevated CO2 levels used with or without reduced O-2 levels regulate many biochemical and physiological processes in higher plants, among them ethylene biosynthesis. The mode of action of elevated CO2 in the

regulation of ethylene biosynthesis is still a subject of much debate. Various hypotheses have been put forward to explain its model(s) of action and most of them have pointed out that CO2 regulates ethylene biosynthesis, at least in part, by counteracting ethylene action. This is thought to be mainly through the regulation of 1- aminocyclopropane-1-carboxylate (ACC) synthase, presumably the rate-limiting enzyme in the ethylene biosynthetic pathway, and in some instances ACC oxidase. The present review brings together recent developments on the biochemical, physiological and molecular bases for the regulation by CO2 of ethylene biosynthesis in higher plants. The mode of activation of ACC oxidase by CO2 is also discussed.

KEYWORDS: CUCURBITA-MAXIMA, ENCODING 1-AMINOCYCLOPROPANE-1-CARBOXYLATE SYNTHASE, FORMING ENZYME, GENES, LEAF-DISKS, LIGHT INHIBITION, MESSENGER-RNA, POSTHARVEST PHYSIOLOGY, TOMATO FRUITS, WOUND ETHYLENE

1470

Mathooko, F.M. 1996. Regulation of respiratory metabolism in fruits and vegetables by carbon dioxide. *Postharvest Biology and Technology 9(3):247-264.*

The respiratory rate of fruits and vegetables can be used as an indicator for designing storage conditions to maximize the longevity of these commodities. One postharvest technique that has been used to prolong the storage life of some of these commodities is the use of a controlled atmosphere. The modulation of respiratory metabolism of such commodities held in controlled atmospheres containing reduced oxygen and/or elevated carbon dioxide levels has been thought of as the primary reason for the beneficial effects on the commodities. However, the mechanism by which elevated carbon dioxide influences the regulation of respiratory metabolism is still obscure and several hypotheses have been proposed for its mode(s) of action. The regulation may be directed towards the glycolytic pathway, the fermentative metabolism, the tricarboxylic acid cycle or the electron transport system, presumably through its influence on the synthesis, degradation, inactivation and/or activation of the respective enzymes. It may also be through the antagonistic effects of carbon dioxide on ethylene action as well as its influence on secondary metabolism through an alteration in cell pH. This article discusses the recent developments on the biochemical and physiological fronts as well as the possible mode(s) of action of elevated carbon dioxide in the regulation of respiratory metabolism in fruits and vegetables.

KEYWORDS: ALCOHOL-DEHYDROGENASE, BARTLETT PEARS, CO2-ENRICHED ATMOSPHERES, CONTROLLED ATMOSPHERES, ELEVATED CO2 CONCENTRATIONS, FRUCTOSE 2;6-BISPHOSPHATE, INDUCTION, OXYGEN, QUALITY, STORAGE

1471

Mathooko, F.M., Y. Kubo, A. Inaba, and R. Nakamura. 1995. Characterization of the regulation of ethylene biosynthesis in tomato fruit by carbon-dioxide and diazocyclopentadiene. *Postharvest Biology and Technology 5(3):221-233.*

The regulation of ethylene biosynthesis by CO2 and diazocyclopentadiene (DACP), both inhibitors of ethylene action, was investigated in tomato (Lycopersicon esculentum Mill. cv. 'Momotaro') fruit held at 25 degrees C. When the tomato fruit at the pink stage of ripeness were treated with 20% CO2 (+ 20% O-2 + 60% N-2) or DACP, ethylene production by the fruit was rapidly decreased. The inhibition of ethylene production resulted primarily, if not solely, from the suppression of the activities of both 1-aminocyclopropane-1- carboxylic acid (ACC) synthase and ACC oxidase. The inhibition of ACC synthase activity subsequently led to low levels of ACC. CO2 treatment further inhibited ACC conjugation into 1- (malonylamino)cyclopropane-1-carboxylic acid (MACC). By contrast, DACP-treated fruit maintained slightly higher levels of MACC relative to the control fruit. When the fruit were transferred from the CO2-enriched atmosphere to air, ethylene production, ACC and MACC contents and the activities of ACC synthase and ACC oxidase increased gradually to the control level after 24 h, while these values, except for MACC content, remained low in DACP-treated fruit throughout the experimental period. These results indicate that CO2 and DACP regulate ethylene production in tomato fruit by inhibiting ACC synthase and ACC oxidase activities and further support the hypothesis that the autocatalytic signal associated with ethylene action during fruit ripening stimulates the activities of both enzymes.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ASSAY, CAPABILITY, CONTROLLED ATMOSPHERES, DACP, PRECLIMACTERIC TOMATO, SYNTHASE

1472

Mathooko, F.M., Y. Kubo, A. Inaba, and R. Nakamura. 1995. Induction of ethylene biosynthesis and polyamine accumulation in cucumber fruit in response to carbon-dioxide stress. *Postharvest Biology and Technology 5(1-2):51-65.*

Carbon dioxide stress-induced ethylene biosynthesis, respiration and polyamine accumulation in cucumber fruit (Cucumis sativus L, cv. Sharp-1) held at 25 degrees C was investigated. Control fruit produced little ethylene and the respiration rate decreased with increase in incubation time while polyamine levels decreased. Elevated CO2 induced ethylene production, respiration and polyamine accumulation. Putrescine and spermidine levels increased in response to CO2 treatment, whereas spermine levels were not significantly affected. No cadaverine was detected in all treatments. The increase in ethylene production paralleled increases in 1- aminocyclopropane-1-carboxylic acid (ACC) and the activities of both ACC synthase and in vitro ACC oxidase. Infiltration of the fruit with aminooxyacetic acid, a potent inhibitor of the conversion of S-adenosylmethionine (AdoMet) to ACC completely blocked CO2 stress-induced ethylene production. Similarly, cycloheximide, an inhibitor of nucleocytoplasmic protein synthesis effectively blocked CO2 stress induction of polyamine accumulation, ethylene production, ACC formation and the development of ACC synthase. Withdrawal of CO2 gas caused cessation of increases in ethylene production, respiration, ACC, putrescine and the activities of ACC synthase and ACC oxidase, but caused increase in spermidine and spermine levels. These data indicate that CO2 induces de novo synthesis of ACC synthase thereby causing accumulation of ACC and increase in ethylene production and suggest that the conversion of AdoMet to ACC is the rate-limiting step in CO2 stress-induced ethylene biosynthesis. The induction, however, requires continuous presence of the stimulus. The results also suggest that protein synthesis might be required for the CO2 stress induction of polyamine biosynthesis. The results further suggest that in cucumber fruit under CO2 stress, at least, the ethylene and polyamine biosynthetic pathways are not competitive.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACTIVATION, C2H4 PRODUCTION, CHILLING INJURY, ELICITOR, OXIDASE, PUTRESCINE, SATIVUS L, SPERMIDINE, STORAGE

1473

Mathooko, F.M., M.W. Mwaniki, A. Nakatsuka, S. Shiomi, Y. Kubo, A. Inaba, and R. Nakamura. 1999. Expression characteristics of CS-ACS1, CS-ACS2 and CS-ACS3, three members of the 1-aminocyclopropane-1-carboxylate synthase gene family in cucumber (Cucumis sativus L.) fruit under carbon dioxide stress. *Plant and Cell Physiology 40(2):164-172.*

Fire investigated the expression pattern of three 1- aminocyclopropane-1-carboxylate (ACC) synthase genes, CS-ACS1, CS-ACS2 and CS-ACS3 in cucumber (Cucumis sativus L.) fruit under CO2 stress. CO2 stress-induced ethylene production paralleled the accumulation of only CS-ACS1 transcripts which disappeared upon withdrawal of CO2. Cycloheximide inhibited the CO2 stress-induced ethylene production but superinduced the accumulation of CS-ACS1 transcript. At higher concentrations, cycloheximide also induced the accumulation of CS-ACS2 and CS- ACS3 transcripts. In the presence of CO2 and cycloheximide, the accumulation of CS-ACS2 transcript occurred within Ih, disappeared after 3h and increased greatly upon withdrawal of CO2. Inhibitors of protein kinase and types 1 and 2A protein phosphatases which inhibited and stimulated, respectively, CO2 stress-induced ethylene production had little effect on the expression of these genes. The results presented here identify CS-ACS1 as the main ACC synthase gene responsible for the increased ethylene biosynthesis in cucumber fruit under CO2 stress and suggest that this gene is a primary response gene and its expression is under negative control since it is expressed by treatment with cycloheximide. The results further suggest that the regulation of CO2 stress-induced ethylene biosynthesis by reversible protein phosphorylation does not result from enhanced ACC synthase transcription.

KEYWORDS: ACID SYNTHASE, ARABIDOPSIS-THALIANA, BINDING PROTEIN, ESCHERICHIA-COLI, ETHYLENE BIOSYNTHESIS, INDOLEACETIC-ACID, MUNG BEAN HYPOCOTYLS, PROTEIN-PHOSPHORYLATION, STRUCTURAL CHARACTERIZATION, TOMATO LYCOPERSICON-ESCULENTUM

1474

Mathooko, F.M., T. Sotokawa, Y. Kubo, A. Inaba, and R. Nakamura. 1993. Retention of freshness in fig fruit by co2-enriched atmosphere treatment or modified atmosphere packaging under ambient-temperature. *Journal of the Japanese Society for Horticultural Science 62(3):661-667.*

At 20-degrees-C. freshness retention of figs (Ficus carica L. cv. Masui Dauphine) by CO2-enriched atmosphere treatment or modified atmosphere packaging were studied in an attempt to reduce deterioration during transportation. CO2-enriched atmosphere treatment inhibited ethylene production, delayed the incidence of mold growth and promoted ethanol production. Majority of the figs exposed to 60% or 80% CO2 for 2 days were still marketable 1 day after transfer to air at 20-degrees-C. Based on mold growth, figs stored in air and in unperforated polyethylene bags deteriorated slightly faster than those stored in perforated bags. A gas mixture of 80% CO2 +20% O2 or 100% CO2 introduced into the polyethylene bags before sealing were more effective in the control of mold growth compared to air or 100% N2 and equally effective in reducing ethylene accumulation as 100% N2. The results suggest that postharvest deterioration of figs can be reduced by either CO2-enriched atmosphere treatment or through modified atmosphere packaging.

KEYWORDS: LIFE, O2, QUALITY, RESPIRATION, STORAGE, STRAWBERRIES

1475

Matsueda, H., and H.Y. Inoue. 1999. Aircraft measurements of trace gases between Japan and Singapore in October of 1993, 1996, and 1997. *Geophysical Research Letters 26(16):2413-2416.*

Carbon dioxide (CO2) methane (CH4), and carbon monoxide (CO) mixing ratios were measured in discrete air samples from aircraft between Japan and Singapore in October. The mixing ratios of all trace gases at 9-12 km were enhanced over the South China Sea in 1997 compared with those in 1993 and 1996. Vertical distributions of all trace gases over Singapore in 1997 also showed largely elevated mixing ratios at all altitudes. These distributions indicate a wide outflow of trace gases from intense biomass burning in the southeast Asia regions in the very strong El Nino year. The enhanced trace gases showed a strong linear correlation between CH4 and CO, and between CO and CO2, with the regression slopes of 0.051 Delta CH(4)ppb/Delta COppb) and 0.089 (Delta COppb/Delta CO(2)ppb). The emission ratios are characteristic of fires with relatively lower combustion efficiency from the tropical rain forest and peat lands in Kalimantan and Sumatra of Indonesia.

KEYWORDS: AFRICAN SAVANNA ECOSYSTEMS, BRAZIL, CARBON-MONOXIDE, DRY SEASON, EMISSIONS, FIRES, METHANE, SOUTHERN AFRICA, UPPER TROPOSPHERE, WESTERN AFRICA

1476

Matsui, T., O.S. Namuco, L.H. Ziska, and T. Horie. 1997. Effects of high temperature and CO2 concentration on spikelet sterility in indica rice. *Field Crops Research 51(3):213-219.*

The effects of increasing temperature and CO2 concentration on floral sterility were examined for rice (cv. IR 72) using open- top chambers located at the International Rice Research Institute in Los Banes, Philippines. The field-based open-top chamber system was used to simulate four different environments: ambient temperature and CO2 concentration (control); ambient temperature, ambient +300 mu l l(-1) CO2; ambient +4 degrees C temperature, ambient CO2 concentration; ambient +4 degrees C temperature, ambient + 300 mu 1 l(-1) CO2. High temperature during flowering resulted in increased pollen sterility with the degree of sterility exacerbated if rice was exposed to both high temperature and increased CO2 concentration. The critical air temperature for spikelet sterility (as determined from the number of germinated pollen grains on the stigma) was reduced by ca 1 degrees C at elevated concentrations of carbon dioxide. We speculate that this downward shift in critical temperature may be due to the observed increase in air temperature within the canopy at high CO2 concentrations. This increase in air temperature, in turn, may be related to stomatal closure and reduced transpirational cooling in an elevated CO2 environment. Data from this experiment indicate that increasing CO2 concentration could limit rice yield if average air temperature increased simultaneously.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, GROWTH, RESPONSES, YIELD

1477

Matthies, D., and P. Egli. 1999. Response of a root hemiparasite to elevated CO2 depends on host type and soil nutrients. *Oecologia 120(1):156-161.*

Although elevated CO2 may affect various forms of ecological interactions, the effect of elevated CO2 on interactions between parasitic plants and their hosts has received little attention. We examined the effect of elevated CO2 (590 mu l l(- 1)) at two nutrient (NPK) levels on the interactions of the facultative root hemiparasite Rhinanthus alectorolophus with two of its hosts, the grass Lolium perenne and the legume Medicago sativa. To study possible effects on parasite mediation of competition between hosts, the parasite was grown with each host separately and with both hosts simultaneously. In addition, all combinations of hosts were grown without the parasite. Both the parasite and the host plants responded to elevated CO2 with increased growth, but only at high nutrient levels. The CO2 response of the hemiparasite was stronger than that of the hosts, but depended on the host species available. With L. perenne and M. sativa simultaneously available as hosts, the biomass of the parasite grown at elevated CO2 was 5.7 times that of parasites grown at ambient CO2. Nitrogen concentration in the parasites was not influenced by the treatments and was not related to

parasite biomass. The presence of the parasite strongly reduced both the biomass of the hosts and total productivity of the system. This effect was much stronger at low than at high nutrient levels, but was not influenced by CO2 level. Elevated CO2 did not influence the competitive balance between the two different hosts grown in mixture. The results of this study support the hypothesis that hemiparasites may influence community structure and suggest that these effects are robust to changes in CO2 concentration.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COMPETITION, GROWTH, PARASITIC PLANT, PERFORMANCE, TRIFOLIUM- REPENS

1478

Matysiak, B., and J. Nowak. 1994. Carbon-dioxide and light effects on photosynthesis, transpiration and ex-vitro growth of homalomena emerald gem plantlets. *Scientia Horticulturae 57(4):353-358.*

Micropropagated plantlets of Homalomena cultivar 'Emerald Gem' were grown ex vitro at two CO2 concentrations (350 and 1200 mumol mol-1) and two light levels (50 and 150 mumol m-2 s-1 photosynthetic photon flux density (PPFD)). Plants grown at 1200 mumol mol-1 CO2 and at 150 mumol m-2 s-1 PPFD accumulated dry weight of shoots and roots three and two times higher, respectively, and had a leaf area 2.4 times higher than that of plants grown at 350 mumol mol-1 CO2 and 50 mumol m-2 s-1 PPFD. These plants also had the highest rate of photosynthesis. Carbon dioxide enrichment was more effective than supplementary light to increase plant growth. The CO2 assimilation rate, photorespiration, transpiration and stomatal conductance to water vapour were strongly promoted by light al 150 mumol m-2 s-1, irrespective Of CO2 concentration. CO2 enrichment enhanced the CO2 assimilation rate and quantum efficiency but decreased the rate of transpiration at 50 mumol m-2 s-1 PPFD and stomatal conductance to water vapour at 50 and 150 mumol m-2 s-1 PPFD.

KEYWORDS: CULTURE

1479

Matysiak, B., and J. Nowak. 1998. Acclimatization and the growth of Ficus benjamina microcuttings as affected by carbon dioxide concentration. *Journal of Horticultural Science & Biotechnology 73(2):185-188.*

The influence of CO2 concentrations (350 and 1200 mu mol mol(- 1)) on the growth of Ficus benjamina microcuttings cv. Golden King and cv. Natasja, was investigated with reference to light levels (50 and 150 mu mol m(-2) s(-1) PPFD, Photosynthetic Photon Flux Density) and the nutrient solution concentrations (0.7, 1.4, 2.1 and 2.8 mS cm(-1) EC, electrical conductivity). Plants grown in peat + perlite at 1,200 mu mol mol(-1) CO2 concentration and simultaneously at high PPFD level (150 mu mol m(-2) s(-1)) had the highest shoot and root fresh weights and the highest leaf area. Elevation of CO2 concentration at low level of PPFD did not affect the growth of F. benjamina. Survival of F. benjamina microcuttings cultivated in rockwool was low (65-90%) and the growth rate was slow, irrespective of nutrient solution concentration. CO2 enrichment increased survival and accelerated the growth of these microcuttings. The best growth of F. benjamina microcuttings cultivated in rockwool was at 1,200 mu mol mol(-1) CO2 and the highest level of electrical conductivity (EC) 2.8 mS cm(-1).

KEYWORDS: ENRICHMENT, INVITRO, PHOTOSYNTHESIS, PLANTLETS, TRANSPIRATION

1480

Mauney, J.R., B.A. Kimball, P.J. Pinter, R.L. Lamorte, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Growth and yield of cotton in response to a free-air carbon- dioxide enrichment (face) environment. *Agricultural and Forest Meteorology 70(1-4):49-67.*

To quantify the growth and yield responses to CO2 enrichment in an open field setting, free-air CO2 enrichment (FACE) technology was used to expose a cotton (Gossypium hirustum L.) crop to 550 mumol mol-1 CO2 throughout the growing seasons of 1989, 1990 and 1991 in fields near Maricopa, Arizona. In 1990 and 1991 a water stress treatment was also imposed. Response data for all years were consistent, and the data for 1991 were the least compromised by unusual weather or equipment failures. In that season the biomass was increased 37% by the 48% increase in CO2 concentration. Harvestable yield was increased 43%. The increase in biomass and yield was attributed to increased early leaf area, more profuse flowering and a longer period of fruit retention. The FACE treatment increased water- use efficiency (WUE) to the same amount in the well-irrigated plots as in the water-stressed plots. The increase in WUE was due to the increase in biomass production rather than a reduction of consumptive use.

1481

Mavrogianopoulos, G.N., J. Spanakis, and P. Tsikalas. 1999. Effect of carbon dioxide enrichment and salinity on photosynthesis and yield in melon. *Scientia Horticulturae 79(1-2):51-63.*

Melon (Cucumis melo L. Cv Parnon) grown in rockwool culture in the greenhouse was CO2 enriched, for 5 h every morning, at 400, 800 and 1200 mu mol mol(-1) and trickle-irrigated with nutrient solutions amended with 0, 25 and 50 mM NaCl. High CO2 level increased fruit yield, the increase being greater in unsalinated plants than in salinated. With total shoot fresh weight, the increase was greater in salinated plants. CO2 enrichment also increased leaf growth and the chlorophyll content of the measured leaves. Addition of NaCl in the nutrient solution caused significant reduction in total yield, the reduction being greater at higher concentrations of CO2, At 25 mM NaCl, the decrease in yield resulted mainly from the smaller fruit size, but at 50 mM yield reduction was due both to smaller fruit size and to fewer fruits per plant. Addition of NaCl caused significant reduction in total shoot fresh weight in all cases, the reduction being greater at the lower level of CO2. Salinity also, significantly reduced leaf surface irrespective of CO2 level. Chlorophyll content was reduced by NaCl mainly at the level of 50 mM NaCl. A stronger correlation was found between salinity and shoot fresh weight, plant height and leaf surface area, than salinity and yield and other characteristics. Measurements of gas exchange showed that, for the above mentioned CO2 and NaCl concentrations, net assimilation was affected by CO2 to a greater degree than by salinity. Stomatal conductance was most affected by salinity at a concentration of 50 mM NaCl.

KEYWORDS: CO2- ENRICHMENT, FRUIT-QUALITY, GROWTH REDUCTION, ION CONCENTRATION, LEAF TISSUE, MUSKMELON, NACL, PLANTS, SALT TOLERANCE, STOMATAL CONDUCTANCE

1482

Mayeux, H.S., H.B. Johnson, H.W. Polley, M.J. Dumesnil, and G.A. Spanel. 1993. A controlled environment chamber for growing plants across a subambient co2 gradient. *Functional Ecology 7(1):125-133.*

1. An elongated, controlled environment chamber is described in which a continuous, reproducible gradient of subambient CO2 Concentration ([CO2]) is maintained during daylight hours to assess plant responses to past increases in atmospheric [CO2]. 2. The [CO2] of air moved unidirectionally through the 37-6-m long chamber by a blower is progressively depleted by photosynthesis of plants growing in the

chamber. 3. Plant top- growth is contained in a transparent film tunnel which rests upon an enclosed soil volume that is 45 cm wide and 76 cm deep. 4. The desired minimum concentration to which CO2 is depleted at the end of the chamber, usually 150 or 200 mul l-1, is maintained by varying the blower speed with a micrologger program dependent upon real-time sensing Of [CO2] and light intensity. 5. Dewpoint and dry bulb temperatures are also controlled by a micrologger- and computer-monitored air- conditioning system.

1483

Mayeux, H.S., H.B. Johnson, H.W. Polley, and S.R. Malone. 1997. Yield of wheat across a subambient carbon dioxide gradient. *Global Change Biology 3(3):269-278.*

Yields and yield components of two cultivars of day-neutral spring wheat (Triticum aestivum L.) were assessed along a gradient of daytime carbon dioxide (CO2) concentrations from about 200 to near 350 mu mol CO2 (mol air)(-1) in a 38 m-long controlled environment chamber. The range in CO2 concentration studied approximates that of Earth's atmosphere since the last ice age. This 75% rise in CO2 concentration increased grain yields more than 200% under well-watered conditions and by 80- 150% when wheat was grown without additions of water during the last half of the 100-day growing season. The 27% increase in CO2 from the pre-industrial level of 150 years ago (275 mu mol mol(-1)) to near the current concentration (350 mu mol mol(-1)) increased grain yields of 'Yaqui 54' and 'Seri M82' spring wheats by 55% and 53%, respectively, under well-watered conditions. Yield increased because of greater numbers of grains per spike, rather than heavier grains or numbers of spikes per plant. Water use increased little with CO2 concentration, resulting in improved water use efficiency as CO2 rose. Data suggest that rising CO2 concentration contributed to the substantial increase in average wheat yields in the U.S. during recent decades.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, BP, DRY-MATTER, ENRICHMENT, EXCHANGE, GROWTH, INCREASING CO2, PHOTOSYNTHESIS, RECORD

1484

Mayr, C., M. Miller, and H. Insam. 1999. Elevated CO2 alters community-level physiological profiles and enzyme activities in alpine grassland. *Journal of Microbiological Methods 36(1-2):35-43.*

Plots of an alpine grassland in the Swiss Alps were treated with elevated (680 mu l l(-1)) and ambient CO2 (355 mu l l(-1)) in open top chambers (OTC). Several plots were also treated with NPK-fertilizer. Community level physiological profiles (CLPPs) of the soil bacteria were examined by Biolog GN microplates and enzyme activities were determined through the release of methylumbelliferyl (MUF) and methylcoumarin (MC) from MUF- or MC-labelled substrates. A canonical discriminant analysis (CDA) followed by multivariate analysis of variance showed a significant effect of elevated CO2 on the CLPPs both under fertilized and unfertilized conditions. Further, the installation of the OTCs caused significant shifts in the CLPPs (chamber effect). Of the four enzyme activities tested, the beta-D-cellobiohydrolase (CELase) and N-acetyl-beta-D- glucosaminidase (NAGase) activity were enhanced under elevated CO2. L-Leucin-7-aminopeptidase (APEase) activity decreased, when the plots received fertilizer. beta-D-Glucosidase (GLUase) remained unaffected. The results suggest effects of elevated CO2 on specific microbial activities even under low mineral nutrient conditions and when bulk parameters like microbial biomass or respiration, which have been investigated on the same site, remain unaffected, The observed medium-term changes point at possible long-term consequences for the ecosystem that may not be specified yet.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATIONS, ENRICHMENT, LITTER DECOMPOSITION, MICROBIAL COMMUNITIES, MYCORRHIZAL COLONIZATION, PINE SEEDLINGS, RESPONSES, RHIZOSPHERE, SOIL

1485

Maytin, C.E., M.F. Acevedo, R. Jaimez, R. Andressen, M.A. Harwell, A. Robock, and A. Azocar. 1995. Potential effects of global climatic-change on the phenology and yield of maize in venezuela. *Climatic Change 29(2):189-211.*

Simulated impacts of global and regional climate change, induced by an enhanced greenhouse effect and by Amazonian deforestation, on the phenology and yield of two grain corn cultivars in Venezuela (CENIAP PB-8 and OBREGON) are reported. Three sires were selected: Turen, Barinas and Yaritagua, representing two important agricultural regions in the country. The CERES-Maize model, a mechanistic process-based model, in the Decision Support System for Agrotechnology Transfer (DSSAT) was used for the crop simulations. These simulations assume non-limiting nutrients, no pest damage and no damage from excess water; therefore, the results indicate only the difference between baseline and perturbed climatic conditions, when other conditions remain the same. Four greenhouse-induced global climate change scenarios, covering different sensitivity levels, and one deforestation-induced regional climate change scenario were used. The greenhouse scenarios assume increased air temperature, increased rainfall and decreased incoming solar radiation, as derived from atmospheric GCMs for doubled CO2 conditions. The deforestation scenarios assume increased air temperature, increased incoming solar radiation and decreased rainfall, as predicted by coupled atmosphere- biosphere models for extensive deforestation of a portion of the Amazon basin. Two baseline climate years for each site were selected, one year with average precipitation and another with lower than average rainfall. Scenarios associated with the greenhouse effect cause a decrease in yield of both cultivars at all three sites, while the deforestation scenarios produce small changes. Sensitivity tests revealed the reasons for these responses. Increasing temperatures, especially daily maximum temperatures, reduce yield by reducing the duration of the phenological phases of both cultivars, as expected from CERES- Maize. The reduction of the duration of the kernel filling phase has the largest effect on yield. Increases of precipitation associated with greenhouse warming have no effects on yield, because these sites already have adequate precipitation; however, the crop model used here does not simulate potential negative effects of excess water, which could have important consequences in terms of soil erosion and nutrient leaching. Increases in solar radiation increased yields, according to the non-saturating light response of the photosynthesis rate: of a C-4 plant like corn, compensating for reduced yields from increased temperatures in deforestation scenarios. In the greenhouse scenarios, reduced insolation (due to increased cloud cover) and increased temperatures combine to reduce yields; a combination of temperature increase with a reduction in solar radiation produces fewer and lighter kernels.

KEYWORDS: CROP RESPONSE, MODEL, NITROGEN, SIMULATION

1486

Mbata, G.N., and C. Reichmuth. 1996. The comparative effectiveness of different modified atmospheres for the disinfestation of Bambarra groundnuts, Vigna subterranea (L) Verde, infested by Callosobruchus subinnotatus (Pic) (Coleoptera:Bruchidae). *Journal of Stored Products Research 32(1):45-51.*

Four atmospheres containing high levels of carbon dioxide (CO2) and different quantities of oxygen (0, 2.0, 3.7, 5.1%) were investigated for their toxicity to Callosobruchus subinnotatus (Pie), The quantity of oxygen contained in atmospheres influenced the disinfestation levels in

bambarra groundnuts infested by C. subinnotatus. The different developmental stages had varying susceptibilities to the atmospheres, Atmospheres containing low concentrations of oxygen (2.0, 3.7%) enhanced the mortality of adults, The anoxic atmosphere of 100% CO2 was more toxic to eggs, larvae, and pupae than the other atmospheres, There was a progressive decrease in toxicity as the quantity of oxygen in the inert atmospheres increased. Copyright (C) 1996 Elsevier Science Ltd

1487

McConnaughay, K.D.M., S.L. Bassow, G.M. Berntson, and F.A. Bazzaz. 1996. Leaf senescence and decline of end-of-season gas exchange in five temperate deciduous tree species grown in elevated CO2 concentrations. *Global Change Biology 2(1):25-33.*

We measured rates of leaf senescence and leaf level gas exchange during autumnal senescence for seedlings of five temperate forest tree species under current and elevated atmospheric CO2 concentrations and low- and high-nutrient regimes. Relative indices of whole canopy carbon gain, water loss and water use efficiency through the senescent period were calculated based on a simple integrative model combining gas exchange per unit leaf area and standing canopy area per unit time. Seedlings grown under elevated [CO2] generally had smaller canopies than their current [CO2]-grown counterparts throughout most of the senescent period. This was a result of smaller pre-senescent canopies or accelerated rates of leaf drop. Leaf-level photosynthetic rates were higher under elevated [CO2] for grey birch canopies and for low-nutrient red maple and high-nutrient ash canopies, but declined rapidly to values below those of their current [CO2] counterparts by midway through the senescent period. CO2 enrichment reduced photosynthetic rates for the remaining species throughout some or all of the senescent period. As a result of smaller canopy sizes and reduced photosynthetic rates, elevated [CO2]-grown seedlings had lower indices of whole canopy end-of-season carbon gain with few exceptions. Leaf level transpiration rates were highly variable during autumnal senescence, and neither [CO2] nor nutrient regime had consistent effects on water loss per unit leaf area or integrated whole canopy water loss throughout the senescent period. Indices of whole canopy, end- of-season estimates of water use efficiency, however, were consistently lower under CO2 enrichment, with few exceptions. These results suggest that whole canopy end-of-season gas exchange may be altered significantly in an elvated [CO2] world, resulting in reduced carbon gain and water use efficiency for many temperate forest tree seedlings. Seedling growth and survivorship, and ultimately temperate forest regeneration, could be reduced in CO2-enriched forests of the future.

KEYWORDS: ECOSYSTEMS, ENRICHMENT, LIGHT, NITROGEN, PLANTS, RESPONSES, SEEDLINGS

1488

McConnaughay, K.D.M., G.M. Berntson, and F.A. Bazzaz. 1993. Limitations to co2-induced growth enhancement in pot studies. *Oecologia 94(4):550-557.*

Recently, it has been suggested that small pots may reduce or eliminate plant responses to enriched CO2, atmospheres due to root restriction. While smaller pot volumes provide less physical space available for root growth, they also provide less nutrients. Reduced nutrient availability alone may reduce growth enhancement under elevated CO2. To investigate the relative importance of limited physical rooting space separate from and in conjunction with soil nutrients, we grew plants at ambient and double-ambient CO2 levels in growth containers of varied volume, shape, nutrient concentration, and total nutrient content. Two species (Abutilon theophrasti, a C3 dicot with a deep tap root and Setaria faberii, a C4 monocot with a shallow diffuse root system) were selected for their contrasting physiology and root architecture. Shoot demography was determined weekly and biomass was determined after eight and ten weeks of growth. Increasing total nutrients, either by increasing nutrient concentration or by increasing pot size, increased plant growth. Further, increasing pot size while maintaining equal total nutrients per pot resulted in increased total biomass for both species. CO2-induced growth and reproductive yield enhancements were greatest in pots with high nutrient concentrations, regardless of total nutrient content or pot size, and were also mediated by the shape of the pot. CO2-induced growth and reproductive yield enhancements were unaffected by pot size (growth) or were greater in small pots (reproductive yield), regardless of total nutrient content, contrary to predictions based on earlier studies. These results suggest that several aspects of growth conditions within pots may influence the CO2 responses of plants; pot size, pot shape, the concentration and total amount of nutrient additions to pots may lead to over- or underestimates of the CO2 responses of real-world plants.

KEYWORDS: ATMOSPHERIC CO2, COMMUNITIES, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, RESPONSES, RESTRICTION, ROOT-GROWTH, TUSSOCK TUNDRA

1489

McConnaughay, K.D.M., and J.S. Coleman. 1999. Biomass allocation in plants: Ontogeny or optimality? A test along three resource gradients. *Ecology 80(8):2581-2593.*

We examined biomass allocation patterns throughout the entire vegetative growth phase for three species of annual plants along three separate gradients of resource availability to determine whether observed patterns of allocational plasticity are consistent with optimal partitioning theory. Individuals of the annual plant species Abutilon theophrasti, Chenopodium album, and Polygonum pensylvanicum were grown from locally field-gathered seed in controlled greenhouse conditions across gradients of light, nutrients, and water. Frequent harvests were used to determine the growth and allocation (root vs. shoot, and leaf area vs. biomass) responses of these plants over a 57-d period. Growth analysis revealed that each species displayed significant plasticity in growth rates and substantial amounts of ontogenetic drift in root: shoot biomass ratios and ratios of leaf area to biomass across each of the three resource gradients. Ontogenetically controlled comparisons of root : shoot and leaf area ratios across light and nutrient gradients were generally consistent with predictions based on optimal partitioning theory; allocation to roots decreased and leaf area increased under low light and high nutrient conditions. These trends were confirmed, though were less dramatic, in allometric plots of biomass allocation throughout ontogeny. These species did not alter biomass allocation (beyond ontogenetic drift) in response to the broadly varying water regimes. Furthermore, many of the observed differences in biomass allocation were limited to a given time during growth and development. We conclude that, for these rapidly growing annual species, plasticity in biomass allocation patterns is only partially consistent with optimal partitioning theory, and that these plastic responses are ontogenetically constrained. Further, while these species did adjust biomass allocation patterns in response to light and nutrient availability, they did not adjust biomass allocation in response to water availability, despite dramatic plasticity in growth rates along all three resource gradients. Our results support a developmentally explicit model of plasticity in biomass allocation in response to limiting resources.

KEYWORDS: ELEVATED CO2, GROWTH, INTERNAL NITROGEN CONCENTRATION, LIGHT-INTENSITY, MODEL, PLASTICITY, RESPONSES, ROOT, SHOOT RATIOS, WILD RADISH

1490

McConnaughay, K.D.M., A.B. Nicotra, and F.A. Bazzaz. 1996. Rooting volume, nutrient availability, and CO2-induced growth enhancements in temperate forest tree seedlings. *Ecological Applications 6(2):619-627.*

We examined growth and allocation responses to CO2 enrichment for three species of co-occurring temperate forest tree seedlings grown in pots of varying rooting volumes and nutrient supply. Under both current and projected future CO2 atmospheres, tree seedling growth was substantially greater with greater total nutrient supply (either due to increased nutrient addition rate or increased rooting volume) for all species. Increasing rooting volume alone, holding total nutrient supply constant, increased growth for gray and yellow birch and decreased growth for red maple. Root/shoot ratios were less and specific leaf masses were greater for plants grown in smaller pots, suggesting that the smaller pots did restrict root growth with consequences for whole-plant carbon allocation. After 12 wk of growth at light levels simulating those found in small gaps in temperate forests, each species exhibited growth, allocational and/or architectural differences due to increased CO2. Of 11 traits measured, 9 were significantly altered by CO2 regime. Gray birch responded in architectural and allocational parameters only; total carbon accumulation after 12 wk of growth was not affected by CO2 regime. Red maple and especially yellow birch grew larger in elevated CO2, and were less responsive in architectural and allocational parameters than gray birch. Increasing N concentration did not increase CO2-induced growth enhancements, except for increased leaf production in gray birch. In fact, CO2-induced increases in branch production were greatest at low nutrient concentration. Pot size had no effect on CO2-induced growth responses, except that CO2-induced enhancement in branch production was greater in smaller pots. With few exceptions, conditions within pots did not influence responses to elevated CO2, despite the many growth and architectural responses manifested by these tree seedlings in response to CO2, nutrient regime, and pot size.

KEYWORDS: AMBIENT, CO2 LEVELS, COMMUNITIES, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, LIGHT, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, RESTRICTION

1491

McDonald, E.P., J. Agrell, and R.L. Lindroth. 1999. CO2 and light effects on deciduous trees: growth, foliar chemistry, and insect performance. *Oecologia 119(3):389-399.*

This study examined the effects of CO2 and light availability on sapling growth and foliar chemistry, and consequences for insect performance. Quaking aspen (Populus tremuloides Michx.), paper birch (Betula papyrifera Marsh.), and sugar maple (Acer saccharum Marsh.) were grown in controlled environment greenhouses under ambient or elevated CO2 (38.7 and 69.6 Pa), and low or high light availability (375 and 855 mu mol m(-2) s(-1)). Because CO2 and light are both required for carbon assimilation, the levels of these two resources are expected to have strong interactive effects on tree growth and secondary metabolism. Results from this study support that prediction, indicating that the relative effect of rising atmospheric CO2 concentrations on the growth and secondary metabolism of deciduous trees may be dependent on light environment. Trees in ambient CO2-low light environments had substantial levels of phytochemicals despite low growth rates; the concept of basal secondary metabolism is proposed to explain allocation to secondary metabolites under growth-limiting conditions. Differences between CO2 and light effects on the responses of growth and secondary metabolite levels suggest that relative allocation is not dependent solely on the amount of carbon assimilated. The relative growth rates and indices of feeding efficiency for gypsy moth (Lymantria dispar L.) larvae fed foliage from the experimental treatments showed no significant interactive effects of light and CO2, although some main effects and many host species interactions were significant. Gypsy moth performance was negatively correlated with CO2- and light-induced increases in the phenolic glycoside content of aspen foliage. Insects were not strongly affected, however, by treatment differences in the nutritional and secondary chemical components of birch and maple.

KEYWORDS: BIRCH BETULA, CARBON NUTRIENT BALANCE, ELEVATED ATMOSPHERIC CO2, FOREST TENT CATERPILLARS, GYPSY-MOTH, NO3 AVAILABILITY, PHENOLIC GLYCOSIDES, QUAKING ASPEN, SECONDARY METABOLITES, TERRESTRIAL ECOSYSTEMS

1492

McElwain, J.C. 1998. Do fossil plants signal palaeoatmospheric CO2 concentration in the geological past? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 353(1365):83-95.*

Fossil, subfossil, and herbarium leaves have been shown to provide a morphological signal of the atmospheric carbon dioxide (CO2) environment in which they developed by means of their stomatal density and index. An inverse relationship between stomatal density/index and atmospheric CO2 concentration has been documented for all the studies to date concerning fossil and subfossil material. Furthermore, this relationship has been demonstrated experimentally by growing plants under elevated and reduced CO2 concentrations. To date, the mechanism that controls the stomatal density response to atmospheric CO2 concentration remains unknown. However, stomatal parameters of fossil plants have been successfully used as a proxy indicator of palaeo-CO2 levels. This paper presents new estimates of palaeoatmospheric CO2 concentrations for the Middle Eocene (Lutetian), based on the stomatal ratios of fossil Lauraceae species from Bournemouth in England. Estimates of atmospheric CO2 concentrations derived from stomatal data from plants of the Early Devonian, Late Carboniferous, Early Permian and Middle Jurassic ages are reviewed in the light of new data. Semi-quantitative palaeo-CO2 estimates based on the stomatal ratio (a ratio of the stomatal index of a fossil plant to that of a selected nearest living equivalent) have in the past relied on the use of a Carboniferous standard. The application of a new standard based on the present-day CO2 level is reported here for comparison. The resultant ranges of palaeo-CO2 estimates made from standardized fossil stomatal ratio data are in good agreement with both carbon isotopic data from terrestrial and marine sources and long-term carbon cycle modelling estimates for all the time periods studied. These data indicate elevated atmospheric CO2 concentrations during the Early Devonian, Middle Jurassic and Middle Eocene, and reduced concentrations during the Late Carboniferous and Early Permian. Such data are important in demonstrating the long-term responses of plants to changing CO2 concentrations and in contributing to the database needed for general circulation model climatic analogues.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, ENVIRONMENTAL-CHANGE, EOCENE, INCREASE, INDEX, OAK LEAVES, ORGANIC-MATTER, RECORD, STOMATAL DENSITY

1493

McElwain, J.C., and W.G. Chaloner. 1995. Stomatal density and index of fossil plants track atmospheric carbon-dioxide in the paleozoic. *Annals of Botany 76(4):389-395.*

It has been demonstrated that the leaves of a range of forest tree species have responded to the rising concentration of atmospheric CO2 over the last 200 years by a decrease in both stomatal density and stomatal index. This response has also been demonstrated experimentally by growing plants under elevated CO2 concentrations. Investigation of Quaternary fossil leaves has shown a corresponding stomatal response to changing CO2 concentrations through a glacial-interglacial cycle, as revealed by ice core data. Tertiary leaves show a similar pattern of stomatal density change, using palynological evidence of palaeo-temperature as a proxy

measure of CO2 concentration. The present work extends this approach into the Palaeozoic fossil plant record. The stomatal density and index of Early Devonian, Carboniferous and Early Permian plants has been investigated, to test for any relationship that they may show with the changes in atmospheric CO2 concentration, derived from physical evidence, over that period. Observed changes in the stomatal data give support to the suggestion from physical evidence, that atmospheric CO2 concentrations fell from an Early Devonian high of 10-12 times its present value, to one comparable to that of the present day by the end of the Carboniferous. These results suggest that stomatal density of fossil leaves has potential value for assessing changes in atmospheric CO2 concentration through geological time. (C) 1995 Annals of Botany Company

KEYWORDS: CO2- ENRICHMENT

1494

McElwain, J.C., and W.G. Chaloner. 1996. The fossil cuticle as a skeletal record of environmental change. *Palaios 11(4):376-388.*

The plant cuticle with its stomatal pores represents an important interface between the plant and its surrounding environment. The potential of cuticular features such as cuticle thickness, stomatal density, stomatal index and stomatal ratio to signal the environment in which they grew and developed have been reviewed. In particular new stomatal data from three Yorkshire Middle Jurassic species, Brachyphyllum crucis Kendall, Brachyphyllum mamillare Lindley and Hutton and Ginkgo huttonii (Sternberg) Heer, have been compared with those of two selected nearest living equivalent (NLE) species Athrotaxis cupressoides and Ginkgo biloba, in an attempt to deduce the atmospheric carbon dioxide concentration from that time, It appears that the development of a thick cuticle can represent an adaptation to more than one kind of environmental constraint and evidently is a feature of certain taxonomic groups. It was concluded therefore that cuticle thickness, taken on its own was nor a suitable palaeo-ecological indicator In contrast however stomatal parameters of fossil plants seem to have great potential as palaeo-atmospheric indicators of carbon dioxide and in this sense as "skeletal evidence of palaeo-ecological change." The stomatal density and index results of the Jurassic species were significantly lower ($P < 0.0001$) than those of their selected NLE species, therefore indicating elevated atmospheric CO2 concentrations for the Middle Jurassic. In addition the stomatal ratios of the Jurassic species were in agreement with those of previous Devonian and Carboniferous stomatal ratio results. These results are consistent with the evidence from carbon cycle modelling and carbon isotopic data which infer elevated atmospheric CO2 concentrations curing the Middle Jurassic of 4 to 5 times and 6 to 10 times the present atmospheric level respectively.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, CYCLE, EVOLUTION, LEAF, LEAVES, PLANT, RESPONSES, STOMATAL DENSITY, TEMPERATURE

1495

McGuire, A.D., L.A. Joyce, D.W. Kicklighter, J.M. Melillo, G. Esser, and C.J. Vorosmarty. 1993. Productivity response of climax temperate forests to elevated- temperature and carbon-dioxide - a north-american comparison between 2 global-models. *Climatic Change 24(4):287-310.*

We assess the appropriateness of using regression- and process- based approaches for predicting biogeochemical responses of ecosystems to global change. We applied a regression-based model, the Osnabruck Model (OBM), and a process-based model, the Terrestrial Ecosystem Model (TEM), to the historical range of temperate forests in North America in a factorial experiment with three levels of temperature (+0-degrees-C, +2-degrees-C, and +5-degrees-C) and two levels Of CO2 (350 ppmv and 700 ppmv) at a spatial resolution of 0.5-degrees latitude by 0.5-degrees longitude. For contemporary climate (+0-degrees-C, 3 50 ppmv), OBM and TEM estimate the total net primary productivity (NPP) for temperate forests in North America to be 2.250 and 2.602 x 10(15) g C . yr-1, respectively. Although the continental predictions for contemporary climate are similar, the responses of NPP to altered changes qualitatively differ; at +0-degrees-C and 700 PPMV CO2, OBM and TEM predict median increases in NPP of 12.5% and 2.5%, respectively. The response of NPP to elevated temperature agrees most between the models in northern areas of moist temperate forest, but disagrees in southern areas and in regions of dry temperate forest. In all regions, the response to CO2 is qualitatively different between the models. These differences occur, in part, because TEM includes known feedbacks between temperature and ecosystem processes that affect N availability, photosynthesis, respiration, and soil moisture. Also, it may not be appropriate to extrapolate regression-based models for climatic conditions that are not now experienced by ecosystems. The results of this study suggest that the process-based approach is able to progress beyond the limitations of the regression-based approach for predicting biogeochemical responses to global change.

KEYWORDS: CO2- ENRICHMENT, DRY-MATTER, GRASSLAND BIOGEOCHEMISTRY, GREAT-PLAINS, GROWTH, NITROGEN, PHOTOSYNTHESIS, SIMULATION, TERRESTRIAL ECOSYSTEMS, VEGETATION

1496

McGuire, A.D., J.M. Melillo, and L.A. Joyce. 1995. The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon-dioxide. *Annual Review of Ecology and Systematics 26:473-503.*

We review experimental studies to evaluate how the nitrogen cycle influences the response of forest net primary production (NPP) to elevated CO2. The studies in our survey report that at the tissue level, elevated CO2 reduces leaf nitrogen concentration an average 21%, but that it has a smaller effect on nitrogen concentrations in stems and fine roots. In contrast, higher soil nitrogen availability generally increases leaf nitrogen concentration. Among studies that manipulate both soil nitrogen availability and atmospheric CO2, photosynthetic response depends on a linear relationship with the response of leaf nitrogen concentration and the amount of change in atmospheric CO2 concentration. Although elevated CO2 often results in reduced tissue respiration rate per unit biomass, the link to changes in tissue nitrogen concentration is not well studied.

KEYWORDS: BETULA-PENDULA ROTH, CASTANEA-SATIVA MILL, CHENOPODIUM-ALBUM L, CO2- ENRICHMENT, GROWTH-RESPONSE, LIRIODENDRON-TULIPIFERA L, LOBLOLLY-PINE SEEDLINGS, QUERCUS-ALBA, USE EFFICIENCY, WATER-STRESS

1497

McGuire, A.D., J.M. Melillo, D.W. Kicklighter, and L.A. Joyce. 1995. Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates. *Journal of Biogeography 22(4-5):785-796.*

We use a new version of the Terrestrial Ecosystem Model (TEM), which has been parameterized to control for reactive soil organic carbon (SOC) across climatic gradients, to evaluate the sensitivity of SOC to a 1 degrees C warming in both empirical and process-based analyses. In the empirical analyses we use the steady state SOC estimates of TEM to derive SOC-response equations that depend on temperature and volumetric soil moisture, and extrapolate them across the terrestrial biosphere at 0.5 degrees spatial resolution. For contemporary climate and atmospheric CO2, mean annual temperature explains 34.8% of the variance in the natural logarithm of TEM-estimated SOC. Because the

inclusion of mean annual volumetric soil moisture in the regression explains an additional 19.6%, a soil moisture term in an equation of SOC response should improve estimates. For a 1 degrees C warming, the globally derived empirical model estimates a terrestrial SOC loss of 22.6 10(15) g (Pg), with 77.9% of the loss in extra-tropical ecosystems. To explore whether loss estimates of SOC are affected by the spatial scale at which the response equations are derived, we derive equations for each of the eighteen ecosystems considered in this study. The sensitivity of terrestrial SOC estimated by summing the losses predicted by each of the ecosystem empirical models is greater (27.9 Pg per degrees C) than that estimated by the global empirical model; the 12.2 Pg loss (43.7%) in tropical ecosystems suggests that they may be more sensitive to warming. The global process-based loss of SOC estimated by TEM in response to a 1 degrees C warming (26.3 Pg) is similar to the sum of the ecosystem empirical losses, but the 13.6 Pg loss (51.7%) in extra-tropical ecosystems suggests that they may be slightly less sensitive to warming. For the modelling of SOC responses, these results suggest that soil moisture is useful to incorporate in empirical models of SOC response and that globally derived empirical models may conceal regional sensitivity pf SOC to warming. The analyses in this study suggest that the maximum loss of SOC to the atmosphere per degrees C warming is less than 2% of the terrestrial soil carbon inventory. Because the NPP response to elevated CO2 has the potential to compensate for this loss, the scenario of warming enhancing soil carbon loss to further enhance warming is unlikely in the absence of land use or changes in vegetation distribution.

KEYWORDS: CO2, DIOXIDE, ECOSYSTEMS, GRASSLAND BIOGEOCHEMISTRY, GREAT-PLAINS, PRODUCTIVITY, SPATIAL VARIABILITY, STORAGE, TEMPERATURE, WORLD

1498

McGuire, A.D., J.M. Melillo, D.W. Kicklighter, Y.D. Pan, X.M. Xiao, J. Helfrich, B. Moore, C.J. Vorosmarty, and A.L. Schloss. 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles 11(2):173-189.*

We ran the terrestrial ecosystem model (TEM) for the globe at 0.5 degrees resolution for atmospheric CO2 concentrations of 340 and 680 parts per million by volume (ppmv) to evaluate global and regional responses of net primary production (NPP) and carbon storage to elevated CO2 for their sensitivity to changes in vegetation nitrogen concentration. At 340 ppmv, TEM estimated global NPP of 49.0 10(15) g (Pg) C yr(-1) and global total carbon storage of 1701.8 Pg C; the estimate of total carbon storage does not include the carbon content of inert soil organic matter. For the reference simulation in which doubled atmospheric CO2 was accompanied with no change in vegetation nitrogen concentration, global NPP increased 4.1 Pg C yr(-1) (8.3%), and global total carbon storage increased 114.2 Pg C. To examine sensitivity in the global responses of NPP and carbon storage to decreases in the nitrogen concentration of vegetation, we compared doubled CO2 responses of the reference TEM to simulations in which the vegetation nitrogen concentration was reduced without influencing decomposition dynamics ("lower N" simulations) and to simulations in which reductions in vegetation nitrogen concentration influence decomposition dynamics ("lower N+D" simulations). We conducted three lower N simulations and three lower N+D simulations in which we reduced the nitrogen concentration of vegetation by 7.5, 15.0, and 22.5%. In the lower N simulations, the response of global NPP to doubled atmospheric CO2 increased approximately 2 Pg C yr(-1) for each incremental 7.5% reduction in vegetation nitrogen concentration, and vegetation carbon increased approximately an additional 40 Pg C, and soil carbon increased an additional 30 Pg C, for a total carbon storage increase of approximately 70 Pg C. In the lower N+D simulations, the responses of NPP and vegetation carbon storage were relatively insensitive to differences in the reduction of nitrogen concentration, but soil carbon storage showed a large change. The insensitivity of NPP in the N+D simulations occurred because potential enhancements in NPP associated with reduced vegetation nitrogen concentration were approximately offset by lower nitrogen availability associated with the decomposition dynamics of reduced litter nitrogen concentration. For each 7.5% reduction in vegetation nitrogen concentration, soil carbon increased approximately an additional 60 Pg C, while vegetation carbon storage increased by only approximately 5 Pg C. As the reduction in vegetation nitrogen concentration gets greater in the lower N+D simulations, more of the additional carbon storage tends to become concentrated in the north temperate- boreal region in comparison to the tropics. Other studies with TEM show that elevated CO2 more than offsets the effects of climate change to cause increased carbon storage. The results of this study indicate that carbon storage would be enhanced by the influence of changes in plant nitrogen concentration on carbon assimilation and decomposition rates. Thus changes in vegetation nitrogen concentration may have important implications for the ability of the terrestrial biosphere to mitigate increases in the atmospheric concentration of CO2 and climate changes associated with the increases.

KEYWORDS: C-4 PLANTS, CHENOPODIUM-ALBUM L, CO2 CONCENTRATION, FORESTS, GROWTH-RESPONSE, LEAF NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, USE EFFICIENCY, WATER

1499

McHale, P.J., M.J. Mitchell, and F.P. Bowles. 1998. Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28(9):1365-1372.*

The response of trace gas fluxes (CO2 CH4 and N-2) and litter decomposition to increased soil temperature was evaluated in a northern hardwood forest. Four experimental plots (10 x 10 m) had heating cables installed within the forest floor. Temperatures at 5 cm were increased 2.5, 5.0, or 7.5 degrees C in individual heated plots during the field season in 1993 and 1994. The fourth plot was a cabled, nonheated reference. Trace gas fluxes were monitored using closed chambers. Soil moisture was monitored using tensiometers and time domain reflectometry. Changes in leaf litter decomposition were quantified using litter bags for American beech (Fagus grandifolia Ehrh.) and sugar maple (Acer saccharum Marsh.) litter. Fluxes of CO2 increased exponentially with increased soil temperatures within treatments and were higher in heated plots than in the reference plot. Temperature coefficients (Q(10)) and mass remaining of American beech leaf litter decreased with the level of heating, suggesting a nonlinear microbial response to elevated temperatures. Soil water content exhibited the most influence on CH4 and N2O flux in the second season. The experimental manipulations showed the importance of evaluating the influence of soil temperature coupled with effects of N and moisture availability.

KEYWORDS: CLIMATE CHANGE, FIELD, METHANE, NITROUS-OXIDE, RESPONSES, TEMPERATE

1500

McIntyre, M., and B. McNeil. 1998. Morphogenetic and biochemical effects of dissolved carbon dioxide on filamentous fungi in submerged cultivation. *Applied Microbiology and Biotechnology 50(3):291-298.*

The inhibitory effects of elevated CO2 in submerged fermentation processes involving bacteria and yeasts have been extensively examined. However, until recently, there have been few similar studies involving filamentous fungi, despite the economic importance of this group of organisms. Many of the investigations that have been carried out have

involved inappropriate simulation methods and, as a result, may have overestimated the morphogenetic and biochemical effects of elevated CO2 on filamentous fungi. Recent studies, involving continuous culture of Aspergillus niger and the use of computerised image analysis systems, have allowed a more detailed and accurate description of elevated CO2 inhibition and quantification of the subtler morphogenetic effects. A critical evaluation of the various experimental methods that have been used to simulate, at laboratory scale, what is assumed to occur in large-scale bioreactors is necessary. The review of simulation methods employed has much broader relevance to many other microbial and cell culture systems, emphasising the need to think about the appropriateness and relevance of experimental design.

KEYWORDS: ASPERGILLUS-NIGER A60, CHRYSOGENUM, CO2, CONTINUOUS CULTURES, EVOLUTION RATE, IMAGE-ANALYSIS, MICROORGANISMS, MORPHOLOGY, PENICILLIN FERMENTATIONS, YEAST GROWTH

1501

McKane, R.B., E.B. Rastetter, J.M. Melillo, G.R. Shaver, C.S. Hopkinson, D.N. Fernandes, D.L. Skole, and W.H. Chomentowski. 1995. Effects of global change on carbon storage in tropical forests of south-america. *Global Biogeochemical Cycles 9(3):329-350.*

We used a process-based model of ecosystem biogeochemistry (MEL-GEM) to evaluate the effects of global change on carbon (C) storage in mature tropical forest ecosystems in the Amazon Basin of Brazil. We first derived a single parameterization of the model that was consistent with all the C stock and turnover data from three intensively studied sites within the Amazon Basin that differed in temperature, rainfall, and cloudiness. The range in temperature, soil moisture, and photosynthetically active radiation (PAR) among these sites is about as large as the anticipated changes in these variables in the tropics under CO2-induced climate change. We then tested the parameterized model by predicting C stocks along a 2400-km transect in the Amazon Basin. Comparison of predicted and measured vegetation and soil C stocks along this transect suggests that the model provides a reasonable approximation of how climatic and hydrologic factors regulate present-day C stocks within the Amazon Basin. Finally, we used the model to predict and analyze changes in ecosystem C stocks under projected changes in atmospheric CO2 and climate. The central hypothesis of this exercise is that changes in ecosystem C storage in response to climate and CO2 will interact strongly with changes in other element cycles, particularly the nitrogen (N) and phosphorus (P) cycles. We conclude that C storage will increase in Amazonian forests as a result of(1) redistribution of nutrients from soil (with low C:nutrient ratios) to vegetation (with high C:nutrient ratios), (2) increases in the C:nutrient ratio of vegetation and soil, and (3) increased sequestration of external nutrient inputs by the ecosystem. Our analyses suggest that C:nutrient interactions will constrain increases in C storage to a maximum of 63 Mg/ha during the next 200 years, or about 16% above present-day stocks. However, it is impossible to predict how much smaller the actual increase in C storage will be until more is known about the controls on soil P availability. On the basis of these analyses, we identify several topics for further research in the moist tropics that must be addressed to resolve these uncertainties.

KEYWORDS: AMAZON BASIN, CLIMATE CHANGE, CYCLE, DIOXIDE, MODEL, NUTRIENT DYNAMICS, PRODUCTIVITY, RESPONSES, SOILS, TERRESTRIAL ECOSYSTEMS

1502

McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin. 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology 78(4):1170-1187.*

We used a process-based model of ecosystem carbon (C) and nitrogen (N) dynamics, MEL-GEM (Marine Biological Laboratory General Ecosystem Model), to integrate and analyze the results of several experiments that examined the response of arctic tussock tundra to manipulations of CO2, temperature, light, and soil nutrients. The experiments manipulated these variables over 3- to 9-yr periods and were intended to simulate anticipated changes in the arctic environment. Our objective was to use the model to extend the analysis of the experimental data so that unmeasured changes in ecosystem C storage and the underlying mechanisms controlling those changes could be estimated and compared. Using an inverse calibration method, we derived a single parameter set for the model that closely simulated the measured responses of tussock tundra to all of the experimental treatments. This parameterization allowed us to infer confidence limits for ecosystem components and processes that were not directly measured in the experiments. Thus, we used the model to estimate changes in ecosystem C storage by inferring key soil processes within the constraints imposed by measured components of the ecosystem C budget. Because tussock tundra is strongly N limited, we hypothesized that changes in ecosystem C storage in response to the experimental treatments would be constrained by several key aspects of C-N interactions: (1) changes in the amount of N in the ecosystem, (2) changes in the C:N ratios of vegetation and soil, and (3) redistribution of N between soil (with a low C:N ratio) and vegetation (with a high C:N ratio). The model results reveal widely differing patterns of change in C-N interactions and constraints on change in ecosystem C storage among treatments. For example, after 9 yr the elevated CO2 (2 x ambient) treatment and the N fertilized (10 g N.m(-2) yr(-1)) treatment increased ecosystem C stocks by 1.4 and 2.9%, respectively. Whereas the increase in the CO2 treatment was due solely to an increase in the C:N ratios of vegetation and soil, the increase in the fertilized treatment was due to increased ecosystem N content and a shift of N from soil to vegetation. In contrast, the greenhouse (3.5 degrees C above ambient) and shade (one-half ambient light) treatments decreased ecosystem C stocks by 1.9 and 2.7%, respectively. The primary reason for the net C losses in these treatments was an increase in respiration relative to photosynthesis, with a consequent decrease in the ecosystem C:N ratio, However, when we simulated the elevated temperatures in the greenhouse treatment without the confounding effects of decreased light intensity (an artifact of the greenhouse structures), there was a long-term increase in ecosystem C stocks because of increased photosynthetic response to the temperature-induced shift of N from soil to vegetation. If our simulated changes in ecosystem C storage are extrapolated for the approximate to 43 Pg C contained in arctic tundras globally, the maximum net gain or loss (approximate to 0.3% per yr) from tundra would be equivalent to 0.13 Pg C/yr. Although fluxes of this magnitude would have a relatively minor impact on current changes in atmospheric CO2, the long-term impact on tundra C stores could be significant. The synthesis and insights provided by the model should make it possible to extrapolate into the future with a better understanding of the processes governing long- term changes in tundra C storage.

KEYWORDS: ALASKAN TUSSOCK TUNDRA, ARCTIC TUNDRA, CO2, ERIOPHORUM VAGINATUM, GLOBAL CHANGE, ORGANIC-MATTER, PLANT GROWTH, TERRESTRIAL ECOSYSTEMS, VEGETATION TYPES, VERTICAL- DISTRIBUTION

1503

McKee, I.F., J.F. Bullimore, and S.P. Long. 1997. Will elevated CO2 concentrations protect the yield of wheat from O-3 damage? *Plant, Cell and Environment 20(1):77-84.*

This study investigated the interacting effects of carbon dioxide and ozone concentrations on the growth and yield of spring wheat (Triticum aestivum L, cv, Wembley), Plants were exposed from time of sowing to harvest to reciprocal combinations of two carbon dioxide and two ozone treatments: [CO2] at 350 or 700 mu mol mol(-1), and [O-3] at <5 or 60

nmol mol(-1), Records of leaf emergence, leaf duration and tillering were taken throughout leaf development, At harvest, biomass, yield and partitioning were analysed. Our data showed that elevated [CO2] fully protected against the detrimental effect of elevated [O-3] on biomass, but not yield.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, EXCHANGE, EXPOSURE, GRAIN QUALITY, GROWTH, OZONE, PHOTOSYNTHESIS, RESPONSES, SPRING WHEAT

1504

McKee, I.F., M. Eiblmeier, and A. Polle. 1997. Enhanced ozone-tolerance in wheat grown at an elevated CO2 concentration: ozone exclusion and detoxification. *New Phytologist 137(2):275-284.*

Elevated [CO2] has been shown to protect photosynthesis and growth of wheat against moderately elevated [O-3]. To investigate the role of ozone exclusion and detoxification in this protection, spring wheat (Triticum aestivum L. cv. Wembley) was grown from seed, in controlled-environment chambers, under reciprocal combinations of [CO2] at 350 or 700 mu mol mol(-1) and [O-3] peaking at < 5 or 60 nmol mol(-1), respectively. Cumulative ozone dose to the mesophyll and antioxidant status were determined throughout flag leaf development. Catalase activity correlated with rates of photorespiration and declined in response to elevated [CO2] and/or [O-3]. Superoxide dismutase activity was not significantly affected by either condition. Neither ascorbate nor glutathione content was enhanced by elevated [CO2]. In wheat, at moderately elevated [O-3], our results show that stomatal exclusion plays a major role in the protective effect of elevated [CO2] against O-3 damage.

KEYWORDS: ATMOSPHERIC CO2, BEAN-LEAVES, CARBON DIOXIDE, HYDROGEN- PEROXIDE, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PICEA-ABIES L, RESPONSES, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

1505

McKee, I.F., P.K. Farage, and S.P. Long. 1995. The interactive effects of elevated co2 and o-3 concentration on photosynthesis in spring wheat. *Photosynthesis Research 45(2):111-119.*

This study investigated the interacting effects of carbon dioxide and ozone on photosynthetic physiology in the flag leaves of spring wheat (Triticum aestivum L. cv. Wembley), at three stages of development. Plants were exposed throughout their development to reciprocal combinations of two carbon dioxide and two ozone treatments: [CO2] at 350 or 700 mu mol mol(-1), [O-3] at < 5 or 60 nmol mol(-1). Gas exchange analysis, coupled spectrophotometric assay for RuBisCO activity, and SDS-PAGE, were used to examine the relative importance of pollutant effects on i) stomatal conductance, ii) quantum yield, and iii) RuBisCO activity, activation, and concentration. Independently, both elevated [CO2] and elevated [O-3] caused a loss of RuBisCO protein and V-cmax. In combination, elevated [CO2] partially protected against the deleterious effects of ozone. It did this partly by reducing stomatal conductance, and thereby reducing the effective ozone dose. Elevated [O-3] caused stomatal closure largely via its effect on photoassimilation.

KEYWORDS: ATMOSPHERIC CO2, EXPOSURE, FIELD, NET PHOTOSYNTHESIS, OXYGENASE, OZONE STRESS, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, TEMPERATURE, TRITICUM-AESTIVUM L

1506

McKee, I.F., P.K. Farage, and S.P. Long. 1995. The interactive effects of elevated CO2 and O-3 concentration on photosynthesis in spring wheat (vol 45, pg 111, 1995). *Photosynthesis Research 46(3):479.*

1507

McKee, I.F., and F.I. Woodward. 1994. Co2 enrichment responses of wheat - interactions with temperature, nitrate and phosphate. *New Phytologist 127(3):447-453.*

Rising levels of atmospheric CO2, climate change, and fertilizer pollution provide the ecological imperative for investigating the interaction between plant responses to atmospheric CO2 concentration, temperature and nutrient supply. In this study spring wheat (Triticum aestivum L. cv. Wembley) was grown at 40, 50, 60 and 70 Pa atmospheric CO2 pressure and three experiments were conducted to investigate interactions between growth responses to the CO2 treatment and: (i) temperature (24/16 degrees C vs. 18/10 degrees C - day/night), (ii) nutrient solution nitrate concentration (2.5, 5, 10 and 15 mM Ca(NO3)(2).4H(2)O), and (iii) phosphate concentration (0.025 and 0.5 mM KH2PO4). Dry mass and root/shoot ratio increased with CO2 level at the higher temperature. These responses were reversed at the lower temperature. The increase in yield with CO2 enhancement was limited by low rates of nutrient supply in both absolute and relative terms. In the elevated CO2 treatments, the shoot nitrogen concentration was reduced, as was the proportional allocation to the uppermost leaves. These results are discussed with respect to possible physiological mechanisms and potential for improved crop performance in a future, elevated CO2 world.

KEYWORDS: AIR- TEMPERATURE, CARBON DIOXIDE, DIFFERENT IRRADIANCES, DRY-MATTER, ELEVATED CO2, PLANT GROWTH, SPRING WHEAT, STOMATAL CONDUCTANCE, WATER-USE, WINTER-WHEAT

1508

McKee, I.F., and F.I. Woodward. 1994. The effect of growth at elevated co2 concentrations on photosynthesis in wheat. *Plant, Cell and Environment 17(7):853-859.*

Rising levels of atmospheric CO2 will have profound, direct effects on plant carbon metabolism. In this study we used gas exchange measurements, models describing the instantaneous response of leaf net CO2 assimilation rate (A) to intercellular CO2 partial pressure (C-i), in vitro enzyme activity assay, and carbohydrate assay in order to investigate the photosynthetic responses of wheat (Triticum aestivum L., cv. Wembley) to growth under elevated partial pressures of atmospheric CO2 (C- a). At flag leaf ligule emergence, the modelled, in vivo, maximum carboxylation velocity for RuBisCO was significantly lower in plants grown at elevated C-a than in plants grown at ambient C-a (70 Pa compared with 40 Pa). By 12 d after ligule emergence, no significant difference in this parameter was detectable. At ligule emergence, plants grown at elevated C-a exhibited reduced in vitro initial activities and activation states of RuBisCO. At their respective growth C-i values, the photosynthesis of 40-Pa-grown plants was sensitive to p(O-2) and to p(CO2), whereas that of 70-Pa-grown plants was insensitive. Both sucrose and starch accumulated more rapidly in the leaves of plants grown at 70 Pa. At flag leaf ligule emergence, modelled non-photorespiratory respiration in the light (R(d)) was significantly higher in 70-Pa-grown plants than in 40-Pa-grown plants. By 12 d after ligule emergence no significant differences in R(d) were detectable.

KEYWORDS: ANTISENSE RBCS, ATMOSPHERIC CO2, CALVIN CYCLE ENZYMES, CARBON DIOXIDE, DARK RESPIRATION, GAS-EXCHANGE, LEAVES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO ACTIVITY

1509

McKeehen, J.D., D.J. Smart, C.L. Mackowiak, R.M. Wheeler, and S.S. Nielsen. UNKNOWN YEAR. Effect of CO2 levels on nutrient content of lettuce and radish. *Natural and Artificial Ecosystems :85-92.*

Atmospheric carbon-dioxide enrichment is known to affect the yield of lettuce and radish grown in controlled environments, but little is known about CO2 enrichment effects on the chemical composition of lettuce and radish. These crops are useful model systems for a Controlled Ecological Life-Support System (CELSS), largely because of their relatively short production cycles. Lettuce (Lactuca sativa L.) cultivar 'Waldmann's Green' and radish (Raphanus sativus L.) cultivar 'Giant White Globe' were grown both in the field and in controlled environments, where hydroponic nutrient solution, light, and temperature were regulated, and where CO2 levels were controlled at 400, 1000, 5000, or 10,000 ppm. Plants were harvested at maturity, dried, and analyzed for proximate composition (protein, fat, ash, and carbohydrate), total nitrogen (N), nitrate N, free sugars, starch, total dietary fiber, and minerals. Total N, protein N, nonprotein N (NPN), and nitrate N generally increased for radish roots and lettuce leaves when grown under growth chamber conditions compared to field conditions. The nitrate-N level of lettuce leaves, as a percentage of total NPN, decreased with increasing levels of CO2 enrichment. The ash content of radish roots and of radish and lettuce leaves decreased with increasing levels of CO2 enrichment. The levels of certain minerals differed between field- and chamber-grown materials, including changes in the calcium (Ca) and phosphorus (P) contents of radish roots and lettuce leaves, resulting in reduced Ca/P ratio for chamber- grown materials. The free-sugar contents were similar between the field and chamber-grown lettuce leaves, but total dietary fiber content was much higher in the field-grown plant material. The starch content of growth-chamber lettuce increased with CO2 level.

KEYWORDS: INCOMPLETE, CARBOHYDRATE, GROWTH, NITRATE, NITRITE

1510

McLaughlin, S., and K. Percy. 1999. Forest health in North America: Some perspectives on actual and potential roles of climate and air pollution. *Water, Air, and Soil Pollution 116(1-2):151-197.*

The perceived health of forest ecosystems over large temporal and spatial scales can be strongly influenced by the frames of reference chosen to evaluate both forest condition and the functional integrity of sustaining forest processes. North American forests are diverse in range, species composition, past disturbance history, and current management practices. Therefore the implications of changes in environmental stress from atmospheric pollution and/or global climate change on health of these forests will vary widely across the landscape. Forest health surveys that focus on the average forest condition may do a credible job of representing the near-term trends in economic value while failing to detect fundamental changes in the processes by which these values are sustained over the longer term. Indications of increased levels of environmental stress on forest growth and nutrient cycles are currently apparent in several forest types in North America. Measurements of forest ecophysiological responses to air pollutants in integrated case studies with four forest types (southern pine, western pine, high elevation red spruce, and northeastern hardwoods) indicate that ambient levels of ozone and/or acidic deposition can alter basic processes of water, carbon, and nutrient allocation by forest trees. These changes then provide a mechanistic basis for pollutant stress to enhance a wider range of natural stresses that also affect and are affected by these resources. Future climatic changes may ameliorate (+ CO2) or axacerbate (+ temperature, + UV-B) these effects. Current projections of forest responses to global climate change do not consider important physiological changes induced by air pollutants that may amplify climatic stresses. These include reduced rooting mass, depth, and function, increased respiration, and reduced water use efficiency. Monitoring and understanding the relative roles of natural and anthropogenic stress in influencing future forest health will require programs that are structured to evaluate responses at appropriate frequencies across gradients in both forest resources and the stresses that influence them. Such programs must also be accompanied by supplemental process -oriented and pattern -oriented investigations that more thoroughly test cause and effect relationships among stresses and responses of both forests and the biogeochemical cycles that sustain them.

KEYWORDS: ABIES L KARST, ACIDIC DEPOSITION, FOLIAR NUTRIENT STATUS, LOBLOLLY-PINE SEEDLINGS, NITROGEN DEPOSITION, PICEA-ABIES, QUEBEC APPALACHIANS, RED SPRUCE SAPLINGS, SOUTHEASTERN UNITED-STATES, SUGAR MAPLE DIEBACK

1511

McMaster, G.S., D.R. LeCain, J.A. Morgan, L. Aiguo, and D.L. Hendrix. 1999. Elevated CO2 increases wheat CER, leaf and tiller development, and shoot and root growth. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 183(2):119-128.*

Whole-plant responses to elevated CO2 throughout the life cycle are needed to understand future impacts of elevated atmospheric CO2. In this study, Triticum aestivum L. leaf carbon exchange rates (CER) and carbohydrates, growth, and development were examined at the tillering, booting, and grain-filling stages in growth chambers with CO2 concentrations of 350 (ambient) or 700 thigh) mu mol mol(-1). Single-leaf CER values measured on plants grown at high CO2 were 50% greater than those measured on plants grown at ambient CO2 for all growth stages, with no photosynthetic acclimation observed at high CO2. Leaves grown in high CO2 had more starch and simple sugars at tillering and booting, and more starch at grain-filling, than those grown in ambient CO2. CER and carbohydrate levels were positively correlated with leaf appearance rates and tillering (especially third-, fourth- and fifth-order tillers). Elevated CO2 slightly delayed tiller appearance, but accelerated tiller development after appearance. Although high CO2 increased leaf appearance rates, final leaf number/culm was not effected because growth stages were reached slightly sooner. Greater plant biomass was related to greater tillering. Doubling CO2 significantly increased both shoot and root dry weight, but decreased the shoot to root ratio. High CO2 plants had more spikes plant(-1) and spikelets spike(-1), but a similar number of fertile spikelets spike(-1). Elevated CO2 resulted in greater shoot, root and spike production and quicker canopy development by increasing leaf and tiller appearance rates and phenology.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, EXCHANGE, NITROGEN, PHOTOSYNTHESIS, SPRING WHEAT, VEGETATIVE DEVELOPMENT, WINTER-WHEAT, YIELD

1512

McMaster, H.J. 1999. The potential impact of global warming on hail losses to winter cereal crops in New South Wales. *Climatic Change 43(2):455-476.*

This study was undertaken to determine the impact of potential global warming on the magnitude of hail losses to winter cereal crops within two areas situated on the western slopes of New South Wales, Australia. A model relating historical crop hail losses to climatic variables was developed for each area. These models included seasonal measures of vertical instability, low- level moisture and the height of the freezing level. In both areas, windshear was not found to be an important factor influencing seasonal crop hail losses. The two crop hail loss models were then used in conjunction with upper-air climatic data from three single

mixed-layer global climate models (GCMs). Each GCM was run for 1 x CO2 conditions and for 2 x CO2 conditions. The enhanced greenhouse effect on climatic variables was taken to be the difference between their values for these two runs. Changes to climatic variables were then translated directly into changes in the percentage value of the winter cereal crop lost due to hail. In both areas, the three GCMs agreed concerning the direction of change in each of the variables used in the crop hail loss model. GCM simulations of the greenhouse effect resulted in a decline in winter cereal crop hail losses, with the exception of one GCM simulation at one location where losses increased slightly. None of the changes due to the enhanced greenhouse effect, however, were significant owing to a large observed seasonal variability of crop hail losses. Also, the simulated seasonal variability of crop hail losses did not change significantly due to the enhanced greenhouse effect. These results depended on two important assumptions. Firstly, it was assumed that the dominant relationships between climatic variables and crop hail losses in the past would remain the same in a future climate. Secondly, it was assumed that the single mixed-layer GCMs used in the study were correctly predicting climate change under enhanced greenhouse conditions.

KEYWORDS: CLIMATE CHANGE, EL-NINO, MODEL, RAINFALL, SIMULATED CONVECTIVE STORMS, TEMPERATURE

1513

McMurtrie, R.E., and H.N. Comins. 1996. The temporal response of forest ecosystems to doubled atmospheric CO2 concentration. *Global Change Biology 2(1):49-57.*

Vegetation responses to high [CO2] include both direct photosynthetic effects and indirect effects associated with various plant and soil feedbacks. Synthesis of these direct and indirect effects requires ecosystem process models describing the cycling of carbon and essential mineral nutrients through plants and soils. Here we use the ecosystem model G'DAY to investigate responses to an instantaneous doubling of [CO2]. The analysis indicates that the magnitude and even direction of the growth response to high [CO2] can vary widely on different timescales, because responses on different timescales are determined by different ecosystem-level feedbacks and hence by different sets of key model parameters. Of particular importance are parameters describing the flexibility of plant and soil nitrogen to carbon (N:C) ratios; large responses occur if N:C ratios decline significantly at high [CO2], with little or no response if N:C ratios are inflexible. According to G'DAY, the CO2-response changes over time because responses on longer timescales are dictated by the N:C ratios of less rapidly cycled organic matter.

KEYWORDS: CARBON, CLIMATE, DECOMPOSITION, DYNAMICS, ELEVATED CO2, LEAF LITTER, NITROGEN, NUTRIENT, PRODUCTIVITY, TERRESTRIAL ECOSYSTEMS

1514

McMurtrie, R.E., H.N. Comins, M.U.F. Kirschbaum, and Y.P. Wang. 1992. Modifying existing forest growth-models to take account of effects of elevated CO2. *Australian Journal of Botany 40(4-5):657-677.*

Most published process models of the growth of forest stands are concerned predominantly with either tree physiology or nutrient cycling, concentrating respectively on photosynthetic carbon gain and allocation, or on decomposition and nutrient uptake processes. Mechanistic formulations of direct CO2 effects on photosynthesis have been incorporated in some physiology-based models, whereas modifications incorporating direct CO2 effects in nutrient-driven models have usually been more empirical. Physiology-based models predict considerable CO2-fertiliser effects, while nutrient driven models tend to be less sensitive to elevated ambient CO2 concentration (C(a)). This paper describes how effects of elevated C(a) can be incorporated in these various types of forest growth models. The magnitude of the simulated response to elevated C(a) varies markedly depending on a particular model's spatial and temporal resolution and on which processes are incorporated. Two physiology-based models of forest canopy processes (MAESTRO and BIOMASS) and a plant-soil model (G'DAY) are considered here. MAESTRO and BIOMASS incorporate mechanistic descriptions of the biochemical basis of photosynthesis by C3 plants, while G'DAY contains a simplified formulation but includes soil processes. All three models are used to simulate the response to an instantaneous doubling of C(a). Simulations of MAESTRO and BIOMASS show that on a clear day total canopy photsynthesis is temperature-dependent with increases of approximately 10, 45 and 70% at 10. 25 and 40-degrees-C respectively. A simulation for a stand of Pinus radiata growing with abundant water and nutrients and mean annual day-time temperature of 14.8-degrees-C shows an increase of 25% in annual canopy photosynthesis. On nutrient-limited sites plant responses to elevated C(a) are constrained by feedbacks associated with rates of decomposition and nutrient cycling. According to the G'DAY model, which incorporates these feedbacks, an instantaneous doubling of C(a) leads to a 27% initial productivity increase lasting less than a decade and a more modest increase of 8% sustained in the long term.

KEYWORDS: C-4 PLANTS, EUCALYPTUS-PAUCIFLORA, LEAF NITROGEN, PAR ABSORPTION, PHOTOSYNTHESIS, PRODUCTIVITY, QUANTUM YIELD, SITKA SPRUCE, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

1515

McMurtrie, R.E., and Y.P. Wang. 1993. Mathematical-models of the photosynthetic response of tree stands to rising co2 concentrations and temperatures. *Plant, Cell and Environment 16(1):1-13.*

Two published models of canopy photosynthesis, MAESTRO and BIOMASS, are simulated to examine the response of tree stands to increasing ambient concentrations of carbon dioxide (C(a)) and temperatures. The models employ the same equations to described leaf gas exchange, but differ considerably in the level of detail employed to represent canopy structure and radiation environment. Daily rates of canopy photosynthesis simulated by the two models agree to within 10% across a range of CO2 concentrations and temperatures. A doubling of C(a) leads to modest increases of simulated daily canopy photosynthesis at low temperatures (10% increase at 10-degrees- C), but larger increases at higher temperatures (60% increase at 30-degrees-C). The temperature and CO2 dependencies of canopy photosynthesis are interpreted in terms of simulated contributions by quantum-saturated and non-saturated foliage. Simulations are presented for periods ranging from a diurnal cycle to several years. Annual canopy photosynthesis simulated by BIOMASS for trees experiencing no water stress is linearly related to simulated annual absorbed photosynthetically active radiation, with light utilization coefficients for carbon of epsilon = 1.66 and 2.07 g MJ-1 derived for C(a) of 350 and 700 mumol mol-1, respectively.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3, CARBOXYLASE-OXYGENASE, CLIMATE CHANGE, ELEVATED CO2, GAS-EXCHANGE, PAR ABSORPTION, RESPIRATION, SITKA SPRUCE, TUSSOCK TUNDRA

1516

Medlyn, B.E. 1996. Interactive effects of atmospheric carbon dioxide and leaf nitrogen concentration on canopy light use efficiency: A modeling analysis. *Tree Physiology 16(1-2):201-209.*

Potential increases in plant productivity in response to increasing atmospheric CO2 concentration are likely to be constrained by nutrient

limitations. However, the interactive effects of nitrogen nutrition and CO2 concentration on growth are difficult to define because both factors affect several aspects of growth, including photosynthesis, respiration, and leaf area. By expressing growth as a product of light intercepted and light use efficiency (epsilon), it is possible to decouple the effects of nutrient availability and CO2 concentration on photosynthetic rates from their effects on other aspects of plant growth. I used measured responses of leaf photosynthesis to leaf nitrogen (N) content and CO2 concentration to parameterize a model of canopy radiation absorption and photosynthesis, and then used the model to estimate the response of E to elevated CO2 concentration for Pinus radiata D. Don, Nothofagus fusca (Hook. f.) Orst. and Eucalyptus grandis W. Hill ex Maiden. Down-regulation of photosynthesis at elevated CO2 was represented as a reduction in either leaf N content or leaf Rubisco activity. The response of epsilon to elevated CO2, which differed among the three species, was analyzed in terms of the underlying relationships between leaf photosynthesis and leaf N content. The response was independent of leaf N content when photosynthesis was down- regulated to the same extent at low and high leaf N content. Interactive effects of N availability and CO2 on growth are thus likely to be the result of either differences in down- regulation of photosynthesis at low and high N availability or interactive effects of CO2 and N availability on other aspects of plant growth.

KEYWORDS: C-3 PLANTS, CO2 CONCENTRATIONS, ELEVATED CO2, ENRICHMENT, FERTILIZATION, GROWTH, LEAVES, MINERAL NUTRITION, PHOTOSYNTHETIC CAPACITY, PINUS-RADIATA

1517

Medlyn, B.E. 1996. The optimal allocation of nitrogen within the C-3 photosynthetic system at elevated CO2. *Australian Journal of Plant Physiology 23(5):593-603.*

The distribution of nitrogen among compounds involved in photosynthesis varies in response to changes in environmental conditions such as photon flux density. However, the extent to which the nitrogen distribution within leaves adjusts in response to increased atmospheric CO2 is unclear. A model was used to determine the nitrogen distribution which maximises photosynthesis under realistic light regimes at both current and elevated levels of CO2, and a comparison was made with observed leaf nitrogen distributions reported in the literature. The model accurately predicted the distribution of nitrogen within the photosynthetic system for leaves grown at current levels of CO2, except at very high leaf nitrogen contents. The model predicted that, under a doubling of CO2 concentration from its current level, the ratio of electron transport capacity to Rubisco activity (J(max):V-cmax) should increase by 40%. In contrast, measurements of J(max):V-cmax taken from the literature show a slight but non-significant increase in response to an increase in CO2. The discrepancy between predicted and observed J(max):V-cmax suggests that leaf nitrogen distribution does not acclimate optimally to elevated CO2. Alternatively, the discrepancy may be due to effects of CO2 which the model fails to take into account, such as a possible decrease in the conductance to CO2 transfer between the intercellular spaces and the sites of carboxylation at elevated CO2.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, DIFFERENT IRRADIANCES, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, LEAF NITROGEN, PHOTON FLUX- DENSITY, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TRANSGENIC TOBACCO

1518

Medlyn, B.E., and P.G. Jarvis. 1999. Design and use of a database of model parameters from elevated [CO2] experiments. *Ecological Modelling 124(1):69-83.*

This paper describes a new approach for linking experiments and models: a searchable database of model parameter values obtained directly from experiments. The experiments were carried out as part of a major European project studying the long-term effects of elevated [CO2] on European forest species. To ensure that the information obtained from these experiments was fully utilised in the modelling component of the project, a database was used to store and synthesise experimental data. Key features of the database include: (1) Data is stored as model parameters rather than raw experimental data, which aids transfer of information from experiments to models. (2) Extensive meta-data is stored, which is crucial for correct interpretation of parameter values. (3) The database has a relational structure, which facilitates data retrieval. In this paper, we document the structure of the database. The structure is flexible and generic and could easily be adapted to suit other fields of research. We illustrate the use of the database with examples from the project.

KEYWORDS: SCOTS PINE

1519

Megonigal, J.P., and W.H. Schlesinger. 1997. Enhanced CH4 emissions from a wetland soil exposed to elevated CO2. *Biogeochemistry 37(1):77-88.*

Methane emissions from wetland soils are generally a positive function of plant size and primary productivity, and may be expected to increase due to enhanced rates of plant growth in a future atmosphere of elevated CO2. We performed two experiments with Orontium aquaticum, a common emergent aquatic macrophyte in temperate and sub-tropical wetlands, to determine if enhanced rates of photosynthesis in elevated CO2 atmospheres would increase CH4 emissions from wetland soils. O. aquaticum was grown from seed in soil cores under ambient and elevated (ca. 2-times ambient) concentrations of CO2 in an initial glasshouse study lasting 3 months and then a growth chamber study lasting 6 months. Photosynthetic rates were 54 to 71% higher under elevated CO2 than ambient CO2, but plant biomass was not significantly different at the end of the experiment. In each case, CH4 emissions were higher under elevated than ambient CO2 levels after 2 to 4 months of treatment, suggesting a close coupling between photosynthesis and methanogenesis in our plant-soil system. Methane emissions in the growth chamber study increased by 136%. We observed a significant decrease in transpiration rates under elevated CO2 in the growth chamber study, and speculate that elevated CO2 may also stimulate CH4 emissions by increasing the extent and duration of flooding in some wetland ecosystems. Elevated CO2 may dramatically increase CH4 emissions from wetlands, a source that currently accounts for 40% of global emissions.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEM, FLUXES, METHANE EMISSIONS, PERSPECTIVE, REDOX, TEMPERATURE, WATER-TABLE

1520

Meheriuk, M. 1990. Effects of diphenylamine, gibberellic-acid, daminozide, calcium, high CO2 and elevated-temperatures on quality of stored bartlett pears. *Canadian Journal of Plant Science 70(3):887-892.*

1521

Meier, M., and J. Fuhrer. 1997. Effect of elevated CO2 on orchard grass and red clover grown in mixture at two levels of nitrogen or water

supply. *Environmental and Experimental Botany 38(3):251-262.*

A mixture of orchard grass (Dactylis glomerata L.) and red clover (Trifolium pratense L.) was grown in microcosms at either ambient (40 Pa) or elevated CO2 (78 Pa) and supplied with two levels of nitrogen (N) or two levels of irrigation. The aim was to study how reduced N or water supply affect the CO2 response of shoot and root growth, in relationship to changes in the plant C/N ratio. Plant growth was monitored non-destructively, and shoot dry mass was determined after 41 days (first growth period) and after 67 days (second growth period). Stubble and root dry mass, and C/N ratios in roots and shoots were measured only after regrowth. Elevated CO2 continuously stimulated growth of the mixture, and increased the shoot biomass in the absence of N or water limitations without changing the shoot/root dry weight ratio, nor the C/N ratio. The CO2-effect on orchard grass tended to be stronger than the effect on red clover, and was more pronounced during the first as compared to the second growth period. At low N, yield of red clover showed the stronger CO2 response, whereas with reduced water supply the relative CO2-stimulation of shoot biomass in orchard grass was more pronounced. Both low-N and reduced water supply decreased shoot, root, and stubble biomass, decreased the shoot/root ratio, and increased the C/N ratio. Elevated CO2 reduced negative effects of limited N or water supply on shoot growth, but the positive CO2 effect at low N declined with time. The interaction between CO2 and N was most pronounced for stubble mass, whereas the interaction between CO2 and reduced water supply was only significant for root mass. It is concluded that changes in shoot/root ratio are mainly caused by low N and reduced water supply via changes in the N-status of the plant, and that elevated CO2 has little effect on the shoot/root ratio, but tends to reduce negative effects of limiting N and water on growth. (C) 1997 Published by Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, MANAGED MODEL-ECOSYSTEMS, PLANT-RESPONSE, RYEGRASS LOLIUM-PERENNE, STRESS, TRIFOLIUM-REPENS L, WHITE CLOVER

1522

Meier, M., M. Saurer, C. Haldemann, and J. Fuhrer. 1997. Effect of elevated CO2 on the carbon balance of a grass-clover mixture. *Acta Oecologica-International Journal of Ecology 18(3):313-317.*

Experiments were carried out to investigate the effect of elevated CO2 (780 mu mol mol(-1)) on the C-balance and carbon release from the roots of a mixture of Dactylis glomerata and Trifolium pratense. The plants were grown for 67 days in a growth chamber with controlled watering and fertilisation, with an intermediate harvest after 41 days. Elevated CO2 increased total net uptake of carbon (C) by about 30% by the end of regrowth. Total net C-uptake and the amount of C recovered in the second harvest were balanced at both CO2 concentrations, and the root: shoot ratio was not affected by elevated CO2. C- 13-allocation to roots, and C-13 released into the root environment were measured following pulse-labelling with (CO2)- C-13 at the end of regrowth. Relative to the amount of C-13 taken up by the shoot, C-13 allocation to roots was 1.6%, and C-13 released from roots was only 0.4%. No significant difference in these proportions was observed at elevated CO2, but in absolute terms, plants grown at elevated CO2 released more C-13 from the roots.

1523

Meinander, O., S. Somersalo, T. Holopainen, and R.J. Strasser. 1996. Scots pines after exposure to elevated ozone and carbon dioxide probed by reflectance spectra and chlorophylla fluorescence transients. *Journal of Plant Physiology 148(1-2):229-236.*

Natural Scots pines have been exposed to filtered air, ambient air and air with elevated O-3 or/and CO2 in open top chambers. The trees showed no differences in their optical responses prior to the fumigations. After the fumigation period of three months the plants were in good health. The position of the maximum derivative of the green light reflectance in carbon dioxide fumigated pines was shifted from the control pines inflection point, by approximately 4 nm towards shorter wavelengths. The position of the red edge derivative maximum showed no significant changes. By fluorescence techniques (as OJIP - fast fluorescence transients) nearly no change was found in the quantum yield for electron transport (phi(o) or excitation energy trapping phi(Po). However, the estimated activities as absorption, trapping or electron transport per cross-section increased considerably for all samples with elevated O-3 or CO2. This increased activity seems to be due to an increased antenna size in O-3 treated samples. At elevated CO2 the antenna size is decreased whereas the density of reaction centers per cross-section increased. This means that two different stress-adaptation mechanisms can lead to a similar macroscopic phenomenon like e.g. an increased metabolic activity.

KEYWORDS: FOREST DECLINE

1524

Melack, J.M., J. Dozier, C.R. Goldman, D. Greenland, A.M. Milner, and R.J. Naiman. 1997. Effects of climate change on inland waters of the Pacific Coastal Mountains and Western Great Basin of North America. *Hydrological Processes 11(8):971-992.*

The region designated as the Pacific Coastal Mountains and Western Great Basin extends from southern Alaska (64 degrees N) to southern California (34 degrees N) and ranges in altitude from sea level to 6200 m. Orographic effects combine with moisture-laden frontal systems originating in the Pacific Ocean to produce areas of very high precipitation on western slopes and dry basins of internal drainage on eastern hanks of the mountains. In the southern half of the region most of the runoff occurs during winter or spring, while in the northern part most occurs in summer, especially in glaciated basins, Analyses of long-term climatic and hydrological records, combined with palaeoclimatic reconstructions and simulations of future climates, are used as the basis for likely scenarios of climatic variations. The predicted hydrological response in northern California to a climate with doubled CO2 and higher temperatures is a decrease in the amount of precipitation falling as snow, and substantially increased runoff during winter and less in late spring and summer. One consequence of the predicted earlier runoff is higher salinity in summer and autumn in San Francisco Bay. In saline lakes, the incidence of meromixis and the associated reduction in nutrient supply and algal abundance is expected to vary significantly as runoff fluctuates. In subalpine lakes, global warming will probably will lead to increased productivity. Lacustrine productivity can also be altered by changes in wind regimes, drought- enhanced forest fires and maximal or minimal snowpacks associated with atmospheric anomalies such as Fl Nino-Southern Oscillation (ENSO) events. Reduced stream temperature from increased contributions of glacial meltwater and decreased channel stability from changed runoff patterns and altered sediment loads has the potential to reduce the diversity of zoobenthic communities in predominately glacier-fed rivers. Climatic warming is likely to result in reduced growth and survival of sockeye salmon in freshwater, which would, in turn, increase marine mortality. Further research activities should include expanded studies at high elevations and of glacier mass balances and glacial runoff, applications of remote sensing to monitor changes, further refinement of regional climatic models to improve forecasts of future conditions and continued analyses of long-term physical, chemical and biological data to help understand responses to future climates. (C) 1997 by John Wiley & Sons, Ltd.

KEYWORDS: HYDROLOGIC SENSITIVITIES, HYPERSALINE MONO-LAKE, INTERANNUAL FLUCTUATIONS, PRECIPITATION

VARIABILITY, SIERRA NEVADA, SOUTHERN OSCILLATION, STREAMFLOW VARIABILITY, TELECONNECTION PATTERN, TREE-RINGS, UNITED-STATES CLIMATE

1525

Melillo, J.M., J. Borchers, J. Chaney, H. Fisher, S. Fox, A. Haxeltine, A. Janetos, D.W. Kicklighter, T.G.F. Kittel, A.D. McGuire, R. McKeown, R. Neilson, R. Nemani, D.S. Ojima, T. Painter, Y. Pan, W.J. Parton, L. Pierce, L. Pitelka, C. Prentice, B. Rizzo, N.A. Rosenbloom, S. Running, D.S. Schimel, S. Sitch, T. Smith, and I. Woodward. 1995. Vegetation ecosystem modeling and analysis project - comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate-change and co2 doubling. *Global Biogeochemical Cycles 9(4):407-437.*

We compare the simulations of three biogeography models (BIOME2, Dynamic Global Phytogeography Model (DOLY), and Mapped Atmosphere-Plant Soil System (MAPSS)) and three biogeochemistry models (BIOME-BGC (BioGeochemistry Cycles), CENTURY, and Terrestrial Ecosystem Model (TEM)) for the conterminous United States under contemporary conditions of atmospheric CO2 and climate. We also compare the simulations of these models under doubled CO2 and a range of climate scenarios. For contemporary conditions, the biogeography models successfully simulate the geographic distribution of major vegetation types and have similar estimates of area for forests (42 to 46% of the conterminous United States), grasslands (17 to 27%), savannas (15 to 25%), and shrublands (14 to 18%). The biogeochemistry models estimate similar continental-scale net primary production (NPP; 3125 to 3772 x 10(12) gC yr(-1)) and total carbon storage (108 to 118 x 10(15) gC) for contemporary conditions. Among the scenarios of doubled CO2 and associated equilibrium climates produced by the three general circulation models (Oregon State University (OSU), Geophysical Fluid Dynamics Laboratory (GFDL), and United Kingdom Meteorological Office (UKMO)), all three biogeography models show both gains and losses of total forest area depending on the scenario (between 38 and 53% of conterminous United States area). The only consistent gains in forest area with all three models (BIOME2, DOLY, and MAPSS) were under the GFDL scenario due to large increases in precipitation. MAPSS lost forest area under UKMO, DOLY under OSU, and BIOME2 under both UKMO and OSU, The variability in forest area estimates occurs because the hydrologic cycles of the biogeography models have different sensitivities to increases in temperature and CO2. However, in general, the biogeography models produced broadly similar results when incorporating both climate change and elevated CO2 concentrations. For these scenarios, the NPP estimated by the biogeochemistry models increases between 2% (BIOME-BGC with UKMO climate) and 35% (TEM with UKMO climate). Changes in total carbon storage range from losses of 33% (BIOME-BGC with UKMO climate) to gains of 16% (TEM with OSU climate). The CENTURY responses of NPP and carbon storage are positive and intermediate to the responses of BIOME-BGC and TEM. The variability in carbon cycle responses occurs because the hydrologic and nitrogen cycles of the biogeochemistry models have different sensitivities to increases in temperature and CO2. When the biogeochemistry models are run with the vegetation distributions of the biogeography models, NPP ranges from no response (BIOME-BGCwith all three biogeography model vegetations for UKMO climate) to increases of 40% (TEM with MAPSS vegetation for OSU climate). The total carbon storage response ranges from a decrease of 39% (BIOME-BGC with MAPSS vegetation for UKMO climate) to an increase of 32% (TEM with MAPSS vegetation for OSU and GFDL climates). The UKMO responses of BIOME-BGC with MAPSS vegetation are primarily caused by decreases in forested area and temperature-induced water stress, The OSU and GFDL responses of TEM with MAPSS vegetations are primarily caused by forest expansion and temperature-enhanced nitrogen cycling.

KEYWORDS: BALANCE, EXCHANGE, FOREST, GENERAL-MODEL, ORGANIC-MATTER DYNAMICS, PHOTOSYNTHESIS, PRODUCTIVITY, REGIONAL APPLICATIONS, SENSITIVITY, TEMPERATURE

1526

Melillo, J.M., R.A. Houghton, D.W. Kicklighter, and A.D. McGuire. 1996. Tropical deforestation and the global carbon budget. *Annual Review of Energy and the Environment 21:293-310.*

The CO2 concentration of the atmosphere has increased by almost 30% since 1800. This increase is due largely to two factors: the combustion of fossil fuel and deforestation to create croplands and pastures. Deforestation results in a net flux of carbon to the atmosphere because forests contain 20-50 times more carbon per unit area than agricultural lands. In recent decades, the tropics have been the primary region of deforestation. The annual rate of CO2 released due to tropical deforestation during the early 1990s has been estimated at between 1.2 and 2.3 gigatons C. The range represents uncertainties about both the rates of deforestation and the amounts of carbon stored in different types of tropical forests at the time of cutting. An evaluation of the role of tropical regions in the global carbon budget must include both the carbon flux to the atmosphere due to deforestation and carbon accumulation, if any, in intact forests. In the early 1990s, the release of CO2 from tropical deforestation appears to have been mostly offset by CO2 uptake occurring elsewhere in the tropics, according to an analysis of recent trends in the atmospheric concentrations of O-2 and N-2. Interannual variations in climate and/or CO2 fertilization may have been responsible for the CO2 uptake in intact forests. These mechanisms are consistent with site-specific measurements of net carbon fluxes between tropical forests and the atmosphere, and with regional and global simulations using process-based biogeochemistry models.

KEYWORDS: ABANDONED PASTURES, ATMOSPHERIC CARBON, BURN AGRICULTURE, EASTERN AMAZONIA, LAND-USE CHANGE, ORGANIC-CARBON, RAIN-FOREST, SATELLITE DATA, SIZE-FRACTIONS, UPPER RIO NEGRO

1527

Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore, C.J. Vorosmarty, and A.L. Schloss. 1993. Global climate-change and terrestrial net primary production. *Nature 363(6426):234-240.*

A process-based model was used to estimate global patterns of net primary production and soil nitrogen cycling for contemporary climate conditions and current atmospheric CO2 concentration. Over half of the global annual net primary production was estimated to occur in the tropics, with most of the production attributable to tropical evergreen forest. The effects of CO2 doubling and associated climate changes were also explored. The responses in tropical and dry temperate ecosystems were dominated by CO2, but those in northern and moist temperate ecosystems reflected the effects of temperature on nitrogen availability.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, ELEVATED CO2, FORESTS, GROWTH, LIMITATION, NITROGEN, NUTRITION, RESPONSES, SENSITIVITY

1528

Melkonian, J., S.J. Riha, and D.S. Wilks. 1998. Simulation of elevated CO2 effects on daily net canopy carbon assimilation and crop yield. *Agricultural Systems 58(1):87-106.*

Three formulations for estimating the impact of elevated CO2 on daily net canopy carbon assimilation (A) are compared. The formulations are all physiologically based but vary in the detail with which A is represented. When implemented in two crop models, all formulations

predict increased yield under elevated CO2, with the formulation incorporating the most detailed representation of A predicting the smallest yield increase. In the crop model with more complex representations of growth and yield, and where increased photoassimilates under elevated CO2 are allowed to affect processes such as leaf area development, yield predictions under elevated CO2 can be substantially greater than the predicted increase in A for each formulation. These results indicate that the representation of A and assumptions regarding adaptation to elevated CO2 of A, crop growth and carbon partitioning will have large impacts on simulation model predictions of crop yields at elevated CO2.

KEYWORDS: CLIMATE CHANGE, DIOXIDE, GROWTH, MODEL, RADIATION, SPRING WHEAT, TEMPERATURE

1529

Menard, C., and B. Dansereau. 1992. Influence of photosynthetic photon flux-density and planting scheme on growth and development of cultivar royalty roses. *Scientia Horticulturae 50(3):197-207.*

The influence of photosynthetic photon flux density (PPFD) and planting scheme on growth, development, yield and quality of RosaXhybrida cultivar 'Royalty' was investigated. Three planting schemes (two, three, and four parallel rows) and three light treatments (ambient light and ambient light Plus supplemental lighting with either 50 or 100-mu-mol s-1 m-2 PPFD (high pressure sodium lamps) were studied. Generally, supplementary PPFD enhanced the vegetative and reproductive growth of the plants compared to plants grown in ambient light conditions. Marketable yield per plant was increased significantly by 79% (P< 0.05) for the crop period from 1 January to 24 March 1988 when a PPFD of 50-mu-mol s-1 m-2 was added to ambient light conditions. Carbon dioxide enrichment increased yield by 113% when a PPFD of 50-mu-mol s-1 m-2 was added to ambient light during the crop period of 1 January to 24 March, 1989. The number of flowers per plant in the superior classes (commercial classification: 'Select' and 'No. 1') was enhanced for this period compared with the same period the previous year when no supplemental carbon dioxide was provided. Generally the planting scheme of two parallel rows gave the best overall results.

KEYWORDS: GREENHOUSE ROSES, SUPPLEMENTARY

1530

Miao, S.L. 1995. Acorn mass and seedling growth in quercus-rubra in response to elevated co2. *Journal of Vegetation Science 6(5):697-700.*

In order to explore whether seed size affects plant response to elevated CO2 plants grown from red oak (Quercus rubra L.) acorns were studied for differences in their first year response to CO2 concentrations of 350 and 700 ul/l. Overall, at final harvest, total biomass of plants grown in elevated CO2 were 47 % larger than that of plants grown in ambient CO2. There were significant interactions between CO2 treatments and initial acorn mass for total biomass, as well as for root, leaf, and stem biomass. Although total biomass increased with increasing initial acorn mass for both high and ambient CO2 plants, high CO2 plants exhibited a greater increase than ambient CO2 plants, as indicated by a steeper slope in high CO2 plants. However, CO2 levels did not affect biomass partitioning traits, such as root/shoot ratio, leaf, stem, and root weight ratios, and leaf area ratio. These results suggest that variation in seed size or initial plant size can cause intraspecific variation in response to elevated CO2.

1531

Miao, S.L., P.M. Wayne, and F.A. Bazzaz. 1992. Elevated co-2 differentially alters the responses of cooccurring birch and maple seedlings to a moisture gradient. *Oecologia 90(2):300-304.*

To determine the effects of elevated CO2 and soil moisture status on growth and niche characteristics of birch and maple seedlings, gray birch (Betula populifolia) and red maple (Acer rubrum) were experimentally raised along a soil moisture gradient ranging from extreme drought to flooded conditions at both ambient and elevated atmospheric CO2 levels. The magnitude of growth enhancement due to CO2 was largely contingent on soil moisture conditions, but differently so for maple than for birch seedlings. Red maple showed greatest CO2 enhancements under moderately moist soil conditions, whereas gray birch showed greatest enhancements under moderately dry soil conditions. Additionally, CO2 had a relatively greater ameliorating effect in flooded conditions for red maple than for gray birch, whereas the reverse pattern was true for these species under extreme drought conditions. For both species, elevated CO2 resulted in a reduction in niche breadths on the moisture gradient; 5% for gray birch and 23% for red maple. Species niche overlap (proportional overall) was also lower at elevated CO2 (0.98 to: 0.88:11%). This study highlights the utility of of experiments crossing CO2 levels with gradients of other resources as effective tools for elucidating the potential consequences of elevated CO2 on species distributions and potential interactions in natural communities.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GROWTH-RESPONSES, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, WATER-STRESS

1532

Micallef, B.J., K.A. Haskins, P.J. Vanderveer, K.S. Roh, C.K. Shewmaker, and T.D. Sharkey. 1995. Altered photosynthesis, flowering, and fruiting in transgenic tomato plants that have an increased capacity for sucrose synthesis. *Planta 196(2):327-334.*

Photosynthesis, leaf assimilate partitioning, flowering, and fruiting were examined in two lines of Lycopersicon esculentum Mill. transformed with a gene coding for sucrose-phosphate synthase (SPS) (EC 2.3.1.14) from Zea mays L. expressed from a tobacco ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) small subunit promoter. Plants were grown at either 35 or 65 Pa CO2 and high light (1000 mu mol photons . m(-2). s(-1)). Limiting and maximum SPS activities were significantly greater (up to 12 times) in the leaves of SPS-transformed lines for all treatments. Partitioning of carbon into sucrose increased 50% for the SPS transformants. Intact leaves of the control lines exhibited CO2-insensitivity of photosynthesis at high CO2 levels, whereas the SPS transformants did not exhibit CO2-insensitivity. The O-2-sensitivity of photosynthesis was also greater for the SPS-transformed lines compared to the untransformed control when measured at 65 Pa CO2. These data indicate that the SPS transformants had a reduced limitation on photosynthesis imposed by end-product synthesis. Growth at 65 Pa CO2 resulted in reduced photosynthetic capacity for control lines but not for SPS-transformed lines. When grown at 65 Pa CO2, SPS transformed lines had a 20% greater photosynthetic rate than controls when measured at 65 Pa CO2 and a 35% greater rate when measured at 105 Pa CO2. Photosynthetic rates were not different between lines when grown at 35 Pa CO2. The time to 50% blossoming was reduced and the total number of inflorescences was significantly greater for the SPS transformants when grown at either 35 or 65 Pa CO2. At 35 Pa CO2, the total fruit number of the SPS transformants was up to 1.5 times that of the controls, the fruit matured earlier, and there was up to a 32% increase in total fruit dry weight. Fruit yield was not significantly different between the lines when grown at 65 Pa CO2. Therefore, there was not a strict relationship between yield and leaf photosynthesis rate. Flowering and fruit development of the SPS-transformed lines grown at 35 Pa CO2 showed similar trends to the controls grown at 65 Pa CO2. Incidences of bios som-end rot were also reduced in the SPS-transformed lines. These data indicate that altering starch/sucrose partitioning by increasing the

capacity for sucrose syn thesis can affect acclimation to elevated CO2 partial pressure and flowering and fruiting in tomato.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, GROWTH, LEAVES, PHASEOLUS-VULGARIS, PHOSPHATE SYNTHASE, TEMPERATURE, YIELD

1533

Micallef, B.J., P.J. Vanderveer, and T.D. Sharkey. 1996. Responses to elevated CO2 of Flaveria linearis plants having a reduced activity of cytosolic fructose-1,6-bisphosphatase. *Plant, Cell and Environment 19(1):10-16.*

Wide variation exists in the growth responses of C-3 plants to elevated CO2 levels. To investigate the role of photosynthetic feedback in this phenomenon, photosynthetic parameters and growth were measured for lines of Flaveria linearis with low, intermediate or high cytosolic fructose-1,6-bisphosphatase (cytFBPase) activity when grown at either 35 or 65 Pa CO2. The effects of pot size on the responses of these lines to elevated CO2 were also examined. Photosynthesis and growth of plants with low cytFBPase activity were less responsive to elevated CO2, and these plants had a reduced maximum potential for photosynthesis and growth. Plants with intermediate cytFBPase activity also showed a lower relative growth enhancement when grown at 65 Pa CO2. There was a significant pot size effect on photosynthesis and growth for line 85-1 (high cytFBPase). This effect was greatest for Line 85-1 when grown at 35 Pa CO2, since these plants showed the greatest downward acclimation of photosynthesis when grown in small pots. There was a minimal pot size effect for line 84-9 (low cytFBPase), and this could be partly attributed to the reduced CO2 sensitivity of this line. It is proposed that the capacity for sucrose synthesis in C-3 plants is partly responsible for their wide variation in CO2 responsiveness.

KEYWORDS: MUTANT, PHOTOSYNTHETIC ACCLIMATION

1534

Michaels, P.J. 1993. Benign greenhouse. *Research & Exploration 9(2):222-233.*

Several lines of evidence are emerging that suggest that the "popular vision" of global warming-major agricultural damage, disastrous sea-level rise, and ecological disequilibrium-is flawed. The popular vision is driven primarily by the prospect of enhanced daytime warming, particularly in summer What has been observed is a warming that is beneath the projections that support the popular vision, and a warming that has occurred virtually all during the night in the Northern Hemisphere. In the Southern Hemisphere there is also evidence of disproportionate night warming. Several sources of data indicate that this night warming has been caused by an increase in cloudiness that could be a consequence of the greenhouse enhancement itself. The results of the night warming-longer growing seasons, little change in moisture stress, and a possible increase in ice volume-are opposite to the popular vision of climatic change.

KEYWORDS: ATMOSPHERE, CLIMATE CHANGE, CO2, GENERAL-CIRCULATION MODEL, SUNSHINE, UNITED-STATES

1535

Midgley, G.F., W.D. Stock, and J.M. Juritz. 1995. Effects of elevated CO2 on Cape Fynbos species adapted to soils of different nutrient status: Nutrient- and CO2-responsiveness. *Journal of Biogeography 22(2-3):185-191.*

The combined effects of elevated atmospheric CO2 and nutrient supply rate on plant biomass accumulation were determined for four Leucadendron species (Proteaceae) of the mediterranean climate Fynbos Biome, South Africa. Juvenile individuals were grown for 6 months in experiments comprising 2X2 factorial combinations of substrate nutrient supply rate and atmospheric CO2 concentration in open-top chambers in a greenhouse. The four selected Leucadendron species included one pair of species common on extremely nutrient-poor acid sands (typical of the Fynbos Biome), and another pair associated with more nutrient rich substrates (rare in the Fynbos Biome). Plant biomass accumulation data were analysed to explore the determinants of plant CO2 responsiveness, particularly the role of plant sink strength characteristics. Results lead us to speculate that the nitrogen:phosphorus supply ratio may have limited plant CO2 responsiveness in three of the four species under conditions of higher nutrient supply rate. Intrinsic plant growth characteristics, possibly related to the relative ability of the species to generate sinks, may ultimately have limited the capacity of all species to respond to elevated CO2.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, MOUNTAIN FYNBOS, NUTRITION, PHOSPHORUS, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, PROTEACEAE, RESPONSES, SINK STRENGTH

1536

Midgley, G.F., S.J.E. Wand, and N.W. Pammenter. 1999. Nutrient and genotypic effects on CO2-responsiveness: Photosynthetic regulation in Leucadendron species of a nutrient-poor environment. *Journal of Experimental Botany 50(333):533-542.*

Four South African Leucadendron congenerics with divergent soil N and P preferences were grown as juveniles at contrasting nutrient concentrations at ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2 levels. Photosynthetic parameters were related to leaf nutrient and carbohydrate status to reveal controls of carbon uptake rate. In ail species, elevated CO2 depressed both the maximum Rubisco catalytic activity (V-c,V-max, by 19-44%) and maximum electron transport rate (J(max) by 13-39%), indicating significant photosynthetic acclimation of both measures. Even so, all species had increased maximum light-saturated rate of net CO2 uptake (A(max)) at the elevated growth CO2 level, due to higher intercellular CO2 concentration (c(i)). Leaf nitrogen concentration was central to photosynthetic performance, correlating with A(max), V-c,V-max and J(max). V-c,V-max and J(max) were linearly cc-correlated, revealing a relatively invariable J(max):V-c,V-max ratio, probably due to N resource optimization between light harvesting (RuBP regeneration) and carboxylation. Leaf total non-structural carbohydrate concentration (primarily starch) increased in high CO2, and was correlated with the reduction in V-c,V-max and J(max). Apparent feedback control of V-c,V-max and J(max) was thus surprisingly consistent across all species, and may regulate carbon exchange in response to end-product fluctuation. If so, elevated CO2 may have emulated an excess end-product condition, triggering both V-c,V-max and J(max) down-regulation. In Leucadendron, a general physiological mechanism seems to control excess carbohydrate formation, and photosynthetic responsiveness to elevated CO2, independently of genotype and nutrient concentration. This mechanism may underlie photosynthetic acclimation to source:sink imbalances resulting from such diverse conditions as elevated CO2, low sink strength, low carbohydrate export, and nutrient limitation.

KEYWORDS: ACCLIMATION, ARABIDOPSIS-THALIANA, CARBOHYDRATE-METABOLISM, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, LEAF NITROGEN, PHOTON FLUX- DENSITY, PLANT-RESPONSES, SOUTH-AFRICA, TEMPERATURE

1537

Miglietta, F., I. Bettarini, A. Raschi, C. Korner, and F.P. Vaccari.

1998. Isotope discrimination and photosynthesis of vegetation growing in the Bossoleto CO2 spring. *Chemosphere 36(4-5):771-776.*

The Bossoleto CO2 spring emits CO2 which has a stable carbon isotopic ratio (delta(13)C = -8 parts per thousand). We determined delta(13)C on leaves of several individual species growing in Bossoleto and in a nearby control site at ambient CO2. delta(13)C was 6% more negative in leaves of species collected from the grassland community of Bossoleto, indicating increased discrimination (Delta) against the heavy carbon isotope. No such changes were found in ruderal species growing in the same spring, suggesting that photosynthetic capacity was much less affected. Delta was substantially increased under elevated CO2 in leaves of Quercus pubescens but not in Quercus ilex, which also did not show any increase in non-structural carbohydrates. Gas-exchange measurements made on Plantago lanceolata, supported the view that photosynthetic capacity is decreased in plants grown under elevated CO2 and on poor soils. (C) 1998 Elsevier Science Ltd.

KEYWORDS: CARBON

1538

Miglietta, F., A. Giuntoli, and M. Bindi. 1996. The effect of free air carbon dioxide enrichment (FACE) and soil nitrogen availability on the photosynthetic capacity of wheat. *Photosynthesis Research 47(3):281-290.*

A. simple system for free air carbon dioxide enrichment (FACE) was recently developed and it is here briefly described. Such a MiniFACE system allowed the elevation of CO2 concentration of small field plots avoiding the occurrence of large spatial and temporal fluctuations. A CO2 enrichment field experiment was conducted in Italy in the season 1993-1994 with wheat (cv. Super-dwarf Mercia). A randomized experimental design was used with the treatment combination CO2 x soil N, replicated twice. Gas exchange measurements showed that photosynthetic capacity was significantly decreased in plants exposed to elevated CO2 and grown under nitrogen deficiency. Photosynthetic acclimation was, in this case, due to the occurrence of reduced rates of rubP saturated and rubP regeneration limited photosynthesis. Gas exchange measurements did not instead reveal any significant effect of elevated CO2 on the photosynthetic capacity of leaves of plants well fertilized with nitrogen, in spite of a transitory negative effect on rubP regeneration limited photosynthesis that was detected to occur in the central part of a day with high irradiance. It is concluded that the levels of nitrogen fertilization will play a substantial role in modulating CO2 fertilization effects on growth and yields of wheat crops under the scenario of future climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2 CONCENTRATIONS, C-3 PLANTS, CARBOXYLASE-OXYGENASE, ELEVATED CO2, LEAVES, PLANT GROWTH, SOURCE-SINK RELATIONS, TEMPERATURE, WINTER-WHEAT

1539

Miglietta, F., M. Lanini, M. Bindi, and V. Magliulo. 1997. Free air CO2 enrichment of potato (Solanum tuberosum, L.): design and performance of the CO2-fumigation system. *Global Change Biology 3(5):417-427.*

Free Air CO2 Enrichment (FACE) systems are used to fumigate unconfined field plots with CO2. As these installations can treat a sufficiently large area without interfering with natural climatic conditions, they are considered important tools for global change research worldwide. However, there is general consensus that elevated capital costs of existing FACE systems as well as high running costs may prevent their application at the required level of scale. A new and small FACE system that was designed to reduce both capital costs and CO2 use, is described in this paper. Due to its intermediate size (8 m diameter) between the smaller Mini-FACE systems that were developed in Italy and the larger systems designed by the Brookhaven National Laboratory in the USA, it was named Mid- FACE. The Mid-FACE was at first developed as a prototype and then used to enrich field grown potato crops in a CO2 concentration gradient experimental design. Technical details of a Mid-FACE prototype and of the operational set-up are presented in this paper together with performance data in terms of temporal and spatial control of CO2 concentrations within the experimental area.

KEYWORDS: CARBON DIOXIDE, COTTON, EXPOSURE, FACE SYSTEM, FACILITY, TRACE GASES, WHEAT

1540

Miglietta, F., V. Magliulo, M. Bindi, L. Cerio, F.P. Vaccari, V. Loduca, and A. Peressotti. 1998. Free air CO2 enrichment of potato (Solanum tuberosum L.): development, growth and yield. *Global Change Biology 4(2):163-172.*

A FACE (Free Air CO2 Enrichment) experiment was carried out on Potato (Solanum tuberosum L., cv. Primura) in 1995 in Italy. Three FACE rings were used to fumigate circular field plots of 8 m diameter while two rings were used as controls at ambient CO2 concentrations. Four CO2 exposure levels were used in the rings (ambient, 460, 560 and 660 mu mol mol-l). Phenology and crop development, canopy surface temperature, above-and below- ground biomass were monitored during the growing season. Crop phenology was affected by elevated CO2, as the date of flowering was progressively anticipated in the 660, 560, 460 mu mol mol(-1) treatments. Crop development was not affected significantly as plant height, leaf area and the number of leaves per plant were the same in the four treatments. Elevated atmospheric CO2 levels had, instead, a significant effect on the accumulation of total nonstructural carbohydrates (TNC = soluble sugars + starch) in the leaves during a sunny day. Specific leaf area was decreased under elevated CO2 with a response that paralleled that of TNC concentrations. This reflected the occurrence of a progressive increase of photosynthetic rates and carbon assimilation in plants exposed to increasingly higher levels of atmospheric CO2. Tuber growth and final tuber yield were also stimulated by rising CO2 levels. When calculated by regression of tuber yield vs. the imposed levels of CO(2)concentration, yield stimulation was as large as 10% every 100 mu mol mol(-1) increase, which translated into over 40% enhancement in yield under 660 mu mol mol(-1). This was related to a higher number of tubers rather than greater mean tuber mass or size. Leaf senescence was accelerated under elevated CO2 and a linear relationship was found between atmospheric CO2 levels and leaf reflectance measured at 0.55 mu m wavelength. We conclude that significant CO2 stimulation of yield has to be expected for potato under future climate scenarios, and that crop phenology will be affected as well.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, COTTON, ELEVATED CO2, IRRADIANCE, LEAVES, PLANTS, TEMPERATURE, WHEAT, WORLD

1541

Miglietta, F., and A. Raschi. 1993. Studying the effect of elevated co2 in the open in a naturally enriched environment in central italy. *Vegetatio 104:391-400.*

A gas vents area was recently localized in Central Italy. The gas emitted from the vents is composed by 92% of carbon dioxide and this produces an anomaly in the composition of the atmosphere over an area of about 2 ha. Atmospheric carbon dioxide concentration was measured by means of an infrared gas analyzer and diffusion tubes in several points and for some days within the area. Measurements revealed that the site can be

at least divided into three sub-areas having increasing CO2 concentration in the air. A preliminary analysis of natural vegetation in the area was conducted by counting stomatal and epidermal cells number and measuring guard cell size on leaves of several oak trees growing both near and far away from the vents. This analysis suggested that elevated CO2 may have reduced the size of guard cells leaving stomatal density and stomatal index unaltered.

KEYWORDS: CARBON DIOXIDE, GROWTH, INCREASES, NUMBERS, STOMATAL DENSITY

1542

Miglietta, F., A. Raschi, I. Bettarini, R. Resti, and F. Selvi. 1993. Natural co2 springs in italy - a resource for examining long- term response of vegetation to rising atmospheric co2 concentrations. *Plant, Cell and Environment 16(7):873-878.*

It is estimated that more than 100 geothermal CO2 springs exist in central-western Italy. Eight springs were selected in which the atmospheric CO2 concentrations were consistently observed to be above the current atmospheric average of 354 mumol mol-1. CO2 concentration measurements at some of the springs are reported. The springs are described, and their major topographic and vegetational features are reported. Preliminary observations made on natural vegetation growing around the gas vents are then illustrated. An azonal pattern of vegetation distribution occurs around every CO2 spring regardless of soil type and phytoclimatic areas. This is composed of pioneer populations of a Northern Eurasiatic species (Agrostis canina L.) which is often associated with Scirpus lacustris L. The potential of these sites for studying the long-term response of vegetation to rising atmospheric CO2 concentrations is discussed.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, INCREASES, NUMBERS, STOMATAL DENSITY

1543

Miglietta, F., A. Raschi, R. Resti, and M. Badiani. 1993. Growth and onto-morphogenesis of soybean (glycine-max merril) in an open, naturally co2-enriched environment. *Plant, Cell and Environment 16(8):909-918.*

Springs emitting carbon dioxide are frequent in Central Italy and provide a way of testing the response of plants to CO2 enrichment under natural conditions. Results of a CO2 enrichment experiment on soybean at a CO2 spring (Solfatara) are presented. The experimental site is characterized by significant anomalies in atmospheric CO2 concentration produced by a large number of vents emitting almost pure CO2 (93%) plus small amounts of hydrogen sulphide, methane, nitrogen and oxygen. Within the gas vent area, plants were grown at three sub-areas whose mean CO2 concentrations during daytime were 350, 652 and 2370 mumol mol-1, respectively. Weekly harvests were made to measure biomass growth, leaf area and ontogenetic development. Biomass growth rate and seed yield were enhanced by elevated CO2. In particular, onto-morphogenetic development was affected by elevated CO2 with high levels of CO2 increasing the total number of main stem leaf nodes and the area of the main stem trifoliolate leaves. Biochemical analysis of plant tissue suggested that there was no effect of the small amounts of H2S on the response to CO2 enrichment. Non-protein sulphydryl compounds did not accumulate in leaf tissues and the overall capacity of leaf extracts to oxidize exogenously added NADH was not decreased. The limitations and advantages of experimenting with crop plants at elevated CO2 in the open and in the proximity of carbon dioxide springs are discussed.

KEYWORDS: CANOPY, CARBON-DIOXIDE ENRICHMENT, CO2 CONCENTRATION, FIELD, INDEX, LEAVES, PHOTOSYNTHESIS, PLANTS, SULFUR, TEMPERATURE

1544

Miglietta, F., M. Tanasescu, and A. Marica. 1995. The expected effects of climate change on wheat development. *Global Change Biology 1(6):407-415.*

Air temperature and the atmospheric concentrations of carbon dioxide are expected to rise. These two factor have a great potential to affect development, growth and yield of crops, including wheat. Rising air temperature may affect wheat development more than rising atmospheric CO2 as there is not yet evidence that elevated CO2 concentrations can directly induce changes in wheat development. In winter wheat, temperature has a complex effect on development due to its strong interaction with vernalization and photoperiod. In this paper, potential effects of rising temperature on the development of winter wheat from sowing to heading are considered in the light of this complex controlling mechanism. Data from a large series of field trials made in Romania is analysed at first and, subsequently, the IATA-Wheat Phenology model is used to calculate the impact of air warming on wheat development under different climate change scenarios. Data from the field trials showed very clearly the occurrence of a complex temperature/photoperiod/vernalization interaction for field sown crops and demostrated that the photoperiodic and vernalization responses have a key role in controlling the duration of the emergence-heading period. Temperature plays, instead, a central role in controlling seed germination and crop emergence as well as leaf inititiation and leaf appearance rate. The results of model analysis showed very well that the impact of an even or uneven distribution of warming effects may be very different. In the first case, the model predicted that the duration of the vegetative period was at least partly reduced in some years. In the second case, the model suggested that if warming will be more pronounced in winter than in spring, as predicted for some areas of the world by General Circulation Models, we may expect an increase in the duration of the vegetative phase of growth. On the contrary, in case of a spring warming but unchanged winter temperatures, we may expect a substantial decrease in the duration of the vegetative period.

KEYWORDS: FIELD, GROWTH, MODEL, NUMBER, PHOTOPERIOD, SPRING WHEAT, VERNALIZATION, WATER

1545

Mikkelsen, T.N., and H. Ropoulsen. 1994. Exposure of norway spruce to ozone increases the sensitivity of current year needles to photoinhibition and desiccation. *New Phytologist 128(1):153-163.*

Physiological effects of ozone exposure over three consecutive growing seasons on current year needles of Norway spruce were studied in open-top chambers, during daily fumigation cycles in the summer, and after the termination of ozone fumigation in autumn 1990. The trees were exposed to two levels of ozone: charcoal filtered air and non-filtered air to which 30 nl l(-1) of ozone was added in three consecutive years from 1988 to 1990, daily from May to September (8 hours a day). Photosynthesis, stomatal conductance, transpiration and chlorophyll fluorescence were studied on selected days. Significant decreases in net photosynthesis and chlorophyll fluorescence (F-v/F-m) were found during periods with co- occurrence of high ozone concentrations and high light intensities, indicating interactions between effects of ozone and photoinhibition. After termination of fumigation enhanced rates of photosynthesis were seen in the trees which had been exposed to ozone. A significant decrease in F-v/F-m was found for twigs from ozone treated trees when exposed to severe desiccation.

KEYWORDS: ABIES L KARST, AIR- POLLUTANTS, BISPHOSPHATE CARBOXYLASE OXYGENASE, CHLOROPHYLL FLUORESCENCE-KINETICS, CO2 ASSIMILATION, GAS-EXCHANGE, LONG-TERM

EXPOSURE, NET PHOTOSYNTHESIS, NONSTOMATAL LIMITATION, OPEN-TOP CHAMBERS

1546

Miller, A., C.H. Tsai, D. Hemphill, M. Endres, S. Rodermel, and M. Spalding. 1997. Elevated CO2 effects during leaf ontogeny - A new perspective on acclimation. *Plant Physiology 115(3):1195-1200.*

For many plants growth in elevated CO2 leads to reduced rates of photosynthesis. To examine the role that leaf ontogeny plays in the acclimation response, we monitored photosynthesis and some related parameters at short intervals throughout the ontogenetic development of tobacco (Nicotiana tabacum L.) leaves under ambient (350 mu L L-1)- and high (950 mu L L-1)- CO2 conditions. The pattern of photosynthetic rate over time was similar between the two treatments and consistent with the expected pattern for a typical dicot leaf. However, the photosynthesis pattern in high-CO2-grown tobacco was shifted temporally to an earlier maximum and subsequent senescent decline. Ribulose-1,5-biphosphate carboxylase/oxygenase activity appeared to be the main factor regulating photosynthetic rates in both treatments. Therefore, we propose a new model for interpreting the acclimation response. Lowered photosynthetic rates observed during acclimation appear to be the result of a shift in the timing of the normal photosynthetic stages of leaf ontogeny to an earlier onset of the natural decline in photosynthetic rates associated with senescence.

KEYWORDS: ATMOSPHERIC CO2, GAS-EXCHANGE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, PROTEINS, TOMATO PLANTS, TRANSFORMED TOBACCO

1547

Miller, C., and D.L. Urban. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems 2(1):76-87.*

In the Sierra Nevada, distributions of forest tree species are largely controlled by the soil-moisture balance. Changes in temperature or precipitation as a result of increased greenhouse gas concentrations could lead to changes in species distributions. In addition, climatic change could increase the frequency and severity of wildfires. We used a forest gap model developed for Sierra Nevada forests to investigate the potential sensitivity of these forests to climatic change, including a changing fire regime. Fuel moisture influences the fire regime and couples fire to climate. Fires are also affected by fuel loads, which accumulate according to forest structure and composition. These model features were used to investigate the complex interactions between climate, fire, and forest dynamics. Eight hypothetical climate-change scenarios were simulated, including two general circulation model (GCM) predictions of a 2 x CO2 world. The response of forest structure, species composition, and the fire regime to these changes in the climate were examined at four sites across an elevation gradient. Impacts on woody biomass and species composition as a result of climatic change were site specific and depended on the environmental constraints of a site and the environmental tolerances of the tree species simulated. Climatic change altered the fire regime both directly and indirectly. Fire frequency responded directly to climate's influence on fuel moisture, whereas fire extent was affected by changes that occurred in either woody biomass or species composition. The influence of species composition on fuel-bed bulk density was particularly important. Future fires in the Sierra Nevada could be both more frequent and of greater spatial extent if GCM predictions prove true.

KEYWORDS: AGE, HISTORY, LANDSCAPES, PROCESS MODEL, SENSITIVITY, VEGETATION

1548

Miller, J.B., D. Yakir, J.W.C. White, and P.P. Tans. 1999. Measurement of O-18/O-16 in the soil-atmosphere CO2 flux. *Global Biogeochemical Cycles 13(3):761-774.*

Measurements of O-18 in atmospheric CO2 can be used to trace gross photosynthetic and respiratory CO2 fluxes between the atmosphere and the terrestrial biosphere. However, this requires knowledge of the O-18 signatures attributable to the fluxes from soil and leaves. Newly developed methods were employed to measure the O-18 of soil-respired CO2 and depth profiles of near-surface soil CO2 in order to evaluate the factors influencing isotopic soil-atmosphere CO2 exchange. The O-18 soil-respired CO2 varied predominantly as a function of the O-18 of soil water which, in turn, changed with soil drying and with seasonal variations in source water. The O-18 of soil- respired CO2 corresponds to full isotopic equilibrium with soil water at a depth ranging between 5 and 15 cm. The O-18 of respired CO2, in reality, results from a weighted average of partial equilibria over a range of depths. Soil water isotopic enrichment of up to 10 parts per thousand in the top 5 cm did not appear to strongly influence the isotopic composition of the respired CO2. We demonstrate that during measurements "invasion" of atmospheric CO2 (the diffusion of ambient CO2 into the soil, followed by partial equilibration and retrodiffusion) must be considered to accurately calculate the O-18 of the soil-respired CO2. The impact of invasion in natural settings is also considered. We also have determined the effective kinetic fractionation of CO2 diffusion out of the soil to be 7.2 +/- 0.3 parts per thousand. High-resolution (1 cm) depth profiles of O-18 of near-surface (top 10 cm) soil CO2 were carried out by gas chromatography-isotope ratio mass spectrometry (IRMS). This novel technique allowed us to observe the competitive diffusion-equilibration process near the soil surface and to test simulations by a diffusion and equilibration model of the soil CO2 O-18 content.

KEYWORDS: CARBON DIOXIDE, DELTA O 18, DIRECT EQUILIBRATION, EXCHANGE, ISOTOPIC COMPOSITION, LEAF WATER, O-18, OXYGEN, SURFACE, VEGETATION

1549

Miller, J.E., A.S. Heagle, and W.A. Pursley. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment: II. Biomass and development. *Crop Science 38(1):122-128.*

Previous research has shown that elevated CO2 concentrations can increase plant growth, whereas the air pollutant O-3 is phytotoxic. Because elevated concentrations of these gases will co-occur, the objective of our experiment was to determine if estimates of plant growth response to future levels of CO2 and O-3 require experiments to test the gases in combination. Soybean plants [Glycine max (L.) Merr. cv. Essex) were exposed in open-top chambers to combinations of O-3 and CO2 from plant emergence through physiological maturity. Ozone treatments were charcoal-filtered air (CF), nonfiltered sir (NF), and NF with O-3 added for 12 h d(-1) (NF+) (seasonal mean 12 h d(-1) O-3 concentrations of 20, 50, or 79 nL L-1, respectively). Carbon dioxide exposures were for 24 h d(-1) giving seasonal mean 12 h d(-1) concentrations of 370, 482, 599, or 713 mu L L-1 Over the season, elevated CO2 usually stimulated growth and O-3 suppressed growth. Elevated CO2 usually increased partitioning of biomass to branches, decreased partitioning to pods, increased specific leaf weight, and decreased leaf area ratio. Ozone suppressed leaf and root weight ratios, increased pod weight ratios, and decreased specific leaf weight. Toward the end of the season, both O-3 and CO2 accelerated reproductive development. Elevated CO2 moderated suppression of growth by O- 3, and the highest CO2 concentration completely ameliorated O-3 effects on main stem biomass, root biomass, and leaf area. Ozone, however, limited some positive growth responses to CO2, especially at less than a doubling of CO2 concentrations. These results indicate that in order to understand the future impacts of atmospheric gases such as elevated CO2 and O-3 On crop growth, their combined effects should be

determined.

KEYWORDS: ATMOSPHERIC CO2, CHAMBERS, GROWTH, PLANT-RESPONSES

1550

Mishra, R.S., M.Z. Abdin, and D.C. Uprety. 1999. Interactive effects of elevated CO2 and moisture stress on the photosynthesis, water relation and growth of Brassica species. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 182(4):223-229.*

Interactive effects of elevated CO2 and moisture stress on photosynthesis, growth and water relation of Brassica species were studied using open top chamber technology. Brassica species responded to the elevated CO2 significantly under moisture stress condition. The adverse effect of moisture stress on the photosynthesis and plant water components were minimized by elevated levels of CO2. Drought susceptible species of B. campestris and B. nigra responded better to elevated CO2 compared to drought tolerant Brassica species such as B. carinata and B, juncea. The plant water potential significantly improved by elevated CO2 coupled with higher stomatal resistance and root growth.

KEYWORDS: ATMOSPHERIC CO2, DEFICITS, LEAF-AREA, SEEDLINGS, WHEAT, YIELD

1551

Mitchell, C.A., C.H. Chun, W.E. Brandt, and S.S. Nielsen. 1997. Environmental modification of yield and nutrient composition of 'Waldmann's Green' leaf lettuce. *Journal of Food Quality 20(1):73-80.*

Leaf number, dry weight, and nutrient composition of Lactuca sativa L. cv. 'Waldmann's Green leaves were compared following 9 days of treatment in a controlled environment room under various combinations of photosynthetic photon flux (PPF:350 vs 800 mu mol m(-2) s(-1)), atmospheric CO2 level (ambient vs 1500 mu mol mol(-1)), and single-strength (1X:15 mM) vs double- strength (2X:30 mM nitrogen (N) as NO3- alone or as NH4+ + NO3- (1:5 molar ratio). CO2 enrichment greatly enhanced leaf number under all PPF and N conditions, but increased leaf dry weight only at high PPF . Conditions favoring high photosynthesis enhanced leaf starch content 3-fold, and protein content increased as much as 64% with 2X NH4++NO3-. Free sugar content was 6 to 9% of leaf dry weight for all treatment combinations, while fat was 1.5 to 3.5%. Ash content varied from 15 to 20% of leaf dry weight. Modified controlled environments can be used to enhance the nutritional content as well as the yield of crops to be used for life support in space-deployed, self- sustaining human habitats. Leaf lettuce is a useful model crop for demonstrating the potential of nutritional value added by environmental manipulation.

KEYWORDS: GROWTH, LIGHT, MANIPULATION, TISSUE

1552

Mitchell, J.F.B. 1990. Greenhouse warming - is the midholocene a good analog. *Journal of Climate 3(11):1177-1192.*

The mid-Holocene period (from approximately 9000 to 6000 years before present) is often suggested as an analogue for enhanced greenhouse warming. The changes in net radiative forcing at the top of atmosphere are very different; increases in greenhouse gases producing a small annual mean warming of little seasonal or latitudinal variation, whereas during the Holocene the annual mean did not change but there were large seasonal and latitudinal variations. Two climate model experiments, one in which CO2 amounts are doubled and the other in which the value of the earth's orbital parameters are altered to those appropriate to 9000 years before present (BP), are compared. Any similarity in the simulated response is found to be limited to the northern continents and, even there, the mechanisms producing the changes differ between the two experiments. Assuming that the gross behavior of the model is realistic, the Holocene is not a good analogue for a "greenhouse" warming. Furthermore, as the mechanisms operating in the two experiments are different, a model which produces a realistic simulation for the mid-Holocene and present climate need not necessarily produce a reliable simulation of greenhouse warming. However, a comparison of simulated climates for the mid-Holocene and that reconstructed from paleoclimatic data may help to constrain the existing range of subgridscale parametrizations used in climate models.

1553

Mitchell, K.A., P.V. Bolstad, and J.M. Vose. 1999. Interspecific and environmentally induced variation in foliar dark respiration among eighteen southeastern deciduous tree species. *Tree Physiology 19(13):861-870.*

We measured variations in leaf dark respiration rate (Rd) and leaf nitrogen (N) across species, canopy light environment, and elevation for 18 co-occurring deciduous hardwood species in the southern Appalachian mountains of western North Carolina. Our overall objective was to estimate leaf respiration rates under typical conditions and to determine how they varied within and among species. Mean dark respi ration rate at 20 degrees C (R- d,R-mass, mu mol CO2 (kg leaf dry mass)(-1) s(-1)) for all 18 species was 7.31 mu mol kg(-1) s(-1). Mean R-d,R-mass of individual species varied from 5.17 mu mol kg(-1) s(-1) for Quercus coccinea Muenchh, to 8.25 mu mol kg(-1) s(-1) for Liriodendron tulipifera L. Dark respiration rate varied by leaf canopy position and was higher in leaves collected from high- light environments. When expressed on an area basis, dark respiration rate (R-d,R-area, mu mol CO2 (kg leaf dry area)(-1) s(-1)) showed a strong linear relationship with the predictor variables leaf nitrogen (N-area, g N (m leaf area)(-2)) and leaf structure (LMA, g leaf dry mass (m leaf area)(-2)) (r(2) = 0.62). This covariance was largely a result of changes in leaf structure with canopy position; smaller thicker leaves occur at upper canopy positions in high-light environments. Mass-based expression of leaf nitrogen and dark respiration rate showed that nitrogen concentration (N-mass, mg N (g leaf dry mass)(- 1)) was only moderately predictive of variation in R-d,R-mass for all leaves pooled (r(2) = 0.11), within species, or among species. We found distinct elevational trends, with both R-d,R- mass and N-mass higher in trees originating from high- elevation, cooler growth environments. Consideration of interspecies differences, vertical gradients in canopy light environment, and elevation, may improve our ability to scale leaf respiration to the canopy in forest process models.

KEYWORDS: ACCLIMATION, BOREAL FOREST ECOSYSTEMS, CANOPY, CARBON GAIN, GROWTH, LEAF LIFE-SPAN, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS- NITROGEN RELATIONS, PLANT, TEMPERATURE

1554

Mitchell, R.A.C., C.R. Black, S. Burkart, J.I. Burke, A. Donnelly, L. de Temmmerman, A. Fangmeier, B.J. Mulholland, J.C. Theobald, and M. van Oijen. 1999. Photosynthetic responses in spring wheat grown under elevated CO2 concentrations and stress conditions in the European, multiple-site experiment 'ESPACE-wheat'. *European Journal of Agronomy 10(3-4):205-214.*

Spring wheat cv. Minaret crop stands were grown under ambient and elevated CO2 concentrations at seven sites in Germany, Ireland, the UK, Belgium and the Netherlands. Six of the sites used open-top chambers and one used a controlled environment mimicking field conditions. The

effect of elevated CO2 for a range of N application regimes, O-3 concentrations, and growth temperatures on flag leaf photosynthesis was studied. Before anthesis, flag leaf photosynthesis was stimulated about 50% by 650 compared with 350 mu mol mol(-1) CO2 at all sites, regardless of other treatments. Furthermore, there was no evidence of a decrease in photosynthetic capacity of flag leaves due to growth at elevated CO2 before anthesis, even for low N treatments. However, photosynthetic capacity, particularly carboxylation capacity, of flag leaves was usually decreased by growth at elevated CO2 after anthesis, especially in low N treatments. Acclimation of photosynthesis to elevated CO2 therefore appears to occur only slowly, consistent with a response to changes in sink-source relationships, rather than a direct response. Effect of elevated CO2 on stomatal conductance was much more variable between sites and treatments, but on average was decreased by similar to 10% at 650 compared with 350 mu mol mol(-1) CO2. Carboxylation capacity of flag leaves was decreased by growth at elevated O-3 both before and after anthesis, regardless of CO2 concentration.

KEYWORDS: PLANTS, PRODUCTIVITY, PROTEINS, RISING ATMOSPHERIC CO2, TEMPERATURE

1555

Mitchell, R.A.C., C.L. Gibbard, V.J. Mitchell, and D.W. Lawlor. 1996. Effects of shading in different developmental phases on biomass and grain yield of winter wheat at ambient and elevated CO2. *Plant, Cell and Environment 19(5):615-621.*

Winter wheat (Triticum aestivum cv, Mercia) was grown in a controlled-environment facility under simulated field conditions at ambient (360 mu mol mol(-1)) and elevated (690 mu mol mol(-1)) CO2 concentrations, Some of the plants were shaded to mimic cloudy conditions during three periods of about 20 d duration between terminal spikelet and start of grain-fill, giving 16 treatments in all, Elevated 20(2), increased grain yield by about 20%, while shading in any period decreased yield, with the greatest effect in the last period, encompassing anthesis, No interactions between these effects were significant for grain yield, but there were complex interactions for mean grain size, Observed effects of shading and elevated CO2 on biomass production were well predicted by a simulation model, Observed effects of treatments on yield could be related to effects on biomass using a simple model which assumes that yield is proportional to biomass production, with coefficients of 0.42 (g grain yield g(-1) biomass) for the first two periods and 0.74 for the last period. Wheat models should therefore include developmental changes in sensitivity of yield to biomass production, but biomass changes induced by different CO2 concentrations or light environments can be treated as having equivalent effects on grain yield.

KEYWORDS: CROPS, GROWTH, MODEL, NITROGEN, NUMBER, SOLAR RADIATION, SPRING WHEAT, TEMPERATURE

1556

Mitchell, R.A.C., D.W. Lawlor, V.J. Mitchell, C.L. Gibbard, E.M. White, and J.R. Porter. 1995. Effects of elevated co2 concentration and increased temperature on winter-wheat - test of arcwheat1 simulation-model. *Plant, Cell and Environment 18(7):736-748.*

Winter wheat (Triticum aestivum L., cv, Mercia) was grown in a controlled-environment facility at two CO2 concentrations (targets 350 and 700 mu mol mol(-1)), and two temperature regimes (tracking ambient and ambient + 4 degrees C), Observations of phenology, canopy growth, dry matter production and grain yield were used to test the ARCWHEAT1 simulation model, Dry-matter production and grain yield were increased at elevated CO2 concentration (27 and 39%, respectively) and reduced at increased temperature (-16 and -35%, respectively), ARCWHEAT1 substantially underestimated canopy growth for all treatments, However, differences in the facility environment from field conditions over the winter, indicated by the unusually rapid canopy growth observed in this period, meant that empirical model relationships were being used outside the conditions for which they were developed, The ARCWHEAT1 productivity submodel, given observed green area indices as inputs, overestimated the effect of CO2 on productivity, An alternative, more mechanistic submodel of productivity, based on the SUCROS87 and Farquhar and von Caemmerer models, simulated observed crop biomass very closely, When these productivity simulations were inputed into the ARCWHEAT1 partitioning and grain-fill submodels, grain yield was predicted poorly, mainly as a result of the assumption that the number of grains is proportional to total growth during a short preanthesis phase, While yield was not correlated with growth in this phase, it was correlated with growth in longer preanthesis phases, indicating that ARCWHEAT1 could be improved by taking into account the contribution of earlier growth in determining yield.

KEYWORDS: CROPS, GENES, GROWTH, NUMBER, PHOTOSYNTHESIS, RBCS, SOLAR RADIATION, SPRING WHEAT, YIELD

1557

Mitchell, R.A.C., V.J. Mitchell, S.P. Driscoll, J. Franklin, and D.W. Lawlor. 1993. Effects of increased co2 concentration and temperature on growth and yield of winter-wheat at 2 levels of nitrogen application. *Plant, Cell and Environment 16(5):521-529.*

Winter wheat (Triticum aestivum L., cv. Mercia) was grown in chambers under light and temperature conditions similar to the UK field environment for the 1990/1991 growing season at two levels each of atmospheric CO2 concentration (seasonal means: 361 and 692 mumol mol-1), temperature (tracking ambient and ambient +4-degrees-C) and nitrogen application (equivalent to 87 and 489 kg ha-1 total N applied). Total dry matter productivity through the season, the maximum number of shoots and final ear number were stimulated by CO2 enrichment at both levels of the temperature and N treatments. At high N, there was a CO2-induced stimulation of grain yield (+15%) similar to that for total crop dry mass (+12%), and there was no significant interaction with temperature. This contrasts with other studies, where positive interactions between the effects of increases in temperature and CO2 have been found. Temperature had a direct, negative effect on yield at both levels of the N and CO2 treatments. This could be explained by the temperature-dependent shortening of the phenological stages, and therefore, the time available for accumulating resources for grain formation. At high N, there was also a reduction in grain set at ambient +4-degrees-C temperature, but the overall negative effect of warmer temperature was greater on the number of grains (-37%) than on yield (-18%), due to a compensating increase in average grain mass. At low N, despite increasing total crop dry mass and the number of ears, elevated CO2 did not increase grain yield and caused a significant decrease under ambient temperature conditions. This can be explained in terms of a stimulation of early vegetative growth by CO2 enrichment leading to a reduction in the amount of N available later for the formation and filling of grain.

KEYWORDS: CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, RADIATION, RESPIRATION, SEED YIELD, STRESS

1558

Mitchell, R.J., G.B. Runion, S.A. Prior, H.H. Rogers, J.S. Amthor, and F.P. Henning. 1995. Effects of nitrogen on pinus-palustris foliar respiratory responses to elevated atmospheric co2 concentration. *Journal of Experimental Botany 46(291):1561-1567.*

Indirect effects of atmospheric CO2 concentration [CO2], on longleaf pine (Pinus palustris Mill.) foliage respiration were studied by growing trees in a factorial arrangement of low and high [CO2] (369 and 729 mu mol CO2 mol(-1)) and low and high N (40 and 400 kg ha(-1) yr(-1)). Direct effects of [CO2] on leaf respiration were tested by measuring respiration rates of foliage from all treatments at two CO2 levels (360 and 720 mu mol CO2 mol(-1)) at the time of measurement. Elevated CO2 did not directly or indirectly affect leaf respiration when expressed on a leaf area or mass basis, but a significant increase in respiration per unit leaf N was observed in trees grown in elevated [CO2] (indirect response to elevated [CO2]). The lack of a [CO2] effect on respiration, when analysed on an area or mass basis, may have resulted from combined effects of [CO2] on factors that increase respiration (e.g. greater availability of non-structural carbohydrates stimulating growth and carbon export from leaves) and on factors that decrease respiration (e.g. lower N concentration leading to lower construction costs and maintenance requirements). Thus, [CO2] affected factors that influence respiration, but in opposing ways.

KEYWORDS: CARBOHYDRATE STATUS, CARBON DIOXIDE, CASTANEA-SATIVA MILL, CLIMATE CHANGE, CONSTRUCTION COST, DARK RESPIRATION, GROWTH, LEAF RESPIRATION, PLANT RESPIRATION, TREE SEEDLINGS

1559

Mitra, A., P.S. Bhattacharya, S. Dey, S.K. Sawarkar, and B.C. Bhattacharyya. 1998. Photoautotrophic in vitro culture of Chrysanthemum under CO2 enrichment. *Biotechnology Techniques 12(4):335-337.*

Photoautotrophic culture of Chrysanthemum was established under CO2 enrichment (2% v/v). The shoot length and number of leaves were almost equal (2.7 cm and 14 respectively) both under photoautotrophic and photomixotrophic cultures, recorded after four weeks of incubation. Similarly, average dry mass of the plantlets were comparable (31 and 28 mg respectively) under both conditions. The number of branches and internode length which influence the number of propagule potential for mass propagation, were also identical. Nevertheless, photoautotrophic cultivation minimized the risk of contamination in cultures, which in turn will reduce the production cost.

KEYWORDS: INVITRO

1560

Mitra, A., S. Dey, and S.K. Sawarkar. 1998. Photoautotrophic in vitro multiplication of the orchid Dendrobium under CO2 enrichment. *Biologia Plantarum 41(1):145-148.*

An attempt to reduce the production cost on tissue cultured plants, photoautotrophic culture of a high value orchid Dendrobium was established under CO2-enriched conditions. The shoot length and the number of leaves were almost equal in plantlets grown on medium with 2 % sucrose or without sucrose and under normal or enhanced (40 g m(-3)) CO2 concentration, whereas the fresh and dry masses were higher in cultures grown in sucrose containing media or under CO2 enrichment. Development of roots was observed only on media without sucrose, but CO2 enrichment did not have significant effects on in vitro rootings.

KEYWORDS: CULTURE, GROWTH, INVITRO

1561

Mitsuda, H. 1999. Toward solutions for food crisis in the 21st century - From basic research to development of innovative food technologies. *Proceedings of the Japan Academy Series B-Physical and Biological Sciences 75(8):246-253.*

The population explosion in the 21st century will have a severe impact on the problems associated with food supply and the environment. Even at present, the shortage of food protein resources is an acute problem. Effective countermeasures to cope with the ever worsening shortage of protein resources in the nest century are absolutely essential. We have developed methods to produce and isolate single cell proteins in an ample yield. We have also found that among food grains rice has the highest protein content, and have found that the protein in the grain is present in discrete particles, for which we coined the name "protein bodies". Rice protein has a relatively good balance of essential amino acids, and hence a relatively high nutritional value. We were able to increase the nutritional value further by fortifying it with L-lysine by a novel soaking method. New methods of food preservation will be important to cope with the 21st century food problems, because a large amount of food is lost either on the farm or during storage, to microorganisms, rodents and insects. We developed the carbon dioxide exchange method (CEM), in in which food is stored under CO2 in helmetically sealed containers (called Hibernation Rice), CO2 is reversiblyv adsorbed to, and desorbed from the amino groups of food pl proteins. We also developed underwater and underground food storage methods earlier (1967-72), to take advantage of constant low temperatures in these conditions. Based on these studies, large scale storage methods in 200 kg steel drums in CO2 have been developed on an industrial scale which is operated on a commercial base. Metylbromide destroys the ozone layer, and will be banned completely from use for food presentation or any ether purposes. Storage under CO2 is far superior to methylbromide because CO2 completely eliminates the rice weevil and other insects, has no toxicity or public health problems, and is economical. CO2 is a very effective synergist when used with the pasteurization gas, ozone, to sterilize foods against the virulent pathogenic strain of E.coli, O-157 and black pepper which are known to be contaminated with bacteria. The use of CO2 may add to an already high production of CO2 from other sources, such as combustion of fossil fuels. Effective measures to prevent leakage of CO2 are needed. We are striving for an innovative idea to pre-vent the escape of CO2 and the consequential warming of the earth.

1562

Miyachi, S., J. Burger, K. Kotzabasis, J. Thielmann, and H. Senger. 1996. Photosynthetic characteristics of three strains of cyanobacteria grown under low- or high-CO2 conditions. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 51(1-2):40-46.*

Quantum requirements of photosynthetic oxygen evolution at 679 nm, fluorescence emission spectra at liquid nitrogen temperature (77 K) and fluorescence induction kinetics in the presence of DCMU, were measured in the cyanobacteria Anabaena variabilis M3, Anabaena variabilis ATCC 29413 and Anacystis nidulans R2, each grown under low- or high-CO2 conditions. Low- CO2 grown cells of the cyanobacteria showed a higher quantum requirement of photosynthetic oxygen evolution and a higher ratio of F-710-740 to F-680-700 fluorescence and a lower variable fluorescence in the presence of DCMU than high-CO2 grown cells. These findings indicate a change in excitation energy distribution in favour of photosystem I. The result might be an enhancement in ATP formation caused by cyclic electron now which in turn provokes dissolved inorganic carbon (DIG) accumulation in these low-CO2 grown cells.

KEYWORDS: ANACYSTIS-NIDULANS, CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, CO2 CONCENTRATION, FIXATION, INDUCTION, INORGANIC CARBON, LIGHT, PHOTOSYSTEM- 2, SYSTEM

1563

Miyashita, Y., Y. Kitaya, C. Kubota, and T. Kozai. 1996.

Photoautotrophic growth of potato plantlets as affected by explant leaf area, fresh weight and stem length. *Scientia Horticulturae 65(2-3):199-202.*

Photoautotrophic growth in vitro of potato (Solanum tuberosum L. cv. Benimaru) explants varied with their initial leaf area and stem length. Photoautotrophic growth was much greater in leafy than in leafless explants. Variability in photoautotrophic growth was smallest in the explants with the greatest leaf area. The results indicated that use of explants with a large leaf area is important to maximize photoautotrophic growth and to minimize variation in photoautotrophic growth of explants in vitro.

1564

Mjwara, J.M., C.E.J. Botha, and S.E. Radloff. 1996. Photosynthesis, growth and nutrient changes in non-nodulated Phaseolus vulgaris grown under atmospheric and elevated carbon dioxide conditions. *Physiologia Plantarum 97(4):754-763.*

The response of Phaseolus vulgaris L. cv. Contender grown under controlled environment at either ambient or elevated (360 and 700 mu mol mol(-1), respectively) CO2 concentrations ([CO2]), was monitored from 10 days after germination (DAG) until the onset of senescence. Elevated CO2 had a pronounced effect on total plant height (TPH), leaf area (LA), leaf dry weight (LD), total plant biomass (TB) accumulation and specific leaf area (SLA). All of these were significantly increased under elevated carbon dioxide with the exception of SLA which was significantly reduced. Other than high initial growth rates in CO2-enriched plants, relative growth rates remained relatively unchanged throughout the growth period. While the trends in growth parameters were dearly different between [CO2], some physiological processes were largely transient, in particular, net assimilation rate (NAR) and foliar nutrient concentrations of N, Mg and Cu. CO2 enrichment significantly increased NAR, but from 20 DAG, a steady decline to almost similar levels to those measured in plants grown under ambient CO2 occurred. A similar trend was observed for leaf N content where the loss of leaf nitrogen in CO2-enriched plants after 20 DAG, was significantly greater than that observed for ambient-CO2 plants. Under enhanced CO2, the foliar concentrations of K and Mn were increased significantly whilst P, Ca, Fe and Zn were reduced significantly. Changes in Mg and Cu concentrations were insignificant. In addition, high CO2 grown plants exhibited a pronounced leaf discoloration or chlorosis, coupled with a significant reduction in leaf longevity.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, LIGHT, MINERAL NUTRITION, NITROGEN, PLANTS, SEEDLINGS, TEMPERATURE, TOMATO, WATER-USE EFFICIENCY

1565

Mo, G., D. Nie, M.B. Kirkham, H. He, L.K. Ballou, F.W. Caldwell, and E.T. Kanemasu. 1992. Root and shoot weight in a tallgrass prairie under elevated carbon-dioxide. *Environmental and Experimental Botany 32(3):193-201.*

The atmospheric concentration of carbon dioxide (CO2) is increasing and knowing how this will affect native vegetation is important. The objective of this study was to determine the effect of elevated CO2 on root growth in a tallgrass prairie kept at a high water level (73 cm of water in a 200 cm soil profile) and a low water level (66 cm of water in 200 cm). Sixteen cylindrical plastic chambers were placed on the prairie to maintain two levels of CO2 (ambient or twice ambient). At the end of two seasons' exposure to the different treatments, dry weight and length of roots in the 0-40 cm depth were determined. Shoot growth also was measured to determine shoot: root ratios. The CO2 and water treatments had no significant effect on root dry weight in the 0-40 cm depth. In the 0-10 cm depth, doubled CO2 reduced dry weight and length of roots of plants grown under the high water level by 47 and 31 %, respectively. Warm-season, C4 grasses had the highest shoot dry weight, which was greatest under the high water, ambient CO2 treatment. The shoot: root ratio did not change with treatment.

KEYWORDS: C-3, CO2, COMMUNITIES, ENRICHMENT, GROWTH, RESPONSES, SOIL, WATER-USE, YIELD

1566

Mohanraju, R., B.S. Rajagopal, and L. Daniels. 1997. Isolation and characterization of a methanogenic bacterium from mangrove sediments. *Journal of Marine Biotechnology 5(2-3):147-152.*

A methanogenic bacterium was enriched with trimethylamine and isolated from mangrove sediments. The isolate was a non-spore- forming regular to slightly irregular coccus (0.4-1 mm in diameter). The isolate required sodium chloride for growth with maximal methanogenesis at 420 mM NaCl at 30 degrees C. The optimal growth temperature was 30-35 degrees C with maximal methane production at 30 degrees C. The maximum growth rate was between pH 6.6 and 7.2 with maximum methane production at pH 6.8. The growth requirement of sulfide was 10-15 mM with maximum methane production at 10 mM at 30 degrees C. Mono-, di-, and trimethylamine or methanol were substrates for the methanogen; sodium acetate and H-2:CO2 were not. The DNA base content is consistent with the type descriptions of Methanoccoides methylutens, a methylotrophic methanogen isolated from submarine sediments. The isolate was found to utilize methylamines that are found in mangroves without having to compete with sulfate-reducing bacteria for H-2.

KEYWORDS: BETAINE, CHOLINE, CO-CULTURE, METABOLISM, METHANOSARCINA-BARKERI, METHYLATED AMINES, SP-NOV, SULFATE REDUCTION, TRIMETHYLAMINE

1567

Mohapatra, P.K. 1990. CO2 enrichment and physiology of inflorescence development in wheat. *Photosynthetica 24(1):9-15.*

1568

Monje, O., and B. Bugbee. 1998. Adaptation to high CO2 concentration in an optimal environment: radiation capture, canopy quantum yield and carbon use efficiency. *Plant, Cell and Environment 21(3):315-324.*

The effect of elevated [CO2] on wheat (Triticum aestivum L, Veery 10) productivity was examined by analysing radiation capture, canopy quantum yield, canopy carbon use efficiency, harvest index and daily C gain, Canopies were grown at either 330 or 1200 mu mol mol(-1) [CO2] in controlled environments, where root and shoot C fluxes were monitored continuously from emergence to harvest. A rapidly circulating hydroponic solution supplied nutrients, water and root zone oxygen, At harvest, dry mass predicted from gas exchange data was 102.8 +/- 4.7% of the observed dry mass in six trials. Neither radiation capture efficiency nor carbon use efficiency were affected by elevated [CO2], but yield increased by 13% due to a sustained increase in canopy quantum yield. CO2 enrichment increased root mass, tiller number and seed mass. Harvest index and chlorophyll concentration were unchanged, but CO2 enrichment increased average life cycle net photosynthesis (13%, $P < 0.05$) and root respiration (24%, $P < 0$ 05). These data indicate that plant communities adapt to CO2 enrichment through changes in C allocation. Elevated [CO2] increases sink strength in optimal environments, resulting in sustained increases in photosynthetic capacity, canopy quantum yield and daily C gain

throughout the life cycle.

KEYWORDS: DARK RESPIRATION, DIOXIDE CONCENTRATION, ELEVATED CO2, LEAVES, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGY, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE, WHEAT

1569
Monz, C.A., H.W. Hunt, F.B. Reeves, and E.T. Elliott. 1994. The response of mycorrhizal colonization to elevated co2 and climate-change in pascopyrum-smithii and bouteloua-gracilis. *Plant and Soil 165(1):75-80.*

Large intact soil cores of nearly pure stands of Pascopyrum smithii (western wheatgrass, C-3) and Bouteloua gracilis (blue grama, C-4) were extracted from the Central Plains Experimental Range in northeastern Colorado, USA and transferred to controlled environment chambers. Cores were exposed to a variety of water, temperature and CO2 regimes for a total of four annual growth cycles. Root subsamples were harvested after the completion of the second and fourth growth cycles at a time corresponding to late winter, and were examined microscopically for the presence of mycorrhizae. After two growth cycles in the growth chambers, 54% of the root length was colonized in P smithii, compared to 35% in blue grama. Field control plants had significantly lower colonization. Elevation of CO2 increased mycorrhizal colonization in B. gracilis by 46% but had no effect in P. smithii. Temperatures 4 degrees C higher than normal decreased colonization in P. smithii by 15%. Increased annual precipitation decreased colonization in both species. Simulated climate change conditions of elevated CO2, elevated temperature and lowered precipitation decreased colonization in P. smithii but had less effect on B. gracilis. After four growth cycles in P. smithii, trends of treatments remained similar, but overall colonization rate decreased.

KEYWORDS: C-3, ECOSYSTEMS, GROWTH

1570
Mooney, H.A. 1991. Biological response to climate change - an agenda for research. *Ecological Applications 1(2):112-117.*

Our knowledge of the structure and functioning of terrestrial ecosystems on a global scale is not developed to a sufficient degree to understand - much less predict - the consequences of climate change either on the systems themselves or on subsequent atmospheric interactions. In many regards we have lagged behind the atmospheric scientists, and to a certain degree the oceanographers, in establishing a global understanding of the dynamics of our respective systems. This is due in part to the inherently greater complexity of biotic systems, but also to the lack of appropriate tools to measure regional biotic processes. These tools are now becoming available and with them a better understanding of terrestrial and atmospheric interactions. Even as these capabilities become a reality we must be realistic in recognizing that we have so far to go along the road to understanding that useful predictive capacity may elude us for a long time to come. What we now need to do is act on the recommendations that have been emerging over the past few years and develop a global program to document more precisely the distribution, structure, and quantity of the earth's biotic systems, their principal functional properties, and - most difficult of all - their changing nature. In order to do this we will have to: (1) perfect some of the emerging new tools for assessing these properties, (2) fill some of the gaps in our knowledge about the relevant processes, and (3) establish an international network of long-term observations and large-scale ecosystem manipulations. We have been aware of these needs and shortcomings for some time and we must move from plans to concerted international action.

KEYWORDS: ELEVATED CO2, PLANTS

1571
Mooney, H.A., B.G. Drake, R.J. Luxmoore, W.C. Oechel, and L.F. Pitelka. 1991. Predicting ecosystem responses to elevated CO2 concentrations. *BioScience 41(2):96-104.*

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ESTUARINE MARSH, GROWTH-RESPONSES, LONG-TERM EXPOSURE, NUTRIENT-UPTAKE, PHOSPHORUS DEFICIENCY, PHOTOSYNTHETIC INHIBITION, PINUS-RADIATA, WATER-STRESS

1572
Mooney, H.A., and G.W. Koch. 1994. The impact of rising co2 concentrations on the terrestrial biosphere. *Ambio 23(1):74-76.*

Large advances have been made in linking terrestrial biospheric and atmospheric processes in real time. Further, it is now possible to model the potential response of the Earth's primary productivity to the changing climate and to changes in atmospheric CO2 concentration. We still have limited information, however, on the total responses of ecosystems to enhanced CO2 because of the complex web of possible interactions. What is needed are experiments on whole ecosystems under enhanced CO2 in which all of the potential interactions and feedbacks can be monitored, including plant- microbe, plant-herbivore, and plant-atmosphere interactions. A global network of experiments in the major biomes of the world is being developed within the International Geosphere-Biosphere Programme (IGBP) to resolve questions related to the implications of a changed pattern of biomass distribution in the biosphere.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ELEVATED CO2, GROWTH, RESPONSES

1573
Moore, B.D., S.H. Cheng, J. Rice, and J.R. Seemann. 1998. Sucrose cycling, Rubisco expression, and prediction of photosynthetic acclimation to elevated atmospheric CO2. *Plant, Cell and Environment 21(9):905-915.*

Photosynthetic acclimation to elevated CO2 cannot presently be predicted due to our limited understanding of the molecular mechanisms and metabolic signals that regulate photosynthetic gene expression. We have examined acclimation by comparing changes in the leaf content of RuBP carboxylase/oxygenase (Rubisco) with changes in the transcripts of Rubisco subunit genes and with leaf carbohydrate metabolism. When grown at 1000 mm(3) dm(-3) CO2, 12 of 16 crop species at peak vegetative growth had a 15-44% decrease in leaf Rubisco protein, but with no specific association with changes in transcript levels measured at midday. Species,vith only modest reductions in Rubisco content (10-20%) often had a large reduction in Rubisco small subunit gene mRNAs (> 30%), with no reduction in large subunit gene mRNAs, However, species with a very large reduction in Rubisco content generally had only small reductions in transcript mRNAs, Photosynthetic acclimation also was not specifically associated with a change in the level of any particular carbohydrate measured at midday. However, a threshold relationship was found between the reduction in Rubisco content at high CO2 and absolute levels of soluble acid invertase activity measured in plants grown at ambient or high CO2, This relationship was valid for 15 of the 16 species examined. There also occurred a similar, albeit less robust, threshold relationship between the leaf hexose/sucrose ratio at high CO2 and a reduced photosynthetic capacity greater than or equal to 20%. These data indicate that carbohydrate repression of photosynthetic gene expression at elevated CO2 may involve leaf

sucrose cycling through acid invertase and hexokinase.

KEYWORDS: CARBON CATABOLITE REPRESSION, CARBOXYLASE SMALL-SUBUNIT, GAS-EXCHANGE, GENE-EXPRESSION, GROWTH, HIGHER-PLANTS, LEAF DEVELOPMENT, MECHANISM, POTATO-TUBERS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE

1574

Moore, B.D., D.E. Palmquist, and J.R. Seemann. 1997. Influence of plant growth at high CO2 concentrations on leaf content of ribulose-1,5-bisphosphate carboxylase/oxygenase and intracellular distribution of soluble carbohydrates in tobacco, snapdragon, and parsley. *Plant Physiology 115(1):241-248.*

We have examined the possible role of leaf cytosolic hexoses and the expression of mannitol metabolism as mechanisms that may affect the repression of photosynthetic capacity when plants are grown at 1000 versus 380 mu L L-1 CO2. In plants grown at high CO2, leaf ribulose-1,5-bisphosphate carboxylase/oxygenase content declined by greater than or equal to 20% in tobacco (Nicotiana sylvestris) but was not affected in the mannitol-producing species snapdragon (Antirrhinum majus) and parsley (Petroselinum hortense). In the three species mesophyll glucose and fructose at midday occurred almost entirely in the vacuole (>99%), irrespective of growth CO2 levels. The estimated cytosolic concentrations of glucose and fructose were less than or equal to 100 mu M. In the three species grown at high CO2, total leaf carbohydrates increased 60 to 100%, but mannitol metabolism did not function as an overflow mechanism for the increased accumulation of carbohydrate. In both snapdragon and parsley grown at ambient or high CO2, mannitol occurred in the chloroplast and cytosol at estimated midday concentrations of 0.1 M or more each. The compartmentation of leaf hexoses and the metabolism of alternate carbohydrates are further considered in relation to photosynthetic acclimation to high levels of CO2.

KEYWORDS: CARBON FLOW, CELERY LEAVES, ELEVATED CO2, GAS-EXCHANGE, MANNITOL, METABOLITE LEVELS, PHOTOSYNTHESIS, SPINACH LEAVES, SUCROSE ACCUMULATION, TRANSGENIC TOBACCO

1575

Moore, T.R., N.T. Roulet, and J.M. Waddington. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change 40(2):229-245.*

Northern peatlands play an important role globally in the cycling of C, through the exchange of CO2 with the atmosphere, the emission of CH4, the production and export of dissolved organic carbon (DOC) and the storage of C. Under 2 x CO2 GCM scenarios, most Canadian peatlands will be exposed to increases in mean annual temperature ranging between 2 and 6 degrees C and increases in mean annual precipitation of 0 to 15 %, with the most pronounced changes occurring during the winter. The increase in CO2 uptake by plants, through warmer temperatures and elevated atmospheric CO2, is likely to be offset by increased soil respiration rates in response to warmer soils and lowered water tables. CH4 emissions are likely to decrease in most peatlands because of lowered water tables, except where the peat surface adjusts to fluctuating water tables, and in permafrost, where the collapse of dry plateau and palsa will lead to increased CH4 emission. There likely will be little change in DOC production, but DOC export to water bodies will decrease as runoff decreases. The storage of C in peatlands is sensitive to all C cycle components and is difficult to predict. The challenge is to develop quantitative models capable of making these predictions for different peatlands. We present some qualitative responses, with levels of uncertainty. There will be, however, as much variation in response to climatic change within a peatland as there will be among peatland regions.

KEYWORDS: ATMOSPHERE, BALANCE, CO2 FLUXES, CONTINENTAL WESTERN CANADA, DISCONTINUOUS PERMAFROST, DISSOLVED ORGANIC-CARBON, METHANE EMISSIONS, POOR FEN, TEMPORAL VARIABILITY, WETLANDS

1576

Moore, T.R., J.A. Trofymow, B. Taylor, C. Prescott, C. Camire, L. Duschene, J. Fyles, L. Kozak, M. Kranabetter, I. Morrison, M. Siltanen, S. Smith, B. Titus, S. Visser, R. Wein, and S. Zoltai. 1999. Litter decomposition rates in Canadian forests. *Global Change Biology 5(1):75-82.*

The effect of litter quality and climate on the rate of decomposition of plant tissues was examined by the measurement of mass remaining after 3 years' exposure of 11 litter types placed at 18 forest sites across Canada. Amongst sites, mass remaining was strongly related to mean annual temperature and precipitation and amongst litter types the ratio of Klason lignin to nitrogen in the initial tissue was the most important litter quality variable. When combined into a multiple regression, mean annual temperature, mean annual precipitation and Klason lignin:nitrogen ratio explained 73% of the variance in mass remaining for all sites and tissues. Using three doubled CO2 GCM climate change scenarios for four Canadian regions, these relationships were used to predict increases in decomposition rate of 4-7% of contemporary rates (based on mass remaining after 3 years), because of increased temperature and precipitation. This increase may be partially offset by evidence that plants growing under elevated atmospheric CO2 concentrations produce litter with high lignin:nitrogen ratios which slows the rate of decomposition, but this change will be small compared to the increased rate of decomposition derived from climatic changes.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECAY-RATES, ELEVATED ATMOSPHERIC CO2, LEAF LITTER, LIGNIN CONTROL, MASS-LOSS, NUTRIENT-UPTAKE, TERM DECOMPOSITION, TERRESTRIAL ECOSYSTEMS

1577

Moorhead, D.L., and A.E. Linkins. 1997. Elevated CO2 alters belowground exoenzyme activities in tussock tundra. *Plant and Soil 189(2):321-329.*

A three-year exposure to a CO2 concentration of 680 mu mol mol(-1) altered the enzymic characteristics of root surfaces, associated ectomycorrhizae, and in soils surrounding roots in a tussock tundra ecosystem of north Alaska, USA. At elevated CO2, phosphatase activity was higher on Eriophorum vaginatum root surfaces, ectomycorrhizal rhizomorphs and mantles associated with Betula nana roots, and in Oe and Oi soil horizons associated with plant roots. Also, endocellulase and exocellulase activities at elevated CO2 were higher in ectomycorrhizal rhizomorphs and lower in Oe and Oi soil horizons associated with roots. These results suggest that arctic plants respond to raised CO2 by increasing activities associated with nutrient acquisition, e.g. higher phosphatase activities on surfaces of roots and ectomycorrhizae, and greater cellulase activity in ectomycorrhizae. Changes in enzyme activities of surrounding soils are consistent with an increase in carbon exudation from plant roots, which would be expected to inhibit cellulase activities and stimulate phosphatase activities of soil microflora. These data were used to modify existing simulation models describing tussock phosphatase activities and litter decay. Model projections suggest that observed increases in phosphatase activities at 680 mu mol mol(-1) CO2, could augment total annual phosphorus release within tussocks by more than 40%, at present levels of root and ectomycorrhizae biomass. This includes a nearly three- fold increase in potential phosphatase activity of E. vaginatum roots, per unit of surface area. Observed

reductions in cellulase activities could diminish cellulose turnover by 45% in soils within rooting zones, which could substantially increase mineral nitrogen availability in soils due to lowered microbial immobilization.

KEYWORDS: ATMOSPHERIC CO2, BACTERIAL-POPULATIONS, CARBON DIOXIDE, CELLULASE ACTIVITY, DECOMPOSING LEAF LITTER, ERIOPHORUM VAGINATUM, FREEZE-THAW CYCLES, MICROBIAL ACTIVITY, MODELING SYNTHESIS, PHOSPHATASE-ACTIVITIES

1578

Moorhead, D.L., R.L. Sinsabaugh, A.E. Linkins, and J.F. Reynolds. 1996. Decomposition processes: Modelling approaches and applications. *The Science of the Total Environment 183(1-2):137-149.*

Decomposition is a fundamental ecosystem process, strongly influencing ecosystem dynamics through the release of organically bound nutrients. Decomposition is also a complex phenomenon that can be modified by changes in the characteristics of the decaying materials or prevailing environmental conditions. For these reasons, the impacts of local, regional or global environmental changes on the quality and turnover of dead organic matter are of considerable interest. However, realistic limits to the complexity, as well as temporal and spatial scales, of experimental studies restrict their usefulness in extrapolating long-term or large- scale results of simultaneous environmental changes. Alternatively, many simulation models have been constructed to gain insight to potential impacts of anthropogenic activities. Because structure and approach determine the strengths and limitations of a model, they must be considered when applying one to a problem or otherwise interpreting model behaviour. There are two basically different types of models: (1) empirical models generally ignore underlying processes when describing system behaviour, while (2) mechanistic models reproduce system behaviour by simulating underlying processes. The former models are usually accurate within the range of conditions for which they are constructed but tend to be unreliable when extended beyond these limits. In contrast, application of a mechanistic model to novel conditions assumes only that the underlying mechanisms behave in a consistent manner. In this paper, we examine models developed at different levels of resolution to simulate various aspects of decomposition and nutrient cycling and how they have been used to assess potential impacts of environmental changes on terrestrial ecosystems.

KEYWORDS: BACTERIAL-POPULATIONS, CLIMATE CHANGE, ELEVATED ATMOSPHERIC CO2, LIGNIN CONTROL, LITTER DECOMPOSITION, LONG-TERM RESPONSE, MODELING SYNTHESIS, ORGANIC-MATTER, TERRESTRIAL ECOSYSTEMS, TUSSOCK TUNDRA

1579

Morcuende, R., P. Perez, R. MartinezCarrasco, I.M. DelMolino, and L.S. DeLaPuente. 1996. Long- and short-term responses of leaf carbohydrate levels and photosynthesis to decreased sink demand in soybean. *Plant, Cell and Environment 19(8):976-982.*

Axillary buds and the apical portion of shoots of soybean [Glycine max (L.) Merr. cultivar Turchina] plants were trimmed to investigate long-term regulation of photosynthesis by sink demand at ambient CO2 and 22 degrees C, Also, in intact and trimmed shoots, the CO2 level was increased to 660 mu mol mol(- 1) and temperature was lowered to 5 degrees C to examine the superimposed short-term responses of photosynthesis to low sink demand, Under growth conditions, trimming the shoots increased leaf photosynthesis and the levels of sucrose, glucose-6- phosphate (G6P) and 3-phosphoglycerate (PGA), as well as the G6P/fructose-6-phosphate (F6P) and sucrose/starch ratios, while it decreased the level of starch and the triose-phosphate (glyceraldehyde 3-phosphate and dihydroxyacetone phosphate, TP)/PGA ratio, Photosynthesis enhancement was accompanied by increased chlorophyll contents and ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) activity. Sink removal consistently increased photosynthesis measured under a variety of conditions (growth CO2 or a short-term change to 660 mu mol mol(-1) CO2; growth temperature or a short-term change to 5 degrees C), except when low temperature was combined with ambient CO2; the increase in photosynthesis was higher under short-term elevated CO2 than at ambient CO2, In contrast with its effect at ambient CO2, shoot trimming increased the levels of TP and ribulose-1,5-bisphosphate (RuBP) and the TP/PGA ratio under high-CO2 conditions.

KEYWORDS: CARBON ASSIMILATION, CARBOXYLASE, ELEVATED CO2, METABOLISM, PLANTS, RIBULOSE 1;5-BISPHOSPHATE, SPINACH LEAVES, SUCROSE PHOSPHATE SYNTHASE, TEMPERATURE, WHEAT

1580

Morgan, J.A., H.W. Hunt, C.A. Monz, and D.R. Lecain. 1994. Consequences of growth at 2 carbon-dioxide concentrations and 2 temperatures for leaf gas-exchange in pascopyrum-smithii (C-3) and bouteloua-gracilis (C-4). *Plant, Cell and Environment 17(9):1023-1033.*

Continually rising atmospheric CO2 concentrations and possible climatic change may cause significant changes in plant communities. This study was undertaken to investigate gas exchange in two important grass species of the short-grass steppe, Pascopyrum smithii (western wheatgrass), C-3, and Bouteloua gracilis (blue grama), C4, grown at different CO2 concentrations and temperatures. Intact soil cores containing each species were extracted from grasslands in north-eastern Colorado, USA, placed in growth chambers, and grown at combinations of two CO2 concentrations (350 and 700 mu mol mol(-1)) and two temperature regimes (field average and elevated by 4 degrees C). Leaf gas exchange was measured during the second, third and fourth growth seasons. All plants exhibited higher leaf CO2 assimilation rates (A) with increasing measurement CO2 concentration, with greater responses being observed in the cool-season C-3 species P. smithii. Changes in the shape of intercellular CO2 response curves of A for both species indicated photosynthetic acclimation to the different growth environments, The photosynthetic capacity of P. smithii leaves tended to be reduced in plants grown at high CO2 concentrations, although A for plants grown and measured at 700 mu mol mol(-1) CO2 was 41% greater than that in plants grown and measured at 350 mu mol mol(-1) CO2. Low leaf N concentration may have contributed to photosynthetic acclimation to CO2. A severe reduction in photosynthetic capacity was exhibited in P. smithii plants grown long-term at elevated temperatures. As a result, the potential response of photosynthesis to CO2 enrichment was reduced in P. smithii plants grown long-term at the higher temperature.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, GRASS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PRAIRIE, PRODUCTIVITY, RESPONSES

1581

Morgan, J.A., W.G. Knight, L.M. Dudley, and H.W. Hunt. 1994. Enhanced root-system C-sink activity, water relations and aspects of nutrient acquisition in mycotrophic bouteloua- gracilis subjected to co2 enrichment. *Plant and Soil 165(1):139-146.*

In order to better elucidate fixed-C partitioning, nutrient acquisition and water relations of prairie grasses under elevated [CO2], we grew the C-4 grass Bouteloua gracilis (H.B.K.) lag ex Steud. from seed in soil-packed, column- lysimeters in two growth chambers maintained at current

ambient [CO2] (350 mu L L(-1)) and twice enriched [CO2] (700 mu L L(- 1)). Once established, plants were deficit irrigated; growth chamber conditions were maintained at day/night temperatures of 25/16 degrees C, relative humidities of 35%/90% and a 14-hour photoperiod to simulate summer conditions on the shortgrass steppe in eastern Colorado. After 11 weeks of growth, plants grown under CO2 enrichment had produced 35% and 65% greater total and root biomass, respectively, and had twice the level of vesicular-arbuscular mycorrhizal (VAM) infection (19.8% versus 10.8%) as plants grown under current ambient [CO2]. The CO2-enriched plants also exhibited greater leaf water potentials and higher plant water use efficiencies. Plant N uptake was reduced by CO2 enrichment, while P uptake appeared little influenced by CO2 regime. Under the conditions of the experiment, CO2 enrichment increased root biomass and VAM infection via stimulated growth and adjustments in C partitioning below-ground.

KEYWORDS: COMMUNITIES, ELEVATED CARBON-DIOXIDE, GROWTH, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, PLANTS, QUERCUS-ALBA, SOIL, STRESS

1582

Morgan, J.A., D.R. LeCain, J.J. Read, H.W. Hunt, and W.G. Knight. 1998. Photosynthetic pathway and ontogeny affect water relations and the impact of CO2 on Bouteloua gracilis (C-4) and Pascopyrum smithii (C-3). *Oecologia 114(4):483-493.*

The eastern Colorado shortgrass steppe is dominated by the C-4 grass, Bouteloua gracilis, but contains a mixture of C-3 grasses as well, including Pascopyrum smithii. Although the ecology of this region has been extensively studied, there is little information on how increasing atmospheric CO2 will affect it. This growth chamber study investigated gas exchange, water relations, growth, and biomass and carbohydrate partitioning in B. gracilis and P. gracilis grown under present ambient and elevated CO2 concentrations of 350 mu l l(-1) and 700 mu l l(-1), respectively, and two deficit irrigation regimes. The experiment was conducted in soil-packed columns planted to either species over a 2-month period under summer- like conditions and with no fertilizer additions. Our objective was to better under stand how these species and the functional groups they represent will respond in future CO2-enriched environments. Leaf CO2 assimilation (A(n)), transpiration use efficiency (TUE, or A(n)/transpiration), plant growth, and whole-plant water use efficiency (WUE, or plant biomass production/water evapotranspired) of both species were greater at elevated CO2, although responses were more pronounced for P. smithii. Elevated CO2 enhanced photosynthesis, TUE, and growth in both species through higher soil water content (SWC) and leaf water potentials (Psi) and stimulation of photosynthesis. Consumptive water use was greater and TUE less for P. smithii than B. gracilis during early growth when soil water was more available. Declining SWC with time was associated with a steadily increased sequestering of total non-structural carbohydrates (TNCs), storage carbohydrates (primarily fructans for P. Smithii) and biomass in belowground organs of P. smithii, but not B. gracilis. The root:shoot ratio of P. smithii also increased at elevated CO2 while the root:shoot ratio of B. gracilis was unresponsive to CO2. These partitioning responses may be the consequence of different ontogenetic strategies of a cool-season and warm-season grass entering a warm, dry summer period; the cool-season P. smithii responds by sequestering TNCs belowground in preparation for summer dormancy, while resource partitioning of the warm-season B. gracilis remains unaltered. One consequence of greater partitioning of resources into P. smithii belowground organs in the present study was maintenance of higher Psi and A(n) rates. This, along with differences in photosynthetic pathway, may have accounted for the greater responsiveness of P. smithii to CO2 enrichment compared to B. gracilis.

KEYWORDS: AGROPYRON-SMITHII, CARBON DIOXIDE, ELEVATED CO2, GAS-EXCHANGE, GRASS, LEAF, NICHE SEPARATION, PRAIRIE ECOSYSTEM, RESPONSES, USE EFFICIENCY

1583

Moriguchi, T., and R.J. Romani. 1995. Mitochondrial self-restoration as an index to the capacity of avocado fruit to sustain atmospheric stress at 2 climacteric states. *Journal of the American Society for Horticultural Science 120(4):643-649.*

A strong association is implicit between mitochondrial function and the energy demands of cells responding to stress, Yet, the dynamics of this organelle-cellular dependency have been difficult to resolve. This study examines a new diagnostic parameter namely, mitochondrial maintenance and self- restoration as exhibited by the course of respiratory functions (States 3 and 4 respiratory rates, respiratory control) of mitochondria extracted during and after exposure of intact 'Hass' avocado (Persea americana) fruit to different stress atmospheres: anoxia (100% N-2) or high (25% and 75%) CO2 for varying durations. Comparisons are made with direct exposure of the mitochondria themselves to similar atmospheres. In general, exposure of the fruit to CO2 rich atmospheres enhanced the capacity of their mitochondria to restore energy-linked functions whereas anoxia caused irreparable damage. The physiological (climacteric) state of the fruit also affected the stress capacity of the mitochondria contained therein, anaerobiosis being more harmful to mitochondria in riper fruit. In contrast to their effects in vivo, in vitro anoxia appeared to sustain mitochondrial energy-linked functions, whereas high CO2 was clearly harmful, These and other observations are discussed in the context of mitochondrial self-restoration or homeostasis and its relevance to postharvest stress-atmosphere storage for purposes such as pathogen suppression or insect control.

1584

Morin, F., M. Andre, and T. Betsche. 1992. Growth-kinetics, carbohydrate, and leaf phosphate content of clover (trifolium-subterraneum L) after transfer to a high co2 atmosphere or to high light and ambient air. *Plant Physiology 99(1):89-95.*

Intact air-grown (photosynthetic photon flux density, 400 microeinsteins per square meter per second) clover plants (Trifolium subterraneum L.) were transferred to high CO2 (4000 microliters CO2 per liter; photosynthetic photon flux density, 400 microeinsteins per square meter per second) or to high light (340 microliters CO2 per liter; photosynthetic photon flux density, 800 microeinsteins per square meter per second) to similarly stimulate photosynthetic net CO2 uptake. The daily increment of net CO2 uptake declined transiently in high CO2, but not in high light, below the values in air/standard light. After about 3 days in high CO2, the daily increment of net CO2 uptake increased but did not reach the high light values. Nightly CO2 release increased immediately in high light, whereas there was a 3-day lag phase in high CO2. During this time, starch accumulated to a high level, and leaf deterioration was observed only in high CO2. After 12 days, starch was two- to threefold higher in high CO2 than in high light, whereas sucrose was similar. Leaf carbohydrates were determined during the first and fourth day in high CO2. Starch increased rapidly throughout the day. Early in the day, sucrose was low and similar in high CO2 and ambient air (same light). Later, sucrose increased considerably in high CO2. The findings that (a) much more photosynthetic carbon was partitioned into the leaf starch pool in high CO2 than in high light, although net CO2 uptake was similar, and that (b) rapid starch formation occurred in high CO2 even when leaf sucrose was only slightly elevated suggest that low sink capacity was not the main constraint in high CO2. It is proposed that carbon partitioning between starch (chloroplast) and sucrose (cytosol) was perturbed by high CO2 because of the lack of photorespiration. Total phosphate pools were determined in leaves.

Concentrations based on fresh weight of orthophosphate, soluble esterified phosphate, and total phosphate markedly declined during 13 days of exposure of the plants to high CO2 but changed little in high light/ambient air. During this time, the ratio of orthophosphate to soluble esterified phosphate decreased considerably in high CO2 and increased slightly in high light/ambient air. It appears that phosphate uptake and growth were similarly stimulated by high light, whereas the coordination was weak in high CO2.

KEYWORDS: ACCLIMATION, CARBON METABOLISM, CHLOROPLASTS, DIOXIDE, ENRICHMENT, LEAVES, LIMITATION, PHOTOSYNTHESIS, SUCROSE, TRANSPORT

1585

Morison, J.I.L. 1993. Response of plants to co2 under water limited conditions. *Vegetatio 104:193-209.*

The influence of increased atmospheric CO2 on the interaction between plant growth and water use is proving to be one of the most profound impacts of the anthropogenic 'Greenhouse Effect'. This paper illustrates the interaction between CO2 and water in plant growth at a range of scales. Most published work has concentrated on water use efficiency, especially at shorter time scales, and has shown large increases of leaf water use efficiency with increased CO2. However, the magnitude of the effect is variable, and does not consistently agree with predictions from simple leaf gas exchange considerations. The longer the time scales considered, the less the information and the more the uncertainty in the response to CO2, because of the additional factors that have to be considered, such as changes in leaf area, respiration of non-photosynthetic tissues and soil evaporation. The need for more detailed studies of the interactions between plant evaporation, water supply, water status and growth is stressed, as increased CO2 can affect all of these either directly, or indirectly through feedbacks with leaf gas exchange, carbon partitioning, leaf growth, canopy development and root growth.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, ROOT-GROWTH, STOMATAL CONDUCTANCE, USE EFFICIENCY, WINTER-WHEAT

1586

Morison, J.I.L. 1998. Stomatal response to increased CO2 concentration. *Journal of Experimental Botany 49:443-452.*

The stomatal response to CO2 is important in understanding stomatal physiology, and important in understanding vegetation- atmosphere exchanges at all scales from the individual plant up to global vegetation. Despite the long history of experiments on stomatal responses to CO2 there are still considerable uncertainties in both these tasks. The difficulty in understanding differences in stomatal conductance between plants grown for any length of time in different CO2 atmospheres is stressed because of the many other possible changes in the plants' carbohydrate, nutrient and water relations. The other key issues that are highlighted are: whether stomata acclimate to CO2 either in parallel with any mesophyll photosynthetic acclimation or independently of changes in the mesophyll; whether stomata on different leaf surfaces respond to CO2 similarly; and whether reported changes in stomatal frequency are important to leaf gas exchange. The need for direct examination of stomatal sensitivity of plants grown in different CO2 concentrations is stressed.

KEYWORDS: ATMOSPHERIC CO2, CONDUCTANCE, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, TEMPERATURE, WATER-USE EFFICIENCY

1587

Morison, J.I.L., and D.W. Lawlor. 1999. Interactions between increasing CO2 concentration and temperature on plant growth. *Plant, Cell and Environment 22(6):659-682.*

The global environment is changing with increasing temperature and atmospheric carbon dioxide concentration, [CO2]. Because these two factors are concomitant, and the global [CO2] rise will affect all biomes across the full global range of temperatures, it is essential to review the theory and observations on effects of temperature and [CO2] interactions on plant carbon balance, growth, development, biomass accumulation and yield, Although there are sound theoretical reasons for expecting a larger stimulation of net CO2 assimilation rates by increased [CO2] at higher temperatures, this does not necessarily mean that the pattern of biomass and yield responses to increasing [CO2] and temperature is determined by this response. This paper reviews the interactions between the effects of [CO2] and temperature on plants. There is little unequivocal evidence for large differences in response to [CO2] at different temperatures, as studies are confounded by the different responses of species adapted and acclimated to different temperatures, and the interspecific differences in growth form and development pattern. We conclude by stressing the importance of initiation and expansion of meristems and organs and the balance between assimilate supply and sink activity in determining the growth response to increasing [CO2] and temperature.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GLOBAL ENVIRONMENT CHANGE, LONG-TERM, NATURAL-POPULATIONS, OPEN-TOP CHAMBERS, TRITICUM-AESTIVUM L, WATER-USE, WINTER-WHEAT

1588

Morokuma, M., M. Yajima, and S. Yonemura. 1996. Effects of elevated CO2 concentration and warming on growth and yield of rice. *Japanese Journal of Crop Science 65(2):222-228.*

Effects of combined treatments of CO2 (400, 660, 1200 ppm) and air temperature (outdoor tracking, outdoor+2 degrees C) on growth and yield of rice (Oryza sativa L. cv. Nipponbare) grown in growth chambers under natural sunlight were investigated. The effects of container size (tank, 3.5 l pot) on growth and yield were also examined. Plants were grown under simulated paddyfield conditions. Growth parameters under the elevated CO2 and temperature conditions were promoted at the maximum tiller number stage but nor at the heading stage, without appreciable difference in such parameters. In the 660HT plot, dry weight increased about 30% at both stages compared with the 400NT plot. In the 1200HT plot, it increased more than that of the 660HT plot at the maximum tiller number stage but at the heading stage, the degree of promotion was decreased substantially. Dry matter distribution to leaf blades was reduced, and the nitrogen ratio in leaf blades were low in plants grown in both 660HT and 1200HT plants. In the 1200HT plot, the yield was remarkably reduced probably due to the high temperature sterility. Potted, limited-root-space plants grew smaller above-ground parts than did tank plants (less limited), without any difference in root production. From these results, the production processes of rice crop are discussed in terms of climate conditions predicted for the future.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, RESPONSES, TEMPERATURE

1589

Morse, S.R., and F.A. Bazzaz. 1994. Elevated co2 and temperature alter recruitment and size hierarchies in C-3 and C-4 annuals. *Ecology 75(4):966-975.*

In order to understand the implications of changes in global CO2 concentrations and temperature for the growth and fitness of individual plants, performance must be investigated in relation to the performance of other plants within a population. In this study we examined patterns of recruitment, mortality, and size structure of monospecific stands in response to ambient (400 mu L/L) and elevated CO2 concentrations (700 mu L/L) across three temperature regimes; 18 degrees, 28 degrees, and 38 degrees C. We created experimental populations of two annual plants that differ in their photosynthetic pathway and water use patterns: Abutilon theophrasti (C-3) and Amaranthus retroflexus (C-4). The effects of CO2, temperature, and their interactions on population structure were complex and species dependent. For both species increasing temperature resulted in higher germination and faster initial growth rates. These initial temperature responses increased the intensity and role of competition in determining stand size and structure. Postemergence responses to elevated CO2 differed markedly between the two species. For Abutilon, the C-3 species, serf-thinning and the mean biomass of the survivors increased under elevated CO2. For Amaranthus, survivorship, but not growth, increased under elevated CO2 conditions. We attribute differences in response between species not only to photosynthetic pathway, but also to differences in the onset of competition mediated through differences in plant form and in resource uptake and deployment. The patterns of stand development in response to CO2 and temperature suggest that the effects of changing CO2 and temperature may be understood within mechanistically based models of resource use. Temperature regulates the rate of resource use and the onset of interference among plants, while CO2 functions both as a resource and a resource regulator. Although mortality was concentrated later in stand development for Abutilon than Amaranthus, overall patterns of stand size and structure were similar for both species; mortality and size inequalities increased with increasing temperature and CO2. Because size is often correlated with fecundity, an increase in size hierarchies in response to elevated CO2, in conjunction with a decrease in survivorship, may result in a smaller effective population size. Our ability to predict changes in effective population size due to changing size hierarchies alone, however, should also consider developmental shifts in response to elevated CO2 that may result in, as in this study, a decrease in the minimum size at the onset of flowering.

KEYWORDS: COMPETITION, DENSITY, ENRICHMENT, FITNESS, GROWTH, MONOCULTURES, PLANT-POPULATIONS, STANDS, VARIABILITY

1590

Morse, S.R., P. Wayne, S.L. Miao, and F.A. Bazzaz. 1993. Elevated co2 and drought alter tissue water relations of birch (betula-populifolia marsh) seedlings. *Oecologia 95(4):599-602.*

The effect of increasing atmospheric CO2 concentrations on tissue water relations was examined in Betula populifolia, a common pioneer tree species of the northeastern U.S. deciduous forests. Components of tissue water relations were estimated from pressure volume curves of tree seedlings grown in either ambient (350 mul l-1) or elevated CO2 (700 mul l-1), and both mesic and xeric water regimes. Both CO2 and water treatment had significant effects on osmotic potential at full hydration, apoplasmic fractions, and tissue elastic moduli. Under xeric conditions and ambient CO2 concentrations, plants showed a decrease in osmotic potentials of 0.15 MPa and an increase in tissue elastic moduli at full hydration of 1.5 MPa. The decrease in elasticity may enable plants to improve the soil- plant water potential gradient given a small change in water content, while lower osmotic potentials shift the zero turgor loss point to lower water potentials. Under elevated CO2, Plants in xeric conditions had osmotic potentials 0.2 MPa lower than mesic plants and decreased elastic moduli at full hydration. The increase in tissue elasticity at elevated CO2 enabled the xeric plants to maintain positive turgor pressures at lower water potentials and tissue water contents. Surprisingly, the elevated CO2 plants under mesic conditions had the most inelastic tissues. We propose that this inelasticity may enable plants to generate a favorable water potential gradient from the soil to the plant despite the low stomatal conductances observed under elevated CO2 conditions.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, GROWTH, LIQUIDAMBAR- STYRACIFLUA, MORPHOLOGY, PINUS-TAEDA SEEDLINGS, PLANTS, PRESSURE, STRESS, WHEAT

1591

Mortensen, L.M. 1992. Diurnal photosynthesis and transpiration of ficus-benjamina L as affected by length of photoperiod, co2 concentration and light level. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 42(2):100-105.*

The diurnal net photosynthesis of Ficus benjamina L., cultivar Cleo, was studied at different daylengths (12, 18 and 24 h day- 1), photosynthetic photon flux densities (40 and 120-mu-mol m-2 s-1 PPFD) and CO2 concentrations (350 and 700-mu-mol mol-1). Net photosynthesis increased to a maximum after 5-6 and 6-7 h of light at 12 and 18 h day-1 photoperiods, respectively, followed by a decrease towards the end of the photoperiod. At a photoperiod of 18 h day-1 similar diurnal curves were found at 350 and 700-mu-mol mol-1 CO2, and at 40 and 120-mu-mol m-2 s-1 PPFD. Five days after the photoperiod was changed from 18 to a 24 h day-1 the diurnal rhythm disappeared. Transpiration followed the same diurnal rhythm as that for photosynthesis. The water-use efficiency was enhanced by raising the CO2 concentration. A decrease in the CO2 concentration from 700 to 350-mu-mol mol-1 after six days at high CO2 first significantly decreased the photosynthesis, but three days later it reached the same level as that at high CO2.

KEYWORDS: BEAN-PLANTS, CARBON-DIOXIDE CONCENTRATIONS, EXCHANGE, GROWTH, INHIBITION, LEAVES, RESPONSES

1592

Mortensen, L.M. 1992. Effects of ozone concentration on growth of tomato at various light, air humidity and carbon-dioxide levels. *Scientia Horticulturae 49(1-2):17-24.*

The effect of ozone (O3) Concentration on the growth of Lycopersicon esculentum was studied at different photosynthetic photon flux densities (PPFD), relative air humidities (RH) and carbon dioxide (CO2) concentrations. Increasing the O3 concentration from < 10 to 85 nl l-1 for 6 h per day reduced the shoot dry weight 35% at 70% RH and 62% at 90% RH. Increasing the PPFD from 100 to 350-mu-mol m-2 s-1 significantly reduced the effect of O3 in one of two experiments. The most pronounced interaction between RH, PPFD and O3 was found on plant height. High O3 levels generally decreased plant height at low PPFD and had no, or a stimulating, effect at high PPFD. Raising the RH from 70 to 90% significantly increased the negative effect of O3 on height. Increasing the O3 concentration from < 10 to 65 nl l-1 significantly decreased plant height at low CO2 concentration (300-340-mu-l l-1), but small effects were found at high CO2 concentration (700-800-mu-l l-1).

KEYWORDS: LEAVES, SUMMER CO2 ENRICHMENT, TEMPERATURES, TRANSPIRATION, YIELD

1593

Mortensen, L.M. 1994. Effects of carbon-dioxide concentration on assimilate partitioning, photosynthesis and transpiration of betula-pendula roth and picea-abies (L) karst seedlings at 2 temperatures. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 44(3):164-169.*

Seedlings of Betula pendula Roth. and Picea abies (L.) Karat. were grown at 350 and 700 mu mol mol(-1) CO2 for 35 or 45 days at 15 and 20 degrees C in eight growth chambers. The mean photosynthetic flux was 15-22 mol m(-2) day(-1). The mean relative growth rate was increased by 7% in Betula and by 10% in Picea at the highest CO2 concentration. This corresponded to an increase in the total plant dry weight of 20 and 19%, respectively The shoot:root and leaf:stem ratios were unaffected by the CO2 concentration in both species. High CO2 levels increased the stem diameter and the number of lateral shoots in Betula. Increasing the temperature did not affect the assimilate partitioning between leaf stem and root in Betula, but the needle:stem ratio decreased in Picea. Elevated CO2 concentration increased the number of lateral shoots in Betula more at 15 than at 20 degrees C, however, the total weight of the lateral shoots was not affected. With this exception the effect of CO2 was generally the same at both temperatures. Measurements of the CO2 exchange rates indicated that a slight acclimation to high CO2 had taken place at the end of the experimental period in the two species. Elevated CO2 slightly decreased the transpiration rate of Betula.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, GROWTH, LIGHT, PLANTS, RESPONSES, TREES, WATER-USE

1594

Mortensen, L.M. 1994. Effects of day-night temperature-variations on growth, morphogenesis and flowering of kalanchoe-blossfeldiana V poelln at different co2 concentrations, daylengths and photon flux densities. *Scientia Horticulturae 59(3-4):233-241.*

Growth and flowering of Kalanchoe blossfeldiana were studied at two temperature treatments (constant, CT; day lower than night temperature, negative DIF) in combination with two CO2 concentrations (360 and 900 mu mol mol(-1)), two daylengths (DL; 12 and 18 h) and two photosynthetic photon flux densities (PPFD; 85 and 130 mu mol m(-2) s(-1)). In addition to the two temperature treatments, a 2-h low temperature pulse (DROP) was included in combination with short days and low CO2 levels. The experiment was conducted in 18 growth chambers with artificial light only. The plant dry weight at saleable stage was the same at the different temperature treatments irrespective of CO2 concentration, DL or PPFD. The dry weight was similarly (31- 40%) increased by CO2 enrichment, or increasing DL or PPFD. Total plant height was slightly, but consistently increased by negative DIF relative to CT, irrespective of the level of the other climate factors. The DROP treatment in short DL increased the height relative to both negative DIF and CT. Negative DIF delayed flowering by 2-4 days at 360 mu mol mol(-1) CO2, but promoted it by 2-4 days at 900 mu mol mol(-1) CO2. Fresh weight of flowers was unaffected by temperatun treatments irrespective of DL and PPFD. It was concluded that the best plant quality was obtained at constant temperature throughout day and night irrespective of the level of the other climate factors.

1595

Mortensen, L.M. 1994. Effects of elevated co2 concentrations on growth and yield of 8 vegetable species in a cool climate. *Scientia Horticulturae 58(3):177-185.*

The effects of elevated CO2 concentrations on the yield of Allium cepa (onion), Allium ampeloprasum (leek), Apium graveolens var. dulce (celery), Apium graveolens var. rapaceum (celery root), Brassica pekinensis (chinese cabbage), Daucus carota (carrot), Lactuca sativa (lettuce) and Petroselinum crispum (parsley) grown in containers, were studied in SiX 9-M2 large field plots surrounded by 1.8-m high plastic foil walls ('field chambers'). Three of the chambers were supplied with pure CO2 gas through perforated tubes. Increasing the CO2 concentration from ambient (355 mumol mol-1) to 800-900 mumol mol-1 increased the yield (fresh weight) by 23% in onion (two cultivars) and by 8% in carrot (three cultivars). The dry weight based yield increase was 18% in lettuce (three cultivars), 19% in carrot and 17% in parsley (one cultivar). The yields of leek (two cultivars), chinese cabbage (three cultivars), celery (one cultivar) and celery root (one cultivar) were not significantly affected by the CO2 concentration. Generally, no 'chamber effect' was found on the yields of the different species.

KEYWORDS: CROP, ENRICHMENT, PLANTS, RESPONSES

1596

Mortensen, L.M. 1994. The influence of carbon-dioxide or ozone concentration on growth and assimilate partitioning in seedlings of 9 conifers. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 44(3):157-163.*

Seedlings of nine different conifers were exposed to 355 and 730 mu mol mol(-1) CO2, or low (< 15 nmol mol(-1)) and elevated O-3 concentration (70 nmol mol(-1)) for 81-116 days. The experiments were conducted in growth chambers placed in a greenhouse. Increased CO2 concentration enhanced the mean relative growth rate (RGR) and total plant dry weight by 4 and 33% in Larix leptolepis, by 4 and 38% in Larix sibirica, by 7 and 47% in Picea glauca and by 3 and 16% in Picea sitchensis, respectively. The growth rates and dry weights of Pinus contorta, Pinus mugo and Pseudotsuga menziesii were not significantly affected. Carbon dioxide enrichment enhanced RGR of two provenances of Picea abies by 4 and 6%, respectively, while a third provenance was unaffected. In Pinus sylvestris, only the RGR of one of three provenances was stimulated by CO2 enrichment (4%). After two growth seasons CO2 enrichment enhanced RGR and total plant dry weight by 11 and 35% in Picea abies and by 12 and 36% in Pinus sylvestris, respectively. Elevated CO2 decreased the shoot:root ratio in Larix leptolepis, and decreased the needle:stem ratio in Picea glauca, but increased it in Pseudotsuga menziesii. Elevated O-3 significantly decreased the plant dry weight in Picea sitchensis, Pseudotsuga menziesii and in one of three provenances of Pinus sylvestris, while the other species and provenances were unaffected. Increased O-3 concentration increased the shoot:root dry weight ratio in one of three Picea abies provenances, in all three Pinus sylvestris provenances and in Pinus contorta. The needle:stem ratio was enhanced by O- 3 in seven of the nine species. The O-3 exposure caused chlorosis of needles in all species except Pseudotsuga menziesii.

KEYWORDS: CO2- ENRICHMENT, PHOTOSYNTHESIS, SOUR ORANGE TREES

1597

Mortensen, L.M. 1995. Diurnal carbon-dioxide exchange-rates of greenhouse roses under artificial-light as compared with daylight conditions in summer. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 45(2):148-152.*

Carbon dioxide exchange rates (CER) of greenhouse roses (cut flowers) were measured under daylight conditions in a greenhouse in July, and under artificial light only (300 mu mol m(-2) s(-1) PPFD in 18 h day(-1)) at two CO2 concentrations (350 and 700 mu mol mol(-1)). The daily CER varied considerably from day to day owing to the large variation in solar radiation. Light saturation of CER seemed not to be reached even on clear days, and a light dose (PAP = number of photosynthetic active photons) produced by variable light over one week in summer gave the same total CER as a similar PAP produced by a constant PPFD. CER at constant PPFD increased rapidly during the first two hours of the photoperiod, followed by a slight increase during the subsequent hours, before CER slightly decreased towards the end of the photoperiod. Raising the CO2 concentration significantly increased CER during the entire photoperiod, and by 32% as a mean for the whole photoperiod.

Elevated CO2 decreased the night respiration of the plants by 30%. As a total of the light and dark period, CO2 enrichment increased CER by 38%.

KEYWORDS: CO2- ENRICHMENT, GROWTH

1598

Mortensen, L.M. 1995. Effect of carbon-dioxide concentration on biomass production and partitioning in betula-pubescens ehrh seedlings at different ozone and temperature regimes. *Environmental Pollution 87(3):337-343.*

Seedlings of Betula pubescens were grown at two CO2 concentrations, in combination with either two O3 concentrations or two air temperatures, during 34-35 days at 24 h day-1 photoperiod in growth chambers placed in a greenhouse. Increasing the CO2 concentration from 350 to 560 mumol mol-1 at 17-degrees-C air temperature increased the dry weight of the main leaves, main stem, branches and root. The mean relative growth rate (RGR) was increased 10% by CO2 enrichment, while increasing the O3 concentration from 7 to 62 nmol mol-1 decreased the RGR by 9%. The relative biomass distribution between the different plant components was not significantly affected by the CO2 concentration irrespective of the O3 concentration. No significant interactions between CO2 and O3 concentration were found except on leaf size, which was stimulated more by elevated CO2 concentration at high, compared to low, O3 levels. In another experiment, elevated CO2 (700 mumol mol-1) significantly increased the dry weight of the different plant components, and more at 20-degrees-C than at 15-degrees-C. Raising the CO2 concentration increased the RGR by 5 and 10% at 15 and 20-degrees-C, respectively. CO2 enrichment increased the branch dry weight relatively more than the dry weight of the other plant parts. Increasing the CO2 concentration or temperature increased the plant height and stem diameter, however, no interactions between CO2 and temperature were found.

KEYWORDS: CO2, GROWTH, O-3, PHOTOSYNTHESIS

1599

Mortensen, L.M. 1997. Effects of carbon dioxide concentrations on three grass species grown in mixture in two soil types at different ozone concentrations or temperatures. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 47(1):14-19.*

A seed mixture of Phleum pratense L., Lolium perenne L. and Festuca pratensis Huds. was grown in spaghnum peat or sandy soil in six growth chambers placed in a greenhouse compartment. Two different experiments were performed. Increasing the CO2 concentration from 375 to 740 mu mol mol(-1) increased the total dry weight of the grass mixture by about 30%, while an increase in the O-3 concentration from < 10 to 50 nmol mol(-1) decreased the dry weight by 18% as a mean in both experiments. The relative dry weights of the three species were not significantly affected by elevated CO2 concentrations at low O- 3, while Lolium increased its relative dry weight at high O-3 concentrations at low CO2 on the expenditure of Phleum dry weight. CO2 enrichment counteracted some of this O-3 effect. No significant interaction between CO2 concentration and temperature (14 and 19 degrees C mean temperature) was found with respect to the dry weights of the three species. The soil type had generally no influence on the effect of CO2 and O-3. However, plant growth was significantly slower in sandy soil than in peat.

KEYWORDS: ELEVATED CO2, LIGHT, NITROGEN, O-3, PASTURE, PERENNIAL RYEGRASS, PLANT-RESPONSES, WHEAT, WHITE CLOVER

1600

Mortensen, L.M. 1998. Effects of elevated CO2 concentration on growth of Betula pubescens Ehrh. in different climatic conditions. *Scandinavian Journal of Forest Research 13(2):197-203.*

Seedlings of Betula pubescens Ehrh. (mountain birch) were grown at ambient and elevated CO2 concentrations in environment- controlled growth chambers, and in chambers or wind tunnels in the field. In the two preliminary experiments in a controlled environment, CO2 enrichment increased the dry weights of six birch provenances grown at a daily mean temperature (MT) of 17 degrees C and 15 provenances grown at 12.5 degrees C MT by 27 and 7%. respectively. In more realistic conditions in field chambers (13.9 degrees C MT), the shoot dry weight of plants grown for 65 days was not significantly affected by the elevated CO2 concentration. In a parallel experiment, CO2 enrichment increased the shoot dry weight by 36% in both unheated (14.7 degrees C MT) and heated (18.1 degrees C MT) wind tunnels. In a final experiment over two seasons in open- top chambers at 850 m a.s.l., elevated CO2 concentrations increased the root (42%) but not the shoot dry weight. The results are discussed in relation to variable climatic conditions.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE, ENRICHMENT, LEAVES, PENDULA ROTH, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS

1601

Mortensen, L.M. 1999. Effects of different carbon dioxide and ozone concentrations on shoot growth of Phleum pratense L. and Betula pubescens Ehrh. as influenced by day length and irradiance. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 49(1):50-56.*

Seedlings of Phleum pratense L. (timothy) and Betula pubescens Ehrh. (mountain birch) were grown for 37 or 42 days at all combinations of two CO2 concentrations (350 and 700 mu mol mol(-1)), two O-3 concentrations (13 and 59 nmol mol(-1) in 8 h day(-1)), two day lengths (17 and 24 h DL) and two levels of supplementary lighting (150 and 210 mu mol m(-2) s(-1) photosynthetic photon flux, PPF) in 16 growth chambers placed in a greenhouse. Elevated CO2 concentration increased the mean shoot dry weight by 47% in timothy and by 39% in birch. No significant interactions were found between CO2 and O-3, DL or PPF with respect to shoot dry weight in the two species. The number of shoots in timothy was generally enhanced by CO2 enrichment. The number of branches in birch was strongly enhanced by elevated CO2 at 17 but not at 24 h DL, and the ratio of the fresh weight of branches to main shoot was significantly increased irrespective of DL, Increasing the O-3 concentration caused visible leaf injuries both in timothy (chlorosis/necrosis) and in birch (yellow stipples/brown spots), while the shoot weight was not significantly affected. The number of O-3-induced injuries in timothy was decreased by increasing the CO2 concentration or the total irradiance (increasing DL and/or PPF). The number of injuries in birch was slightly decreased by increasing PPF; however, CO2 enrichment had no effect.

KEYWORDS: CLOVER, ELEVATED CO2 CONCENTRATION, ENRICHMENT, PENDULA ROTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, TEMPERATURE

1602

Mortensen, L.M. 1999. Foliar injuries caused by ozone in Betula pubescens Ehrh. and Phleum pratense L. as influenced by climatic conditions before and during O-3 exposure. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 49(1):44-49.*

Seedlings of Betula pubescens Ehrh. (mountain birch) and Phleum pratense L. (timothy) were grown for 42 days under full light or 50% shade in the field at 12 degrees C, and at comparable photosynthetic active radiation (PAR) levels in a greenhouse at 18 degrees C. Plants from the four pretreatments were exposed to 78 nmol mol(-1) (ppb) O-3 (8 h day(-1)) under two temperatures (15 and 25 degrees C), two relative air humidities (50 and 80% RH) or two CO2 concentrations (400 and 750 mu mol mol(-1)) during 7 days. The accumulated O-3 dose over 40 nmol mol(-1) O-3 (AOT40) was 2.6 mu mol mol(-1)-hours (ppm-h). Decreasing the temperature during exposure significantly increased the amount of injury induced by O-3 in leaves of birch (yellow mottling/bronzing) as well as timothy (chlorosis/necrosis). Increasing the air humidity or decreasing the CO2 concentration strongly enhanced the injuries caused by O-3 in timothy, but not in birch. In general, both birch and timothy plants grown in the greenhouse and in the field had the same O-3 sensitivity. However, decreasing the PAR level during the pretreatment enhanced leaf injury in birch but not in timothy. At the most sensitive exposure climate, 15 degrees C/80% RH, leaf injury developed at an AOT40 of 0.7-0.9 ppm-h in both species.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, GROWTH, HUMIDITY, PENDULA ROTH, PHOTOSYNTHESIS, RESPIRATION, SEEDLINGS, TEMPERATURE, TRANSPIRATION

1603

Mortensen, L.M., and R. Moe. 1992. Effects of co2 enrichment and different day night temperature combinations on growth and flowering of rosa L and kalanchoe- blossfeldiana V poelln. *Scientia Horticulturae 51(1-2):145-153.*

The effects of increasing the CO2 concentration from 350 to 700-mu-l l-1 on growth and flowering of Rosa L. and Kalanchoe blossfeldiana at four different day/night temperature combinations (20/20-degrees-C, 23/14-degrees-C and 17/26- degrees-C day/night, and 20/20-degrees-C with 2 h at 14- degrees-C in the morning) were studied in 16 growth chambers. An increase in the CO2 concentration resulted in enhanced total dry weight, stem: leaf fresh weight ratio, flower fresh weight, length and diameter of the rose shoot, while the number of days until flowering was not affected. With the 17/26-degrees-C treatment, rose shoots were 3-4 cm shorter, and with the 23/14- degrees-C treatment flowering occurred about 2 days earlier than with the other temperature treatments. The results were the same for Rosa cultivars 'Frisco' and 'Kiss'. No significant interactions between CO2 and temperature were found. Plant dry weight and fresh weight of flowers in Kalanchoe were generally enhanced by CO2 enrichment. The effects of CO2 on dry weight, plant height and flower stem length were greater with the 23/14-degrees-C treatment compared with the effects of the other temperature treatments. A constant temperature (20/20- degrees-C) and the 23/14-degrees-C treatments gave the shortest and tallest plants, respectively.

1604

Mortensen, L.M., and A. Saebo. 1996. The effect of elevated CO2 concentration on growth of Phleum pratense L in different parts of the growth season. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 46(2):128-134.*

Seedlings of Phleum pratense L. (timothy) of the same age were grown in five sequential four-week periods during one growth season (May 5-September 23) at low (380 mu mol mol(-1)) and high (650 mu mol mol(-1)) CO2 concentration. The experiment was performed in 10 9 m(2) field plots surrounded by plastic foil walls ("field chambers") in the relatively cool climate (10- 13 degrees C mean temperature) of the west coast of Norway (59 degrees N latitude). Raising the CO2 concentration generally decreased the height of the grass (8-23%), especially at the beginning and end of the growth season. The number of shoots was significantly increased (13-42%) by CO2 enrichment in all growth periods except the last. Elevated CO2 did not influence the above-ground biomass (dry weight) in the first (May) and last (September) period, but increased it by 14-51% in the intervening periods (June-August). Positive effects of CO2 enrichment on plant biomass were correlated with positive effects on the number of shoots. Elevated CO2 concentrations resulted in 25-64% denser plant biomass (dry weight per unit air volume) in the different growth periods. In general, a positive "chamber effect" on plant height and dry weight was found in spite of the small air temperature differences between the insides and the outsides of the chambers. A greenhouse experiment showed that wind speeds above 3 m s(-1) strongly decreased height and dry weight of timothy seedlings. The reduced wind speeds inside the chambers could therefore explain the "chamber effects" found.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, PLANT-RESPONSES, TEMPERATURE

1605

Mosier, A.R. 1998. Soil processes and global change. *Biology and Fertility of Soils 27(3):221-229.*

Contributors to the Intergovernmental Panel on Climate Change (IPCC) generally agree that increases in the atmospheric concentration of greenhouse trace gases (i.e., CO2, CH4, N2O, O-3) since preindustrial times, about the year 1750, have led to changes in the earth's climate. During the past 250 years the atmospheric concentrations of CO2, CH4, and N2O have increased by 30, 145, and 15%, respectively. A doubling of preindustrial CO2 concentrations by the end of the twenty-first century is expected to raise global mean surface temperature by about 2 degrees C and increase the frequency of severe weather events. These increases are attributed mainly to fossil fuel use, land-use change, and agriculture. Soils and climate changes are related by bidirectional interactions. Soil processes directly affect climatic changes through the production and consumption of CO2, CH4, and N2O and, indirectly, through the production and consumption of NH,, NO,, and CO. Although CO2 is primarily produced through fossil fuel combustion, land-use changes, conversion of forest and grasslands to agriculture, have contributed significantly to atmospheric increase of CO2. Changes in land use and management can also result in the net uptake, sequestration, of atmospheric CO2. CH4 and N2O are produced (30% and 70%, respectively) in the soil, and soil processes will likely regulate future changes in the atmospheric concentration of these gases. The soil-atmosphere exchange of CO2, CH4, and N2O are interrelated, and changes in one cycle can im part changes in the N cycle and resulting soil-atmosphere exchange of N2O. Conversely, N addition increases C sequestration. On the other hand, soil processes are influenced by climatic change through imposed changes in soil temperature, soil water, and nutrient competition. Increasing concentrations of atmospheric CO2 alters plant response to environmental parameters and frequently results in increased efficiency in use of N and water. In annual crops increased CO2 generally leads to increased crop productivity. In natural systems, the long-term impact of increased CO2 on ecosystem sustainability is not known. These changes may also-result in altered CO2, CH4, and N2O exchange with the soil. Because of large temporal and spatial variability in the soil-atmosphere exchange of trace gases, the measurement of the absolute amount and prediction of the changes of these fluxes, as they are impacted by global change on regional and global scales, is still difficult. in recent years, however, much progress has been made in decreasing the uncertainty of field scale flux measurements, and efforts are being directed to large scale field and modeling programs. This paper briefly relates soil process and issues akin to the soil-atmosphere exchange of CO2, CH4, and N2O. The impact of climate change, particularly increasing atmospheric CO2 concentrations, on soil processes is also briefly discussed.

KEYWORDS: CARBON DIOXIDE, CULTIVATION,

DENITRIFICATION, FERTILIZATION, FOREST, GAS FLUXES, INVENTORY, LAND-USE, N2O, NITROUS-OXIDE EMISSIONS

1606

Mousseau, M. 1993. Effects of elevated co2 on growth, photosynthesis and respiration of sweet chestnut (castanea-sativa mill). *Vegetatio 104:413-419.*

Two year old sweet chestnut seedlings (Castanea sativa Mill) were grown in pots at ambient (350 mumol.mol-1) and double (700 mumol.mol-1) atmospheric CO2 concentration in constantly ventilated greenhouses during entire growing seasons. CO2 enrichment caused either no significant change or a decrease in shoot growth response, depending on yearly weather condition either reduced or unchanged under elevated CO2. However, when grown under controlled conditions in a growth chamber, leaf area was enlarged with elevated CO2. The CO2 exchanges of whole plants were measured during the growing season. In elevated CO2, net photosynthetic rate was maximum in May and then decreased, reaching the level of the control at the end of the season. End of night dark respiration of enriched plants was significantly lower than that of control plants; this difference decreased with time and became negligible in the fall. The original CO2 level acted instantaneously on the respiration rate: a double concentration in CO2 decreased the respiration of control plants and a reduced concentration enhanced the respiration of enriched plants. The carbon balance of a chestnut seedling may then be modified in elevated CO2 by increased carbon inputs and decreased carbon outputs.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, DARK RESPIRATION, ENRICHMENT, FORESTS, HIGH ATMOSPHERIC CO2, SEEDLINGS, TREES

1607

Mousseau, M., and B. Saugier. 1992. The direct effect of increased co2 on gas-exchange and growth of forest tree species. *Journal of Experimental Botany 43(253):1121-1130.*

CO2 enrichment of the atmosphere is now well documented and its effect on the growth of world forests is being questioned by the scientific community. The direct effects of increased CO2 on tree species are reviewed: the different experimental approaches are described, as well as the principal results already obtained. Short-term experiments have shown an increased photosynthetic rate, as predicted by leaf models. In longer experiments this increase is reduced after a few weeks or months by mechanisms that remain to be found. Elevated CO2 seems to decrease the dark respiration rate, but the results are still controversial. Biomass partitioning in elevated CO2 is clearly related to the mineral supply of the trees: An increase in root investment in elevated CO2 is related to a poor mineral status. The mineral content of trees grown in elevated CO2 is generally lowered compared to controls. No general rule has yet been found for the effect of increased CO2 on leaf area development. The paper emphasizes large areas of ignorance: the reasons for the different responses of different species, which may be related to their developmental strategies, are largely ignored. Much experimental effort is needed to parameterize all the physiological processes which are susceptible to change with an increase in atmospheric CO2, leading to a change in forest tree growth.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, DARK RESPIRATION, ENRICHMENT, LEAF, NUTRIENT-UPTAKE, PLANTS, RESPONSES, SEEDLINGS, SHORT-TERM

1608

Moya, T.B., L.H. Ziska, O.S. Namuco, and D. Olszyk. 1998. Growth dynamics and genotypic variation in tropical, field- grown paddy rice (Oryza sativa L.) in response to increasing carbon dioxide and temperature. *Global Change Biology 4(6):645-656.*

While previous studies have examined the growth and yield response of rice to continued increases in CO2 concentration and potential increases in air temperature, little work has focused on the long-term response of tropical paddy rice (i.e. the bulk of world rice production) in situ, or genotypic differences among cultivars in response to increasing CO2 and/or temperature. At the International Rice Research Institute, rice (cv IR72) was grown from germination until maturity for 4 field seasons, the 1994 and 1995 wet and the 1995 and 1996 dry seasons at three different CO2 concentrations (ambient, ambient + 200 and ambient + 300 mu L L-1 CO2) and two air temperatures (ambient and ambient + 4 degrees C) using open-top field chambers placed within a paddy site. Overall, enhanced levels of CO2 alone resulted in significant increases in total biomass at maturity and increased seed yield with the relative degree of enhancement consistent over growing seasons across both temperatures. Enhanced levels of temperature alone resulted in decreases or no change in total biomass and decreased seed yield at maturity across both CO2 levels. In general, simultaneous increases in air temperature as well as CO2 concentration offset the stimulation of biomass and grain yield compared to the effect of CO2 concentration alone. For either the 1995 wet and 1996 dry seasons, additional cultivars (N-22, NPT1 and NPT2) were grown in conjunction with IR72 at the same CO2 and temperature treatments. Among the cultivars tested, N-22 showed the greatest relative response of both yield and biomass to increasing CO2, while NPT2 showed no response and IR72 was intermediate. For all cultivars, however, the combination of increasing CO2 concentration and air temperature resulted in reduced grain yield and declining harvest index compared to increased CO2 alone. Data from these experiments indicate that (a) rice growth and yield can respond positively under tropical paddy conditions to elevated CO2, but that simultaneous exposure to elevated temperature may negate the CO2 response to grain yield; and, (b) sufficient intraspecific variation exists among cultivars for future selection of rice cultivars which may, potentially, convert greater amounts of CO2 into harvestable yield.

KEYWORDS: CO2- ENRICHMENT, YIELD

1609

Msudoe, N.N.A. 1990. 2 mutants of Arabidopsis thaliana that become chlorotic in atmospheres enriched with CO2. *Plant, Cell and Environment 13(6):575-580.*

1610

Mtolera, M.S.P., J. Collen, M. Pedersen, and A.K. Semesi. 1995. Destructive hydrogen peroxide production in Eucheuma denticulatum (Rhodophyta) during stress caused by elevated pH, high light intensities and competition with other species. *European Journal of Phycology 30(4):289-297.*

Growth of Eucheuma denticulatum was studied in the field and in laboratory experiments. Field co-cultivation of E, denticulatum with the green alga Ulva reticulata or the seagrass Thalassia sp, reduced daily growth rate (DGR)bf a Tanzanian and a Philippine strain of E. denticulatum by 10-100% and 10-55%, respectively, depending upon the type of water current: a unidirectional water current produced the best growth. Laboratory co-cultivation of a Tanzanian strain of E. denticulatum with U, reticulata also reduced DGR (to 8% of the control) and nitrate-nitrogen uptake rate (to < 30% of the control) of E, denticulatum and, moreover, it increased epiphytism of a red filamentous alga on E, denticulatum. E, denticulatum monoculture at pH 8.6 +/- 0.5 or at photosynthetic photon flux densities (PPFDs) higher than its growth optimum (350 +/- 50 mu mol photons m(-1) s(-1)) also

increased epiphytism. The lack of a competitive mechanism for inorganic carbon uptake in Eucheuma may have contributed to its reduced growth during co-cultivation. During co-cultivation, elevated pH regimes (PH > 8.5) were created around the Eucheuma thalli as a result of photosynthesis, thus decreasing the concentration of CO2 in the seawater to values around 1 mu mM. As Eucheuma depends mainly on the CO2 in the seawater for its growth a higher pH can cause CO2 limitation by decreasing CO2 concentration. Hydrogen peroxide (H2O2) production from the Tanzanian strain was also determined by luminol-dependent chemiluminescence. H2O2 production was found to increase with increased pH and PPFD (probably as a result of oxidative stress). Preincubation of plants with catalase for 5 min before addition of luminol prevented chemiluminescence, confirming H2O2 as the substrate of the luminol reaction. We suggest that the inefficiency of E, denticulatum in HCO3- utilisation contributes to its poor growth during field coexistence with seagrasses or Ulva sp. and that carbon deficiency induces H2O2 production in E, denticulatum.

KEYWORDS: GROWTH, HYPERSENSITIVE REACTION, INORGANIC CARBON, KAPPAPHYCUS-ALVAREZII, LIPID-PEROXIDATION, METABOLISM, OXYGEN, PHOTOSYNTHESIS, RED SEAWEEDS, ULVA-FASCIATA

1611

Muchow, R.C., and T.R. Sinclair. 1991. Water deficit effects on maize yields modeled under current and greenhouse climates. *Agronomy Journal 83(6):1052-1059.*

The availability of water imposes one of the major limits on rainfed maize (Zea mays L.) productivity. This analysis was undertaken in an attempt to quantify the effects of limited water on maize growth and yield by extending a simple, mechanistic model in which temperature regulates crop development and intercepted solar radiation is used to calculate crop biomass accumulation. A soil water budget was incorporated into the model by accounting for inputs from rainfall and irrigation, and water use by soil evaporation and crop transpiration. The response functions of leaf area development and crop gas exchange to the soil water budget were developed from experimental studies. The model was used to interpret a range of field experiments using observed daily values of temperature, solar radiation, and rainfall or irrigation, where water deficits of varying durations developed at different stages of growth. The relative simplicity of the model and its robustness in simulating maize yields under a range of water-availability conditions allows the model to be readily used for studies of crop performance under alternate conditions. One such study, presented here, was a yield assessment for rainfed maize under possible "greenhouse" climates where temperature and atmospheric CO2 concentration were increased. An increase in temperature combined with decreased rainfall lowered grain yield, although the increase in crop water use efficiency associated with elevated CO2 concentration, ameliorated the response to the greenhouse climate. Grain yields for the greenhouse climates as compared to current conditions increased, or decreased only slightly, except when the greenhouse climate was assumed to result in severely decreased rainfall.

KEYWORDS: ARID TROPICAL ENVIRONMENT, COMPONENTS, EVAPORATION, FIELD, NITROGEN LIMITATIONS, PEARL-MILLET, SOIL, SORGHUM, SOYBEAN GRAIN PRODUCTION, WHEAT

1612

Mudrik, V.A., A.K. Romanova, B.N. Ivanov, N.S. Novichkova, and V.A. Polyakova. 1997. Effect of increased CO2 concentration on growth, photosynthesis, and composition of Pisum sativum L plants. *Russian Journal of Plant Physiology 44(2):141-146.*

Pea (Pisum sativum L.) plants grown for 3 weeks at 0.03 (control plants) or 0.5% CO2 (CO2-plants) concentration were used to study the effects of increased CO2 concentration on plant growth, CO2 exchange, morphological pattern, and the content of carbohydrates and protein in plant leaves. The fresh and dry weights, the ratio of plant dry weight to the total area of its leaves and stipules, and the root/shoot dry weight ratio were 150, 42, and 24%, respectively, higher in the CO2- plants. Protein content was similar in the leaves of CO2- exposed and control plants, whereas the content of sugars and starch was significantly higher in the leaves of the CO2- plants. The rate of CO2 exchange per plant measured at 0.5% CO2 in plants grown under this carbon dioxide concentration was 1.8 times higher than in control plants grown and measured at a low CO2 concentration. Within the range of the studied CO2 concentrations, the net photosynthesis measured at 0.5% CO2 in the plants previously grown at this level of CO2 content in the air was enhanced only due to the rise in CO2 concentration used by plants as a substrate for carboxylation. However, in the CO2-plants, the rate of photosynthesis measured at 0.03 and 0.5% CO2 and calculated per dry weight unit was lower than that in the control plants. The causes of limitations imposed on photosynthesis at a higher CO2 concentration are discussed. It is proposed that accumulation of sugars induced a nonstomatal limitation of photosynthesis in the CO2-plants. An increase in the root/shoot ratio indicates some changes in the hormonal status of plants under the influence of a high CO2 concentration.

KEYWORDS: CARBON DIOXIDE, CHLOROPLAST

1613

Muellerdombois, D. 1992. Potential effects of the increase in carbon-dioxide and climate change on the dynamics of vegetation. *Water, Air, and Soil Pollution 64(1-2):61-79.*

The continued CO2 loading of the atmosphere appears to be responsible for inducing three new force factors controlling dynamic changes in the world's vegetation. They come from (1) enhanced fertilization with the single most important plant nutrient, (2) the widely expected global temperature increase, and (3) aggravated weather disturbances. Increased CO2 absorption may enhance plant growth but it may also increase soil-nutrient limitations. It surely will enhance the metabolism of forest trees similarly as global warming will enhance plant metabolism, but both factors may also shorten the lifespan of perennial plants. Increased weather disturbances can be expected to produce new physiological stresses on the standing vegetation, particularly on habitats with poor soils. Since wide-spread forest decline has been reported from both the Atlantic and Pacific region, it seems possible that the roughly synchronic mass mortality of trees during the past two decades is related to the global increase in CO2. The paper gives an overview of forest decline and dieback as known from past and present research and suggests how the changing atmospheric environment may interact in this widely observed contemporary Phenomenon of vegetation dynamics.

KEYWORDS: CANOPY DIEBACK, DECLINE, ECOSYSTEMS, EL-NINO, FORESTS, ISLANDS, MORTALITY, NEW-ZEALAND, SENESCENCE, STAND-LEVEL DIEBACK

1614

Mulchi, C., B. Rudorff, E. Lee, R. Rowland, and R. Pausch. 1995. Morphological responses among crop species to full-season exposures to enhanced concentrations of atmospheric CO2 and O-3. *Water, Air, and Soil Pollution 85(3):1379-1386.*

Field studies using open-top chambers were conducted at USDA- BARC involving the growth of soybeans ('89 & '90), wheat ('91 & '92), and corn ('91), under increased concentrations of atmospheric CO2 and O-3. Treatment responses were compared in all cases to plants grown in charcoal-filtered (CF) air (seasonal 7-h mean = 25 +/- 3 n mol O-3 mol(-1)) having 350 or 500 mu mol CO2 mol(-1). Elevated seasonal O-3

levels for the soybean, wheat, and corn studies averaged 72.2 +/- 4, 62.7 +/- 2, and 70.2 n mol O-3 mol(-1), respectively. Results presented were obtained for plants grown in silt loam soil under well- watered conditions. Grain yield increases in response to elevated CO2 in the absence of O-3 stress averaged 9.0, 12.0, and 1.0% for soybean, wheat, and corn:respectively. Reductions in grain yields in response to the elevated O-3 treatments at 350 mu mol CO2 mol(-1) averaged 20.0, 29.0 and 13.0% for soybean, wheat, and corn, respectively. Reductions in grain yields in response to elevated O-3 at 500 mu mol CO2 mol(-1) averaged 20.0, 8.0, and 7.0% for soybean, wheat, and corn, respectively. Dry biomass and harvest index in wheat were significantly reduced by O-3 stress at 350 mu mol mol(-1) CO2 but not at 500 u mol mol(-1) CO2. Seed weight 1000(-1) for soybeans and wheat was significantly increased by CO2 enrichment and decreased by O-3 stress. Seed weight 1000(-1) in corn was increased by O-3 stress suggesting that O-3 affected pollination resulting in fewer kernels per ear.

KEYWORDS: CARBON DIOXIDE

1615

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1997. Effects of elevated carbon dioxide and ozone on the growth and yield of spring wheat (Triticum aestivum L). *Journal of Experimental Botany 48(306):113-122.*

Spring wheat cv. Minaret was grown under three carbon dioxide (CO2) and two ozone (O-3) concentrations from seedling emergence to maturity in open-top chambers. Under elevated CO2 concentrations, the green leaf area index of the main shoot was increased, largely due to an increase in green leaf area duration. Biomass increased linearly in response to increasing CO2 (ambient, 550 and 680 ppm). At anthesis, stem and ear dry weights and plant height were increased by up to 174%, 5% and 9 cm, respectively, and biomass at maturity was 23% greater in the 680 ppm treatment as compared to the ambient control. Grain numbers per spikelet and per ear were increased by 0.2 and 5 grains, respectively, and this, coupled with a higher number of ears bearing tillers, increased grain yield by up to 33%. Exposure to a 7 h daily mean O-3 concentration of 60 ppb induced premature leaf senescence during early vegetative growth (leaves 1-7) under ambient CO2 concentrations. Damage to the main shoot and possible seedling mortality during the first 3 weeks of exposure altered canopy structure and increased the proportion of tillers 1 and 2 which survived to produce ears at maturity was increased; as a result, grain yield was not significantly affected. In contrast to the older leaves, the flag leaf (leaf 8) sustained no visible O-3 damage, and mean grain yield per ear was not affected. Interactions between elevated CO2 and O-3 influenced the severity of visible leaf damage (leaves 1-7), with elevated CO2 apparently protecting against O-3-induced premature senescence during early vegetative growth. The data suggest that the flag leaf of Minaret, a major source of assimilate during grain fill, may be relatively insensitive to O-3 exposure. Possible mechanisms involved in damage and/or recovery are discussed.

KEYWORDS: CEREALS, CO2- ENRICHMENT, DRY-WEIGHT, GRAIN QUALITY, IMPACTS, NITROGEN, O-3, PHOTOSYNTHESIS, PLANT-RESPONSES, VEGETATION

1616

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1997. Impact of elevated atmospheric CO2 and O-3 on gas exchange and chlorophyll content in spring wheat (Triticum aestivum L.). *Journal of Experimental Botany 48(315):1853-1863.*

Stands of spring wheat grown in open-top chambers (OTCs) were used to assess the individual and interactive effects of season-long exposure to elevated atmospheric carbon dioxide (CO2) and ozone (O-3) on the photosynthetic and gas exchange properties of leaves of differing age and position within the canopy. The observed effects were related to estimated ozone fluxes to individual leaves. Foliar chlorophyll content was unaffected by elevated CO2, but photosynthesis under saturating irradiances was increased by up to 100% at 680 mu mol mol(-1) CO2 relative to the ambient CO2 control; instantaneous water use efficiency was improved by a combination of increased photosynthesis and reduced transpiration. Exposure to a seasonal mean O-3 concentration (7 h d(-1)) of 84 nmol mol(-1) under ambient CO2 accelerated leaf senescence following full expansion, at which time chlorophyll content was unaffected. Stomatal regulation of pollutant uptake was limited since estimated O-3 fluxes to individual leaves were not reduced by elevated atmospheric CO2. A common feature of O-3-treated leaves under ambient CO2 was an initial stimulation of photosynthesis and stomatal conductance for up to 4 d and 10 d, respectively, after full leaf expansion, but thereafter both variables declined rapidly. The O-3-induced decline in chlorophyll content was less rapid under elevated CO2 and photosynthesis was increased relative to the ambient CO2 treatment. A/C-i analyses suggested that an increase in the amount of in vivo active RuBisCO may be involved in mitigating O-3-induced damage to leaves. The results obtained suggest that elevated atmospheric CO2 has an important role in restricting the damaging effects of O-3 on photosynthetic activity during the vegetative growth of spring wheat, and that additional direct effects on reproductive development were responsible for the substantial reductions in grain yield obtained at final harvest, against which elevated CO2 provided little or no protection.

KEYWORDS: AIR- POLLUTANTS, BISPHOSPHATE CARBOXYLASE OXYGENASE, BRASSICA-NAPUS L, CARBON DIOXIDE, NET PHOTOSYNTHESIS, PHOTOSYNTHETIC ACCLIMATION, PLANT-RESPONSES, REPRODUCTIVE DEVELOPMENT, VICIA-FABA L, WATER-USE EFFICIENCY

1617

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1998. Effects of elevated CO2 and O-3 On the rate and duration of grain growth and harvest index in spring wheat (Triticum aestivum L.). *Global Change Biology 4(6):627-635.*

Wheat (Triticum aestivum L.) cv. Minaret was grown in open-top chambers (OTCs) in 1995 and 1996 under three carbon dioxide (CO2) and two ozone (O-3) levels. Plants were harvested regularly between anthesis and maturity to examine the rate of grain growth (dG/dt; mg d(-1)) and the rate of increase in harvest index (dHI/dt;% d(-1)). The duration of grain filling was not affected by elevated CO2 or O-3, but was 12 days shorter in 1995, when the daily mean temperature was over 3 degrees C higher than in 1996. Season-long exposure to elevated CO2 (680 mu mol mol(-1)) significantly increased the rate of grain growth in both years and mean grain weight at maturity (MGW) was up to 11% higher than in the chambered ambient air control (chAA; 383 mu mol mol(-1)). However, the increase in final yield obtained under elevated CO2 relative to the chAA control in 1996 resulted primarily from a 27% increase in grain number per unit ground area. dG/dt was significantly reduced by elevated O-3 under ambient CO2 conditions in 1995, but final grain yield was not affected because of a concurrent increase in grain number. Neither dG/dt nor dHI/dt were affected by the higher mean O-3 concentrations applied in 1996 (77 vs. 66 nmol mol(-1)); the differing effects of O-3 on grain growth in 1995 and 1996 observed in both the ambient and elevated CO2 treatments may reflect the contrasting temperature environments experienced. Grain yield was nevertheless reduced under elevated O-3 in 1996, primarily because of a substantial decrease in grain number. The data obtained show that, although exposure to elevated CO2 and O-3 individually or in combination may affect both dG/dt and dHI/dt, the presence of elevated CO2 does not protect against substantial O-3-induced yield losses resulting from its direct deleterious impact on reproductive processes. The implications of these results for food production under future climatic conditions are considered.

KEYWORDS: BRASSICA-NAPUS L, CARBON DIOXIDE, CHRONIC OZONE, ENRICHMENT, IMPACT, QUALITY, RED WINTER-WHEAT, REPRODUCTIVE DEVELOPMENT, TEMPERATURE, YIELD

1618

Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1998. Growth, light interception and yield responses of spring wheat (Triticum aestivum L.) grown under elevated CO2 and O-3 in open-top chambers. *Global Change Biology 4(2):121-130.*

Spring wheat cv. Minaret was grown to maturity under three carbon dioxide (CO2) and two ozone (O-3) concentrations in open-top chambers (OTC). Green leaf area index (LAI) was increased by elevated CO2 under ambient O-3 conditions as a direct result of increases in tillering, rather than individual leaf areas. Yellow LAI was also greater in the 550 and 680 mu mol mol(-1) CO2 treatments than in the chambered ambient control; individual leaves on the main shoot senesced more rapidly under 550 mu mol mol(-1) CO2, but senescence was delayed at 680 mu mol mol(-1) CO2. Fractional light interception (f) during the vegetative period was up to 26% greater under 680 mu mol mol(-1) CO2 than in the control treatment, but seasonal accumulated intercepted radiation was only increased by 8%. As a result of greater carbon assimilation during canopy development, plants grown under elevated CO2 were taller at anthesis and stem and ear biomass were 27 and 16% greater than in control plants. At maturity, yield was 30% greater in the 680 mu mol mol(-1) CO2 treatment, due to a combination of increases in the number of ears per m(- 2), grain number per ear and individual grain weight (IGW). Exposure to a seasonal mean (7 h d(-1)) of 84 nmol mol(-1) O-3 under ambient CO2 decreased green LAI and increased yellow LAI, thereby reducing both f and accumulated intercepted radiation by approximate to 16%. Individual leaves senesced completely 7- 28 days earlier than in control plants. At anthesis, the plants were shorter than controls and exhibited reductions in stem and ear biomass of 15 and 23%. Grain yield at maturity was decreased by 30% due to a combination of reductions in ear number m(-2), the numbers of grains per spikelet and per ear and IGW. The presence of elevated CO2 reduced the rate of O-3- induced leaf senescence and resulted in the maintenance of a higher green LAI during vegetative growth under ambient CO2 conditions. Grain yields at maturity were nevertheless lower than those obtained in the corresponding elevated CO2 treatments in the absence of elevated O-3. Thus, although the presence of elevated CO2 reduced the damaging impact of ozone on radiation interception and vegetative growth, substantial yield losses were nevertheless induced. These data suggest that spring wheat may be susceptible to O-3-induced injury during anthesis irrespective of the atmospheric CO2 concentration. Possible deleterious mechanisms operating through effects on pollen viability, seed set and the duration of grain filling are discussed.

KEYWORDS: BRASSICA-NAPUS L, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, FIELD CHAMBERS, GRAIN QUALITY, OZONE, PHOTOSYNTHESIS, REPRODUCTIVE DEVELOPMENT, WINTER-WHEAT

1619

Muller, C., W. Reuter, W. Wehrmeyer, H. Dau, and H. Senger. 1993. Adaptation of the photosynthetic apparatus of anacystis- nidulans to irradiance and co2-concentration. *Botanica Acta 106(6):480-487.*

Homocontinuous cultures of the cyanobacterium Anacystis nidulans (syn. Synechococcus sp. PCC 6301) were grown at white light intensities of 2 and 20 W/M2, and supplied with 0.03 and 3 % CO2 enriched air. The mutual influence of these growth factors on the development of the photosynthetic apparatus was studied by analyses of the pigment content, by low temperature absorbance and fluorescence spectroscopy, by analyses of oxygen evolution light-saturation curves, and by SDS PAGE of isolated phycobilisomes. The two growth factors, light and CO2, distinctly affect the absorption cross section of the photosynthetic apparatus, which is expressed by its pigment pattern, excitation energy distribution and capacity. In response to low CO2 concentrations, the phycocyanin/allophycocyanin ratios were lower and one linker polypeptide L(R)30, of the phycobilisomes was no longer detectable in SDS PAGE. Apparently, low CO2 adaptation results in shorter phycobilisome rods. Specifically, upon adaptation to low light intensities, the chlorophyll and the phycocyanin content on a per cell basis increase by about 50 % suggesting a parallel increase in the amount of phycobilisomes and photosystem core-complexes. Low light adaptation and low CO2 adaptation both cause a shift of the excitation energy distribution in favor of photosystem I. Variations in the content of the "anchor" polypeptides L(CM)60 and L(CM)75 are possibly related to changes in the excitation energy transfer from phycobilisomes to the photosystem II and photosystem I core-complexes.

KEYWORDS: ACCLIMATION, ALGA, ANABAENA, CYANOBACTERIA, LIGHT-INTENSITY, MASTIGOCLADUS-LAMINOSUS, MICROCYSTIS- AERUGINOSA, ORGANIZATION, PHYCOBILISOME STRUCTURE, REACTION CENTERS

1620

Muller, J. 1993. Dry-matter production, co2 exchange, carbohydrate and nitrogen- content of winter-wheat at elevated co2 concentration and drought stress. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 171(4):217-235.*

Methods of mathematical modelling and simulation are being used to an increasing degree in estimating the effects of rising atmospheric CO2 concentration and changing climatic conditions on agricultural ecosystems. In this context, detailed knowledge is required about the possible effects on crop growth and physiological processes. To this aim, the influence of an elevated CO2 concentration and of drought stress on dry matter production, CO2 exchange, and on carbohydrate and nitrogen content was studied in two winter wheat varieties from shooting to milk ripeness. Elevated CO2 concentration leads to a compensation of drought stress and at optimal water supply to an increase of vegetative dry matter and of yield to the fourfold value. This effects were caused by enhanced growth of secondary tillers which were reduced in plants cultivated at atmospheric CO2 concentration. Analogous effects in the development of ear organs were influenced additionally by competitive interactions between the developing organs. The content and the mass of ethanol soluble carbohydrates in leaves and stems were increased after the CO2 treatment and exhausted more completely during the grain filling period after drought stress. Plants cultivated from shooting to milk ripeness at elevated CO2 concentration showed a reduced response of net photosynthesis rate to increasing CO2 concentration by comparison with untreated plants.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CROP RESPONSES, DIFFERENT IRRADIANCES, ENVIRONMENTS, LEAVES, PHOTOSYNTHESIS, PLANT GROWTH, SPRING WHEAT, WATER-USE, YIELD

1621

Muller, M., D. Grill, and H. Guttenberger. 1994. The effects of interactions between ozone and co2 on the chromosomes of norway spruce root-meristems. *Phyton-Annales Rei Botanicae 34(2):321-335.*

A Norway spruce (Picea abies (L.) Karsten) test system was used to study the immediate and after effects of increased ozone or elevated CO2 or both, on root tip chromosomes. Five-year-old potted spruce trees were exposed in environmental chambers to elevated concentrations of ozone (0.1 cm3m-3) for the study of an immediate effect and to elevated concentrations of carbon dioxide (750 cm3m-3) and ozone (0.08 cm3m-

3) as single variables or in combination and then transferred to a field for the observation of an after effect. Elevated ozone caused an increased number of chromosomal abnormalities directly after finishing the fumigation and also 21 months later. Elevated CO2 more likely induced a decrease rather than an increase in the number of chromosomal aberrations. The most common abnormalities were chromsome stickiness, in the form of connections, clumped metaphases and amorphous chromatin masses. An increased number of chromosomal aberrations especially chromosome stickiness reflects highly toxic effects, usually of an irreversible type leading to cell death.

1622

Munoz, M.T., P. Aguado, N. Ortega, M.I. Escribano, and C. Merodio. 1999. Regulation of ethylene and polyamine synthesis by elevated carbon dioxide in cherimoya fruit stored at ripening and chilling temperatures. *Australian Journal of Plant Physiology 26(3):201-209.*

In this study we focused on the effect of high CO2 level (20%) on ethylene and polyamine biosynthesis in cherimoya (Annona cherimola Mill.) fruits stored at ripening (20 degrees C) and chilling (6 degrees C) temperatures. At ripening temperature, CO2 inhibited ethylene production, but 1-aminocyclopropane-1- carboxylate (ACC) oxidase activity was similar to that in ripe control fruits. CO2 treatment led to a decline in putrescine (Put) and a major accumulation of spermidine (Spd) and spermine (Spm) without any effect on arginine decarboxylase (ADC) activity. These results confirm the preferential transformation of Put to Spd and Spm in CO2-treated fruits. At chilling temperature, the increase in ACC oxidase activity was inhibited and the V-max of ADC increased. A combination of chilling temperature storage and high CO2 level led to suppression of basal ethylene production while ACC oxidase activity remained unchanged. In addition, fruits held at these conditions had higher polyamine titres than the untreated control. We propose that, in CO2-treated fruits, the absence of autocatalytic or basal ethylene production, depending on the temperature, may be due to deviation of the S-adenosylmethionine (SAM) pool towards polyamine synthesis, primarily Spd and Spm.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACC SYNTHASE, ACCUMULATION, ARGININE DECARBOXYLASE, BIOSYNTHESIS, PEA-SEEDLINGS, SENESCENCE, SPERMIDINE, TOMATO FRUIT, ZUCCHINI SQUASH

1623

Munoz, M.T., M.I. Escribano, and C. Merodio. 1997. Ethanolic metabolism in cherimoya fruit during storage at ambient and under high CO2 atmospheres. *Journal of Horticultural Science 72(3):363-370.*

Cherimoya fruits (Annona cherimola, Mill.) were kept in 20% O-2 + 20% CO2 for UP to 3 d at 20 degrees C and then transferred to air to study the effect of high CO2 levels on fermentation enzymes, ethanol and acethaldehyde content and ripening evolution. Ethanol and acetaldehyde content increased during ripening in air mainly associated with the first respiration peak. At the end of the short-term high CO2 treatment, cherimoya fruit had a lower aerobic respiration rate while concentrations of acethaldehyde and ethanol were greatly increased compared with those of air-control fruit. The activation of fermentation pathway by high CO2 atmosphere is mainly due to an enhancement in pyruvate decarboxylase (PDC) activity. High CO2 treatment prevented the ripening process but, after transfer to air a decrease in fermentation metabolism was recorded and fruit was able to ripen, showing a typical decrease in tissue pH.

KEYWORDS: ACETALDEHYDE, ALCOHOL-DEHYDROGENASE, ETHYLENE PRODUCTION, MILL, PEAR, PLANTS, PYRUVATE DECARBOXYLASE, RESPIRATION

1624

Murage, E.N., N. Watashiro, and M. Masuda. 1996. Leaf chlorosis and carbon metabolism of eggplant in response to continuous light and carbon dioxide. *Scientia Horticulturae 67(1-2):27-37.*

Leaf chlorosis and carbon metabolism were examined in the youngest fully expanded leaves of eggplants (Solanum melongena L. cultivar 'Senryo') grown starting from the third true leaf stage (acropetally) under 12-h and 24-h (continuous) light periods for 6 days, and under continuous illumination with either 0, 6 or 12 h of carbon dioxide (CO2)-free air per day for 10 days at a photosynthetic photon flux density (PPFD) of 100 mu mol m(-2) s(-1). The amount of (CO2)-C-13 assimilated under continuous light was lower on Day 3 and declined even further on Day 6. On the contrary, starch accumulation and the levels of glucose and fructose were highest under continuous illumination and were at their maximum on the fourth day. However, no difference was observed in the amount of leaf sucrose formed in the 12- and 24-h light treatments. Leaves of plants continuously lit developed leaf chlorosis starting from the fourth day. Growing plants with 12 h of CO2-free air per day drastically reduced the amounts of starch and sugar accumulated in the leaves, inhibited the development of chlorosis and enhanced the chlorophyll content. With either the 6 or 0 h of CO2-free air per day, the plants grew better but the leaves accumulated large amounts of starch and sugars and finally developed mild and severe chlorosis, respectively. The results strongly implicated the involvement of carbon metabolism in the predisposition of leaf chlorosis observed under continuous light.

KEYWORDS: MAGNESIUM, PHOSPHATE SYNTHASE ACTIVITY, PHOTOPERIOD, PHOTOSYNTHETIC PERIOD DURATION, PLANTS, POTASSIUM, RHYTHMS, SOYBEAN LEAVES, STARCH

1625

Murakami, A., S.J. Kim, and Y. Fujita. 1997. Changes in photosystem stoichiometry in response to environmental conditions for cell growth observed with the cyanophyte Synechocystis PCC 6714. *Plant and Cell Physiology 38(4):392-397.*

Changes in photosystem stoichiometry in response to shift of environments for cell growth other than light regime were studied with the cyanophyte Synechocystis PCC 6714 in relation to the change induced by light-quality shift. Following two environment-shifts were examined: the shift of molecular form of inorganic carbon source for photosynthesis from CO2 to HCO3- (CO2 stress) and the increase in salinity of the medium with NaCl (0.5 M) (Na+ stress). Both CO2 and Na+ stresses induced the increase in PSI abundance resulting in a higher PSI/PSII stoichiometry. CO2 stress was found to elevate simultaneously Cyt c oxidase activity (V-max). The feature was the same as that caused by light-quality shift from preferential excitation of PSI to PSII (light stress) though the enhancement by either stress was smaller than that by light stress. Under our experimental conditions, PSI/PSII stoichiometry appeared to increase at a fairly constant rate to the basal level even when the basal level had been differently determined by the light- quality. Enhancing rates for PSI/PSII stoichiometry and for Cyt c oxidase activity were also similar to each other. Since the two stresses affect the thylakoid electron transport similarly to the shift of light-quality, we interpreted our results as follows: three environmental stresses, CO2, Na+, and light stresses, cause changes in electron turnover capacity of PSI and Cyt c oxidase under a similar, probably a common, mechanism for monitoring redox state of thylakoid electron transport system.

KEYWORDS: ANACYSTIS-NIDULANS, COMPLEX, CYANOBACTERIAL PHOTOSYNTHETIC SYSTEM, CYTOCHROME-OXIDASE, ELECTRON-TRANSPORT COMPOSITION, II LIGHT,

LIGHT REGIME, PCC-6714, REDOX STATE, STEADY-STATE

1626

Murchie, E.H., and P. Horton. 1997. Acclimation of photosynthesis to irradiance and spectral quality in British plant species: Chlorophyll content, photosynthetic capacity and habitat preference. *Plant, Cell and Environment 20(4):438-448.*

Twenty-two common British angiosperms were examined for their ability to acclimate photosynthetically to sun and shade conditions, Plants were grown under low irradiance, far-red enriched light (50 mu mol m(-2) s(-1)), selected to mimic as closely as possible natural canopy shade, and moderately high light of insufficient irradiance to induce photoinhibitory or photoprotective responses (300 mu mol m(-2) s(-1)), Light- and CO2-saturated photosynthetic rates of m s oxygen evolution (P- max) and chlorophyll content were measured, Large variation was found in both parameters, and two 'strategies' for long-term acclimation were identified: firstly a change in chlorophyll per unit leaf area which was found to correlate positively with photosynthetic capacity, and secondly changes in chlorophyll a/b ratio and P-max, indicative of alterations at the chloroplast level, which were not associated with a change in chlorophyll content per unit leaf area, Combinations of these two strategies may occur, giving rise to the observed diversity in photosynthetic acclimation, The extent and nature of photosynthetic acclimation were compared with an index of shade association, calculated from the association each species has with woodland, It was found that the greatest flexibility for change at the chloroplast level was found in those species possessing an intermediate shade association, whilst acclimation in 'sun' species proceeded by a change in chlorophyll content; obligate shade species showed little capacity for acclimation at either the chloroplast or leaf level, A framework for explaining the variation between plant species in leaf-level photosynthetic capacity, in relation to the natural light environment, is presented, This is the first time the potential for light acclimation of photosynthesis in different plant species has been satisfactorily linked to habitat distribution.

KEYWORDS: ARABIDOPSIS-THALIANA, COMPONENTS, ELECTRON-TRANSPORT, GROWTH-CONDITIONS, LEAVES, LIGHT ENVIRONMENT, PEA-CHLOROPLASTS, PHOTOSYSTEM, SHADE PLANTS, THYLAKOID MEMBRANES

1627

Murchie, E.H., C. Sarrobert, P. Contard, T. Betsche, C.H. Foyer, and N. Galtier. 1999. Overexpression of sucrose-phosphate synthase in tomato plants grown with CO2 enrichment leads to decreased foliar carbohydrate accumulation relative to untransformed controls. *Plant Physiology and Biochemistry 37(4):251-260.*

Tomato plants expressing the maize sucrose-phosphate synthase (SPS) cDNA under the control of the promoter of the small subunit of ribulose-1,5-bisphosphate carboxylase oxygenase (rbcS) promoter were grown 5 weeks in air (450 mu mol.m(-2) s(- 1) irradiance, 350 ppm CO2) and then either maintained in air or exposed to CO2 enrichment (1 000 ppm CO2) for 8 d. A linear relationship between the foliar sucrose to starch ratio and maximal extractable SPS activity was found both in air and high CO2. Starch accumulation was dramatically increased in all plants subjected to CO2 enrichment but the CO2-dependent increase in foliar starch accumulation was much lower in the leaves of the SPS transformants than in those of the untransformed controls in the same conditions. Maximal extractable ribulose-1,5-bisphosphate carboxylase/ oxygenase activity was reduced by growth at high CO2 to a similar extent in both plant types. The carbon/nitrogen ratios were similar in both plant lines in both growth conditions after 20 d exposure to high CO2. A small (5 %) increase in carbon export capacity was observed at high CO2 in the leaves of transformed plants compared to leaves from untransformed controls. Increased foliar SPS activity did not, however, prevent acclimation of photosynthesis in plants grown with long-term CO2 enrichment. (C) Elsevier, Paris.

KEYWORDS: ACCLIMATION, CARBON, ELEVATED CO2, EXPRESSION, GENES, METABOLISM, NITROGEN, PHOTOSYNTHESIS, SINK REGULATION, TRANSCRIPT LEVELS

1628

Murphy, K.P., J.M. Santamaria, W.J. Davies, and P.J. Lumsden. 1998. Ventilation of culture vessels. I. Increased growth in vitro and survival ex vitro of Delphinium. *Journal of Horticultural Science & Biotechnology 73(6):725-729.*

Inclusion of small circular apertures covered with filters in the sides of plastic culture vessels led to a small but significant increase in the multiplication rate of Delphinium cultured in vitro and greater survival following transfer ex vitro. Filters had no effect on the multiplication rate and survival of Hosta. In vessels with apertures there was a large increase in the rate of water loss, but relative humidity was greater than 95% in both intact vessels and in vessels with filters. It is suggested that in vessels with apertures there was an increase in the flow of water vapour from the vessel atmosphere to the external atmosphere, due to a reduced diffusive resistance. The improved performance of Delphinium plants could have resulted from an increase in transpiration and movement of water (and therefore some nutrients) through the plants.

KEYWORDS: AERATION, CARBON DIOXIDE, CO2- ENRICHMENT, ETHYLENE, INVITRO, PLANTLETS, REDUCED HUMIDITY, RESISTANCE

1629

Murray, D.R. 1995. Plant-responses to carbon-dioxide. *American Journal of Botany 82(5):690-697.*

The average atmospheric concentration of CO2 will probably double before the end of next century. Many of the consequences for plant growth can and should be determined now. In this review the effects of [CO2] on a variety of plant processes are summarized: stomatal opening and closing; stomatal density; respiration; root morphogenesis; and flowering. The effects of growth under elevated [CO2] on crop yield and seed composition are also discussed. Adverse effects on the composition of C-3 cereal grains are clearly indicated.

KEYWORDS: DARK RESPIRATION, DRY-MATTER, ELEVATED ATMOSPHERIC CO2, GROWTH, GUARD-CELLS, PERENNIAL RYEGRASS, STOMATAL DENSITY, WATER-USE EFFICIENCY, WHITE CLOVER, ZOSTERA-CAPRICORNI

1630

Murray, M.B., I.D. Leith, and P.G. Jarvis. 1996. The effect of long term CO2 enrichment on the growth, biomass partitioning and mineral nutrition of Sitka spruce (Picea sitchensis (Bong) Carr). *Trees-Structure and Function 10(6):393-402.*

Sitka spruce [Picea sitchensis (Pong.) Carr.] seedlings were grown for 3 years in an outside control plot or in ambient (similar to 355 mu mol mol(-1)) or elevated (ambient + 350 mu mol mol(-1)) atmospheric CO2 environments, within open top chambers (OTCs) at the Institute of Terrestrial Ecology, Edinburgh. Sequential harvests were carried out at the end of each growing season and throughout the 1991 growing season, five in all. Plants grown in elevated CO2 had, (i) 35 and 10% larger root/shoot ratios at the end of the first and third season, respectively, (ii) significantly higher summer leader extension relative growth rates, which declined more rapidly in early autumn than ambient grown plants, (iii) after three growing seasons a significantly increased

mean annual relative growth rate, (iv) consistently lower foliar nutrient concentrations, and (v) after two growing seasons smaller total projected needle areas. Plants grown inside OTCs were taller, heavier and had a smaller root/shoot ratio than those grown outside the chambers. There was no effect of CO2 concentration on Sitka spruce leaf characteristics, although leaf area ratio, specific leaf area and leaf weight ratio all fell throughout the course of the 3 year experiment.

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, CARBON DIOXIDE, CASTANEA-SATIVA MILL, ELEVATED ATMOSPHERIC CO2, NITROGEN, NUTRIENTS, PLANT-RESPONSES, SEEDLINGS, TREES

1631

Murray, M.B., R.I. Smith, I.D. Leith, D. Fowler, H.S.J. Lee, A.D. Friend, and P.G. Jarvis. 1994. Effects of elevated co2, nutrition and climatic warming on bud phenology in sitka spruce (picea-sitchensis) and their impact on the risk of frost damage. *Tree Physiology 14(7-9):691-706.*

Effects of elevated CO2, clone and plant nutrition on bud dormancy of Sitka spruce (Picea sitchensis (Bong.) Carr.) were examined. Sitka spruce seedlings were fumigated with ambient or elevated (ambient + 350 mumol mol-1) concentrations of CO2 in open-top chambers for three growing seasons. In 1991 and 1992, elevated CO2 delayed bud burst in the spring and advanced bud set in the autumn. The effect of the open-top chamber on the thermal requirement for bud burst was greater than the effect of elevated CO2 (50 and 30 day degrees (D(d)), respectively). In a second study, four clones of Sitka spruce taken from two provenances, at 43 and 54-degrees-N, were fumigated with ambient or elevated CO2. There was a large natural variation in the timing of bud burst and bud set among the clones. Elevated CO2 had no effect on bud dormancy of the Skidegate a clone, but it reduced the growing season of the North Bend b clone by 20 days. In a third study, Sitka spruce seedlings growing in ambient or elevated CO2, were supplied with one of three nutrient regimes, low (0.1 x potential), medium (0.5 x potential) or high (2.0 x potential), using a method and solution based on the Ingestad technique. Elevated CO2 did not affect bud dormancy in the high-nutrient treatment, but it reduced the growing season of plants in the low-nutrient treatment by 22 days. Increasing plant nutrient supply lengthened the growing season, plants flushed earlier in the spring and set bud later in the autumn. The effects of elevated CO2 plus a 0, 2 or 4-degrees-C climatic warming on the timing of bud burst and the subsequent risk of frost damage were assessed using a simulation model and meteorological data from three sites, Edinburgh, Braemar and Masset. The model predicted that (i) doubling the CO2 concentration in die absence of climatic warming, will delay the onset of bud burst at all three sites, (ii) climatic warming in ambient CO2 will hasten bud burst and (iii) climatic warming in elevated CO2 will hasten bud burst at Edinburgh and Braemar but to a lesser extent than climatic warming alone. At Masset, a 4-degrees-C warming was required to advance the date of bud burst of seedlings in the elevated CO2 treatment. At all three sites, elevated CO2 and climatic warming increased the mean daily temperature on the date of bud burst, thus reducing the risk of subsequent frost damage.

1632

Murthy, R., and P.M. Dougherty. 1997. Effect of carbon dioxide, fertilization and irrigation on loblolly pine branch morphology. *Trees-Structure and Function 11(8):485-493.*

Foliage and wood parameters of branches of 12-year-old loblolly pine (Pinus taeda L.) trees were characterized after 21 months of exposure to fertilizer, irrigation and elevated CO2 treatments. Branches of loblolly pine trees were enclosed in plastic chambers and exposed to ambient, ambient +175 and ambient +350 umol mol(-1) CO2 concentrations. Measurements of foliage and wood at the fascicle, flush and branch levels were made at the end of the 21 month study period. The +350 CO2 treatment did not significantly increase fascicle radius or length but did increase the number of fascicles on the first flush. Fertilization significantly increased fascicle radius and length, while irrigation significantly increased number of fascicles and flush length of first flush. The +350 CO2 treatment also significantly increased flush length of the first flush. Significant interaction of fertilization and irrigation with CO2 was observed for fascicle length. Significant interactions of fertilization and irrigation were also observed for flush length, number of fascicles and fascicle length. Observed increases in fascicle radius, fascicle length, number of fascicles and flush length may have been responsible for the significantly higher flush leaf area observed for the all three treatments. Also, a combination of fertilization and irrigation increased leaf area by 82% compared to that in the control when averaged across CO2 treatments. At the branch level +350 CO2 treatment significantly increased shoot length but not the number of flushes on the branch. In general with the exception of bark density and total number of needle scales, neither fertilization nor irrigation had any significant effect on other branch level parameters. Results from this study indicate that with 'global change' an increase in CO2 alone may increase leaf area via an increase in flush length and number of fascicles. Combining increases in CO2 with fertilization and irrigation could greatly enhance leaf area which when coupled to observed increases in net photosynthesis as a result of elevated CO2 could greatly increase productivity of loblolly pine trees.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, ELEVATED CO2, GROWTH-RESPONSES, LEAF-AREA, LIQUIDAMBAR-STYRACIFLUA, MINERAL NUTRITION, SEASONS, SPRUCE SEEDLINGS, TAEDA SEEDLINGS, WATER-STRESS

1633

Murthy, R., P.M. Dougherty, S.J. Zarnoch, and H.L. Allen. 1996. Effects of carbon dioxide, fertilization, and irrigation on photosynthetic capacity of loblolly pine trees. *Tree Physiology 16(6):537-546.*

Branches of nine-year-old loblolly pine trees grown in a 2 x 2 factorial combination of fertilization and irrigation were exposed for 11 months to ambient, ambient + 175, or ambient + 350 mu mol mol(-1) CO2. Rates of light-saturated net photosynthesis (A(max)), maximum stomatal conductance to water vapor (g(max)), and foliar nitrogen concentration (% dry mass) were assessed monthly from April 1993 until September 1993 on 1992 foliage (one-year-old) and from July 1993 to March 1994 on 1993 foliage (current-year). Rates of A(max) of foliage in the ambient + 175 CO2 treatment and ambient + 350 were 32-47 and 83-91% greater, respectively, than that of foliage in the ambient CO2 treatment. There was a statistically significant interaction between CO2 treatment and fertilization or irrigation treatment on A(max) on only one measurement date for each age class of foliage. Light-saturated stomatal conductance to water vapor (g(max)) was significantly affected by CO2 treatment on only four measurement dates. Light-saturated g(max) in winter was only 42% of summer g(max) even though soil water during winter was near field capacity and evaporative demand was low. Fertilization increased foliar N concentration by 30% over the study period when averaged across CO2 treatments. During the study period, the ambient + 350 CO2 treatment decreased average foliar N concentration of one-year- old foliage in the control, irrigated, fertilized and irrigated + fertized plots by 5, 6.4, 9.6 and 11%, respectively, compared with one-year-old foliage in the corresponding ambient CO2 treatments. The percent increase in A(max) due to CO2 enrichment was similar in all irrigation and fertilization treatments and the effect persisted throughout the 11-month study period for both one-year-old and current-year foliage.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, ELEVATED

CO2, ENRICHMENT, GAS-EXCHANGE, GROWTH, NUTRITION, RESPONSES, SEEDLINGS, SOUR ORANGE TREES, WATER

1634

Murthy, R., S.J. Zarnoch, and P.M. Dougherty. 1997. Seasonal trends of light-saturated net photosynthesis and stomatal conductance of loblolly pine trees grown in contrasting environments of nutrition, water and carbon dioxide. *Plant, Cell and Environment 20(5):558-568.*

Repeated measures analysis was used to evaluate the effect of long-term CO2 enhancement on seasonal trends of light-saturated rates of net photosynthesis (A(sat)) and stomatal conductance to water vapour (g(sat)) of 9-year-old loblolly pine (Pious taeda L.) trees grown in a 2 x 2 factorial experimental design of nutrition and water. A significant interaction effect of CO2 and nutrition on mean A(sat) was observed for juvenile foliage. Also, juvenile foliage exposed to + 350 mu mol mol(-1) CO2 had a higher rate of increase of A(sat) between late summer and early autumn. This would lead to a greater potential for recharging carbohydrate reserves for winter. Mature foliage was affected by CO2, water and nutrient treatments in two ways. First, A(sat) was significantly increased as a result of elevated CO2 in January, a period when stomatal conductance was only 47% of the maximum observed rate. Secondly, the rate of increase of A(sat) from winter to early spring was accelerated asa result of both nutrient + water and + 350 mu mol mol(-1) CO2 treatments. This accelerated response resulted in a greater potential for photosynthate production during the period when growth initiation occurred. Nutrient, water or carbon dioxide treatments did not significantly alter trends in g(sat) for mature or juvenile foliage. A significant nutrition x CO2 interaction was observed for the mature foliage, suggesting that g(sat) increased with increasing CO2 and nutrition. These results may have important consequences for the determination of the water use efficiency of loblolly pine. In spite of low g(sat) in the winter to early spring period, there was a substantial gain in A(sat) attributable to elevated CO2 concentrations.

KEYWORDS: ATMOSPHERIC CO2, BRANCH BAG, DIFFERENT IRRADIANCE LEVELS, ELEVATED CO2, ENRICHMENT, FOLIAR GAS-EXCHANGE, LEAF, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, TAEDA SEEDLINGS

1635

Muschak, M., L. Willmitzer, and J. Fisahn. 1999. Gas-exchange analysis of chloroplastic fructose-1,6- bisphosphatase antisense potatoes at different air humidities and at elevated CO2. *Planta 209(1):104-111.*

Gas-exchange measurements were performed to analyze the leaf conductances and assimilation rates of potato (Solanum tuberosum L. cv. Desiree) plants expressing an antisense construct against chloroplastic fructose-1,6-bisphosphatase (FBPase, EC 3.1.3.11) in response to increasing photon flux densities, different relative air humidities and elevated CO2 concentrations. Assimilation rates (A) and transpiration rates (E) were observed during a stepwise increase of photon flux density. These experiments were carried out under atmospheric conditions and in air containing 500 mu mol mol(-1) CO2. In both gas atmospheres, two levels of relative air humidity (60- 70% and 70-80%) were applied in different sets of measurements. Intercellular CO2 concentration, leaf conductance, air-to-leaf vapour pressure deficit, and instantaneous water-use efficiency (A/E) were determined. As expected, assimilation rates of the FBPase antisense plants were significantly reduced as compared to the wild type. Saturation of assimilation rates in transgenic plants occurred at a photon flux density of 200 mu mol m(-2) s(-1), whereas saturation in wild type plants was observed at 600 mu mol m(-2) s(-1). Elevated ambient CO2 levels did not effect assimilation rates of transgenic plants. At 70- 80% relative humidity and atmospheric CO2 concentration the FBPase antisense plants had significantly higher leaf conductances than wild-type plants while no difference. emerged at 60-70%. These differences in leaf conductance vanished at elevated levels of ambient CO2. Stomatal response to different relative air humidities was not affected by mesophyll photosynthetic activity. It is suggested that the regulation of stomatal opening upon changes in photon flux density is merely mediated by a signal transmitted from mesophyll cells, whereas the intercellular CO2 concentration plays a minor role in this kind of stomatal response. The results are discussed with respect to stomatal control by environmental parameters and mesophyll photosynthesis.

KEYWORDS: ABSCISIC- ACID, CARBON DIOXIDE, GROWTH, GUARD-CELLS, HIGHER-PLANTS, PHOTOSYNTHESIS, STOMATAL RESPONSES, VICIA-FABA L, VIOLAXANTHIN CYCLE, ZEAXANTHIN

1636

Musil, C.F., G.F. Midgley, and S.J.E. Wand. 1999. Carry-over of enhanced ultraviolet-B exposure effects to successive generations of a desert annual: interaction with atmospheric CO2 and nutrient supply. *Global Change Biology 5(3):311-329.*

The performance of fifth generation offspring of a desert annual (Dimorphotheca sinuata DC.) were compared in the absence of UV-B, under variable atmospheric CO2 and nutrient supply after four consecutive generations of concurrent exposure of their progenitors to UV-B at ambient (seasonal range: 2.55-8.85 kJ m(-2) d(-1)) and enhanced (seasonal range: 4.70-11.41 kJ m-2 d(-1)) levels. Offspring of progenitors grown under elevated UV-B exhibited a diminished photosynthetic rate, a consequence of a reduced leaf density, and diminished foliar levels of carotenoids, polyphenolics and anthocyanins. Conversely nonstructural carbohydrate and chlorophyll b levels were increased. Altered physiology was accompanied by reduced apical dominance and earlier flowering, features generally considered under photomorphogenic control, increased branching and inflorescence production and greater partitioning of biomass to reproductive structures, but diminished seed production. Many of these changes were magnified under nutrient limitation and intensified under atmospheric CO2 enriched conditions. The latter disagrees with current opinion that elevated CO2 may reduce detrimental UVB effects, at least over the long-term. Observed correlations between seed production and polyphenolic, especially anthocyanin, levels in offspring, and indications of diminished lignification (thinner leaves, less robust stems and fewer lignified seeds set) all pointed to the involvement of the phenylpropanoid pathway in seed formation and plant structural development and its disruption during long-term UV-B exposure. Comparisons with earlier generations revealed trends with cumulative generations of enhanced UVB exposure of increasing chlorophyll b and nonstructural carbohydrates, decreasing polyphenolics and biomass allocation to vegetative structures, and diminishing seed production despite increasing biomass allocation to reproductive structures. Notwithstanding some physiological compensation (increased chlorophyll b), the accumulation and persistence of these ostensibly inherited changes in physiological and reproductive performance suggest a greater impact of elevated UV-B on vegetation, primary production and regeneration over the long-term than presently envisaged.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL CONTENT, ELEVATED CO2, ELEVATIONAL GRADIENT, ETIOLATING TOMATO SEEDLINGS, HYPOCOTYL ELONGATION, PHOTON FLUX- DENSITY, POLYMORPHIC DIASPORES, TERRESTRIAL ECOSYSTEMS, UV-B

1637

Myers, D.A., R.B. Thomas, and E.H. Delucia. 1999. Photosynthetic capacity of loblolly pine (Pinus taeda L.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell and Environment 22(5):473-481.*

Our objective was to assess the photosynthetic responses of loblolly pine trees (Pinus taeda L,) during the first full growth season (1997) at the Brookhaven National Lab/Duke University Free Air CO2 Enrichment (FACE) experiment. Gas exchange, fluorescence characteristics, and leaf biochemistry of ambient CO2 (control) needles and ambient + 20 Pa CO2 (elevated) needles were examined five times during the year. The enhancement of photosynthesis by elevated CO2 in mature loblolly pine trees varied across the season and was influenced by abiotic and biotic factors. Photosynthetic enhancement by elevated CO2 was strongly correlated with leaf temperature. The magnitude of photosynthetic enhancement was zero in March but was as great as 52% later in the season. In March, reduced sink demand and lower temperatures resulted in lower net photosynthesis, lower carboxylation rates and higher excess energy dissipation from the elevated CO2 needles than from control needles, The greatest photosynthetic enhancement by CO2 enrichment was observed in July during a period of high temperature and low precipitation, and in September during recovery from this period of low precipitation, In July, loblolly pine trees in the control rings exhibited lower net photosynthetic rates, lower maximum rates of photosynthesis at saturating CO2 and light, lower values of carboxylation and electron transport rates (modelled from A-C-i curves), lower total Rubisco activity, and lower photochemical quenching of fluorescence in comparison to other measurement periods. During this period of low precipitation trees in the elevated CO2 rings exhibited reduced net photosynthesis and photochemical quenching of fluorescence, but there was little effect on light- and CO2-saturated rates of photosynthesis, modelled rates of carboxylation or electron transport, or Rubisco activity. These first-year data will be used to compare with similar measurements from subsequent years of the FACE experiment in order to determine whether photosynthetic acclimation to CO2 occurs in these canopy loblolly pine trees growing in a forest ecosystem.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, C-3 PLANTS, ELEVATED CO2, GAS-EXCHANGE, LEAF, LEAVES, NET PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TEMPERATURE

1638

Myers, R.E., D.E. Deyton, and C.E. Sams. 1996. Applying soybean oil to dormant peach trees alters internal atmosphere, reduces respiration, delays bloom, and thins flower buds. *Journal of the American Society for Horticultural Science 121(1):96-100.*

Dormant 'Georgia Belle' peach [Prunus persica (L.) Batsch.] trees were sprayed in early February 1992 with single applications of 0%, 2.5%, 5.0%, 10.0%, or 20.0% (v/v) crude soybean oil. 'Redhaven' trees were sprayed in February 1993 with single applications of 0%, 2.5%, 5.0%, 10.0%, or 15% degummed soybean oil, Additional treatments of two applications of 2.5% or 5.0% oil were included each year, Both crude and degummed soybean oil treatments interfered with escape of respiratory CO2 from shoots and increased internal CO2 concentrations in shoots for up to 8 days compared to untreated trees, Respiration rates, relative to controls, were decreased for 8 days following treatment, indicating a feedback inhibition of respiration by the elevated CO2. Thus, an internal controlled atmosphere condition was created, Ethylene evolution was elevated for 28 days after treatment. Flower bud development was delayed by treating trees with 5% crude or degummed soybean oil. Trees treated with 10% crude or degummed soybean oil bloomed 6 days later than untreated trees. Repeated sprays of one half concentration delayed bloom an additional four days in 1992, but <1 day in 1993 compared to a single spray of the same total concentration, Application of soybean oil caused bud damage and reduced flower bud density (number of flower buds/cm branch length) at anthesis, In a trial comparing petroleum oil and degummed soybean oil, yields of trees treated with 6% or 9% soybean oil were 17% greater than the untreated trees and 29% more than petroleum treated trees, These results suggest that applying soybean oil delays date of peach bloom and may be used as a bloom thinner.

1639

Nadelhoffer, K.J., B.A. Emmett, P. Gundersen, O.J. Kjonaas, C.J. Koopmans, P. Schleppi, A. Tietema, and R.F. Wright. 1999. Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature 398(6723):145-148.*

Humans have altered global nitrogen cycling such that more atmospheric N-2 is being converted ('fixed') into biologically reactive forms by anthropogenic activities than by all natural processes combined(1). In particular, nitrogen oxides emitted during fuel combustion and ammonia volatilized as a result of intensive agriculture have increased atmospheric nitrogen inputs (mostly NO3 and NH4) to temperate forests in the Northern Hemisphere(2-4). Because tree growth in northern temperate regions is typically nitrogen-limited(5), increased nitrogen deposition could have the effect of attenuating rising atmospheric CO2 by stimulating the accumulation of forest biomass. Forest inventories indicate that the carbon contents of northern forests have increased concurrently with nitrogen deposition since the 1950s(6-8). In addition, variations in atmospheric CO2 indicate a globally significant carbon sink in northern mid-latitude forest regions(9-12). It is unclear, however, whether elevated nitrogen deposition or other factors are the primary cause of carbon sequestration in northern forests. Here we use evidence from N-15-tracer studies in nine forests to show that elevated nitrogen deposition is unlikely to be a major contributor to the putative CO2 sink in forested northern temperature regions.

KEYWORDS: ADDITIONS, BIOSPHERE, CO2, CYCLE, MAINE, NITRATE, SINK, STORAGE, TERRESTRIAL ECOSYSTEMS, USA

1640

Naeem, S., L.J. Thompson, S.P. Lawler, J.H. Lawton, and R.M. Woodfin. 1995. Empirical-evidence that declining species-diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 347(1321):249-262.*

We examined experimentally the association between species diversity and ecosystem processes in a series of terrestrial mesocosms. We developed and maintained 14 mesocosms whose biota were assembled from a single pool of plant and animal species and whose environmental conditions were identically controlled. Each community contained four trophic levels: primary producers (annual herbs), consumers (herbivorous molluscs and phloem sucking insects), secondary consumers (parasitoids) and decomposers (earthworms, Collembola and microbes). All mesocosms received the same diurnal pattern of light, temperature, relative humidity and water. The initial volume of soil, soil structure, composition, nutrient content and inocula of both soil microbes and nematodes were also identical among replicates. The only experimentally manipulated factor was the number of plant and animal species within each trophic level. High, medium and low diversity communities had nine, 15 or 31 plant and animal species, respectively. We measured five ecosystem processes as response variables in these mesocosms over the course of 206 days: (i) community respiration; (ii) productivity; (iii) decomposition; (iv) nutrient retention; and (v) water retention. The manipulation of diversity produced communities that differed significantly in their ecosystem processes. Our results provide the first evidence (obtained by a direct manipulation of diversity under controlled environmental conditions) that ecosystem processes may be affected by loss of diversity.

KEYWORDS: BIODIVERSITY, CO2, ELEVATED CARBON-DIOXIDE

1641

Nagy, J., K.F. Lewin, G.R. Hendrey, E. Hassinger, and R. Lamorte.

1994. Face facility co2 concentration control and co2 use in 1990 and 1991. *Agricultural and Forest Meteorology 70(1-4):31-48.*

CO2 treatment level control and CO2 use are reported for free- air carbon dioxide enrichment (FACE) facility operations at the University of Arizona's Maricopa Agricultural Center in 1990 and 1991. These are required for evaluation of the validity of biological experiments conducted in four replicates of paired experimental and control plots in a large cotton field and the cost-effectiveness of the plant fumigation facility. Gas concentration was controlled to 550 mumol mol-1 at the center of each experimental plot, just above the canopy. In both years, season-long (April-September) average CO2 levels during treatment hours (05:00-19:00 h Mountain Standard Time) were 550 mumol mol-1 measured at treatment plot centers when the facility was operating. Including downtime, the season average was 548 mumol mol-1 in 1991. In 1990, the season averages for the four elevated CO2 treatments varied from 522 to 544 mumol mol-1, owing to extended periods of downtime after lightning damage. Ambient CO2 concentration during treatment was 370 mumol mol-1. Instantaneous measurements of CO2 concentration were within 10% of the target concentration of 550 mumol mol-1 more than 65% of the time when the facility was operating, and 1 min averages were within 10% of the target concentration for 90% of the time. The long-term average of CO2 concentration measured over the 20 m diameter experimental area of one array at the height of the canopy was in the range 550-580 mumol mol- 1 during July 1991, with the higher values near the edges. In 1991, CO2 demand averaged 1250 kg per array per 14 h treatment day, or 4 kg m-2 of fumigated plant canopy. The FACE facility provided good temporal and spatial control of CO2 concentration and was a cost-effective method for large-scale field evaluations of the biological effects of CO2.

KEYWORDS: FIELD CROPS, SYSTEM

1642

Naidu, S.L., and E.H. DeLucia. 1999. First-year growth response of trees in an intact forest exposed to elevated CO2. *Global Change Biology 5(5):609-613.*

Although elevated atmospheric CO2 has been shown to increase growth of tree seedlings and saplings, the response of intact forest ecosystems and established trees is unclear. We report results from the first large-scale experimental system designed to study the effects of elevated CO2 on an intact forest with the full complement of species interactions and environmental stresses, During the first year of exposure to approximate to 1.5 x ambient CO2, canopy loblolly pine (Pinus taeda, L.) trees increased basal area growth rate by 24% but understorey trees of loblolly pine, sweetgum (Liquidambar styraciflua L.), and red maple (Acer rubrum L.) did not respond. Winged elm (Ulmus alata Michx.) had a marginally significant increase in growth rate (P=0.069). These data suggest that this ecosystem has the capacity to respond immediately to a step increase in atmospheric CO2; however, as exposure time increases, nutrient limitations may reduce this initial growth stimulation.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON DIOXIDE, GAS-EXCHANGE, LOBLOLLY-PINE, NITROGEN, PHOTOSYNTHESIS, PLANTS, SEEDLINGS, TAEDA

1643

Naidu, S.L., J.H. Sullivan, A.H. Teramura, and E.H. Delucia. 1993. The effects of ultraviolet-b radiation on photosynthesis of different aged needles in field-grown loblolly-pine. *Tree Physiology 12(2):151-162.*

We examined the effect of supplemental UV-B radiation (290-320 nm) on photosynthetic characteristics of different aged needles of 3-year-old, field-grown loblolly pine (Pinus taeda L.). Needles in four age classes were examined: I, most recently fully expanded, year 3; II, first flush, year 3; III, final flush, year 2; and IV, oldest needles still present, year 2. Enhanced UV-B radiation caused a statistically significant decrease (6%) in the ratio of variable to maximum fluorescence (F(v)/F(m)) following dark adaptation only in needles from the youngest age class, suggesting transient damage to photosynthesis. However, no effects of enhanced UV-B radiation on other instantaneous measures of photosynthesis, including maximum photosynthesis, apparent quantum yield and dark respiration, were seen for needles of any age. Foliar nitrogen concentration was unaffected by UV-B treatment. However, the C- 13/C-12 carbon isotope ratios (deltaC-13-a time integrated measure of photosynthetic function) of needles in age classes II and IV were 3% ($P < 0.01$) and 2% ($P < 0.05$) more negative. respectively, in treated plants than in control plants. Exposure to enhanced UV-B radiation caused a 20% decrease in total biomass and a 4% ($P < 0.05$), 25% ($P < 0.01$), and 9% ($P < 0.01$) decrease in needle length of needles in age classes I, II, and IV, respectively. The observed decreases in delta-C-13, and F(v)/F(m) of the needles in the youngest needle age class suggest subtle damage to photosynthesis, although overall growth reductions were probably a result of decreased total leaf surface rather than decreased photosynthetic capacity. Needles of age class IV had lower light- and CO2-saturated maximum photosynthetic rates (39%), lower dark respiration (34%), lower light saturation points (37%), lower foliar nitrogen concentration (28%), and lower delta-C-13 (14%) values than needles of age class I. Apparent quantum yield and F(v)/F(m) did not change with needle age. The observed changes in photosynthesis and foliage chemical composition with needle age are consistent with previous studies of coniferous trees and may represent adaptations of older needles to shaded conditions within the canopy.

1644

Nakadai, T., H. Koizumi, Y. Usami, M. Satoh, and T. Oikawa. 1993. Examination of the method for measuring soil respiration in cultivated land - effect of carbon-dioxide concentration on soil respiration. *Ecological Research 8(1):65-71.*

An acceleration of soil respiration with decreasing CO2 concentration was suggested in the field measurements. The result supports that obtained in laboratory experiments in our previous study. The CO2 concentrations in a chamber of the alkali absorption method (the AA-method) were about 150-250 parts/10(6) lower than that in the atmosphere (about 350 parts/ 10(6)), while those observed in the open-flow IRGA method (the OF-method) were nearly equal to the soil surface CO2 levels. The AA-method at such low CO2 levels in the chamber appears to overestimate the soil respiration. Our results showed that the rates obtained by the AA-method were about twice as large as those by the OF-method in field and laboratory measurements. This finding has important consequences with respect to the validity of the existing data obtained by the AA-method and the estimation of changes in the terrestrial carbon flow with elevated CO2 concentrations.

KEYWORDS: DYNAMICS, ECOSYSTEMS, EVOLUTION, GRASSLAND, LITTER, STORAGE, TEMPERATURE

1645

Nakamura, T., M. Osaki, T. Koike, Y.T. Hanba, E. Wada, and T. Tadano. 1997. Effect of CO2 enrichment on carbon and nitrogen interaction in wheat and soybean. *Soil Science and Plant Nutrition 43(4):789-798.*

Effect of CO2 enrichment on the carbon-nitrogen balance in whole plant and the acclimation of photosynthesis was studied in wheat (spring wheat) and soybean (A62-1 [nodulated] and A62- 2 [non-nodulated]) with a combination of two nitrogen application rates (0 g N land area m(-2) and 30 g N land area m(-2)) and two temperature treatments (30/20 degrees C (day/night) and 26/16 degrees C), Results were as

follows. 1. Carbon (dry matter)-nitrogen balance of whole plant throughout growth was remarkably different between wheat and soybean, as follows: 1) in wheat, the relationship between the amount of dry matter (DMt) and amount of nitrogen absorbed (Nt) in whole plant was expressed by an exponential regression, in which the regression coefficient was affected by only the nitrogen application rate, and not by CO2 and temperature treatments, and 2) in soybean the DMt-Nt relationship was basically expressed by a linear regression, in which the regression coefficient was only slightly affected by the nitrogen treatment (at ON, DMt-Nt balance finally converged to a linear regression), Thus, carbon-nitrogen interaction in wheat was strongly affected by the underground environment (nitrogen nutrition), but not by the above ground environment (CO2 enrichment and temperature), while that in soybean was less affected by both under and above ground environments, 2. The photosynthetic response curve to CO2 concentration in wheat and soybean was less affected by the CO2 enrichment treatment, while that in wheat and soybean (A62-2) was affected by the nitrogen treatment, indicating that nitrogen nutrition is a more important factor for the regulation of photosynthesis regardless of the CO2 enrichment, 3. Carbon isotope discrimination (d) in soybean was similar to that in wheat under ambient CO2, while lower than that in wheat under CO2 enrichment, suggesting that the carbon metabolism is considerably different between wheat and soybean under the CO2 enrichment conditions.

KEYWORDS: ACCLIMATION, DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO2, FIELD CROPS, GAS-EXCHANGE, GROWTH, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE

1646

Nakano, H., A. Makino, and T. Mae. 1997. The effect of elevated partial pressures of CO2 on the relationship between photosynthetic capacity and N content in rice leaves. *Plant Physiology 115(1):191-198.*

The effects of growth CO2 levels on the photosynthetic rates; the amounts of ribulose-1,5-bisphosphate carboxylase (Rubisco), chlorophyll (Chl), and cytochrome f;sucrose phosphate synthase activity; and total N content were examined in young, fully expanded leaves of rice (Oryza sativa L.). The plants were grown hydroponically under two CO2 partial pressures of 36 and 100 Pa at three N concentrations. The light-saturated photosynthesis at 36 Pa CO2 was lower in the plants grown in 100 Pa CO2 than those grown in 36 Pa CO2. Similarly, the amounts of Rubisco, Chl, and total N were decreased in the leaves of the plants grown in 100 Pa CO2. However, regression analysis showed no differences between the two CO2 treatments in the relationship between photosynthesis and total N or in the relationship between Rubisco and Chl and total N. Although a relative decrease in Rubisco to cytochrome for sucrose phosphate synthase was found in the plants grown in 100 Pa CO2, this was the result of a decrease in total N content by CO2 enrichment. The activation state of Rubisco was also unaffected by growth CO2 levels. Thus, decreases in the photosynthetic capacity of the plants grown in 100 Pa CO2 could be simply accounted for by a decrease in the absolute amount of leaf N.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, ELECTRON-TRANSPORT, GAS-EXCHANGE, LONG-TERM EXPOSURE, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOYBEAN LEAVES, SUCROSE SYNTHESIS ENZYMES

1647

Nakayama, F.S., G. Huluka, B.A. Kimball, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1994. Soil carbon-dioxide fluxes in natural and co2-enriched systems. *Agricultural and Forest Meteorology 70(1-4):131-140.*

Carbon dioxide fluxes between the soil and atmosphere were determined on the 1991 free-air carbon dioxide enrichment (FACE) experiment at the Maricopa Agricultural Center, Maricopa, Arizona. The study was conducted on drip-irrigated cotton in conjunction with other physical and physiological measurements. Fluxes were measured with a 1.6 l closed-chamber static sampling system. The main treatment for the open-air release study had two levels of CO2-ambient air with CO2 concentration of approximately 370 mumol mol-1 (control) and CO2-enriched air with CO2 concentration of approximately 550 mumol mol-1 (FACE). The enrichment was made over the daylight hours (05:00-19:00 h). Two quantities of water application, 'wet' (1050 mm) and 'dry' (790 mm), were superimposed on the two CO2 levels. The observed soil CO2 fluxes ranged from 2 to 8 mumol m-2 s-1 over the cultivation period. The CO2 fluxes were significantly higher in the FACE than in the control plots, and also higher for the wet than for the dry irrigation level. In addition, an interaction between CO2 and water levels was present. The CO2 enrichment effect on soil CO2 flux remained for approximately 4 weeks after the enrichment was ended. A detailed study on the procedure for determining flux indicated that some of the random and inconsistent flux values observed in the field could be attributed to a high CO2 concentration present in the first of the two gas samples taken to estimate flux.

KEYWORDS: RESPIRATION

1648

Nakazawa, T., S. Murayama, M. Toi, M. Ishizawa, K. Otonashi, S. Aoki, and S. Yamamoto. 1997. Temporal variations of the CO2 concentration and its carbon and oxygen isotopic ratios in a temperate forest in the central part of the main island of Japan. *Tellus Series B-Chemical and Physical Meteorology 49(4):364-381.*

Using discrete air sampling, values of delta(13)C and delta(18)O in atmospheric CO2, as well as its concentration, were measured in a forest in the central part of the main island of Japan during the period from June 1994 to June 1996 to examine the biospheric contribution to their temporal variations. delta(13)C shows a prominent diurnal variation with high values in the daytime and low values in the nighttime, especially during the warm season. delta(13)C also vary seasonally, showing a maximum in summer and a minimum in spring. The diurnal and seasonal variations of delta(13)C are opposite in phase with those of the CO2 concentration. The rate of change in delta(13)C with respect to the CO2 concentration is found to be approximately -0.05 parts per thousand/ppmv. This suggests that the diurnal and seasonal variations of the CO2 concentration are produced primarily by diurnally-and seasonally-dependent photosynthetic-respiratory processes of the biosphere near the observation site, respectively. In the warm season, delta(18)O also increases in the daytime and decreased in the nighttime, which is similar to the diurnal variation of delta(13)C, but opposite to that of the CO2 concentration. The diurnal delta(18)O variation is thought to be caused by the release of isotopically heavy CO2 during photosynthesis, and light CO2 during respiration. However, an interpretation of the seasonal delta(18)O variation is found to be much more difficult than those of delta(13)C and the CO2 concentration. This is likely due to complicated combinations of different seasonally varying fluxes of biospheric CO2 into the atmosphere, as well as to various weather-dependent factors governing the delta(18)O composition in CO2.

KEYWORDS: ABUNDANCE, ATMOSPHERIC WATER-VAPOR, DIOXIDE, ENRICHMENT, EXCHANGE, LEAF WATER, PACIFIC-OCEAN, REGION, SECULAR VARIATIONS, VEGETATION

1649

Napolitano, R., and M.P. Juarez. 1997. Entomopathogenous fungi degrade epicuticular hydrocarbons of Triatoma infestans. *Archives of*

Biochemistry and Biophysics 344(1):208-214.

Studies were undertaken to analyze the ability of entomopathogenous fungi to degrade insect hydrocarbons. Strains of Beauveria bassiana and Metarhizium anisopliae pathogenic to the blood-sucking bug Triatoma infestans were grown on hydrocarbon and non-hydrocarbon insect lipid extracts and on synthetic hydrocarbon-enriched media as the sole carbon source. Entomopathogenous fungi were shown to utilize hydrocarbons as the only carbon source for their growth. Insect-derived hydrocarbons served more efficiently as metabolic fuel rather than synthetic compounds of similar structure. [H-3]n- Pentacosane, [11,12-H-3]3,11-dimethylnonacosane, and [C-14]n- hexadecane were catabolized into different amounts of polar lipids, free fatty acids, and acylglycerols. In experiments using the branched alkane, labeled hydrocarbons of different chain length than the precursor were also synthesized. Evidence of complete catabolism was obtained by a significant release of (CO2)-C-14 from [1-C-14]n-hexadecane. (CO2)-C-14 production might be used as a simple method to compare hydrocarbon utilization by fungal strains. These data demonstrate that entomopathogenous fungi are able to transform a variety of hydrocarbon structures into different lipid products, part of which may be subsequently utilized for energy production and for the biosynthesis of cellular components. These data are the first evidence of hydrocarbon catabolism and synthesis in entomopathogenous fungi. (C) 1997 Academic Press.

KEYWORDS: ALKANES, INTEGUMENT, LIPIDS, NONHEME IRON PROTEIN, OMEGA- HYDROXYLASE, PSEUDOMONAS-OLEOVORANS

1650

Navarro, C., C. Teisson, F. Cote, and J. Ganry. 1994. Effects of light-intensity and co2 concentration on growth of banana plants (musa aaa, cultivar petite-naine) in-vitro and subsequent growth following acclimatization. *Scientia Horticulturae 60(1-2):41-54.*

The development of micropropagated banana plants during the in vitro growth phase prior to acclimatization was studied both in tight vessels under two different photosynthetic photon flux densities (PPFD of 30 and 240 mu mol m(-2) s(-1)) and in continuously flushed vessels under three atmospheric CO2 concentrations (0.034, 0.24 and 4.0%) at 240 mu mol m(-2) s(-1) PPFD. In tight vessels at low PPFD, the CO2 originating from dark respiration was partially fixed during the light period, indicating photosynthetic activity by the plants in vitro. At high PPFD, CO2 originating from dark respiration was rapidly fixed in the early hours of the light period and CO2 concentration became the limiting factor for photosynthetic activity. Plants in vitro grown under high PPFD accumulated 2.3 times the dry matter achieved by plants in low PPFD. However, this developmental advantage acquired in vitro was not maintained ex vitro at the end of the acclimatization phase (on a leaf area basis). In continuously flushed vessels, treatments with 0.24% and 4.0% CO2-enriched atmospheres enhanced dry matter accumulation in vitro by 1.6 and 2.3 times, respectively, as compared to a 0.034% CO2 treatment. Twenty days after transfer ex vitro, the development of plants (on a leaf area basis) from these CO2 treatments was no longer significantly different. The relative growth rate ex vitro was lower for plants cultured in a CO2-enriched atmosphere in vitro than for those cultured at 0.034% CO2.

KEYWORDS: AERATION, CARBON DIOXIDE, CULTURES, ENRICHMENT, INVITRO, RASPBERRY, SOIL, STRAWBERRY

1651

Navas, M.L. 1998. Individual species performance and response of multispecific communities to elevated CO2: a review. *Functional Ecology 12(5):721-727.*

KEYWORDS: ATMOSPHERIC CO2, BIOMASS CARBON, CARBON DIOXIDE, COMPETITION, GROWTH-RESPONSES, PERENNIAL RYEGRASS, PLANT-POPULATIONS, POPULATION-DYNAMICS, SIZE HIERARCHIES, WHITE CLOVER

1652

Navas, M.L., E. Garnier, M.P. Austin, and R.M. Gifford. 1999. Effect of competition on the responses of grasses and legumes to elevated atmospheric CO2 along a nitrogen gradient: differences between isolated plants, monocultures and multi- species mixtures. *New Phytologist 143(2):323-331.*

The responses to CO2 of perennial grasses (Danthonia richardsonii and Phalaris aquatica) and legumes (Lotus pedunculatus and Trifolium repens) were compared under controlled conditions for isolated plants, monoculture stands and mixed-species stands along a N gradient to test whether: plant-plant interactions between species in mixed stands changed with concentration of CO2; responses to CO2 of species in mixtures could be related to their responses as single stands; responses of mixtures to CO2 could be related to the responses of individual species to CO2 and to competition. Plants were grown for 60 d in sand, using nutrient solutions (six nitrate concentrations from 0.25 to 16 mM NO3), at ambient (c. 357 mu l l(-1)) or elevated CO2 (c. 712 mu l l(-1)). Species dominance in the mixtures depended more on the range of N than of CO2 concentration provided: T. repens and L. pedunculatus dominated at low concentrations of N; L. pedunculatus and P. aquatica performed better at high concentrations. Responses of species in mixtures to CO2 were related to their responses in monocultures but not to those of isolated plants. Species biomass proportions in mixtures under ambient CO2 determined the outcome of mixture responses to CO2 more than of individual species responses to CO2. These results emphasize the influence of plant-plant interactions on community responses to CO2, since mixture behaviour under elevated CO2 could not be scaled-up from responses by isolated plants in this experiment.

KEYWORDS: ANNUALS, BIOMASS, COMMUNITY, ENRICHMENT, FACE, GRASSLAND, GROWTH, LIGHT, SEASONS

1653

Navas, M.L., J.L. Guillerm, J. Fabreguettes, and J. Roy. 1995. The influence of elevated co2 on community structure, biomass and carbon balance of mediterranean old-field microcosms. *Global Change Biology 1(5):325-335.*

We studied the effects of a doubling of atmospheric CO2 concentration on intact monoliths of Mediterranean grassland in growth chambers where climatic field conditions were simulated. During the six month growing season, changes in community structure were monitored by quantifying species richness and cover. The CO2 exchange of microcosms was measured continuously and the resulting quantity and quality of biomass were evaluated. Species richness and cover did not respond to elevated C02. After one month of treatment, CO2 exchange measured during the day did not differ between CO2 levels but the night respiration was two-fold higher under elevated CO2. Stimulations of both day and night CO2 flux by short-term CO2 enrichment were recorded several times during the growing season. These results suggest that despite some downward adjustment of photosynthesis, net canopy photosynthesis was stimulated by elevated CO2, but this stimulation was compensated for by an increased respiration. The 20% stimulation of final phytomass under elevated CO2 was not significant: it resulted from unchanged live plant matter but a significant, 100% increase in litter accumulation. These results suggest that in low-productivity Mediterranean herbaceous systems, the greatest effect of CO2 is not on the storage of carbon in biomass but on the turnover of the carbon in the plants.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, C-3, DIOXIDE, ECOSYSTEM, ESTUARINE MARSH, GLOBAL CLIMATE-CHANGE, GROWTH, PLANTS, TUSSOCK TUNDRA

1654

Navas, M.L., L. Sonie, J. Richarte, and J. Roy. 1997. The influence of elevated CO2 on species phenology, growth and reproduction in a Mediterranean old-field community. *Global Change Biology 3(6):523-530.*

We studied the effects on the phenology, growth and reproduction of 19 Mediterranean species, of elevating the atmospheric CO2 concentration ([CO2]) to twice-ambient. Intact monoliths were taken from an old-field and put, during a six month growing season, into growth chambers in which external climatic conditions were mimicked and [CO2] was regulated. Fruit set time was significantly changed in six species under elevated [CO2] and leaf and branch senescence accelerated in most species. Grasses had fewer leaves and legumes were more branched at peak production under elevated [CO2] than under ambient. Plant seed number was not significantly changed under elevated [CO2], whereas the reproductive effort of grasses was significantly depressed. Reproductive and vegetative characteristics showed related responses to [CO2], as species with enhanced biomass had a hastened fruit set time, a higher number of fruits per plant and a higher reproductive biomass under elevated [CO2] than under ambient conditions, while species with depressed biomass had a delayed fruit set time, a lower number of fruits per plant and a lower reproductive biomass. Our results also show a high interspecific variability in [CO2] response, but some trends emerged at the family level: the production of vegetative and reproductive modules were depressed in grasses and slightly stimulated in legumes.

KEYWORDS: ALLOCATION, ALPINE GRASSLAND, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, DENSITY, DYNAMICS, PLANT GROWTH, RESPONSES, TEMPERATURE, YIELD

1655

Nederhoff, E.M. 1992. Effects of CO2 on greenhouse grown eggplant (solanum-melongena L) .1. Leaf conductance. *Journal of Horticultural Science 67(6):795-803.*

Leaf conductance of eggplant (Solanum melongena L., cv. Cosmos) was measured comparatively in two glasshouse compartments, with continuously low or high CO2 (on average 415 or 685 mumol mol-1, respectively). Measurements were carried out on eight days between February and June 1991 in an early planted crop. A regression equation was fitted to the data to account for the effects of PAR, air humidity and CO2 on leaf conductance. Calculations with this equation demonstrated that leaf conductance was reduced by 10.2% per 100 mumol mol-1 increase in CO2, which is a three to four times stronger response than in other fruit vegetable crops. When, on some occasional days, CO2 was kept equal in the two compartments, leaf conductance was not different, indicating that stomatal behaviour had not adapted to long lasting CO2 conditions. The rate of crop transpiration, as estimated with the Penman-Monteith combination equation, was reduced by elevated CO2 by only a few percent on average and by about 15% in a period of some weeks in spring.

KEYWORDS: ABSCISIC- ACID, AIR HUMIDITY, CROPS, ENRICHMENT, LEAVES, RESPONSES, WATER-STRESS

1656

Nederhoff, E.M., and R. Degraaf. 1993. Effects of co2 on leaf conductance and canopy transpiration of greenhouse-grown cucumber and tomato. *Journal of Horticultural Science 68(6):925-937.*

The effects of carbon dioxide (CO2) on stomatal opening and canopy transpiration were investigated in cucumber (Cucumis sativus L., cv. Jessica) and tomato (Lycopersicon esculentum Mill., cv. Calypso). Stomatal opening (i.e. leaf conductance, g) was measured with a porometer, and canopy transpiration rate (E) with weighing lysimeters on intact plants in large greenhouses. Regression analysis was applied to account for the effects of radiation, air humidity, leaf temperature and CO2 on g. The effect of CO2 on E, which is primarily through g and secondarily through adjusted air humidity, was investigated by combining the regression equation for g with the Penman- Monteith equation for E. The relative effect of CO2, as calculated with the fitted regression equations, was a decrease of about 4% in g for cucumber and of about 3% for tomato, per 100 muol mol-1 increase in CO2, in the range of about 300 to 1200 mumol mol-1 CO2. The effect of CO2 on E was smaller than on g and the extent of the effect depended on the conditions, mainly ventilation rate. The ratio K (relative change in calculated E divided by relative change in calculated g) was estimated at less than 0.2, except at low radiation. In reality, K will be even lower, because feedback mechanisms enforce the reduction in g and counteract the reduction in E. So the reduction of the transpiration rate of greenhouse cucumber and tomato caused by moderate CO2 enrichment is small and mostly negligible, except under low light conditions.

KEYWORDS: CROPS, RADIATION, RESISTANCES

1657

Nederhoff, E.M., A.N.M. Dekoning, and A.A. Rijsdijk. 1992. Leaf deformation and fruit production of glasshouse grown tomato (lycopersicon-esculentum mill) as affected by co-2 plant-density and pruning. *Journal of Horticultural Science 67(3):411-420.*

During summer, glasshouse grown tomato plants (Lycopersicon esculentum Mill.) often demonstrate leaf deformation, reduced leaf area (short leaves) and low Specific Leaf Area (SLA), sometimes accompanied by higher dry matter content of leaves and stems and higher leaf starch content. This so-called "Short Leaves Syndrome" (SLS), which decreases the production capacity, was investigated with emphasis on the effects of CO2 concentration. As a working hypothesis it was postulated that SLS is indirectly caused by an oversupply of assimilates relative to the sink capacity. An experiment was conducted between 10 May and 31 July 1990 in 12 glasshouse compartments. The sink/source ratio was varied by maintaining two levels of CO2, multifactorially combined with two plant densities and three pruning treatments. CO2 enrichment and wider planting enhanced SLS and decreased leaf area and SLA of upper leaves. Leaf pruning and fruit pruning, however, did not give clear effects on vegetative characteristics, although the impact on the sink/source ratio was of the same order of magnitude. As a mechanism for these effects, we suggest that SLS is caused by calcium deficiency in the apex, a condition more severe when much phloem sap (with low calcium content) is available, i.e. when the sink/source ratio is lower. Stronger effects of CO2 and plant density than of pruning on the incidence of SLS, may be due to local effects of sink/source relationships or to involvement of other processes, like transpiration. In crops with little SLS-symptoms, CO2 enrichment increased the weight of fruits grown during the treatment period by 31%, whereas in crops with severe SLS, CO2 enrichment aggravated SLS and had no significant effect on fruit production. CO2 enrichment in summer is beneficial if SLS is prevented, which can be achieved by maintaining a higher plant density or, in an early crop, an extra shoot on the plants in spring and summer.

KEYWORDS: CALCIUM, CO2- ENRICHMENT, DRY-MATTER

1658

Nederhoff, E.M., A.A. Rijsdijk, and R. Degraaf. 1992. Leaf conductance and rate of crop transpiration of greenhouse grown sweet-

pepper (capsicum-annuum-L) as affected by carbon- dioxide. *Scientia Horticulturae 52(4):283-301.*

The effects of carbon dioxide concentration (CO2) in the range 300-1100 mumol mol-1 on leaf conductance (g) and rate of crop transpiration (E) of sweet pepper (Capsicum annuum L.) were investigated in spring 1990. In two greenhouse compartments (154 m2) that were simultaneously exposed to different CO2 levels, leaf conductance of the upper leaves was measured with a steady state diffusion porometer and crop transpiration rates were measured with three weighing lysimeters per greenhouse compartment. Multiple regression equations, describing the effects of photosynthetic active radiation (PAR), vapour pressure deficit (VPD)-leaf-air, CO2 and optionally leaf temperature on g, were fitted to the measured data. The fitted regression curves demonstrated that 100 mumol mol-1 increase in CO2 reduced g by about 3%, at any level of CO2, VPD and PAR, if VPD and PAR would remain constant. Measured rates of crop transpiration were highly correlated to radiation and were in reasonable accordance with the Penman-Monteith combination equation. With this equation it was estimated that a 10% decrease in g would reduce E by 1.5-3% at high levels of g (high radiation) and by 4-7% at low g (dark weather), at least if VPD would remain constant. In a greenhouse-crop system, however. owing to thermal and hydrologic feedbacks, an increase in CO2 leads to a considerable increase in VPD-leaf-air. This enforces the effect of CO2 on g and counteracts the effect of CO2 on E, because the driving force for transpiration is enhanced. Thus, in general the apparent response of g to changes in CO2 is far greater than the mentioned percentage, whereas the apparent response of E is relatively small.

KEYWORDS: CO2, LEAVES, RESISTANCES

1659

Neilson, R.P., and R.J. Drapek. 1998. Potentially complex biosphere responses to transient global warming. *Global Change Biology 4(5):505-521.*

Feedback interactions between terrestrial vegetation and climate could alter predictions of the responses of both systems to a doubling of atmospheric CO2. Most previous analyses of biosphere responses to global warming have used output from equilibrium simulations of current and future climate, as compared to more recently available transient GCM simulations. We compared the vegetation responses to these two different classes of GCM simulation (equilibrium and transient) using an equilibrium vegetation distribution model, MAPSS. Average climatologies were extracted from the transient GCM simulations for current and doubled (2 x) CO2 concentrations (taken to be 2070-2099) for use by the equilibrium vegetation model. However, the 2 x CO2 climates extracted from the transient GCM simulations were not in equilibrium, having attained only about 65% of their eventual 2 x CO2 equilibrium temperature change. Most of the differences in global vegetation response appeared to be related to a very different simulated change in the pole to tropic temperature gradient. Also, the transient scenarios produced much larger increases of precipitation in temperate latitudes, commensurate with a minimum in the latitudinal temperature change. Thus, the (equilibrium) global vegetation response, under the transient scenarios, tends more to a greening than a decline in vegetation density, as often previously simulated. It may be that much of the world could become greener during the early phases of global warming, only to reverse in later, more equilibrial stages. However, whether or not the world's vegetation experiences large drought-induced declines or perhaps large vegetation expansions in early stages could be determined by the degree to which elevated CO2 will actually benefit natural vegetation, an issue still under debate. There may occur oscillations, perhaps on long timescales, between greener and drier phases, due to different frequency responses of the coupled ocean-atmosphere-biosphere interactions. Such oscillations would likely, of themselves, impart further reverberations to the coupled Earth System.

KEYWORDS: ATMOSPHERE, BOREAL FOREST, CO2, FEEDBACKS, HOLOCENE, MODEL, REGIONAL CLIMATE, SENSITIVITY, TROPICAL DEFORESTATION, VEGETATION

1660

Nemry, B., L. Francois, J.C. Gerard, A. Bondeau, and M. Heimann. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of the seasonal atmospheric CO2 signal. *Global Change Biology 5:65-76.*

Eight terrestrial biospheric models (TBMs) calculating the monthly distributions of both net primary productivity (NPP) and soil heterotrophic respiration (R-H) in the Potsdam NPP Model Intercomparison workshop are used to simulate seasonal patterns of atmospheric CO2 concentration. For each model, we used net ecosystem productivity (NEP=NPP-R-H) as the source function in the TM2 atmospheric transport model from the Max- Planck Institute for Meteorology. Comparing the simulated concentration fields with detrended measurements from 25 monitoring stations spread over the world, we found that the decreasing seasonal amplitude from north to south is rather well reproduced by all the models, though the amplitudes are slightly too low in the north. The agreement between the simulated and observed seasonality is good in the northern hemisphere, but poor in the southern hemisphere, even when the ocean is accounted for. Based on a Fourier analysis of the calculated zonal atmospheric signals, tropical NEP plays a key role in the seasonal cycle of the atmospheric CO2 in the whole southern hemisphere. The relatively poor match between measured and predicted atmospheric CO2 in this hemisphere suggests problems with all the models. The simulation of water relations, a dominant regulator of NEP in the tropics, is a leading candidate for the source of these problems.

KEYWORDS: CARBON DIOXIDE, CYCLE, EXCHANGE, LAND BIOSPHERE, TRANSPORT, VEGETATION

1661

Newberry, R.M., and J. Wolfenden. 1996. Effects of elevated CO2 and nutrient supply on the seasonal growth and morphology of Agrostis capillaris. *New Phytologist 132(3):403-411.*

Responses to elevated CO2 have been studied using an upland grass species, Agrostis capillaris L. The plants were grown in sand culture with a range of N, P and K concentrations, in 'Solardome' growth chambers with either ambient air or a CO2 concentration of 250 mu mol CO2 mol(-1) above ambient. The interactive effects of high CO2 and nutrient supply on plant growth and morphology were monitored throughout the growing season. A. capillaris exhibited positive growth responses to enhanced CO2, even at limiting supplies of N and P. Moreover, greater shoot mass at elevated CO2 was attributed to disproportionate increases in leaf and tiller number, resulting in an increase in the average leaf number per tiller. However, total leaf area remained unaffected, indicating that leaf size was reduced. There was no evidence of any acclimation in the growth response of A. capillaris to additional CO2, even in N and P-stressed plants. On the contrary, a stimulation in leaf production was observed later in the growing season. A consistent interaction was observed between N and P concentrations, whereby the response to one element was greater at higher concentrations of the other. In addition, there were indications of competition among the three elements for uptake at the root. These findings indicate the importance of multifactorial nutrient experiments in developing an understanding of the complex relationships during CO2 enrichment.

KEYWORDS: CARBON DIOXIDE, CROP RESPONSES,

ENRICHMENT, NITROGEN, NUTRITION, PHOTOSYNTHESIS, PLANTS, SEEDLINGS

1662

Newbery, R.M., J. Wolfenden, T.A. Mansfield, and A.F. Harrison. 1995. Nitrogen, phosphorus and potassium uptake and demand in agrostis-capillaris - the influence of elevated co2 and nutrient supply. *New Phytologist 130(4):565-574.*

Responses to elevated CO2 have been studied using Agrostis capillaris L., an upland grass which is abundant on nutrient- poor soils. Plants were grown in sand culture with a wide range of nitrogen, phosphorus and potassium concentrations, and the impact of CO2 on the demand for nutrients was determined using isotopic root bioassays. Plants grown with the smallest concentrations of N and P showed typical foliar symptoms associated with deficiency of these elements. However, even when supplies of N and P were limiting to growth, additional CO2 (250 ppm above ambient) influenced neither total N nor total P in above-ground tissues, nor nutrient demands as indicated by the bioassay. The estimates of the demand of the plants for K from the Rb-86 bioassay indicated an appreciable increase when plants were raised in elevated CO2. For plants of the same size with the same nutrient supply, those grown in elevated CO2 consistently displayed an increased internal demand for K. Uptake of K was not, however, enhanced by elevated CO2 even in non-limiting conditions and it might therefore be limited by a factor other than K supply. The overall conclusion from the experiments is that when A. capillaris is grown in elevated CO2, uptake of N, P and K fails to increase proportionally with dry mass. This was true even when nutrient supplies were adequate, and it appears that nutrient-use-efficiency might increase to enable the plants to maintain growth in elevated CO2.

KEYWORDS: ALLOCATION, AVAILABILITY, CARBON DIOXIDE, DRY-MATTER, ENRICHMENT, GROWTH, LIMITATION, NUTRITION, PHOTOSYNTHESIS, PLANTS

1663

Newman, J.A., D.J. Gibson, E. Hickam, M. Lorenz, E. Adams, L. Bybee, and R. Thompson. 1999. Elevated carbon dioxide results in smaller populations of the bird cherry-oat aphid Rhopalosiphum padi. *Ecological Entomology 24(4):486-489.*

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO2, CO2- ENRICHMENT, HOMOPTERA, INFECTION, INSECT HERBIVORE, PLANTS, RESPONSES, SAGEBRUSH

1664

Newton, P.C.D. 1991. Direct effects of increasing carbon-dioxide on pasture plants and communities. *New Zealand Journal of Agricultural Research 34(1):1-24.*

The atmospheric carbon dioxide (CO2) level is rising and is expected to double during the next century. This paper reviews information on the responses of pasture species and communities to elevated CO2. Data for some further non-arable species are included where relevant. The effect of CO2 on yield and on morphological and physiological characteristics are considered together with aspects of particular relevance to pasture, for example, herbivory, plant community relationships, and experimental methods for the exposure of pasture to elevated CO2. At the plant level, physiological responses to CO2 include enhanced net photosynthesis and reduced stomatal conductance; morphological changes include greater leaf areas, shoot production, and root: shoot ratios. Little is known about community responses or about plant-herbivore dynamics at elevated CO2. Changes in herbage quality, tissue turnover, and botanical composition may be expected but confirmation of these responses will only be possible when data are available from long-term studies of grazed pasture at elevated CO2.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CLOVER TRIFOLIUM-REPENS, ELEVATED CO2, GAS-EXCHANGE, LOLIUM-PERENNE, OLD- FIELD PERENNIALS, ORDERED DEVELOPMENT, PHOTOSYNTHETIC RESPONSE, WATER-USE, WHITE CLOVER

1665

Newton, P.C.D., C.C. Bell, and H. Clark. 1996. Carbon dioxide emissions from mineral springs in Northland and the potential of these sites for studying the effects of elevated carbon dioxide on pastures. *New Zealand Journal of Agricultural Research 39(1):33-40.*

Sites in Northland with mineral springs were examined for their potential as experimental areas to study the effects of elevated carbon dioxide (CO2) on grassland. A suitable site was defined as having: (1) grassland species; (2) cold springs; (3) high levels of gas flow; and (4) high concentrations of CO2. Two sites were selected for detailed study- Hakanoa Springs near Kamo and Waiare Spring near Kaeo. At Hakanoa, the vegetation was scrubby but at least 10 grassland species were present. Two vents released large volumes of CO2 resulting in concentrations at 10 cm above ground level that ranged from 5000 mu l/litre near the vent to 400 mu l/litre 10 m downwind. At Waiare, the spring was situated in a grazed grass paddock that contained 10 grass species as well as Trifolium repens and Lotus spp. There was little enrichment of CO2 above the canopy but high concentrations were measured at mid-canopy height with a maximum value exceeding 2000 mu l/litre. Because of the nature of the enrichment within, but not above the canopy, it appeared that the enrichment was from the soil. This was confirmed by measurements of soil CO2 efflux that were consistently very high (greater than 9.9 g CO2/m(2) per h in some instances). The springs have existed for decades and the sites offer the potential to study plant material that has been exposed to elevated CO2 for very long periods.

KEYWORDS: CO2 CONCENTRATIONS, COMMUNITIES, ENVIRONMENT, ESTUARINE MARSH, GROWTH

1666

Newton, P.C.D., H. Clark, C.C. Bell, and E.M. Glasgow. 1996. Interaction of soil moisture and elevated CO2 on the above- ground growth rate, root length density and gas exchange of turves from temperate pasture. *Journal of Experimental Botany 47(299):771-779.*

Interactions between water availability and elevated atmospheric CO2 concentrations have the potential to be important factors in determining future forage supply from temperate pastures, Using large turves from an established pasture, the response of these communities at 350 or 700 mu l l(-1) CO2 to a soil moisture deficit and to recovery from the deficit in comparison to turves that were well-watered throughout was measured, Prior to this experiment the turves had been exposed to the CO2 treatments for 324 d. Net CO2 exchange continued at elevated CO2 even when the volumetric soil moisture content was less than 0.10 m(3) m(-3) soil; at the same moisture deficit gas exchange at ambient CO2 was zero. The additional carbon fixed by the elevated CO2 turves was primarily allocated below-ground as shown by the maintenance of root length density at the same level as in well-watered turves, When the dry turves were rewatered there was compensatory growth at ambient CO2 so that the above-ground growth rate exceeded that of turves that had not experienced a moisture deficit, At the start of this experiment, the turves that were growing at 700 mu l l(-1) CO2 had a greater proportion of legume (principally white clover, Trifolium repens L.) in the harvested herbage, There was a trend for the legume content at elevated CO2 to be reduced under a soil moisture deficit. The results indicate different strategies in response to soil moisture deficits depending on the CO2

concentration, At ambient CO2, growth stopped, but plants were able to respond strongly on rewatering; while at elevated CO2 growth continued (particularly belowground), but no additional growth was evident on rewatering. Ecosystem gas exchange measurements taken at the end of the experiment (after 429 d of exposure to CO2) showed 33% more CO2 was fixed at elevated CO2 with only a small (12%) and nonsignificant downward regulation.

KEYWORDS: ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, COMPETITION, ENRICHMENT, LOLIUM-PERENNE, PLANT GROWTH, RESPONSES, SEEDLINGS, WATER-USE

1667

Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow, and B.D. Campbell. 1994. Effects of elevated co2 and simulated seasonal-changes in temperature on the species composition and growth-rates of pasture turves. *Annals of Botany 73(1):53-59.*

KEYWORDS: ANNUALS, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, ECOSYSTEM, ENRICHMENT, NITROGEN, PERENNIAL RYEGRASS, PLANT GROWTH, RESPIRATION, WHITE CLOVER

1668

Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow, K.R. Tate, D.J. Ross, G.W. Yeates, and S. Saggar. 1995. Plant growth and soil processes in temperate grassland communities at elevated CO2. *Journal of Biogeography 22(2-3):235-240.*

Turves of a Mollic Psammaquent soil were used in controlled environment rooms to examine the response of managed temperate pasture communities to 350, 525 or 700 p.p.m. CO2. Yield of herbage (regrowth over 3-week intervals) increased only slightly with higher CO2; however, the botanical composition was markedly different. At elevated CO2 Paspalum dilatatum (C4) and Lolium perenne (C3) declined as a proportion of harvested yield despite a stimulation of single leaf photosynthesis that was comparable to that found in Trifolium repens, a species that increased in abundance. Changes in species composition were largely a consequence of CO2-induced differences in axillary bud activity. Net primary productivity below-ground was stimulated by CO2. Soil CO2-C production was greater in elevated CO2 treatments, and was consistent with a greater input of herbage and root mass and/or metabolites and of more readily decomposable material. Levels of microbial biomass were unchanged, but enchytraeids were more abundant at elevated CO2. Tracking of (CO2)-C-14 into the various C pools also indicated a more rapid turnover of C at elevated CO2 but no change in pool sizes. No consistent effects on net mineralization of N were observed.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, FEEDBACK, NITROGEN

1669

Nguyen, Q.T., T. Kozai, G. Niu, and U.V. Nguyen. 1998. Photosynthetic characteristics of coffee (Coffea arabusta) plantlets in vitro in response to different CO2 concentrations and light intensities. *Plant Cell Tissue and Organ Culture 55(2):133-139.*

The photosynthetic characteristics of coffee (Coffea arabusta) plantlets cultured in vitro in response to different CO2 concentrations inside the culture vessel and photosynthetic photon flux (PPF) were investigated preliminarily. The estimation of net photosynthetic rate (P-n) of coffee plantlets involved three methods: (1) estimating time courses of actual P-n in situ based on measuring CO2 concentrations inside and outside the vessel during a 45-day period, (2) estimating P-n in situ at different CO2 concentrations and PPFs using the above measuring approach for 10-day and 30-day old in vitro plantlets, and (3) estimating P-n of a single leaf at different CO2 concentrations and PPFs by using a portable photosynthesis measurement system for 45-day old in vitro coffee plantlets. The results showed that coffee plantlets in vitro had relatively high photosynthetic ability and that the P-n increased with the increase in CO2 concentration inside the vessel. The CO2 saturation point of in vitro coffee plantlets was high (4500-5000 mu mol mol(-1)); on the other hand, the PPF saturation point was not so high as compared to some other species, though it increased with increasing CO2 concentration inside the vessel.

KEYWORDS: INVITRO

1670

Nicolas, M.E., R. Munns, A.B. Samarakoon, and R.M. Gifford. 1993. Elevated co2 improves the growth of wheat under salinity. *Australian Journal of Plant Physiology 20(3):349-360.*

Wheat plants (Triticum aestivum cv. Matong and T. durum cv. Modoc) were grown at ambient and elevated CO2 (350 cm3 m-3 above ambient) in soil with or without 150 mol m-3 NaCl for 6 weeks. The increase in dry matter, leaf area and tillering under high CO2 was relatively greater under saline than non- saline conditions for both cultivars. Tillering was the primary component of growth affected by both salinity and high CO2. Salinity greatly reduced tillering and high CO2 partly reversed the effects of salinity. High CO2 increased dry matter accumulation of the salt-sensitive Modoc to a greater extent (+ 104%) than that of the more salt-tolerant Matong (+ 73 %) in the salt treatment. Transpiration rates were greatly reduced by salinity for both cultivars. Under high CO2, increased leaf areas compensated for reduced transpiration rates per unit leaf area (i.e. greater stomatal closure), and total transpiration was little affected by CO2 level within each treatment. The more salt-tolerant Matong showed greater stomatal closure and higher transpiration efficiencies than the salt-sensitive Modoc under salinity. High CO2 reduced transpiration rate (per unit dry weight) by 40 to 50%, but did not significantly change the rate of sodium accumulation (per unit dry weight), indicating that salt uptake was largely independent of water uptake, and that high CO2 did not increase growth by reducing the salt load. Our results suggest that high CO2 increased growth by stimulating the development of tiller buds that would otherwise have been inhibited.

KEYWORDS: ATMOSPHERIC CO2, BARLEY, CARBON DIOXIDE, CL CONCENTRATIONS, DRY-WEIGHT, ENRICHMENT, LEAF-AREA, NACL-TREATED PLANTS, PHOTOSYNTHESIS, WATER-STRESS

1671

Nicolussi, K., S. Bortenschlager, and C. Korner. 1995. Increase in tree-ring width in sub-alpine pinus-cembra from the central alps that may be co2-related. *Trees-Structure and Function 9(4):181-189.*

It has been suggested many times that elevated atmospheric CO2 levels should stimulate radial increment of stem growth. However, interpretation of dendrochronologies with respect to a CO2 signal is a difficult task, since a multitude of environmental and tree factors influence the growth of stems. Here we provide a data set from subalpine stone pine which covers the period from 1750 to 1988, and from which growth rings of the 80- to 90-year age class were analysed. The most common climatological effects are taken into consideration. We found a steady and significant increase of mean ring width for the considered age class from approximately 1 mm per year in the middle of the last century to about 1.4 mm per year at present. Selected periods of equal mean summer temperatures in the last century and in more recent decades still yield a mean stimulation of about 25% for which atmospheric CO2 enrichment appears to be the most plausible

explanation. The recent dramatic increase of atmospheric N-deposition could confound this interpretation, but chronologies of the last 2 decades during which wet and dry deposition of N-compounds showed the most dramatic increase exhibit no deviation from the long term trend. In contrast to the so far conflicting evidence of tree- ring responses to atmospheric changes the clear signal obtained here may be explained as follows: (1) stone pine produces little late season wood and moisture is never a limiting factor (particularly not in the early season); (2) comparatively good climatic records permitted the selection of thermally comparable periods; (3) trees grew under little spatial competition, (4) cores were collected well below the upper altitudinal range-limit of stone pine, leaving enough physiological leeway under episodic climatic stress, but (5) trees grew at altitudes high enough so that the reduction of the partial pressure of CO2 could be expected to cause CO2 to become relatively more limiting than at low elevations.

1672

Nie, D., H. He, M.B. Kirkham, and E.T. Kanemasu. 1992. Photosynthesis of a C3 grass and a C4 grass under elevated co2. *Photosynthetica 26(2):189-198.*

The net photosynthetic rate (P(N)), intercellular CO2 concentration (C(i)), transpiration rate (E), stomatal resistance (r(s)), and water potential (PSI(W)) of a C3 grass (Kentucky bluegrass, Poa pratensis L.) and a C4 grass (big bluestem, Andropogon gerardii Vitman) growing in the spring in a tallgrass prairie under two levels of CO2 (ambient and twice ambient) were compared. Elevated CO2 (HC) increased P(N) of Kentucky bluegrass (C3) by 47.0 % but did not affect P(N) of big bluestem (C4). HC increased C(i) of both grasses by about the same amount (is-approximately-equal-to cm3 m-3), but reduced E (and parallelly increased r(s)) of big bluestem more than those of Kentucky bluegrass. HC increased PSI(W) of both grasses by about 30 %. Kentucky bluegrass had a lower PSI(W) than big bluestem, but HC increased PSI(W) of Kentucky bluegrass to values more similar to those of big bluestem under ambient CO2 (LC). Hence a high PSI(W), resulting from HC, was necessary for a high P(N).

KEYWORDS: ANNUALS, ATMOSPHERIC CO2, C-3, CARBON DIOXIDE, CLIMATE CHANGE, COMPETITION, ECOSYSTEMS, GROWTH, PLANTS

1673

Nie, D., H. He, G. Mo, M.B. Kirkham, and E.T. Kanemasu. 1992. Canopy photosynthesis and evapotranspiration of rangeland plants under doubled carbon-dioxide in closed-top chambers. *Agricultural and Forest Meteorology 61(3-4):205-217.*

It is important to know how the increasing atmospheric concentration of carbon dioxide (CO2) will affect growth of agricultural plants. The objective of this study was to determine the effect of elevated CO2 on canopy photosynthetic rate of prairie (rangeland) plants growing under natural field conditions. The dominant plants were warm-season grasses with the C4 type of photosynthesis. Sixteen closed-top, cylindrical, plastic chambers (1.5 m in diameter; 1.8 m tall) were placed on the prairie to maintain two levels of CO2 (ambient and twice ambient) over a full growing season in 1990. The soil (silty clay loam) was kept at a high water (field capacity) or a low water level (no water added). Carbon dioxide concentration, air temperature, net radiation, canopy photosynthetic rate, and canopy evapotranspiration rate were measured in the 16 chambers on 49 sunny days during the season. The target value for high- CO2 chambers was 720 cm3 CO2 m-3; the measured mean concentrations varied from 710.8 to 720.1 cm3 CO2 m-3. For chambers with ambient CO2, the chamber-to-chamber variation was minor, with mean values ranging from 350.8 to 356.0 cm3 CO2 m- 3. Daytime air temperatures at 100 cm aboveground in the chambered plots averaged 2.7-degrees-C warmer than outside. Early in the season, net radiation was usually similar among chambers with the different CO2 and water treatments, but late in the season, differences occurred among chambers, possibly because of the amount of tall grasses that shaded the radiometers. Under the high-water treatment, canopy photosynthesis of plants grown with doubled and ambient CO2 averaged 41.8 mumol m-2 s-1 and 44.5 mumol m-2 s-1, respectively. These results are consistent with previous findings, which showed that the photosynthetic rate of C4 plants on rangeland was not augmented when the CO2 concentration was increased. Under the low-water treatment, photosynthesis of plants grown with doubled CO2 was slightly more (36.9 mumol m-2 s-1) than that of plants grown with ambient CO2 (31.7 mumol m-2 s-1). This observation is in agreement with other results, which have shown that high CO2 alleviates water-stress effects on plants. Elevated CO2 reduced canopy evapotranspiration rate by 18 and 8%, under the high- and low-water levels, respectively. The results suggested that, as the CO2 concentration in the atmosphere increases, water lost from rangelands will be reduced.

KEYWORDS: AMBIENT, WATER-USE

1674

Nie, D., M.B. Kirkham, L.K. Ballou, D.J. Lawlor, and E.T. Kanemasu. 1992. Changes in prairie vegetation under elevated carbon-dioxide levels and 2 soil-moisture regimes. *Journal of Vegetation Science 3(5):673-678.*

It is important to know how increasing levels of atmospheric CO2 will affect native vegetation. The objective of this study was to determine the effect of elevated CO2 concentrations on species composition in a tallgrass prairie kept at a high water level (730 mm of water in a 2000 mm soil profile) and a low water level (660 mm of water in 2000 mm). 16 cylindrical plastic chambers were placed on the prairie to maintain two levels of CO2 (ambient or twice ambient) during two growing seasons in 1989 and 1990. Frequency of species was determined on 25 July 1989 and on 5 and 10 October 1990. At the beginning of the study, Poa pratensis (Kentucky bluegrass), the dominant C3 species, had the highest frequency of 43.3%, but decreased with time. However, at the end of the experiment and under the high soil-water level, there were more P. pratensis plants in the elevated CO2 treatment (frequency: 13.5%) than in the ambient CO2 treatment (1.0%). Under the low soil water regime, the reverse occurred (frequencies: 3.6 % and 11.0 % for high and low CO2, respectively). The frequency of major C4 plants, Andropogon gerardii (big bluestem), A. scoparius (little bluestem) and Sorghastrum nutans (Indian grass) was not affected by CO2. However, water did affect their frequency. Under low water, the frequency of A. gerardii decreased between 1989 and 1990. Under both soil moisture levels, the frequencies of S. nutans and A. scoparius increased. At the end of the study, Indian grass grown with high water had the highest frequency of all species on the prairie (frequency at the end of the study in October, 1990, of 44.4% and 47.4% for the high and low CO2 levels, respectively). Unlike Indian grass, little bluestem grew better under low water conditions than under high water conditions. These results suggest that, if the climate becomes drier, A. scoparius will flourish more than S. nutans or A. gerardii, and P. pratensis may die out. Elevated CO2 might not increase survival of C3 Plants under dry conditions, if temperatures are too high for them.

1675

Nie, G.Y., D.L. Hendrix, S.P. Long, and A.N. Webber. 1995. The effect of elevated co2 concentration throughout the growth of a wheat crop in the field on the expression of photosynthetic genes in relation to carbohydrate accumulation. *Plant Physiology 108(2):92.*

1676

Nie, G.Y., D.L. Hendrix, A.N. Webber, B.A. Kimball, and S.P. Long. 1995. Increased accumulation of carbohydrates and decreased photosynthetic gene transcript levels in wheat grown at an elevated co2 concentration in the field. *Plant Physiology 108(3):975-983.*

Repression of photosynthetic genes by increased soluble carbohydrate concentrations may explain acclimation of photosynthesis to elevated CO2 concentration. This hypothesis was examined in a field crop of spring wheat (Triticum aestivum L.) grown at both ambient (approximately 360 mu mol mol(-1)) and elevated (550 mu mol mol(-1)) atmospheric CO2 concentrations using free-air CO2 enrichment at Maricopa, Arizona. The correspondence of steady-state levels of mRNA transcripts (coding for the 83-kD photosystem I apoprotein, sedoheptulose-1,7-bisphosphatase, phosphoribulokinase, phosphoglycerokinase, and the large and small subunits of ribulose-1,5-bisphosphate carboxylase/oxygenase) with leaf carbohydrate concentrations (glucose-6-phosphate, glucose, fructose, sucrose, fructans, and starch) was examined at different stages of crop and leaf development and through the diurnal cycle. Overall only a weak correspondence between increased soluble carbohydrate concentrations and decreased levels for nuclear gene transcripts was found. The difference in soluble carbohydrate concentration between leaves grown at elevated and current ambient CO2 concentrations diminished with crop development, whereas the difference in transcript levels increased. In the flag leaf, soluble carbohydrate concentrations declined markedly with the onset of grain filling; yet transcript levels also declined. The results suggest that, whereas the hypothesis may hold well in model laboratory systems, many other factors modified its significance in this field wheat crop.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, EXPRESSION, HIGH ATMOSPHERIC CO2, LEAVES, LONG-TERM EXPOSURE, MESSENGER-RNA, NUCLEAR, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, STARCH

1677

Nie, G.Y., S.P. Long, R.L. Garcia, B.A. Kimball, R.L. Lamorte, P.J. Pinter, G.W. Wall, and A.N. Webber. 1995. Effects of free-air co2 enrichment on the development of the photosynthetic apparatus in wheat, as indicated by changes in leaf proteins. *Plant, Cell and Environment 18(8):855-864.*

A spring wheat crop was grown at ambient and elevated (550 mu mol mol(-1)) CO2 concentrations under free-air CO2 enrichment (FACE) in the field, Four experimental blocks, each comprising 21-m-diameter FACE and control experimental areas, were used, CO2 elevation was maintained day and night from crop emergence to final grain harvest, This experiment provided a unique opportunity to examine the hypothesis that CO2 elevation in the field would lead to acclimatory changes within the photosynthetic apparatus under open field conditions and to assess whether acclimation was affected by crop developmental stage, leaf ontogeny and leaf age, Change in the photosynthetic apparatus was assessed by measuring changes in the composition of total leaf and thylakoid polypeptides separated by SDS-PAGE, For leaves at completion of emergence of the blade, growth at the elevated CO2 concentration had no apparent effect on the amount of any of the major proteins of the photosynthetic apparatus regardless of the leaf examined, Leaf 5 on the main stem was in full sunlight at emergence, but then became shaded progressively as 3-4 further leaves formed above with continued development of the crop, By 35 d following completion of blade emergence, leaf 5 was in shade, At this point, the chlorophyll alb ratio had declined by 26% both in plants grown at the control CO2 concentration and in those grown at the elevated CO2 concentration, which is indicative of shade acclimation. The ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content declined by 45% in the control leaves, but by 60% in the leaves grown at the elevated CO2 concentration, The light- harvesting complex of photosystem II (LHCII) and the chlorophyll content showed no decrease and no difference between treatments, indicating that the decrease in Rubisco was not an effect of earlier senescence in the leaves at the elevated CO2 concentration. Following completion of the emergence of the flag-leaf blade, the elevated-CO2 treatment inhibited the further accumulation of Rubisco which was apparent in control leaves over the subsequent 14 d, From this point onwards, the flag leaves from both treatments showed a loss of Rubisco, which was far more pronounced in the elevated- CO2 treatment, so that by 36 d the Rubisco content of these leaves was just 70% of that of the controls and by 52 d it was only 20%, At 36 d, there was no decline in chlorophyll, LHCII or the chloroplast ATPase coupling factor (CFI) in the elevated CO2 concentration treatment relative to the control, By 52 d, all of these proteins showed a significant decline relative to the control, This indicates that the decreased concentration of Rubisco at this final stage probably reflected earlier senescence in the elevated-CO2 treatment, but that this was preceded by a CO2-concentration-dependent decline in Rubisco.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, LEAVES, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SENESCENCE, TEMPERATURES

1678

Nie, G.Y., S.P. Long, and A. Webber. 1993. The effect of nitrogen supply on down-regulation of photosynthesis in spring wheat grown in an elevated co2 concentration. *Plant Physiology 102(1):138.*

1679

Nielsen, M.V. 1995. Photosynthetic characteristics of the coccolithophorid emiliania-huxleyi (prymnesiophyceae) exposed to elevated concentrations of dissolved inorganic carbon. *Journal of Phycology 31(5):715-719.*

Light-saturated photosynthesis (P-max) of Emiliania huxleyi (Lohmann) Hay et Mohler is known to be carbon-limited at natural concentrations of dissolved inorganic carbon (DIC). In the present study, light-limited and light-saturated photosynthetic rates of E. huxleyi were studied at three concentrations of DIC (2.4, 7.4, and 12.4 mM) for high-calcite (C-in/C-tot = 0.48) and low-calcite (C-in/C-tot = 0.08) cells of the same strain. The photosynthetic efficiency (alpha) and the maximum quantum yield (Phi(max)) increased by more than a factor of 2 from the lowest to the highest DIC level. P-max, alpha, and Phi(max) were always higher for the high-calcite than for the low-calcite cells at identical DIC levels. This may indicate that the calcification process acts as an extra supplier of CO2 for photosynthesis making the CO2 shortage at natural DIC levels a little smaller for high-calcite than for low-calcite E. huxleyi. A dependency of Phi(max) on DIC has not previously been shown for marine phytoplankton. Phi(max) is a key parameter in recent biooptical models of phytoplankton productivity, and the results from the present study are therefore important for modeling the productivity of E. huxleyi.

KEYWORDS: ALGAE, CALCIFICATION, DIATOMS, DIOXIDE, GROWTH, LIGHT, LOHMANN KAMPTNER, PHYTOPLANKTON

1680

Niewiadomska, E., C. Gaucher-Veilleux, N. Chevrier, Y. Mauffette, and P. Dizengremel. 1999. Elevated CO2 does not provide protection against ozone considering the activity of several antioxidant enzymes in the leaves of sugar maple. *Journal of Plant Physiology 155(1):70-77.*

Seedlings of sugar maple (Acer saccharum Marsch.) were exposed for 46 days to 700 ppm of CO2, 200 ppb of ozone, and 700 ppm of CO2 + 200 ppb of ozone. A significant increase in the activity of H2O2 scavenging enzymes, i.e. ascorbate peroxidase [EC 1.11.1.11] and catalase [EC 1.11.1.6], was measured due to the action of O-3 This increase was rather negatively affected by elevated CO2. A tendency of decreased activity of glutathione reductase [EC 1.6.4.2] and superoxide dismutase [EC 1.15.1.1] due to the action of O-3 was detected. Elevated CO2 does not provide enhanced tolerance to oxidative stress in the seedlings of sugar maple. Changes in the activity of antioxidant enzymes were more pronounced in the young leaves (developed during the experiment) than in the old leaves (developed before starting the experiment). Stimulation of chloroplastic FeSOD by elevated CO2 was observed, indicating oxidative stress in chloroplasts evoked by elevated CO2 level. This effect did not result in enhanced protection against the detrimental effect of ozone, most probably due to compartmentation of CO2 and O-3 effects within the cell.

KEYWORDS: ASCORBATE PEROXIDASE, CARBON DIOXIDE, ENHANCED OZONE, GLUTATHIONE-REDUCTASE, HYDROGEN-PEROXIDE, NORWAY SPRUCE, PICEA-ABIES, PLANTS, STRESS RESPONSES, TOBACCO

1681

Niinemets, U., J.D. Tenhunen, N.R. Canta, M.M. Chaves, T. Faria, J.S. Pereira, and J.F. Reynolds. 1999. Interactive effects of nitrogen and phosphorus on the acclimation potential of foliage photosynthetic properties of cork oak, Quercus suber, to elevated atmospheric CO2 concentrations. *Global Change Biology 5(4):455-470.*

Leaf gas-exchange and chemical composition were investigated in seedlings of Quercus suber L. grown for 21 months either at elevated (700 mu mol mol(-1)) or normal (350 mu mol mol-l) ambient atmospheric CO2 concentrations, [CO2], in a sandy nutrient-poor soil with either 'high' N (0.3 mol N m(-3) in the irrigation solution) or with 'low' N (0.05 mol N m(-3)) and with a constant suboptimal concentration of the other macro- and micronutrients. Although elevated [CO2] yielded the greatest total plant biomass in 'high' nitrogen treatment, it resulted in lower leaf nutrient concentrations in all cases, independent of the nutrient addition regime, and in greater nonstructural carbohydrate concentrations. By contrast, nitrogen treatment did not affect foliar N concentrations, but resulted in lower phosphorus concentrations, suggesting that under lower N, P use-efficiency in foliar biomass production was lower. Phosphorus deficiency was evident in all treatments, as photosynthesis became CO2 insensitive at intercellular CO2 concentrations larger than approximate to 300 mu mol mol-l, and net assimilation rates measured at an ambient [CO2] of 350 mu mol mol(-1) or at 700 mu mol mol(-1) were not significantly different. Moreover, there was a positive correlation of foliar P with maximum Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) carboxylase activity (V-cmax), which potentially limits photosynthesis at low [CO2], and the capacities of photosynthetic electron transport (J(max)) and phosphate utilization (P-max), which are potentially limiting at high [CO2]. None of these potential limits was correlated with foliar nitrogen concentration, indicating that photosynthetic N use-efficiency was directly dependent on foliar P availability. Though the tendencies were towards lower capacities of potential limitations of photosynthesis in high [CO2] grown specimens, the effects were statistically insignificant, because of (i) large within-treatment variability related to foliar P, and (ii) small decreases in P/N ratio with increasing [CO2], resulting in balanced changes in other foliar compounds potentially limiting carbon acquisition. The results of the current study indicate that under P-deficiency, the down-regulation of excess biochemical capacities proceeds in a similar manner in leaves grown under normal and elevated [CO2], and also that foliar P/N ratios for optimum photosynthesis are likely to increase with increasing growth CO2 concentrations.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, ELECTRON-TRANSPORT, LEAF GAS- EXCHANGE, NUTRIENT CONCENTRATIONS, PHASEOLUS-VULGARIS L, PHOSPHATE CONCENTRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1682

Nijs, I., T. Behaeghe, and I. Impens. 1995. Leaf nitrogen content as a predictor of photosynthetic capacity in ambient and global change conditions. *Journal of Biogeography 22(2-3):177-183.*

Leaf assimilation capacity in Lolium perenne, grown in elevated CO2 level (700 mu mol mol(-1)) and/or increased air temperature (ambient + 4 degrees C) could be predicted from leaf N content expressed on an area basis, although the linear relationships between maximum carboxylation rate (Vc(max)) Or maximum electron transport rate (J(max)) and leaf N depended on treatment. The model, based on Farquhar, Von Caemmerer & Berry (1980) showed negative long-term effects of increased air temperature on Vc(max) and J(max) while longterm exposure to increased CO2 level affected only Vc(max). Acclimation responses to these global changes therefore could not be explained by changes in N-content alone, but also in terms of changes in photosynthetic nitrogen use efficiency. Stimulation of photosynthesis by elevated CO2 was not affected by reduction of leaf N in leaves developed in ambient air temperature, while part of the CO2 benefit was lost in leaves developed in increased air temperature. This suggests that N-deficient ecosystems maintain the potential to respond to elevated CO2 concentration, unless other processes than the primary carbon metabolism become limiting at low N supply. Similar to nitrogen content, changes in photon flux density did not change the CO2 benefit either, unless a transition occurred from one limiting process to another (electron transport to carboxylation or vice versa). Hypotheses on interaction between CO2 level, nitrogen status of the leaf and light intensity are formulated to support these findings.

KEYWORDS: ASSIMILATION, C-3 PLANTS, CANOPY PHOTOSYNTHESIS, CO2- ENRICHMENT, ELEVATED CO2, GROWTH-RESPONSE, LEAVES, LIGHT, PLANT GROWTH, TEMPERATURE

1683

Nijs, I., R. Ferris, H. Blum, G. Hendrey, and I. Impens. 1997. Stomatal regulation in a changing climate: a field study using Free Air Temperature Increase (FATI) and Free Air CO2 enrichment (FACE). *Plant, Cell and Environment 20(8):1041-1050.*

This study investigates effects of climate warming (+2.5 degrees C above ambient) and elevated CO2 concentration (600 mu mol mol(-1)) on the stomatal functioning and the water relations of Lolium perenne, using Free Air Temperature Increase (FATI) and Free Air CO2 Enrichment (FACE), Compared to growth at ambient temperature, whole-season temperature increase reduced leaf stomatal conductance, but only at the top of the canopy (-14.6 and -8.8% at ambient and elevated CO2, respectively), However, because higher canopy temperature raised the leaf-to-air vapour pressure difference, leaf transpiration rate increased (+28% at ambient and +48% at elevated CO2) and instantaneous leaf water use efficiency, derived from short-term measurements of assimilation and transpiration rate, declined (-11% at ambient and -13% at elevated CO2). Nevertheless, at the stand level, growth at +2.5 degrees C reduced transpiration due to fewer tillers per plant and a smaller leaf area per tiller, This sparser vegetation was also more closely coupled to the atmosphere and maintained a drier internal microclimate. To assess whether the stomatal behaviour observed in this experiment could be explained by prevailing concepts of stomatal functioning, three models were applied (Cowan 1977; Ball,

Woodrow & Berry 1987; Leuning 1995), The latter model accounted for the highest proportion of variability in the data (58%) and was insensitive to CO2 and temperature regime, which suggests that the principles of stomatal regulation are not affected by changes in CO2 or climate.

KEYWORDS: CARBON DIOXIDE, COTTON, ELEVATED CO2, GROWTH, LEAF, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, TRANSPIRATION, WATER RELATIONS

1684

Nijs, I., and I. Impens. 1993. Effects of long-term elevated atmospheric carbon-dioxide on lolium-perenne and trifolium-repens, using a simple photosynthesis model. *Vegetatio 104:421-431.*

Changes in gross canopy photosynthetic rate (PGc), produced by long-term exposure to an elevated atmospheric CO2 level (626 +/- 50 mumol mol-1), were modelled for Lolium perenne L. cv. Vigor and Trifolium repens L. cv. Blanca, using a simple photosynthesis model, based on biochemical and physiological information (leaf gross CO2 uptake in saturating light, P(max), and leaf quantum efficiency, alpha) and structural vegetation parameters (leaf area index, LAI, canopy extinction coefficient, k, leaf transmission, M). Correction of PGc for leaf respiration allowed comparison with previously measured canopy net CO2 exchange rates, with the average divergence from model prediction amounting to about 6%. Sensitivity analysis showed that for a three-week old canopy, the PGc increase in high CO2 could be attributed largely to changes in P(max) and alpha, while differences in canopy architecture were no longer important for the PGc-stimulation (which they were in the early growth stages). As a consequence of this increasing LAI with canopy age, the gain of daytime CO2 uptake is progressively eroded by the increasing burden of canopy respiration in high- CO2 grown Lolium perenne. Modelling canopy photosynthesis in different regrowth stages after cutting (one week, two weeks,...), revealed that the difference in a 24-h CO2 balance between the ambient and the high CO2 treatment is reduced with regrowth time and completely disappears after 6 weeks.

KEYWORDS: CO2

1685

Nijs, I., and I. Impens. 1996. Effects of elevated CO2 concentration and climate-warming on photosynthesis during winter in Lolium perenne. *Journal of Experimental Botany 47(300):915-924.*

Long-term effects of atmospheric carbon dioxide concentration (ambient or 700 mu mol mol(-1)) and air temperature (simulation of field conditions or +4 degrees C) on leaf photosynthetic rate were examined in Lolium perenne L. cv. Vigor, exposed to natural illumination during winter. Photosynthetic capacity was compared over a range of air temperatures and photon flux densities of photosynthetically active radiation which were representative of winter climate (5-15 degrees C and 0-500 mu mol m(-2) s(-1)), with CO2 level during measurement similar to that during the experimental period, Long-term exposure to increased air temperature reduced leaf CO2 fixation capacity by 23% (averaged over all measurement conditions), resulting from a decline in light-saturated uptake rate, but not in incident- light quantum efficiency, CO2-stimulation was largely absent in plants grown in ambient temperature, but pronounced in plants grown under +4 degrees C, where it compensated for two-thirds of the 23% drop. This enhancing effect of elevated CO2 level on leaf CO2 uptake rate observed in the warmer treatment, was strongly dependent on measurement temperature, increasing from 5% at 5 degrees C, to up to 32% at 15 degrees C. Measurements of chlorophyll fluorescence and dry matter corresponded with the observed changes in assimilation capacity, which could not be attributed to a deteriorated nitrogen status of the leaves as there was a similar N content on an area basis. Several hypotheses are considered to explain the observed CO2- temperature interactions.

KEYWORDS: AIR- TEMPERATURE, ASSIMILATION, CARBON-DIOXIDE CONCENTRATION, LEAF, LEAVES, LIMITATION, NITROGEN, PLANTS, PRODUCTIVITY, QUANTUM YIELD

1686

Nijs, I., and I. Impens. 1997. An analysis of the balance between root and shoot activity in Lolium perenne cv Melvina. Effects of CO2 concentration and air temperature. *New Phytologist 135(1):81-91.*

This study investigated the mechanisms which control the partitioning between roots and shoots in plants subjected to changes in environment. Two types of analyses were used: firstly, an examination of the cost and revenue associated with investment in different plant parts, and secondly, a test of the principle of functional equilibrium between roots and shoots, i.e. whether root dry matter x root specific activity balances shoot dry matter x shoot specific activity. Measurements were made on individual plants of Lolium perenne in sunlit controlled environments, grown from germination to canopy closure under optimal nitrogen supply. At the final harvest, increased air temperature (+4 degrees C above ambient) reduced whole-plant dry matter by 12% relative to the control, whereas elevated CO2 mole fraction (700 mu mol mol(-1)) led to a 38% gain. The combined treatment yielded an intermediate result (+19%). Plants grown at +4 degrees C maintained balanced activity between roots and shoots throughout the experimental period, irrespective of CO2 concentration. This required enhanced allocation to roots in young plants to compensate for a strong negative effect of higher temperature on root specific activity, which suggests that plants conserve balanced activity by adjusting dry matter partitioning. The extra cost involved with the adjustment at +4 degrees C significantly enhanced the cost:revenue ratio of plant investment. In ambient temperature, the balance between roots and shoots departed from equilibrium, slightly at ambient but substantially at elevated CO2: the plants accumulated excess carbon relative to nitrogen, and this imbalance increased with plant age. At elevated CO2, the cost:revenue ratio increased in young plants but this was later reversed owing to loss of root specific activity, which explains the gradually declining CO2 stimulation with time. The strategies in equilibrating root and shoot functioning observed in the different treatments are discussed in the light of whole plant performance.

KEYWORDS: ALLOCATION, BIOMASS, CARBON DIOXIDE, ENRICHMENT, LEAF, MODEL, NITROGEN CONCENTRATION, OPTIMIZATION, PHOTOSYNTHESIS, RESPONSES

1687

Nijs, I., I. Impens, and P. Vanhecke. 1992. Diurnal changes in the response of canopy photosynthetic rate to elevated co2 in a coupled temperature-light environment. *Photosynthesis Research 32(2):121-130.*

The relative increase with elevated CO2 of canopy CO2 uptake rate (A), derived from continuous measurements during the day, was examined in full-cover vegetative Lolium perenne canopies after 17 days of regrowth. The stands were grown at ambient (358 +/- 50-mu-mol mol-1) and increased (626 +/- 50-mu-mol mol- 1) CO2 concentration in sunlit growth chambers. Over the entire range of temperature and light conditions (which were strongly coupled and increased simultaneously), A was on average twice as large in high compared to ambient CO2. This response (called M = A in high CO2/A in ambient CO2) could not be explained by changes in canopy conductance for CO2 diffusion (GC). In spite of interaction and strong coupling between temperature and light intensity, there was evidence that temperature rather than light determined M. Further, high CO2 treatment was found to alleviate the afternoon depression in A observed in ambient CO2. A temperature

optimum shift or/and a larger carbohydrate sink capacity through altered root/shoot ratio are proposed in explanation.

KEYWORDS: AIR- TEMPERATURE, CARBON-DIOXIDE CONCENTRATION, GROWTH, PLANTS, YIELD

1688

Nijs, I., F. Kockelbergh, H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Free air temperature increase (FATI): A new tool to study global warming effects on plants in the field. *Plant, Cell and Environment 19(4):495-502.*

A new technique, called Free Air Temperature Increase (FATI), was developed to artificially induce increased canopy temperature in field conditions without the use of enclosures. This acronym was chosen in analogy with FACE (Free Air CO2 Enrichment), a technique which produces elevated CO2 concentrations [CO2] in open field conditions. The FATI system simulates global warming in small ecosystems of limited height, using infrared heaters from which all radiation below 800 nm is removed by selective cut-off filters to avoid undesirable photomorphogenetic effects. An electronic control circuit tracks the ambient canopy temperature in an unheated reference plot with thermocouples, and modulates the radiant energy from the lamps to produce a 2 5 degrees C increment in the canopy temperature of an associated heated plot (continuously day and night). This pre-set target differential is relatively constant over time due to the fast response of the lamps and the use of a proportional action controller (the standard deviation of this increment was <1 degrees C in a 3 week field study with 1007 measurements). Furthermore, the increase in leaf temperature does not depend on the vertical position within the canopy or on the height of the stand. Possible applications and alternative designs are discussed.

KEYWORDS: CARBON DIOXIDE, CO2, ENVIRONMENT, GROWTH, LIGHT, PHOTOSYNTHESIS

1689

Nijs, I., H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Simulation of climate change with infrared heaters reduces the productivity of Lolium perenne L in summer. *Environmental and Experimental Botany 36(3):271-280.*

Field-grown perennial ryegrass was subjected to climate warming and elevated CO2 concentration during summer in free air conditions (no enclosure of the vegetation). Increased foliage temperature (2.5 degrees C above fluctuating ambient) was induced by heating the stand with infrared radiation sources, modulated by an electronic control device (FATI, Free Air Temperature Increase). Enhanced CO2 was produced by a FACE system (Free Air CO2 Enrichment). Exposure to simulated climate warming drastically reduced above-ground harvestable dry matter (52% loss). The nitrogen allocated to the leaf fraction was thus concentrated into less dry matter, which enhanced the nitrogen concentration on a mass basis (+17%) but also per unit leaf area (+47%). As a consequence, CO, assimilation rates were not affected in these slower growing plants in the +2.5 degrees C treatment, and the photochemical efficiency of non-cyclic electron transport of photosystem II was also unaffected. Although the plants were grown in the field without root restrictions, long-term exposure to elevated CO, concentration induced noticeable acclimation of the photosynthetic apparatus (40% loss of fixation potential), which largely outweighed the direct stimulation in this summer period. Part of the reduced rates could be attributed to lower N concentration on a leaf area basis. The results are compared with responses of this species in sunlit conditioned greenhouses, which indicates that experiments in enclosures may underestimate effects in the field. This also emphasizes the need to validate other plant responses to climate warming and CO2 enrichment in free air conditions.

KEYWORDS: ACCLIMATION, ELEVATED CO2, GROWTH, NITROGEN, PLANTS, TEMPERATURE, TISSUE

1690

Niklaus, P.A. 1998. Effects of elevated atmospheric CO2 on soil microbiota in calcareous grassland. *Global Change Biology 4(4):451-458.*

Microbial responses to three years of CO2 enrichment (600 mu L L-1) in the field were investigated in calcareous grassland. Microbial biomass carbon (C) and soil organic C and nitrogen (N) were not significantly influenced by elevated CO2. Microbial C:N ratios significantly decreased under elevated CO2 (-15%, P = 0.01) and microbial N increased by + 18% (P = 0.04). Soil basal respiration was significantly increased on one out of 7 sampling dates (+ 14%, P = 0.03; December of the third year of treatment), whereas the metabolic quotient for CO2 (qCO(2) = basal respiration/microbial C) did not exhibit any significant differences between CO2 treatments. Also no responses of microbial activity and biomass were found in a complementary greenhouse study where intact grassland turfs taken from the field site were factorially treated with elevated CO2 and phosphorus (P) fertilizer (1 g P m(-2) y(-1)). Previously reported C balance calculations showed that in the ecosystem investigated growing season soil C inputs were strongly enhanced under elevated CO2. It is hypothesized that the absence of microbial responses to these enhanced soil C fluxes originated from mineral nutrient limitations of microbial processes. Laboratory incubations showed that short- term microbial growth (one week) was strongly limited by N availability, whereas P was not limiting in this soil. The absence of large effects of elevated CO2 on microbial activity or biomass in such nutrient-poor natural ecosystems is in marked contrast to previously published large and short-term microbial responses to CO2 enrichment which were found in fertilized or disturbed systems. It is speculated that the absence of such responses in undisturbed natural ecosystems in which mineral nutrient cycles have equilibrated over longer periods of time is caused by mineral nutrient limitations which are ineffective in disturbed or fertilized systems and that therefore microbial responses to elevated CO2 must be studied in natural, undisturbed systems.

KEYWORDS: BIOMASS, CARBON DIOXIDE, CYCLE, ECOSYSTEM, FEEDBACK, NITROGEN, PLANT, RESPONSES, SYSTEM, TUNDRA

1691

Niklaus, P.A., and C. Korner. 1996. Responses of soil microbiota of a late successional alpine grassland to long term CO2 enrichment. *Plant and Soil 184(2):219-229.*

We investigated microbial responses in a late successional sedge-dominated alpine grassland to four seasons of CO2 enrichment. Part of the plots received fertilizer equivalent to 4.5g N m(-2) a(-1). soil basal respiration (R(mic)), the metabolic quotient for CO2 (qCO(2) = R(mic)/C-mic), microbial C and N (C-mic and N-mic) as well as total soil organic C and N showed no response to CO2 enrichment alone. However, when the CO2 treatment was combined with fertilizer addition R(mic) and qCO(2) were statistically significantly higher under elevated CO2 than under ambient conditions (+57% and +71%, respectively). Fertilizer addition increased microbial N pools by 17%, but this was not influenced by elevated CO2. Microbial C was neither affected by elevated CO2 nor fertilizer. The lack of a CO2-effect in unfertilized plots was surprising in the light of our evidence (based on C balance) that enhanced soil C inputs must have occurred under elevated CO2 regardless of fertilizer treatment. Based on these data and other published work we suggest that microbial responses to elevated CO2 in such stable, late-successional ecosystems are limited by the availability

of mineral nutrients and that results obtained with fertile or heavily disturbed substrates are unsuitable to predict future microbial responses to elevated CO2 in natural systems. However, when nutrient limitation is removed (e.g. by wet nitrogen deposition) microbes make use of the additional carbon introduced into the soil system. We believe that the response of natural ecosystems to elevated CO2 must be studied in situ in natural, undisturbed systems.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON DIOXIDE, ELEVATED CO2, FEEDBACK, FLOW, NITROGEN

1692

Niklaus, P.A., P.W. Leadley, J. Stocklin, and C. Korner. 1998. Nutrient relations in calcareous grassland under elevated CO2. *Oecologia 116(1-2):67-75.*

Plant nutrient responses to 4 years of CO2 enrichment were investigated in situ in calcareous grassland. Beginning in year 2, plant aboveground C:N ratios were increased by 9% to 22% at elevated CO2 (P < 0.01), depending on year. Total amounts of N removed in biomass harvests during the first 4 years were not affected by elevated CO2 (19.9 +/- 1.3 and 21.1 +/- 1.3 g N m(- 2) at ambient and elevated CO2), indicating that the observed plant biomass increases were solely attained by dilution of nutrients. Total aboveground P and tissue N:P ratios also were not altered by CO2 enrichment (12.5 +/- 2 g N g(-1) P in both treatments). In contrast to non-legumes (>98% of community aboveground biomass), legume C/N was not reduced at elevated CO2 and legume N:P was slightly increased. We attribute the less reduced N concentration in legumes at elevated CO2 to the fact that virtually all legume N originated from symbiotic N-2 fixation (%N-dfa approximate to 90%), and thus legume growth was not limited by soil N. While total plant N was not affected by elevated CO2, microbial N pools increased by +18% under CO2 enrichment (P = 0.04) and plant available soil N decreased. Hence, there was a net increase in the overall biotic N pool, largely due increases in the microbial N pool. In order to assess the effects of legumes for ecosystem CO2 responses and to estimate the degree to which plant growth was P-limited, two greenhouse experiments were conducted, using firstly undisturbed grassland monoliths from the field site, and secondly designed 'microcosm' communities on natural soil. Half the microcosms were planted with legumes and half were planted without. Both monoliths and microcosms were exposed to elevated CO2 and P fertilization in a factored design. After two seasons, plant N pools in both unfertilized monoliths and microcosm communities were unaffected by CO2 enrichment, similar to what was found in the field. However, when P was added total plant N pools increased at elevated CO2. This community-level effect originated almost solely from legume stimulation. The results suggest a complex interaction between atmospheric CO2 concentrations, N and P supply. Overall ecosystem productivity is N-limited, whereas CO2 effects on legume growth and their N-2 fixation are limited by P.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLOVER TRIFOLIUM-REPENS, ENRICHMENT, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, NITROGEN-FIXATION, RESPONSES, TALLGRASS PRAIRIE, WHITE CLOVER, WOODY-PLANTS

1693

Niklaus, P.A., D. Spinnler, and C. Korner. 1998. Soil moisture dynamics of calcareous grassland under elevated CO2. *Oecologia 117(1-2):201-208.*

Water relations of nutrient-poor calcareous grassland under long-term CO2 enrichment were investigated. Understanding CO2 effects on soil moisture is critical because productivity in these grasslands is water limited. In general, leaf conductance was reduced at elevated CO2, but responses strongly depended on date and species. Evapotranspiration (measured as H2O gas exchange) revealed only small, non-significant reductions at elevated CO2, indicating that leaf conductance effects were strongly buffered by leaf boundary layer and canopy conductance (leaf area index was not or only marginally increased under elevated CO2). However, these minute and non-significant responses of water vapour loss accumulated over time and resulted in significantly higher soil moisture in CO2-enriched plots (gravimetric spot measurements and continuous readings using a network of time-domain reflectometry probes). Differences strongly depended on date, with the smallest effects when soil moisture was very high (after heavy precipitation) and effects were largest at intermediate soil moisture. Elevated CO2 also affected diurnal soil moisture courses and rewetting of soils after precipitation. We conclude that ecosystem-level controls of the water balance (including soil feedbacks) overshadow by far the physiological effects observed at the leaf level. Indirect effects of CO2 enrichment mediated by trends in soil moisture will have far-ranging consequences on plant species composition, soil bacterial and faunal activity as well as on soil physical structure and may indirectly also affect hydrology and trace gas emissions and atmospheric chemistry.

KEYWORDS: ATMOSPHERIC CO2, CARBON, FLUXES, GROWTH, PLANT, RESPONSES, STOMATAL CONDUCTANCE, WATER-USE EFFICIENCY

1694

Nikolaidis, N.P., H.L. Hu, and C. Ecsedy. 1994. Effects of climatic variability on the hydrologic response of a fresh-water watershed. *Aquatic Sciences 56(2):161-178.*

A generalized watershed model was used to evaluate the effects of global climate changes on the hydrologic responses of freshwater ecosystems. The Enhanced Trickle Down (ETD) model was applied to W-3 watershed located near Danville, Vermont. Eight years of field data was used to perform model calibration and verification and the results were presented in Nikolaidis et al., (1993). Results from the Goddard Institute for Space Studies (GISS) and the Geophysical Fluid Dynamics Laboratory (GFDL) general circulation models which simulated the doubling of present day atmospheric CO2 scenarios were used to perform the hydrologic simulations for the W-3 watershed. The results indicate that the W-3 watershed will experience increases in annual evapotranspiration and decreases in annual outflow and soil moisture. Stochastic models that simulate collective statistical properties of meteorological time series were developed to generate data to drive the ETD model in a Monte- Carlo fashion for quantification of the uncertainty in the model predictions due to input time series. This coupled deterministic and stochastic model was used to generate probable scenarios of future hydrology of the W-3 watershed. The predicted evapotranspiration and soil moisture under doubling present day atmospheric CO2 scenarios exceed the present day uncertainty due to input time series by a factor greater than 2. The results indicate that the hydrologic response of the W-3 watershed will be significantly different than its present day response. The Enhanced Trickle Down model can be used to evaluate land surface feedbacks and assessing water quantity management in the event of climate change.

KEYWORDS: ACIDIFICATION, CALIFORNIA, DEPOSITION, MODELS, RESOURCES, RIVER BASIN

1695

Nilsen, E.T., P.W. Rundel, and M.R. Sharifi. 1996. Diurnal gas exchange characteristics of two stem photosynthesizing legumes in relation to the climate at two contrasting sites in the California desert. *Flora 191(2):105-116.*

The diurnal and seasonal patterns of climate, shoot water potential, stem

photosynthesis (Pn), stem conductance, and stem intercellular CO2 were measured for two legume shrubs in the southern California desert at two elevations at four seasons of the year. One species (Senna armata), is restricted to the Mojave desert and was studied at 950 m elevation, while the other species (Caesalpinia virgata) is endemic to the Sonoran desert and was studied at 180 m elevation. The Sonoran desert site was characterized by higher temperatures, higher vapor pressure deficits, and more consistent solar radiation than the Mojave desert site. During the summer, the differences between the microclimates of the two sites were maximal. Both species have high predawn and midday shoot water potentials compared with other desert species, most likely because they have vertical stem orientation and low stem conductance. Stem Pn was positive all year, but Pn(max) decreased for C. virgata during the summer. Stem temperature, and its impact on vapor pressure deficit, was the most important regulator of stem photosynthesis. Although there were large changes in stem Pn between winter and summer, there was little change in intercellular CO2 among seasons inferring no change in water use efficiency. Stem Pn most likely provides most of the carbon gain for both species because leaves are small and ephemeral, and stems are present and actively gaining carbon all year.

KEYWORDS: ERIOGONUM-INFLATUM, LEAF, MORPHOLOGY, STOMATAL CONDUCTANCE

1696

Ning, B., Y. Kubo, A. Inaba, and R. Nakamura. 1997. Physiological responses of Chinese pear 'Yali' fruit to CO2- enriched and/or O-2-reduced atmospheres. *Journal of the Japanese Society for Horticultural Science 66(3-4):613-620.*

Respiration and ethylene production rates of Chinese pear 'Yali' fruit (Pyrus ussuriensis Maxim. var. sinensis Kikuchi) stored in CO2-enriched and/or O-2-reduced atmospheres. In addition, several types of polyethylene film packaging were also applied to the long-term storage of 'Yali' fruit. 1. Oxygen uptake and ethylene production in 'Yali' fruit at 20 degrees C decreased with increasing CO2 concentration up to 40%. Ethylene production under 60% CO2 was markedly inhibited, whereas O-2 uptake was promoted; a physiological disorder in the flesh developed. 2. Under the same storage condition, oxygen uptake and ethylene production consistently decreased with decreasing O-2 concentration. However, when O-2 was decreased to less than 5%, CO2 output exceeded O-2 uptake, suggesting that anaerobic respiration was occurring. 3. Respiration was inhibited in fruit kept at 10 or 20 degrees C under 5% CO2 + 3% O-2 during the first 4 days of storage and then increased suddenly thereafter accompanied by the development of a physiological disorder. 4. The storage life of the fruit packed in a film with soda lime at 10 degrees C, in which O-2 became to about 8%, was prolonged by about a month, as compared to that of those packed in a perforated bag. The gas concentration higher than 5% CO2 and/or lower than 5% O-2 within a plastic bag caused an accumulation of ethanol and the development of disorder in flesh, thus shortening storage life of fruit. Our results suggest that 'Yali' fruit is sensitive to both CO2-enriched and O-2-reduced atmospheres, and that 2% CO2 and 8% O-2 are about optimal for its long-term storage.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ETHYLENE, QUALITY

1697

Ning, L., B.E. Petersen, G.E. Edwards, L.S. Daley, and J.B. Callis. 1997. Recovery of digital information stored in living plant leaf photosynthetic apparatus as fluorescence signals. *Applied Spectroscopy 51(1):1-9.*

A CCD (charge-coupled device)-equipped, imaging spectroscopic instrument is discussed that can be reversible and rapidly reconfigured to image photosynthetic fluorescence, allowing two-dimensional spatial estimates of fluorescence quantum yield (Y'). Y' images of leaf areas with immediately functional photosynthetic apparatus appear smooth and uniform and are much less affected by variations in chlorophyll content and light path through the leaf, However, areas of the leaf where the photosynthetic apparatus has different light history, pathology, or other damage generate different Y' value images, This characteristic allowed storage and recovery of images from leaves, Extending this finding, we prepared binary data coding for the value of pi to 99 decimal places (100 digits), on living leaves, The images containing the binary codes for these digits can be "read" by eye, because the human brain interprets visual data with great skill. However, it was necessary to enhance the images to facilitate instrument "reading", A program was developed to enhance the images and "read" the data images with no errors. The photosynthetic mechanism involved (nonphotochemical quenching), the role of leaf age and germplasm variation, and the potential applications of this finding in terms of bioelectronics are discussed.

KEYWORDS: CHLOROPHYLL-A FLUORESCENCE, CO2 ASSIMILATION, COMPLEX, LEAVES, MUTANTS, PHOTOCURRENTS, PHOTOSYSTEM, PLATINIZED CHLOROPLASTS, SPECTRA, TRANSIENT

1698

Nitschelm, J.J., A. Luscher, U.A. Hartwig, and C. VanKessel. 1997. Using stable isotopes to determine soil carbon input differences under ambient and elevated atmospheric CO2 conditions. *Global Change Biology 3(5):411-416.*

Quantitative estimates of soil C input under ambient (35 Pa) and elevated (60 Pa) CO2-partial pressure (pCO(2)) were determined in a Free-Air Carbon dioxide Enrichment (FACE) experiment. To facilitate C-13-tracing, Trifolium repens L. was grown in a soil with an initial delta(13)C distinct by at least 5 parts per thousand from the delta(13)C of T. repens grown under ambient or elevated pCO(2). A shift in delta(13)C Of the soil organic C was detected after one growing season. Calculated new soil C inputs in soil under ambient and elevated pCO(2) were 2 and 3 t ha(-1), respectively. Our findings suggest that under elevated CO2 conditions, soil C sequestration may be altered by changes in plant biomass production and quality.

KEYWORDS: C-13 NATURAL ABUNDANCE, DIOXIDE ENRICHMENT, DYNAMICS, LITTER QUALITY, NITROGEN, ORGANIC-MATTER, PERENNIAL RYEGRASS, PLANTS, TALLGRASS PRAIRIE, WHITE CLOVER

1699

Niu, G., T. Kozai, M. Hayashi, and M. Tateno. 1997. Time course simulations of CO2 concentration and net photosynthetic rates of potato plantlets cultured under different lighting cycles. *Transactions of the Asae 40(6):1711-1718.*

Potato (Solanum tuberosum L. cv. Benimaru) plantlets were cultured under four lighting cycles with the same ratio of photo/dark period (16 h/8 h, 4 h/2 h, I h/0.5 h, and 0.25 h/0.125 h) photoautotrophically (without sugar-in the medium) and photomixotrophically (with sugar in the medium) in vitro for 28 days. Simulations of time courses of CO2 concentration in the vessel (C-i) for plantlets cultured photoautotrophically, and photomixotrophically and dry weight accumulations of the plantlets cultured photoautotrophically were conducted using the same model and parameter values as those in Niu and Kozai (1997). While underestimation and overestimation of the time courses of C-i in some treatments were observed the simulated values of C-i and the dry weight accumulation of the plantlets generally agreed with the measured values. The simulated responses of net photosynthetic

rate of the plantlets to C-i indicated that in the early, culture period, plantlets have higher photosynthetic ability under photoautotrophic than under photomixotrophic culture conditions. The quantitative relationship between daily net photosynthetic rate (daily net production) and vessel ventilation rate per plantlet was simulated under various CO2 levels outside the vessel for given sizes of potato plantlets cultured in vitro photoautotrophically, to aid appropriate CO2 enrichment and vessel design in commercial micropropagation systems.

KEYWORDS: ENRICHMENT, GROWTH, INVITRO

1700

Nobel, P.S. 1991. Environmental productivity indexes and productivity for Opuntia ficus-indica under current and elevated atmospheric CO2 levels. *Plant, Cell and Environment 14(7):637-646.*

The productivity of the prickly-pear cactus Opuntia ficus- indica, which is cultivated worldwide for its fruits and stem segments, was predicted based on the responses of its net CO2 uptake to soil water status, air temperature and photosynthetic photon flux density (PPFD). Each of these environmental factors was represented by an index with a maximum value of unity when that factor was not limiting net CO2 uptake over a 24-h period. The water index, the temperature index, and the PPFD index were determined for 87 sites in the contiguous United States using data from 189 weather stations and for 148 sites worldwide using data from 1464 weather stations. The product of these three indices, the environmental productivity index (EPI), was used to predict the productivity of O. ficus-indica under current climatic conditions and under those accompanying a possible increase in the atmospheric CO2 level to 650-mu-mol mol-1. Sites with temperatures always above -10-degrees-C and hence suitable for prickly-pear cultivation numbered 37 in the United States and 110 worldwide; such sites increased by 43 and 5%, respectively, for the global warming accompanying the elevated CO2. Productivity of O. ficus-indica was at least 15 tonnes dry weight hectare-1 year-1, comparable to that of many agronomic crops, for 20 sites with temperatures always above -10-degrees-C in the contiguous United States and for 12 such sites worldwide under current climatic conditions; such sites increased by 85 and 117%, respectively, under the elevated CO2 condition, mainly because of direct effects of the atmospheric CO2 level on net CO2 uptake. In summary, simulations based on EPI indicate that O. ficus-indica may presently be advantageously cultivated over a substantial fraction of the earth's surface, such regions increasing markedly with a future doubling in atmospheric CO2 levels.

KEYWORDS: AGAVE-DESERTI, PAR INTERCEPTION, PREDICTIONS, RESPONSES, TEMPERATURE, UNITED-STATES, WATER

1701

Nobel, P.S. 1996. Responses of some North American CAM plants to freezing temperatures and doubled CO2 concentrations: Implications of global climate change for extending cultivation. *Journal of Arid Environments 34(2):187-196.*

Environmental influences on the cultivation of Crassulacean acid metabolism (CAM) plants, which are especially well adapted to arid regions with limited rainfall, were evaluated with respect to two aspects of global climate change. Cellular uptake of a vital stain, which occurs in living cells only, was halved at -6+/-1 degrees C for the cultivated CAM species Agave salmiana, Opuntia ficus indica and Stenocereus queretaroensis growing at day/night air temperatures of 30 degrees C/20 degrees C compared with -12 degrees C for the wild species Opuntia humifusa. When plants were grown at reduced temperatures of 10 degrees C/0 degrees C, stain uptake was halved at about -8 degrees C for the cultivated species but at -24 degrees C for O. humifusa. The greater low-temperature sensitivity and the lesser low-temperature acclimation of the cultivated species severely limit the regions where they can presently be grown, but such regions will expand as air temperatures rise accompanying global climate change. When the atmospheric CO2 concentration was doubled from the current ambient value of 360 mu mol mol(-1) to 7201 mu mol mol(-1), net CO2 uptake over 24-h periods increased 36% for A. salmiana and S. queretaroensis; about one-third of the increase resulted from higher net CO2 uptake rates in the last 4 h of daytime and two-thirds from higher rates during the first 8 h of the night. The doubled atmospheric CO, concentration predicted to occur before the end of the twenty-first century will increase CO2 uptake and hence biomass productivity of such CAM species, further expanding the regions where they may be profitably cultivated. (C) 1996 Academic Press Limited.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CO2, CACTACEAE, ELEVATED CARBON-DIOXIDE, FRUIT CROP, GROWTH, OPUNTIA FICUS INDICA, PRODUCTIVITY, TOLERANCE, UNITED-STATES

1702

Nobel, P.S. 1996. Shading, osmoticum, and hormone effects on organ development for detached cladodes of Opuntia ficus-indica. *International Journal of Plant Science 157(6):722-728.*

To help understand what conditions lead to the development of new organs on shoots of Opuntia ficus-indica, a widely cultivated prickly pear cactus, detached cladodes were kept in a glasshouse and were shaded, exposed to full sunlight, or exposed to full sunlight and injected with various osmotica and hormones. Daughter cladodes emerged more slowly on cladodes detached in January (mean time of 12.6 wk) than in May (4.2 wk). In the field, new organ development was more rapid and more fruits were produced compared with cladodes detached in January and kept in a glasshouse. Shading by 94% essentially eliminated the development of daughter cladodes for cladodes harvested in both seasons over the 18-wk observation period. Daughter cladodes had a lower percentage dry mass and a higher water potential than the detached cladodes on which they developed, suggesting that water entered them primarily via the phloem. Compared with detached cladodes injected weekly with 1% of the cladode fresh mass of water for 6 wk, injection of 1.5 M sucrose accelerated daughter cladode development by 1.4 wk 750 mM KCl by 3.0 wk, and 750 mM KNO3 by 4.8 wk. Injection of 20 mu M gibberellic acid (GA(3) and GA(4)) virtually eliminated the development of daughter cladodes. Injection of 800 mu M indole- 3-acetic acid accelerated cladode development by 3.1 wk and 800 mu M kinetin by 4.0 wk, both resulting in a greater biomass for the new organs. Thus production of daughter cladodes by detached cladodes of O. ficus-indica was enhanced by a higher tissue osmotic pressure, indole-acetic acid, and kinetin and was inhibited by shading and gibberellic acid.

KEYWORDS: CACTACEAE, CACTUS, CO2, FRUIT-DEVELOPMENT, GIBBERELLIC-ACID, GROWTH, METABOLISM, PHOTOPERIOD, PLANTS, TIME

1703

Nobel, P.S., M.Y. Cui, and A.A. Israel. 1994. Light, chlorophyll, carboxylase activity and co2 fixation at various depths in the chlorenchyma of opuntia-ficus-indica (L) miller under current and elevated co2. *New Phytologist 128(2):315-322.*

Mature cladodes of Opuntia ficus-indica (L.) Miller have a thick chlorenchyma (about 4 mm) with a relatively high chlorophyll content (0.65 g m(-2)), suggesting that light may be greatly attenuated and hence CO2 fixation negligible in the inner part of this tissue. Indeed, blue light (400-470 nm) and red light (670-685 nm) were 99 % attenuated in the

outer 2 mm of the chlorenchyma when the cladodes developed under both current and elevated CO2 concentrations. Nevertheless, the nocturnal acidity increase and C-14 accumulation following a brief exposure to (CO2)-C-14 night decreased only 22 to 47 % for a layer 2-3 mm deep in the chlorenchyma of this CAM plant. Under a particular growth CO2, the activities of both ribulose- 1,5-bisphosphate carboxylase/oxygenase and phosphoenolpyruvate carboxylase were similar for each of the outer three 1-mm-thick layers of the chlorenchyma. Therefore, although the light level and total chlorophyll decreased sharply with depth and the chlorophyll a/b ratio also decreased, substantial CO2 fixation apparently occurs throughout most of the chlorenchyma. When O. ficus-indica was grown under 720 mu mol CO2 mol(-1), the chlorenchyma nas 20 % thicker but contained 11 % less chlorophyll and had a lower absorptance than under the current CO2 concentration (370 mu mol(-1)). Greater nocturnal acidity increases and C-14 accumulation following exposure to (CO2)-C- 14 at night occurred at the doubled CO2 concentration despite 29-39% reductions in the activities of the two carboxylating enzymes, the lower absorptance, and a 24 % increase in the cladode reflectance from 400 to 700 nm.

KEYWORDS: CRASSULACEAN ACID METABOLISM, ENVIRONMENT, GRADIENTS, LEAF, LEAVES, PALISADE TISSUE, PHOTOSYNTHETIC PROPERTIES, PLANTS, REFLECTANCE, TRANSMITTANCE

1704

Nobel, P.S., M.Y. Cui, P.M. Miller, and Y.Q. Luo. 1994. Influences of soil volume and an elevated co2 level on growth and co2 exchange for the crassulacean acid metabolism plant opuntia-ficus-indica. *Physiologia Plantarum 90(1):173-180.*

Effects of the current (38 Pa) and an elevated (74 Pa) CO2 partial pressure on root and shoot areas, biomass accumulation and daily net CO2 exchange were determined for Opuntia ficus- indica (L.) Miller, a highly productive Crassulacean acid metabolism species cultivated worldwide. Plants were grown in environmentally controlled rooms for 18 weeks in pots of three soil volumes (2 600, 6 500 and 26 000 cm3), the smallest of which was intended to restrict root growth. For plants in the medium-sized soil volume, basal cladodes tended to be thicker and areas of main and lateral roots tended to be greater as the CO2 level was doubled. Daughter cladodes tended to be initiated sooner at the current compared with the elevated CO2 level but total areas were similar by 10 weeks. At 10 weeks, daily net CO2 uptake for the three soil volumes averaged 24% higher for plants growing under elevated compared with current CO2 levels. but at 18 weeks only 3% enhancement in uptake occurred. Dry weight gain was enhanced 24% by elevated CO2 during the first 10 weeks but only 8% over 18 weeks. Increasing the soil volume 10-fold led to a greater stimulation of daily net CO2 uptake and biomass production than did doubling the CO2 level. At 18 weeks, root biomass doubled and shoot biomass nearly doubled as the soil volume was increased 10-fold; the effects of soil volume tended to be greater for elevated CO2. The amount of cladode nitrogen per unit dry weight decreased as the CO2 level was raised and increased as soil volume increased, the latter suggesting that the effects of soil volume could be due to nitrogen limitations.

KEYWORDS: AGAVE-VILMORINIANA, ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, RESPONSES, SOURCE-SINK RELATIONS, TEMPERATURE, TERM

1705

Nobel, P.S., and V.G. Decortazar. 1991. Growth and predicted productivity of Opuntia ficus-indica for current and elevated carbon-dioxide. *Agronomy Journal 83(1):224-230.*

Opuntia ficus-indica (L.) Mill., a prickly pear cactus cultivated worldwide for its fruits and stem segments, can have an annual dry weight productivity exceeding that of many crops. Using a recently introduced environmental productivity index (EPI), the influences of water status, temperature, and photosynthetically active radiation (PAR) on its productivity can be predicted. This investigation calculated the water index the temperature index, and the PAR index, whose product equals EPI, for 169 sites distributed approximately uniformly across the contiguous USA for present climatic conditions as well as for those associated with an elevated CO2 concentration of 650-mu-L L-1. The effect of elevated CO2 on growth of O. ficus-indica was directly measured, and low temperature limitations on productivity were considered. The dry weight gain of O. ficus-indica during 6 mo in an environmental growth chamber was 23% greater at 650 compared with 350-mu-L L-1 CO2 and increased as the duration of the wet period increased, in agreement with predictions of the water index (the fraction of maximal net CO2 uptake during a 24-h period for the prevailing plant water status). For closely spaced plants that lead to a high productivity per unit ground area, EPI averaged about 0.10, except in desert regions where the water index lowered EPI, in the far North or South and at high elevations where the temperature index lowered EPI, and in the Northeast and Northwest where the PAR index lowered EPI. The predicted annual dry weight productivity for O. ficus-indica was 12.8 Mg ha-1 yr-1 under current conditions, and 16.3 Mg ha-1 yr-1 under those associated with 650-mu-L L-1 CO2. Both productivities are relatively high compared with other agronomic plants. The percentage of sites where temperatures fall below - 15-degrees- C at least once during the 10 years simulated, which would be lethal to most prickly pear cacti, was reduced from 49 to 18% by the general warming expected to accompany an approximate doubling of the atmospheric CO2 concentration.

KEYWORDS: CACTUS, CO2, DESERT, PAR INTERCEPTION, PLANT, RESPONSES

1706

Nobel, P.S., and A.A. Israel. 1994. Cladode development, environmental responses of co2 uptake, and productivity for opuntia-ficus-indica under elevated co2. *Journal of Experimental Botany 45(272):295-303.*

Opuntia ficus-indica, an extremely productive CAM plant cultivated in many countries, was exposed to 36, 52, and 72-73 Pa CO, in field plots and open-top chambers. Initiation of new cladodes (stem segments) was monitored until the canopy closed, after which bimonthly harvests maintained the plants for one year at a cladode area per unit ground area that is optimal for biomass production. Doubling the CO2 partial pressure slightly increased the number of first-order daughter cladodes growing on the basal (planted) cladodes after 3 months and nearly doubled the number and area of second-order cladodes. When the CO2 level was doubled, cladodes were 5% thicker after a few months and 11 to 16% thicker after one year. Although the productivity enhancement by elevated CO2 tended to decrease during the year, the annual above-ground dry-mass gain was 37 to 40% higher when the CO2 level was doubled, reaching 65 tons hectare(-1) year-l in a field plot. Well-watered cladodes at day/night air temperatures of 25 degrees C/15 degrees C and a total daily photosynthetic photon flux (PPF) of 15 mol m(-2) d(-1) in controlled environment chambers had 74% more net CO2 uptake over 24 h at 73 Pa than at 37 Pa CO2. With doubled CO2, the percentage enhancement of net CO2 uptake increased as the PPF was lowered, as the temperature was raised, and during drought. Using an environmental productivity index based on such factors, net CO2 uptake and hence productivity of O. ficus-indica can be predicted for elevated CO2 levels and other variations accompanying global climate change.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH, PHOTOSYNTHETIC ACCLIMATION,

PHYSIOLOGICAL-RESPONSES, PREDICTION, PRICKLY PEAR CACTUS, RISING CO2, TEMPERATURE

1707

Nobel, P.S., A.A. Israel, and N. Wang. 1996. Growth, CO2 uptake, and responses of the carboxylating enzymes to inorganic carbon in two highly productive CAM species at current and doubled CO2 concentrations. *Plant, Cell and Environment 19(5):585-592.*

In Agave salmiana Otto ex Salm. var. salmiana grown for 41/2 months in open-top chambers, 55% more leaves unfolded and 52% more fresh mass was produced at 730 than at 370 mu mol CO2 mol(-1). A doubling of the CO2 concentration also stimulated growth in another highly productive CAM species, Opuntia ficus- indica (L.) Miller, leading to earlier initiation and 37% more daughter cladodes. Substantial net CO2 uptake occurred earlier in the afternoon and lasted longer through the night for A, salmiana at 730 than at 370 mu mol CO2 mol(-1), resulting in 59% more total daily net CO2 uptake, The Michaelis constant (HCO3-) for PEPCase was 15% lower for A, salmiana and 44% lower for O. ficus-indica when the CO2 concentration was doubled; the percentage of Rubisco in the activated state in vivo was on average 64% higher at the doubled CO2 concentration, Thus the substantial increases in net CO2 uptake and biomass production that occurred in these two CAM species when the ambient CO2 concentration was doubled resulted mainly from higher inorganic carbon levels for their carboxylating enzymes, a greater substrate affinity for PEPCase, and a greater percentage of Rubisco in the activated state.

KEYWORDS: AGAVE-VILMORINIANA, CRASSULACEAN ACID METABOLISM, DIOXIDE, ELEVATED CO2, PHOTOSYNTHESIS, PLANTS, TERM, WATER-STRESS

1708

Noble, R., K.F. Jensen, B.S. Ruff, and K. Loats. 1992. Response of acer-saccharum seedlings to elevated carbon-dioxide and ozone. *Ohio Journal of Science 92(3):60-62.*

Newly germinated seedlings of Acer saccharum were grown in atmospheres of elevated carbon dioxide (CO2) or ozone (O3) for 85 days. Net photosynthesis measured on initial leaves and recently formed leaves tended (though not always statistically significant) to increase with an increase in CO2. Biomass measured at the end of the study also increased with and increase in CO2. Ozone at 0.15 ppm did not have a significant impact on either net photosynthesis or growth; however, with O3-treatment, biomass increased at elevated CO2 levels.

KEYWORDS: CO2, GROWTH, VEGETATION

1709

Noctor, G., A.C.M. Arisi, L. Jouanin, and C.H. Foyer. 1999. Photorespiratory glycine enhances glutathione accumulation in both the chloroplastic and cytosolic compartments. *Journal of Experimental Botany 50(336):1157-1167.*

Transformed poplars overexpressing gamma-glutamylcysteine synthetase (gamma-ECS) in the chloroplast (Lggs) were used to investigate chloroplastic biosynthesis of glutathione (GSH), In Lggs leaves, GSH contents were! enhanced by up to 3.7-fold. In general, the highest GSH contents were observed in lines with highest gamma-glutamylcysteine (gamma-EC) contents. These lines had relatively low glycine, In darkness, foliar GSH decreased and gamma-EC increased. Illumination of pre-darkened Lggs in air resulted in a 5-fold decrease in the gamma-EC:GSH ratio, This light-induced decrease was largely abolished if leaves were illuminated at high CO2. Con Consequently, the gamma-EC:GSH ratio of illuminated leaves was much higher at high CO2 than in air. At high CO2 total foliar amino acids were higher, but glycine and serine were lower, than in air, These results suggest that photorespiratory glycine is used in chloroplastic GSH synthesis, Despite this, net CO2 fixation was similar in Lggs to untransformed poplars. Pre-illuminated leaf discs from Lggs, and poplars overexpressing gamma-ECS in the cytosol (ggs), were incubated in darkness with a range of metabolites. After 15 h, discs from both types of transformant incubated on water had accumulated high levels of gamma-EC and showed marked increases in the y-EC:GSH ratio. Feeding glycine, serine, glycollate or phosphoserine, attenuated the dark-induced changes in the gamma-EC:GSH ratio, whereas 3-phosphoglycerate (PGA), phosphoenolpyruvate, glycerate, and hydroxypyruvate did not. Glycine produced from glycollate was therefore required for maximal GSH accumulation in both the chloroplastic and cytosolic compartment Production of glycine from PGA failed to meet the demand of increased GSH synthetic capacity.

KEYWORDS: ARABIDOPSIS-THALIANA, DEFICIENT MUTANT, EXCESS SULFUR, FOLIAR GLUTATHIONE, GAMMA-GLUTAMYLCYSTEINE SYNTHETASE, LEAF PEROXISOMES, METABOLITE CONCENTRATIONS, SERINE, SPINACH LEAVES, SUBCELLULAR VOLUMES

1710

Nonhebel, S. 1996. Effects of temperature rise and increase in CO2 concentration on simulated wheat yields in Europe. *Climatic Change 34(1):73-90.*

A crop-growth-simulation model based on SUCROS87 was used to study effects of temperature rise and increase of atmospheric CO2 concentration on wheat yields in several regions in Europe. The model simulated potential and water-limited crop production (growth with ample supply of nutrients and in the absence of damage by pests, diseases and weeds). Historic daily weather data from 13 sites in Western Europe were used as starting point. For potential production (optimal water) a 3 degrees C temperature rise led to a yield decline due to a shortening of the growing period on all locations. Doubling of the CO2 concentration caused an increase in yield of 40% due to higher assimilation rates. It was found that effects of higher temperature and higher CO2 concentration were nearly additive and the combination of both led to a yield increase of 1-2 ton ha(-1). A very small CO2-temperature interaction was found: the effect of doubled CO2 concentration on crop yield was larger at higher temperatures. The inter-annual yield variability was hardly affected. When water was Limiting crop-production effects of temperature rise and higher CO2 levels were different than for the potential production. Rise in temperature led to a smaller yield reduction, doubled CO2 concentration to a larger yield increase and combination of both led to a large yield increase (3 ton ha(-1)) in comparison with yields simulated for the present situation. Both rise in temperature and increase in the CO2 concentration reduced water requirements of the crop. Water shortages became smaller, leading to a reduction in inter-annual variability. It is concluded that when no major changes in precipitation pattern occur a climate change will not affect wheat yields since negative effects of higher temperatures are compensated by positive effects of CO2 enrichment.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CO2, CO2-INDUCED CLIMATIC-CHANGE, GROWTH, MODELS

1711

Norby, R.J. 1994. Issues and perspectives for investigating root responses to elevated atmospheric carbon-dioxide. *Plant and Soil 165(1):9-20.*

A thorough assessment of how plants and ecosystems will respond to increasing concentrations of atmospheric CO2 requires that the

responses of root systems and associated belowground processes be understood. Static measures of root-to-shoot ratio have not been satisfactory for describing the integrated responses of plants to CO2-enriched atmospheres, but research with a process orientation has suggested that elevated CO2 can stimulate root growth or root activity and provide a positive feedback on plant growth. There are, however, critical questions concerning the relevance of root data from short-term studies with potted plants when scaling to questions about plants in the field. Data on root responses to CO2 enrichment in the field are fragmentary, but they allow us to more clearly define research questions for further investigation. Three perspectives for analyzing the significance of root responses as a component of the overall response of the terrestrial biosphere to increasing atmospheric CO2 are suggested: (1) roots as a platform for nutrient acquisition and a mediator of whole-plant response to CO2; (2) carbon storage in roots as a component of whole-plant carbon storage; and (3) effects of CO2 enrichment on root turnover and the implications for carbon storage as soil organic matter. The relative importance of these different perspectives will vary depending on the ecosystem of interest and the larger-scale issues being considered.

KEYWORDS: CLIMATE CHANGE, CO2- ENRICHMENT, FINE ROOTS, FORESTED ECOSYSTEMS, GROWTH, MINERAL NUTRITION, ORGANIC-MATTER, PARTIAL-PRESSURE, SOUR ORANGE TREES

1712

Norby, R.J. 1996. Oaks in a high-CO2 world. *Annales Des Sciences Forestieres 53(2-3):413-429.*

The concentration of carbon dioxide in the atmosphere is one environmental factor that is certain to influence the physiology and productivity of oak trees everywhere. Direct assessment of the impact of increasing CO2 is very difficult, however, because of the long-term nature of CO2 effects and the myriad potential interactions between CO2 and other environmental factors that can influence the physiological and ecological relationships of oaks. The CO2 responses of at least 11 Quercus species have been investigated, primarily in experiments with seedlings. The growth response varies considerably among these experiments, and there appears to be no basis for differentiating the response of oaks as a group from those of other woody plants. The more important challenge is to find a basis for addressing questions about the responses of oak forest ecosystems from experimental data on individual seedlings and saplings. A series of experiments with white oak (Quercus alba L) seedlings and saplings was focused toward larger-scale questions, such as whether N limitations would preclude growth responses to elevated CO2 and whether short- term physiological responses could be sustained over longer time scales. These experiments suggested three issues that are particularly important for addressing forest responses: leaf area dynamics, fine root production, and biotic interactions. By focusing seedling and sapling experiments toward these issues, we gain insight into the important processes that will influence ecosystem response and, at least in a qualitative sense, the sensitivity of those processes to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH, LEAVES, QUERCUS-ALBA, RESPONSES, STOMATAL DENSITY, TREE SEEDLINGS

1713

Norby, R.J. 1998. Nitrogen deposition: a component of global change analyses. *New Phytologist 139(1):189-200.*

The global cycles of carbon and nitrogen are being perturbed by human activities that increase the transfer from large pools of non-reactive forms of the elements to reactive forms that are essential to the functioning of the terrestrial biosphere. The cycles are closely linked at all scales, and global change analyses must consider C and N cycles together. The increasing amount of N originating from fossil fuel combustion and deposited to terrestrial ecosystems as nitrogen oxides could increase the capacity of ecosystems to sequester C, thereby removing some of the excess carbon dioxide from the atmosphere and slowing the development of greenhouse warming. Several global and ecosystem models have calculated the amount of C sequestration that can be attributed to N deposition, based on assumptions about the allocation of N among ecosystem components with different C:N ratios. They support the premise that, since industrialization began, N deposition has been responsible for an increasing terrestrial C sink, but there is great uncertainty whether ecosystems will continue to retain exogenous N. Whether terrestrial ecosystems continue to sequester additional C will depend in part on their response to increasing concentrations of atmospheric carbon dioxide, widely thought to be constrained by limited N availability. Ecosystem models generally support the conclusion that responses to increasing concentrations of carbon dioxide will be greater, and the range of possible responses will be wider, in ecosystems where increased N inputs originate as atmospheric deposition. The interactions between N deposition and increasing carbon dioxide concentrations could be altered considerably, however, by additional factors, including N saturation of ecosystems, changes in community composition, and climate change, Nitrogen deposition is also linked to global change issues through the volatile losses of nitrous oxide, which is a potent greenhouse gas, and the role of nitrogen oxides in the production of tropospheric ozone, which could interact with plant responses to elevated carbon dioxide. Any consideration of the role of N deposition in global change issues must also balance the projected responses against the serious detrimental impact of excess N on the environment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2 CONCENTRATION, ELEVATED CO2, FOREST ECOSYSTEMS, LEAF-AREA, LOBLOLLY-PINE, PHOTOSYNTHESIS, PRODUCTIVITY, RESPONSES, TERRESTRIAL ECOSYSTEMS

1714

Norby, R.J., and M.F. Cotrufo. 1998. Global change - A question of litter quality. *Nature 396(6706):17-18.*

KEYWORDS: DECOMPOSITION, ELEVATED CO2

1715

Norby, R.J., N.T. Edwards, J.S. Riggs, C.H. Abner, S.D. Wullschleger, and C.A. Gunderson. 1997. Temperature-controlled open-top chambers for global change research. *Global Change Biology 3(3):259-267.*

To enable experiments on the interactive effects of elevated atmospheric CO2 and increased air temperature on physiological processes in trees to be carried out, we altered the standard design of open-top chambers by replacing blowers with evaporative coolers and in-line heaters, with a feedback control system to maintain ambient or elevated air temperatures within the chambers. Ambient and elevated (+ 4 degrees C) temperature regimes were attained consistently and reliably throughout the growing season, with high reproducibility between chambers. From May through December the average of nearly 300,000 temperature measurements was 18.5 degrees C in ambient air, 18.9 +/- 0.6 degrees C in six ambient chambers, and 22.4 +/- 0.9 degrees C in six elevated temperature chambers. The difference in soil temperature between ambient and elevated chambers was 1.2 degrees C. Absolute humidity (vapour pressure) in the chambers was higher than that of ambient air, but it was generally similar between temperature treatments. Vapour pressure deficit therefore was higher in elevated temperature

chambers than in ambient chambers, and this difference is considered an inseparable part of the temperature treatment. The addition of a temperature control system to open-top chambers removes what has been an important flaw in this important tool for global change research.

KEYWORDS: AIR-POLLUTION, BIOMASS PRODUCTION, ELEVATED CO2, FIELD, PLANT-RESPONSES, SEEDLINGS

1716

Norby, R.J., C.A. Gunderson, S.D. Wullschleger, E.G. Oneill, and M.K. McCracken. 1992. Productivity and compensatory responses of yellow-poplar trees in elevated co2. *Nature 357(6376):322-324.*

INCREASED forest growth in response to globally rising CO2 concentrations could provide an additional sink for the excess carbon added to the atmosphere from fossil fuels 1,2. The response of trees to increased CO2, however, can be expected to be modified by the interactions of other environmental resources and stresses, higher-order ecological interactions and internal feedbacks inherent in the growth of large, perennial organisms 3,4. To test whether short-term stimulation of tree growth by elevated CO2 can be sustained without inputs from other environmental resources, we grew yellow-poplar (Liriodendron tulipifera L.) saplings for most of three growing seasons with continuous exposure to ambient or elevated concentrations of atmospheric CO2. Despite a sustained increase in leaf-level photosynthesis and lower rates of foliar respiration in CO2-enriched trees, whole-plant carbon storage did not increase. The absence of a significant growth response is explained by changes in carbon allocation patterns, specifically a relative decrease in leaf production and an increase in fine root production. Although these compensatory responses reduced the potential increase in carbon storage in increased CO2 concentrations, they also favour the efficient use of resources over the longer term.

1717

Norby, R.J., and E.G. Oneill. 1991. Leaf-area compensation and nutrient interactions in CO2- enriched seedlings of yellow-poplar (Liriodendron tulipifera L). *New Phytologist 117(4):515-528.*

The responses of yellow-poplar (Liriodendron tulipifera L.) seedlings to elevated levels of atmospheric CO2 were investigated to identify attributes governing growth and physiological responses to CO2. Based on the pattern of leaf initiation and nutrient requirements of the species, it was predicted that (1) CO2 enrichment would enhance growth of yellow-poplar seedlings both through accelerated leaf area production and through higher rates of carbon assimilation per unit leaf area; and (2) growth enhancement of yellow-poplar by CO2 enrichment would be reduced by nutrient limitations. The hypotheses were tested in an experiment in which yellow-poplar plants were grown from seed for 24 weeks in controlled- environment chambers. The experimental design comprised three atmospheric CO2 concentrations (371, 493, and 787 cm3 m-3), two levels of mineral nutrients (unfertilized or weekly additions of complete nutrient solution), and three harvests (6, 12, and 24 weeks). Plant growth rate, water use, foliar gas exchange, component dry weights, and nutrient contents were measured. Both hypotheses were rejected. Whole-plant dry weight increased similarly with CO2 enrichment in plants provided with additional mineral nutrients and in unfertilized plants, although the fertilized plants grew 10-fold larger. The increase in dry weight resulting from elevated CO2 occurred only in root systems. Although leaves were produced continuously during the experiment, leaf area was slightly reduced in elevated CO2, and the whole-plant growth response was wholly attributable to an increase in carbon assimilation per unit leaf area. Although the compensation between photosynthesis and leaf area reduced the potential growth response to CO2, the reduction in leaf area ratio was associated with a significant increase in water-use efficiency. This unexpected result demonstrated the importance of feedbacks and interactions between resources in shaping the response of a plant to CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CONDUCTANCE, DROUGHT, ENRICHMENT, GROWTH-RESPONSES, HIGH CO2, PHOSPHORUS DEFICIENCY, PINUS-RADIATA, STRESS, WATER-USE EFFICIENCY

1718

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, D.W. Johnson, and R. Ceulemans. 1999. Tree responses to rising CO2 in field experiments: implications for the future forest. *Plant, Cell and Environment 22(6):683-714.*

The need to assess the role of forests in the global cycling of carbon and how that role will change as the atmospheric concentration of CO2 increases has spawned many experiments over a range of scales. Experiments using open-top chambers have been established at many sites to test whether the short- term responses of tree seedlings described in controlled environments would be sustained over several growing seasons under field conditions. Here we review the results of those experiments, using the framework of the interacting cycles of carbon, water and nutrients, because that is the framework of the ecosystem models that are being used to address the decades-long response of forests. Our analysis suggests that most of what was learned in seedling studies was qualitatively correct, The evidence from field-grown trees suggests a continued and consistent stimulation of photosynthesis of about 60% for a 300 p.p.m, increase in [CO2], and there is little evidence of the long-term loss of sensitivity to CO2 that was suggested by earlier experiments with tree seedlings in pots. Despite the importance of respiration to a tree's carbon budget, no strong scientific consensus has yet emerged concerning the potential direct or acclimation response of woody plant respiration to CO2 enrichment. The relative effect of CO2 on above-ground dry mass was highly variable and greater than that indicated by most syntheses of seedling studies. Effects of CO2 concentration on static measures of response are confounded with the acceleration of ontogeny observed in elevated CO2. The trees in these open-top chamber experiments were in an exponential growth phase, and the large growth responses to elevated CO2 resulted from the compound interest associated with an increasing leaf area. This effect cannot be expected to persist in a closed-canopy forest where growth potential is constrained by a steady-state leaf area index, A more robust and informative measure of tree growth in these experiments is the annual increment in wood mass per unit leaf area, which increased 27% in elevated CO2. There is no support for the conclusion from many studies of seedlings that root-to- shoot ratio is increased by elevated CO2; the production of fine roots may be enhanced, but it is not clear that this response would persist in a forest. Foliar nitrogen concentrations were lower in CO2-enriched trees, but to a lesser extent than was indicated in seedling studies and only when expressed on a leaf mass basis, The prediction that leaf litter C/N ratio would increase was not supported in field experiments. Also contrasting with seedling studies, there is little evidence from the field studies that stomatal conductance is consistently affected by CO2; however, this is a topic that demands more study. Experiments with trees in open- top chambers under field conditions have provided data on longer-term, larger-scale responses of trees to elevated CO2 under field conditions, confirmed some of the conclusions from previous seedling studies, and challenged other conclusions. There remain important obstacles to using these experimental results to predict forest responses to rising CO2, but the studies are valuable nonetheless for guiding ecosystem model development and revealing the critical questions that must be addressed in new larger-scale CO2 experiments.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO2, GLOBAL CLIMATE MODEL, LIRIODENDRON-TULIPIFERA L, LONG-TERM ELEVATION, NET PRIMARY PRODUCTION, PONDEROSA PINE- SEEDLINGS, SOIL N-

AVAILABILITY, SOUR ORANGE TREES, SPRUCE MODEL-ECOSYSTEMS

1719

Norby, R.J., S.D. Wullschleger, C.A. Gunderson, and C.T. Nietch. 1995. Increased growth efficiency of quercus-alba trees in a co2-enriched atmosphere. *New Phytologist 131(1):91-97.*

Forests have a prominent role in the global carbon cycle, but their response to a changing atmosphere cannot be measured directly. Experimental observations of small trees in CO2- enriched atmospheres must be interpreted carefully if they are to be relevant to the potential responses of forest trees. We grew white oak (Quercus alba L.) saplings for four complete growing seasons in open-top chambers with different partial pressures of atmospheric CO2. White oak saplings produced 58% more dry mass in 50 Pa CO2 and 135% more in 65 Pa, compared with plants in ambient (35 Pa) CO2. Although this result might suggest a substantial potential for increased carbon storage in forests, the large difference in growth rate could be attributed to a stimulation of growth very early in the experiment. There was not a sustained effect of CO2 on relative growth rate after the first year, and the increased absolute growth rate could persist only so long as leaf area could increase, a condition that would not occur indefinitely in a forest. Nevertheless, annual stem wood production per unit area (growth efficiency) was 37% greater in elevated CO2. This increase in growth efficiency, a response that is consistent across diverse studies, implies a potential increase in carbon sequestration by forests, subject to critical assumptions about forest canopy development in a CO2-enriched atmosphere.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, ELEVATED CO2, FORESTS, RESPONSES, SEEDLINGS, SOIL

1720

Norris, T.S., and B.J. Bailey. 1996. Use of simulation analysis to improve the design of open-top chambers. *Agricultural and Forest Meteorology 78(3-4):259-275.*

A greenhouse climate simulation model, employing linked first- order integral and differential equations, was adapted to predict the microclimate within carbon-dioxide-enriched open- top chambers (OTCs) suitable for climate change research. The simulation model was validated using experimental measurements from a prototype OTC test rig constructed at Silsoe Research Institute; this model was then used to investigate the effect of employing a controlled combination of air recirculation and ventilation on carbon dioxide consumption for a chamber containing wheat plants. Control criteria for a controlled-ventilation OTC were investigated using the simulation and verified experimentally; results showed that a 2 degrees C temperature excess limit within the chamber could be achieved in practice for a chamber exhibiting minimal wind incursion through the open-top, provided that a mechanical ventilation rate of 6 air changes minute(-1) was provided during periods of peak solar flux. Furthermore, the simulation suggested that, by applying controlled ventilation and recirculation to OTCs, it is feasible to reduce the daily consumption of enrichment gas to achieve 560 mu mol mol(-1) concentration within a 3 m- diameter and 3 m-high chamber located at an exposed site to 15 kg in comparison to the estimated 100 kg required when continuous ventilation is employed.

KEYWORDS: CO2 CONCENTRATION, FIELD CHAMBERS, GAS-EXCHANGE, OZONE

1721

North, G.B., T.L. Moore, and P.S. Nobel. 1995. Cladode development for opuntia-ficus-indica (cactaceae) under current and doubled co2 concentrations. *American Journal of Botany 82(2):159-166.*

Morphological and anatomical changes for first-order daughter cladodes (flattened stem segments) of a prickly pear cactus, Opuntia ficus-indica, were monitored to determine the effects of a doubled atmospheric CO2 concentration on their development and mature form. For daughter cladodes developing in controlled environment chambers for 60 d, maximal elongation rates were similar under a photosynthetic photon flux density (PPFD) of 6 mol m(-2) d(-1) and a CO2 concentration of 370 mu l liter(-1), an increased PPFD (10 mol m(-2) d(-1)), and an increased PPFD and a doubled CO2 concentration. These maximal rates, however, occurred at 20, 15, and 12 d, respectively. The maximal relative growth rate under the doubled CO2 concentration was about twice that under the other conditions. For cladodes at 60 d as well as after 4 and 16 mo in open-top chambers, doubling the CO2 concentration had no effect on final length or width. At 4 mo, cladodes under doubled CO2 were 27% thicker, perhaps allowing the earlier production of second-order daughter cladodes. The chlorenchyma was then 31% thicker and composed of longer cells. At 16 mo, the difference in cladode thickness diminished, but the chlorenchyma remained thicker under doubled CO2, which may contribute to greater net CO2 uptake for O. ficus-indica under elevated CO2 concentrations. Two other persistent differences were a 20% lower stomatal frequency and a 30% thicker cuticle with more epicuticular wax for cladodes under doubled CO2, both of which may help reduce transpirational water loss.

KEYWORDS: ANATOMY, CRASSULACEAN ACID METABOLISM, ELEVATED CO2, ENRICHMENT, EPICUTICULAR WAX, GROWTH, LEAVES, MORPHOLOGY, POLYACANTHA CACTACEAE, RESPONSES

1722

Norton, L.R., L.G. Firbank, and H. Blum. 1999. Effects of free-air CO2 Enrichment (FACE) on experimental grassland communities. *Functional Ecology 13:38-44.*

1. Experimental grassland communities (turves) were exposed to elevated (60 Pa) and ambient (35 Pa) CO2 partial pressures (pCO(2)) in a Free-air Carbon Dioxide Enrichment (FACE) experiment between 30 March 1995 and 4 July 1996. The vegetation was cut once during the experiment prior to the final harvest (harvest 2). 2, No significant treatment effects on total plant biomass at the whole turf level were detected, although biomass was typically about 25% higher under fumigation in year 1 and about 15% higher in year 2, 3, Biomass for two of the six sown species was significantly higher at harvest 2 than at harvest 1. There were no significant differences between individual species biomass under the two CO2 treatments at either harvest I or 2 or in terms of overall cumulative biomass. However, in four of the five sown species in both years biomass tended to be higher in the fumigated than in the control rings (Cerastium holosteiodes, Phleum pratense, Plantago lanceolata and Poa trivialis). In contrast, Lolium perenne showed increased biomass under the control treatment relative to the fumigated treatment in both years. Owing to the high variance both within and between rings for each of the two treatments the statistical power of most, but not all, of the analyses carried out was poor. 4, The relative proportions of each species in the turves under fumigated and control treatments was broadly similar after the first summer, with differences in die second year being mainly owing to the negative response of L. perenne to CO2 fumigation.

KEYWORDS: ALPINE GRASSLAND, COMPETITION, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, PHLEUM-PRATENSE, PLANTS, RESPONSES, TREES, TRIFOLIUM-REPENS L

1723

Norton, L.R., L.G. Firbank, A.J. Gray, and A.R. Watkinson. 1999. Responses to elevated temperature and CO2 in the perennial grass Agrostis curtisii in relation to population origin. *Functional Ecology*

13:29-37.

1. Evolutionary responses to climate change will depend on the presence of heritable variation within species populations for traits that increase fitness under the changing conditions. Patterns of ecotypic differentiation in relation to latitude in some species suggest that such variation exists in relation to temperature responses. Response to elevated CO2, whether heritable or not, is not expected to be related to latitudinal or climatic differences within temperate regions. 2. To test these ideas, seeds were collected from 10 populations of the outbreeding perennial grass Agrostis curtisii across its range in Europe from south Wales to Portugal. Plants were grown under ambient and elevated temperature and CO2 conditions, in a factorial design, in solardomes; two half sibs from each population were planted in separate pots in each of the two replicate domes with each combination of treatments. One half sib was harvested at the end of the first summer, the second at the end of the second summer. 3. Survival was uniformly high and flowering uniformly low across treatments and populations. 4. Responses to temperature and CO2 treatments varied over time for almost all populations. Treatment effects were not significant on plants harvested in year 1, although there was a trend towards higher shoot biomass under the elevated temperature and CO2 treatment. Tn year 2 shoot biomass was significantly higher under the elevated temperature treatment across all populations and there was a strong trend towards decreased biomass under elevated CO2 5. There were no significant correlations of plant response to either CO2 or temperature with climate at origin. 6. These results warn of the dangers of extrapolating evolutionary plant responses to CO2 from short-term experiments.

KEYWORDS: BIOMASS, CARBON, ENRICHMENT, ENVIRONMENTS, GROWTH, INTRASPECIFIC VARIATION, PHOTOSYNTHESIS, PLANT-RESPONSES

1724

Norton, L.R., L.G. Firbank, and A.R. Watkinson. 1995. Ecotypic differentiation of response to enhanced co2 and temperature levels in arabidopsis-thaliana. *Oecologia 104(3):394-396.*

Five ecotypes of Arabidopsis thaliana, from widely dispersed origins, were grown under combinations of ambient and elevated atmospheric CO2 concentrations and ambient and elevated temperatures within solardomes. Total above-ground plant biomass was measured when the majority of plants across all ecotypes and treatments had formed seed pods. There were substantial differences in biomass between the ecotypes across all treatments. Temperature had no effect on biomass whilst CO2 had a significant effect both alone and in interaction with ecotype. The CO2 x ecotype interaction was mostly due to the enhancement of a single ecotype from the Cape Verde Islands.

KEYWORDS: ENRICHMENT

1725

Nosberger, J., and B. Campbell. 1997. Interactions between elevated CO2 and water supply in grasslands - an introduction. *Global Change Biology 3(3):175.*

1726

Novero, R., D.H. Smith, F.D. Moore, J.F. Shanahan, and R. Dandria. 1991. Field-grown tomato response to carbonated water application. *Agronomy Journal 83(5):911-916.*

Direct release of CO2 gas to achieve a cost-effective method of atmospheric CO2 enrichment has not been proven feasible under field conditions. We hypothesized that greater efficiency of application would occur by applying CO2 via carbonated water and that application would also result in beneficial modifications of the soil environment. Our objectives were to evaluate crop, soil, and atmospheric CO2 responses to application of carbonated water under pressure through a drip irrigation system. Studies were conducted under mulched and unmulched conditions in 1988 using tomato (Lycopersicon esculentum Mill.). In 1989, carbonated water was applied at approximately 2-, 4-, and 6-d intervals to determine the effect of irrigation frequency. In 1988, a positive yield response of 9% was obtained in the presence of mulch. No response was observed in open beds. Fruit yields were increased at all three irrigation frequencies in 1989, with increases in fresh-market and total fruit yields averaging 16.4 and 15.9%, respectively. Atmospheric enrichment was observed during carbonated water application, but residual enrichment between irrigations was difficult to detect. Significant increase in soil-air CO2 from carbonated water application was noted throughout the intervals between successive irrigation events. Carbonated water application also decreased soil pH for periods of up to 5 d after irrigation and increased apparent uptake of P, K, Ca, Mg, Zn, Fe, Mn, Cu, and B. Based on the limited duration of enrichment relative to the entire growing season for any of the carbonated water treatments, the yield responses observed could not be attributed solely to atmospheric enrichment. Thus, we conclude that yield increases resulted from the combined effects of limited atmospheric CO2 enrichment and soil environment modifications leading to improved nutrient uptake.

KEYWORDS: ATMOSPHERIC CO2, COTTON, DIOXIDE

1727

Nowak, E.J., and C.E. Martin. 1995. Effect of elevated co2 on nocturnal malate accumulation in the cam species tillandsia-ionantha and crassula-arborescens. *Photosynthetica 31(3):441-444.*

The effect of elevated CO2 on overnight malate accumulation in the CAM epiphyte Tillandsia ionantha and the CAM terrestrial species Crassula arborescens was compared. Both species showed an increase in nocturnal accumulation of malate with increasing CO2 concentrations. This study is the first to show an increase in nighttime malate accumulation with increasing levels of CO2 at near-ambient concentrations in a CAM plant. The results indicate that some CAM plants can respond to increasing levels of CO2 in the atmosphere, potentially leading to an increase in productivity.

KEYWORDS: ACID METABOLISM, GROWTH, KALANCHOE-DAIGREMONTIANA, OPUNTIA FICUS INDICA, PLANTS

1728

Nunes, M.A., J.D.C. Ramalho, and M.A. Dias. 1993. Effect of nitrogen supply on the photosynthetic performance of leaves from coffee plants exposed to bright light. *Journal of Experimental Botany 44(262):893-899.*

Although Coffea arabica L. grows naturally in shaded habitats, it can be cultivated under high light intensity, but not without severe photoinhibition mainly during the period of transfer from the nursery into the field. The present work examines some of the changes in the photosynthetic performance induced by exposure to high light and the possibility of using enhanced nitrogen levels to overcome photoinhibition. For that purpose, young plants of Coffea arabica L. (cv. Catuai) grown in a shaded greenhouse were treated with 0, 1 and 2 mmol of nitrogen and 4 weeks later exposed to full solar irradiation, outside. Visible damage due to exposure to full sunlight appeared within 2 d in all plants, resulting in a reduced photosynthetic leaf area and drastic shedding of leaves in the unfertilized plants. These effects were considerably less in plants with the highest N dose. After 130 d of exposure, there was 100% mortality in plants receiving no extra

nitrogen, compared with 30% in the plants treated with 2 mmol nitrogen. Photosynthesis rates, leaf conductance and transpiration presented minimum values after 4 d of light stress. Large changes in the photosynthetic capacity (measured at high CO2 concentration and high light intensity), quantum efficiency and fluorescence yield (F(v)/F(m)) indicate that net photosynthesis rate in the air had been reduced by both stomatal closure and by changes at the photochemical level. All indicators show that N-fertilized plants were less affected by photoinhibition.

KEYWORDS: ANACYSTIS-NIDULANS, BARLEY LEAVES, CHLOROPHYLL FLUORESCENCE, CO2 ASSIMILATION, PHOTOINHIBITION, RECOVERY, SOLANUM- DULCAMARA, TEMPERATURE, WATER RELATIONS, WILLOW LEAVES

1729

Nungesser, M.K., L.A. Joyce, and A.D. McGuire. 1999. Effects of spatial aggregation on predictions of forest climate change response. *Climate Research 11(2):109-124.*

We investigated the influence of spatial aggregation on modeled forest responses to climate change by applying the profess- based Terrestrial Ecosystem Model (TEM) to a fine resolution spatial grid (100 km(2)) and to a coarse resolution spatial grid (2500 km(2)). Three climate scenarios were simulated: baseline (present) climate with ambient CO2 and 2 future climates derived from the general circulation models OSU and GFDL-Q with elevated atmospheric CO2. For baseline climate, the aggregation error of the national (U.S.) study area was very small, -0.4%. Forest-level aggregation error ranged from -1.6 to 11.8%, with the largest aggregation error occurring in boreal forest types. Coarse grid resolution inputs underestimated production for boreal and forested boreal wetland forests and overestimated net primary production (NPP) for temperate conifer, temperate deciduous, and temper ate forested wetland forests. Aggregation error for coarse grid cells ranged between -25.6 and 27.3%. Aggregation errors were especially large in transition regions between temperate and boreal forest types. An analysis that homogenized inputs for the 10 km grid cells within a 50 km grid indicated that aggregation of forest types and air temperature from fine to coarse grid cells contributed most to the spatial aggregation error. The aggregation error for the OSU climate was similar to the GFDL-Q climate and both results were similar to the aggregation error of the baseline climate in magnitude, sign, and spatial pattern. While aggregation error was similar across the baseline, GFDL-Q and OSU scenarios, NPP response to the GFDL-Q and OSU climates increased 13 to 30% above the baseline NPP. Within each climate scenario, the estimated NPP response to climate change differed by less than 1% between the coarse and fine resolutions. Except for transition regions and regions with substantial variability in air temperature, our simulations indicate that the use of 0.5 degrees resolution provides an acceptable level of aggregation error at the 3 scales of analysis in this study. Improvements could be made by focusing computational intensity in heterogeneous regions and avoid computational intensity in regions that are relatively homogeneous with respect to vegetation and air temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2 EXCHANGE, EQUILIBRIUM RESPONSES, FRANKFURT BIOSPHERE MODEL, NET PRIMARY PRODUCTION, PRECIPITATION, SCALE, TERRESTRIAL ECOSYSTEMS, VARIABILITY, VEGETATION

1730

Nussbaumer, U., J. Ascher, A. Kraft, and H. Insam. 1997. Litter decomposition of a tropical understory species (Ctenanthe lubbersiana) grown under ambient and elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):377-381.*

A CO2 evolution and a disserved organic carbon (DOC)-die-away test were used to determine the inherent decomposability of plant litter of Ctenanthe lubbersiana grown under ambient (340 ppm) and elevated CO2 (610 ppm). The CO2 evolution of leaf lifter in a 10 day decomposition assay was retarded by 7% (P = 0.046). Tn the DOG-die-away test, the decomposition of a leaf litter hot water extract was retarded by 8% (P = 0.039). The decomposition of the solid litter fraction was retarded by 16% (P = 0.101). The decomposition rate of petioles was not affected by elevated CO,. Despite the differences were small, the results suggest possible effects on ecosystem C cycling.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON, COMMUNITIES, QUALITY, SOIL

1731

Obenland, D.M., L.H. Aung, and R.E. Rij. 1994. Timing and control of methanethiol emission from broccoli florets induced by atmospheric modification. *Journal of Horticultural Science 69(6):1061-1065.*

Storage of broccoli (Brassica oleracea L., Italica Group) under conditions of low O-2 concentration extends its shelf life. Excessively low O-2, however, leads to the formation of an offensive odour which is primarily due to the emission of methanethiol. In this study, we investigated the initial induction and control of methanethiol production of broccoli florets exposed to various levels of O-2 and CO2 over short-term periods of 10 h or less. Lowering the O-2 concentration surrounding the broccoli florets by continuously flowing N-2 through the sample containers acted to initiate the production of methanethiol within 1 h after the 0(2) concentration had reached 0.5 %. After initiation the rate of production showed a slow but steady increase during the 10 h of experimentation. In contrast, introduction of O-2 into the sample containers while the broccoli florets were actively producing methanethiol led to a rapid 79% drop in the amount of methanethiol detected within 15 min, followed by a complete absence of methanethiol within another 15 min. Resumption of N-2 flow acted to reinitiate methanethiol production, with the initiation requiring a lesser amount of time than that required for the initial induction of methanethiol production. Experiments with elevated CO2 concentrations of up to 26.5% determined that CO2 is an inhibitor of methanethiol production.

KEYWORDS: STORAGE

1732

Oechel, W.C., S. Cowles, N. Grulke, S.J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis. 1994. Transient nature of co2 fertilization in arctic tundra. *Nature 371(6497):500-503.*

THERE has been much debate about the effect of increased atmospheric CO2 concentrations on plant net primary production(1,3) and on net ecosystem CO2 flux(3-10). Apparently conflicting experimental findings could be the result of differences in genetic potential(11-15) and resource availability(16-20), different experimental conditions(21-24) and the fact that many studies have focused on individual components of the system(2,21,25-27) rather than the whole ecosystem. Here we present results of an in situ experiment on the response of an intact native ecosystem to elevated CO2. An undisturbed patch of tussock tundra at Toolik Lake, Alaska, was enclosed in greenhouses in which the CO2 level, moisture and temperature could be controlled(28), and was subjected to ambient (340 p.p.m.) and elevated (680 p.p.m.) levels of CO2 and temperature (+4 degrees C). Air humidity, precipitation and soil water table were maintained at ambient control levels. For a doubled CO2 level alone, complete homeostasis of the CO2 flux was re-established within three Sears, whereas the regions exposed to a combination of higher temperatures and doubled CO2 showed persistent fertilization effect on net ecosystem carbon sequestration over this time.

This difference may be due to enhanced sink activity from the direct effects of higher temperatures on growth(16,29-33) and to indirect effects from enhanced nutrient supply caused by increased mineralization(10,11,19,27,34). These results indicate that the responses of native ecosystems to elevated CO2 may not always be positive, and are unlikely to be straightforward. Clearly, CO2 fertilization effects must always be considered in the context of genetic limitation, resource availability and other such factors.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS PRODUCTION, CLIMATE CHANGE, ELEVATED CO2, MINERAL NUTRITION, PHOTOSYNTHETIC ACCLIMATION, SOIL TEMPERATURE, TRANSGENIC TOBACCO PLANTS, TUSSOCK TUNDRA, UNMANAGED ECOSYSTEMS

1733

Oechel, W.C., G. Riechers, W.T. Lawrence, T.J. Prudhomme, N. Grulke, and S.J. Hastings. 1992. Co2lt an automated, null-balance system for studying the effects of elevated co2 and global climate change on unmanaged ecosystems. *Functional Ecology 6(1):86-100.*

An automated, CO2-controlled, long-term greenhouse system ('CO2LT') has been developed to provide replicated in situ ecosystem-level manipulation of atmospheric CO2 concentration and temperature for intact plots of tussock tundra, and to measure the instantaneous ecosystem-level CO2 exchange rates within each of the plots under the treatments imposed. This is a computer-controlled, closed, null-balance greenhouse system consisting of 12 chambers with individual control of CO2 concentration and temperature. Carbon dioxide can be maintained in each chamber at concentrations from well below ambient (150-200-mu-l l-1) to more than 900-mu-l l-1. Air temperature can be fixed, set to track ambient, or can track ambient temperature with a specified offset allowing studies of the interaction of CO2 and temperature. Despite the complications involved in tracking a naturally fluctuating environment, the CO2LT system performs very well. Temperatures in individual chambers average within 1-degrees-C of ambient or target temperatures over a 24-h period and carbon dioxide concentration control rivals that of laboratory-based, control- environment systems. Photon flux density within the chambers is within 93% of ambient values. Comparison to unenclosed tundra indicates minimal chamber effects on depth of thaw, air, leaf, or soil temperatures, or net ecosystem CO2 flux. Chamber effects are generally small, and the experimental design allows separation and interpretation of treatment effects despite any unavoidable chamber effects. Both diurnal and seasonal patterns of net ecosystem CO2 flux can be accurately tracked with this system. Field measurements indicate net ecosystem CO2 loss under current environmental conditions, a possible response to recent climate change. Field measurements also indicate initial enhancement of net ecosystem CO2 uptake with elevated atmospheric CO2. Photosynthetic adjustment to elevated CO2 lowers ecosystem response to that of ambient chambers by mid-season. Also indicated is the possibility of delayed senescence of photosynthetic capacity at elevated CO2.

1734

Oechel, W.C., and G.L. Vourlitis. 1994. The effects of climate-change on land atmosphere feedbacks in arctic tundra regions. *Trends in Ecology and Evolution 9(9):324-329.*

Recently reported high-latitude warming has the potential to affect arctic ecosystem structure and function in the short and long term. Arctic ecosystems are known sources of atmospheric CH4, and recent CO2 flux measurements indicate that these ecosystems are now, at least regionally, net sources of atmospheric CO2. It appears that over the short term (decades to centuries), arctic ecosystems may represent a positive feedback on global atmospheric CO2 concentrations and associated greenhouse gas-induced climate change. In addition, short-term feedbacks may be large enough to affect both local and global surface temperatures. Over the long term, changes in the structure, function and composition of arctic ecosystems may increase C accumulation relatively more than the amount lost, thus restoring the sink status of arctic ecosystems.

KEYWORDS: ACID PEAT, ALASKAN TUNDRA, BALANCE, CARBON DIOXIDE, ECOSYSTEMS, ELEVATED CO2, EMISSIONS, METHANE, TEMPERATURE, TUSSOCK TUNDRA

1735

Oechel, W.C., G.L. Vourlitis, S. Brooks, T.L. Crawford, and E. Dumas. 1998. Intercomparison among chamber, tower, and aircraft net CO2 and energy fluxes measured during the Arctic System Science Land- Atmosphere-Ice Interactions (ARCSS-LAII) Flux Study. *Journal of Geophysical Research-Atmospheres 103(D22):28993-29003.*

Measurements of net ecosystem CO2 exchange (NEE) and energy balance were made using chamber-, tower-, and aircraft-based measurement techniques in Alaskan arctic tundra ecosystems during the 1994-1995 growing seasons (June-August). One of our objectives was to quantify the interrelationships between the NEE and the energy balance measurements made from different sampling techniques. Qualitative and quantitative intercomparisons revealed that on average the correspondence between the mass and energy fluxes measured by these sampling methods was good despite potential spatial and temporal mismatches in sampling scale. Quantitative comparisons using least squares linear regression analyses with the tower-based measurements of NEE as the independent variable indicate that the chamber- and aircraft-based NEE measurements were generally lower relative to the tower-based measurements (slope = 0.76- 0.86). Similarly, tower-aircraft comparisons of latent (L-e) and sensible (H) heat exchange indicated that the aircraft- based measurements were lower than the tower-based measurements (slope = 0.72-0.80). Qualitative comparisons, however, indicate that the correspondence among the chamber-, tower-: and aircraft-measured fluxes varied both seasonally and interannually, suggesting the lack of a consistent bias between the sampling techniques. The results suggest that differences observed between the chamber, tower, and aircraft flux measurements were primarily due to the failure to account for the spatial distribution of surface types in the tower and aircraft sampling footprint, problems involved in the comparison of temporal and spatial averages, and temporal (e.g., seasonal and interannual) variance in rates of mass and energy flux for a given point. Other potential sources of variance include the underestimation of nocturnal NEE by the tower-based eddy covariance system, and the periodic occurrence of an elevated CO2 plume in the atmosphere over the Prudhoe Bay oil field. Even with these potential sources of variation, the results reveal that the various methods,give comparable estimates of NEE and energy flux within a range of temporal or spatial variability.

KEYWORDS: ALASKA, BROOKS-RANGE, CARBON DIOXIDE, CLIMATE CHANGE, EDDY-COVARIANCE, HEAT, OPEN-PATH, TUNDRA ECOSYSTEMS, VAPOR, WATER

1736

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, R.P. Ault, and P. Bryant. 1998. The effects of water table manipulation and elevated temperature on the net CO2 flux of wet sedge tundra ecosystems. *Global Change Biology 4(1):77-90.*

lit situ manipulations were conducted in a naturally drained lake on the arctic coastal plain near Prudhoe Bay, Alaska (70 degrees 21.98' N, 148 degrees 33.72' W) to assess the potential shortterm effects of decreased water table and elevated temperature on net ecosystem CO2 flux. The

experiments were conducted over a 2-year period, and during that time, water table depth of drained plots was maintained on average 7 cm lower than the ambient water table, and surface temperatures of plots exposed to elevated temperature were increased on average 0.5 degrees C. Water table drainage, and to a lesser extent elevated temperature, resulted in significant increases in ecosystem respiration (ER) rates, and only small and variable changes in gross ecosystem productivity (GEP). As a result, drained plots were net sources of approximate to 40 gC m(-2) season(-1) over both years of manipulation, while control plots were net sinks of atmospheric CO2 of about 10 gC m(-2) season(- 1) (growing season length was an estimated 125 days). Control plots exposed to elevated temperatures accumulated slightly more carbon than control plots exposed to ambient temperatures. The direct effects of elevated temperature on net CO2 flux, ER, and GEP were small, however, elevated temperature appeared to interact with drainage to exacerbate the amount of net carbon loss. These data suggest that many currently saturated or nearly saturated wet sedge ecosystems of the north slope of Alaska may become significant sources of CO2 to the atmosphere if climate change predictions of increased evapotranspiration and reduced soil water status are realized. There is ample evidence that this may be already occurring in arctic Alaska, as a change in net carbon balance has been observed for both tussock and wet-sedge tundra ecosystems over the last 2-3 decades, which coincides with a recent increase in surface temperature and an associated decrease in soil water content. In contrast, if precipitation increases relatively more than evapotranspiration, then increases in soil moisture content will likely result in greater carbon accumulation.

KEYWORDS: ALASKA, ARCTIC TUNDRA, ATMOSPHERE, BROOKS-RANGE, CARBON DIOXIDE, CLIMATE CHANGE, METHANE FLUXES, SOILS, TUSSOCK TUNDRA, VEGETATION

1737

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, and S.A. Bochkarev. 1995. Change in arctic co2 flux over 2 decades - effects of climate-change at barrow, alaska. *Ecological Applications 5(3):846-855.*

A significant difference in net ecosystem carbon balance of wet sedge ecosystems in the Barrow, Alaska region was observed between CO2 flux measurements obtained during the International Biological Program in 1971 and measurements made during the 1991-1992 growing seasons. Currently, high-center polygons are net sources of CO2 to the atmosphere of approximate to 14 gC . m(-2). yr(-1), while low-center polygons are losing approximate to 3.6 gC . m(-2). yr(-1), and ice wedge habitats are accumulating 4.0 gC . m(-2). yr(-1). On average, moist meadow habitats characteristic of the IBP-II site are currently sources of approximate to 1.3 gC . m(-2). yr(-1) to the atmosphere compared to the reported accumulation of approximate to 25 gC . m(-2). yr(-1) determined in 1971. This difference in ecosystem function over the last two decades may be due to the recently reported increase in surface temperatures resulting in decreases in the soil moisture status. These results point to the importance of long-term research sites and databases for determining the potential effects of climate change on ecosystem function.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BALANCE, ECOSYSTEMS, GROWTH, NUTRIENT, PERMAFROST, SOIL, TEMPERATURE, TUNDRA, WATER

1738

Oeschger, H. 1992. Atmospheric co2 - global change and regulation mechanisms. *Berichte Der Bunsen-Gesellschaft-Physical Chemistry Chemical Physics 96(3):252-257.*

For the estimate of the distribution in the carbon system of the CO2 emitted into the atmosphere due to human activities, the exchange of carbon between atmosphere and ocean, and between atmosphere and biosphere needs to be considered. Information on this spreading of excess CO2 can be obtained from measurements of a.o. CO2, C-13/C-12, C-14/C in the atmosphere, of natural and nuclear weapon produced C-14 in the ocean and in the biota and of other natural or anthropogenic tracers. - Based essentially on such information, models for the CO2 uptake by the carbon system have been developed which are capable of reproducing the result of the drop in the rate of increase of CO2 emissions from 4.5% to 2% per year following the oil-embargo in 1973. - Of special interest regarding the understanding of the carbon cycle and its role in controlling the climate of the Earth are the observations in polar ice cores covering the past 160.000 years, corresponding to one and a half glaciation cycles. They show variations of atmospheric CO2, CH4, and N2O parallel to the climatic variations. Measurements of C-13/C-12 in shells of foraminiferas support the hypothesis that these CO2 changes are caused by changes in the ocean's biological pump, i.e. the flux of detrital organic carbon from the surface to the deep ocean, which affects the total inorganic carbon in the surface ocean and the partial pressure of CO2.

KEYWORDS: ICE CORE, RECORD

1739

Ogasawara, N., H. Inden, and T. Asahira. 1996. Effects of lighting cycle on Caladium plantlets grown under ventilated and airtight culture vessels in relation to net daily CO2 uptakes. *Journal of the Japanese Society for Horticultural Science 65(1):129-134.*

Caladium plantlets were cultured in vitro under a long lighting cycle (16 hr light/8 hr dark) and a short lighting cycle (2 hr light/1 hr dark). When gas exchange between the inside and outside of the culture vessel was allowed, the short lighting cycle enhanced growth, but when the culture vessel was airtight, the lighting cycle had no effect on growth. The estimated net daily CO2 uptake under the short lighting cycle is greater than that under the long lighting cycle only when gas exchange occurs between the inside and outside of the vessel. These results demonstrate that the enhancement of growth by the short lighting cycle is due to an increase in the amount of available CO2 resulting from the reduced escape of CO2 from the vessel.

KEYWORDS: INVITRO

1740

Ojala, A., P. Kankaala, J. Haapamaki, and T. Tulonen. 1995. Immediate responses of photosynthesis and dark respiration of late summer stands of Equisetum fluviatile L to increasing concentrations of atmospheric CO2. *Journal of Applied Botany-Angewandte Botanik 69(5-6):169-176.*

Short-term responses of net photosynthesis, apparent dark respiration and gross photosynthesis of Equisetum fluviatile to increasing concentrations of atmospheric CO2 were studied by using transplanted stands of natural origin. Three transplantations with biomasses of 274, 407, and 401 g dry weight m(-2) were established six weeks before the measurements in late August. Net photosynthesis and apparent dark respiration was measured from the change of CO2 concentration inside polycarbonate chambers with diameter of 0.455 m and volume of 0.207 m(3). Altogether 50 experiments for determination of CO2 influx rates and 24 for efflux rates were run without any pre-treatment to higher CO2 and each of them lasted 20-30 min. The response of net photosynthesis of E. fluviatile to CO2 enrichment was less clear than the response to temperature or irradiance. Nevertheless, the stands showed an increase of ca. 25 % in net photosynthesis when the CO2 concentration in air was increased from ambient to 500-600 ppm. When the CO2 concentration was > 600 ppm the increase was ca. 60 %. A multilinear regression model combining solar radiation, temperature and CO2 concentration

could only explain 46.4 % of the variation in the observed rates of net photosynthesis. The apparent dark respiration was positively correlated with temperature but inversely related to CO2 concentration. When the CO2 concentration was doubled from ambient the stands of E. fluviatile reduced their apparent dark respiration by ca. 50 %. Under higher CO2 concentration E. fluviatile appeared more effective than in the ambient concentration, as the production lost through respiration decreased. When the concentration of atmospheric CO2 was < 500 ppm, 57.5 % of gross production was respired whereas above 500 ppm of CO2 the corresponding proportion was only 34.2 %. As the enrichment with CO2 resulted in decreased respiration rates and it was known from long-term growth and photosynthesis experiments that neither shoot growth in length in E. fluviatile is stimulated by higher CO2 concentrations nor do the stands show down-regulation of photosynthesis after several weeks of CO2 enrichment, it was concluded that the extra carbon fixed was allocated to storage through growth of below-ground biomass.

KEYWORDS: AQUATIC MACROPHYTES, CARBON DIOXIDE, COMMUNITIES, ENRICHMENT, GROWTH, LAKE PAAJARVI, PLANTS, SHORT- TERM, SOUTHERN FINLAND, WATER HYACINTH

1741

Ojima, D.S., W.J. Parton, D.S. Schimel, J.M.O. Scurlock, and T.G.F. Kittel. 1993. Modeling the effects of climatic and co2 changes on grassland storage of soil-C. *Water, Air, and Soil Pollution 70(1-4):643-657.*

We present results from analyses of the sensitivity of global grassland ecosystems to modified climate and atmospheric CO2 levels. We assess 31 grassland sites from around the world under two different General Circulation Models (GCM) double CO2 climates. These grasslands are representative of mostly naturally occurring ecosystems, however, in many regions of the world, grasslands have been greatly modified by recent land use changes. In this paper we focus on the ecosystem dynamics of natural grasslands. The climate change results indicate that simulated soil C losses occur in all but one grassland ecoregion, ranging from 0 to 14% of current soil C levels for the surface 20 cm. The Eurasian grasslands lost the greatest amount of soil C (approximately 1200 g C m-2) and the other temperate grasslands losses ranged froM 0 to 1000 g C m-2, averaging approximately 350 g C m-2. The tropical grasslands and savannas lost the least amount of soil C per unit area ranging from no change to 300 g C m-2 losses, averaging approximately 70 g C m-2. plant production varies according to modifications in rainfall under the altered climate and to altered nitrogen mineralization rates. The two GCM's differed in predictions of rainfall with a doubling of CO2, and these differences are reflected in plant production. Soil decomposition rates responded most predictably to changes in temperature. Direct CO2 enhancement effects on decomposition and plant production tended to reduce the net impact of climate alterations alone.

KEYWORDS: TERRESTRIAL

1742

Olaizola, M., E.O. Duerr, and D.W. Freeman. 1991. Effect of co2 enhancement in an outdoor algal production system using tetraselmis. *Journal of Applied Phycology 3(4):363-366.*

One of the objectives of microalgal culture is to provide reliable production technology for important live aquaculture feed organisms. Presented here are the results of experiments designed to provide a better understanding of the relationship between inorganic carbon availability and algal production. Our results suggest that through additions of CO2 gas we were able to maintain sufficient dissolved carbon to stabilize outdoor algal cultures. Increases in the rate of addition of CO2 increased levels of dissolved CO2, total dissolved inorganic carbon (SIGMA-CO2), and decreased pH in the growth medium. This translated into improved buffering capacity of the culture medium and higher growth rate. A minimum of 2.4 mM SIGMA-CO2 was found necessary to maintain a maximal growth rate of 0.7 doublings/day. We also found that the increased productivity more than offsets the cost of adding the CO2.

1743

Olesniewicz, K.S., and R.B. Thomas. 1999. Effects of mycorrhizal colonization on biomass production and nitrogen fixation of black locust (Robinia pseudoacacia) seedlings grown under elevated atmospheric carbon dioxide. *New Phytologist 142(1):133-140.*

Interactive effects of elevated atmospheric CO2 and arbuscular mycorrhizal (AM) fungi on biomass production and N-2 fixation were investigated using black locust (Robinia pseudoacacia). Seedlings were grown in growth chambers maintained at either 350 mu mol mol(-1) or 710 mu mol mol(-1) CO2. Seedlings were inoculated with Rhizobium spp. and were grown with or without AM fungi. The N-15 isotope dilution method was used to determine N source partitioning between N, fixation and inorganic fertilizer uptake. Elevated atmospheric CO2 significantly increased the percentage of fine roots that were colonized by AM fungi. Mycorrhizal seedlings grown under elevated CO2 had the greatest overall plant biomass production, nodulation, N and P content, and root N absorption. Additionally, elevated CO2 levels enhanced nodule and root mass production, as well as N, fixation rates, of nonmycorrhizal seedlings. However, the relative response of biomass production to CO2 enrichment was greater in non-mycorrhizal seedlings than in mycorrhizal seedlings. This study provides strong evidence that arbuscular mycorrhizal fungi play an important role in the extent to which plant nutrition of symbiotic N-2-fixing tree species is affected by enriched atmospheric CO2.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, CO2-ENRICHMENT, EXTERNAL HYPHAE, GLOMUS-RHIZOBIUM SYMBIOSIS, N-UPTAKE, N2 FIXATION, PHOSPHATE NUTRITION, SOIL N, TRIFOLIUM-SUBTERRANEUM L

1744

Olszyk, D.M., H.G.S. Centeno, L.H. Ziska, J.S. Kern, and R.B. Matthews. 1999. Global climate change, rice productivity and methane emissions: comparison of simulated and experimental results. *Agricultural and Forest Meteorology 97(2):87-101.*

Irrigated rice production is a major food source for a large portion of the world's population, and a major anthropogenic source of the greenhouse gas methane (CH4). Potential impacts of global climate change [elevated carbon dioxide (CO2) and/or elevated temperature] on rice can be predicted with simulation models, but experiments are necessary to determine how well these models mimic the responses of the field crop. This paper compares grain yield, biomass, and methane emissions from experiments at the international Rice Research Institute (IRRI) at Los Banos, the Philippines, with potential responses based on simulations using the ORYZA1 process model and the climate data from those experiments. Yield and biomass were compared for the 1995 and 1996 dry seasons (DS) and the 1994 wet season (WS). Emissions of CH4 from rice fields were evaluated for the 1995 WS and 1996 DS, Simulated and experimental responses (adjusted for effects of the open-top chambers on plant growth) differed with climate change scenario, response parameter, and season Under current climate conditions (ambient CO2 and ambient temperature), simulated grain yield was 14% lower than the adjusted experimental grain yield in the 1996 DS, but was 17 and 37% higher than experimental grain yield in the 1995 DS and 1994 WS, respectively. With current climate, simulations underestimated experimental aboveground, belowground, and total biomass. The

simulated CH4 emissions were the same as the experimental emissions, assuming CH4 emissions were 2.9% of the simulated total biomass carbon. With elevated CO7 and ambient temperature, simulations predicted greater increases (compared with current climate) in grain yield, aboveground biomass, and total biomass, but generally smaller increases in belowground biomass and CH4 emissions than the significant (at $p < 0.05$) increases that were found experimentally. With ambient CO2 and elevated temperature, both simulations and experiments generally showed either no change or a decrease in grain yield and biomass, but none of the responses in the experiments wen statistically significant. Simulated ambient CO2 and elevated temperature resulted in a smaller decrease in CH4 emissions than the significant decrease found in the experiments. For both elevated CO2 and elevated temperature, simulated grain yield increased in all three seasons, whereas there were no significant effects on experimental grain yield. The simulations predicted smaller increases in belowground biomass and CH4 emissions with elevated CO2 and elevated temperature than the significant increases in the experiments. To better correspond to experimental results, this study suggested that current simulation models could be improved in terms of effects of temperature on grain yield and use of belowground biomass to estimate CH4 emissions.

KEYWORDS: CO2, GROWTH, IMPACT, INCREASING CARBON-DIOXIDE, ORYZA-SATIVA, PADDY RICE, PLANTS, TEMPERATURE, TROPICAL RICE, YIELD

1745

Olszyk, D.M., and C. Wise. 1997. Interactive effects of elevated CO2 and O-3 on rice and flacca tomato. *Agriculture Ecosystems & Environment 66(1):1-10.*

Atmospheric concentrations of both carbon dioxide (CO2) and ozone (O-3) are increasing, with potentially dramatic effects on plants. This study was conducted to determine interactive effects of CO2 and O-3 on rice (Oryza sativa L. cv. IR 74) and a 'wilty' mutant of tomato (Lycopersicon esculentum Mill. flacca). Plants were grown from seed in a glasshouse and exposed for 28 days to ambient or elevated CO2 (approximate to 400 or 700 mu l l(-1) CO2) and/or ambient or elevated O-3 (peak/valley pattern of exposure with cumulative totals of approximate to 1 or 44 mu l l(-1) h). Elevated CO2 alleviated O-3-associated decreases in allocation of biomass to roots, as indicated by a decreased root:shoot ratio ($p < 0.05$), and also reduced injury from O-3 as indicated by leaf greenness readings for one experiment($p < 0.05$). By itself, elevated CO2 resulted in increases in total plant and individual organ(root, leaf, stem) dry weights and root:shoot ratio and elevated O-3 resulted in increases in main culm leaf number and a decrease in stem dry weight ($p < 0.05$). Elevated CO2 had no significant effect on the tendency for O-3-induced biomass reductions of flacca tomato. For flacca, elevated CO2 alone increased shoot and root biomass ($p < 0.05$), and elevated O-3 alone tended to decrease biomass for both parameters, but only at $p = 0.09$ and O.11, respectively. This study was preliminary, as the environmental conditions in these experiments may have altered O-3 and CO2 responses of the plants. However, these results provided additional evidence that elevated CO2 inhibits adverse effects of O-3 on plants, and that the interactive response may be mediated by stomata.

KEYWORDS: AIR- POLLUTANTS, B RADIATION, BIOMASS, CARBON-DIOXIDE CONCENTRATION, CHRONIC OZONE, EXPOSURE, GROWTH, REGIMES, RESPONSES, SEEDLINGS

1746

Olszyk, D., C. Wise, E. VanEss, M. Apple, and D. Tingey. 1998. Phenology and growth of shoots, needles, and buds of Douglas- fir seedlings with elevated CO2 and (or) temperature. *Canadian Journal of Botany-Revue Canadienne De Botanique 76(12):1991-2001.*

Increased atmospheric CO2 and global warming may affect overall tree growth, but impacts of these combined stresses are largely unknown in terms of multiple growing season impacts on specific flushes. Thus, the effects of ambient or elevated CO2 (approximately 200 mu mol.mol(-1) above ambient) and ambient or elevated temperature (approximately 4 degrees C above ambient) were evaluated for both main and second (lammas) flushes of Douglas-fir (Pseudotsuga menziesii (Mirb.) France). Established seedlings were grown for three full growing seasons in outdoor, sunlit chambers, which maintained diel and seasonal variation in climate. A reconstructed forest soil was used with a seasonal wet and dry cycle and without added fertilizer. Compared with ambient CO2 elevated CO2 had no impact on overall phenology and growth of terminal shoots, needles, or buds. In contrast, compared with ambient temperature, elevated temperature resulted in higher shoot and needle growth rates early in the season; reduced final terminal shoot length; and either reduced, increased, or unchanged final needle length, depending on season. Initiation of the lammas flush was delayed and (or) decreased at elevated temperature. Leading terminal bud break and growth occurred earlier; however, resting bud length was reduced, and bud width tended to increase with elevated temperature. Thus, at least during early seedling growth, elevated temperatures may reduce both main- and lammas- flush growth, thereby altering tree productivity, whereas elevated CO2 may have little effect on main or lammas growth at either the current or elevated temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BURST, HARDINESS, PINE, RESPONSES, SEASONALITY, TREES, WOODY-PLANTS

1747

Olszyk, D., C. Wise, E. VanEss, and D. Tingey. 1998. Elevated temperature but not elevated CO2 affects long-term patterns of stem diameter and height of Douglas-fir seedlings. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 28(7):1046-1054.*

Global climatic change may impact forest productivity, but data are lacking on potential effects of elevated CO2 and temperature on tree growth. We determined changes in shoot growth for Douglas-fir (Pseudotsuga menziesii (Mirb.) France) seedlings exposed to ambient or elevated CO2 (+approximate to 179 mu mol.mol(-1)),and ambient or elevated temperature (+approximate to 3.5 degrees C). Seedings were grown for 4 years (three complete growing seasons) in outdoor, sunlit chambers. In each season, height growth was initiated earlier and, in two seasons, ceased earlier for elevated compared with ambient temperature trees. Elevated temperature reduced intermediate and final plant heights. Stem diameter growth began earlier each season at the elevated compared with the ambient temperature, but temperature had no affect on final stem diameter. Elevated temperature tended to reduce leaf ($p = 0.07$) but not woody biomass. Elevated CO2 had no significant effects on stem diameter, height, and leaf or woody biomass, and there were no significant CO2 x temperature interactions. Thus, elevated temperatures (but not elevated CO2) associated with climate change may decrease seedling canopy growth as indicated by reduced height and leaf biomass but have little or no effect on overall woody growth as indicated by stem diameter and woody biomass.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS ALLOCATION, CLIMATE CHANGE, FORESTS, GROWTH, PONDEROSA PINE

1748

Oltchev, A., A. Ibrom, K. Morgenstern, H. Kreilein, and G. Gravenhorst. 1999. Evaluation of the response of a spruce forest

ecosystem on climatic changes: Results of modelling experiments. *Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere 24(1-2):103-110.*

The physical and chemical environment of forests will change in the future. How forests will react to new conditions is not known yet. In order to get an idea of the sensitivity of present forests to possible atmospheric changes, it is helpful to investigate the physiological response of forest ecosystem to a change of key environmental parameters. In order to estimate the response of a mountain spruce forest to different atmospheric conditions during the summer a six-layer non-steady-state SVAT model (SLODSVAT) was used Eight scenarios were used for modelling energy and mass exchange during an eleven day summer period, combining different combinations of microclimatic conditions. All atmospheric scenarios were examined for three various CO2 mixing ratio levels: 350ppm (current condition), 450ppm and 550ppm. A scenario "0" assuming the current climatic features at different CO2 contents was considered as well. Structural and physiological adaptation of the forest to the new atmospheric conditions were not taken into account. For all scenarios the modelling results show increased net CO2 flux into the forest with increasing ambient CO2 concentration. Maximum net CO2 uptake was simulated for dry climate scenarios. Transpiration and evapotranspiration rates had similar trends independently of the ambient CO2 concentration used: at cold and wet conditions they decreased, while at warm and dry conditions transpiration and evapotranspiration rates increased The influence of CO2 concentrations on transpiration rates is of minor importance if compared to changes of temperature, water vapour pressure, cloud amount and atmospheric precipitation as considered in this investigation.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2-ENRICHMENT, PINE

1749

Ommen, O.E., A. Donnelly, S. Vanhoutvin, M. van Oijen, and R. Manderscheid. 1999. Chlorophyll content of spring wheat flag leaves grown under elevated CO2 concentrations and other environmental stresses within the 'ESPACE-wheat' project. *European Journal of Agronomy 10(3-4):197-203.*

Spring wheat cv. Minaret was grown in open-top chambers at four sites across Europe. The effect of different treatments (CO2 enrichment, O-3 fumigation, drought stress and temperature) on the chlorophyll content of the flag leaf was investigated using the MINOLTA SPAD-502 meter. Under optimum growth conditions the maximum chlorophyll content, which was reached at anthesis, was consistent among the sites ranging from 460 to 500 mg chlorophyll m(-2). No significant effect of elevated CO2 or O-3 was observed at anthesis. Leaf senescence, indicated by the chlorophyll breakdown after anthesis, was relatively constant in the control chambers. Under control conditions, thermal time until 50% chlorophyll loss was reached was 600 degrees C day. Elevated CO2 caused a faster decline in chlorophyll content (thermal time until 50% chlorophyll loss was reduced to 500-580 degrees C day) indicating a faster rate of plant development at two experimental sites. The effect of ozone on chlorophyll content depended on the time and dose of O-3 exposure. During grain filling, high O-3 concentrations induced premature senescence of the flag leaves (up to -130 degrees C day). This deleterious effect was mitigated by elevated CO2. Drought stress led to faster chlorophyll breakdown irrespective of CO2 treatment.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, OPEN-TOP CHAMBERS, OZONE, PHOTOSYNTHESIS, TRITICUM-AESTIVUM L, WATER-STRESS, WINTER-WHEAT, YIELD

1750

Oneill, E.G. 1994. Responses of soil biota to elevated atmospheric carbon-dioxide. *Plant and Soil 165(1):55-65.*

Increasing concentrations of atmospheric CO2 could have dramatic effects upon terrestrial ecosystems including changes in ecosystem structure, nutrient cycling rates, net primary production, C source-sink relationships and successional patterns. All of these potential changes will be constrained to some degree by below ground processes and mediated by responses of soil biota to indirect effects of CO2 enrichment. A review of our current state of knowledge regarding responses of soil biota is presented, covering responses of mycorrhizae, N-fixing bacteria and actinomycetes, soil microbiota, plant pathogens, and soil fauna. Emphasis will be placed on consequences to biota of increasing C input through the rhizosphere and resulting feedbacks to above ground systems. Rising CO2 may also result in altered nutrient concentrations of plant litter, potentially changing decomposition rates through indirect effects upon decomposer communities. Thus, this review will also cover current information on decomposition of litter produced at elevated CO2.

KEYWORDS: CO2- ENRICHMENT, DOUGLAS-FIR ECOSYSTEM, DYNAMICS, INDUCED NITROGEN MINERALIZATION, MYCORRHIZAL, PISUM-SATIVUM, QUERCUS-ALBA, RHIZOSPHERE, ROOT, SEEDLING GROWTH

1751

Ong, B.L., C.K.K. Koh, and Y.C. Wee. 1998. Effects of CO2 on growth and photosynthesis of Pyrrosia piloselloides (L.) Price gametophytes. *Photosynthetica 35(1):21-27.*

The effects of CO2 concentration on spore germination, growth, and net photosynthetic rate (P-N) Of gametophytes of a tropical epiphytic fern, Pyrrosia piloselloides, were investigated over a 100-d period. Increasing CO2 concentration stimulated spore germination and enhanced gametophytic growth. The appearance of sexual organs and formation of sporophytes were accelerated with higher CO2 during growth. Radiant energy saturated P-N and dark respiration rate also increased with increasing CO2 concentrations during growth.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CROP RESPONSES, ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, LEAF AGE, RESPIRATION, SEEDLINGS, STOMATAL CONDUCTANCE

1752

Ormrod, D.P., V.M. Lesser, D.M. Olszyk, and D.T. Tingey. 1999. Elevated temperature and carbon dioxide affect chlorophylls and carotenoids in douglas-fir seedlings. *International Journal of Plant Science 160(3):529-534.*

The objective of this study was to determine whether increased temperature and CO2 concentration would decrease or increase the concentrations of foliar pigments in S-yr-old seedlings of Douglas-fir Pseudotsuga menziesii [Mirb,] France var, menziesii). Seedlings were grown for 3 yr in sunlit, controlled environment chambers under ambient conditions or with a 179 mu L L-1 elevation of CO2 and/or a 3.5 degrees C elevation of temperature. Current- and previous-year needles were extracted with methanol for determination of chlorophylls and b, total carotenoids, and UV-absorbing compounds. Interactive effects of elevated temperature and CO2 on the measured responses were not significant. Current-year needles from the elevated CO2 treatment had the lowest chlorophyll and carotenoid concentrations, whereas needles of both age classes in the elevated temperature treatment had the highest concentrations of chlorophylls; current-year needles had the highest carotenoid concentration at elevated temperature. Neither temperature

nor CO2 affected the concentrations of UV-absorbing compounds or needle fresh mass significantly. Chlorophyll a was correlated with carotenoids across all treatments (r = 0.75- 0.89) in both needle age classes and with chlorophyll b in most treatments.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, AVAILABILITY, B RADIATION, LEAVES, LIGHT, PACIFIC NORTHWEST, PHOTOSYNTHESIS, PLANT GROWTH, SCOTS PINE, UV-B

1753

Osborne, C.P., B.G. Drake, J. LaRoche, and S.P. Long. 1997. Does long-term elevation of CO2 concentration increase photosynthesis in forest floor vegetation? Indian strawberry in a Maryland forest (vol 114, pg 337, 1997). *Plant Physiology 114(4):1571.*

As the partial pressure of CO2 (pCO(2)) in the atmosphere rises, photorespiratory loss of carbon in C-3 photosynthesis will diminish and the net efficiency of light-limited photosynthetic carbon uptake should rise. We tested this expectation for Indian strawberry (Duchesnea indica) growing on a Maryland forest floor. Open-top chambers were used to elevate the pCO(2) of a forest floor habitat to 67 Pa and were paired with control chambers providing an ambient pCO(2) of 38 Pa. After 3.5 years, D. indica leaves grown and measured in the elevated pCO(2) showed a significantly greater maximum quantum efficiency of net photosynthesis (by 22%) and a lower light compensation point (by 42%) than leaves grown and measured in the control chambers. The quantum efficiency to minimize photorespiration, measured in 1% O-2, was the same for controls and plants grown at elevated pCO(2). This showed that the maximum efficiency of light-energy transduction into assimilated carbon was not altered by acclimation and that the increase in light-limited photosynthesis at elevated pCO(2) was simply a function of the decrease in photorespiration. Acclimation did decrease the ribulose-1,5-bisphospbate carboxylase/oxygenase and light-harvesting chlorophyll protein content of the leaf by more than 30%. These changes were associated with a decreased capacity for light-saturated, but not light-limited, photosynthesis. Even so, leaves of D. indica grown and measured at elevated pCO(2) showed greater light- saturated photosynthetic rates than leaves grown and measured at the current atmospheric pCO(2). In situ measurements under natural forest floor lighting showed large increases in leaf photosynthesis at elevated pCO(2), relative to controls, in both summer and fall. The increase in efficiency of light- limited photosynthesis with elevated pCO(2) allowed positive net photosynthetic carbon uptake on days and at locations on the forest floor that light fluxes were insufficient for positive net photosynthesis in the current atmospheric pCO(2).

1754

Osborne, C.P., B.G. Drake, J. LaRoche, and S.P. Long. 1997. Does long-term elevation of CO2 concentration increase photosynthesis in forest floor vegetation? Indiana strawberry in a Maryland forest. *Plant Physiology 114(1):337-344.*

As the partial pressure of CO2 (pCO(2)) in the atmosphere rises, photorespiratory loss of carbon in C-3 photosynthesis will diminish and the net efficiency of light-limited photosynthetic carbon uptake should rise. We tested this expectation for Indiana strawberry (Duchesnea indica) growing on a Maryland forest floor. Open-top chambers were used to elevate the pCO(2) of a forest floor habitat to 67 Pa and were paired with control chambers providing an ambient pCO(2) of 38 Pa. After 3.5 years, D. indica leaves grown and measured in the elevated pCO(2) showed a significantly greater maximum quantum efficiency of net photosynthesis (by 22%) and a lower light compensation point (by 42%) than leaves grown and measured in the control chambers. The quantum efficiency to minimize photorespiration, measured in 1% O-2, was the same for controls and plants grown at elevated pCO(2). This showed that the maximum efficiency of light-energy transduction into assimilated carbon was not altered by acclimation and that the increase in light-limited photosynthesis at elevated pCO(2) was simply a function of the decrease in photorespiration. Acclimation did decrease the ribulose-1,5-bisphosphate carboxylase/oxygenase and light-harvesting chlorophyll protein content of the Leaf by more than 30%. These changes were associated with a decreased capacity for light-saturated, but not light-limited, photosynthesis. Even so, leaves of D. indica grown and measured at elevated pCO(2) showed greater light- saturated photosynthetic rates than leaves grown and measured at the current atmospheric pCO(2). In situ measurements under natural forest floor lighting showed large increases in leaf photosynthesis at elevated pCO(2), relative to controls, in both summer and fall. The increase in efficiency of light- limited photosynthesis with elevated pCO(2) allowed positive net photosynthetic carbon uptake on days and at locations on the forest floor that light fluxes were insufficient for positive net photosynthesis in the current atmospheric pCO(2).

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, EXPRESSION, GROWTH, NITROGEN, PROTEINS, QUANTUM YIELD, RUBISCO, VASCULAR PLANTS

1755

Osborne, C.P., J. LaRoche, R.L. Garcia, B.A. Kimball, G.W. Wall, P.J. Pinter, R.L. LaMorte, G.R. Hendrey, and S.P. Long. 1998. Does leaf position within a canopy affect acclimation of photosynthesis to elevated CO2? Analysis of a wheat crop under free-air CO2 enrichment. *Plant Physiology 117(3):1037-1045.*

Previous studies of photosynthetic acclimation to elevated CO2 have focused on the most recently expanded, sunlit leaves in the canopy. We examined acclimation in a vertical profile of leaves through a canopy of wheat (Triticum aestivum L.). The crop was grown at an elevated CO2 partial pressure of 55 Pa within a replicated field experiment using free-air CO2 enrichment. Cas exchange was used to estimate in vivo carboxylation capacity and the maximum rate of ribulose-1,5-bisphosphate-limited photosynthesis. Net photosynthetic CO2 uptake was measured for leaves in situ within the canopy. Leaf contents of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), light-harvesting-complex (LHC) proteins, and total N were determined. Elevated CO2 did not affect carboxylation capacity in the most recently expanded leaves but led to a decrease in lower, shaded leaves during grain development. Despite this acclimation, in situ photosynthetic CO2 uptake remained higher under elevated CO2. Acclimation at elevated CO2 was accompanied by decreases in both Rubisco and total leaf N contents and an increase in LHC content. Elevated CO2 led to a larger increase in LHC/Rubisco in lower canopy leaves than in the uppermost leaf. Acclimation of leaf photosynthesis to elevated CO2 therefore depended on both vertical position within the canopy and the developmental stage.

KEYWORDS: APPARATUS, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, NITROGEN, PERSPECTIVE, PLANTS, REDISTRIBUTION

1756

Osborne, J.L., C.S. Awmack, S.J. Clark, I.H. Williams, and V.C. Mills. 1997. Nectar and flower production in Vicia faba L (field bean) at ambient and elevated carbon dioxide. *Apidologie 28(1):43-55.*

Atmospheric CO2 has been predicted to double by the year 2100. Elevated CO2 causes an increase in photosynthetic rate and extra assimilate is allocated to plant growth, seed and fruit production. Increased investment in flowers may have implications for pollination in entomophilous plants. Floral nectar standing crop, flower production and longevity were examined in Vicia faba, field bean, at ambient and

elevated CO2. Nectar standing crop did not differ significantly between treatments but plants grown at elevated CO2 produced approximately 25% more flowers per plant and these lived 17% longer than those grown at ambient CO2. A plant grown at elevated CO2 may thus produce more nectar in total and, together with its increased floral display, may be more attractive to pollinators, but pollen flow will not necessarily be improved.

KEYWORDS: CO2, FLORAL NECTARY, HONEY BEES, MODIFIED STOMATA, PLANTS, TEMPERATURE

1757

Osorio, J., M.L. Osorio, M.M. Chaves, and J.S. Pereira. 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in Eucalyptus globulus. *Tree Physiology 18(6):363-373.*

Potted cuttings of three Eucalyptus globulus Labill, clones (AR3, CN44, MP11) were either well watered or subjected to one of two soil water deficit regimes for six months in a greenhouse. Reductions in lateral branching, leaf production and leaf expansion were the leading contributors to the large differences observed in biomass production between well-watered and water-stressed plants. Although no significant differences among clones were observed in dry matter accumulation or in the magnitude of the response to soil water deficits, sensitivity of lateral branching, leaf initiation and whole-plant foliage to water stress was significantly lower in CN44 than in AR3 and MP11. When the confounding effect of differences in plant size resulting from the different watering regimes was removed, allometric analysis indicated that the genotypes differed in biomass allocation patterns. In addition to a drought-induced reduction in leaf number, water deficits also resulted in smaller leaves because leaf expansion was inhibited during dehydration events. Resumption of leaf expansion following stress relief occurred in all of the clones, but was particularly evident in severely stressed plants of Clone AR3, possibly as a result of the osmotic adjustment observed in this genotype.

KEYWORDS: AREA, DISCRIMINATION, DROUGHT, ELEVATED CO2, LEAF GROWTH, NITROGEN, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS, SEEDLINGS, SOIL-MOISTURE STRESS

1758

Ottosen, C.O. 1994. Net photosynthesis of schefflera-arboricola hayata clones at different co2 concentration and photosynthetic flux densities. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 44(4):248-250.*

KEYWORDS: CO2, ENRICHMENT, FICUS-BENJAMINA, GROWTH, LEAVES

1759

Overdieck, D. 1993. Effects of atmospheric co2 enrichment on co2 exchange-rates of beech stands in small model-ecosystems. *Water, Air, and Soil Pollution 70(1-4):259-277.*

CO2 enrichment experiments were performed during two vegetation periods on young beech stands in four closed mini-greenhouses. The houses were climatized according to the outside microclimate (+/- 0,5-degrees-C, +/- 15 % rel. air humidity, wind speed approximately to outside in the range of 0.5 - 2.5 m s-1, max. 17 % PAR reduction). The model ecosystems - consisting of 36 young beech (2.5 yr-old) in a soil block of 0.38 m3 and an air volume of 0.64 m3 - were exposed to CO2 concentrations of the unchanged ambient air (350 +/- 34 ppmv, control) and of 700 ppmv (698 +/- 10 ppmv). Plant growth parameters were measured non distructively and at the end of the 1st season samples were taken for weighing the phytomass. CO2 gas exchange of the stands taken as a whole were continuously measured with two entire mini-greenhouses and, in addition, a compact mini-cuvette system (CMS 400, Walz) was used for measuring dark respiration and CO2 net assimilation rates of single leaves in both stands. Under the influence of the additional CO2 supply stem diameter (2 cm above the first lateral roots) was increased by 13.5 %, stem height by 27.4 %, and the number of leaves/tree by 33 % at the end of the 2nd season. The number of buds was not significantly different and the effect on mean area per leaf was insignificant. Leaf area index was by 1.4 units greater. All dry weights of the main organs were increased after the 1st season: leaf 60 %, stem 34 %, bud 54 %. Roots < 2 mm phi weighed 1.5-fold more and roots > 2 mm phi 1.7-fold more under elevated CO2. CO2 gas exchange of two systems was measured. Whole system CO2 losses during night as well as photosynthetic CO2 gains during days were greater at 700 ppmv than in the control system. However, if one balances CO2 gains with CO2 losses over a period of five days in August both model-ecosystems taken as a whole were sinks for CO2. During this selected time period of 5 days at the peak of the season the beech stand at 350 ppmv was the greater sink. At 350 ppmv CO2 (control) the average leaf respiration for 20-degrees- C amounted to 0.31 +/- 0.18 and at 700 ppmv to 0.57 +/- 0.42 mumol CO2 m-2 s-1 (n = 35/40, t = 3.48, alpha < 0.05), and correlated positively with leaf temperature. At light saturation the mean net assimilation rate was 4.48 mumol m-2 (leaf area) s-1 in the control and 6.21 mumol m-2 s-1 at the high CO2 concentration corresponding with an enhancement factor of 1.39 for the selected time period. Results from the whole stand and from single leaf measurements are compared by means of mathematical modelling procedures in order to quantify CO2 enrichment effects on beech model ecosystems.

KEYWORDS: ELEVATED CARBON-DIOXIDE, FIELD, GAS-EXCHANGE, PLANTS, QUERCUS-ALBA, SEEDLING GROWTH, VEGETATION

1760

Overdieck, D. 1993. Elevated co2 and the mineral-content of herbaceous and woody- plants. *Vegetatio 104:403-411.*

The CO2 enrichment effects (300-650 mumol mol-1) on mineral concentration (N, P, K, Ca, Mg, Mn, Fe, Zn), absolute total mineral contents per individual and of whole stands of four herbaceous (Trifolium repens L., Trifolium pratense L., Lolium perenne L., Festuca pratensis HUDS.) and two woody species (Acer pseudo-platanus L., Fagus sylvatica L.) were investigated. In general, the mineral concentration of the plant tissues decreased (all six species: N > Ca > K > Mg) with the exception of P. Mn and Fe were only determined for the tree species. Both decreased in concentration (Mn > Fe). Zn was only analysed for Trifolium pratense and Festuca pratensis and decreased significantly in the grass. Despite of decreases in concentrations of as much as 20 % in some cases there were increases in absolute amounts per individual and, therefore, in the whole vegetation up to 25 % because of the enhanced dry matter accumulation at elevated CO2 supply.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLOVER TRIFOLIUM-REPENS, ENRICHMENT, GAS-EXCHANGE, GROWTH, LOLIUM-PERENNE L, MANAGED MODEL-ECOSYSTEMS, NUTRIENT-UPTAKE, RYEGRASS, WHITE CLOVER

1761

Overdieck, D. 1996. CO2 gas exchange and mass production during germination of radish at elevated atmospheric CO2 concentration. *Journal of Applied Botany-Angewandte Botanik 70(5-6):205-210.*

The influence of elevated CO2 concentration (similar to 700 mu mol mol(-1)) on dry mass accumulation and CO2 net assimilation of

germinating Raphanus sativus L.-seeds was investigated during growth over 10 days at low light during the day (16 h, photosynthetic photon flux density (PPFD: 20-70 mu mol m(-2)s(- 1)) and at darkness (8 h). Investigations at similar to 360 (unchanged ambient air) and at similar to 400 mu mol CO2 mol-L served as controls. At germination and development in a WALZ- mini-cuvette (part of CMS 400) with constant microclimatic conditions (20 degrees C, PPFD during day: 20-60 mu mol m(-2) s(-1), vapor pressure deficit: similar to 0.5 kPa) dry mass decreased by 14% in the course of the experiment without measurable influence of CO2 concentration. In a subsequent experiment with continuous CO2 gas exchange measurements on groups of 10 germinating radishes over 10 days at similar to 360 (n = 6) and at similar to 700 mu mol CO2 mol(-1) (n = 5) and, except for PPFD (70 mu mol m(-2) s(-1)), under unchanged microclimatic conditions no measurable CO2 effect on dark respiration (R(d)) could be found. In light and in both CO2 treatments maximum respiration was reached at day 3 or 4; whereas during darkness its level remained unchanged until the 10(th) day. At 700 mu mol CO2 mol(-1) during the day compensation of respiratory CO2 losses by photosynthetic gains was reached one day earlier than in the control. CO2 net assimilation during the light phase of the 10(th) day was enhanced by the elevated CO2 supply by a factor of 2.2 relative to the control. Results of CO2 gas exchange measurements on groups of 10 germinating radish seeds taken day by day from phytotron chambers with the same microclimatic conditions as before (similar to 400 and similar to 700 mu mol CO2 mol(-1), n = 3/day and CO2 concentration) again showed no CO2 effect on dark respiration; however, a positive effect on CO2 net assimilation clearly occurred once more in light (with an enhancement factor after 10 days of similar to 1.5). The mean dry mass balance - calculated by means of all CO2 gas exchange rates and the C-content [%] of seeds and seedlings of the last experiment - resulted after 10 days in a photosynthetically not yet compensated loss of 8.7% from the starting seed dry mass at 400 mu mol CO2 mol(-1) and of only 3.3% at 700 mu mol CO2 mol(- 1). The reported positive CO2 effect on growth and net production of radish reported in literature could, therefore, be explained at least in the germinating phase by enhanced CO2 net assimilation with unchanging CO2 losses by simultaneous dark respiration.

KEYWORDS: CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, ENRICHMENT, GROWTH, INHIBITION, PLANTS, TEMPERATURE

1762

Overdieck, D., and M. Forstreuter. 1994. Evapotranspiration of beech stands and transpiration of beech leaves subject to atmospheric co2 enrichment. *Tree Physiology 14(7-9):997-1003.*

Beech trees (Fagus sylvatica L.) show reduced stomatal conductance and increased leaf area index in response to increased atmospheric CO2 concentration. To determine whether the reduction in stomatal conductance results in lower stand evapotranspiration, we compared transpiration on a leaf-area basis and stand evapotranspiration on a ground-area basis in young European beech trees growing in greenhouses at ambient (360 +/- 34 mumol mol-1) and elevated (698 +/- 10 mumol mol-1) CO2 concentrations. Trees were grown in homogenized natural soil at constant soil water supply for two growing seasons. At light saturation, leaf transpiration rates were, on average, 18% lower in the elevated CO2 treatment than in the ambient C02 treatment. Mean transpiration coefficients (transpiration/net CO2 uptake) of leaves were 179 and 110 in the ambient and elevated CO2 treatments, respectively, indicating improved water use efficiency in trees in the elevated CO2 treatment. Total leaf conductance was decreased by 32% at light saturation. The elevated CO2 treatment resulted in a 14% reduction in stand evapotranspiration. In both CO2 treatments, evapotranspiration increased linearly at a rate of 0.2 kg H2O m-2 day-1 for each 1-degrees-C rise in air temperature between 14 and 25-degrees-C. We conclude that, under Central European conditions, water losses from deciduous forest stands will be reduced by a doubling of tropospheric CO2 concentration.

1763

Owensby, C.E. 1993. Potential impacts of elevated co2 and aboveground and belowground litter quality of a tallgrass prairie. *Water, Air, and Soil Pollution 70(1-4):413-424.*

Increased atmospheric CO2 will likely impact the productivity of arid and semiarid ecosystems through increased C, N, and water use efficiencies at the individual plant level. Tallgrass prairie has had increased above- and belowground biomass production under elevated CO2, primarily due to increased water use efficiency. There is an apparent decreased N requirement to sustain increased productivity in CO2-enriched tallgrass prairie, and C:N ratios of plant litter above and below ground have increased. The tallgrass prairie ecosystem level response to elevated CO2 on the C cycle could potentially increase C storage. Reduced litter quality associated with elevated CO2 in tallgrass prairie has the potential to reduce decomposition rates, and ruminant digestion rate of plant biomass apparently has been lowered. Reduced intake by ruminants would shunt more of the plant biomass directly into the detrital food chain, thereby slowing decomposition further. The potential impact is for increased C to be retained as soil organic matter in the tallgrass prairie.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, COMMUNITIES, DECOMPOSITION, ESTUARINE MARSH, GRASSLAND ECOSYSTEMS, GROWTH, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES

1764

Owensby, C.E., L.M. Auen, and P.I. Coyne. 1994. Biomass production in a nitrogen-fertilized, tallgrass prairie ecosystem exposed to ambient and elevated levels of co2. *Plant and Soil 165(1):105-113.*

Increased biomass production in terrestrial ecosystems with elevated atmospheric CO2 may be constrained by nutrient limitations as a result of increased requirement or reduced availability caused by reduced turnover rates of nutrients. To determine the short-term impact of nitrogen (N) fertilization on plant biomass production under elevated CO2, we compared the response of N-fertilized tallgrass prairie at ambient and twice-ambient CO2 levels over a 2-year period. Native tallgrass prairie plots (4.5 m diameter) were exposed continuously (24 h) to ambient and twice-ambient CO2 from 1 April to 26 October. We compared our results to an unfertilized companion experiment on the same research site. Above- and belowground biomass production and leaf area of fertilized plots were greater with elevated than ambient CO2 in both years. The increase in biomass at high CO2 occurred mainly aboveground in 1991, a dry year, and belowground in 1990, a wet year. Nitrogen concentration was lower in plants exposed to elevated CO2, but total standing crop N was greater at high CO2. Increased root biomass under elevated CO2 apparently increased N uptake. The biomass production response to elevated CO2 was much greater on N-fertilized than unfertilized prairie, particularly in the dry year. We conclude that biomass production response to elevated CO2 was suppressed by N limitation in years with below-normal precipitation. Reduced N concentration in above-and belowground biomass could slow microbial degradation of soil organic matter and surface litter, thereby exacerbating N limitation in the long term.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, DYNAMICS, ENRICHMENT, ESTUARINE MARSH, GROWTH, PLANTS, RESPONSES

1765

Owensby, C.E., P.I. Coyne, and L.M. Auen. 1993. Nitrogen and phosphorus dynamics of a tallgrass prairie ecosystem exposed to elevated carbon-dioxide. *Plant, Cell and Environment 16(7):843-850.*

A tallgrass prairie ecosystem was exposed to ambient and twice- ambient CO2 ConCentrations in open-top chambers and compared to unchambered ambient CO2 during the entire growing season from 1989 through 1991. Dominant species were Andropogon gerardii (C4), A. scoparius (C4), Sorghastrum nutans (C4) and Poa pratensis (C3). Nitrogen and phosphorus concentrations in A. gerardii, P. pratensis and dicotyledonous herbs above ground biomass were estimated by periodic sampling throughout the growing season in 1989 and 1990. In 1991, N and P concentrations in peak biomass were estimated by an early August harvest. N and P concentrations in root production as a function of treatment were estimated using root ingrowth bags that remained in place throughout the growing season. Total N and P in above- and belowground biomass were calculated as products of concentration and peak biomass by species groups. N concentration in A. gerardii and dicotyledonous herb aboveground biomass was lower and total N higher in elevated CO2 plots than in ambient CO2 PlOts. N concentration in P. pratensis aboveground biomass was lower in elevated CO2 plots than in ambient, but total N did not differ among treatments in 2 out of 3 years. In 1990, N concentration in root ingrowth bag biomass was lower and total N greater in elevated CO2 than in ambient CO2 plots. Root ingrowth bag biomass N concentration did not differ among treatments in 1991, but total N was greater in elevated CO2 plots than in ambient CO2 Plots. P concentration was lower under elevated CO2 compared to ambient in 1989, but did not differ substantially among treatments in 1990 or 1991. In all years, total P in aboveground A. gerardii and root ingrowth bag biomass was greater under elevated CO2 than ambient. P concentration and total P in P. pratensis was similar among treatments.

KEYWORDS: ATMOSPHERIC CO2, C-3, COMMUNITIES, ENRICHMENT, ESTUARINE MARSH, GROWTH, INSECT HERBIVORE, MYCORRHIZAL FUNGI, PLANTS, TEMPERATURE

1766

Owensby, C.E., P.I. Coyne, J.M. Ham, L.M. Auen, and A.K. Knapp. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated co2. *Ecological Applications 3(4):644-653.*

Responses to elevated CO2 have not been measured for natural grassland ecosystems. Global carbon budgets will likely be affected by changes in biomass production and allocation in the major terrestrial ecosystems. Whether ecosystems sequester or release excess carbon to the atmosphere will partly determine the extent and rate that atmospheric CO2 concentration rises. Elevated CO2 also may change plant community species composition and water status. We determined above- and belowground biomass production, plant community species composition, and measured and modeled water status of a tallgrass prairie ecosystem in Kansas exposed to ambient and twice-ambient CO2 concentrations in open-top chambers during the entire growing season from 1989 through 1991. Dominant species were Andropogon gerardii, A. scoparius, and Sorghastrum nutans (C-4 metabolism) and Poa pratensis (C-3). Aboveground biomass and leaf area were estimated by periodic sampling throughout the growing season in 1989 and 1990. In 1991, peak biomass and leaf area were estimated by an early August harvest. Relative root production among treatments was estimated using root ingrowth bags which remained in place throughout the growing season. Latent heat flux was simulated with and without water stress. Botanical composition was estimated annually. Compared to ambient CO2 levels, elevated CO2 increased production of C-4 grass species, but not of C-3 grass species. Species composition of C-4 grasses did not change, but Poa pratensis (C-3) declined, and C-3 forbs increased in the stand with elevated CO2 compared to ambient. Open-top chambers appeared to reduce latent heat flux and increase water-use efficiency similar to the elevated CO2 treatment when water stress was not severe, but under severe water stress, the chamber effect on water-use efficiency was limited. In natural ecosystems with periodic moisture stress, increased water-use efficiency under elevated CO2 apparently would have a greater impact on productivity irrespective of photosynthetic pathway.

KEYWORDS: BALANCE, BLUESTEM, CARBON DIOXIDE, COMMUNITIES, ESTUARINE MARSH, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RESPONSES, WATER-USE EFFICIENCY

1767

Owensby, C.E., J.M. Ham, A.K. Knapp, and L.M. Auen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO2. *Global Change Biology 5(5):497-506.*

To determine the long-term impact of elevated CO2 on primary production of native tallgrass prairie, we compared the responses of tallgrass prairie at ambient and twice-ambient atmospheric CO2 levels over an 8-year period. Plots in open-top chambers (4.5 m diameter) were exposed continuously (24 h) to ambient and elevated CO2 from early April to late October each year. Unchambered plots were monitored also. Aboveground peak biomass was determined by clipping each year in early August, and root growth was estimated by harvesting roots from root ingrowth bags. Plant community composition was censused each year in early June. In the last 2 years of the study, subplots were clipped on 1 June or 1 July, and regrowth was harvested on 1 October. Volumetric soil water content of the 0-100 cm soil layer was determined using neutron scattering, and was generally higher in elevated CO2 plots than ambient. Peak aboveground biomass was greater on elevated CO2 plots than ambient CO2 plots with or without chambers during years with significant plant water stress. Above-ground regrowth biomass was greater under elevated CO2 than under ambient CO2 in a year with late-season water stress, but did not differ in a wetter year. Root ingrowth biomass was also greater in elevated CO2 plots than ambient CO2 plots when water stress occurred during the growing season. The basal cover and relative amount of warm-season perennial grasses (C4) in the stand changed little during the 8-year period, but basal cover and relative amount of cool-season perennial grasses (C3) in the stand declined in the elevated CO2 plots and in ambient CO2 plots with chambers. Forbs (C3) and members of the Cyperaceae (C3) increased in basal cover and relative amount in the stand at elevated compared to ambient CO2. Greater biomass production under elevated CO2 in C4-dominated grasslands may lead to a greater carbon sequestration by those ecosystems and reduce peak atmospheric CO2 concentrations in the future.

KEYWORDS: AMBIENT, C-4 GRASS, CARBON DIOXIDE, COMPETITIVE INTERACTIONS, DECOMPOSITION, LEAF LITTER, NITROGEN, RESPONSES, TERRESTRIAL ECOSYSTEMS, WATER RELATIONS

1768

Owensby, C.E., J.M. Ham, A.K. Knapp, D. Bremer, and L.M. Auen. 1997. Water vapour fluxes and their impact under elevated CO2 in a C4-tallgrass prairie. *Global Change Biology 3(3):189-195.*

We measured leaf-level stomatal conductance, xylem pressure potential, and stomate number and size as well as whole plant sag now and canopy-level water vapour fluxes in a C4-tallgrass prairie in Kansas exposed to ambient and elevated CO2. Stomatal conductance was reduced by as much as 50% under elevated CO2 compared to ambient. In addition, there was a reduction in stomate number of the C4 grass, Andropogon gerardii Vitman, and the C3 dicot herb, Salvia pitcheri Torr., under elevated CO2 compared to ambient. The result was an improved water status for plants exposed to elevated CO2 which was

reflected by a less negative xylem pressure potential compared to plants exposed to ambient CO2. Sap flow rates were 20 to 30% lower for plants exposed to elevated CO2 than for those exposed to ambient CO2. At the canopy level, evapotranspiration was reduced by 22% under elevated CO2. The reduced water use by the plant canopy under elevated CO2 extended the photosynthetically-active period when water became limiting in the ecosystem. The result was an increased above- and belowground biomass production in years when water stress was frequent.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, C-4 GRASS, CARBON DIOXIDE, CHAMBER, ECOSYSTEMS, FLOW, INCREASE, RESPONSES, STOMATAL DENSITY

1769
Pacala, S.W., and D.H. Deutschman. 1995. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos 74(3):357-365.*

This paper shows that the processes controlling tree-scale spatial heterogeneity in forests have large effects on system- level properties such as standing crop, and on community-level properties such as successional species turnover. A "mean field" version of the forest simulation model SORTIE is developed in which horizontal spatial heterogeneity is eliminated while vertical structure is retained. The mean-field model maintains only approximately one half the standing crop and looses successional diversity approximately twice as fast as the full spatial model. Data from natural stands support the spatial model. A partial differential equation limit of the mean-field simulator is also derived. The results are set in the context of ongoing efforts to develop models intended to predict the biosphere's response to global change. The importance of processes governing fine-scale spatial heterogeneity implies that biospheric models will agree with nature only ii they are phenomenological (e.g. fitted to data) at large scale, or if spatial scaling rules are discovered that allow one to derive system-level properties from individual- level processes.

KEYWORDS: CO2, MODEL, RESPONSES

1770
Pachepsky, L.B., and B. Acock. 1996. An adequate model of photosynthesis .2. Dependence of parameters on environmental factors. *Agricultural Systems 50(2):227-238.*

Models of photosynthesis are commonly written as functions of light, temperature and CO2 concentration ([CO2]). In an ideal model, the parameter values would be independent of these environmental factors. However, there is no ideal photosynthesis model, so it is necessary to know how the parameters vary in response to the environment. Three of the most popular models of photosynthesis were fitted to experimental data for tomato plants, including light response curves measured at temperatures of 18, 25 and 32 degrees C and [CO2] of 100, 350, 700 and 1000 vpm. Statistical analysis of parameter values allowed us to find their dependencies on environmental factors. Light utilization efficiency oc proved to be constant at ambient and elevated [CO2]. Values of alpha at 100 mu l l(-1) [CO2] were approximately half of those at 350, 700 and 1000 mu l l(-1) [CO2]. Leaf conductance for CO2 transfer tau depended on temperature as well as on [CO2]. Two other parameters, one connected with respiration, R and Farquhar's 'curvature factor' theta, were both linearly dependent on temperature.

KEYWORDS: C-3, CO2, LIGHT, O2, PLANTS, TEMPERATURE

1771
Pachepsky, L.B., and B. Acock. 1996. A model 2DLEAF of leaf gas exchange: Development, validation, and ecological application. *Ecological Modelling 93(1-3):1-18.*

A two-dimensional model (2DLEAF) of leaf photosynthesis and transpiration has been developed that explicitly accounts for gas diffusion through the boundary layer and the intercellular space as well as for stomatal regulation. The model has been validated for tomato. It was used to study the effect of stomatal density on photosynthesis and transpiration rate. It has been demonstrated by varying stomatal density in the model that the stomatal density measured on tomato leaves provides the maximal photosynthesis rate for both 300 and 600 mu l l(-1) [CO2]. The transpiration rate varied in direct proportion to stomatal density at all values of stomatal aperture, but transpiration efficiency (photosynthesis rate/transpiration rate) was higher at 600 mu l l(-1) [CO2] with a normal stomatal density than at 300 mu l l(-1) [CO2] with a stomatal density reduced 25%, Such calculations with 2DLEAF can be useful for analysis of contradicting data presented in publications on possible changes in stomatal density in a future high [CO2] atmosphere.

KEYWORDS: CONDUCTANCE, DENSITY, ELEVATED CO2, INCREASES, LEAVES, NUMBERS, PHOTOSYNTHESIS, TRANSPORT

1772
Pachepsky, L.B., J.D. Haskett, and B. Acock. 1995. A two-dimensional model of leaf gas exchange with special reference to leaf anatomy. *Journal of Biogeography 22(2-3):209-214.*

This model of leaf gas exchange includes (1) two-dimensional CO2, O-2 and water vapour diffusion in intercellular space schematized according to leaf anatomy, (2) CO2 assimilation by mesophyll cells as described by Farquhar's model of photosynthesis and (3) stomatal movements as a regulating factor. Parameters describing the leaf cross-section and gas diffusion properties replace the empirical parameters of earlier models. The model was tested for soybean and performed well in representing light, CO2 concentration ([CO2]), and temperature response curves as well as the dependence of transpiration on temperature and water vapour deficit. The model allows the calculation of the steady state distribution of CO2 and water vapour concentrations in the intercellular space and the boundary layer. The direct calculation of diffusion in leaves showed that stomatal aperture effectively regulates the transpiration rate but usually has a much smaller effect on the rate of assimilation.

KEYWORDS: LEAVES, MATHEMATICAL-MODEL, PHOTOSYNTHESIS, TRANSPIRATION, WATER-USE EFFICIENCY

1773
Paffen, B.G.P., and J.G.M. Roelofs. 1991. Impact of carbon-dioxide and ammonium on the growth of submerged Sphagnum cuspidatum. *Aquatic Botany 40(1):61-71.*

In a culture experiment, the influence of carbon dioxide and ammonium on the growth of Sphagnum cuspidatum Hoffin. was studied. During a 12-week period, S. cuspidatum was grown in a solution with various concentrations of carbon dioxide and ammonium. The culture experiment clearly demonstrated that the biomass and the length of S. cuspidatum only increased strongly when the carbon dioxide concentration of the water was high. Further it is shown that ammonium enrichment without CO2 enrichment does not lead to an increase in biomass of S. cuspidatum.

KEYWORDS: ACIDIFICATION, EUTROPHICATION, MACROPHYTE COMMUNITIES, NITRATE REDUCTASE-ACTIVITY, SOFT WATERS

1774
Pajari, B. 1995. Soil respiration in a poor upland site of scots pine stand

subjected to elevated-temperatures and atmospheric carbon concentration. *Plant and Soil 169:563-570.*

Soil respiration rates under elevated temperature and atmospheric CO2 concentrations were studied in eastern Finland (62 degrees 47'N, 30 degrees 58'E, 144 m.a.s.l.) around naturally regenerated 20 - 30 years old Scots pine trees, enclosed in open top chambers. The production of CO2 varied spatially and temporally, but clearly followed the changes in temperature measured at the soil surface. However, soil respiration in the open control was higher than that in chambers; i.e. the chamber itself changed the conditions by increasing the temperature, altering the movement of water, and thereby soil moisture, Nevertheless, an elevation in the concentration of atmospheric CO2 raised soil respiration and brought it nearer to the level in the open control. An increase in temperature seemed to inhibit this rise, possibly because of an imbalance between temperature and moisture.

KEYWORDS: CO2, DIOXIDE, ECOSYSTEMS, MODEL

1775

Pal, R.K., and R.W. Buescher. 1993. Respiration and ethylene evolution of certain fruits and vegetables in response to carbon-dioxide in controlled- atmosphere storage. *Journal of Food Science and Technology-Mysore 30(1):29-32.*

Respiration was depressed by 10-30% CO2 in ripening bananas, pink tomatoes and pickling cucumbers; increased by 20-30% in carrot roots and unaffected by CO2 exposure in guava, orange and onion bulb. Changes in respiration seldom coincided with changes in C2H4 evolution. Evolution of C2H4 from guavas and tomatoes was substantially reduced by all levels of CO2. However, 30% CO2, accelerated C2H4 evolution in bananas, carrot roots, cucumbers, onions and potatoes which may have been due to an early injury response.

1776

Palet, A., M. Ribascarbo, J.M. Argiles, and J. Azconbieto. 1991. Short-term effects of carbon-dioxide on carnation callus cell respiration. *Plant Physiology 96(2):467-472.*

The addition of potassium bicarbonate to the electrode cuvette immediately stimulated the rate of dark O2 uptake of photomixotrophic and heterotrophic carnation (Dianthus caryophyllus L.) callus, of Elodea canadensis (Michx) leaves, and of other plant tissues. This phenomenon occurred at pH values lower than 7.2 to 7.8, and the stimulation depended on the concentration of gaseous CO2 in the solution. These stimulatory responses lasted several minutes and then decreased, but additional bicarbonate or gaseous CO2 again stimulated respiration, suggesting a reversible effect. Carbonic anhydrase in the solution increased the stimulatory effect of potassium bicarbonate. The CO2/bicarbonate dependent stimulation of respiration did not occur in animal tissues such as rat diaphragm and isolated hepatocytes, and was inhibited by salicylhydroxamic acid in carnation callus cells and E. canadensis leaves. This suggested that the alternative oxidase was engaged during the stimulation in plant tissues. The cytochrome pathway was severely inhibited by CO2/bicarbonate either in the absence or in the presence of the uncoupler carbonyl-cyanide m-chlorophenyl hydrazone. The activity of cytochrome c oxidase of callus tissue homogenates was also inhibited by CO2/bicarbonate. The results suggested that high carbon dioxide levels (mainly free CO2) Partially inhibited the cytochrome pathway (apparently at the oxidase level), and this block in electron transport elicited a large transient engagement of the alternative oxidase when present uninhibited.

KEYWORDS: CYANIDE-INSENSITIVE RESPIRATION, ELEVATED CO2 CONCENTRATIONS, LEAF, LEAVES, METABOLISM, PATHWAY, PEAR FRUIT, PH, PHOTOSYNTHESIS, PLANT-MITOCHONDRIA

1777

Palutikof, J.P., C.M. Goodess, and X. Guo. 1994. Climate-change, potential evapotranspiration and moisture availability in the mediterranean basin. *International Journal of Climatology 14(8):853-869.*

Simple methods for estimating potential evapotranspiration, requiring only temperature and day length data, are compared by reference to the results from the Penman method. A modification of the Blaney and Criddle method, in which the c parameter is calculated from seasonal regression equations with the mean monthly temperature as the independent variable, is proposed and tested. It is found to work sufficiently well in the area of interest, the Mediterranean Basin. For a network of 248 Mediterranean temperature stations, present-day seasonal mean potential evapotranspiration is estimated by this method. Using the results from four equilibrium-mode general circulation models, seasonal mean scenarios of potential evapotranspiration per 1-degree-C rise in global mean temperature caused by the enhanced greenhouse effect are presented. Comparison of scenarios of the change in potential evapotranspiration and scenarios of the change in precipitation indicates an unfavourable shift in moisture availability due to the enhanced greenhouse effect, throughout the Mediterranean region.

KEYWORDS: CO2, SENSITIVITY

1778

Pan, Q., Z. Wang, and B. Quebedeaux. 1998. Responses of the apple plant to CO2 enrichment: changes in photosynthesis, sorbitol, other soluble sugars, and starch. *Australian Journal of Plant Physiology 25(3):293-297.*

There is no information on the effects of elevated [CO2] on whole-plant photosynthesis and carbohydrate metabolism in apple (Malus domestica Borkh.) and other sorbitol-translocating plants. Experiments were conducted in controlled growth chambers to evaluate how increases in [CO2] affect plant photosynthesis and carbon partitioning into soluble sugars and starch in apple leaves. Apple plants (cv, Gala), 1-year-old, were exposed to [CO2] of 200, 360, 700, 1000, and 1600 mu L L-1 up to 8 d. Whole-plant net photosynthetic rates were analysed daily after [CO2] treatments. Newly expanded mature leaves were sampled at 1, 2, 4, and 8 d after [CO2] treatments for sorbitol, sucrose, glucose, fructose, and starch analysis. Midday whole-plant net photosynthetic rates increased linearly with increasing [CO2], but the differences in whole-plant photosynthesis between CO2-enrichment and ambient [CO2] treatments were less significant as apple plants acclimated to high atmospheric [CO2] for 8 d. Increases in [CO2] significantly increased sorbitol and starch, but did not affect sucrose concentrations. As a result, the ratios of starch to sorbitol and starch to sucrose at 8 d after [CO2] treatments were increased from 0.05 and 0.06 to 0.8 and 1.6 as [CO2] increased from ambient [CO2] (360 mu L L-1) to 1000 mu L L-1 [CO2], respectively. The sorbitol to sucrose ratio also increased from 1.3 to 2.2 as [CO2] increased from 360 to 1000 mu L L-1. Elevated [CO2] enhanced the photosynthesis of apple plants and altered carbohydrate accumulation in mature leaves in favour of starch and sorbitol over sucrose.

KEYWORDS: CARBOHYDRATE ACCUMULATION, CARBON DIOXIDE, ELEVATED CO2, EXCHANGE, GROWTH, RICE, WATER-STRESS

1779

Pan, Y.D., J.M. Melillo, A.D. McGuire, D.W. Kicklighter, L.F.

Pitelka, K. Hibbard, L.L. Pierce, S.W. Running, D.S. Ojima, W.J. Parton, and D.S. Schimel. 1998. Modeled responses of terrestrial ecosystems to elevated atmospheric CO2: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia 114(3):389-404.*

Although there is a great deal of information concerning responses to increases in atmospheric CO2 at the tissue and plant levels, there are substantially fewer studies that have investigated ecosystem-level responses in the context of integrated carbon, water, and nutrient cycles. Because our understanding of ecosystem responses to elevated CO2 is incomplete, modeling is a tool that can be used to investigate the role of plant and soil interactions in the response of terrestrial ecosystems to elevated CO2. In this study, we analyze the responses of net primary production (NPP) to doubled CO2 from 355 to 710 ppmv among three biogeochemistry models in the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP): BIOME-BGC (BioGeochemical Cycles), Century, and the Terrestrial Ecosystem Model (TEM). For the conterminous United States, doubled atmospheric CO2 causes NPP to increase by 5% in Century, 8% in TEM, and 11% in BIOME-BGC. Multiple regression analyses between the NPP response to doubled CO2 and the mean annual temperature aid annual precipitation of biomes or grid cells indicate that there are negative relationships between precipitation and the response of NPP to doubled CO2 for all three models. In contrast, there are different relationships between temperature and the response of NPP to doubled CO2 for the three models: there is a negative relationship in the responses of BIOME-BGC, no relationship in the responses of Century, and a positive relationship in the responses of TEM. In BIOME-BGC, the NPP response to doubled CO2 is controlled by the change in transpiration associated with reduced leaf conductance to water vapor. This change affects soil water, then leaf area development and, finally, NPP. In Century, the response of NPP to doubled CO2 is controlled by changes in decomposition rates associated with increased soil moisture that results from reduced evapotranspiration. This change affects nitrogen availability for plants, which influences NPP. In TEM, the NPP response to doubled CO2 is controlled by increased carboxylation which is modified by canopy conductance and the degree to which nitrogen constraints cause down-regulation of photosynthesis. The implementation of these different mechanisms has consequences for the spatial pattern of NPP responses, and represents, in part, conceptual uncertainly about controls over NPP responses. Progress in reducing these uncertainties requires research focused at the ecosystem level to understand how interactions between the carbon, nitrogen, and water cycles influence the response of NPP to elevated atmospheric CO2.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, FOREST-BGC, GAS-EXCHANGE, GENERAL-MODEL, NET PRIMARY PRODUCTION, REGIONAL APPLICATIONS, SOIL CARBON, TALLGRASS PRAIRIE, WATER-USE

1780

Panina, L.I., I.V. Motorina, M.N. Mamedov, and S.A. Makhmudov. 1997. Physicochemical conditions of the development of the tertiary trachybasalt-phonolite formation in the Talysh zone (Azerbaijan). *Geologiya I Geofizika 38(4):730-739.*

It has been established by mineral thermobarogeochemistry that the magmas initial of the trachybasalt-phonolite series in the Talysh zone were crystallized according to Bowen's scheme at the following temperatures and order of phenocryst formation: O1 (>1350 degrees C) --> Cpx (1280-1170 degrees C) --> Ap (1240-1030 degrees C) --> P1 (1190-1035 degrees C). The fluid phase at the time of olivine phenocryst crystallization was composed of 90 mol. % CO2 and 10 mol. % N-2, while at the stage of pyroxene and plagioclase formation it was 100 mol. % N-2. A drastic change in fluid composition is related to a discontinuity in time and place of phenocryst formation: olivine crystallization in deep-seated conditions, and formation of pyroxene and plagioclase in shallow depth of the Earth's crust. A microprobe study of silicate melt inclusions has shown that the evolution of the initial magma proceeded by means of differentiation and fractionation of minerals. In the process of crystallization the derivative melts were enriched in SiO2 (up to 64%), Al2O3 (up to 21%), alkalies (up to 10-11 wt.%) and were depleted in femic components (totalled to few per cent). Residual rhyolite-dacite alkali-enriched melts (67- 73% SiO2, 14-17% Al2O3, 4-8% alkalies) appeared in the final stages of magma evolution. The presence of alkalies brings us back to the problem of the mantle, <<basalt>>, origin of some siliceous rocks, as well as of the possibility to overcome an <<impassable>> barrier between quartz-normative acid melts and alkaline leucite-bearing rocks.

1781

Paoletti, E., G. Nourrisson, J.P. Garrec, and A. Raschi. 1998. Modifications of the leaf surface structures of Quercus ilex L in open, naturally CO2-enriched environments. *Plant, Cell and Environment 21(10):1071-1075.*

Two Italian CO2 springs allowed us to study the long-term effect of a 350-2600 mu mol mol(-1) increase in CO2 concentrations on the surface structures of leaves of Quercus ilex L. Carbon dioxide increased the quantity of cuticular waxes, above an apparent threshold of 750 mu mol mol(-1) CO2. Leaf wettability was not modified by CO2 concentrations. Reduction in stomatal frequency was observable up to 750 mu mol mol(-1) CO2, the slope being almost the same as that estimated for the increase in CO2 concentration from preindustrial times to the present. At higher concentrations, CO2 seemed to exert no more impact on stomatal frequency.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, CARBON DIOXIDE, CUTICLES, ELEVATED CO2, EPICUTICULAR WAX, LEAVES, NEEDLES, NORWAY SPRUCE, RESPONSES, STOMATAL DENSITY

1782

Papadopoulos, A.P., and X.M. Hao. 1997. Effects of three greenhouse cover materials on tomato growth, productivity, and energy use. *Scientia Horticulturae 70(2-3):165-178.*

Effects of single-layered glass (glass), double inflated polyethylene film (D-poly), and rigid-twin wall acrylic panels (acrylic), as greenhouse covers on tomato (Lycopersicon esculentum Mill) growth, productivity and energy use were investigated over two spring seasons in 1993 and 1994. There was no significant difference in early marketable yield (harvested until April 30) between the D-poly and glass houses. Early marketable yield in the acrylic houses was similar to that in the glass houses, but higher than that in the D-poly houses in 1994. Mid-season yield in the D-poly houses was lower than in the glass houses. Final marketable yield in the D-poly and acrylic houses was similar to that in the glass houses. Fruit size during the early and mid-season in the D-poly houses was smaller than in the glass or acrylic houses. This reduction in fruit size shifted 6-12% of grade #1 fruit from extra large to large. Fruit size in the glass and acrylic houses was similar. In 1993, there was a higher BER (blossom-end rot) incidence in the glass houses than in D-poly or acrylic houses, but a higher percentage of grade #1 fruit in the D-poly houses than in the glass or acrylic houses. The D-poly and acrylic houses saved 30% in heating energy compared to the glass houses. (C) 1997 Elsevier Science B.V.

KEYWORDS: CO2- ENRICHMENT, CUCUMBERS, GLASSHOUSE TOMATOES, HUMIDITY, QUALITY, TEMPERATURES, YIELD

1783

Parton, W.J., D.S. Ojima, and D.S. Schimel. 1994. Environmental-change in grasslands - assessment using models. *Climatic Change 28(1-2):111-141.*

Modeling studies and observed data suggest that plant production, species distribution, disturbance regimes, grassland biome boundaries and secondary production (i.e., animal productivity) could be affected by potential changes in climate and by changes in land use practices. There are many studies in which computer models have been used to assess the impact of climate changes on grassland ecosystems. A global assessment of climate change impacts suggest that some grassland ecosystems will have higher plant production (humid temperate grasslands) while the production of extreme continental steppes (e.g., more arid regions of the temperate grasslands of North America and Eurasia) could be reduced substantially. All of the grassland systems studied are projected to lose soil carbon, with the greatest losses in the extreme continental grassland systems. There are large differences in the projected changes in plant production for some regions, while alterations in soil C are relatively similar over a range of climate change projections drawn from various General Circulation Models (GCM's). The potential impact of climatic change on cattle weight gains is unclear. The results of modeling studies also suggest that the direct impact of increased atmospheric CO2 on photosynthesis and water use in grasslands must be considered since these direct impacts could be as large as those due to climatic changes. In addition to its direct effects on photosynthesis and water use, elevated CO2 concentrations lower N content and reduce digestibility of the forage.

KEYWORDS: BIOGEOCHEMISTRY, CLIMATE CHANGE, ECOSYSTEMS, GLOBAL CHANGE, GREAT-PLAINS, NITROGEN, SENSITIVITY, SOIL, TALLGRASS PRAIRIE, UNITED-STATES

1784

Parton, W.J., J.M.O. Scurlock, D.S. Ojima, D.S. Schimel, and D.O. Hall. 1995. Impact of climate-change on grassland production and soil carbon worldwide. *Global Change Biology 1(1):13-22.*

The impact of climate change and increasing atmospheric CO2 was modelled for 31 temperate and tropical grassland sites, using the CENTURY model. Climate change increased net primary production, except in cold desert steppe regions, and CO2 increased production everywhere. Climate change caused soil carbon to decrease overall, with a loss df 4 Pg from global grasslands after 50 years. Combined climate change and elevated CO2 increased production and reduced global grassland C losses to 2 Pg, with tropical savannas becoming small sinks for soil C. Detection of statistically significant change in plant production would require a 16% change in measured plant production because of high year to year variability in plant production. Most of the predicted changes in plant production are less than 10%.

KEYWORDS: DECOMPOSITION, GREAT-PLAINS, MODEL, NITROGEN, ORGANIC-MATTER DYNAMICS, STORAGE

1785

Pasquier-Cardin, A., P. Allard, T. Ferreira, C. Hatte, R. Coutinho, M. Fontugne, and M. Jaudon. 1999. Magma-derived CO2 emissions recorded in C-14 and C-13 content of plants growing in Furnas caldera, Azores. *Journal of Volcanology and Geothermal Research 92(1-2):195-207.*

The environmental impact of fumarolic and soil emanations of ma,oma-derived carbon dioxide across Furnas caldera has been investigated by measuring the C-14 and C-13 content of 40 specimens of different C3 plants (leaves) growing within and outside the degassing areas. The results demonstrate a significant to large C-14 depletion in many of the plants due to assimilation of C-14-free endogenous CO2 during photosynthesis and leading to artificial radiocarbon ageing of up to 4400 years. The extent of C-14 ageing broadly correlates with the intensity of gas manifestations at the sampling sites, as inferred from field observations and measurements of excess CO2 concentrations in the volcanic ground. It also provides a time-integrated measure of the amount of volcanic CO2 locally admired to the ambient air; at several sites this accounts for 15 to 40% of total CO2 (420 to 600 ppm) in enriched air, In some of the plant species (Azalea, Camellia and fern) C-14 depletion is correlated with an enrichment of C-13 due to assimilation of magma-derived CO2 with a 4 parts per thousand higher delta(13)C than normal atmosphere. The rate of C-13 enrichment averages ca. 0.18 parts per thousand by percent of volcanic carbon fixed in the plant and includes enhanced C-13 discrimination during photosynthesis as a consequence of increased ambient pCO(2) (inferred at - 0.0306 parts per thousand per added ppm of volcanic CO2). Furnas is one of the few Volcanoes where clear C-13 enrichment in plants due to endogenous degassing has been evidenced. Our results can be used to estimate the local intensity of volcanic soil gas fluxes in the emanating areas of Furnas caldera. They also have implications for radiocarbon dating of past eruptive events in the caldera, since plants artificially aged by previous degassing could be trapped in volcanic deposits.

KEYWORDS: ATMOSPHERIC CO2, CARBON, CRATER, SAO-MIGUEL, VULCANO-ISLAND

1786

Pataki, D.E., R. Oren, and D.T. Tissue. 1998. Elevated carbon dioxide does not affect average canopy stomatal conductance of Pinus taeda L. *Oecologia 117(1-2):47-52.*

While photosynthetic responses of C-3 plants to elevated CO2 are fairly well documented, whole-plant water use under such conditions has been less intensively studied. Woody species, in particular, have exhibited highly variable stomatal responses to high CO2 as determined by leaf-level measurements. In this study, sap flux of Pinus taeda L. saplings was periodically monitored during the 4th year of an open-top chamber CO2 fumigation experiment. Water use per unit sapwood area did not differ between treatments. Furthermore, the ratio of leaf area to sapwood area did not change under high CO2, so that average canopy stomatal conductance (on a unit leaf area basis) remained unaffected by the CO2 treatment. Thus, the only effect of high CO2 was to increase whole-plant water use by increasing sapling leaf area and associated conducting sapwood area. Such an effect may not directly translate to forest-level responses as the feedback effects of higher leaf area at the canopy scale cannot be incorporated in a chamber study. These feedbacks include the potential effect of higher leaf area index on rainfall and light interception, both of which may reduce average stomatal conductance in intact forest canopies.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, ENRICHMENT, FOREST, GROWTH, LEAF GAS- EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, RESPONSES, SAP FLOW, SEEDLINGS, WATER-STRESS

1787

Paterson, E., J.M. Hall, E.A.S. Rattray, B.S. Griffiths, K. Ritz, and K. Killham. 1997. Effect of elevated CO2 on rhizosphere carbon flow and soil microbial processes. *Global Change Biology 3(4):363-377.*

Direct effects of increased above-ground CO2 concentration on soil microbial processes are unlikely, due to the high pCO(2) of the soil atmosphere in most terrestrial ecosystems. However, below-ground microbial processes are likely to be affected through altered plant inputs at elevated CO2. A major component of plant input is derived from litter

fall and root turnover. Inputs also derive from rhizodeposition (loss of C-compounds from active root systems) which may account for up to 40% of photoassimilate. This input fuels the activity of complex microbial communities around roots. These communities are centrally important not only to plant-microbe interactions and consequent effects on plant growth, but also, through their high relative activity and abundance, to microbially mediated processes in soil generally. This review focuses on approaches to measure C-flow from roofs, in particular, as affected by increased atmospheric CO2 concentration. The available evidence for impacts on microbial communities inhabiting this niche, which constitutes an interface for possible perturbations on terrestrial ecosystems through the influence of environmental change, will also be discussed. While methodologies for measuring effects of increased CO2 concentration on plant growth, physiology and C-partitioning are abundant and widely reported, there is relatively little information on plant- mediated effects on soil microbial communities and processes. Importantly, many studies have also neglected to recognize that any secondary effects on microbial communities may have profound effects on plant parameters measured in relation to environmental change. We critically review approaches which have been used to measure rhizodeposition under conditions of increased atmospheric CO2 concentration, and then consider evidence for changes in microbial communities and processes, and the methodologies which have been recently developed, and are appropriate to study such changes.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, LOLIUM-PERENNE, ORGANIC-CARBON, PERENNIAL RYEGRASS, PSEUDOMONAS- FLUORESCENS, ROOT EXUDATION, TERRESTRIAL ECOSYSTEMS, WHITE CLOVER, ZEA MAYS L

1788

Paterson, E., A. Hodge, B. Thornton, P. Millard, and K. Killham. 1999. Carbon partitioning and rhizosphere C-flow in Lolium perenne as affected by CO2 concentration, irradiance and below-ground conditions. *Global Change Biology 5(6):669-678.*

Plant responses to increasing atmospheric CO2 concentrations have received considerable interest. However, major uncertainties in relation to interactive effects of CO2 with above- and below-ground conditions remain. This microcosm study investigated the impacts of CO2 concentration on plant growth, dry matter partitioning and rhizodeposition as affected by: (i) photon flux density (PFD), and (ii) growth matrix. Plants were grown in a sandy loam soil for 28 d under two photon flux densities: 350 (low PFD) and 1000 mu mol m(-2) s(-1) (high PFD) and two CO2 concentrations: 450 (low CO2) and 720 mu mol mol(- 1) (high CO2). Partitioning of recent assimilate amongst plant and rhizosphere C-pools was determined by use of (CO2)-C-14 pulse-labelling. In treatments with high PFD and/or high CO2, significant (P< 0.05) increases in dry matter production were found in comparison with the low PFD/low CO2 treatment. In addition, significant (P < 0.05) reductions in shoot %N and SLA were found in treatments imposing high PFD and/or high CO2. Root weight ratio (RWR) was unaffected by CO2 concentration, however, partitioning of C-14 to below ground pools was significantly (P< 0.05) increased. In a separate study, L. perenne was grown for 28 d in microcosms percolated with nutrient solution, in either a sterile sand matrix or nonsterile soil, under high or low CO2. Dry matter production was significantly (P< 0.01) increased for both sand and soil grown seedlings. Dry matter partitioning was affected by matrix type. C-14-allocation below ground was increased for sand grown plants. Rhizodeposition was affected by CO2 concentration for growth in each matrix, but was increased for plants grown in the soil matrix, and decreased for those in sand. The results illustrate that plant responses to CO2 are potentially affected by (i) PFD, and (ii) by feedbacks from the growth matrix. Such feedbacks are discussed in relation to soil nutrient status and interactions with the rhizosphere microbial biomass.

KEYWORDS: DIOXIDE, DRY-MATTER, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, GROWTH, NITROGEN, RESPONSES, ROOT EXUDATION, SOIL SYSTEM, WHOLE-PLANT LEVEL

1789

Paterson, E., E.A.S. Rattray, and K. Killham. 1996. Effect of elevated atmospheric CO2 concentration on C- partitioning and rhizosphere C-flow for three plant species. *Soil Biology and Biochemistry 28(2):195-201.*

The effects of elevated atmospheric CO2- concentration on the partitioning of dry matter and recent assimilate was investigated for three plant species (rye grass, wheat and Bermuda grass). This was evaluated in plant-soil microcosm systems maintained at specific growth conditions, under two CO2 regimes (450 and 720 mu mol mol(-1)). The distribution of recent assimilate between plant, microbial and soil pools was determined by (CO2)-C-14 pulse chase, for each plant species at both CO2 concentrations. Growth of rye grass and wheat (both C- 3) was Ca. doubled al the higher CO2 concentration. Dry matter partitioning was also significantly affected, with an increased root-to-shoot ratio for heat (0.72-1.03), and a decreased root- to-shoot ratio for rye grass (0.68-0.47) at elevated CO2. For Bermuda grass (C-4), growth and partitioning of dry matter and C-14 were not affected by CO2 concentration. C-14-allocation to the rhizospheres of rye-grass and wheat was found to be increased by 62 and 19%, respectively, at the higher CO2 concentration. The partitioning of C-14 within the rhizospheres of the two C-3 species was also found to be affected by CO2 concentralion. At the higher CO2 concentration. proportionately less C-14 was present in the microbial fraction, relative to that in the soil. This indicates altered microbial utilisation of root-released compounds at the higher CO2 concentration, which may be a consequence of altered quantity or quality of rhizodeposits derived from recent assimilate.

KEYWORDS: CARBON, ENRICHMENT, GROWTH, MAINTENANCE, MAIZE, NITROGEN, PHOTOSYNTHESIS, RESPIRATION, SOIL MICROBIAL BIOMASS, VEGETATION

1790

Patterson, B.W., X.J. Zhang, Y.P. Chen, S. Klein, and R.R. Wolfe. 1997. Measurement of very low stable isotope enrichments by gas chromatography mass spectrometry: Application to measurement of muscle protein synthesis. *Metabolism-Clinical and Experimental 46(8):943-948.*

Measurement of muscle protein synthesis using stable isotopically labeled tracers usually requires isotope ratio mass spectrometry (IRMS) because of the need to measure very low enrichments of stable isotopically labeled tracers (tracer to tracee ratio [TTR], 0.005% to 0.10%). This approach is laborious, requiring purification of the metabolite of interest and combustion to a gas for IRMS analysis, and is best suited for use with C-13 tracers. We have developed an approach whereby low enrichments can be conveniently measured by a conventional gas chromatography/mass spectrometry (GC/MS) instrument. The approach includes three critical elements: (1) use of a highly substituted tracer containing three or more labeled atoms, to measure enrichment above a very low natural abundance of highly substituted isotopomers; (2) use of a highly substituted natural abundance isotopomer as a base ion for comparison rather than the most abundant m + 0 isotopomer, to reduce the dynamic range of the isotopomer ratio measurement; and (3) a sensitive mass spectrometric analysis that measures the natural abundance of the isotopomer used as a tracer with a high signal to noise ratio (> 100:1). This approach was used to measure the rate of synthesis of muscle protein following a primed continuous infusion of L-[C-13(6)]- phenylalanine (PHE) in eight fasted dogs and L-[H-2(3)]-leucine in five fasted human subjects. Values for [C-13(6)]-PHE enrichment by GC/MS rates were virtually identicalthose obtained by a conventional approach using high-

performance liquid chromatography (HPLC) to isolate PHE, combustion to CO2, and measurement of (CO2)-C-13 enrichment by IRMS (IRMS enrichment = 0.9988 x GC/MS enrichment, R-2 = .891), resulting in identical values for muscle fractional synthesis rates ([FSRs] mean +/- SEM: 2.7 +/- 0.2 and 2.5 +/- 0.2%/d for GC/MS and IRMS, respectively). Human muscle synthesis rates measured by GC/MS analysis of [H-2(3)]-leucine enrichment (1.90 +/- 0.17%/d) were similar to published values based on IRMS analysis using a 1-C-13-leucine tracer. We conclude that compared with the IRMS approach, the GC/MS approach offers faster throughput, has a lower sample requirement, and is suitable for a wider variety of tracers such as H-2. The principles outlined here should be applicable to the measurement of low enrichments by GC/MS in a wide variety of stable isotope tracer applications. Copyright (C) 1997 by W.B. Saunders Company.

KEYWORDS: AMINO-ACIDS, HUMAN SKELETAL-MUSCLE

1791

Patterson, D.T. 1995. Effects of environmental-stress on weed/crop interactions. *Weed Science 43(3):483-490.*

All environmental factors that influence plant growth potentially can affect the ability of weeds and crops to exploit the environmental resources for which plants compete, Stressful levels of environmental factors such as temperature, light, and water and nutrient availability influence weed/crop interactions directly and also may interfere with (or enhance) weed control. Weed and crop species differing in photosynthetic pathway (C-3 VS C-4) are likely to respond differently to many of these factors. Long-term changes in the atmospheric concentrations of CO2 and other radiatively-active "greenhouse gases" may exert direct physiological and indirect climatic effects on weed/crop interactions and influence weed management strategies. This review focuses on the effects of temperature, light, soil nutrients, water stress, and CO2 concentration on weed/crop interactions with consideration of the potential impact of climate change.

KEYWORDS: ANODA ANODA-CRISTATA, BROADLEAF WEEDS, CORN ZEA-MAYS, COTTON GOSSYPIUM- HIRSUTUM, GROWTH-ANALYSIS, JIMSONWEED DATURA-STRAMONIUM, PIGWEED AMARANTHUS-RETROFLEXUS, SOYBEANS GLYCINE-MAX, VELVETLEAF ABUTILON-THEOPHRASTI, WATER RELATIONS

1792

Patterson, D.T. 1995. Weeds in a changing climate. *Weed Science 43(4):685-700.*

Current and projected increases in the concentrations of CO2 and other radiatively-active gases in the Earth's atmosphere lead to concern over possible impacts on agricultural pests, All pests would be affected by the global warming and consequent changes in precipitation, wind patterns, and frequencies of extreme weather events which may accompany the "greenhouse effect." However, only weeds are likely to respond directly to the increasing CO2 concentration, Higher CO2 will stimulate photosynthesis and growth in C-3 weeds and reduce stomatal aperture and increase water use efficiency in both C-3 and C-4 weeds, Respiration, and photosynthate composition, concentration, and translocation may be affected, Perennial weeds may become more difficult to control, if increased photosynthesis stimulates greater production of rhizomes and other storage organs, Changes in leaf surface characteristics and excess starch accumulation in the leaves of C-3 weeds may interfere with herbicidal control, Global warming and other climatic changes will affect the growth, phenology, and geographical distribution of weeds, Aggressive species of tropical and subtropical origins, currently restricted to the southern U.S., may expand northward. Any direct or indirect consequences of the CO2 increase that differentially affect the growth or fitness of weeds and crops will alter weed-crop competitive interactions, sometimes to the detriment of the crop and sometimes to its benefit.

KEYWORDS: ANODA ANODA-CRISTATA, ATMOSPHERIC CO2 ENRICHMENT, COTTON GOSSYPIUM- HIRSUTUM, ELEVATED CARBON-DIOXIDE, LONG-TERM EXPOSURE, PANICUM PANICUM-TEXANUM, PLANT GROWTH, SOYBEAN GLYCINE-MAX, VELVETLEAF ABUTILON-THEOPHRASTI, WATER-USE EFFICIENCY

1793

Paul, M.J., and S.P. Driscoll. 1997. Sugar repression of photosynthesis: The role of carbohydrates in signalling nitrogen deficiency through source:sink imbalance. *Plant, Cell and Environment 20(1):110-116.*

The aim of this work was to examine whether carbohydrates are involved in signalling N deficiency through source:sink imbalance. Photosynthetic metabolism in tobacco was studied over 8 d during the withdrawal of N from previously N- sufficient plants in which the source:sink ratio was manipulated by shading leaves on some of the plants, In N- sufficient plants over this timescale, there was a small decline in photosynthetic rate, Rubisco protein and amino acid content, with a larger decrease in carbohydrate content, Withdrawal of N from the growing medium induced a large decrease in the rate of photosynthesis (35% reduction after 8 d under the growing conditions, with a reduction also apparent at high and low measuring CO2), which was caused by a large decrease in the amount of Rubisco protein (62% after 8 d) and Rubisco activity, Higher amounts of hexoses preceded the loss of photosynthetic activity and sucrose and starch accumulation, Reduction of the source:sink ratio by shading prevented the loss of photosynthetic activity and the increase in hexoses and other carbohydrates, These data indicate that the reduction of photosynthesis that accompanies N deficiency in intact plants has the characteristics of sugar repression of photosynthesis observed in model systems, but that the accumulation of hexose prior to the decline in photosynthesis is small, The possibility that sugar repression of photosynthesis under physiological conditions depends more crucially on the C:N status of leaves than the carbohydrate status alone is discussed.

KEYWORDS: ACCLIMATION, CARBON METABOLISM, ELEVATED CO2, GAS-EXCHANGE, HIGHER-PLANTS, LEAF DEVELOPMENT, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPINACH LEAVES, SUCROSE, TEMPERATURE

1794

Paustian, K., E.T. Elliott, H.P. Collins, C.V. Cole, and E.A. Paul. 1995. Use of a network of long-term experiments for analysis of soil carbon dynamics and global change: The North American model. *Australian Journal of Experimental Agriculture 35(7):929-939.*

Soils contain a large proportion of the carbon (C) in the terrestrial biosphere, yet the role of soils as a sink or a source of net atmospheric C flux is uncertain. In agricultural systems, soil C is highly influenced by management practices and there is considerable interest in adapting management systems to promote soil C sequestration, thereby helping to mitigate atmospheric CO2 increases. Long-term field experimental sites represent a unique source of information on soil C dynamics, and networks of such sites provide a key ingredient for making large-scale assessments of soil C change across ranges in climate and soil conditions and management regimes. Currently, there are collaborative efforts to develop such site networks in Australia, Europe, and North America. A network of long-term experiments in North America was established to provide baseline information on the effects of management (i.e. tillage, crop rotations, fertilisation, organic amendments) on soil organic matter. Historical data on soils, primary productivity, climate, and management

were synthesised by scientists from the individual field sites, representing a total of 35 long-term field experiments. An additional cross-site soil sampling campaign was carried out to provide uniform comparisons of soil C and nitrogen (N), both within and across sites. Long-term field experiments are a principle component necessary for regional assessments of soil C dynamics. We describe a general methodology for combining long-term data with process-oriented simulation models and regional-level, spatially resolved databases. Such analyses are needed to assess past and present changes in soil C at regional to global scales and to make projections of the potential impacts of changes in climate, CO2, and landuse patterns on soil C in agroecosystems.

KEYWORDS: NITROGEN, ORGANIC-MATTER

1795

Paustian, K., E.T. Elliott, G.A. Peterson, and K. Killian. 1996. Modelling climate, CO2 and management impacts on soil carbon in semi-arid agroecosystems. *Plant and Soil 187(2):351-365.*

In agroecosystems, there is likely to be a strong interaction between global change and management that will determine whether soil will be a source or sink for atmospheric C. We conducted a simulation study of changes in soil C as a function of climate and CO2 change, for a suite of different management systems, at four locations representing a climate sequence in the central Great Plains of the US. Climate, CO2 and management interactions were analyzed for three agroecosystems: a conventional winter wheat-summer fallow rotation, a wheat-corn-fallow rotation and continuous cropping with wheat. Model analyses included soil C responses to changes in the amount and distribution of precipitation and responses to changes in temperature, precipitation and CO2 as projected by a general circulation model for a 2xCO(2) scenario. Overall, differences between management systems at all the sites were greater than those induced by perturbations of climate and/or CO2. Crop residue production was increased by CO2 enrichment and by a changed climate. Where the frequency of summer fallowing was reduced (wheat-corn-fallow) or eliminated (continuous wheat), soil C increased under all conditions, particularly with increased (640 mu L L-1) CO2. For wheat-fallow management, the model predicted declines in soil C under both ambient conditions and with climate change alone. Increased CO2 with wheat-fallow management yielded small gains in soil C at three of the sites and reduced losses at the fourth site. Our results illustrate the importance of considering the role of management in determining potential responses of agroecosystems to global change. Changes in climate will determine changes in management as farmers strive to maximize profitability. Therefore, changes in soil C may be a complex function of climate driving management and management driving soil C levels and not be a simple direct effect of either climate or management.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CO2, CROP RESPONSES, DYNAMICS, ENRICHMENT, FERTILIZATION, GREAT-PLAINS, ORGANIC-MATTER, ROTATIONS, SIMULATION

1796

Pearson, M., R.T. Besford, and D.W. Hand. 1994. The effects of oxides of nitrogen and carbon-dioxide enrichment on growth and content of ribulose-1, 5-bisphosphate carboxylase-oxygenase and nitrite reductase in glasshouse lettuce. *Journal of Horticultural Science 69(2):257-266.*

Different systems of CO2 enrichment and heating were used to produce glasshouse atmospheres with varying concentrations of NO(x) and CO2 (ambient NO(x) and CO2, ambient NO(x) and 1000 vpm CO2, and three concentrations of NO(x) varying between 0.5 and 2.5 vpm with concurrent CO2 concentrations between 1000- 2500 vpm). The growth response of winter lettuce in these environments was assessed for three contrasting cultivars (Ambassador, Berlo and Pascal). Contents of ribulose-1, 5- bisphosphate carboxylase-oxygenase (RuBPco) and nitrite reductase (NiR) in the leaf tissue were also determined using immunoblotting and enzyme-linked immunosorbent assay (ELISA). 'Ambassador' produced the heaviest "head" weights, but on marketable criteria 'Berlo' performed better. CO2 enrichment enhanced yields, but the High NO(x) treatments reduced growth relative to that in the Low NO(x) and unpolluted environments. Growth assessments suggested a greater tolerance of NO(x) in cvs Berlo and Pascal than in cv. Ambassador. Immunoblots showed that the antibodies used here were specific. Using these antibodies in ELISA, 'Pascal' was found to contain more RuBPco and NiR on a leaf area basis than 'Ambassador'. There were reductions in RuBPco and NiR contents in response to growth in elevated CO2. Elevated CO2 caused a reduction in RuBPco and NiR in 'Ambassador', but in 'Pascal' only RuBPco levels were reduced. This may account for the greater relative tolerance of 'Pascal' and the sensitivity of 'Ambassador' to NO(x) pollution.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, C-3 PLANTS, CALVIN CYCLE ENZYMES, LEAVES, PHOTOSYNTHETIC CO2 ASSIMILATION, RESPIRATION

1797

Pearson, M., and G.L. Brooks. 1995. The influence of elevated co2 on growth and age-related-changes in leaf gas-exchange. *Journal of Experimental Botany 46(292):1651-1659.*

Rumex obtusifolius plants were grown far several months in daylit environment chambers (Solardomes) force-ventilated with air containing 350 or 600 mu mol mol(-1) CO2. Elevated CO2 was found to accelerate the natural ontogenic decline in photosynthesis, but did not reduce leaf duration, In both CO2 treatments photosynthetic rates declined progressively with increasing leaf age, the decline being greater for plants grown in elevated CO2 such that rates became lower than in ambient CO2. The degree of CO2-induced photosynthetic down-regulation as determined by A/C-I analysis was found to be dependent on leaf age, The major contribution to the decline in photosynthesis was likely to be a reduction in Rubisco activity as changes in stomatal and mesophyll limitations were small. Instantaneous water use efficiency (WUE(i)) was greater for plants in elevated CO2, but these values declined rapidly with leaf age, whereas in ambient CO2 values were always lower, but were maintained for longer. Growth analysis indicated an increased root: shoot ratio for plants grown in elevated CO2, this occurring almost entirely as a result of increased root growth. Greater root proliferation and increased WUE(i) are characteristics which should give this persistent and troublesome weed an increased competitive under projected conditions of climate change.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE, PHOTOSYNTHESIS, PROTEIN, RESPONSES, RUMEX-OBTUSIFOLIUS L, TRANSPIRATION, WATER-USE EFFICIENCY

1798

Pearson, M., and G.L. Brooks. 1996. The effect of elevated CO2 and grazing by Gastrophysa viridula on the physiology and regrowth of Rumex obtusifolius. *New Phytologist 133(4):605-616.*

Plants of Rumex obtusifolius L. were grown in Solardomes under ambient and elevated (+ 250 mu mol mol-l) mole fractions of CO2 and were exposed to two levels of herbivory by Gastrophysa viridula Degeer larvae. The herbivory treatment lasted 1 month, thereafter half of the plants were harvested and over the following month during a period of regrowth physiological measurements were made on the remaining plants. At the termination of the herbivory treatment uninfested plants

showed no damage, whereas the low and high herbivore treatments caused 20-40% and 50-70% loss of leaf area as a proportion of total leaf area, respectively. The CO2 treatment did not affect the degree of defoliation. Total leaf area was not significantly affected by either CO2 or herbivory. Uninfested plants grown in elevated concentrations of CO2 showed increased growth, root- to-shoot ratios (RS), rates of photosynthesis and reduced stomatal conductance compared with uninfested plants grown in ambient CO2. A/C-i analysis revealed that plants grown in elevated CO2 showed reductions in Vc(max). For plants grown in ambient CO2 the high herbivory treatment led to increased rates of photosynthesis and decreased rates of dark respiration per unit leaf area, and caused increases in stomatal conductance and RS. For plants grown in elevated CO2 the high herbivory treatment increased plant biomass and RS. The increases in RS in response to elevated CO2 and herbivory appeared to be additive. Defoliation did not reduce the degree of photosynthetic down-regulation caused by growth in elevated concentrations of CO2, but appeared to reduce the rate of ontogenic decline in photosynthesis in ambient CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CHRYSOMELID BEETLE, GROWTH, HERBIVORY, PHOTOSYNTHETIC CAPACITY, PLANTS, RESPIRATION, SHORT-TERM, SOURCE-SINK RELATIONS

1799

Pearson, M., W.J. Davies, and T.A. Mansfield. 1995. Asymmetric responses of adaxial and abaxial stomata to elevated co2 - impacts on the control of gas-exchange by leaves. *Plant, Cell and Environment 18(8):837-843.*

The response of adaxial and abaxial stomatal conductance in Ruiner obtusifolius to growth at elevated atmospheric concentrations of CO2 (250 mu mol mol(-1) above ambient) was investigated over two growing seasons, The conductance of both the adaxial and abaxial leaf surfaces was found to be reduced by elevated concentrations of CO2. Elevated CO2 caused a much greater reduction in conductance for the adaxial surface than for the abaxial surface, The absence of effects upon stomatal density indicated that the reductions were probably the result of changes in stomatal aperture, Partitioning of gas exchange between the leaf surfaces revealed that increased concentrations of CO2 caused increased rates of photosynthesis only via the abaxial surface, Additionally, leaf thickness was found to increase during growth at elevated concentrations of CO2. The tendency for these amphistomatous leaves to develop a distribution of conductance approaching that of hypostomatous leaves clearly reduced their maximum photosynthetic potential. This conclusion was supported by measurements of stomatal limitation, which showed greater values for the adaxial surfaces, and greater values at elevated CO2. This reduction in photosynthesis may in part be caused by higher diffusive limitations imposed because of increased leaf thickness, in an uncoupled canopy, asymmetrical stomatal responses of the kind identified here may appreciably reduce transpiration, Species which show symmetrical responses are less likely to show reduced transpirational rates, and a redistribution of water loss between species may occur. The implications of asymmetrical stomatal responses for photosynthesis and canopy transpiration are discussed.

KEYWORDS: ACCLIMATION, CONDUCTANCE, GROWTH, PHOTOSYNTHESIS, SCALE, TOMATO

1800

Pearson, S., T.R. Wheeler, P. Hadley, and A.E. Wheldon. 1997. A validated model to predict the effects of environment on the growth of lettuce (Lactuca sativa L): Implications for climate change. *Journal of Horticultural Science 72(4):503-517.*

A mechanistic model is described that predicts the effects of changes to the environment on the growth, yield and maturity of lettuce. The model assumes that lettuce has structural and storage carbon pools. The storage pool is supplied by photosynthesis and depleted by respiratory losses and the conversion of assimilate to the structural pool. The model incorporated both instantaneous effects of temperature and CO2, and long term effects of thermal time on photosynthetic rate. The rate of structural dry-matter production was related to a simple temperature dependent partitioning coefficient. The model was calibrated on eight separate crops of lettuce and validated With independent data from seven sources. The validated model was then used to simulate changes in head weight and time to maturity with systematic changes in temperature (-2 to +5 degrees C in 1K steps) and carbon dioxide (350 to 700 ppm in 50 ppm steps) superimposed on baseline meteorological data from Rothamsted (1984-1995). These predicted that changes to temperature of up to +3 degrees C would reduce the production time from about 96 to 79 d for April plantings, and from 63 to 52 d for August plantings. Head weight would increase by approximately 32% with an increase in CO2 of from 350 to 700 ppm, whilst the magnitude of this response varied little with planting date. For any sowing date, increasing temperature was predicted to have little effect on final head weight, however, head weight was predicted to decrease with later transplanting. The potential effects of changes to climate on lettuce production are discussed.

KEYWORDS: CARBON DIOXIDE, CARROT, CO2, CROPS, ENRICHMENT, GREENHOUSE, LIGHT INTERCEPTION, TEMPERATURE, YIELD

1801

Pedersen, O., and K. SandJensen. 1997. Transpiration does not control growth and nutrient supply in the amphibious plant Mentha aquatica. *Plant, Cell and Environment 20(1):117-123.*

Mentha aquatica L. was grown at different nutrient availabilities in water and in air at 60% RH, The plants were kept at 600 mmol m(-3) free CO2 dissolved in water (40 times air equilibrium) and at 30 mmol m(-3) CO2 in air to ensure CO2 saturation of growth in both environments, We quantified the transpiration-independent water transport from root to shoot in submerged plants relative to the transpiration stream in emergent plants and tested the importance of transpiration in sustaining nutrient flux and shoot growth. The acropetal water flow was substantial in submerged Mentha aquatica, reaching 14% of the transpiration stream in emergent plants, The transpiration-independent mass flow of water from the roots, measured by means of tritiated water, was diverted to leaves and adventitious shoots in active growth, The plants grew well and at the same rates in water and air, but nutrient fluxes to the shoot were greater in plants grown in air than in those that were submerged when they were rooted in fertile sediments, Restricted O-2 supply to the roots of submerged plants may account for the smaller nutrient concentrations, though these exceeded the levels required to saturate growth, In hydroponics, the root medium was aerated and circulated between submerged and emergent plants to minimize differences in medium chemistry, and here the two growth forms behaved similarly and could fully exploit nutrient enrichment. It is concluded that the lack of transpiration from leaf surfaces in a vapour- saturated atmosphere, or under water, is not likely to constrain the transfer of nutrients from root to shoot in herbaceous plants, Nutrient deficiency under these environmental conditions is more likely to derive from restricted development and function of the roots in waterlogged anoxic soils or from low porewater concentrations of nutrients.

KEYWORDS: INORGANIC CARBON, ION-TRANSPORT, MACROPHYTES, PRESSURE, SAP, WATER TRANSPORT

1802

Peiris, D.R., J.W. Crawford, C. Grashoff, R.A. Jefferies, J.R.

Porter, and B. Marshall. 1996. A simulation study of crop growth and development under climate change. *Agricultural and Forest Meteorology 79(4):271-287.*

Climate changes of the order predicted by Global Circulation Models have important implications for arable crop production. We have studied the impact in Scotland using simulation models for three crops of contrasting developmental type: faba or field bean, potato, spring and winter wheat. The models used were the FABEAN, SCRI water-constrained potato model and AFRCWHEAT2 models respectively. Consideration has been made of the natural year-to-year variation in weather which causes yield variability by using 100 years of input weather data produced by a weather generator. The models were run for four Scottish sites and five Scottish soils. Based on GCM predictions, we used eight scenarios of future climate which combine both temperature and rainfall changes. Current temperature (T-0) and rainfall (R(0)) were used as a baseline, and each of T-0 + 1 degrees C, T-0 + 2 degrees C, T-0 + 3 degrees C were used with rainfall unchanged at R(0), and increased by seasonally adjusted amounts ranging from 0 to 1.5 mm per wet day. Possible enhancements due to CO2 fertilisation were not included in the study. Increased temperatures increase crop development rate, which shortens the growing season for wheat and faba bean, but, given a fixed harvest date, lengthens the season for potatoes. Yields of potato increased by up to 33% over all our sites and scenarios, whereas wheat yields decreased by 5-15% and faba bean by 11-41%. Rainfall increases of the amount suggested here do not affect the yield of potatoes or spring wheat, but winter wheat yields are reduced, due to leaching, and faba bean yields increase through alleviation of water shortage. Faba beans also show a reduction in yield variability as a result of increased rainfall. Changes in variability in wheat and potato were less pronounced and tended to reflect the increase in variability which was assumed to accompany the increased rainfall. Predictions for the changes in the frequencies of high and low yields are also presented. The results give an indication of the level of changes in crop production which would be expected in these future climates.

KEYWORDS: MODEL, SENSITIVITY, VARIABILITY, WATER

1803

Peisker, M., I. Heinemann, and M. Pfeffer. 1998. A study on the relationship between leaf conductance, CO2 concentration and carboxylation rate in various species. *Photosynthesis Research 56(1):35-43.*

Leaf conductance g(L) is strongly influenced by environmental factors like CO2, irradiance and air humidity. According to Ball et al. (1987), g(L) is correlated with an index calculated as the product of net CO2 exchange rate A and ambient water vapour concentration W-a, divided by ambient CO2 concentration c(a). However, this empirical model does not apply to high values of g(L) observed at c(a) below CO2 compensation concentration Gamma. Therefore, we applied modified indices in which A is replaced by estimates for the rate of carboxylation. Such estimates, P-1 and P-2, were determined by adding to A the quotient of Gamma and the sum of gas phase resistance r(g) and intracellular resistance for CO2 exchange r(i), P-1 = A+Gamma/(r(g) + r(i)). or the quotient of Gamma and r(i), P-2 = A + Gamma/r(i). If P-2 is chosen, c(a) in the Ball index has to be replaced by the intercellular CO2 concentration c(i). By using the modified indices P-1.W-a/c(a) and P-2.W-a/c(i), we analysed data from the C-3 species Nicotiana tabacum and Nicotiana plumbaginifolia, the C-3-C-4 intermediate species Diplotaxis tenuifolia, and the C-4 species Zea mays. The data were collected at widely varying levels of irradiance and CO2 concentration. For all species uniform relationships between g(L) and the new indices were found for the whole range of CO2 concentrations below and above Gamma. Correlations between g(L) and P-1.W-a/c(a) were closer than those between g(L) and P-2.W- a/c(i) because P-1/c(a) implicitly contains g(L). Highly significant correlations were also obtained for the relationships between g(L) and the ratios P-1/c(a) and P- 2/c(i).

KEYWORDS: C-3 PLANTS, ELEVATED CO2, EMPIRICAL-MODEL, GAS-EXCHANGE, GUARD-CELLS, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, STOMATAL CONDUCTANCE

1804

Peker, H., M.P. Srinivasan, J.M. Smith, and B.J. McCoy. 1992. Caffeine extraction rates from coffee beans with supercritical carbon-dioxide. *Aiche Journal 38(5):761-770.*

The extraction of caffeine from whole coffee beans with supercritical carbon dioxide was studied in a continuous-flow extraction apparatus. Decaffeination rates were determined as a function of CO2 flow rate, temperature and pressure by continuously monitoring the caffeine in the effluent with aflame ionization detector. Soaking the raw beans in water prior to decaffeination enhanced the rate of extraction, which increased markedly with water content. Using CO2 saturated with water also increased the rate of extraction. The rate of decaffeination increased with pressure and temperature and was influenced by both intraparticle diffusion in the water-soaked beans and external mass transfer. A mathematical model based on a linear-driving-force approximation of mass transfer and partitioning of caffeine between the water and the supercritical CO2 describes the time-dependent process. The partition coefficient for caffeine distributed between water and supercritical CO2, the only parameter determined from the dynamic extraction rate data, increases with temperature and pressure.

KEYWORDS: ACTIVATED CARBON, DESORPTION, MASS-TRANSFER

1805

Peng, C.H., and M.J. Apps. 1998. Simulating carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada - 2. Sensitivity to climate change. *Global Biogeochemical Cycles 12(2):393-402.*

The effects of climate change and doubling atmospheric CO2 on carbon dynamics of the boreal forest in the area of the Boreal Forest Transect Case Study in central Canada were investigated using the process-based plant-soil model CENTURY 4.0. The results presented here suggest that (1) across the transect climate change would result in increased total carbon in vegetation biomass but decreased overall carbon in soil; (2) increased atmospheric CO2 concentration under current climatic patterns would result in increased total carbon in vegetation and in soil organic matter; and (3) combined climate change and elevated CO2 would increase both net primary productivity and decomposition rates relative to the current climate condition, but their combined action would be a reduction of soil carbon losses relative to those due to climate change alone. The interactive effects of climate change and elevated CO2, however, are not a simple additive combination of the individual responses. The responses to climate change and elevated CO2 vary across the climate gradient from southern to northern sites on the transect. The present simulations indicate that the northern sites are more sensitive to climate change than the southern sites are, but these simulations do not consider likely changes in the disturbance regime or changes in forest species distribution.

KEYWORDS: BIOSPHERE-MODEL, C STORAGE, ECOSYSTEM PROCESSES, ELEVATED CO2, GENERAL-MODEL, LAND-USE, REGIONAL APPLICATIONS, RESPONSES, SOIL ORGANIC MATTER, TERRESTRIAL ECOSYSTEMS

1806

Peng, C.H., and M.J. Apps. 1999. Modelling the response of net

primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modelling 122(3):175-193.*

This study reports on the use of the process-based ecosystem model CENTURY 4.0 to investigate the patterns of net primary productivity (NPP) along a transect across the boreal forests of central Canada and the influence of climate change, CO2 fertilization and changing fire disturbance regimes on changes in NPP over time. Simulated NPP was tested against observed NPP data from northern sites near Thompson (Manitoba) and southern sites near Prince Albert (Saskatcheuan) and shown to be consistent with the data. The temporal dynamics of NPP were very different for the southern, central and northern sites, consistent with the hypothesis that different climate-driven processes regulate forest growth in the various regions of the boreal forest transect case study (BFTCS). The simulations suggest that climate change would result in increased NPP for most sites across the transect. According to the model results, increases in atmospheric CO2 also show increased NPP. The combined influence of climate change and elevated CO2 appear to interact in a positive, but non-linear manner. Statistical analysis of the simulation results indicate that changes in NPP are also positively correlated with changes in net N mineralization (R-2 = 0.89). This supports the conclusion that feedback via N cycling - a coupling of aboveground production with changes in belowground decomposition - is very important for understanding the NPP dynamics of the boreal forest under a changing climate. It was also found that NPP increases with greater fire frequency under current climate conditions, at least over the range of fire return intervals considered (50- 200 years). The influence of other changes in disturbance regimes (e.g. altered fire severity and concurrent changes in climate or CO2 fertilization), however, were not considered.

KEYWORDS: ATMOSPHERIC CO2, CASE-STUDY BFTCS, CENTRAL CANADA, ELEVATED CO2, GLOBAL-MODEL, MISSING CO2 SINK, SIMULATING CARBON DYNAMICS, SOIL ORGANIC MATTER, TALLGRASS PRAIRIE, TERRESTRIAL BIOSPHERE

1807

Peng, C.H., J. Guiot, and E. Van Campo. 1998. Past and future carbon balance of European ecosystems from pollen data and climatic models simulations. *Global and Planetary Change 18(3-4):189-200.*

As climate changes, there is considerable uncertainty whether northern hemisphere ecosystems will act as atmospheric CO2 sinks or sources. Here, we used statistical models calibrated on field measurements, past terrestrial biomes and climates inferred from pollen and future climatic change scenarios simulated by General Circulation Models (GCMs), to investigate the processes controlling past, present and future CO2 fluxes in the European ecosystems. Our results suggest that climatic change can significantly affect spatial and temporal variations of net primary production and soil respiration, and alter the net ecosystem exchange of CO2. Most of the potential terrestrial biomes in Europe will likely change from a net CO2 sink, which provided a negative feedback for atmospheric CO2 during the last 13 000 yr BP, to a net CO2 source, providing a positive feedback following global warming. The results further illustrate that there is no analogue in the recent past (Late Quaternary) for the probable future ecosystem dynamics.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERIC CO2, CYCLE, ELEVATED CO2, MISSING CO2 SINK, SOIL RESPIRATION, STORAGE, TERRESTRIAL BIOSPHERE, VEGETATION, YR BP

1808

Pennanen, A., V. Kemppi, D. Lawlor, and E. Pehu. 1992. The effect of elevated co2 on photosynthesis and chloroplast thylakoid structure of crop plants. *Photosynthesis Research 34(1):243.*

1809

Pennanen, A.H., J.C.V. Vu, L.H. Allen, and G. Bowes. 1995. Elevated co2 and temperature effects on enzymes of sucrose and starch synthesis in soybean. *Plant Physiology 108(2):90.*

1810

Penuelas, J., C. Biel, and M. Estiarte. 1995. Growth, biomass allocation, and phenology responses of pepper to elevated co2 concentrations and different water and nitrogen supply. *Photosynthetica 31(1):91-99.*

Fifty-day old plants of Capsicum annuum L. with two developed leaves were placed into controlled environment chambers at atmospheric (350 cm(3) m(-3), ACO(2)) and elevated (700 cm(3) m(-3), ECO(2)) CO2 concentrations under different nitrogen and water supply. Plant response to ECO(2) and the modulating effect of the availability of nitrogen and water were evaluated. CO2 effects were significant only after 40 d of treatment. An increase in plant growth and yield was found in ECO(2) plants only under a good supply of both water (HW) and nitrogen (HN). Chlorophyll concentration responded only to N supply. Root/shoot ratio was higher under ECO(2) only under low N (LN) and low water (LW) supply. Leaf area and specific leaf area decreased under ECO2. Flowering and fructification took place earlier in ECO(2) under HN and HW. Thus, all CO2 effects were modulated by the N and water supply and the duration of exposure.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, COTTON, CROP RESPONSES, LAST 3 CENTURIES, LEAF-AREA, MINERAL NUTRITION, PLANTS, TEMPERATURE, YIELD

1811

Penuelas, J., C. Biel, R. Save, and M. Estiarte. 1995. Detrimental effects of fluctuating high co2 concentrations on peppers. *Photosynthetica 31(3):361-370.*

Plants of pepper (Capsicum annuum L.) were grown in controlled environment chambers at ambient (360 mu mol mol(-1)) and fluctuating pulse-enriched CO2 concentrations (700 mu mol mol(- 1) daily average, ranging from 500 to 3500 mu mol mol(-1) = ECO(2)) under two water regimes. A decrease in plant growth and yield together with frequent visual injuries was found in plants growing under ECO(2). Root/shoot ratio was greater, chlorophyll concentration and respiration rates were lower, and stomatal conductance and relative importance of alternative pathway respiration were higher under ECO(2). The negative effects of ECO(2) were more intense under high water availability. The symptoms produced by ECO(2) were similar to those of resource limitation, and were alleviated with increased nutrient supply. Constant elevated CO2 concentrations (700 mu mol mol(-1)) increased pepper production and did not produce any of the injuries described for this erratic ECO(2) treatment. Thus, it is probably the erratic nature of the CO2 concentration and not the gas itself that was causing the injury.

KEYWORDS: CARBON DIOXIDE, CUCUMBERS, ENRICHMENT, FOLIAR DEFORMATION, LAST 3 CENTURIES, PLANTS, RESPONSES, STARCH, TOMATO, YIELD

1812

Penuelas, J., and M. Estiarte. 1997. Trends in plant carbon

concentration and plant demand for N throughout this century. *Oecologia 109(1):69-73.*

Atmospheric CO2 concentration has increased by 25% over the preindustrial level. A parallel increase in C concentration and decreases in N concentration and delta(13)C Of plants grown throughout this century have been observed in plant specimens stored in herbaria. We tested our previous results in a study of 12 more species collected in the western Mediterranean throughout this century (1920-1930, 1945-1955, and 1985-1990) and tree rings of Quercus pubescens from the same area. These changes were accompanied by apparent increases in condensed tannin concentration. A decreasing trend in delta(15)N both in herbarium material and tree rings was also found, indicating that ecosystems might cope with higher plant N demand by decreasing N losses and increasing N fixation and mineralization. These results may contribute to a better understanding of the effects of global change on carbon and nitrogen cycling.

KEYWORDS: ABUNDANCE, BALANCE, CO2, DIOXIDE, ECOSYSTEMS, FRACTIONATION, INCREASE, N-15, NITROGEN, NUTRITION

1813

Penuelas, J., M. Estiarte, B.A. Kimball, S.B. Idso, P.J. Pinter, G.W. Wall, R.L. Garcia, D.J. Hansaker, R.L. LaMorte, and D.L. Hendrix. 1996. Variety of responses of plant phenolic concentration to CO2 enrichment. *Journal of Experimental Botany 47(302):1463-1467.*

A wide range of responses to elevated CO2 was found for leaf total phenolic concentration of one grass species (wheat) growing in a Free-Air CO2 Enrichment (FACE) system and two woody species (orange and pine trees) growing in Open-Top Chambers (OTC). The total phenolic concentration of wheat flag leaves grown at elevated [CO2] was increased for most of the grain-filling stages studied; there was no significant change in phenolic concentration of CO2-enriched orange tree leaves and CO2-enriched pine tree needles had reduced total phenolic concentration. There was an inverse relationship between the increase in leaf total phenolic concentration and increase in biomass of these pine trees. Different rates of increase in growth (carbon sink) produced by different environmental conditions or different resource availabilities apart from CO2 itself must be considered in order to understand the response of carbon-based-secondary-compounds to elevated CO2.

KEYWORDS: AIR, ALLELOCHEMICALS, ATMOSPHERIC CO2, CARBON NUTRIENT BALANCE, DIOXIDE, ELEVATED CO2, GROWTH, LAST 3 CENTURIES, SECONDARY METABOLITES, SUSCEPTIBILITY

1814

Penuelas, J., M. Estiarte, and J. Llusia. 1997. Carbon-based secondary compounds at elevated CO2. *Photosynthetica 33(2):313-316.*

From literature sources we compiled the data on carbon-based-secondary compounds CBSC (phenolics and terpenoids) and biomass of 17 plant species grown at different CO2 concentrations under low and high nutrient availabilities. With a low nutrient availability a possible inverse correlation was found between the biomass and CBSC changes. On the contrary, under a high nutrient availability, both the CBSC and biomass increased with elevated CO2. The wide variation in the CBSC production among species and compounds (larger responses in phenolics than in terpenoids) indicates that the allocation to CBSC may not completely be governed by changes in CO2 and nutrient availabilities per se. Yet the comparison shows that elevated CO2 generally loads the carbon into CBSC [their leaf concentration increased an overall average of 14 % at 700 mu mol(CO2) mol(-1)] which may improve our understanding of the carbon storage and cycling in ecosystems under the "global change" of climate.

KEYWORDS: ALLELOCHEMICALS, BIRCH, DECOMPOSITION, DIOXIDE, ENRICHMENT, GROWTH, METABOLITES, NUTRIENT BALANCE, PLANTS, WATER-STRESS

1815

Penuelas, J., S.B. Idso, A. Ribas, and B.A. Kimball. 1997. Effects of long-term atmospheric CO2 enrichment on the mineral concentration of Citrus aurantium leaves. *New Phytologist 135(3):439-444.*

Leaf mineral concentration of Citrus aurantium (sour orange tree) was measured at bi-monthly intervals from 30 to 85 months of exposure in a long-term study on the effects of a 300 mu mol mol(-1) enrichment of atmospheric CO2, under conditions of high nutrient and water supply. There were clear seasonal trends in the concentrations of most of the elements studied. There were initial decreases in the leaf concentrations of N and the xylem-mobile, phloem-immobile elements Mn, Ca and Mg, as well as a significant and sustained increase in the leaf concentration of B, and no changes in the concentrations of K, Fe, Na, P, S, Zn and Cu. Interestingly, the initial reductions in the leaf concentrations of Mn, N, Ca and Mg gradually disappeared with time.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, INSECT HERBIVORE INTERACTIONS, LAST 3 CENTURIES, NUTRIENT-UPTAKE, SOUR ORANGE TREES, TEMPERATURE, TERRESTRIAL ECOSYSTEMS

1816

Penuelas, J., and J. Llusia. 1997. Effects of carbon dioxide, water supply, and seasonality on terpene content and emission by Rosmarinus officinalis. *Journal of Chemical Ecology 23(4):979-993.*

Rosmarinus officinalis L. plants were grown under carbon dioxide concentrations of 350 and 700 mu mol/mol (atmospheric CO2 and elevated CO2) and under two levels of irrigation (high water and low water) from October 1, 1994 to May 31, 1996. Elevated CO2 led to increasingly larger monthly growth rates than the atmospheric CO2 treatments. The increase was 9.5% in spring 1995, 23% in summer 1995, and 53% in spring 1996 in the high-water treatments, whereas in low-water treatments the growth response to elevated CO2 was constrained until the second year spring, when there was a 47%, increase. The terpene concentration was slightly larger in the elevated CO2 treatments than in atmospheric CO2 treatments and reached a maximum 37% difference in spring 1996. There was no significant effect of water treatment, likely as a result of a mild low water treatment for a Mediterranean plant. Terpene concentration increased throughout the period of study, indicating possible age effects. The most abundant terpenes were alpha-pinene, cineole, camphor, borneol, and verbenone, which represented about 75% of the total. No significant differences were found in the terpene composition of the plants in the different treatments or seasons. The emission of volatile terpenes was much larger in spring (about 75 mu g/dry wt/hr) than in autumn (about 10 mu g/dry wt/hr), partly because of higher temperature and partly because of seasonal effect, but no significant difference was found because of CO2 or water treatment. The main terpene emitted was alpha-pinene, which represented about 50% of the total. There was no clear correlation between content and emission, either quantitatively or qualitatively. More volatile terpenes were proportionally more important in the total emission than in total content and in autumn than in spring.

KEYWORDS: ALLOCATION, BIRCH, CO2, FIR PSEUDOTSUGA-MENZIESII, MONOTERPENES, PLANTS, RESPONSES

1817

Penuelas, J., and R. Matamala. 1993. Variations in the mineral-composition of herbarium plant- species collected during the last 3 centuries. *Journal of Experimental Botany 44(266):1523-1525.*

Mineral content (dry weight basis) was determined for herbarium specimens of 12 C3 plants (trees, shrubs and herbs) collected during the last 250 years in N.E. Spain. Present values of Al, Ca, Cu, Sr, Fe, P, Mg, Mn, K, Na, S, and Zn were always lower than in any other period of the last three centuries. Only one C4 plant was analysed. It presented a similar pattern to the C3 plants. These results are in accordance with experimental results that have shown that the mineral content of plants grown in elevated CO2 is generally lowered. Increased atmospheric CO2 and other anthropogenic environmental changes are suggested as possible causes of the changes in mineral content.

KEYWORDS: ATMOSPHERIC CO2, INCREASE, PAST 2 CENTURIES

1818

Percival, D.C., J.T.A. Proctor, and M.J. Tsujita. 1996. Whole-plant net CO2 exchange of raspberry as influenced by air and root-zone temperature, CO2 concentration, irradiation, and humidity. *Journal of the American Society for Horticultural Science 121(5):838-845.*

The influence of irradiance, CO2, and temperature on whole- plant net CO2 exchange rate (NCER) of Rubus idaeus L. 'Heritage' micropropagated raspberries was examined, Within the set of environmental conditions examined, irradiation was the most important factor, accounting for 58% of the whole-plant irradiance/CO2 concentration/temperature NCER model variation, followed by CO2 concentration (28%) and temperature (2.5%), Net photosynthesis (Pn) required irradiance levels >600 mu mol . m(-2). s(-1) PPF for saturation, greatly increased under CO2 enrichment (up to 1500 mu L . L(-1)), and was optimum at a whole-plant temperature of 20 degrees C. Temperature effects were partitioned in an experiment using varying air and root-zone temperatures (15, 20, 25, 30, and 35 degrees C) under saturated light and ambient CO2 levels (350 mu L . L(-1)). Air and root-zone temperature influenced Pn, with maximum rates occurring at an air x root-zone temperature of 17/25 degrees C. The contribution of air and root-zone temperature to the NCER model varied, with air and root-zone temperature contributing 75% and 24%, respectively, to the total model variation (R(2) = 0.96). Shoot dark respiration increased with air and root-zone temperature, and root respiration rates depended on air and root-zone temperature and shoot assimilation rate, Humidity also influenced Pn with a saturated vapor pressure deficit threshold >0.25 kPa resulting in a Pn decrease. Quantifying the physiological response of raspberries to these environmental parameters provides further support to recent findings that cool shoot/warm root conditions are optimum for raspberry plant growth.

KEYWORDS: ACQUISITION, CO2 EXCHANGE, ENRICHMENT, GROWTH, LEAVES, NUTRITION, PHOTOSYNTHESIS, RED RASPBERRY, RESPIRATION, RESPONSES

1819

Perezsoba, M., T.A. Dueck, G. Puppi, and P.J.C. Kuiper. 1995. Interactions of elevated co2, nh3 and o-3 on mycorrhizal infection, gas-exchange and n-metabolism in saplings of scots pine. *Plant and Soil 176(1):107-116.*

Four-year-old saplings of Scots pine (Pinus sylvestris L.) were exposed for 11 weeks in controlled-environment chambers to charcoal-filtered air, or to charcoal-filtered air supplemented with NH3 (40 mu g m(-3)), O-3 (110 mu g m(-3) during day/ 40 mu g m(-3) during night) or NH3 + O-3. All treatments were carried out at ambient (350 mu L L(-1)) and at elevated CO2 concentration (700 mu L L(-1)). Total tree biomass, mycorrhizal infection, net CO2 assimilation (P-n), stomatal conductance (g(s)), transpiration of the shoots and NH3 metabolization of the needles were measured. In ambient CO2 (1) gaseous NH3 decreased mycorrhizal infection, without significantly affecting tree biomass or N concentration and it enhanced the activity of glutamine synthetase (GS) and glutamate dehydrogenase (GDH) in one-year-old needles; (2) ozone decreased mycorrhizal infection and the activity of GS in the needles, while it increased the activity of GDH; (3) exposure to NH3 + O-3 lessened the effects of single exposures to NH3 and O-3 on reduction of mycorrhizal infection and on increase in GDH activity. Similar lessing effects on mycorrhizal infection as observed in trees exposed to NH3 + O-3 at ambient CO2, were measured in trees exposed to NH3 + O-3 at elevated CO2. Exposure to elevated CO2 without pollutants did not significantly affect any of the parameters studied, except for a decrease in the concentration of soluble proteins in the needles. Elevated CO2 + NH3 strongly decreased root branching and mycorrhizal infection and temporarily stimulated P-n and g(s). The exposure to elevated CO2 + NH3 + O-3 also transiently stimulated P-n. The possible mechanisms underlying and integrating these effects are discussed. Elevated CO2 clearly did not alleviate the negative effects of NH3 and O-3 on mycorrhizal infection. The significant reduction of mycorrhizal infection after exposure to NH3 or O-3, observed before significant changes in gas exchange or growth occurred, suggest the use of mycorrhizal infection as an early indicator for NH3 and O-3 induced stress.

KEYWORDS: ACCLIMATION, AMMONIUM-SULFATE, ATMOSPHERIC CARBON-DIOXIDE, DOUGLAS-FIR, FIR PSEUDOTSUGA-MENZIESII, GROWTH, OZONE, RESPONSES, SEEDLINGS, STRESS

1820

Perezsoba, M., L.J.M. Vandereerden, I. Stulen, and P.J.C. Kuiper. 1994. Gaseous ammonia counteracts the response of scots pine needles to elevated atmospheric carbon-dioxide. *New Phytologist 128(2):307-313.*

Four-year-old saplings of Scots pine (Pinus sylvestris L.) were exposed for 8 wk in controlled-environment chambers to charcoal-filtered air (FB), FA supplemented with 754 mg m(-3) (650 mu l l(-1)) CO2, FA supplemented with 100 mu g m(-3) NH3 and FA + CO2 + NH3. Elevated CO2 induced a significant increase in the concentrations of NH4+ and NO3- in the soil solution, while exposure to NH3 enhanced the soil NH4+ concentration. Elevated CO2 significantly increased needle biomass and area, and decreased specific leaf area (SLA) and N concentration in the needles. The activity of peroxidase (POD) was decreased, while the activities of glutamine synthetase (GS) and glutamate dehydrogenase (GDH) were only slightly affected. Gaseous NH3 enhanced the concentration of N, soluble proteins and the GS activity in the needles, while it decreased the POD and GDH activities. The effects of elevated CO2 + NH3 on needle biomass production, N metabolism and POD activity were smaller than the effects of single exposures to elevated CO2 or NH3, suggesting that elevated CO2 and NH3 counteract each other and disturb needle physiology. The possible mechanisms underlying the negative interactions of elevated CO2 and NH3 are discussed. The expected stimulation of biomass production by elevated CO2 may be reduced in the presence of atmospheric NH3.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, FORESTS, LEAVES, NH3, NITROGEN, PLANT GROWTH, SEEDLINGS, SOIL, SYLVESTRIS

1821

Perruchoud, D., F. Joos, A. Fischlin, I. Hajdas, and G. Bonani. 1999. Evaluating timescales of carbon turnover in temperate forest soils with radiocarbon data. *Global Biogeochemical Cycles 13(2):555-573.*

Timescales of soil organic carbon (SOC) turnover in forests were investigated with soil radiocarbon data. The C-12/C-14 ratios were measured by accelerated mass spectroscopy on soil sampled from a deciduous temperate forest in Switzerland during 1969-1995. The resulting Delta(14)C values (125-174 parts per thousand) were in line with previously published C-14 soil data. We applied FORCLIM-D, a model of nonliving organic matter decomposition including nine litter and two soil compartments to estimate SOC turnover times for this forest type. Carbon 14 aging in woody vegetation was explicitly accounted for. Parameters were calibrated to match radiocarbon ratios observed for forest soils at Meathop Wood, United Kingdom [Harkness et al., 1986]. We estimated that roughly 50-94% (best estimate, 49%) of foliar litter carbon and 11-74% (73%) of fine root litter carbon are eventually respired as CO2 at Meathop Wood; the rest is transferred to soil humus, where it undergoes further decomposition. Turnover times for the 0-20 cm mineral soil layer ranged from 9-50 years (25 years) for a fast overturning soil compartment comprising 38-74% (68%) of bulk SOC and 155-10,018 years (3,570 years) for a slowly overturning compartment. For the Swiss site, SOC turnover times were in the same range. Parameter uncertainties were correlated and induced by uncertainties in C-14 observations from small-scale spatial inhomogeneities, sample preparation and by lack of reliable C- 14 observations for the "prebomb" test period. Model-based estimates of soil organic C turnover derived from C-14 data must be used cautiously since they depend on the underlying model structure: bypassing litter in FORCLIM-D overestimated SOC turnover by a factor of 2.5. Such an error might remain undetected in studies lacking samples from the late 1960s and early 1970s. Thus litter C turnover should be included when estimating SOC turnover in temperate forests from C-14 data.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, ECOSYSTEMS, ELEVATED CO2, LAND-USE, LITTER PRODUCTION, NITROGEN, ORGANIC-MATTER TURNOVER, STORAGE, TERRESTRIAL

1822

Perumal, J.V., and M.A. Maun. 1999. The role of mycorrhizal fungi in growth enhancement of dune plants following burial in sand. *Functional Ecology 13(4):560-566.*

1, Burial in sand of Agropyron psammophilum and Panicum virgatum plants had a stimulating effect on carbon dioxide exchange rate, leaf area and biomass, irrespective of whether sand used for burial did or did not contain mycorrhizal fungi. 2, Plants of both A. psammophilum and P. virgatum species grown in mycorrhiza-containing sand and then buried with mycorrhiza- containing sand had the highest CO2 exchange rate, leaf area and biomass. 3, The growth stimulation following a burial episode is probably a composite response of several factors. The major contribution of mycorrhizal fungi will possibly be the exploitation of resources in the burial deposit.

KEYWORDS: AMMOPHILA-BREVILIGULATA, CALAMOVILFA-LONGIFOLIA, COMMUNITY STRUCTURE, MORPHOLOGY, PHOTOSYNTHESIS, SOIL

1823

Pesheva, I., M. Kodama, M.L. Dionisiosese, and S. Miyachi. 1994. Changes in photosynthetic characteristics induced by transferring air-grown cells of chlorococcum-littorale to high- co2 conditions. *Plant and Cell Physiology 35(3):379-387.*

When air-grown cells of Chlorococcum littorale was enriched with CO2, growth was enhanced after a lag period of one to two days at 20% CO2, and 3 to 6 days at 40% CO2. Changes in the rate of photosynthesis measured as oxygen evolution and CO2 fixation, were similar to those observed for growth. During the initial inhibition of photosynthesis in 40% CO2, the activity of PSII was suppressed. In contrast, PSI activity was greatly enhanced. Air-grown cells of C. littorale possessed comparatively high carbonic anhydrase (CA) activity which was localized inside the cells and on the cell surface. Under high CO2 concentrations extracellular CA activity was greatly suppressed and intracellular activity almost completely abolished. Phosphoenol pyruvate carboxylase activity was also suppressed in high CO2-grown cells. Ribulose-1,5-bisphosphate carboxylase activity was higher in high-CO2 grown cells than in air-grown cells. The above results indicated that the lag phase induced by 40% CO2 was due to suppression of PSII activity.

KEYWORDS: BISPHOSPHATE, CARBONIC-ANHYDRASE, CARBOXYLASE OXYGENASE CONTENT, CHLORELLA, CO2 CONCENTRATION, DIOXIDE, FIXATION, INDUCTION, INORGANIC CARBON, PLANTS

1824

Peterson, A.G., J.T. Ball, Y. Luo, C.B. Field, P.S. Curtis, K.L. Griffin, C.A. Gunderson, R.J. Norby, D.T. Tissue, M. Forstreuter, A. Rey, and C.S. Vogel. 1999. Quantifying the response of photosynthesis to changes in leaf nitrogen content and leaf mass per area in plants grown under atmospheric CO2 enrichment. *Plant, Cell and Environment 22(9):1109-1119.*

Previous modelling exercises and conceptual arguments have predicted that a reduction in biochemical capacity for photosynthesis (A(area)) at elevated CO2 may be compensated by an increase in mesophyll tissue growth if the total amount of photosynthetic machinery per unit leaf area is maintained (i.e. morphological upregulation). The model prediction was based on modelling photosynthesis as a function of leaf N per unit leaf area (N-area), where N-area = N-mass x LMA. Here, N-mass is percentage leaf N and is used to estimate biochemical capacity and LMA is leaf mass per unit leaf area and is an index of leaf morphology. To assess the relative importance of changes in biochemical capacity versus leaf morphology we need to control for multiple correlations that are known, or that are likely to exist between CO2 concentration, N-area, N-mass, LMA and A(area). Although this is impractical experimentally, we can control for these correlations statistically using systems of linear multiple-regression equations. We developed a linear model to partition the response of A(area), to elevated CO2 into components representing the independent and interactive effects of changes in indexes of biochemical capacity, leaf morphology and CO2 limitation of photosynthesis. The model was fitted to data from three pine and seven deciduous tree species grown in separate chamber-based field experiments. Photosynthetic enhancement at elevated CO2 due to morphological upregulation was negligible for most species. The response of A(area), in these species was dominated by the reduction in CO2 limitation occurring at higher CO2 concentration. However, some species displayed a significant reduction in potential photosynthesis at elevated CO2 due to an increase in LMA that was independent of any changes in N-area. This morphologically based inhibition of A(area) combined additively with a reduction in biochemical capacity to significantly offset the direct enhancement of A(area) caused by reduced CO2 limitation in two species. This offset was 100% for Acer rubrum, resulting in no met effect of elevated CO2 on A(area) for this species, and 44% for Betula pendula. This analysis shows that interactions between biochemical and morphological responses to elevated CO2 can have important effects on photosynthesis.

KEYWORDS: ACCLIMATION, C-3 PLANTS, ELEVATED CARBON-DIOXIDE, FIELD, GAS-EXCHANGE, LEAVES, MODEL, OPEN-TOP CHAMBERS, TEMPERATURE, TREES

1825

Peterson, A.G., J.T. Ball, Y.Q. Luo, C.B. Field, P.B. Reich, P.S. Curtis, K.L. Griffin, C.A. Gunderson, R.J. Norby, D.T. Tissue, M.

Forstreuter, A. Rey, and C.S. Vogel. 1999. The photosynthesis leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biology 5(3):331-346.*

Estimation of leaf photosynthetic rate (A) from leaf nitrogen content (N) is both conceptually and numerically important in models of plant, ecosystem, and biosphere responses to global change. The relationship between A and N has been studied extensively at ambient CO2 but much less at elevated CO2. This study was designed to (i) assess whether the A-N relationship was more similar for species within than between community and vegetation types, and (ii) examine how growth at elevated CO2 affects the A-N relationship. Data were obtained for 39 C3 species grown at ambient CO2 and 10 C3 species grown at ambient and elevated CO2. A regression model was applied to each species as well as to species pooled within different community and vegetation types. Cluster analysis of the regression coefficients indicated that species measured at ambient CO2 did not separate into distinct groups matching community or vegetation type. Instead, most community and vegetation types shared the same general parameter space for regression coefficients. Growth at elevated CO2 increased photosynthetic nitrogen use efficiency for pines and deciduous trees. When species were pooled by vegetation type, the A-N relationship for deciduous trees expressed on a leaf-mass basis was not altered by elevated CO2, while the intercept increased for pines. When regression coefficients were averaged to give mean responses for different vegetation types, elevated CO2 increased the intercept and the slope for deciduous trees but increased only the intercept for pines. There were no statistical differences between the pines and deciduous trees for the effect of CO2. Generalizations about the effect of elevated CO2 on the A-N relationship, and differences between pines and deciduous trees will be enhanced as more data become available.

KEYWORDS: CO2, FIELD, GAS-EXCHANGE, GROWTH, LEAVES, LIFE-SPAN, MODEL, NET PRIMARY PRODUCTION, OPEN-TOP CHAMBERS, USE EFFICIENCY

1826

Peterson, R.B. 1991. Effects of O2 and CO2 concentrations on quantum yields of photosystem-I and photosystem-II in tobacco leaf tissue. *Plant Physiology 97(4):1388-1394.*

The interactive effects of irradiance and O2 and CO2 levels on the quantum yields of photosystems I and II have been studied under steady-state conditions at 25-degrees-C in leaf tissue of tobacco (Nicotiana tabacum). Assessment of radiant energy utilization in photosystem II was based on changes in chlorophyll fluorescence yield excited by a weak measuring beam of modulated red light. Independent estimates of photosystem I quantum yield were based on the light-dark in vivo absorbance change at 830 nanometers, the absorption band of P700+. Normal (i.e. 20.5%, v/v) levels of O2 generally enhanced photosystem II quantum yield relative to that measured under 1.6% O2 as the irradiance approached saturation. Photorespiration is suspected to mediate such positive effects of O2 through increases in the availability of CO2 and recycling of orthophosphate. Conversely, at low intercellular CO2 concentrations, 41.2% O2 was associated with lower photosystem II quantum yield compared with that observed at 20.5% O2. Inhibitory effects of 41.2% O2 may occur in response to negative feedback on photosystem II arising from a build-up in the thylakoid proton gradient during electron transport to O2. Covariation between quantum yields of photosystems I and II was not affected by concentrations of either O2 or CO2. The dependence of quantum yield of electron transport to CO2 measured by gas exchange upon photosystem II quantum yield as determined by fluorescence was unaffected by CO2 concentration.

KEYWORDS: ABSORBANCE CHANGES, ASSIMILATION, CHLOROPHYLL FLUORESCENCE, CHLOROPLASTS, ELECTRON-TRANSPORT, EXCHANGE, LEAVES, PHOSPHATE, PHOTOREDUCTION, PHOTOSYNTHESIS

1827

Petschel- Held, G., H.J. Schellnhuber, T. Bruckner, F.L. Toth, and K. Hasselmann. 1999. The tolerable windows approach: Theoretical and methodological foundations. *Climatic Change 41(3-4):303-331.*

The tolerable windows (TW) approach is presented as a novel scheme for integrated assessment of climate change. The TW approach is based on the specification of a set of guardrails for climate evolution which refer to various climate-related attributes. These constraints, which define what we call tolerable windows, can be purely systemic in nature - like critical thresholds for the North Atlantic Deep Water formation - or of a normative type - like minimum standards for per- capita food production worldwide. Starting from this catalogue of knock-out criteria and using appropriate modeling techniques, those policy strategies which are compatible with all the constraints specified are sought to be identified. In addition to the discussion of the basic elements and the general theory of the TW approach, a modeling exercise is carried out, based on simple models and assumptions adopted from the German Advisory Council on Global Change (WBGU). The analysis shows that if the global mean temperature is restricted to 2 degrees C beyond the preindustrial level, the cumulative emissions of CO2 are asymptotically limited to about 1550 Gt C. Yet the temporal distribution of these emissions is also determined by the climate and socio-economic constraints: using, for example, a maximal tolerable rate of temperature change of 0.2 degrees C/ dec and a smoothly varying emissions profile, we obtain the maximal cumulative emissions, amounting to 370 Gt C in 2050 and 585 Gt C in 2100.

KEYWORDS: CLIMATE CHANGE, ECONOMICS, MODEL, THERMOHALINE CIRCULATION

1828

Pettersson, R., and A.J.S. McDonald. 1992. Effects of elevated carbon-dioxide concentration on photosynthesis and growth of small birch plants (betula-pendula roth) at optimal nutrition. *Plant, Cell and Environment 15(8):911-919.*

Small birch plants (Betula Pendula Roth.) were grown from seed for periods of up to 70 d in a climate chamber at optimal nutrition and at present (350 mumol mol-1)or elevated (700 mumol mol-1) concentrations of atmospheric CO2. Nutrients were sprayed over the roots in Ingestad-type units. Relative growth rate and net assimilation rate were slightly higher at elevated CO2, whereas leaf area ratio was slightly lower. Smaller leaf area ratio was associated with lower values of specific leaf area. Leaves grown at elevated CO2 had higher starch concentrations (dry weight basis) than leaves grown at present levels Of CO2. Biomass allocation showed no change with CO2, and no large effects on stem height, number of side shoots and number of leaves were found. However, the specific root length of fine roots was higher at elevated CO2. No large difference in the response of carbon assimilation to intercellular CO2 concentration (A/C(i) curves) were found between CO2 treatments. When measured at the growth environments, the rates of photosynthesis were higher in plants grown at elevated CO2 than in plants grown at present CO2. Water use efficiency of single leaves was higher in the elevated treatment. This was mainly attributable to higher carbon assimilation rate at elevated CO2. The difference in water use efficiency diminished with leaf age. The small treatment difference in relative growth rate was maintained throughout the experiment, which meant that the difference in plant size became progressively greater. Thus, where plant nutrition is sufficient to maintain maximum growth, small birch plants may potentially increase in size more rapidly at elevated CO2.

KEYWORDS: CO2 CONCENTRATION, ENRICHMENT, FORESTS,

LEAVES, ORANGE, RISING CO2, SEEDLINGS, SOURCE-SINK RELATIONS, WATER-USE EFFICIENCY, YIELD

1829

Pettersson, R., and A.J.S. McDonald. 1994. Effects of nitrogen supply on the acclimation of photosynthesis to elevated co2. *Photosynthesis Research 39(3):389-400.*

A common observation in plants grown in elevated CO2 concentration is that the rate of photosynthesis is lower than expected from the dependence of photosynthesis upon CO2 concentration in single leaves of plants grown at present CO2 concentration. Furthermore, it has been suggested that this apparent down regulation of photosynthesis may be larger in leaves of plants at low nitrogen supply than at higher nitrogen supply. However, the available data are rather limited and contradictory. In this paper, particular attention is drawn to the way in which whole plant growth response to N supply constitutes a variable sink strength for carbohydrate usage and how this may affect photosynthesis. The need for further studies of the acclimation of photosynthesis at elevated CO2 in leaves of plants whose N supply has resulted in well-defined growth rate and sink activity is emphasised, and brief consideration is made of how this might be achieved.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, BETULA-PENDULA ROTH, CARBON-DIOXIDE CONCENTRATION, CHENOPODIUM-ALBUM L, DRY-MATTER, LONG-TERM EXPOSURE, MINERAL NUTRITION, PHASEOLUS-VULGARIS L, PHOTON FLUX- DENSITY, PLANT GROWTH

1830

Pettersson, R., A.J.S. McDonald, and I. Stadenberg. 1993. Response of small birch plants (betula-pendula roth) to elevated co2 and nitrogen supply. *Plant, Cell and Environment 16(9):1115-1121.*

Small birch plants were grown for up to 80 d in a climate chamber at varied relative addition rates of nitrogen in culture solution, and at ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) concentrations of CO2. The relative addition rate of nitrogen controlled relative growth rate accurately and independently of CO2 concentration at sub- optimum levels. During free access to nutrients, relative growth rate was higher at elevated CO2. Higher values of relative growth rate and net assimilation rate were associated with higher values of plant N-concentration. At all N-supply rates, elevated CO2 resulted in higher values of net assimilation rate, whereas leaf weight ratio was independent of CO2. Specific leaf area (and leaf area ratio) was less at higher CO2 and at lower rates of N-supply. Lower values of specific leaf area weight partly because of starch accumulation. Nitrogen productivity (growth rate per unit plant nitrogen) was higher at elevated CO2. At sub-optimal N-supply, the higher net assimilation rate at elevated CO2 was offset by a lower leaf area ratio. Carbon dioxide did not affect root/shoot ratio, but a higher fraction of plant dry weight was found in roots at lower N-supply. In the treatment with lower N-supply, five times as much root length was produced per amount of plant nitrogen in comparison with optimum plants. The specific fine root length at all N-supplies was greater at elevated CO2. These responses of the root system to lower N- supply and elevated CO2 may have a considerable bearing on the acquisition of nutrients in depleted soils at elevated CO2. The advantage of maintaining steady-state nutrition in small plants while investigating the effects of elevated CO2 on growth is emphasized.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GROWTH, INCREASE, NUTRITION, PHOTON FLUX- DENSITY, PRODUCTIVITY, SEEDLINGS, SOURCE-SINK RELATIONS, TEMPERATURE

1831

Pfirrmann, T., J.D. Barnes, K. Steiner, P. Schramel, U. Busch, H. Kuchenhoff, and H.D. Payer. 1996. Effects of elevated CO2, O-3 and K deficiency on Norway spruce (Picea abies): Nutrient supply, content and leaching. *New Phytologist 134(2):267-278.*

Two clones of 5-yr-old Norway spruce (Picea abies [L.] Karst.) were exposed to two atmospheric concentrations of CO2 (350 and 750 mu mol mol(-1)) and of O-3 (20 and 75 nmol mol(-1)) in a phytotron at the GSF-Forschungszentrum (Munich) over the course of a single season (April-October). The phytotron was programmed to recreate an artificial climate similar to that at a high elevation site in the Inner Bavarian forest, and trees were grown in 401 containers of soil (pH 3.5) fertilized to achieve two levels of potassium nutrition; well fertilized and K-deficient. Foliar nutrient analyses performed at the beginning of the exposure indicated that the fertilization programmes achieved their goal without significantly altering the levels of other nutrients or the soil pH. At the beginning of the fumigation, foliar K concentrations were 7-9 mg g(-1) d. wt for well fertilized trees and 4-5 mg g(-1) d. wt for trees receiving no supplemental K. Over the course of the season, differences between K treatments intensified so that by the end of the experiment there was a five to sixfold difference between foliar K concentrations. This was associated with slight, but significant ($P < 0.05$), decreases in S and Zn (and of Cu in the 1989 needle year age class) and higher levels of C, N and Mg in K-deficient trees. Foliar N concentrations were low for all trees (9-15 mg g(-1) needle d. wt) but were similar to levels found in the field. Elevated O-3 was found to decrease significantly the C ($P < 0.05$) and N ($P < 0.001$) content of both current-year (1989) and previous-pear (1988) needles independent of CO2 concentration, but apart from some minor changes in the concentrations of Cu and Mn in the current-year needles no other effects of the pollutant on plant nutrient status were found. In contrast, CO2 enrichment resulted in significantly ($P < 0.01$) lower concentrations of K and P (effects on Mg were also on the borderlines of statistical significance) in current-year needles, but there was no influence on the nutrient composition of the previous- year needles (although effects on N were on the borderlines of statistical significance). CO2 enrichment also increased ($P < 0.05$) the C:N ratio of both current-year and previous-year needles. One factor contributing to the decline in foliar K at elevated CO2 appeared to be a marked increase (25-30%) in the rate at which cations were leached from the canopy by repeated simulated acid mist (pH 4.0) events, and this effect occurred independently of the O-2 concentration. The information presented will aid the interpretation of parallel studies examining the effects of elevated CO2 and/or O-2 on seasonal changes in photosynthesis, non-structural carbohydrate content, antioxidants, tree growth and water use efficiency, and sheds further light on the growing scepticism concerning the role of O-2 in the development of Mg and K-deficiency symptoms characteristic of certain types of forest decline in central Europe.

KEYWORDS: ACID MIST, ATMOSPHERIC CO2, BIOMASS PRODUCTION, CARBON DIOXIDE, GROWTH, L KARST, MINERAL NUTRITION, OZONE, TREES, TRITICUM-AESTIVUM L

1832

Phillips, D.L., J.J. Lee, and R.F. Dodson. 1996. Sensitivity of the US corn belt to climate change and elevated CO2 .1. Corn and soybean yields. *Agricultural Systems 52(4):481-502.*

Climate models indicate that increasing atmospheric concentrations of CO2 and other greenhouse gases could alter climate globally. The EPIC (Erosion Productivity Impact Calculator) model was used to examine the sensitivity of corn and soybean yields over the US corn belt to changes in temperature, precipitation, wind and atmospheric CO2 concentration. A statistically representative sample of 100 corn and soybean production sites was selected from the 1987 National Resources Inventory (NRI). One-hundred-year simulations were run for each site under 36 different

climate/CO2 scenarios. The results were area weighted according to the NRI area expansion factor's to produce a regionally aggregated estimate of yields. EPIC did an excellent job of reproducing current regional mean expected yields under the baseline scenario. There were 3% decreases in both corn and soybean yields in response to a 2 degrees C temperature increase at baseline precipitation levels, with larger and smaller temperature effects under drier and wetter conditions, respectively. Crop yields increased and decreased in response to increases and decreases of 10% or 20% precipitation. A 10% precipitation increase roughly balanced the negative effect of the 2 degrees C temperature increase. Whether the precipitation changes resulted from altered precipitation event frequency or amount per event had little effect on mean crop yields; however interannual yield variability was higher when precipitation decreases were due to frequency rather than intensity. The opposite was true, though to a lesser extent, far precipitation increases. Potential evapotranspiration responded linearly to changes in mean wind speed, leading to modest changes of 1-3 days of water stress per growing season, yield increases of up to 2% for decreased wind, and yield decreases of up to 6% for increased wind. Elevated CO2 concentrations of 625 ppmv gave the greatest yield increases, +17% for corn and +27% for soybean at baseline temperature and precipitation levels. The relative CO2 effect was larger under drier conditions. Copyright (C) 1996 Published by Elsevier Science Ltd

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CROP RESPONSES, ENRICHMENT, GROWTH, MODEL, PLAINS, TEMPERATURE

1833

Phillips, O.L., and A.H. Gentry. 1994. Increasing turnover through time in tropical forests. *Science 263(5149):954-958.*

Tree turnover rates were assessed at 40 tropical forest sites. Averaged across inventoried forests, turnover, as measured by tree mortality and recruitment, has increased since the 1950s, with an apparent pantropical acceleration since 1980. Among 22 mature forest sites with two or more inventory periods, forest turnover also increased. The trend in forest dynamics may have profound effects on biological diversity.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATIC CHANGE, DEFORESTATION, ECOSYSTEMS, ENRICHMENT, GROWTH, MOUNTAINS, PRODUCTIVITY, TREES

1834

Piastuch, W.C., and E.C. Stryjewski. 1995. Arabidopsis-thaliana growth, morphology and ultrastructure at elevated and super-elevated co2 concentrations. *Plant Physiology 108(2):62.*

1835

Picon, C., A. Ferhi, and J.M. Guehl. 1997. Concentration and delta C-13 of leaf carbohydrates in relation to gas exchange in Quercus robur under elevated CO2 and drought. *Journal of Experimental Botany 48(313):1547-1556.*

The variations of leaf carbohydrate concentration, carbon isotope discrimination (Delta) of leaf soluble carbohydrate, gas-exchange and growth during a soil drying cycle under 350 and 700 mu mol mol(-1) CO2 concentrations ([CO2]) in Quercus robur seedlings were analysed. In well-watered conditions, a doubling of [CO2] caused an increase of CO2 assimilation rate (A) (+47%) and a decrease of stomatal conductance for water vapour (g) (-25%), and doubled the intrinsic water-use efficiency (A/g). The values of Delta were not affected by elevated [CO2] which was consistent with the 2-fold increase of A/g. Elevated [CO2] also significantly increased sucrose and starch leaf concentrations as well as aerial growth and plant dry weight. The stimulating effect of CO2 enrichment on A and A/g was maintained in moderate drought conditions, but disappeared in the most severe drought conditions, Drought induced an increase of hexose concentrations in both [CO2], but this effect was more pronounced under elevated [CO2], which may contribute to increase osmoregulation, From the onset of drought, starch was depleted in both [CO2]. Carbon isotope discrimination decreased in response to drought, which corresponded to an increase in A/g according to the two-step model of isotopic discrimination, In contrast, the A/g values derived from instantaneous leaf gas-exchange measurements decreased along the drying cycle, The discrepancy observed between the two independent estimates of water-use efficiency is discussed in terms of time-scale integration. The results obtained with the isotopic approach using soluble carbohydrate suggest a predominant stomatal limitation of CO2 assimilation in response to drought.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON ISOTOPE DISCRIMINATION, FIELD CONDITIONS, LEAVES, OAK SEEDLINGS, OSMOTIC ADJUSTMENT, RISING CO2, STRESS, WATER-USE EFFICIENCY

1836

Picon, C., J.M. Guehl, and G. Aussenac. 1996. Growth dynamics, transpiration and water-use efficiency in Quercus robur plants submitted to elevated CO2 and drought. *Annales Des Sciences Forestieres 53(2-3):431-446.*

Seedlings of pedunculate oak (Quercus robur L) were grown for one growing season under ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2 concentration ([CO2]) either in well-watered or in droughted (the water supply was 40% of the well-watered plants transpiration in both [CO2]) conditions. In the droughted conditions, gravimetric soil water content (SWC) was on average 4 10(-2) g g(-1) lower under elevated [CO2]. In well-watered conditions, biomass growth was 39% higher in the elevated [CO2] treatment than under ambient [CO2]. However relative growth rate (RGR) was stimulated by the elevated [CO2] only for 17 days, in July, at the end of the stem elongation phase (third growing flush), which corresponded also to the phase of maximum leaf expansion rate. Both the number of leaves per plant and the plant leaf area were 30% higher in the elevated [CO2] treatment than under ambient [CO2]. In the droughted conditions, no significant enhancement in biomass growth and in plant leaf area was brought about by the elevated [CO2]. Transpiration rate was lower in the elevated [CO2] conditions, but whole plant water use was similar in the two [CO2] treatments, reflecting a compensation between leaf area and stomatal control of transpiration. Transpiration efficiency (W = biomass accumulation/plant water use) was improved by 47% by the elevated [CO2] in well-watered conditions but only by 18% in the droughted conditions. Carbon isotope discrimination (Delta) was decreased by drought and was increased by the elevated [CO2]. A negative linear relationship was found between transpiration efficiency divided by the atmospheric [CO2] and Delta, as predicted by theory.

KEYWORDS: ALBA L, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GAS-EXCHANGE, ISOTOPIC COMPOSITION, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PHOSPHORUS, PINUS-TAEDA SEEDLINGS, STRESS

1837

Picon, C., J.M. Guehl, and A. Ferhi. 1996. Leaf gas exchange and carbon isotope composition responses to drought in a drought-avoiding (Pinus pinaster) and a drought- tolerant (Quercus petraea) species under present and elevated atmospheric CO2 concentrations. *Plant, Cell and Environment 19(2):182-190.*

The responses of predawn leaf water potential (Psi(wp)), leaf conductance to water vapour diffusion (g), CO2 assimilation rate (A) and carbon isotope competition (delta(13)C) to a soil drying cycle were assessed in Pinus pinaster, a drought- avoiding species with high stomatal sensitivity to drought, and Quercus petraea, a drought-tolerant species with lower stomatal sensitivity to drought, under present (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2 concentrations ([CO2]). In P, pinaster, decreasing A in response to drought was associated with increasing plant intrinsic water use efficiency (A/g) and with decreasing calculated intercellular [CO2] (C-i), suggesting a stomatal limitation of A, In contrast, in Q, pefraea, A/g declined and Ci increased during the drying cycle, which suggests a non-stomatal origin for the decrease in A, In P, pinaster, a negative relationship was observed between the gas exchange-derived values of C-i/C-a, and delta(13)C, which conforms to the classical two-step carbon isotope discrimination model, In Q, petraea, the relationship between C-i/C-a and delta(13)C was positive, Possible causes of this discrepancy are discussed, Lower g values were observed under elevated [CO2] than under present [CO2] in Q. pefraea, whereas g was unaffected in P, pinaster, A stimulation of A by elevated [CO2] was found in P, pinaster but not in Q, petraea, In both species, A/g was markedly higher under elevated than under present [CO2], Whether the differences in the g response to elevated [CO2] found here can be generalized to other drought-avoiding and non-avoiding species remains to be assessed.

KEYWORDS: DIOXIDE, DISCRIMINATION, LEAVES, PHOTOSYNTHESIS, PLANTS, RISING CO2, SEEDLINGS, SOIL, STRESS, WATER-USE EFFICIENCY

1838

Picon-Cochard, C., and J.M. Guehl. 1999. Leaf gas exchange and carbohydrate concentrations in Pinus pinaster plants subjected to elevated CO2 and a soil drying cycle. *Annals of Forest Science 56(1):71-76.*

Plants of maritime pine (Pinus pinaster Ait.) were acclimated for 2 years under ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2 concentrations ([CO2]). In the summer of the second growing season, the plants were subjected to a soil drying cycle for 6 days. Drought reduced plant transpiration rate and net CO2 assimilation rate (A) by about 80 %. Elevated [CO2] induced a substantial increase of A (+105 % and +229 % in well-watered and in droughted plants, respectively) and of the needle starch (+145 %) and sucrose (+20 %) concentrations, whatever the watering regime. Drought did not significantly affect starch acid sucrose concentrations, while hexose concentrations were slightly increased in the most severe drought condition (predawn water potential value equal to -1.5 MPa). The stimulating effect of elevated [CO2] on A was maintained along the drying cycle, whereas no significant CO2 effect was observed on the soluble carbohydrate concentration. These compounds did not contribute to an enhance ment of osmotic adjustment under elevated [CO2] in P. pinaster. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ATMOSPHERIC CO2, DROUGHT, LEAVES, OSMOREGULATION, OSMOTIC ADJUSTMENT, RESPONSES, SEEDLINGS, WATER-STRESS

1839

Pinter, P.J., S.B. Idso, D.L. Hendrix, R.R. Rokey, R.S. Rauschkolb, J.R. Mauney, B.A. Kimball, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effect of free-air co2 enrichment on the chlorophyll content of cotton leaves. *Agricultural and Forest Meteorology 70(1-4):163-169.*

In vivo chlorophyll concentrations were estimated using a Minolta SPAD 502 meter on upper-canopy leaves of cotton plants exposed to air enriched to an atmospheric CO2 concentration of approximately 550 mumol mol-1 in a free-air CO2 enrichment (FACE) study. Measurements were made on 27 days during the final 90 days of the 1991 growing season. In both well-watered and moderately water-stressed plants, leaves in the FACE plots had greater chlorophyll a concentrations than leaves in the ambient air control plots (about 370 mumol CO2 mol-1): season- long chlorophyll a averages were 7.1% greater in the 'wet' treatment and 8.2% greater in the 'dry' treatment. This finding differs from what has been observed in a number of studies where experimental plants were grown in small pots. It is, however, typical of what has been observed in studies employing larger pots and open fields, and is a compelling rationale for conducting additional studies of this nature in FACE projects.

KEYWORDS: CARBON DIOXIDE, DENSITY, DRY-MATTER, EXTRACTABLE CHLOROPHYLL, GROWTH, LEAF GREENNESS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, ROOT

1840

Pinter, P.J., B.A. Kimball, J.R. Mauney, G.R. Hendrey, K.F. Lewin, and J. Nagy. 1994. Effects of free-air carbon-dioxide enrichment on par absorption and conversion efficiency by cotton. *Agricultural and Forest Meteorology 70(1-4):209-230.*

Anticipated changes in global climate and atmospheric CO2 concentrations have very important, albeit poorly understood consequences for production agriculture. Effects of these changes on plants have usually been examined in controlled- environment enclosures, glass-houses, or open-top field chambers. Beginning in 1989, an innovative experimental free- air CO2 enrichment (FACE) facility was operated in central Arizona to evaluate crop response to increased CO2 levels within a large, open-field production environment. Cotton (Gossypium hirsutum L.) was grown for three consecutive seasons under exposed to either ambient (control, about 370 mumol mol- 1) or elevated (FACE, 550 mumol mol-1) CO2 concentrations. Deficit irrigation regimes supplying 75% (beginning in July 1990) or 67% (beginning in mid-May 1991) of the crop's evapotranspiration requirement were included as additional treatment variables. Plant growth was monitored by periodic sampling. Canopy reflectances in visible (blue, 0.45-0.52 mum; green, 0.05-0.59 mum; red, 0.61-0.68 mum) and near-infrared (NIR; 0.79-0.89 mum) wavebands were measured frequently with an Exotech radiometer and related to absorbed photosynthetically active radiation (PAR; 0.4-0.7 mum) measured with a line quantum sensor. Dry biomass of plants in the FACE treatment was significantly ($P < 0.05$) greater than control values during each year of the study. The FACE plant canopy also absorbed significantly more PAR than controls during the early and middle portion of the 1990 and 1991 seasons. Light use efficiency (LUE, biomass produced per unit absorbed PAR) was significantly higher in FACE plots during each year. In the well-watered irrigation treatment, the 3 year mean LUE was 1.97 g MJ-1 for FACE and 1.56 g MJ-1 for controls. The deficit irrigation treatment in 1991 produced significantly smaller plants, which absorbed less PAR and had lower LUE than plants in the well-watered treatment ($P < 0.05$). No interaction was observed between CO2 and irrigation treatments. FACE research under realistic field conditions revealed positive consequences of increased CO2 on cotton plant biomass, PAR absorption, and LUE. It also demonstrated the effectiveness of this new technology for examining community-level plant responses to possible changes in global environment.

KEYWORDS: CANOPY REFLECTANCE, CO2, CORN CANOPIES, FIELD, GROWTH, PHOTOSYNTHETICALLY ACTIVE RADIATION, SOLAR RADIATION, VEGETATION INDEXES, WINTER-WHEAT, YIELD

1841

Pirjola, L. 1999. Effects of the increased UV radiation and biogenic

VOC emissions on ultrafine sulphate aerosol formation. *Journal of Aerosol Science 30(3):355-367.*

A sectional model (AEROFOR) for the formation of sulphuric acid-water particles has been developed. The model includes gas-phase chemistry and aerosol dynamics. An increased UV-B irradiation penetrating into the troposphere due to stratospheric ozone depletion causes via the SO2 oxidation route an enhanced nucleation potential for new H2SO4-H2O particles as well as the growth of particles to CCN size. Using AEROFOR we show that after a nucleation event the nucleated particle concentration is linearly dependent on increased UV-B irradiation with a positive slope. On the other hand, due to increased CO2 concentration photosynthetic rates of plants will increase, and it is likely that enhanced photosynthesis in forests will increase emissions of biogenic volatile organic compounds (BVOC) such as isoprene and monoterpenes, We show that the nucleated particle concentration decreases with increasing BVOC emission, but this dependence is not linear. We investigate the strength of these opposite effects and fit a straight line for such UV-B and BVOC conditions which yield a certain particle number density. The coupling between O-3, OH and particle concentrations as a function of UV-B and BVOC emission is also demonstrated.

KEYWORDS: ATMOSPHERIC CO2, CLOUD CONDENSATION NUCLEI, GREENHOUSE GASES, ISOPRENE EMISSION, MARINE BOUNDARY-LAYER, OZONE DEPLETION, SOUTHEASTERN UNITED-STATES, STRATOSPHERIC OZONE, SULFATE AEROSOLS, SULFURIC-ACID

1842

Pitelka, L.F. 1994. Ecosystem response to elevated co2. *Trends in Ecology and Evolution 9(6):204-207.*

KEYWORDS: ATMOSPHERIC CO2

1843

Plaut, Z., and E. Federman. 1991. Acclimation of CO2 assimilation in cotton leaves to water- stress and salinity. *Plant Physiology 97(2):515-522.*

Cotton (Gossypium hirsutum L. cv Acala SJ2) plants were exposed to three levels of osmotic or matric potentials. The first was obtained by salt and the latter by withholding irrigation water. Plants were acclimated to the two stress types by reducing the rate of stress development by a factor of 4 to 7. CO2 assimilation was then determined on acclimated and nonacclimated plants. The decrease of CO2 assimilation in salinity-exposed plants was significantly less in acclimated as compared with nonacclimated plants. Such a difference was not found under water stress at ambient CO2 partial pressure. The slopes of net CO2 assimilation versus intercellular CO2 partial pressure, for the initial linear portion of this relationship, were increased in plants acclimated to salinity of -0.3 and -0.6 megapascal but not in nonacclimated plants. In plants acclimated to water stress, this change in slopes was not significant. Leaf osmotic potential was reduced much more in acclimated than in nonacclimated plants, resulting in turgor maintenance even at -0.9 megapascal. In nonacclimated plants, turgor pressure reached zero at approximately -0.5 megapascal. The accumulation of Cl- and Na+ in the salinity-acclimated plants fully accounted for the decrease in leaf osmotic potential. The rise in concentration of organic solutes comprised only 5% of the total increase in solutes in salinity- acclimated and 10 to 20% in water-stress-acclimated plants. This acclimation was interpreted in light of the higher protein content per unit leaf area and the enhanced ribulose bisphosphate carboxylase activity. At saturating CO2 Partial pressure, the declined inhibition in CO2 assimilation of stress-acclimated plants was found for both salinity and water stress.

KEYWORDS: CHLOROPLASTS, COWPEA LEAVES, GROWTH, INTACT LEAVES, ION CONTENT, LEAF CONDUCTANCE, OSMOTIC ADJUSTMENT, PHOTOSYNTHETIC CAPACITY, PLANTS, SALT STRESS

1844

Pleijel, H., J. Sild, H. Danielsson, and L. Klemedtsson. 1998. Nitrous oxide emissions from a wheat field in response to elevated carbon dioxide concentration and open-top chamber enclosure. *Environmental Pollution 102:167-171.*

Soil emissions of nitrous oxide (N2O) were measured using static field chambers, which were installed in a wheat field. The treatments were: open-top chambers with ambient CO2 concentrations (OTC350), open-top chambers with 700 ppm CO2 (OTC700) and ambient air plots without open-top chambers (AA). Measurements of N2O emissions were made weekly starting at anthesis. The measurements continued for ten weeks, until two weeks after the harvest of the mature crop. During the first eight weeks the N2O emissions were higher in the OTC350 treatment compared to OTC700. At the last two measurements, after the plants were harvested, the N2O emissions of the chamber treatments were similar to each other and higher than during the preceding period. The accumulation of grain protein per unit area was higher in OTC700 compared with OTC350. These results suggest that a competition for soil nitrogen exists between plants and the microbial community. The AA plots emitted less N2O during the green canopy period compared with the chamber treatments. After harvest, the emissions from AA increased up to the same magnitude as the chamber treatments. The lower emissions of the ambient air plots during the pre- harvest period can be explained partly by lower ambient temperatures and drier soil.

KEYWORDS: FLUXES, SOILS, YIELD

1845

Polderdijk, J.J., and G.J.P.M. van den Boogaard. 1998. Effect of reduced levels of O-2 and elevated levels of CO2 on the quality of bunched radishes. *Gartenbauwissenschaft 63(6):250-253.*

In two trials bunched radishes were stored at 12 degrees C and different levels of O-2 (21%, 10%, 5%, 1%, 0.5%) combined with different levels of CO2 (0%, 1%, 5%, 10%, 15%, 20%). Decreased levels of O-2 and increased levels of CO2 proved to inhibit the yellowing of the leaves and the growth of new roots. The incidence of decay was inhibited by increased CO2 concentrations. Levels of 1% and 0.5% O-2 caused abnormal discolouration of the radishes and increased the incidence of decay. Off-odours and/or off-taste were found at O-2 levels df 0.5% and/or CO2 levels of 20%.

1846

Polglase, P.J., and Y.P. Wang. 1992. Potential co2-enhanced carbon storage by the terrestrial biosphere. *Australian Journal of Botany 40(4-5):641-656.*

Geochemical models that deduce latitudinal source/sink relationships of atmospheric CO2 suggest that, in tropical regions, there is almost zero net exchange of CO2 between the atmosphere and the terrestrial biosphere. The implication is that CO2-enhanced carbon storage (CO2-ECS) by tropical biomes is negating the output of CO2 from deforestation. We describe here a 10-biome model for CO2-ECS, in which carbon accumulation in living vegetation is coupled to the Rothamsted soil carbon model. A biotic growth factor (beta) was used to describe the relationship between literature estimates of net primary production (NPP) and atmospheric CO2 concentration. Using beta = 0.3 as a reference state, CO2-ECS by the global biosphere in 1990 was 1.1

Gt. When more appropriate values of beta were used (derived from a theoretical response of vegetation to increasing temperature and CO2), CO2-ECS was 1.3 Gt, of which tropical biomes accounted for 0.7 Gt. There are many uncertainties in this (and other) models; total CO2-ECS is particularly sensitive to changes in NPP. Unless published surveys have underestimated tropical NPP by a factor of about 2, then it is unlikely that CO2-ECS could have negated the 1.5- 3.0 Gt of carbon that are estimated to have been emitted by tropical deforestation in 1990.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, DIOXIDE, ECOSYSTEMS, GROWTH, INSECT HERBIVORE, LATITUDINAL DISTRIBUTION, PRODUCTIVITY, SOIL, TROPICAL FORESTS, WATER-USE EFFICIENCY

1847

Polle, A., M. Eiblmeier, L. Sheppard, and M. Murray. 1997. Responses of antioxidative enzymes to elevated CO2 in leaves of beech (Fagus sylvatica L.) seedlings grown under a range of nutrient regimes. *Plant, Cell and Environment 20(10):1317-1321.*

To study whether responses of antioxidative enzymes to enhanced atmospheric CO2 concentrations are affected by plant nutrition, the activities of superoxide dismutase, catalase and peroxidase were investigated in leaves of 3-year-old beech trees grown with low (0.1 x optimum), intermediate (0.5 x optimum) and high (2 x optimum) nutrient supply rates in open-top chambers at either ambient (approximate to 355 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 concentrations, These treatments resulted in foliar C/N ratios of about 20 in the presence of high and > 30 in the presence of low nutrient supply rates, Pigment and malondialdehyde contents were determined to assess plant stress levels, Low nutrient supply rates caused pigment loss, whereas elevated CO2 had no effect on pigmentation, Guaiacol peroxidase activities did not respond to either CO2 or nutrient treatment, Catalase activity decreased with decreasing nutrient supply rate and also in response to elevated CO2. Superoxidase dismutase activity was affected by both nutrient supply and CO2 concentration, In leaves from trees grown with the high-nutrient treatment, superoxide dismutase activity was low irrespective of CO2 concentration, In chlorotic leaves, superoxide dismutase activity was increased, suggesting an enhanced need for detoxification of reactive oxygen species, Leaves from plants grown under elevated CO2 with medium nutrient supply rates showed decreased malondialdehyde contents and superoxide dismutase activities, This suggests that the intrinsic oxidative stress of leaves was decreased under these conditions, These results imply that intrinsic oxidative stress is modulated;by the balance between N and C assimilation.

KEYWORDS: ATMOSPHERIC CO2, CHLOROSIS, DROUGHT STRESS, MAGNESIUM-DEFICIENCY, NEEDLES, PHOTORESPIRATION, PICEA-ABIES L, PLANTS, POTASSIUM, SYSTEMS

1848

Polle, A., T. Pfirrmann, S. Chakrabarti, and H. Rennenberg. 1993. The effects of enhanced ozone and enhanced carbon-dioxide concentrations on biomass, pigments and antioxidative enzymes in spruce needles (picea-abies L). *Plant, Cell and Environment 16(3):311-316.*

During one growing period, 5-year-old spruce trees (Picea abies L., Karst.) were exposed in environmental chambers to elevated concentrations of carbon dioxide (750 cm3 m-3) and ozone (0.08 cm3 m-3) as single variables or in combination. Control concentrations of the gases were 350 cm 3 m-3 CO2 and 0.02 cm3 m-3 ozone. To investigate whether an elevated CO2 concentration can prevent adverse ozone effects by reducing oxidative stress, the activities of the protective enzymes superoxide dismutase, catalase and peroxidase were determined. Furthermore, shoot biomass, pigment and protein contents of two needle age classes were investigated. Ozone caused pigment reduction and visible injury in the previous year's needles and growth reduction in the current year's shoots. In the presence of elevated concentrations of ozone and CO2, growth reduction in the current year's shoots was prevented, but emergence of visible damage in the previous year's needles was only delayed and pigment reduction was still found. Elevated concentrations of ozone or CO2 as single variables caused a significant reduction in the activities of superoxide dismutase and catalase in the current year's needles. Minimum activities of superoxide dismutase and catalase and decreased peroxidase activities were found in both needle age classes from spruce trees grown at enhanced concentrations of both CO2 and ozone. These results suggest a reduced tolerance to oxidative stress in spruce trees under conditions of elevated concentrations of both CO2 and ozone.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, ELEVATED CO2, EXPOSURE, FIELD, GROWTH, NORWAY SPRUCE, RED SPRUCE, SEASONAL-CHANGES, SUPEROXIDE-DISMUTASE ACTIVITY

1849

Polley, H.W. 1997. Implications of rising atmospheric carbon dioxide concentration for rangelands. *Journal of Range Management 50(6):562-577.*

Extensive rangelands and other vegetation types that we know today formed while atmospheric carbon dioxide (CO2) concentration was low (50 to 75% of today's concentration). Fossil fuel burning and deforestation and other land me changes during the last 200 years have increased CO2 concentration by about 30%, to the present 360 parts per million (ppm). Atmospheric CO2 will continue to rise during the next century, possibly to concentrations that are unprecedented for the last several million years. Much of the potential importance of CO2 concentration to vegetation derives from its influence on plant carbon balance and water relations. Plants grow by assimilating CO2 that diffuses into leaves through stomatal pores. Inevitably associated with CO2 uptake is transpirational loss of water vapor through stomata. Transpiration rates usually decline as CO2 increases, while, in many plants, photosynthesis and growth increase. These "primary" responses to CO2 can lead to a multitude of changes at the plant and ecosystem levels, ranging from alteration of the chemical composition of plant tissues to changes in ecosystem function and the species composition of plant communities. The direct physiological responses of plants to CO2 and expression of these responses at higher scales differ among species and growing conditions. Growth response to CO2 is usually highest in rapidly-growing plants that quickly export the carbohydrates formed in leaves and use them for storage or new growth and allocate a high proportion of fixed carbon to produce leaves. Growth is also more responsive to CO2 in plants with the C-3 (most woody plants and 'cool-season' grasses) than C-4 photosynthetic pathway (most 'warm-season' grasses), These and other differences among species could lead to changes in the composition of rangeland vegetation, but generalizations are difficult. On many rangelands, species abundances are determined more by morphological and phenological attributes that influence plant access to essential resources like nitrogen and light and reaction to fire, grazing, and other disturbances than by physiological traits that are sensitive to CO2 concentration. Species composition probably will be most responsive to CO2 on moderately water-limited and disturbed rangelands where multiple positive effects of CO2 on plant water relations can be expressed and competition for light is minimized. Greatest initial changes in species composition likely will occur on C-3/C-4 grasslands and at the transition between grasslands and woodlands. Plant production should also increase on water-limited rangelands, but CO2 may have little influence on production when nutrient elements like nitrogen are severely Limiting.

KEYWORDS: C-4 GRASS, CLIMATE CHANGE, ELEVATED CO2 CONCENTRATIONS, ICE-CORE RECORD, LONG-TERM EXPOSURE, PLANT GROWTH, SEASON GAS- EXCHANGE, STOMATAL DENSITY, TALLGRASS PRAIRIE, WATER-USE EFFICIENCY

1850

Polley, H.W., H.B. Johnson, B.D. Marino, and H.S. Mayeux. 1993. Increase in C3 plant water-use efficiency and biomass over glacial to present co2 concentrations. *Nature 361(6407):61-64.*

ATMOSPHERIC CO2 concentration was 160 to 200 mumol mol-1 during the Last Glacial Maximum (LGM; about 18,000 years ago)1, rose to about 275 mumol mol-1 10,000 years ago2,3, and has increased to about 350 mumol mol-1 since 1800 (ref. 4). Here we present data indicating that this increase in CO2 has enhanced biospheric carbon fixation and altered species abundances by increasing the water-use efficiency of biomass production of C3 plants, the bulk of the Earth's vegetation. We grew oats (Avena sativa), wild mustard (Brassica kaber) and wheat (Triticum aestivum cv. Seri M82 and Yaqui 54), all C3 annuals, and selected C4 grasses along daytime gradients of Glacial to present atmospheric CO2 concentrations in a 38-m-long chamber. We calculated parameters related to leaf photosynthesis and water-use efficiency from stable carbon isotope ratios (C-13/C- 12) of whole leaves. Leaf water-use efficiency and above-ground biomass/plant of C3 species increased linearly and nearly proportionally with increasing CO2 concentrations. Direct effects of increasing CO2 on plants must be considered when modelling the global carbon cycle and effects of climate change on vegetation.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, BALANCE, CARBON-DIOXIDE CONCENTRATION, GROWTH, ISOTOPIC COMPOSITION, VEGETATION

1851

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1992. Growth and gas-exchange of oats (avena-sativa) and wild mustard (brassica-kaber) at subambient co2 concentrations. *International Journal of Plant Science 153(3):453-461.*

A repeated sequence of monocultures and mixtures of oats (A vena sativa L.) and wild mustard (Brassica kaber (DC.) Wheeler) was grown along a daytime gradient of CO2 concentrations ([CO2]) from near 330 to a minimum of 150 mumol mol-1. The objectives were to determine effects of subambient [CO2] on leaf gas exchange, biomass production, and competitive interactions of these C3 species. A decrease in stomatal conductance did not prevent a nearly linear increase in leaf internal [CO2] and net assimilation of oat leaves as [CO2] increased. Net assimilation of oats and wild mustard increased from 5.0 and 2.5 mumol m-2 s-1 at 150 mumol mol-1, respectively, to 16.1 and 15.9 mumol m-2 s-1 at 330 mumol mol-1 CO2, respectively, when measured at 1,200-1,500 mumol m-2 s-1 incident light. Aboveground biomass per plant of wild mustard and oats increased 106% and 198%, respectively, and leaf area rose more than two- and threefold, respectively, from 154 to 331 mumol mol-1 CO2. The CO2-induced increase in aboveground biomass of plants of each species did not vary among monocultures and mixtures. Responses of oats and wild mustard to higher subambient [CO2] were large relative to reported responses of C3 species to comparable increases above the current atmospheric [CO2]. This suggests that past changes in atmospheric [CO2], including the 27% rise since the beginning of the nineteenth century, may have profoundly altered the productivity of C3 plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, COTTON, ELEVATED CO2, LEAVES, PHOTOSYNTHETIC ACCLIMATION, PLANT DRY- WEIGHT, RESPONSES, STOMATAL DENSITY, WATER-USE EFFICIENCY

1852

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1994. Increasing co2 - comparative responses of the C-4 grass schizachyrium and grassland invader prosopis. *Ecology 75(4):976-988.*

The woody C-3 Prosopis glandulosa (honey mesquite) and C-4 perennial grass Schizachyrium scoparium (little bluestem) were grown along a gradient of daytime carbon dioxide concentrations from near 340 to 200 mu mol/mol air in a 38 m long controlled environment chamber. We sought to determine effects of historical and prehistorical increases in atmospheric CO2 concentration on growth, resource use, and competitive interactions of a species representative of C-4-dominated grasslands in the southwestern United States and the invasive legume P. glandulosa. Increasing CO2 concentration stimulated N-2 fixation by individually grown P. glandulosa and elicited in C-3 seedlings a similar relative increase in leaf intercellular CO2 concentration, net assimilation rate, and intrinsic water use efficiency (leaf net assimilation rate/stomatal conductance). Aboveground biomass of P. glandulosa was not altered by CO2 concentration, but belowground biomass and whole-plant water and nitrogen use efficiencies increased linearly with CO2 concentration in seedlings that were grown alone. Biomass produced by P. glandulosa that was grown with S. scoparium was not affected by CO2 concentration. Stomatal conductance declined and leaf assimilation rates of S. scoparium at near maximum incident light increased at higher CO2 concentration, but there was no effect of CO2 concentration on biomass production or whole- plant water use efficiency of the C-4 grass. Rising CO2 concentration, especially the 27% increase since the beginning of the 19th century, may have contributed to more abundant P. glandulosa on C-4 grasslands by stimulating the shrub's growth or reducing the amount of resources that the C-3 required. Much of the potential response of P. glandulosa to CO2 concentration, however, appears to be contingent on the shrub's escaping competition with neighboring grasses.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, DESERT, ELEVATED CO2, GAS-EXCHANGE, GLANDULOSA, GREAT-BASIN, GROWTH, PLANTS, WATER-USE EFFICIENCY

1853

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1995. Nitrogen and water requirements of C3 plants grown at glacial to present carbon-dioxide concentrations. *Functional Ecology 9(1):86-96.*

1. Nitrogen- and water-use efficiencies in biomass production were determined for three C3 plant species at carbon dioxide concentrations ([CO2]) that spanned glacial to present atmospheric levels [200-350 mumol CO2 (mol air)-1]. The species were annual grasses Bromus tectorum and Triticum aestivum (two cultivars) and a woody perennial Prosopis glandulosa (alone and in mixtures with the C4 grass, Schizachyrium scoparium). 2. Changes in nitrogen- and water- use efficiencies were used to investigate effects of increasing [CO2] on the relative requirements of C3 plants for these frequently limiting resources. 3. Water-use efficiency (biomass produced/evapotranspiration; WUE) increased at higher [CO2] in all species but relative responses to [CO2] varied among species, cultivars and watering regimes. 4. Intrinsic WUE (net assimilation/stomatal conductance to water), calculated from stable carbon isotopes in plants, increased by about the same relative amount as did [CO2] in all species. 5. Nitrogen-use efficiency (biomass produced/plant N; NUE) rose at higher [CO2] only in well-watered B. tectorum and in P. glandulosa grown alone. 6. The more consistent increase in WUE than NUE in these species at higher [CO2] implies that rising [CO2] may have reduced the amount of water relative to nitrogen that some C3 plants require and

thereby altered the composition and function of terrestrial ecosystems.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, ECOSYSTEMS, ELEVATED CO2, GAS-EXCHANGE, ISOTOPE DISCRIMINATION, MARSH PLANTS, NUTRIENT USE EFFICIENCY, RESPONSES, SUBAMBIENT

1854

Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1997. Leaf physiology, production, water use, and nitrogen dynamics of the grassland invader Acacia smallii at elevated CO2 concentrations. *Tree Physiology 17(2):89-96.*

Invasion by woody legumes can alter hydrology, nutrient accumulation and cycling, and carbon sequestration on grasslands. The rate and magnitude of these changes are likely to be sensitive to the effects of atmospheric CO2 enrichment on growth and water and nitrogen dynamics of leguminous shrubs. To assess potential effects of increased atmospheric CO2 concentrations on plant growth and acquisition and utilization of water and nitrogen, seedlings of Acacia smallii Isely (huisache) were grown for 13 months at CO2 concentrations of 385 (ambient), 690, and 980 mu mol mol(-1). Seedlings grown at elevated CO2 concentrations exhibited parallel declines in leaf N concentration and photosynthetic capacity; however, at the highest CO2 concentration, biomass production increased more than 2.5-fold as a result of increased leaf photosynthetic rates, leaf area, and N-2 fixation. Measurements of leaf gas exchange and aboveground biomass production and soil water balance indicated that water use efficiency increased in proportion to the increase in atmospheric CO2 concentration. The effects on transpiration of an accompanying decline in leaf conductance were offset by an increase in leaf area, and total water loss was similar across CO2 treatments. Plants grown at elevated CO2 fixed three to four times as much N as plants grown at ambient CO2 concentration. The increase in N-2 fixation resulted from an increase in fixation per unit of nodule mass in the 690 mu mol mol(-1) CO2 treatment and from a large increase in the number and mass of nodules in plants in the 980 mu mol mol(-1) CO2 treatment. Increased symbiotic Nz fixation by woody invaders in response to CO2 enrichment may result in increased N deposition in litterfall, and thus increased productivity on many grasslands.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GROWTH, HONEY MESQUITE, NATURAL ABUNDANCE, PHOTOSYNTHESIS, STOMATAL RESPONSES, TALLGRASS PRAIRIE

1855

Polley, H.W., H.B. Johnson, H.S. Mayeux, D.A. Brown, and J.W.C. White. 1996. Leaf end plant water use efficiency of C-4 species grown at glacial to elevated CO2 concentrations. *International Journal of Plant Science 157(2):164-170.*

Leaf gas exchange was measured on C-4 plants grown from near glacial to current CO2 concentrations (200-350 mu mol mol(-1)) and from the current concentration to possible future levels (near 700 and 1000 mu mol mol(-1)) to test the prediction that intrinsic water use efficiency (CO2 assimilation [A]/stomatal conductance to water [g]) would rise by a similar relative amount as CO2 concentration. Studied were species differing in growth form or life history, the perennial grass Schizachyrium scoparium (little bluestem), perennial shrub Atriplex canescens (four-wing saltbush), and annual grass Zea mays (maize). Contrary to our prediction, leaf A/g of the C-4 species examined was stimulated proportionally more by a given relative increase in CO2 over subambient than by elevated concentrations. The ratio of the relative increase in A/g to that in CO2 exceeded unity in S. scoparium and, in 1 of 2 yr, in Z. mays as CO2 rose from 200 to 350 mu mol mol(-1), but declined to near zero in S. scoparium and A, canescens as CO2 rose from 700 to 1000 mu mol mol(-1). At higher CO2 concentrations, A/g of the C-4 perennials was similar to that expected for C-3 plants. Since much of the potential response of C-4 plants to CO2 often derives from higher water use efficiency (WUE), these results indicated that potential productivity of some C-4 plants increased relatively more since glaciation than it will in the future. There also were large (>100%) differences in A/g and plant WUE (production/transpiration) at a given CO2 level among the plants examined that could influence the relative productivities of C-4 species or growth forms and their interactions with C-3 plants.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS, CONDUCTANCE, GRADIENT, HUMIDITY, IRRADIANCE, PHOTOSYNTHESIS, RESPONSES, SENSITIVITY, STOMATA

1856

Polley, H.W., H.B. Johnson, H.S. Mayeux, and S.R. Malone. 1993. Physiology and growth of wheat across a subambient carbon- dioxide gradient. *Annals of Botany 71(4):347-356.*

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, ELEVATED CO2, ENRICHMENT, PLANTS, RESPIRATION, RESPONSES, SOYBEAN CANOPY PHOTOSYNTHESIS, TEMPERATURE, TRANSPIRATION

1857

Polley, H.W., H.B. Johnson, H.S. Mayeux, C.R. Tischler, and D.A. Brown. 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (Prosopis glandulosa) seedlings. *Tree Physiology 16(10):817-823.*

Low water availability reduces the establishment of the invasive shrub Prosopis on some grasslands. Water deficit survival and traits that may contribute to the postponement or tolerance of plant dehydration were measured on seedlings of Fl glandulosa Torr. var. glandulosa (honey mesquite) grown at CO2 concentrations of 370 (ambient), 710, and 1050 mu mol mol(-1). Because elevated CO2 decreases stomatal conductance, the number of seedlings per container in the elevated CO2 treatments was increased to ensure that soil water content was depleted at similar rates in all treatments. Seedlings grown at elevated CO2 had a greater root biomass and a higher ratio of lateral root to total root biomass than those grown at ambient CO2 concentration; however, these seedlings also shed more leaves and retained smaller leaves. These changes, together with a reduced transpiration/leaf area ratio at elevated CO2, may have contributed to a slight increase in xylem pressure potentials of seedlings in the 1050 mu mol mol(-1) CO2 treatment during the first 37 days of growth (0.26 ro 0.40 MPa). Osmotic potential was not affected by CO2 treatment. Increasing the CO2 concentration to 710 and 1050 mu mol mol(-1) more than doubled the percentage survival of seedlings from which water was withheld for 65 days. Carbon dioxide enrichment significantly increased survival from 0% to about 40% among seedlings that experienced the lowest soil water content. By increasing seedling survival of drought, rising atmospheric CO2 concentration may increase abundance of P. glandulosa on grasslands where low water availability limits its establishment.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, ELEVATED CO2, ESTABLISHMENT, GRASSLAND, OLD- FIELD PERENNIALS, PLANTS, RESPONSES, SONORAN DESERT, STRESS

1858

Polley, H.W., H.B. Johnson, C.R. Tischler, and H.A. Torbert. 1999. Links between transpiration and plant nitrogen: Variation with atmospheric CO2 concentration and nitrogen availability. *International Journal of Plant Science 160(3):535-542.*

Transpiration is closely linked to plans nitrogen (N) content, indicating that global or other changes that alter plant N accumulation or the relative requirements of plants for water and N will affect transpiration. We studied effects of N availability and atmospheric CO2 concentration, two components of global biogeochemistry that are changing, on relationships between whole-plant transpiration and N in two perennial C-3 species, Pseudoroegneria spicata (a tussock grass) and Gutierrezia microcephala ia half-shrub). Two indices of plant N requirement were used: N accretion (N in live and dead tissues) and N loss in litter (N in dead tissues). Transpiration was analyzed as the product of N accretion or loss by plants and the ratio of transpiration to N accretion or loss. The two indices of plant N requirement led to different conclusions as to the effects of N availability on plant use of water relative to N. Transpiration scaled proportionally with N accretion, but transpiration per unit of N loss declined at high N. Carbon dioxide enrichment had little effect on the ratio of transpiration to N accretion and no effect on transpiration per unit of N lass. The two species accumulated similar amounts of N, but the half-shrub used more than twice as much water as the grass. Nitrogen availability and CO2 concentration influenced whole-plant transpiration more by changing plant N accumulation than by altering the stoichiometry between transpiration and plant N. Species differences in total water use, by contrast, reflected differences in the scaling of transpiration to plant N. A better under standing of species differences in water and N dynamics may thus be required to predict transpiration reliably.

KEYWORDS: DESERT EVERGREEN SHRUB, ECOLOGY, ELEVATED CO2, LARREA-TRIDENTATA, PHOTOSYNTHESIS, USE EFFICIENCY, VARYING NITROGEN, WATER

1859

Polley, H.W., H.S. Mayeux, H.B. Johnson, and C.R. Tischler. 1997. Viewpoint: Atmospheric CO2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management 50(3):278-284.*

The abundance of woody plants on grasslands and savannas often is controlled by the availability of water and its location in soil. Water availability to plants is limited by precipitation, but the distribution of soil water and period over which it is available in these ecosystems are influenced by the transpiration rates of grasses, We discuss implications of recent and projected increases in atmospheric CO2 concentration for transpiration, soil water availability, and the balance of grasses and shrubs, An increase in CO2 concentration often reduces potential transpiration/leaf area by reducing stomatal conductance. On grasslands where effects of stomatal closure on transpiration are not negated by an increase in leaf temperature and leaf area, rising CO2 concentration should slow the depletion of soil water by grasses and potentially favor shrubs and other species that might otherwise succumb to water stress. Predicted effects of CO2 are supported by results from CO2-enrichment studies in the field and are compatible with recent models of interactions between resource levels and vegetation pattern and structure.

KEYWORDS: ANDROPOGON-GERARDII, BIOMASS PRODUCTION, C-4 GRASS, CANOPY PHOTOSYNTHESIS, CLIMATIC CONTROL, ELEVATED CARBON-DIOXIDE, PHOTOSYNTHETIC RESPONSE, PLANT- COMMUNITIES, STOMATAL RESPONSES, TALLGRASS PRAIRIE

1860

Polley, H.W., C.R. Tischler, H.B. Johnson, and R.E. Pennington. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (Prosopis glandulosa): responses to CO2 enrichment. *Tree Physiology 19(6):359-366.*

Low water availability is a leading contributor to mortality of woody seedlings on grasslands, including those of the invasive shrub Prosopis. Increasing atmospheric CO2 concentration could favor some genotypes of this species over others if there exists intraspecific variation in the responsiveness of survivorship to CO2. To investigate such variation, we studied effects of CO2 enrichment on seedling survival in response to uniform rates of soil water depletion in six maternal families of honey mesquite (P. glandulosa Torr. var, glandulosa). Three families each from the arid and mesic extremes of the species' distribution in the southwestern United States were studied in environmentally controlled glasshouses. Relative water content at turgor loss and osmotic potential were not affected by CO2 treatment. Increased atmospheric CO2 concentration, however, increased growth, leaf production and area, and midday xylem pressure potential, and apparently reduced transpiration per unit leaf area of seedlings as soil dried. Consequently, CO2 enrichment about doubled the fraction of seedlings that survived soil water depletion. Maternal families of honey mesquite differed in percentage survival of drought and in several other characteristics, but differences were of similar or of smaller magnitude compared with differences between CO2 treatments. There was no evidence for genetic variation in the responsiveness of survivorship to CO2. By increasing seedling survival of drought, increasing atmospheric CO2 concentration could increase the abundance of honey mesquite where establishment is limited by water availability. Genetic types with superior ability to survive drought today, however, apparently will maintain that advantage in the future.

KEYWORDS: AVAILABILITY, BALANCE, BIRCH, ELEVATED CARBON-DIOXIDE, EMERGENCE, GAS-EXCHANGE, GRASSLAND, POPULATIONS, STRESS, TEXAS

1861

Pons, T.L., and R.W. Pearcy. 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiologia Plantarum 92(4):636-644.*

The first trifoliate of soybean was shaded when fully expanded, while the plant remained in high light; a situation representative for plants growing in a closed crop. Leaf mass and respiration rate per unit area declined sharply in the first few days upon shading and remained rather constant during the further 12 days of the shading treatment. Leaf nitrogen per unit area decreased gradually until the leaves were shed. Leaf senescence was enhanced by the shading treatment in contrast to control plants growing in low light. Shaded leaves on plants grown at low nutrient availability senesced earlier than shaded leaves on plants grown at high nutrient availability. The light saturated rate of photosynthesis decreased also gradually during the shading treatment, but somewhat faster than leaf N, whereas chlorophyll contents declined somewhat slower than leaf N. Partitioning of N in the leaf over main photosynthetic functions was estimated from parameters derived from the response of photosynthesis to CO2. It appeared that the N exported from the leaf was more at the expense of compounds that make up photosynthetic capacity than of those involved in photon absorption, resulting in a change in partitioning of N within the photosynthetic apparatus. Photosynthetic nitrogen use efficiency increased during the shading treatment, which was for the largest part due to the decrease in leaf N content, to some extent to the decrease in respiration rate and only for a small part to change in partitioning of N within the photosynthetic apparatus.

KEYWORDS: ALOCASIA-MACRORRHIZA, CANOPY PHOTOSYNTHESIS, DIFFERENT IRRADIANCES, INDUCTION STATE, LEAF NITROGEN, LEAVES, LIGHT, LUCERNE CANOPY, USE EFFICIENCY, VULGARIS L

1862

Poorter, H. 1993. Interspecific variation in the growth-response of

plants to an elevated ambient co2 concentration. *Vegetatio 104:77-97.*

The effect of a doubling in the atmospheric CO2 concentration on the growth of vegetative whole plants was investigated. In a compilation of literature sources, the growth stimulation of 156 plant species was found to be on average 37%. This enhancement is small compared to what could be expected on the basis of CO2-response curves of photosynthesis. The causes for this stimulation being so modest were investigated, partly on the basis of an experiment with 10 wild plant species. Both the source-sink relationship and size constraints on growth can cause the growth-stimulating effect to be transient. Data on the 156 plant species were used to explore interspecific variation in the response of plants to high CO2. The growth stimulation was larger for C3 species than for C4 plants. However the difference in growth stimulation is not as large as expected as C4 plants also significantly increased in weight (41% for C3 vs. 22 % for C4). The few investigated CAM species were stimulated less in growth (15%) than the average C4 species. Within the group of C3 species, herbaceous crop plants responded more strongly than herbaceous wild species (58% vs. 35%) and potentially fast-growing wild species increased more in weight than slow-growing species (54% vs. 23%). C3 species capable of symbiosis with N2-fixing organisms had higher growth stimulations compared to other C3 species. A common denominator in these 3 groups of more responsive C3 plants might be their large sink strength. Finally, there was some tendency for herbaceous dicots to show a larger response than monocots. Thus, on the basis of this literature compilation, it is concluded that also within the group of C3 species differences exist in the growth response to high CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHED ATMOSPHERE, DRY-MATTER, LIQUIDAMBAR- STYRACIFLUA, LONG-TERM EXPOSURE, MINERAL NUTRITION, PHOTOSYNTHETIC INHIBITION, PINUS-TAEDA SEEDLINGS, RADIATA D-DON

1863

Poorter, H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO2? *Global Change Biology 4(6):693-697.*

Mainly based on a simulation model, Lloyd & Farquhar (1996; Functional Ecology, 10, 4-32) predict that inherently slow- growing species and nutrient-stressed plants show a relatively strong growth response to an increased atmospheric CO2 concentration. Compiling published experiments, I conclude that these predictions are not supported by the available data. On average, inherently fast-growing species are stimulated proportionately more in biomass than slow-growing species and plants grown at a high nutrient supply respond more strongly than nutrient-stressed plants.

KEYWORDS: ATMOSPHERIC CO2, AVAILABILITY, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, MINERAL NUTRITION, NITROGEN, PHOSPHORUS, PHOTOSYNTHESIS, RADIATA D-DON, SEEDLINGS

1864

Poorter, H., and R. De Jong. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytologist 143(1):163-176.*

Laboratory experiments have shown a large difference in specific leaf area (SLA, leaf area:leaf mass) between species from nutrient-poor and nutrient-rich habitats, but no systematic difference in the construction costs (the amount of glucose required to construct 1 g biomass). We examined how far these patterns are congruent with those from field-grown plants. An analysis was made of the vegetation in a range of grasslands and heathlands differing in productivity. The SLA of the dominant species in 15 different habitats was determined, as well as chemical composition and construction costs of bulk samples of leaves. SLA in the field was generally lower than in the laboratory, but showed consistency in that the ranking across species remained the same. Species from highly productive habitats had higher SLA than those from sites of low productivity, although individual species sometimes deviated substantially from the general trend. Construction costs were similar for plants from different habitats. This was mainly due to the positive correlation between an expensive class of compounds (proteins) and a cheap one (minerals).

KEYWORDS: CARBON, EFFICIENCY, ELEVATED CO2, FLUX-DENSITY, LEAVES, LIGHT, NET ASSIMILATION RATE, NITROGEN-AVAILABILITY, NUTRITION, RELATIVE GROWTH-RATE

1865

Poorter, H., R.M. Gifford, P.E. Kriedemann, and S.C. Wong. 1992. A quantitative-analysis of dark respiration and carbon content as factors in the growth-response of plants to elevated CO2. *Australian Journal of Botany 40(4-5):501-513.*

An analysis of elevated CO2 effects (2-4 times ambient) on dark respiration rate and carbon content was undertaken for a wide range of plant species, using both published reports and new data. On average, leaf respiration per unit leaf area was slightly higher for plants grown at high CO2 (16%), whereas a small decrease was found when respiration was expressed on a leaf weight basis (14%). For the few data on root respiration, no significant change due to high CO2 could be detected. Carbon content of leaves and stem showed a small increase (1.2 and 1.7% respectively), whereas C-content of roots was not significantly affected. In both data sets direction of responses was variable. A sensitivity analysis of carbon budgets under elevated CO2 identified changes in respiration rate, and to a lesser extent carbon content, as important factors affecting the growth response to elevated CO2 in quite a number of cases. Any comprehensive analysis of growth responses to increased CO2 should therefore include measurements of these two variables.

KEYWORDS: CARBOHYDRATE CONTENT, DIOXIDE EFFLUX, ENRICHMENT, EXCHANGE, NITROGEN, PHOTOSYNTHESIS, TEMPERATURE, TERM, WHITE CLOVER, YIELD

1866

Poorter, H., Y. VanBerkel, R. Baxter, J. DenHertog, P. Dijkstra, R.M. Gifford, K.L. Griffin, C. Roumet, J. Roy, and S.C. Wong. 1997. The effect of elevated CO2 on the chemical composition and construction costs of leaves of 27 C-3 species. *Plant, Cell and Environment 20(4):472-482.*

We determined the proximate chemical composition as well as the construction costs of leaves of 27 species, grown at ambient and at a twice-ambient partial pressure of atmospheric CO2, These species comprised wild and agricultural herbaceous plants as well as tree seedlings, Both average responses across species and the range in response were considered, Expressed on a total dry weight basis, the main change in chemical composition due to CO2 was the accumulation of total non- structural carbohydrates (TNC), To a lesser extent, decreases were found for organic N compounds and minerals, Hardly any change was observed for total structural carbohydrates (cellulose plus hemicellulose), lignin and lipids, When expressed on a TNC-free basis, decreases in organic N compounds and minerals were still present. On this basis, there was also an increase in the concentration of soluble phenolics, In terms of glucose required for biosynthesis, the increase in costs for one chemical compound - TNC - was balanced by a decrease in the costs for organic N compounds, Therefore, the construction costs,

the total amount of glucose required to produce 1 g of leaf, were rather similar for the two CO2 treatments; on average a small decrease of 3% was found, This decrease was attributable to a decrease of up to 30% in the growth respiration coefficient, the total CO2 respired [mainly for NAD(P)H and ATP] in the process of constructing 1 g of biomass, The main reasons for this reduction were the decrease in organic N compounds and the increase in TNC.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GROWTH-RESPONSE, LEAF RESPIRATION, LITTER DECOMPOSITION, MAINTENANCE, MAX L MERR, NITROGEN, PARTIAL-PRESSURE, PLANTS

1867

Popova, L.P., T.D. Tsonev, G.N. Lazova, and Z.G. Stoinova. 1996. Drought- and ABA-induced changes in photosynthesis of barley plants. *Physiologia Plantarum 96(4):623-629.*

The changes caused by drought stress and abscisic acid (ABA) on photosynthesis of barley plants (Hordeum vulgare L. cv. Alfa)have been studied. Drought stress was induced by allowing the leaves to lose 12% of their fresh weight. Cycloheximide (CHI), an inhibitor of stress-induced ABA accumulation, was used to distinguish alterations in photosynthetic reactions that are induced after drought stress in response to elevated ABA levels from those that are caused directly by altered water relations. Four hours after imposition of drought stress or 2 h after application of ABA, the bulk of the leaf's ABA content measured by enzyme-amplified ELISA, increased 14- and 16-fold, respectively. CHI fully blocked the stress-induced ABA accumulation. Gas exchange measurements and analysis of enzyme activities were used to study the reactions of photosynthesis to drought stress and ABA. Leaf dehydration or ABA treatment led to a noticeable decrease in both the initial slope of the curves representing net photosynthetic rate versus intercellular CO2 concentration and the maximal rate of photosynthesis; dehydration of CHI treated plants showed much slower inhibition of the latter. The calculated values of the intercellular CO2 concentration, CO2 compensation point and maximal carboxylating efficiency of ribulose 1,5-bisphosphate (RuBP) carboxylase support the suggestion that biochemical factors are involved in the response of photosynthesis to ABA and drought stress. RuBP carboxylase activity was almost unaffected in ABA- and CHI-heated, non-stressed plants. A drop in enzyme activity was observed after leaf dehydration of the control and ABA-treated plants. When barley plants were supplied with ABA, the activity of carbonic anhydrase (CA, EC 4.2.2.1) increased more than 2-fold. Subsequent dehydration caused an over 1.5-fold increase in CA activity of the control plants and a more than 2.5-fold increase in ABA-treated plants. Dehydration of CHI-treated plants caused no change in enzyme activity. It is suggested that increased activity of CA is a photosynthetic response to elevated ABA concentration.

KEYWORDS: ABSCISIC- ACID, INDUCTION, INHIBITORS, LEAVES, METABOLISM, STOMATA

1868

Porte, A., and D. Loustau. 1998. Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old Pinus pinaster. *Tree Physiology 18(4):223-232.*

Photosynthetic characteristics of 1- and 2-year-old needles were determined in excised shoots of maritime pine (Pinus pinaster Ait.) with an open gas exchange system. We used the nonlinear least mean squares method to derive values for quantum yield of electron transport (alpha), maximum carboxylation velocity (V-cmax), and maximum electron transport rate (J(max)), from photosynthetic response curves to light and CO2. Crown height had no significant effect on any of the parameters; however, V-cmax and J(max), as well as a were 43, 26 and 35% higher, respectively, in 1-year-old needles than in 2-year-old needles. The main effect of irradiance on needles was a small decline in leaf concentrations of nitrogen and phosphorus from the top to the bottom of the canopy. Only J(max) demonstrated a linear relationship with both nitrogen content (R-2 = 0.42) and irradiance at the shoot level. Because needle age accounted for most of the variability in photosynthesis, we incorporated needle age into the photosynthesis model of Farquhar et al. (1980). The modified model underestimated the daily assimilation rate of 1-year-old needles in the field, especially when assimilation rates were high.

KEYWORDS: C-3 PLANTS, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CO2/O2 SPECIFICITY, ELEVATED CO2, EUCALYPTUS-GRANDIS, LEAF NITROGEN, QUANTUM YIELD, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE

1869

Portielje, R., and L. Lijklema. 1995. Carbon-dioxide fluxes across the air-water-interface and its impact on carbon availability in aquatic systems. *Limnology and Oceanography 40(4):690-699.*

Diffusion of CO2 across the air-water interface was analyzed with a model that simulates both transport and reaction of CO2 in a stagnant boundary layer. The atmospheric C influx was determined in relation to several environmental variables: pH, total dissolved inorganic C, temperature, and the thickness of the stagnant boundary layer in relation to ambient windspeed. We used the model to calculate the atmospheric CO2 influx into six experimental ditches for a period of 6 or 8 months, starting in early spring. Three of the six ditches were dominated by aquatic macrophytes and three by benthic algae. Each series received three levels of external N and P input. A comparison with net C assimilation during the same period, as estimated from continuous oxygen measurements, showed that, especially in the ditches dominated by submersed macrophytes, a sizable fraction of the C requirements during this period could have been obtained from atmospheric CO2. In the ditches dominated by benthic algae, this fraction was considerably less, but nonetheless substantial, and was related to the level of N and P loading. Increased primary production due to enhanced external N and P loading increased the atmospheric C input due to the resultant higher pH values. The trophic state with respect to N and P and the availability of C are therefore interrelated.

KEYWORDS: ELODEA, INORGANIC CARBON, PHOTOSYNTHESIS, PLANTS, STRATEGIES

1870

Pospisilova, J., and J. Catsky. 1999. Development of water stress under increased atmospheric CO2 concentration. *Biologia Plantarum 42(1):1-24.*

The increase in water use efficiency (the ratio of photosynthetic to transpiration rates) is likely to be the commonest positive effect of long-term elevation in CO2 concentration (CE), This may not necessarily lead to decrease in long-term water use owing to increased leaf area. However, some plant species seem to cope better with drought stress under CE, because increased production of photosynthates might enhance osmotic adjustment and decreased stomatal conductance and transpiration rate under CE enable plants to maintain a higher leaf water potential during drought. In addition, at the same stomatal conductance, internal CO2 concentration might be higher under CE which results in higher photosynthetic rate. Therefore plants under CE of the future atmosphere will probably survive eventual higher drought stress and some species may even be able to extend their biotope into less favourable sites.

KEYWORDS: ABIES L KARST, CARBON-DIOXIDE ENRICHMENT,

DRY-MATTER PRODUCTION, FAGUS-SYLVATICA L, LEAF GAS-EXCHANGE, OPEN-TOP CHAMBERS, SITCHENSIS BONG CARR, TERM ELEVATED CO2, USE EFFICIENCY, VAPOR-PRESSURE DEFICIT

1871

Pospisilova, J., J. Solarova, and J. Catsky. 1992. Photosynthetic responses to stresses during invitro cultivation. *Photosynthetica 26(1):3-18.*

Present knowledge of photosynthesis, biomass production and water relations of plantlets cultivated in vitro and their responses to environmental conditions is reviewed. Acclimation of plantlets, firstly to very special in vitro conditions and secondly after transplantating to ex vitro conditions, is considered. Low irradiance and CO2 concentration inside cultivation vessels restrict photosynthetic rate and accumulation of biomass by plantlets in situ. Nevertheless the photosynthetic apparatus is often fully developed. Therefore net photosynthetic rate and hence biomass accumulation can increase immediately after artificial increase in CO2 concentration inside the vessels (this enables autotrophic cultivation of plantlets as one of important future technologies) or after transplanting to glasshouse or field. On the other hand, under very high humidity and low irradiance in vitro, efficient regulation of gas exchange does not operate. The development of functional stomata and cuticle requires some weeks of acclimation to natural conditions.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, LEAF ANATOMY, LIQUIDAMBAR-STYRACIFLUA HAMAMELIDACEAE, MERISTEM CULTURE, PLANTS CULTURED INVITRO, PROLINE ACCUMULATION, STRAWBERRY PLANTLETS, TAEDA L CALLUS, WATER-STRESS

1872

Pospisilova, J., H. Synkova, D. Haisel, J. Catsky, N. Wilhelmova, and F. Sramek. 1999. Effect of elevated CO2 concentration on acclimation of tobacco plantlets to ex vitro conditions. *Journal of Experimental Botany 50(330):119-126.*

Nicotiana tabacum L, plants grown in vitro were transferred to ex vitro conditions and grown for 28 d in a greenhouse under normal CO2 concentration (C, 330 pmol mol(-1)) or elevated CO2 concentration (E, 1000 mu mol mol(-1)). Stomatal conductances of abaxial and adaxial epidermes measured under optimal conditions were not significantly affected by growth under E, but the stomatal regulation of gas exchange was better. Leaf photosynthetic rate (A) of elevated CO2 plants was similar to that of control plants when both were measured under normal CO2, but higher when both were measured under elevated CO2. The A of elevated CO2 plants was much higher than the A of control plants when measured under their respective growth CO2 concentration, which resulted in their higher growth rate. Chlorophyll a and b contents, and activities of whole electron transport chain and of photosystem (PS) II were not markedly affected by growth under E, and the maximum efficiency of PSII measured as the ratio of variable to maximum fluorescence was even slightly increased. Hence no down-regulation of photosynthesis occurred in transplanted plants grown for 4 weeks under E. The contents of p-carotene and of xanthophyll cycle pigments (violaxanthin + antheraxanthin+zeaxanthin) were lower in E plants. The degree of de-epoxidation of xanthophyll cycle pigments was not changed or was even lower after transfer to ex vitro conditions, which indicated that no photoinhibition occurred, Therefore, CO2 enrichment can improve acclimation of in vitro-grown plantlets to ex vitro conditions.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWN IN-VITRO, INVITRO, LIGHT-INTENSITY, PHOTOSYNTHESIS, SUBSEQUENT GROWTH, SUGAR-FREE MEDIUM, TEMPERATURE

1873

Pospisilova, J., N. Wilhelmova, H. Synkova, J. Catsky, D. Krebs, I. Ticha, B. Hanackova, and J. Snopek. 1998. Acclimation of tobacco plantlets to ex vitro conditions as affected by application of abscisic acid. *Journal of Experimental Botany 49(322):863-869.*

Plantlets of Nicotiana tabacum L. cv, Petit Havana SR1 were grown in vitro on Murashige and Skoog medium containing 2% saccharose, and then transplanted ex vitro into pots with coarse sand and Hewitt nutrient solution, In the first day after transplantation, the antitranspirant abscisic acid (ABA; 0.01, 0.05 or 0.10 mM) was added to the substrate. Leaf stomatal conductance (g(s)), which was high in plants during the first days after transplantation similarly as in plantlets grown in vitro, was considerably decreased by ABA-treatment, However, in the further days g(s) decreased more quickly in control than in ABA-treated plants, and after 2 or 3 weeks g(s) was significantly lower than that of plantlets grown in vitro but similar in control and ABA-treated plants. Two weeks after transplantation, net photosynthetic rate, chlorophyll a + b content, maximal photochemical efficiency, and actual quantum yield of photosystem II in plant leaves were higher in comparison with those in plantlets grown in vitro. ABA- treatment had slight positive or insignificant effect on photosynthetic parameters and enhanced plant growth. Thus ABA application can alleviate 'transplant shock' and speed up acclimation of plantlets to ex vitro conditions.

KEYWORDS: CO2- ENRICHMENT, CULTURED APPLE SHOOTS, GAS-EXCHANGE, GROWN IN-VITRO, INVITRO, MICROPROPAGATED PLANTS, PHOTOSYNTHESIS, ROSE PLANTS, STOMATAL CONDUCTANCE, WATER RELATIONS

1874

Possingham, H.P. 1993. Impact of elevated atmospheric co2 on biodiversity - mechanistic population-dynamic perspective. *Australian Journal of Botany 41(1):11-21.*

Biodiversity is characteristically defined on three levels: genetic diversity, species diversity and ecosystem diversity. In this paper I consider the impact of elevated CO2 and associated climate change on the biodiversity of terrestrial systems at the species level. I attempt to understand the impact of a rapidly changing physical environment mechanistically. The direct impact of elevated CO2 is emphasised. A changing physical environment will cause behavioural and physiological responses in organisms that will affect population dynamics and interspecific relationships. In the short term, extinctions will occur via the direct interaction of species with their changing environment. Species exposed to new diseases, and species dependent on mutualists or keystone species that become extinct or change geographical range, may become extinct rapidly through interactions with other species. I hypothesise that the effect of environmental change on competitive interactions will play a minor role in causing declines in biodiversity. Existing literature on the impact of climate change on terrestrial ecosystems emphasises the way in which ecosystems and species should track suitable climates across the landscape. Here I argue that each species will be affected in one, or a combination, of the following ways: range change to track shifting climate zones, tolerating the environmental change, microevolutionary change, and extinction.

KEYWORDS: CLIMATE CHANGE, CONSEQUENCES, ECOSYSTEMS, FORESTS, GLOBAL CHANGE, GROWTH, INCREASING CO2, PLANTS, RESPONSES, VEGETATION

1875

Post, W.M., J. Pastor, A.W. King, and W.R. Emanuel. 1992. Aspects

of the interaction between vegetation and soil under global change. *Water, Air, and Soil Pollution 64(1-2):345-363.*

Responses of terrestrial ecosystems to a world undergoing a change in atmospheric CO2 concentration presents a formidable challenge to terrestrial ecosystem scientists. Strong relationships among climate, atmosphere, soils and biota at many different temporal and spatial scales make the understanding and prediction of changes in net ecosystem production (NEP) at a global scale difficult. Global C cycle models have implicitly attempted to account for some of this complexity by adapting lower pool sizes and smaller flux rates representing large regions and long temporal averages than values appropriate for a small area. However, it is becoming increasingly evident that terrestrial ecosystems may be experiencing a strong transient forcing as a result of increasing levels of atmospheric CO2 that will require a finer temporal and spatial representation of terrestrial systems than the parameters for current global C cycle models allow. To adequately represent terrestrial systems. in the global C cycle it is necessary to explicitly model the response of terrestrial systems to primary environmental factors. While considerable progress has been. made experimentally and conceptually in aspects of photosynthetic responses, and gross and net primary production, the application of this understanding to NEP at individual sites is not well developed. This is an essential step in determining effects of plant physiological responses on the global C cycle. We use a forest stand succession model to explore the effects of several possible plant responses to elevated atmospheric CO2 concentration. These simulations show that ecosystem C storage can be increased by increases in individual tree growth rate, reduced transpiration, of increases in fine root production commensurate with experimental observations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CO2, CO2-INDUCED CLIMATE CHANGE, FORESTS, LITTER DECOMPOSITION, MOUNTAIN HEMLOCK, NITROGEN MINERALIZATION, NORTH-AMERICA, NUTRIENT, TERRESTRIAL ECOSYSTEMS

1876

Potosnak, M.J., S.C. Wofsy, A.S. Denning, T.J. Conway, J.W. Munger, and D.H. Barnes. 1999. Influence of biotic exchange and combustion sources on atmospheric CO2 concentrations in New England from observations at a forest flux tower. *Journal of Geophysical Research-Atmospheres 104(D8):9561-9569.*

Hourly data for concentrations and fluxes of CO2 at 30 m in Harvard Forest (Petersham, Massachusetts) are analyzed using linear modeling to obtain regionally representative CO2 concentrations at a continental site. The time series is decomposed into contributions due to regional combustion, local canopy exchange, monthly average regional biotic exchange (as modulated by the daily cycle of growth and decay of the planetary boundary layer (PBL)), and the regional monthly background concentration Attributions are derived using time series analysis, data for a tracer for combustion (CO or acetylene (C2H2)), and measurements of indicators of proximate canopy exchange (CO2 flux and momentum flux). Results are compared to observations at Cold Bay, Alaska. Combustion contributes on average 4-5 ppm to ambient CO2 at Harvard Forest in winter and 2-3 ppm in summer. Regional biotic emissions elevate daily mean CO2 by 4-6 ppm in winter, and the covariance of the biotic cycle of uptake and emission with PBL height enhances daily mean CO2 by 1-2 ppm in summer; minimum values in late afternoon average 10 ppm lower than at Cold Bay in summer. The study shows that regionally representative concentrations of CO2 can be determined at continental sites if suitable correlates (tracers, fluxes of CO2, and momentum) are measured simultaneously with CO2 itself.

KEYWORDS: CARBON DIOXIDE

1877

Potter, C.S., and S.A. Klooster. 1999. Detecting a terrestrial biosphere sink for carbon dioxide: Interannual ecosystem modeling for the mid-1980s. *Climatic Change 42(3):489-503.*

There is considerable uncertainty as to whether interannual variability in climate and terrestrial ecosystem production is sufficient to explain observed variation in atmospheric carbon content over the past 20-30 years. In this paper, we investigated the response of net CO2 exchange in terrestrial ecosystems to interannual climate variability (1983 to 1988) using global satellite observations as drivers for the NASA- CASA (Carnegie-Ames-Stanford Approach) simulation model. This computer model of net ecosystem production (NEP) is calibrated for interannual simulations driven by monthly satellite vegetation index data (NDVI) from the NOAA Advanced Very High Resolution Radiometer (AVHRR) at 1 degree spatial resolution. Major results from NASA-CASA simulations suggest that from 1985 to 1988, the northern middle-latitude zone (between 30 and 60 degrees N) was the principal region driving progressive annual increases in global net primary production (NPP; i.e., the terrestrial biosphere sink for carbon). The average annual increase in NPP over this predominantly northern forest zone was on the order of +0.4 Pg (10(15) g) C per year. This increase resulted mainly from notable expansion of the growing season for plant carbon fixation toward the zonal latitude extremes, a pattern uniquely demonstrated in our regional visualization results. A net biosphere source flux of CO2 in 1983-1984, coinciding with an El Nino event, was followed by a major recovery of global NEP in 1985 which lasted through 1987 as a net carbon sink of between 0.4 and 2.6 Pg C per year. Analysis of model controls on NPP and soil heterotrophic CO2 fluxes (R-h) suggests that regional warming in northern forests can enhance ecosystem production significantly. In seasonally dry tropical zones, periodic drought and temperature drying effects may carry over with at least a two-year lag time to adversely impact ecosystem production. These yearly patterns in our model-predicted NEP are consistent in magnitude with the estimated exchange of CO2 by the terrestrial biosphere with the atmosphere, as determined by previous isotopic (delta(13)C) deconvolution analysis. Ecosystem simulation results can help further target locations where net carbon sink fluxes have occurred in the past or may be verified in subsequent field studies.

KEYWORDS: CLIMATE VARIABILITY, EXCHANGE, GLOBAL-SCALE, NDVI DATA SET, SATELLITE, VEGETATION

1878

Potvin, C., and D. Tousignant. 1996. Evolutionary consequences of simulated global change: Genetic adaptation or adaptive phenotypic plasticity. *Oecologia 108(4):683-693.*

During the next century, natural and agricultural systems might need to adjust to a rapid increase in atmospheric CO2 concentration and global temperature. Evolution of genotypes adapted to this global change could play a central role in plants' response. The main purpose of this study was to determine the relative importance of phenotypic and genotypic responses of plants to global change. To do so, we selected two populations of the short-lived Brassica juncea, one under ambient conditions and another one under conditions simulating global change. After seven generations of selection, differences between the two populations were examined using a reciprocal transplant garden. We monitored 14 different traits and found evidence for genetic adaptation only once, for vegetative biomass early in the growth cycle. Of the 14 traits, 11 responded plastically to the environment, but only one of these plastic changes had a possible adaptive value. Overall, the long-term evolutionary consequences of global change will depend on the response of fitness-related traits. None of the five reproductive traits measured showed any evolutionary responses. The main conclusion of our study is that Brassica juncea was apparently unable to respond evolutionarily to simulated global change either by genetic adaptation or by adaptive

phenotypic plasticity. The Limit to selection was apparently due to inbreeding depression induced by the harsh conditions of the "predicted" environment.

KEYWORDS: BRASSICA, CLIMATE CHANGE, CO2, HIGH-TEMPERATURE, IMPATIENS-CAPENSIS, INBREEDING DEPRESSION, OUTCROSSED PROGENY, PLANTS, POPULATIONS, STRESS

1879

Potvin, C., and L. Vasseur. 1997. Long-term CO2 enrichment of a pasture community: Species richness, dominance, and succession. *Ecology 78(3):666-677.*

The present study addresses responses of a pasture community to CO2 enrichment in situ. It focused on two levels of organization. We examined changes in both community properties and species-specific responses during long-term exposure to high CO2 concentration. The underlying hypothesis is that CO2 enrichment could change community composition. At the community level, we observed higher species richness and lesser dominance under enriched than ambient CO2. Two species were apparently central in explaining our results, Agropyron repens and Plantago major. The cover of this first species increased only under ambient CO2. Conversely, the cover of the latter species decreased under ambient CO2 but remained stable under enriched CO2. Species were pooled into dicots and monocots to examine space acquisition. Changes in monocot cover through time were more tightly coupled with that of dicots under ambient than high CO2. Enrichment with CO2 appeared to have a positive effect on the early-successional species, preventing the complete dominance by late-successional species. In fact, under elevated CO2 early- and late-successional species were coexisting. Therefore, our results suggest the possibility that succession patterns might be altered by CO2 enrichment apparently because enriched CO2 stimulates the growth of dicots.

KEYWORDS: AVAILABILITY, COMPETITION, DISTURBANCE, ECOSYSTEM, ELEVATED CO2, FERTILIZATION, FIELD PLANT COMMUNITY, GLOBAL CHANGE, GRASSLAND, RESPONSES

1880

Poulin, M.J., R. Belrhlid, Y. Piche, and R. Chenevert. 1993. Flavonoids released by carrot (daucus-carota) seedlings stimulate hyphal development of vesicular-arbuscular mycorrhizal fungi in the presence of optimal co2 enrichment. *Journal of Chemical Ecology 19(10):2317-2327.*

Carbon dioxide has been previously identified as a critical volatile factor that stimulates hyphal growth of Gigaspora margarita, a vesicular-arbuscular mycorrhizal fungus, and we determined the optimal concentration at 2.0%. The beneficial effect of CO2 On fungal development is also visible in the presence of stimulatory (quercetin, myricetin) or inhibitory (naringenin) flavonoids. Sterile root exudates from carrot seedlings stimulate the hyphal development of G. margarita in the presence of optimal CO2 enrichment. Three flavonols (quercetin, kaempferol, rutin or quercetin 3-rutinoside) and two flavones (apigenin, luteolin) were identified in carrot root exudates by means of HPLC retention time. Flavonols like quercetin and kaempferol are known to have stimulatory effects on hyphal growth of G. margarita.

KEYWORDS: ACTIVATION, DNA TRANSFORMED ROOTS, GIGASPORA-MARGARITA, GROWTH, HOST, INFECTION, INVITRO, NODULATION GENES, PLANTS, SPORE GERMINATION

1881

Prade, K., and V. Hagelgans. 1993. Enrichment of n2 and ar in the atmosphere of co2-consuming soils. *Zeitschrift Fur Pflanzenernahrung Und Bodenkunde 156(5):421-426.*

The phenomenon of unexplained N2/Ar-enrichment in soil air is quite frequently to be encountered in soil air studies on anthropogenically influenced sites. In the present study two anthropogenic deposits and a calcareous fluvisol were investigated for their soil air composition. While in the alkaline deposits extreme enrichments of N2 and Ar (N2 + Ar: up to 99%, v/v) were found as persistent site characteristics, the fluvisol showed only slight (about 1%, v/v) transient N2/Ar- enrichments in summer. All sites, which did not show substantial vertical seepage percolation, exhibited enhanced CO2-Solubility either due to strong calcite precipitation or dissolution. So, it was concluded that intensive continuous depletion Of CO2 was responsible for the subsequent convective influx of atmospheric air. From the results obtained it was concluded that an encasement of the concerned soil volume rather impermeable to gas transport as well as intense dissolution of CO2 in the pore water are prerequisites for substantial N2/Ar-enrichments in soil air.

1882

Prakash, O., A. Sood, M. Sharma, and P.S. Ahuja. 1999. Grafting micropropagated tea [Camellia sinensis (L.) O. Kuntze] shoots on tea seedlings - a new approach to tea propagation. *Plant Cell Reports 18(10):883-888.*

Tea microshoots excised from well-established multiple shoot cultures grown in vitro and 8-week-old, three- to five-leaved seedlings from a local chinery stock (Banuri-96) and UPASI-9 (from southern India) were selected as scions and root stocks, respectively, for grafting. In addition, 4-month- and 12-month- old seedlings of Banuri-96 were also used as root stocks. Cut ends of root stocks and scions were pretreated with varying concentrations of BAP and NAA for 10 min. A treatment of BAP (5 mg/l) and NAA (5 mg/l) to both scion and stocks in water renewed foliar development at a relatively early stage (40-60 days). The grafted plants were kept in hardening chambers with CO2-enriched air. No significant difference was observed between autograft (scion and root stock of Banuri clone) and heterograft (scion of the Banuri clone and root stock of UPASI- 9). Of the three types (in terms of age) of seedling-raised root stocks employed, grafts on young tea (4-month-old) performed the best (88.33%). Grafts made in early summer established relatively faster and at a high rate of success. The percentage survival of plants transferred to the field was 88.33%.

KEYWORDS: INVITRO

1883

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri, and C.S. Vogel. 1995. Atmospheric co2, soil-nitrogen and turnover of fine roots. *New Phytologist 129(4):579-585.*

In most natural ecosystems a significant portion of carbon fixed through photosynthesis is allocated to the production and maintenance of fine roots, the ephemeral portion of the root system that absorbs growth-limiting moisture and nutrients. In turn, senescence of fine roots can be the greatest source of C input to forest soils. Consequently, important questions in ecology entail the extent to which increasing atmospheric CO2 may alter the allocation of carbon to, and demography of, fine roots. Using microvideo and image analysis technology, we demonstrate that elevated atmospheric CO2 increases the rates of both fine root production and mortality. Rates of root mortality also increased substantially as soil nitrogen availability increased, regardless of CO2 concentration. Nitrogen greatly influenced the proportional allocation of carbon to leaves vs. fine roots. The amount of available nitrogen in the soil appears to be the most important factor regulating fine root

demography in Populus trees.

KEYWORDS: CARBON DIOXIDE, FORESTS, PLANTS, RESPONSES

1884

Prentice, I.C., M.T. Sykes, M. Lautenschlager, S.P. Harrison, O. Denissenko, and P.J. Bartlein. 1993. Modeling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. *Global Ecology and Biogeography Letters 3(3):67-76.*

Global patterns of potential natural vegetation were simulated for present and last glacial maximum (LGM) climates. The LGM simulation showed good agreement with available evidence, most importantly in the humid tropics. Simple calculations based on these simulations indicate that terrestrial carbon storage increased by 300-700 Pg C after the LGM. The range is due to uncertainties in the mean carbon storage values for different biomes, and in the amount of carbon in boreal peats. These results are consistent with the global change in ocean delta-C- 13, inferred from measurements on benthic foraminifera, reflecting the increased storage of isotopically light carbon on land.

KEYWORDS: AMAZON, ATMOSPHERIC CO2, CLIMATE, CORE, ICE-AGE, LATE QUATERNARY, RECORD, SIMULATIONS, SURFACE

1885

Price, D.T., and M.J. Apps. 1995. The boreal forest transect case-study - global change effects on ecosystem processes and carbon dynamics in boreal canada. *Water, Air, and Soil Pollution 82(1-2):203-214.*

The Boreal Forest Transect Case Study (BFTCS) is a multi- disciplinary ecological study organised around a 1000 km transect located in central Canada. The transect is oriented along an ecoclimatic gradient in a region likely to undergo significant environmental change within the next: few decades, and crosses the climate-sensitive boreal forest biome, including the transitions north and south into tundra and grassland respectively. Originally conceived as an extension to the BOReal Ecosystem Atmosphere Study (BOREAS), the 10-year BFTCS project projects the intensive canopy-scale measurements and modelling advances obtained from BOREAS to a wider range of sites with a longer-term perspective. In addition to considering ecophysiological processes with time-frames of the order of one year or shorter, BFTCS addresses the effects of larger scale, longer term processes including vegetation succession and ecosystem disturbances. The BFTCS currently provides practical linkages among ecosystem monitoring, field experiments and regional scale modelling. It will ultimately provide a knowledge-base of key processes and their environmental sensitivities, and assessments of possible climate feedbacks, which can be used to assess the possible consequences of global change both regionally and globally.

KEYWORDS: BIOSPHERE, CLIMATE CHANGE, CO2, CYCLE, DECOMPOSITION, MODEL, NORTHWESTERN MINNESOTA, PEATLANDS, SENSITIVITY, VEGETATION

1886

Prince, T.A., and M.S. Cunningham. 1991. Forcing characteristics of easter lily bulbs exposed to elevated-ethylene and elevated-carbon dioxide and low-oxygen atmospheres. *Journal of the American Society for Horticultural Science 116(1):63-67.*

Exposure of bulbs of Easter Lily (Lilium longiflorum Thunb.) to a maximum of 2-mu-l ethylene/liter during vernalization delayed flowering by 5 to 7 days and decreased the number of flower buds. Ethylene exposure for 5 days at 21C after vernalization accelerated shoot emergence and flowering by up to 3 days. No floral or plant abnormalities were observed after bulb exposure to ethylene. Exposure to atmospheres with 0%, 0.5%, or 1% O2 at 21C for up to 2 weeks before or 10 days after vernalization did not significantly impair subsequent bulb forcing. Storage in 1% O2 at 21C for 1 week before vernalization resulted in nearly one additional secondary bud initiated per plant. Exposure to up to 15% CO2 at 21C for up to 2 weeks before or 10 days after vernalization did not significantly impair subsequent forcing.

1887

Prior, L.D., D. Eamus, and G.A. Duff. 1997. Seasonal and diurnal patterns of carbon assimilation, stomatal conductance and leaf water potential in Eucalyptus tetrodonta saplings in a wet-dry savanna in northern Australia. *Australian Journal of Botany 45:241-258.*

Seasonal and diurnal trends in carbon assimilation, stomatal conductance and leaf water potential were studied using 1-3 m tall saplings of Eucalyptus tetrodonta (F.Muell.). The study site was in an unburnt savanna near Darwin, where rainfall is strongly seasonal. Mean daily maximum assimilation rates ranged from 14.5 mu mol m(-2) s(-1) in May to 4.8 mu mol m(-2) s(-1) in October. There was a linear relationship between daily maximum assimilation rates and pre-dawn leaf water potential (r = 0.62, n = 508) and a log-log linear relationship between daily maximum stomatal conductance and pre-dawn leaf water potential (r = 0.68, n = 508). Assimilation rates and stomatal conductance were always higher in the morning than in the afternoon, irrespective of season. Stomatal conductance responded more strongly to leaf-to-air vapour pressure difference when pre-dawn leaf water potentials were moderately low (-0.5 to -1.5 MPa) than when they were very low (< -1.5 MPa) or high (> -0.5 MPa). Assimilation decreased sharply when temperature exceeded 35 degrees C. Seasonal trends in assimilation rate could be attributed primarily to stomatal closure, but diurnal trends could not. High leaf temperatures were a major cause of lower assimilation rates in the afternoon. Approximately 90% of leaves were lost by the end of the dry season, and above-ground growth was very slow. It is hypothesised that E. tetrodonta saplings allocate most photosynthate to root and lignotuber growth in order to tolerate seasonal drought and the high frequency of fire in northern Australian savannas.

KEYWORDS: CO2, DEFICITS, ENRICHMENT, HUMIDITY, LEAVES, PHOTOSYNTHESIS, RESPONSES, TEMPERATURE, TRANSPIRATION, TREE

1888

Prior, S.A., S.G. Pritchard, G.B. Runion, H.H. Rogers, and R.J. Mitchell. 1997. Influence of atmospheric CO2 enrichment, soil N, and water stress on needle surface wax formation in Pinus palustris (Pinaceae). *American Journal of Botany 84(8):1070-1077.*

Interactive effects of increasing atmospheric CO2 with resource limitations on production of surface wax in plants have not been studied. Pinus palustris seedlings were grown for 1 yr at two levels of soil N (40 or 400 kg N.ha(-1).yr(-1)) and water stress (-0.5 or -1.5 MPa xylem pressure potential) in open-top field chambers under two levels of CO2 (365 or 720 mu mol/mol). Needle surface wax content was determined at 8 mo (fall) and 12 mo (spring) and epicuticular wax morphology was examined using scanning electron microscopy (SEM) at 12 mo. Wax content expressed on both a leaf area and dry mass basis was increased due to main effects of low N and water stress. No main effects of CO2 were observed; however, a CO2 x N interaction at 12 mo indicated that under low soil N the elevated CO2 treatment had less wax (surface area or dry mass basis) compared to its ambient counterpart. Morphologically, low N needle surfaces appeared rougher compared to those of high N needles due to more extensive wax ridges. Although the

main effect of water treatment on wax density was not reflected by changes in wax morphology, the CO2 x N interaction was paralleled by alterations in wax appearance. Decreases in density and less prominent epicuticular wax ridges resulting from growth under elevated CO2 and limiting N suggest that dynamics of plant/atmosphere and plant/pathogen interactions may be altered.

KEYWORDS: ELEVATED CARBON-DIOXIDE, EPICUTICULAR WAX, GROWTH, LEAF, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS, ULTRASTRUCTURE

1889

Prior, S.A., and H.H. Rogers. 1995. Soybean growth-response to water-supply and atmospheric carbon- dioxide enrichment. *Journal of Plant Nutrition 18(4):617-636.*

Growth response of soybean [Glycine max (L.) Merr. 'Bragg'] grown in open top field chambers at five carbon dioxide (CO2) concentrations ranging from 349 to 946 mu LL(-1) and under two water regimes was examined. During reproductive growth, plants grown under CO2 enrichment exhibited increases in total leaf area and dry weight. Water stress inhibited growth at all CO2 levels, but the relative enhancement of growth due to CO2 enrichment under water-stressed (WS) conditions was greater than under well-watered (WW) conditions. Water-stressed plants grown under 946 mu LL(-1) CO2 were larger than WW plants grown under 349 mu LL(-1) CO2. Reproductive yield increases were represented by increases in seed number rather than larger seeds. Although water stress reduced yield, the relative increase in seed number in response to elevated CO2 was greater for WS plants. Leaf tissue analysis suggested that a phosphorus deficiency may have restricted the seed dry weight response to elevated CO2. The mean relative growth rate (RGR) and mean net assimilation rate (NAR) increased with CO2 concentration in the first interval (5 to 14 days after planting) and diminished with time thereafter for each CO2 level. At the second interval (14 to 63 days), the direct effect of NAR was offset by lower leaf area ratio (LAR). However, the LAR was greater for WS plants but the response of RGR to CO2 was similar under both water treatments. At the third interval (63 to 98 days), the RGR for WS plants remained constant across CO2 treatments, whereas under WW conditions a level response of NAR coupled with a negative response of LAR resulted in a decrease in RGR under CO2-enriched conditions. The decrease in LAR was attributed to a decrease in specific leaf area. Leaf weight ratio was unaffected by Co-2.

KEYWORDS: CO2- ENRICHMENT, ELEVATED CO2, FIELD, PHOSPHORUS, PHOTOSYNTHETIC ACCLIMATION, PLANTS, SEEDLINGS, STRESS, WHEAT, YIELD

1890

Prior, S.A., H.H. Rogers, and G.B. Runion. 1993. Effects of free-air co2 enrichment on cotton root morphology. *Plant Physiology 102(1):173.*

1891

Prior, S.A., H.H. Rogers, G.B. Runion, and G.R. Hendrey. 1994. Free-air co2 enrichment of cotton - vertical and lateral root distribution patterns. *Plant and Soil 165(1):33-44.*

The objective of this investigation was to determine how free- air carbon dioxide enrichment (FACE) of cotton (Gossypium hirsutum L.) affects root distribution in a natural soil environment. For two years cotton was grown on a Trix clay loam under two atmospheric CO2 concentrations (370 and 550 mu mol mol(-1)) and two water treatments [wet, 100% of evapotranspiration (ET) replaced and dry, 75% (1990) and 67% (1991) of ET replaced] at Maricopa, AZ. At early vegetative and mid-reproductive growth, 90 cm soil cores were taken at 0, 0.25, and 0.5 m perpendicular to row center; root variables were ascertained at three 30 cm depth increments. The effect of water stress alone or its interaction with CO2 on measured variables during both samplings were rare and showed no consistent pattern. There was a significant CO2 x position interaction for root length density at the vegetative stage (both years) and reproductive stage (1990 only); the positive effects of extra CO2 were more evident at interrow positions (0.25 and 0.5 m). A CO2 x depth x position interaction at the vegetative phase (1990) indicated that FACE increased root dry weight densities for the top soil depth increment at all positions and at the middle increment at the 0.5 m position. Similar trends were seen at the reproductive sampling for this measure as well as for root length density at both sample dates in 1990. In 1991, a CO2 x depth interaction was noted at both periods; CO2 enhancement of root densities (i.e., both length and dry weight) were observed within the upper and middle depths. Although variable in response, increases for root lineal density under high CO2 were also seen. In general, results also revealed that the ambient CO2 treatment had a higher proportion of its root system growing closer to the row center, both on a root length and dry wight basis. On the other hand, the FACE treatment had proportionately more of its roots allocated away from row center (root length basis only). Results from this field experiment clearly suggest that increased atmospheric CO2 concentration will alter root distribution patterns in cotton.

KEYWORDS: AGRICULTURE, ATMOSPHERIC CARBON-DIOXIDE, GROWTH, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, SOIL, SYSTEM, VEGETATION, WATER-USE, YIELD

1892

Prior, S.A., H.H. Rogers, G.B. Runion, B.A. Kimball, J.R. Mauney, K.F. Lewin, J. Nagy, and G.R. Hendrey. 1995. Free-air carbon-dioxide enrichment of cotton - root morphological-characteristics. *Journal of Environmental Quality 24(4):678-683.*

The response of plants to rising global CO2 concentration is of critical research interest but one neglected aspect is its effect on roots. Root morphological changes in cotton [Gossypium hirsutum (L.) 'Delta Pine 77'] were examined in a 2- yr held study. The test crop was grown under two water regimes (wet, 100% of evapotranspiration [ET] replaced and dry, 75% [1990] and 67% [1991] of ET replaced) and two atmospheric CO2 concentrations (ambient = 370 mu mol mol(-1) and free-air CO2 enrichment [FACE] = 550 pmol mol(-1)). A FACE technique that allows for CO2 exposure under held conditions with minimal alteration of plant microclimate was used. Excavated root systems were partitioned into taproot and lateral roots at two growth phases (vegetative and reproductive). Vertical root- pulling resistance was determined at the second sampling; this measure was higher because of CO2 enrichment but was unaffected by water stress. Water stress affected root variables only at the second sampling; water stress reduced taproot variables more than lateral variables. The larger diameter taproots seen at all sample dates under FACE exhibited large increases in dry weight and volume. FACE often increased lateral root number and lateral dry weights were higher at all sample dates. The development of more robust taproot systems in CO2-enriched environments may allow for greater carbohydrate storage for utilization during periods such as hop filling and to ensure root growth for continued exploration of the soil profile to meet nutrient and water demands during peak demand periods.

KEYWORDS: ATMOSPHERIC CO2, GROWTH, PHOTOSYNTHETIC ACCLIMATION, RESISTANCE, RESPONSES, VEGETATION, WATER-USE, YIELD

1893

Prior, S.A., H.H. Rogers, G.B. Runion, and J.R. Mauney. 1994.

Effects of free-air co2 enrichment on cotton root-growth. *Agricultural and Forest Meteorology 70(1-4):69-86.*

The rise in atmospheric CO2 concentration is predicted to have a positive effect on agro-ecosystem productivity. However, an area which requires further investigation centers on responses of crop root systems to elevated atmospheric CO2 under field conditions. The advent of free-air CO2 enrichment (FACE) technology provides a new method of CO2 exposure with minimal alteration of plant microclimate. In 1990 and 1991, cotton (Gossypium hirsutum (L.) 'Deltapine 77') was grown under two atmospheric CO2 levels (370 and 550 mumol mol-1) and two water regimes (wet (100% of ET replaced) and dry (75% of ET replaced in 1990 and 67% in 1991)). Plant root samples were collected at early vegetative and mid-reproductive growth. Taproots of CO2-enriched plants displayed greater volume, dry weight, length, and tissue density. Water treatment effects were noted for length, volume and dry weight of roots at the second sampling in 1991. In general, whole soil profile root densities (both length and dry weight densities) and root weight per unit length at the initial sampling were increased under CO2 enrichment at each of three positions (0.00, 0.25, and 0.50 m) from row center to the middle of the inter-row space. At the second sampling, root length density and root dry weight density were generally unaffected by water stress, whereas root weight per unit length was somewhat higher. In addition, extra CO2 increased whole profile root length density only at the 0.50 m inter-row position, whereas whole profile root dry weight density and root weight per unit length were generally higher under elevated CO2 at all three positions. The results from this field experiment strongly indicated that increased atmospheric CO2 level would enhance plant root growth.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, PHOTOSYNTHETIC ACCLIMATION, RESISTANCE, RESPONSES, SEEDLINGS, STRESS, VEGETATION, WATER RELATIONS, WHEAT, YIELD

1894

Prior, S.A., H.H. Rogers, G.B. Runion, H.A. Torbert, and D.C. Reicosky. 1997. Carbon dioxide-enriched agroecosystems: Influence of tillage on short-term soil carbon dioxide efflux. *Journal of Environmental Quality 26(1):244-252.*

Increasing atmospheric carbon dioxide (CO2) concentration can increase biomass production that may influence carbon (C) dynamics in terrestrial ecosystems. Soil CO2 efflux as affected by crop residues from high CO2 environments managed under different tillage systems has not been explored. This study examined the effects of tillage systems in a legume soybean [Glycine max (L.) Merr.] and nonlegume grain sorghum [Sorghum bicolor] (L.) Moench. CO2-enriched agroecosystem on the rates of short-term CO2 evolution from a Blanton loamy sand (loamy siliceous, thermic Grossarenic Paleudults). In the spring of 1993, CO2 efflux observations initiated within 5 s after a tillage event were compared to no-tillage conditions for 8 d in plots where both crop species had been grown in open top field chambers under two CO2 conditions (ambient and twice ambient) for two seasons (1992 and 1993). Added CO2 increased yields, residue, and root biomass; higher percent ground cover was also observed in CO2-enriched plots prior to the tillage treatment. Differences in C/N ratio of the residue may have influenced CO2 efflux rates; C/N ratio was highest for sorghum and was increased by elevated CO2. Efflux patterns were characterized by flushes of CO2 following initial tillage and rainfall events. Species x tillage and CO2 x species interactions were noted on several days and for total CO2 efflux values. Our results suggest that short-term CO2 fluxes may be greater for tilled soybean and for soybean grown under elevated CO2; however, short-term flux rates in the sorghum crop were affected by tillage, but not by CO2 level. These short-term results should be viewed with caution when predicting long-term C turnover in agroecosystems.

KEYWORDS: AIR, ATMOSPHERIC CO2 ENRICHMENT, CROP ROTATIONS, ELEVATED CO2, GLOBAL CLIMATE-CHANGE, NITROGEN, ORGANIC-MATTER, PLANT-RESPONSES, TALLGRASS PRAIRIE, TERRESTRIAL BIOSPHERE

1895

Prior, S.A., H.H. Rogers, N. Sionit, and R.P. Patterson. 1991. Effects of elevated atmospheric CO2 on water relations of soya bean. *Agriculture Ecosystems & Environment 35(1):13-25.*

Soya bean (Glycine max (L.) Merr. 'Bragg') plants were grown in large containers in open-top field chambers under five atmospheric CO2 concentrations (349-946-mu-l-l-1) and two water regimes. Rate of soil water depletion for the high CO2 treatments started to decrease under well-watered conditions during anthesis and by early pod formation under water-stressed conditions. During reproductive growth, normal and stressed plants at 349-mu-l-l-1 (ambient level) received irrigation water 29 and 12 times, respectively, compared with 21 and 9 times, respectively, at 946-mu-l-l-1 CO2. At both anthesis and pod fill, plants grown under CO2 enrichment exhibited greater leaf area. Nevertheless, water use per plant either remained constant (stressed plants at anthesis) or else declined (well- watered plants at pod fill; both moisture levels during pod fill) in response to CO2 enrichment. At pod fill, leaves of CO2-enriched plants generally displayed a higher stomatal resistance, except near the end of the sampling period when a sudden increase in resistance was observed under low CO2 owing to low soil water availability. Midday xylem potential for well-watered plants was greater than values for stressed plants and was unaffected by CO2 treatment. Under low moisture conditions, elevated CO2 had no effect on xylem potential at anthesis; however, during pod fill potential increased significantly with increasing CO2 concentration, as elevated CO2 decreased water use rates, lowering soil water stress. Alleviation of water stress during critical reproductive phases was strongly suggested.

KEYWORDS: CARBON DIOXIDE, FIELD, GROWTH, PHOTOSYNTHESIS, RESPONSES, SOYBEANS, STRESS, WHEAT, YIELD

1896

Prior, S.A., G.B. Runion, R.J. Mitchell, H.H. Rogers, and J.S. Amthor. 1997. Effects of atmospheric CO2 on longleaf pine: Productivity and allocation as influenced by nitrogen and water. *Tree Physiology 17(6):397-405.*

Longleaf pine (Pinus palustris Mill.) seedlings were exposed to two concentrations of atmospheric CO2 (365 or 720 mu mol mol(- 1)) in combination with two N treatments (40 or 400 kg N ha(-1) year(-1)) and two irrigation treatments (target values of -0.5 or -1.5 MPa xylem pressure potential) in open-top chambers from March 1993 through November 1994. Irrigation treatments were imposed after seedling establishment (i.e., 19 weeks after planting). Seedlings were harvested at 4, 8, 12, and 20 months. Elevated CO2 increased biomass production only in the high-N treatment, and the relative growth enhancement was greater for the root system than for the shoot system. In water-stressed trees, elevated CO2 increased root biomass only at the final harvest. Root:shoot ratios were usually increased by both the elevated CO2 and low-N treatments. In the elevated CO2 treatment, water-stressed trees had a higher root:shoot ratio than well-watered trees as a result of a drought-induced increase in the proportion of plant biomass in roots. Well- watered seedlings consistently grew larger than water-stressed seedlings only in the high-N treatment. We conclude that available soil N was the controlling resource for the growth response to elevated CO2 in this study. Although some growth enhancement was observed in water-stressed trees in the elevated CO2 treatment, this response was contingent on available soil N.

KEYWORDS: AVAILABILITY, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, LIQUIDAMBAR- STYRACIFLUA, PHOSPHORUS, PLANT-RESPONSES, STRESS, TAEDA SEEDLINGS

1897

Prior, S.A., H.A. Torbert, G.B. Runion, G.L. Mullins, H.H. Rogers, and J.R. Mauney. 1998. Effects of carbon dioxide enrichment on cotton nutrient dynamics. *Journal of Plant Nutrition 21(7):1407-1426.*

The rise in atmospheric carbon dioxide (CO2) concentration is predicted to have positive effects on agro-ecosystem productivity. However, an area which requires further study centers on nutrient dynamics of crops grown under elevated CO2 in the field. In 1989 and 1990, cotton [Gossypium hirsutum (L.) Deltapine 77'] was grown under two CO2 levels [370 mu mol mol(- 1)=ambient and 550 mu mol mol(-1)=free-air CO2 enrichment(FACE)]. At physiological maturity, nutrient concentration and content of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) were determined for whole plant and individual plant organs. While the effects of added CO2 on whole plant nutrient concentrations and contents were consistent, some differences among plant organs were observed between years. FACE often decreased tissue nutrient concentration, but increased total nutrient accumulation. Results indicate that under elevated CO2, field grown cotton was more nutrient efficient in terms of nutrient retrieval from the soil and nutrient utilization in the plant. This implies more efficient fertilizer utilization, better economic return for fertilizer expenditures, and reduced environmental impact from agricultural fertilization practices in the future.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, ENVIRONMENT, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, RHIZOSPHERE, ROOT-GROWTH, SEEDLINGS, YIELD

1898

Prior, S.A., H.A. Torbert, G.B. Runion, H.H. Rogers, C.W. Wood, B.A. Kimball, R.L. LaMorte, P.J. Pinter, and G.W. Wall. 1997. Free-air carbon dioxide enrichment of wheat: Soil carbon and nitrogen dynamics. *Journal of Environmental Quality 26(4):1161-1166.*

The predicted positive impact of elevated atmospheric carbon dioxide (CO2) concentration on crop biomass production suggests that more C will reach the soil. An aspect of soil C sequestration that requires further study is the effect of elevated CO2 on C and N dynamics; this relationship is the keg to understanding potential longterm C storage in soil. Soil samples (0-5, 5-10, and 10-20 cm increments) were collected after 2 yr of wheat (Triticum aestivum L.) production under two CO2 levels [370 (ambient) and 550 mu L L-1 (free-air CO2 enrichment) (FACE)] and two water treatments [100% of ET replaced (wet) and 50% of ET replaced (dry)] on a Trix clay loam [fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvents] at Maricopa, AZ. Organic C, total N, potential C and N mineralization, and C turnover were determined during a 60-d incubation study. Organic C content increased at all three soil depths under FACE and the total N content increased at the 5 to 10 and 10 to 20 cm depths. In general, increased N mineralization under dry conditions corresponded well with patterns of higher C mineralization and turnover. Nitrogen mineralization was unaffected by CO2 treatment, indicating that factors other than N may limit C mineralization and turnover. Soil respiration and C turnover patterns were not affected by CO2 treatment level at the 0 to 5 cm depth; however, these measures were Lower under FACE at the lower depths. Soil respiration and C turnover at the 10 to 20 cm depth were increased by water stress under ambient CO2; these measures under both water levels for FACE were similar to the ambient CO2/wet treatment, suggesting that more C storage in wheat cropping systems is likely under elevated CO2 regardless of mater treatment.

KEYWORDS: DECOMPOSITION, ELEVATED ATMOSPHERIC CO2, PLANT, RESPONSES

1899

Pritchard, S.G., C. Mosjidis, C.M. Peterson, G.B. Runion, and H.H. Rogers. 1998. Anatomical and morphological alterations in longleaf pine needles resulting from growth in elevated CO2: Interactions with soil resource availability. *International Journal of Plant Science 159(6):1002-1009.*

Studies of anatomical changes in longleaf pine (Pinus palustris Mill.) needles for plants exposed to elevated atmospheric CO2 may provide insight into the potential influences of global CO2 increases on plant productivity. Longleaf pine seedlings were grown in open-top field chambers supplied with either ambient (similar to 365 mu mol mol(-1)) or elevated (similar to 720 mu mol mol(-1)) atmospheric CO2 for 20 mo. Two levels of soil nitrogen (40 and 400 g ha(-1) yr(-1)) and two soil moisture regimes (-0.5 or -1.5 MPa predawn xylem pressure potential) were used in combination with CO2 treatments. Needle tissue was collected 12 and 20 mo after treatment initiation and subjected to light and scanning electron microscopy. There was no effect of elevated CO2 on stomatal distribution or the proportion of internal leaf area allocated to a given tissue type at either sampling date. Although the relationships between vascular, transfusion, mesophyll, and epidermal tissue cross-sectional areas to total leaf cross-sectional areas appear nonplastic, leaves grown in elevated CO2 with low N availability exhibit anatomical characteristics suggestive of reduced capacity to assimilate carbon, including decreased mesophyll cell surface area per unit needle volume (in low-N soil). Significantly greater (8%) needle fascicle volume as a result of growth in elevated CO2 was observed after 12 mo because of thicker needles. After 20 mo of exposure, there was a trend indicating smaller fascicle volume (8%) in plants grown with elevated CO2 compared with those grown in ambient conditions, resulting from shorter needles and smaller mesophyll, vascular tissue, and epidermal cell cross-sectional areas. These results indicate short-term stimulation and longterm inhibition of needle growth in longleaf pine as a result of exposure to elevated CO2 and suggest at the leaf level that pine species are less responsive to elevated CO2 than are dicotyledons, including other tree species.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, LEAF ANATOMY, PALUSTRIS, PLANT GROWTH, POPLAR CLONES, RESPONSES, SEEDLINGS, STOMATAL DENSITY

1900

Pritchard, S.G., C.M. Peterson, S.A. Prior, and H.H. Rogers. 1997. Elevated atmospheric CO2 differentially affects needle chloroplast ultrastructure and phloem anatomy in Pinus palustris: Interactions with soil resource availability. *Plant, Cell and Environment 20(4):461-471.*

The response of forest species to increasing atmospheric CO2, particularly under resource limitations, will require study in order to predict probable changes which may occur at the plant, community and ecosystem levels, Longleaf pine (Pinus palustris Mill.) seedlings were grown for 20 months at two levels of CO2 (365 and 720 mu mol mol(-1)) in two levels of soil nitrogen (4 and 40 g m(-2)), and with two levels of soil moisture (-0.5 and -1.5 MPa xylem pressure potential), Leaf tissue was collected in the spring (12 months exposure) and autumn (20 months exposure) and examined using transmission electron microscopy (TEM) and light microscopy, During early spring, elevated CO2 magnified effects of N and water treatment on starch accumulation and in some cases contributed to altered organization of mesophyll chloroplasts. Disruption of chloroplast integrity was pronounced under elevated CO2, low N and water stress, In autumn, needles contained little starch; however, chloroplasts grown under high CO2 exhibited

stress symptoms including increased plastoglobuli and shorter grana, A trend for reduced needle phloem cross-sectional area resulting from fewer sieve cells was also observed under elevated CO2, These results suggest that, in nature, longleaf pine seedlings may not benefit from a doubling of CO2, especially when soil resources are limiting.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE ENRICHMENT, GROWTH, LEAVES, PHOSPHORUS, PHOTOSYNTHESIS, PLANT-RESPONSES, SEEDLINGS, SPRUCE NEEDLES, TRANSLOCATION

1901

Pritchard, S., C. Peterson, G.B. Runion, S. Prior, and H. Rogers. 1997. Atmospheric CO2 concentration, N availability, and water status affect patterns of ergastic substance deposition in longleaf pine (Pinus palustris Mill.) foliage. *Trees-Structure and Function 11(8):494-503.*

Leaf chemistry alterations due to increasing atmospheric CO2 will reflect plant physiological changes and impact ecosystem function. Longleaf pine was grown for 20 months at two levels of atmospheric CO2 (720 and 365 mu mol mol(-1)), two levels of soil N (4 g m(-2) year(-1) and 40 g m(-2) year(-1)), and two soil moisture levels (-0.5 and -1.5 MPa) in open top chambers. After 20 months of exposure, needles were collected and ergastic substances including starch grains and polyphenols were assessed using light microscopy, and calcium oxalate crystals were assessed using light microscopy, scanning electron microscopy, and transmission electron microscopy. Polyphenol content was also determined using the Folin-Denis assay and condensed tannins were estimated by precipitation with protein. Evaluation of phenolic content histochemically was compared to results obtained using the Folin-Denis assay. Total leaf polyphenol and condensed tannin content were increased by main effects of elevated CO2, low soil N and well-watered conditions. Elevated CO2 and low soil N decreased crystal deposition within needle phloem. Elevated CO2 had no effect on the percentage of cells within the mesophyll, endodermis, or transfusion tissue which contained visible starch inclusions. With respect to starch accumulation in response to N stress, mesophyll > endodermis > transfusion tissue. The opposite was true in the case of starch accumulation in response to main effects of water stress: mesophyll < endodermis < transfusion tissue. These results indicate that N and water conditions significantly affect deposition of leaf ergastic substances in longleaf pine, and that normal variability in leaf tissue quality resulting from gradients in soil resources will be magnified under conditions of elevated CO2.

KEYWORDS: ALLELOCHEMICALS, CALCIUM-OXALATE CRYSTALS, CARBON NUTRIENT BALANCE, DIOXIDE, LEAVES, NEEDLES, NITROGEN, PLANTS, RESPONSES, TANNIN

1902

Pritchard, S.G., H.H. Rogers, S.A. Prior, and C.M. Peterson. 1999. Elevated CO2 and plant structure: a review. *Global Change Biology 5(7):807-837.*

Consequences of increasing atmospheric CO2 concentration on plant structure, an important determinant of physiological and competitive success, have not received sufficient attention in the literature. Understanding how increasing carbon input will influence plant developmental processes, and resultant form, will help bridge the gap between physiological response and ecosystem level phenomena. Growth in elevated CO2 alters plant structure through its effects on both primary and secondary meristems of shoots and roots. Although not well established, a review of the literature suggests that cell division, cell expansion, and cell patterning may be affected, driven mainly by increased substrate (sucrose) availability and perhaps also by differential expression of genes involved in cell cycling (e.g. cyclins) or cell expansion (e.g. xyloglucan endotransglycosylase). Few studies, however, have attempted to elucidate the mechanistic basis for increased growth at the cellular level. Regardless of specific mechanisms involved, plant leaf size and anatomy are often altered by growth in elevated CO2, but the magnitude of these changes, which often decreases as leaves mature, hinges upon plant genetic plasticity, nutrient availability, temperature, and phenology. Increased leaf growth results more often from increased cell expansion rather than increased division. Leaves of crop species exhibit greater increases in leaf thickness than do leaves of wild species. Increased mesophyll and vascular tissue cross-sectional areas, important determinates of photosynthetic rates and assimilate transport capacity, are often reported. Few studies, however, have quantified characteristics more reflective of leaf function such as spatial relationships among chlorenchyma cells (size, orientation, and surface area), intercellular spaces, and conductive tissue. Greater leaf size and/or more leaves per plant are often noted; plants grown in elevated CO2 exhibited increased leaf area per plant in 66% of studies, compared to 28% of observations reporting no change, and 6% reported a decrease in whole plant leaf area. This resulted in an average net increase in leaf area per plant of 24%. Crop species showed the greatest average increase in whole plant leaf area (+37%) compared to tree species (+14%) and wild, nonwoody species (+15%). Conversely, tree species and wild, nontrees showed the greatest reduction in specific leaf area (-14% and -20%) compared to crop plants (-6%). Alterations in developmental processes at the shoot apex and within the vascular cambium contributed to increased plant height, altered branching characteristics, and increased stem diameters. The ratio of internode length to node number often increased, but the length and sometimes the number of branches per node was greater, suggesting reduced apical dominance. Data concerning effects of elevated CO2 on stem/branch anatomy, vital for understanding potential shifts in functional relationships of leaves with stems, roots with stems, and leaves with roots, are too few to make generalizations. Growth in elevated CO2 typically leads to increased root length, diameter, and altered branching patterns. Altered branching characteristics in both shoots and roots may impart competitive relationships above and below the ground. Understanding how increased carbon assimilation affects growth processes (cell division, cell expansion, and cell patterning) will facilitate a better understanding of how plant form will change as atmospheric CO2 increases. Knowing how basic growth processes respond to increased carbon inputs may also provide a mechanistic basis for the differential phenotypic plasticity exhibited by different plant species/functional types to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, LEAF-AREA, NATURAL-POPULATIONS, PERENNIAL RYEGRASS, PINUS-TAEDA SEEDLINGS, POPLAR CLONES, SEEDLINGS CASTANEA-SATIVA, SOIL RESOURCE AVAILABILITY, SOURCE-SINK RELATIONS

1903

Prusky, D., H. Hamdan, R. Ardi, and N.T. Keen. 1996. Induction of biosynthesis of epicatechin in avocado suspension cells treated with an enriched CO2 atmosphere. *Physiological and Molecular Plant Pathology 48(3):171-178.*

Exposure to an atmosphere of 30% carbon dioxide caused increased levels of phenylalanine ammonia-lyase (PAL) activity in avocado cell suspension cultures. The carbon dioxide treatment also enhanced chalcone synthase activity by 30% and resulted in a 1 . 5-2 fold greater accumulation of epicatechin than in untreated cells. It was concluded that the level of epicatechin in avocado suspension cells can be increased by carbon dioxide, and this increase appears to be regulated by PAL and CHS activation. (C) 1996 Academic Press Limited.

KEYWORDS: ANTIFUNGAL DIENE, COLLETOTRICHUM-GLOEOSPORIOIDES, FRUITS, INVOLVEMENT, LATENCY, LIPOXYGENASE

1904

Prusky, D., R.A. Plumbley, I. Kobiler, G. Zauberman, and Y. Fuchs. 1993. The effect of elevated co2 levels on the symptom expression of colletotrichum-gloeosporioides on avocado fruits. *Plant Pathology 42(6):900-904.*

Exposure of freshly harvested avocado fruits to different concentrations of CO2 (11, 16 and 30%) for different lengths of time (4, 17 and 26 h) affected the decay development caused by Colletotrichum gloeosporioides. The delay in symptom development depended on the treatment given, the temperature regime of the fruit and time after harvest for treatment application. The most appropriate treatment was the application of 30% CO2 for 24 h at a temperature of 20-25 degrees C on the day of harvest. Treatment for shorter time periods, at lower temperatures or 50 h after harvest, resulted in a reduced response and, in some cases, enhanced symptom expression. Concentrations of 11 or 16% CO2 were less effective than 30% CO2 as the fruits became more mature. It is concluded that treatment of avocado fruits with high levels of CO2 for a short period has the potential to provide an alternative means of controlling anthracnose.

KEYWORDS: ANTHRACNOSE, ATMOSPHERE, CARBON DIOXIDE, INVOLVEMENT, LATENCY, RESISTANCE, STORAGE

1905

Pukhalskaya, N.V. 1997. Generative development of barley at an elevated atmospheric concentration of CO2 and varying temperature conditions. *Russian Journal of Plant Physiology 44(2):152-157.*

Ear development in barley (Hordeum vulgare L.) was studied at normal (350 mu l/l) and elevated (700 mu l/l) atmospheric CO2 concentrations and two temperature regimes. Plant productivity was found to increase by 63 and 47% at temperatures of 20/14 and 23/17 degrees C (day/night), respectively. Analysis of production showed that elevated CO2 may induce an increase in the number of spikelets in the inflorescence primordium and in the size of the primordium beginning from the early stages of development. At 20/14 degrees C, a high level of CO2 significantly elevated the yield of the main ear, increasing the number of caryopses by 18-28% and the grain weight in the main ear by 42-49%. At 23/17 degrees C, a double concentration of CO2 increased plant production due to increased tiller formation (by 75-106%). It was found that the CO2 concentration did not affect pollen fertility in barley at low temperature, but at elevated temperature, the number of sterile pollen grains increased. Thus, the experiments showed that an elevated CO2 concentration affected the development of the barley ear during its whole ontogeny, including the early stages.

KEYWORDS: ENRICHMENT, GROWTH, MODEL, SENSITIVITY, SPRING WHEAT, YIELD

1906

Pukhal'skaya, N.V., and L.V. Osipova. 1999. Drought resistance of wheat plants in an atmosphere enriched with CO2. *Russian Journal of Plant Physiology 46(2):219-226.*

Wheat (Triticum aestivum L.) plants were grown under natural (350 mu l/l) and elevated (700 mu l/l) CO2 concentrations. Watering was discontinued for a portion of the plants during floret development in the primordial ear (the sixth stage of morphogenesis after Kuperman). The evapo-transpiration of the stand, leaf water deficit, membrane permeability for electrolytes, and final grain yield were evaluated. At the beginning of the growth period of the normally watered plants, the elevated CO2 concentration reduced the evapo-transpiration of the stand, providing for slower tissue dehydration during drought. Under equal stress "doses," the drought-induced decrease in the grain yield was deeper in the CO2-enriched atmosphere (37%) than in normal air (27%), although the elevated CO2 level alleviated some metabolic damages (increased membrane permeability in particular). However, the total grain yield was higher in the CO2-enriched atmosphere under both normal watering (by 49%) and drought conditions (by 25%). It was concluded that, under a high CO2 concentration in the air, plant sensitivity to tissue dehydration declined. However, this change was not always correlated with plant drought resistance.

KEYWORDS: CARBON DIOXIDE, GROWTH, PHOTOSYNTHESIS, WATER-USE, WINTER-WHEAT, YIELD

1907

Pukhalskaya, N.V., N. Romin, and E.N. Akanov. 1997. Growth and CO2 exchange in wheat seedlings grown at an elevated concentration of CO2. *Russian Journal of Plant Physiology 44(2):147-151.*

The effect of an elevated concentration of CO2 (700 mu l/l) on the growth and gas exchange of wheat (Triticum aestivum L.) seedlings was studied on the 4th day (germination), the 8th day (etiolated seedlings), and the 13th day (2-leaf stage) after sowing. The elevated concentration of CO2 activated respiration of seeds germinating in the air but did not significantly affect their growth, gas exchange, and the time of shoot formation when the seeds were in soil. The increase in CO2 concentration lowered the rate of respiration in etiolated seedlings by 25-40% and in the 13-day-old seedlings-by 30-35%. In the 13-day-old seedlings, the elevated concentration of CO2 in the air increased the rate of photosynthesis and, as a result, augmented twofold the net (per day) assimilation of CO2 and activated growth processes. Thus, it was found that the CO2 concentration in the air significantly affected the growth and gas exchange of the seedlings before the formation of assimilating machinery.

KEYWORDS: ENRICHMENT, YIELD

1908

Pulleman, M., and A. Tietema. 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. *Soil Biology and Biochemistry 31(2):275-285.*

Microbial C and N transformation rates in air-dried and subsequently rewetted coniferous forest floor material were examined in a laboratory incubation study. Gross N transformation rates were determined through parallel (NH4+)-N- 15 and (NO3-)-N-15 enrichment experiments. After drying of the litter for 12 d to a water content of 10% of dry weight, CO2 respiration, net N mineralization and nitrification rates were strongly restricted. Microbial biomass C was reduced to 67% of the amount in the continuously moist material. Remoistening of the dry litter to a water content of 340% resulted in a flush in C and net N mineralization within a few hours after rewetting. The increase in net N mineralization could be attributed to a larger increase in gross N mineralization relative to the increase in gross N immobilization. Gross N immobilization had increased to the same rate as gross N mineralization after 26 h, and a small secondary peak in respiration and microbial C was observed 48 h after rewetting. It was concluded that both biomass-derived substrate with a low C-to-N ratio and 'nonbiomass'-derived substrate with a high C- to-N ratio have been released, and metabolized, as a result of the drying-rewetting treatment. Despite the very extreme drying treatment, the mineralization flush after rewetting could not compensate for the large reduction in CO2 and mineral N production during dry conditions due to its short duration. Since there was no increase in nitrification rate after drying and rewetting, the NO3- concentration at the end of the incubation was strongly reduced due to the extremely slow net nitrification rates during desiccation.

KEYWORDS: BIOMASS-C, CARBON, EXTRACTION METHOD,

FUMIGATION, GROSS NITROGEN TRANSFORMATIONS, N-15, NITRATE, RATES, SOIL

1909

Pushnik, J.C., R.S. Demaree, J.L.J. Houpis, W.B. Flory, S.M. Bauer, and P.D. Anderson. 1995. The effect of elevated carbon dioxide on a Sierra-Nevadan dominant species: Pinus ponderosa. *Journal of Biogeography 22(2-3):249-254.*

The impact of increasing atmospheric CO2 has not been fully evaluated on western coniferous forest species. Two year old seedlings of Pinus ponderosa were grown in environmentally controlled chambers under increased CO2 conditions (525 mu L L(-1) and 700 mu L L(-1)) for 6 months. These trees exhibited morphological, physiological and biochemical alterations when compared to our controls (350 mu L L(-1)). Analysis of whole plant biomass distribution has shown no significant treatment effect to the root to shoot ratios. However, while stem diameter and height growth generally increased with elevated CO2, needles exhibited an increased overall specific needle mass and a decreased total needle area. Morphological changes at the needle level included decreased mesophyll to vascular tissue ratio and variations in starch storage in chloroplasts. The elevated CO2 increased internal CO2 concentrations and assimilation of carbon. Biochemical assays revealed that ribulose-bis-phosphate carboxylase (RuBPCase) specific activities increased on per unit area basis with CO2 treatment levels. Sucrose phosphate synthase (SPS) activities exhibited an increase of 55% in the 700 mu L(-1) treatment. These results indicate that the sink-source relationships of these trees have shifted carbon allocation toward above ground growth, possibly due to transport limitations.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, FORMS, GROWTH, LEAF ANATOMY, PHOTOSYNTHETIC ACCLIMATION, RADIATA, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1910

Pushnik, J.C., D. Garcia-Ibilcieta, S. Bauer, P.D. Anderson, J. Bell, and J.L.J. Houpis. 1999. Biochemical responses and altered genetic expression patterns in ponderosa pine (Pinus ponderosa Doug ex P. Laws) grown under elevated CO2. *Water, Air, and Soil Pollution 116(1-2):413-422.*

Biochemical and gene expression changes in response to elevated atmospheric CO2 were investigated in five maternal half-sibling breeding families of Ponderosa pine. Seedlings were grown in a common garden located at Lawrence Livermore National Laboratory, in open-topped chambers (OTC) for two years. Chamber atmospheres were maintained at ambient, ambient + 175 mu L L-1, CO2, or ambient + 350 mu L L-1CO2. Growth measurements showed significant increases in stem volumes and volume enhancement ratios in three of the five families studied when grown under elevated CO2. Biochemical and gene expression studies were undertaken to gain a mechanistic understanding of these phenotypic responses. Biochemical studies focused on sucrose phosphate synthase (SPS) specific activities at increase CO2 levels. Kinetic evaluations of SPS showed an increase in V-Max. Specific SPS probes revealed increases in the transcriptional levels of one SPS gene with exposure to increasing CO2. RT-PCR differential gene displays showed that overall only a small fraction of visualized gene transcripts responded to elevated CO2 (8-10%). There were also significant differences between the gene expression patterns of the different families, some of which correlated with alterations in growth at elevated CO2 levels.

KEYWORDS: ALLOCATION, ANATOMY, CARBON-DIOXIDE ENRICHMENT, ENZYMES, LEAVES, METABOLISM, PROTEIN-PHOSPHORYLATION, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1911

Qi, J.E., J.D. Marshall, and K.G. Mattson. 1994. High soil carbon-dioxide concentrations inhibit root respiration of douglas-fir. *New Phytologist 128(3):435-442.*

Total and basal respiration (R(t) and R(b), respectively) of intact and undisturbed roots of one-year-old Douglas fir seedlings, Pseudotsuga menziesii var. glauca [Beissn] France, were measured at experimentally varied soil carbon dioxide concentrations ([CO2]). Use of specially designed root boxes and a CO2 gas-flow compensating system designed around an infrared gas analyzer (IRGA) allowed controlled delivery of CO2 to roots and simultaneous measurements of CO2 released by roots. Root respiration rate responded to each inlet [CO2], independent of whether the previous concentration had been higher or lower, within two to three hours (paired t test = 0.041, P = 0.622, and n = 13). Total and basal respiration rates decreased exponentially as soil [CO2] rose from 130 ppm, well below atmospheric [CO2], to 7015 ppm, a concentration not uncommon in field soils. Analyses of variance (ANOVA) showed that the effects of soil [CO2] on rates of total and basal root respiration were statistically significant. Root respiration rates decreased by 4 to 5 nmol CO2 g(-1) dry weight of roots s(-1) for every doubling of [CO2] according to the following equations: ln(R(t)) (nmol CO2 g(-1) s(-1)) = 5.24-0.30*ln[CO2] with r = 0.78, P < 0.0001, and n = 70; and ln(R(b)) (nmol CO2 g(-1) s(-1)) = 6.29-0.52*ln[CO2] with r = 0.82, P < 0.0001, and n = 35. The sensitivity of root respiration to [CO2] suggests that some previous laboratory measurements of root respiration at atmospheric [CO2], which is 3 to 10-fold lower than [CO2] in field soils, overestimated root respiration in the field. Further, the potential importance of soil [CO2] indicates that it should be accounted for in models of below-ground carbon budgets.

KEYWORDS: CO2- ENRICHMENT, DARK RESPIRATION, EFFLUX, FIELD, GROWTH, LEAVES, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, PERENNIAL RYEGRASS, SEEDLINGS

1912

Rabbinge, R., H.C. Vanlatesteijn, and J. Goudriaan. 1993. Assessing the greenhouse-effect in agriculture. *Ciba Foundation Symposia 175:62-79.*

Evidence that concentrations of CO2 and trace gases in the atmosphere have increased is irrefutable. Whether or not these increased concentrations will lead to climate changes is still open to debate. Direct effects of increased CO2 concentrations on physiological processes and individual plants have been demonstrated and the consequences for crop growth and production under various circumstances are evaluated with simulation models. The consequences of CO2 enrichment are considerable under optimal growing conditions. However, the majority of crops are grown under sub-optimal conditions where the effects of changes in CO2 are often less. The same holds for the possible indirect effects of environmental changes such as temperature rise. Studies on individual plants under optimal conditions are therefore not sufficient for evaluating the effects at a farm, regional, national or supra-national level. Simulation studies help to bridge the gap between the various aggregation levels and provide a basis for various studies of policy options at various aggregation levels.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, GROWTH, PHOTOSYNTHESIS, RESPONSES, SOYBEAN LEAVES, YIELD

1913

Rabha, B.K., and D.C. Uprety. 1998. Effects of elevated CO2 and moisture stress on Brassica juncea. *Photosynthetica 35(4):597-602.*

The interactive effect of elevated CO2 (EC) and moisture stress (MS) on

Brassica juncea cv. Pusa Bold was studied using open- top chambers. The EC markedly increased net photosynthetic rate and internal CO2 concentration and reduced variable and maximal chlorophyll fluorescence. Under MS, EC increased water potential and relative water content, and reduced transpiration rate. The greater allocation of biomass to the roots, which serve as a strong sink for assimilated carbon under EC, helped in better root growth.

KEYWORDS: GROWTH, PHOTOSYNTHESIS, RESPONSES

1914
Raddatz, R.L., and C.F. Shaykewich. 1998. Impact of warm summers on the actual evapotranspiration from spring wheat grown on the eastern Canadian prairies. *Canadian Journal of Soil Science 78(1):171-179.*

How do warm summers (June-July-August) influence the actual evapotranspiration totals from cropped land sown to spring wheat on the eastern Canadian Prairies? The eastern Prairies is a semi-arid region where over 60% of the land is cultivated. Over a third of the cropped land is usually sown to spring wheat. A comparison of mean summer temperatures and modelled evapotranspiration, for the years 1988 to 1996, demonstrated that with the current environmental conditions and farming practices, warm summers have lower actual evapotranspiration totals from spring wheat than cool summers. The average daily actual evapotranspiration rate is generally higher in years with higher mean summer temperatures; however, the crop growth- period is shorter. The net effect is lower total actual evapotranspiration from spring wheat. This suggests that climate warming on the eastern Canadian Prairies, if the current trend continues and all other factors remain equal, will reduce, on average, the total actual evapotranspiration from spring wheat. A reduction in the growth-period actual evapotranspiration from lands sown to spring wheat will likely decrease the total actual evapotranspiration for the entire warm season as growth-period evapotranspiration currently makes up about three-quarters of the seasonal total. However, the magnitude and timing of the reduction is far from certain. The consequence for agriculture may be a reduction in the average spring wheat yield because yield is positively correlated with the actual evapotranspiration total from the crop.

KEYWORDS: AIR CO-2 ENRICHMENT, ENERGY-BALANCE, MODELS, WATER-USE

1915
Radoglou, K.M., P. Aphalo, and P.G. Jarvis. 1992. Response of photosynthesis, stomatal conductance and water-use efficiency to elevated co2 and nutrient supply in acclimated seedlings of phaseolus-vulgaris L. *Annals of Botany 70(3):257-264.*

KEYWORDS: ACCUMULATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GROWTH, INHIBITION, IRRADIANCE, LEAVES, PHOSPHORUS, POPLAR CLONES, RIBULOSE BISPHOSPHATE CARBOXYLASE

1916
Radoglou, K.M., and P.G. Jarvis. 1990. Effects of CO2 enrichment on 4 poplar clones .1. Growth and leaf anatomy. *Annals of Botany 65(6):617-626.*

1917
Radoglou, K.M., and P.G. Jarvis. 1990. Effects of CO2 enrichment on 4 poplar clones .2. Leaf surface- properties. *Annals of Botany 65(6):627-632.*

1918
Radoglou, K.M., and P.G. Jarvis. 1992. The effects of co2 enrichment and nutrient supply on growth- morphology and anatomy of phaseolus-vulgaris L seedlings. *Annals of Botany 70(3):245-256.*

KEYWORDS: AREA, ATMOSPHERIC CARBON-DIOXIDE, FORESTS, LEAF ANATOMY, LEAVES, MINERAL NUTRITION, N,N-DIMETHYLFORMAMIDE, PHOTOSYNTHESIS, PLANTS, POPLAR CLONES

1919
Radoglou, K.M., and P.G. Jarvis. 1993. Effects of atmospheric co2 enrichment on early growth of vivia- faba, a plant with large cotyledons. *Plant, Cell and Environment 16(1):93-98.*

Seedlings of Vicia faba L. were grown in open-top growth chambers at present (P=350 mumol-1) and at elevated (E=700 mumol mol-1) atmospheric CO2 concentration. The effects Of CO2 enrichment on the first phase of growth after germination were examined over 45d. There were no positive effects Of CO2 enrichment on growth of the seedlings during this early phase. No differences were observed in leaf area or in total dry weight. No differences were found in morphology or anatomy of the leaves. The numbers of stomatal and epidermal cells, thickness of leaf, of epidermis and of mesophyll cell-layers were unaffected by CO2 enrichment. Also, no differences were observed in leaf concentrations of chlorophyll, reducing carbohydrates or starch. These results contrast markedly with results from similar experiments on poplar hybrids and Phaseolus vulgaris obtained in the same growth facility. It seems that the intitial growth is under internal control such that the atmospheric CO2 concentration has no effects. The lack of response in this case may be attributed to the presence and longevity of the large cotyledons which provided available substrate for growth.

KEYWORDS: POPLAR CLONES

1920
Rafarel, C.R., T.W. Ashenden, and T.M. Roberts. 1995. An improved Solardome system for exposing plants to elevated CO2 and temperature. *New Phytologist 131(4):481-490.*

Ventilated Solardomes (hemispherical glasshouses) have been used for 20 yr for studying the effects of gaseous pollutants on plants. This paper describes a computer-operated facility for studying the effects of CO2 x temperature regimes on plants. The eight chambers were set up for factorial design experiments - with two levels of CO2 (ambient and ambient+340 ppmv), two levels of temperature (ambient and 3 degrees C tracked continuously above ambient) and two replicates of each CO(2)xtemperature treatment. Monitoring of environmental conditions within the chambers over a 2 yr period has shown highly effective control of CO2 and temperature regimes. Even with high-quality and u.v.-B transmitting glass, the irradiance in the PAR region was reduced by 18 % within the domes. Variation in temperature across the radii of the domes increased with higher photosynthetic photon flux density (PPFD). Vapour pressure deficits (VPDs) in the ambient temperature domes compared well with outside conditions but were higher in the elevated temperature domes. The watering regime within the domes affected intermittently the relationship between 'dome' and 'outside' VPDs. The Solardome facility has been used extensively for studies of the impacts of climate change within the UK Programme on Terrestrial Initiative on Global Environmental Research (TIGER).

KEYWORDS: AIR-POLLUTION, CHAMBERS, ECOSYSTEMS, EXPOSURE, FIELD, OZONE, POLLUTANTS, STRESS, TREES

1921

Raich, J.W., and A. Tufekciogul. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry 48(1):71-90.*

Soil respiration rates vary significantly among major plant biomes, suggesting that vegetation type influences the rate of soil respiration. However, correlations among climatic factors, vegetation distributions, and soil respiration rates make cause-effect arguments difficult. Vegetation may affect soil respiration by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of that detritus, and the overall rate of root respiration. At the global scale, soil respiration rates correlate positively with litterfall rates in forests, as previously reported, and with aboveground net primary productivity in grasslands, providing evidence of the importance of detritus supply. To determine the direction and magnitude of the effect of vegetation type on soil respiration, we collated data from published studies where soil respiration rates were measured simultaneously in two or more plant communities. We found no predictable differences in soil respiration between cropped and vegetation-free soils, between forested and cropped soils, or between grassland and cropped soils, possibly due to the diversity of crops and cropping systems included. Factors such as temperature, moisture availability, and substrate properties that simultaneously influence the production and consumption of organic matter are more important in controlling the overall rate of soil respiration than is vegetation type in most cases. However, coniferous forests had similar to 10% lower rates of soil respiration than did adjacent broad-leaved forests growing on the same soil type, and grasslands had, on average, similar to 20% higher soil respiration rates than did comparable forest stands, demonstrating that vegetation type does in some cases significantly affect rates of soil respiration.

KEYWORDS: BOREAL FOREST ECOSYSTEMS, CARBON-DIOXIDE EVOLUTION, CLIMATIC CHANGE, LAND-USE, MAINTENANCE RESPIRATION, NITROGEN MINERALIZATION, PINE PLANTATIONS, PRIMARY PRODUCTIVITY, ROOT RESPIRATION, SEASONAL PATTERN

1922

Raiesi, F.G., and P. Buurman. 1998. Effects of CO2 enrichment on quality of leaf litter and on soil C dynamics in a Mediterranean forest ecosystem. *Fresenius Environmental Bulletin 7(5A-6A):429-436.*

We discuss the effect of long-term elevated CO2 on quality and decomposability of litter from mature trees, and its influence on soil organic matter (SOM) dynamics by evaluating the available data from mineral CO2 springs in Central Italy. Results from the vegetation around these natural CO2 springs demonstrate that elevated CO2 did not affect litter quality. Consequently, C and N mineralization rates remained unaffected by CO2 level. However, there were significant differences in litter quality and decomposition between species. Results from soil analysis indicate that elevated CO2 increased the total organic C content and C pool sizes in the F layer, but not in HA and 0-10 cm layers. Neither were soil N, C/N ratio and the decomposition of SOM affected by elevated CO2. Soil N mineralization in the forest floor seems to be enhanced by CO2 enrichment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOSPHERE, DECOMPOSITION RATES, ELEVATED CO2, GRASSLAND, RESPONSES

1923

Ranasinghe, S., and G. Taylor. 1996. Mechanism for increased leaf growth in elevated CO2. *Journal of Experimental Botany 47(296):349-358.*

The effect of exposure to elevated CO2 on the processes of leaf cell production and leaf cell expansion was studied using primary leaves of Phaseolus vulgaris L. Cell division and expansion were separated temporally by exposing seedlings to dim red light for 10 d (when leaf cell division was completed) followed by exposure to bright white light for 14 d (when leaf growth was entirely dependent on cell expansion). When plants were exposed to elevated CO2 during the phase of cell expansion, epidermal cell size and leaf area development were stimulated, Three pieces of evidence suggest that this occurred as a result of increased cell wall loosening and extensibility, (i) cell wall extensibility (WEx, measured as tensiometric extension using an Instron) was significantly increased, (ii) cell wall yield turgor (Y, MPa) was reduced and (iii) xyloglucan endotransglycosylase (XET) enzyme activity was significantly increased. When plants were exposed to elevated CO2 during the phase of cell division, the number of epidermal cells was increased whilst final cell size was significantly reduced and this was associated with reduced final leaf area, WEx and XET activity, When plants were exposed to elevated CO2 during both phases of cell division and expansion, leaf area development was not affected. For this treatment, however, the number of epidermal cells was increased, but cell expansion was inhibited, despite exposure to elevated CO2 during the expansion phase. Assessments were also made of the spatial patterns of WEx across the expanding leaf lamina and the data suggest that exposure to elevated CO2 during the phase of leaf expansion may lead to enhanced extensibility particularly at basal leaf margins which may result in altered leaf shape. The data show that both cell production and expansion were stimulated by elevated CO2, but that leaf growth was only enhanced by exposure to elevated CO2 in the cell expansion phase of leaf development. Increased leaf cell expansion is, therefore, an important mechanism for enhanced leaf growth in elevated CO2, whilst the importance of increased leaf cell production in elevated CO2 remains to be elucidated.

KEYWORDS: CELL, ELONGATION, ENRICHMENT, EXPANSION, WALL EXTENSIBILITY, XYLOGLUCAN ENDOTRANSGLYCOSYLASE ACTIVITY

1924

Randerson, J.T., M.V. Thompson, and C.B. Field. 1999. Linking C-13-based estimates of land and ocean sinks with predictions of carbon storage from CO2 fertilization of plant growth. *Tellus Series B-Chemical and Physical Meteorology 51(3):668-678.*

The residence times of carbon in plants, litter, and soils are required for partitioning land and ocean sinks using measurements of atmospheric delta(13)CO(2) and also for estimating terrestrial carbon storage in response to net primary production (NPP) stimulation by elevated levels of atmospheric CO2. While C-13-based calculations of the land sink decline with increasing estimates of terrestrial carbon residence times (through the fossil fuel-induced isotopic disequilibrium term in equations describing the global atmospheric budgets of (CO2)-C-13 and CO2), estimates of land sinks based on CO2 fertilization of plant growth are directly proportional to carbon residence times. Here we used a single model of terrestrial carbon turnover, the Carnegie Ames- Stanford Approach (CASA) biogeochemical model, to simultaneously estimate 1984-1990 terrestrial carbon storage using both approaches. Our goal was to identify the fraction of the (CO2)-C-13-based land sink attributable to CO2 fertilization. Uptake from CO2 fertilization was calculated using a beta factor of 0.46 to describe the response of NPP to increasing concentrations of atmospheric CO2 from 1765 to 1990. Given commonly used parameters in the C-13-based sink calculation and assuming a deforestation flux of 0.8 Pg C/yr, CO2 fertilization accounts for 54% of the missing terrestrial carbon sink from 1984 to 1990. CO2 fertilization can account for all of the missing terrestrial sink only when the terrestrial mean residence time (MRT) and the land isodisequilibrium forcing are greater than many recent estimates.

KEYWORDS: ATMOSPHERIC CO2, C-13, C-13/C-12 RATIO,

DIOXIDE, DISCRIMINATION, ICE CORE, NET PRIMARY PRODUCTION, NITROGEN, SEASONAL CYCLE, TERRESTRIAL BIOSPHERE

1925

Randlett, D.L., D.R. Zak, K.S. Pregitzer, and P.S. Curtis. 1996. Elevated atmospheric carbon dioxide and leaf litter chemistry: Influences on microbial respiration and net nitrogen mineralization. *Soil Science Society of America Journal 60(5):1571-1577.*

Elevated atmospheric CO2 has the potential to influence rates of C and N cycling in terrestrial ecosystems by altering plant litter chemistry and slowing rates of organic matter decomposition, We tested the hypothesis that the chemistry of leaf litter produced at elevated CO2 would slow C and N transformations in soil. Soils were amended with Populus leaf litter produced under two levels of atmospheric CO2 (ambient and twice-ambient) and soil N availability (low and high). Kinetic parameters for microbial respiration and net N mineralization were determined on soil with and without litter during a 32-wk lab incubation, Product accumulation curves for CO2-C and inorganic N were fit to a first order rate equation [y = A(1 - e(-kt))] using nonlinear regression analyses, Although CO2 treatment affected soluble sugar concentration in leaf litter (ambient = 120 g kg(-1), elevated = 130 g kg(-1)), it did not affect starch concentration or C/N ratio, Microbial respiration, microbial biomass, and leaf litter C/N ratio were affected by soil N availability but not by atmospheric CO2, Net N mineralization was a linear function of time and was not significantly different for leaves grown at ambient (50 mg N kg(-1)) and elevated CO2 (35 mg N kg(-1)). Consequently, we found no evidence for the hypothesis that leaf litter produced at elevated atmospheric CO2 will dampen the rates of C and N cycling in soil.

KEYWORDS: CO2, DECOMPOSITION, EFFICIENCY, ENRICHMENT, GROWTH, PRODUCTIVITY, RESPONSES, SEEDLINGS, SOIL-NITROGEN, TERRESTRIAL ECOSYSTEMS

1926

Rao, M.V., and L.J. Dekok. 1994. Interactive effects of high co2 and so2 on growth and antioxidant levels in wheat. *Phyton-Annales Rei Botanicae 34(2):279-290.*

The impact of elevated CO2 and/or SO2 on the growth and antioxidant levels of wheat (Triticum aestivum L. cv. Urban) plants has been studied. High CO2 (0.7 ml l-1) significantly enhanced shoot biomass and photosynthetic capacity, while exposure to SO2 (0.14 mul l-1) resulted in a decreased shoot biomass and in an injured photosynthetic aparatus, illustrated by a loss of chlorophyll and a decreased ratio of variable to maximal fluorescence (F(v)/F(m)) and A(max). However, combined exposure of plants to high CO2 and SO2 eliminated the negative effects of SO2. Sulfate accumulation was almost equal in plants exposed to SO2 and, high CO2 and SO2. A significant increase in ascorbate, glutathione and their redox state was observed in plants exposed to high CO2 and SO2, compared to that of plants exposed to solely SO2. The absence of the negative efects of SO2 in the presence of high CO2 might be related to a high redox state of ascorbate and glutathione. Abbreviations: A(max), maximum rate of oxygen evolution at saturated light and CO2 (mumol m-2 s-1); ASA, reduced ascorbic acid; DHA, dehydroascorbic acid; F(m), maximum emission of photosystem-II chlorophyll fluorescence; F(v), variable component of F(m); GSH, reduced glutathione; GSSG, oxidized glutathione.

1927

Rao, M.V., B.A. Hale, and D.P. Ormrod. 1995. Amelioration of ozone-induced oxidative damage in wheat plants grown under high-carbon dioxide - role of antioxidant enzymes. *Plant Physiology 109(2):421-432.*

O-3-induced changes in growth, oxidative damage to protein, and specific activities of certain antioxidant enzymes were investigated in wheat plants (Triticum aestivum L. cv Roblin) grown under ambient or high CO2. High CO2 enhanced shoot biomass of wheat plants, whereas O-3 exposure decreased shoot biomass. The shoot biomass was relatively unaffected in plants grown under a combination of high CO2 and O-3. O-3 exposure under ambient CO2 decreased photosynthetic pigments, soluble proteins, and ribulose-1,5-bisphosphate carboxylase/oxygenase protein and enhanced oxidative damage to proteins, but these effects were not observed in plants exposed to O-3 under high CO2. O-3 exposure initially enhanced the specific activities of superoxide dismutase, peroxidase, glutathione reductase, and ascorbate peroxidase irrespective of growth in ambient or high CO2. However, the specific activities decreased in plants with prolonged exposure to O-3 under ambient CO2 but not in plants exposed to O-3 under high CO2. Native gels revealed preferential changes in the isoform composition of superoxide dismutase, peroxidases, and ascorbate peroxidase of plants grown under a combination of high CO2 and O-3. Furthermore, growth under high CO2 and O-3 led to the synthesis of one new isoform of glutathione reductase. This could explain why plants grown under a combination of high CO2 and O-3 are capable of resisting O-3-induced damage to growth and proteins compared to plants exposed to O-3 under ambient CO2.

KEYWORDS: AIR- POLLUTANTS, ASCORBATE PEROXIDASE, ATMOSPHERIC CO2 CONCENTRATION, B RADIATION, ELEVATED CO2, ENRICHMENT, PHOTOSYNTHETIC RESPONSE, PROTEINS, SULFUR-DIOXIDE, SUPEROXIDE-DISMUTASE

1928

Rastetter, E.B. 1996. Validating models of ecosystem response to global change. *BioScience 46(3):190-198.*

KEYWORDS: BIOMASS, CARBON BUDGET, CLIMATE, ELEVATED CO2, PHOTOSYNTHESIS, TEMPERATURE, TUNDRA

1929

Rastetter, E.B., and G.R. Shaver. 1992. A model of multiple-element limitation for acclimating vegetation. *Ecology 73(4):1157-1174.*

In this paper we present a simple model of multiple-element limitation of plant production and biomass accumulation. The primary aim of this model is to develop a theoretical framework for examining multiple-element limitation vs. single-element limitation and for examining the relationship between short- term and long-term responses to changes in element availability. In the model we assume that there is an "optimal" ratio of mineral elements in vegetation biomass, and that the vegetation continually adjusts its relative element uptake capacities to compensate for shifts away from this optimum. We examine the responses of this model to changes in element availability in the plant environment, where "availability" is defined either as fixed concentrations of non-depletable elements or as fixed replenishment rates of depletable elements. The model results suggest that the nature of the controls on element availability has a major impact on whether single- or multiple-element limitation prevails, even when plants can acclimate so as to maintain an "optimal" nutritional balance. Single-element limitation occurs when the replenishment rate of an essential element to the available pool is limited and sustainable plant uptake of that element equals the replenishment rate. Furthermore, when single- element limitation prevails, there is little or no correlation between short-term responses to a change in element availability and long-term, equilibrium responses. In general, previous experimental studies and models of plant growth in response to changes in relative availability of multiple, essential elements have either not specified how those resources are controlled, or have examined only one

type of control. Our results help to explain the diversity of results of past studies of multiple-element limitation, suggest some improvements in experimental design for future studies, and have important implications for the extrapolation of the results of controlled experiments to field situations.

KEYWORDS: CO2- ENRICHMENT, COMPETITION, ECOSYSTEMS, EFFICIENCY, GROWTH, NITROGEN-AVAILABILITY, PHOTOSYNTHESIS, PLANTS, TAIGA TREES, TEMPERATURE

1930

Ratanachinakorn, B., A. Klieber, and D.H. Simons. 1997. Effect of short-term controlled atmospheres and maturity on ripening and eating quality of tomatoes. *Postharvest Biology and Technology 11(3):149-154.*

Mature green, breaker, and pink 'Bermuda' tomatoes (Lycopersicon esculentum Mill.) were treated in air, 0.5% O-2 for 1 day, or 80% CO2 for 1 or 2 days at 22 degrees C before ripening in air at 22 degrees C. Headspace ethanol (EtOH) and acetaldehyde (AA), soluble solids (SS), titratable acidity (TA), and pH were measured, and sensory quality was determined using descriptive analysis with a trained panel. Some ripening delay of 1-2 days was observed due to low O-2 and 2 days of high CO2. EtOH and AA production increased more with increasing fruit maturity and with low O-2 at these maturities; both volatiles dissipated to trace amounts before fruit were eating ripe in all treatments. Aroma and taste were not enhanced by any treatment/ripeness combinations, although 80% CO2 for 2 days marginally increased the sweetness and blandness of the fruit. Soluble solids, titratable acidity and pH were not different between treatments or ripening stages. (C) 1997 Elsevier Science B.V.

KEYWORDS: ACETALDEHYDE VAPOR, ANAEROBIC CONDITIONS, EXPRESSION, FRUIT, ORANGES, POSTHARVEST APPLICATION, STORAGE, VOLATILES

1931

Rathgeber, C., J. Guiot, P. Roche, and L. Tessier. 1999. Quercus humilis increase of productivity in the Mediterranean area. *Annals of Forest Science 56(3):211-219.*

Several recent studies have shown an increasing long-term growth trend for various forest tree species in western Europe. Nevertheless such studies have not yet, been performed in Mediterranean Europe. The aim of this work is to analyse changes in productivity of some Mediterranean forest ecosystems compared with other medioeuropean forest ecosystems. Sixteen Quercus humilis (Miller) populations were sampled in south-east France. Tree ring widths were measured for each tree according to three radius, and annual basal area increments were calculated. Two growth indexes (IP and IC) were calculated with two different standardization techniques, in order to remove age and interstation productivity effects. From the IP and IC indexes we can see that there was a productivity increase during the last century, this increase being evaluated at 100 % (IC index). These results indicate that the Mediterranean forest ecosystems have shown a high productivity increase over the last century, as have the medioeuropean forest ecosystems. The best hypothesis to explain this increasing long-term growth trend is a direct CO2 fertilization along with N deposition fertilization. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE, ENERGY-PRODUCTION, FERTILIZATION, FOREST ECOSYSTEMS, GROWTH-RESPONSES, NORTHEASTERN FRANCE, TREE-RING CHRONOLOGY, TRENDS

1932

Rattray, E.A.S., E. Paterson, and K. Killham. 1995. Characterization of the dynamics of C-partitioning within lolium-perenne and to the rhizosphere microbial biomass using C-14 pulse-chase. *Biology and Fertility of Soils 19(4):280-286.*

The dynamics of C partitioning with Lolium perenne and its associated rhizosphere was investigated in plant-soil microcosms using C-14 pulse-chase labelling. The CO2(C-14) pulse was introduced into the shoot chamber and the plants allowed to assimilate the label for a fixed period. The microcosm design facilitated independent monitoring of shoot and root/soil respiration during the chase period. Partitioning between above- and below-ground pools was determined between 30 min and 168 h after the pulse, and the distribution was found to vary with the length of the chase period. Initially (30 min after the pulse), C-14 was predominantly (99%) in the shoot biomass and declined thereafter. The results indicate that translocation of recent photoassimilate is rapid, with C-14 detected below ground within 30 min of pulse application. The translocation rate of C-14 below ground was maximal (6.2% h-1) between 30 min and 3h after the pulse, with greatest incorporation into the microbial biomass detected at 3 h. After 3 h, the microbial biomass C-14 pool accounted for 74% of the total C-14 rhizosphere pool. By 24 h, approximately 30% of C-14 assimilate had been translocated below ground; thereafter C-14 translocation was greatly reduced. Partitioning of recent assimilate changed with increasing CO2 concentration. The proportion of C-14 translocated below ground almost doubled from 17.76% at the ambient atmospheric CO2 concentration (450 ppm) to 33.73% at 750 ppm CO2 concentration. More specifically, these changes occurred in the root biomass and the total rhizosphere pools, with two- and threefold C-14 increases at an elevated CO2 concentration compared to ambient, respectively. The pulse- labelling strategy developed in this study provided sufficient sensitivity to determine perturbations in C dynamics in L. perenne, in particular rhizosphere C pools, in response to an elevated atmospheric CO2 concentration.

KEYWORDS: ATMOSPHERIC CO2, CARBON FLOW, FIELD PLOTS, GROWTH-RESPONSE, NITROGEN, PLANTS, ROOTS, SANDY LOAM, SOIL, WHEAT

1933

Raveh, E., M. Gersani, and P.S. Nobel. 1995. Co2 uptake and fluorescence responses for a shade-tolerant cactus hylocereus-undatus under current and doubled co2 concentrations. *Physiologia Plantarum 93(3):505-511.*

Hylocereus undatus (Haworth) Britton and Rose growing in controlled environment chambers at 370 and 740 mu mol CO2 mol(- 1) air showed a Crassulacean acid metabolism (CAM) pattern of CO2 uptake, with 34% more total daily CO2 uptake under the doubled CO2 concentration and most of the increase occurring in the late afternoon. For both CO2 concentrations, 90% of the maximal daily CO2 uptake occurred at a total daily photosynthetic photon flux density (PPFD) of only 10 mol m(-2) day(-1) and the best day/night air temperatures were 25/15 degrees C. Enhancement of the daily net CO2 uptake by doubling the CO2 concentration was greater under the highest PPFD (30 mol m(-2) day(-1)) and extreme day/night air temperatures (15/5 and 45/35 degrees C). After 24 days of drought, daily CO2 uptake under 370 mu mol CO2 mol(-1) was 25% of that under 740 mu mol CO2 mol(-1). The ratio of variable to maximal chlorophyll fluorescence (F-v/F-m) decreased as the PPFD was raised above 5 mol m(-2) day(-1), at extreme day/night temperatures and during drought, suggesting that stress occurred under these conditions. F-v/F-m was higher under the doubled CO2 concentration, indicating that the current CO2 concentration was apparently limiting for photosynthesis. Thus net CO2 uptake by the shade-tolerant H. undatus, the photosynthetic efficiency of which was greatest at low PPFDs, showed a positive response to doubling the CO2 concentration, especially under stressful environmental conditions.

KEYWORDS: AGAVE-VILMORINIANA, CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ELEVATED CO2, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, OPUNTIA FICUS INDICA, PLANT

1934

Raven, J.A. 1994. Carbon fixation and carbon availability in marine-phytoplankton. *Photosynthesis Research 39(3):259-273.*

It is widely believed that inorganic C does not limit the rate of short-term photosynthesis, the net productivity, or the maximum biomass, of marine phytoplankton. This lack of inorganic C restriction is less widely believed to hold for phytoplankton in many low alkalinity freshwaters or for seaweed in nutrient-enriched rock pools. These views are examined in the context of the physical chemistry of the inorganic C system in natural waters and of the ways in which various taxa of phytoplankton deal with inorganic C and discriminate between C- 12 and C-13. Using this information to interpret data obtained in the ocean or in freshwater suggests that short-term photosynthesis, production rate, and achieved biomass, of phytoplankton are rarely limited by inorganic C supply but, rather, that the widely suggested factors of limited light, nitrogen or phosphorus supply are the resource inputs which restrict productivity. Global change, by increasing atmospheric CO2 partial pressure and global mean temperatures, is likely to increase the mean CO2 concentration in the atmosphere, but the corresponding change in the oceans will be much less. There are, however, genotypic differences in the handling of inorganic C among the diversity of marine phytoplankton, and in impact on use of limiting nutrients, so increases in the mean CO2 and HCO3- concentrations in surface ocean waters could cause changes in species composition. However, the rarity of inorganic C limitation of marine phytoplankton short-term photosynthesis, net productivity, or the maximum biomass, in today's ocean means that global change is unlikely to increase these three values in the ocean.

KEYWORDS: ATMOSPHERIC CO2, DELTA C 13, GROWTH-RATES, ICE CORE, INORGANIC CARBON, NATURAL ABUNDANCE, PLANTS, PRODUCTIVITY, SURFACE OCEAN, TEMPERATURE

1935

Rawson, H.M. 1992. Plant-responses to temperature under conditions of elevated CO2. *Australian Journal of Botany 40(4-5):473-490.*

A literature survey of the interactive effects of CO2 enrichment and temperature on plant development and growth, indicated that the responses cannot be interpreted within a simple framework. For example, although plant development is generally accelerated by increased temperature, CO2 enrichment can accelerate it even further in some instances, or CO2 enrichment may have neutral or even retarding effects in other cases. Where the temperature and CO2 effects are additive, it is argued that CO2 is operating in the same way as radiation to reduce a carbon limitation. If this were true, CO2 enrichment would be most likely to accelerate development in tropical regions during the low-radiation monsoon season. Similarly, while it would be expected that CO2-enrichment would have increasingly enhancing effects with increasing temperature on phytomass growth, this is not invariably the case. In extreme examples which followed the expected trend, plants grown in twice-normal CO2-enriched atmospheres performed progressively better than those grown at current levels of CO2 by 8.7% for every 1-degrees-C rise in temperature. However, the difference between the two CO2 treatments more commonly increased by only around 2% for every 1-degrees-C rise in temperature. Of examples examined, both sunflower and nodulated cowpea showed the reverse response to temperature, while non-nodulated cowpea, supplied with luxuriant levels of nutrition, showed no interaction with temperature but a strong interaction between CO2 and radiation. Other aspects of the environment such as nutrition and radiation strongly modify the responses to temperature. It is also clear that plant factors such as stage of development can alter the response to CO2. Long-term studies with several species are required which will take into account many environmental variables within a realistic envelope. One methodology for doing this is presented. There was no evidence among species that responses to CO2 arise through any consistent change in morphology such as via increased branching or increased leaf number. Plant plasticity is such that responses can be expressed in a variety of ways determined by other environmental variables.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, KUDZU PUERARIA-LOBATA, LEAF EXPANSION, SEED YIELD, SPRING WHEAT, WATER-USE, WINTER-WHEAT, YIELD COMPONENTS

1936

Rawson, H.M. 1995. Yield responses of 2 wheat genotypes to carbon-dioxide and temperature in-field studies using temperature-gradient tunnels. *Australian Journal of Plant Physiology 22(1):23-32.*

Clear, plastic-coated, temperature gradient tunnels (TGTs), 8 X 1.25 X 1.25 m were designed and built to examine how temperature and CO2 affect the yield of wheat in the field. Each of the three modules of each TGT was maintained at a different temperature above the ambient temperature using solar heating during the day and electric heating at night. The maximum day-time increment above ambient for the warmest module was 5 degrees C and full-season averages were close to 2 degrees C. TGTs were paired, with air in one being enriched to 700 mu L L(-1) CO2, and in the other being maintained at ambient CO2. Crops were planted in the TGTs at two sites in either summer (December) or winter (April and July) and they remained there until maturity. CO2 enrichment increased the yield in summer plantings by up to 36%. In winter plantings, with mean temperatures between sowing and anthesis of around 10 degrees C, the responses to CO2 were small averaging only 7% (range 1-12%). Though yield declined with increasing temperature in the TGTs in summer, there was a clear trend for an increasing response to CO2 at these higher temperatures, i.e. yield declined less. In summer, there was no convincing evidence for a different relative response to CO2 in two isolines which differed in maturity date, though the later line yielded more under the highest temperature regime (mean of 22- 24 degrees C between sowing and anthesis). In winter there was a strong trend for the isoline requiring less vernalisation to respond more to CO2. It is suggested that early progress towards flowering might predispose wheat to a greater CO2 response. Overall, the data indicated that the positive response to CO2 in grain yield is likely to increase at approximately 1.8% per 1 degrees C in wheat crops that are not limited by water. Extrapolation indicated that the temperature at which there was no response to CO2 was 5 degrees C. All yield responses reflected biomass responses as harvest index was unchanged by CO2.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CULTIVAR, ELEVATED CO2, PHOTOPERIOD, PHOTOSYNTHESIS, PLANT GROWTH, POA-PRATENSIS, PRODUCTIVITY, STRESS, WATER

1937

Read, J.J., and J.A. Morgan. 1996. Growth and partitioning in Pascopyrum smithii (C-3) and Bouteloua gracilis (C-4) as influenced by carbon dioxide and temperature. *Annals of Botany 77(5):487-496.*

This study investigated how CO2 and temperature affect dry weight (d.wt) accumulation, total nonstructural carbohydrate (TNC) concentration, and partitioning of C and N among organs of two important grasses of the shortgrass steppe, Pascopyrum smithii Rydb. (C-3) and Bouteloua gracilis (H.B.K.) Lag. ex Steud. (C-4). Treatment combinations comprised two temperatures (20 and 35 degrees C) at two

concentrations of CO2 (380 and 750 mu mol mol(-1)), and two additional temperatures of 25 and 30 degrees C at 750 mu mol mol(-1) CO2. Plants were maintained under favourable nutrient and soil moisture and harvested following 21, 35, and 49 d of treatment. CO2-induced growth enhancements were greatest at temperatures considered favourable for growth of these grasses. Compared to growth at 380 mu mol mol(-1) CO2, final d.wt of CO2-enriched P. smithii increased 84% at 20 degrees C but only 4% at 35 degrees C. Final d.wt of B. gracilis was unaffected by CO2 at 20 degrees C, but was enhanced by 28% at 35 degrees C. Root:shoot ratios remained relatively constant across CO2 levels, but increased in P. smithii with reduction in temperature. These partitioning results were adequately explained by the theory of balanced root and shoot activity. Favourable growth temperatures led to CO2-induced accumulations of TNC in leaves of both species, and in stems of P. smithii, which generally reflected responses of above-ground d.wt partitioning to CO2. However, CO2-induced decreases in plant tissue N concentrations were more evident for P. smithii. Roots of CO2-enriched P. smithii had greater total N content at 20 degrees C, an allocation of N below- ground that may be an especially important adaptation for C-3 plants. Tissue N contents of B. gracilis were unaffected by CO2. Results suggest CO2 enrichment may lead to reduced N requirements for growth in C-3 plants and lower shoot N concentration, especially at favourable growth temperatures. (C) 1996 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, BIOMASS, ENRICHMENT, MODEL, NITROGEN, RESPONSES

1938

Read, J.J., J.A. Morgan, N.J. Chatterton, and P.A. Harrison. 1997. Gas exchange and carbohydrate and nitrogen concentrations in leaves of Pascopyrum smithii (C-3) and Bonteloua gracilis (C-4) at different carbon dioxide concentrations and temperatures. *Annals of Botany 79(2):197-206.*

Pascopyrum smithii (C-3) and Bouteloua gracilis (C-4) are important forage grasses native to the Colorado shortgrass steppe. This study investigated photosynthetic responses of these grasses to long-term CO2 enrichment and temperature in relation to leaf nonstructural carbohydrate (TNC) and [N]. Glasshouse-grown seedlings were transferred to growth chambers and grown for 49 d at two CO2 concentrations (380 and 750 mu mol mol(-1)) al 20 and 35 degrees C, and two additional temperatures (25 and 30 degrees C) at 750 mu mol mol(-1) CO2. Leaf CO2 exchange rate (CER) was measured at a plant's respective growth temperature and at two CO2 concentrations of approx. 380 and 700 mu mol mol(-1). Long-term CO2 enrichment stimulated CER in both species, although the response was greater in the CER P. smithii. Doubling the [CO2] from 380 to 750 mu mol mol(-1) stimulated CER of P. smithii slightly more in plants grown and measured al 30 degrees C compared to plants grown at 20, 25 or 35 degrees C. CO2-enriched plants sometimes exhibited lower CER when compared to ambient-grown controls measured at the same [CO2], indicating photosynthetic acclimation to CO2 growth regime. In P. smithii, such reductions in CER were associated with increases in TNC and specific leaf mass, reductions in leaf [N] and, in one instance, a reduction in leaf conductance compared to controls. In B. gracilis, photosynthetic acclimation was observed more often, but significant changes in leaf metabolite levels from growth at different [CO2] were generally less evident. Temperatures considered optimal for growth (C-3: 20 degrees C; C-4: 35 degrees C) sometimes led to CO2-induced accumulations of TNC in both species, with starch accumulating in the leaves of both species, and fructans accumulating only in P. smithii. Photosynthesis of both species is likely to be enhanced in future CO2-enriched and warmer environments, although responses will sometimes be attenuated by acclimation. (C) 1997 Annals of Botany Company.

KEYWORDS: ACCLIMATION, ACCUMULATION, ATMOSPHERIC CO2 CONCENTRATIONS, BOUTELOUA-GRACILIS, COOL TEMPERATURES, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, PLANTS, STARCH

1939

Reddy, A.R., K.R. Reddy, and H.F. Hodges. 1998. Interactive effects of elevated carbon dioxide and growth temperature on photosynthesis in cotton leaves. *Plant Growth Regulation 26(1):33-40.*

Cotton (Gossypium hirsutum L., cv DPL 5415) plants were grown in naturally lit environment chambers at day/night temperature regimes of 26/18 (T26/18), 31/23 (T-31/23) and 36/28 degrees C (T-36/28) and CO2 concentrations of 350 (C-350), 450 (C-450) and 700 IA L L-1 (C-700). Net photosynthesis rates, stomatal conductance, transpiration, RuBP carboxylase activity and the foliar contents of starch and sucrose were measured during different growth stages. Net CO2 assimilation rates increased with increasing CO2 and temperature regimes. The enhancement of photosynthesis was from 24 mu mol CO2 m(-2) s(-1) (with C-350 and T-26/18) to 41 mu mol m-2 s(-1) (with C-700 and T-36/28). Stomatal conductance decreased with increasing CO2 while it increased up to T-31/23 and then declined. The interactive effects of CO2 and temperature resulted in a 30% decrease in transpiration. Although the leaves grown in elevated CO2 had high starch and sucrose concentrations, their content decreased with increasing temperature. Increasing temperature from T- 26/18 to 36/28 increased RuBP carboxylase activity in the order of 121, 172 and 190 mu mol mg(-1) chi h(-1) at C-350, C-450 and C-700 respectively. Our data suggest that leaf photosynthesis in cotton benefited more from CO2 enrichment at warm temperatures than at low growth temperature regimes.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERIC CO2, ENRICHMENT, PLANTS, PROTEIN, RATES, RICE

1940

Reddy, K.R., G.H. Davidonis, A.S. Johnson, and B.T. Vinyard. 1999. Temperature regime and carbon dioxide enrichment alter cotton roll development and fiber properties. *Agronomy Journal 91(5):851-858.*

Temperature and atmospheric carbon dioxide concentration [CO2] affect cotton (Gossypium hirsutum L.) growth and development, but the interaction of these two factors on boil and fiber properties has not been studied. An experiment aas conducted in naturally lit plant growth chambers to determine the influence of temperature and atmospheric [CO2] on cotton (cv. DPL-51) boll and fiber growth parameters. Five temperature regimes were evaluated: the 1995 temperature at Mississippi State, MS; the 1995 temperature minus 2 degrees C; and the 1995 temperature plus 2, 5, and 7 degrees C. Daily and seasonal variation and amplitudes were maintained. Atmospheric [CO2] treatments were 360 (ambient) and 720 mu L L-1. Boll number, bell growth, and fiber properties were measured. Boll size and maturation periods decreased as temperature increased. Boll growth increased with temperature to 25 degrees C and then declined at the highest temperature. Boll maturation period, size, and growth rates were not affected by atmospheric [CO2]. The most temperature-sensitive aspect of cotton development is boll retention. Almost no bells were retained to maturity at 1995 plus 5 or 7 degrees C, but squares and bells were continuously produced even at those high temperatures. Therefore, the upper limit for cotton boil survival is 32 degrees C, or 5 degrees C warmer than the 1995 U.S. Mid-South ambient temperatures. The 720 mu L L-1 atmospheric [CO2] had about 40% more squares and bells across temperatures than the 360 mu L L-1 [CO2], Fibers were longer when bells grew at less than optimal temperatures (25 degrees C) for boll growth. As temperature increased, fiber length distributions were more uniform. Fiber fineness and maturity increased linearly with the increase in temperature up to 26 degrees C, but decreased at 32 degrees C. Short-fiber content declined linearly from 17 to 26 degrees C, but was higher at higher temperature.

As for boll growth and developmental parameters, elevated atmospheric [CO2] did not affect any of the fiber parameters. Changes in temperature, however, had a dramatic effect on boll set and tiber properties. The relationships between temperature and boll growth and developmental rate functions and fiber properties provide the necessary functional parameters to build fiber models under optimum water and nutrient conditions.

KEYWORDS: CROP MANAGEMENT, GROWTH, RAY-FLUORESCENCE SPECTROSCOPY, RICE, SIMULATION-MODEL, SYSTEM

1941

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1995. Carbon-dioxide and temperature effects on pima cotton development. *Agronomy Journal 87(5):820-826.*

Predicting plant responses to changing atmospheric CO2 and to the possible global warming are important concerns. Effects of CO2 on developmental events are poorly documented, as is the interaction of CO2 and other major climate variables on crop development. The objective of this experiment was to determine the effects of an altered CO2 environment and interactions of CO2 and temperature on pima cotton developmental rates. Pima cotton (Gossypium barbadense L. cv. S-6) was grown from seed in sun-lit plant growth chambers. Air temperatures were controlled from 20/12 to 40/32 degrees C (day/night) in 5-degree increments. Daytime CO2 was maintained at 350 or 700 mu L L(- 1). In a second experiment, the temperature was maintained at 30/22 degrees C day/night and the plants were grown in 350, 450, or 700 mu L L(-1) CO2. Days required to develop nodes on the mainstem, days from emergence to first square, number of vegetative and fruiting branches, number of fruiting sites produced, number of bells and squares produced, and number of bells and squares retained by the plants were determined. Rates of mainstem node formation and the time required to produce the first square and first flower were not sensitive to atmospheric CO2, but were very sensitive to temperature. Prefruiting branch nodal positions required longer to develop than nodes with fruiting branches. Carbon dioxide levels did not affect the time required to produce nodes. Number of branches produced was sensitive to both temperature and CO2. The larger number of bells set on the lower branches of plants grown at high CO2 provided a larger sink for photosynthate than plants grown at low CO2. This may be the reason for the observed reduction in number of fruit at the upper nodes of high-CO2-grown plants. More bells and squares were produced and retained on plants grown in high-CO2 environments, except that none were produced in either CO2 environment at 40/32 degrees C. Our results indicate that high-temperature-tolerant cotton cultivars would be more productive in the present-day CO2 world, and they would be essential in the future if global temperature increases.

KEYWORDS: ELEVATED CO2, ENRICHMENT, GROWTH, PLANTS, RESPONSES

1942

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1995. Carbon-dioxide and temperature effects on pima cotton growth. *Agriculture Ecosystems & Environment 54(1-2):17-29.*

Temperature and CO2 are major environmental variables that affect plant growth and development. Limited information is available concerning how these factors affect plants, as well as specific interactions between the two. We conducted two experiments in controlled environmental chambers were temperature and CO2 were controlled and other environmental factors were not limiting. The purpose was to determine how cotton grew and responded to a range of temperatures and CO2 concentrations. During vegetative development, stem growth was quite sensitive to CO2 resulting in more effective early-season light capture. Plants did not develop more nodes when exposed to additional CO2, while node number increased more at higher temperatures. Individual leaf growth was about 18% greater at optimum temperature in 450 mul 1(-1) than in 350 mul 1(-1) CO2, but did not increase from 450 mul 1(-1) CO2 to 700 mul 1(-1) CO2. However, the time required for a leaf to reach mature size was not influenced by CO2. Leaf area, on the whole plant basis, was about 33% greater on plants grown at optimum temperature in high CO2 than in ambient CO2. The greater leaf area on a whole plant basis was achieved by a combination of larger leaves and additional leaves produced primarily on the branches. There was a 28% increase in number of bolls produced at 700 mul 1(-1) CO2 at optimum temperature compared with bolls produced at 350 mul 1(-1) CO2. There was not, however, an increase in boll size due to high CO2. At 35.5-degrees-C, little growth response to high CO2 environments occurred at 700 mul 1(-1) CO2 compared with 350 mul 1(-1) CO2, but approximately a 45% increase occurred in the plants grown at 18.9-26.9-degrees-C. Less total biomass was produced at 35.5-degrees-C than at 26.9-degrees-C and no bolls were produced in either CO2 environment at the higher temperature. The most important response to temperature and CO2 occurred at high temperatures where the effects of elevated CO2 on plant growth were masked by apparent high-temperature injury that limited growth of all plant organs, particularly, reproductive growth.

KEYWORDS: ELEVATED CO2, RESPONSES, RETENTION

1943

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1997. A comparison of scenarios for the effect of global climate change on cotton growth and yield. *Australian Journal of Plant Physiology 24(6):707-713.*

If global surface temperatures change as projected because of radiative and physiological effects of a changing environment, we should expect important changes in crop production in the 21st Century. Experiments were conducted at ambient and twice ambient atmospheric CO2 concentrations at five temperatures. The 1995 temperature in Mississippi was used as a reference with the other temperatures being 1995 minus 2 degrees C, and 1995 plus 2, 5 and 7 degrees C. Daily and seasonal variation and amplitudes were maintained. Seedlings had 4-6 times as much leaf area and dry weight at 20 d after emergence when grown at 28 degrees C as at 23 degrees C (1995 ambient) average temperature during that growth period. Number of days to first square, flower, and open boil decreased as temperature increased. Double atmospheric CO2 did not affect these developmental rates. Temperatures above 28 degrees C, or 1995 average whole-season temperatures, were detrimental to mid-and late-season boil retention and growth. No fruits were retained to maturity at 1995 plus 5 or 7 degrees C. However, whole season vegetative growth was not significantly reduced by temperature 5-7 degrees C above the 1995 ambient conditions. Twice ambient CO2 caused about 40% increase in vegetative dry matter accumulation across temperatures. In a separate experiment, similar results were obtained on fruiting cotton grown at a range of temperatures based on long-term average US Midsouth July temperatures. Therefore, if global warming occurs as predicted, food and fibre production in such high- temperature and humid environments may be more limited to vegetative structures and the animals that consume vegetative structures.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, PIMA COTTON, RESPONSES, RICE

1944

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1997. Modeling temperature effects on cotton internode and leaf growth. *Crop Science 37(2):503-509.*

Cotton (Gossypium hirsutum L.) is grown commercially in temperatures that vary greatly during the season. The purpose of this study was to develop potential growth and developmental rates of cotton leaves and internodes as a function of temperature in a temperature-limiting environment. That information may be used with growth duration and appropriate stress factors to develop a crop canopy development model. Plants were grown in sunlit plant growth chambers in five temperatures, 20/12 degrees C to 40/32 degrees C (day/night), at ambient (350 mu L L-1 CO2) and twice ambient carbon dioxide levels in well-watered and fertilized conditions. Plants were monitored daily for leaf unfolding dates, areas of leaves, and lengths of internodes at leaf unfolding, and growth of leaves and internodes. Durations of leaf and internode expansion were also determined. Leaf unfolding interval rates of both mainstem and fruiting branches increased as temperature increased; the rate of mainstem leaf unfolding interval increased more than the rate of branch leaf unfolding. Irrespective of sizes, leaves, and internodes fit a single relationship of relative expansion rates and age for each temperature condition. Enriching CO2 to twice the ambient level did not change these relationships. Increasing temperature increased maximum growth rate, decreased the decay in the rate of expansion due to age, and reduced growth duration of both leaves and internodes. Internodes typically took less time than leaves to elongate at all temperatures. Leaf area and internode length at leaf unfolding increased as temperature increased to 27 to 30 degrees C, then decreased at higher temperatures.

KEYWORDS: CARBON DIOXIDE, GOSSYPIUM HIRSUTUM L, INITIATION, LEAVES, YIELD

1945

Reddy, K.R., R.R. Robana, H.F. Hodges, X.J. Liu, and J.M. McKinion. 1998. Interactions of CO2 enrichment and temperature on cotton growth and leaf characteristics. *Environmental and Experimental Botany 39(2):117-129.*

Studies on the interactive effects of atmospheric CO2 and temperature on growth and leaf morphology, particularly on stomatal index and density are limited. Upland cotton was grown in naturally-lit plant growth chambers al 30/22 degrees C day/night temperatures from planting until squaring or the fifth or sixth leaf emerged. Five growth chambers were maintained at ambient (350 mu l l(-1)) CO2 and another five at twice ambient (700 mu l l(-1)) CO2 throughout the experiment. Day/night temperature treatments of 20/12, 25/17, 30/22, 35/27 and 40/32 degrees C were imposed at each CO2 treatment for 42 days after squaring. The plants were irrigated with half- strength Hoagland's nutrient solution three times per day. Growth of plant parts was determined at the end of the experiment. Stomatal characteristics, nonstructural carbohydrates and specific leaf weight were measured on the fully expanded tenth mainstem leaf, Stomatal density and index were not affected by elevated CO2. Stomata and epidermal cell numbers pet leaf increased in high CO2 and were positively correlated with final leaf sizes irrespective of CO2 level. Our results suggest that plants do not acclimate to elevated CO2 by changing stomatal density within a single generation. Leaves had greater area and accumulated more biomass when grown in high CO2. Growth stimulation expressed as dry weight at 700 mu l l(-1) over dry weight al 350 mu l l(-1) CO2 was uniform across temperatures. Temperature optimum for vegetative and reproductive growth was 30/22 degrees C and was not altered by CO2 enrichment. Fruit retention was severely curtailed at the two higher temperatures compared to 30/22 degrees C in both CO2 environments. increased carbohydrate storage in leaves may be an added advantage for initiation and growth of vegetative structures such as branches at all temperatures. However, it is unlikely that high temperature effects on flower abortion will be ameliorated by high CO2. Species/cultivars that retain fruits at high temperatures would be more productive both in the present-day cotton producing environments and are even more desirable in the future warmer world.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CLIMATE SENSITIVITY, ELEVATED CO2, INCREASES, LEAVES, PIMA COTTON, PLANTS, RESPONSES, STOMATAL DENSITY

1946

Reddy, S.R.C., and C. Price. 1999. Carbon sequestration and conservation of tropical forests under uncertainty. *Journal of Agricultural Economics 50(1):17-35.*

Concern for global warming has focused attention on the rob of tropical forests in the reduction of ambient CO2 levels and mitigation of climate change. Deforestation is a major land use change in the tropics, with forest resources undergoing degradation through the influence of logging and conversion to other uses. Land use change is a product of varied local and regional resource use policies. Management of forest resources is one such major temporal factor, influencing resource stability and the carbon pool. Under a given management policy, both the long period of forest growth, and the slow turnover and decay of the carbon pool, enhance the relevance of stand level management policies as cost-effective mechanisms mitigating climate change. Apart from regional level uncertainties like the nature of land use and the estimation of carbon storage in vegetation and soil, the carbon flux of tropical forests is greatly influenced by uncertainty in regenerative capacity of forests and in harvest and management policies. A case study from India is used to develop a transition matrix model of natural forest management, and to explore the economic implications of maintaining and expanding existing carbon sinks. The study further explores the significance of investments in additional carbon sink in plantation forests, given continued uncertainty in natural forest management.

KEYWORDS: BIOMASS, CLIMATE, DAMAGE, LAND, MANAGEMENT, SOUTHEAST-ASIA, STORAGE, TRANSITION

1947

Reddy, V.R., K.R. Reddy, and B. Acock. 1995. Carbon-dioxide and temperature interactions on stem extension, node initiation, and fruiting in cotton. *Agriculture Ecosystems & Environment 55(1):17-28.*

Understanding the response of agricultural crops to rising carbon dioxide concentration (CO2) and temperature is critical for modeling the effects of future climate change on crop productivity. The objective of this study was to evaluate the direct and interactive effects of temperature and CO2 on mainstem and branch expansion rates, node initiation rates, and fruiting in cotton to be used for the development of a cotton simulation model. Cotton plants (Gossypium hirsutum L., cv. DPL 50) were grown in plant growth chambers exposed to natural light levels with temperature and C4 as treatments. The average temperatures were 17.8, 18.7, 22.7, 26.6, and 30.6 degrees C during a 70 day experimental period with CO2 treatments of 350 and 700 mu l l(-1) at each temperature. Plant height and number of mainstem nodes increased with increase in temperature and CO2. A nine-fold increase was observed in number of fruiting branches with increase in temperature from 17.8 to 30.6 degrees C, however, no significant differences were observed in fruiting branch number due to doubling of CO2 except at 30.6 degrees C. The number of days from emergence to first square was strongly influenced by temperature, and CO2 had no effect on this process. The number of squares and bells were increased at higher temperatures, and the rate of increase was greater at 700 mu l l(-1) CO2.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2 ENRICHMENT, GROWTH, PHOTOSYNTHESIS, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES, YIELD

1948

Reddy, V.R., K.R. Reddy, and H.F. Hodges. 1995. Carbon-dioxide

enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency. *Field Crops Research 41(1):13-23.*

The objectives of this study were to evaluate effects of ambient and double ambient [CO2] at a range of growing temperatures on photosynthesis, respiration, transpiration, water-use efficiency and dry matter accumulation of cotton plants (Gossypium hirsutum L., cv. DPL 50). In Experiment I, plants were grown outdoors until first bloom, then transferred into naturally lit growth chambers and grown for 22 days at 30/ 18 degrees C with five CO2 concentrations varying from 350 to 900 mu l l(-1). In Experiment II, air temperatures were maintained at 20/12, 25/17, 30/22, and 35/27 degrees C day/night during a 70-day experimental period with [CO2] of 350 and 700 mu l l(-1) at each temperature, Photosynthesis increased with [CO2] from 350 to 700 mu l l(-1) and with temperature. Plants grown at 35/27 degrees C produced fewer bells due to abscission compared with plants grown at optimum temperatures (30/20 degrees C). At higher [CO2], water-use efficiency increased at all temperatures due mainly to increased canopy photosynthesis but also to more limited extent to reduced canopy transpiration. Increased photosynthesis at higher [CO2] resulted in greater dry matter accumulation at all temperatures except at 20/12 degrees C. Respiration increased as dry matter and temperature increased. Plants grown at higher [CO2] had less respiration per unit dry matter but more per unit area. These results indicate that future increases in [CO2] are likely to benefit cotton production by increasing carbon assimilation under temperatures favorable for cotton growth. Reduced fruit weights at higher temperatures indicate potential negative effects on production if air temperatures increase as projected in a high-CO2 world.

KEYWORDS: CLIMATE, CO2, CROP YIELD, GROWTH, LEAVES, RESPIRATION, RESPONSES, SIMULATION

1949

Reddy, V.R., K.R. Reddy, and Z. Wang. 1997. Cotton responses to nitrogen, carbon dioxide, and temperature interactions (Reprinted from Plant nutrition for sustainable food production and environment, 1997). *Soil Science and Plant Nutrition 43:1125-1130.*

Several studies were conducted to evaluate how increases in the global atmospheric carbon dioxide concentration [CO2] and temperature affect growth and development rates, dry matter production, photosynthesis, and water use efficiency of cotton and how these responses are influenced by leaf N levels. In one study, cotton (cv. DPL 50) plants were grown at four temperatures (20/12, 25/17, 30/22, and 35/27 degrees C day/night) until harvest at 70 days after emergence (DAE). Each temperature treatment was combined with [CO2] of 350 or 700 mu L L-1. In another study, cotton (cv. DES 119) grown at two [CO2] received five N treatments (0, 1, 2, 6, and 10 mM NO3 in Hoagland's nutrient solution) at 17 DAE and every 2 days thereafter. Canopy gross photosynthetic rates increased with increasing [CO2] and temperature. The increased photosynthesis resulted in higher plant growth and dry matter accumulation rates except at the highest temperature. At 70 DAE, the maximum canopy dry matter accumulation rate occurred in 30/22 degrees C. The 35/27 degrees C treatment induced fruit abortion, resulting in greater dry matter accumulation in vegetative structures. Increases in plant dry weights by CO2 enrichment were greater in the two high temperature regimes than in the two lower temperature regimes. Water-use efficiency increased with increased [CO2] and decreased with increased temperature. Increases in water-use efficiency were due mainly to increased photosynthesis and partly to reduced canopy transpiration. Increase in leaf N concentration increased cotton photosynthesis and vegetative growth rates, and the increases were higher at 700 mu L L-1 than at 350 mu L L-1 [CO2].

KEYWORDS: CANOPY PHOTOSYNTHESIS, CROP YIELD, DEFICIENCY, ENRICHMENT, TRANSPIRATION, USE EFFICIENCY, WATER RELATIONS

1950

Reece, C.F., S.V. Krupa, H.J. Jager, S.W. Roberts, S.J. Hastings, and W.C. Oechel. 1995. Evaluating the effects of elevated levels of atmospheric trace gases on herbs and shrubs - a prototype dual array field exposure system. *Environmental Pollution 90(1):25-31.*

In the context of global climate change, an understanding of the long-term effects of increasing concentrations of atmospheric trace gases (carbon dioxide, CO2, ozone, O-3, oxides of nitrogen, NOx etc.) on both cultivated and native vegetation is of utmost importance. Over the years, under field conditions, various trace gas-vegetation exposure methodologies with differing advantages and disadvantages have been used. Because of these variable criteria, with elevated O-3 or CO2 levels, at the present time the approach of free-air experimental-release of the gas into study plots is attracting much attention. However, in the case of CO2, this approach (using 15 m diameter study plot with a single circular array of vent pipes) has proven to be cost prohibitive (about $59000- 98000/year/replicate) due to the consumption of significant quantities of the gas to perform the experiment (CO2 level elevated to 400 ppm above the ambient). Therefore, in this paper, we present a new approach consisting of a dual concentric exposure array of vertical risers or vent pipes. The purpose of the outer array (17 m diameter) is to vent ambient air outward and toward the incoming wind thus providing an air curtain to reduce the velocity of that incoming wind to simulate the mode or the most frequently occurring wind speed at the study site. The inner array (15 m diameter) vents the required elevated levels of trace gases (CO2, O-3, etc.) into the study plot. This dual array system is designed to provide spatial homogeneity (shown through diffusion modeling) of the desired trace-gas levels within the study plot and to also reduce its consumption. As an example, while in the single- array free-air CO2-release system the consumption of CO2 to elevate its ambient concentration by 400 ppm is calculated to be about 980 tons/year/replicate, it is estimated that in the dual array system it would be approximately 590 tons/year/replicate. Thus, the dual array system may provide substantial cost savings ($24000-39000/year/replicate) in the CO2 consumption ($60-100/ton of CO2) alone. Similarly, benefits in the requirements of other trace gases (O-3, NOx, etc.) are expected, in future multivariate studies on global climate change.

KEYWORDS: AIR, ENRICHMENT

1951

Reekie, E.G., and F.A. Bazzaz. 1991. Phenology and growth in 4 annual species grown in ambient and elevated co2. *Canadian Journal of Botany-Revue Canadienne De Botanique 69(11):2475-2481.*

The objectives of this study were (i) to test the hypothesis that changes in phenology with CO2 are a function of the effect of CO2 upon growth and (ii) to determine if CO2-induced changes in phenology can influence competitive outcome. We examined the effect of 350, 525, and 700-mu-L.L-1 CO2 on Guara brachycarpa, Gailardia pulchella, Oenothera laciniata, and Lupinus texensis. Plants were grown as individuals in 150-, 500-, or 1000-mL pots and in competition in 1000-mL pots. Growth and development were monitored at twice-weekly intervals, by recording the number of leaves and noting the presence or absence of stem elongation, branching, flower buds, and open flowers. Elevated CO2 affected both growth and phenology, but the direction and magnitude of effects varied with species and soil volume. Elevated CO2 did not appear to affect development through its effect on growth. Those treatments in which there were significant effects of CO2 on growth were generally different from those treatments in which CO2 affected phenology. Rather than affecting phenology by changing plant size, CO2 appeared to affect phenology by modifying the size at which plants

switched from one stage to the next. The level of CO2 changed competitive outcome; the importance of Lupinus increased whereas that of Oenothera decreased with increased CO2. These changes were more closely related to the effect of CO2 on growth than its effect on phenology.

KEYWORDS: CARBON DIOXIDE, FATE, PHARBITIS, PREDICTIONS, ROSETTE SIZE

1952

Reekie, E.G., C. MacDougall, I. Wong, and P.R. Hicklenton. 1998. Effect of sink size on growth response to elevated atmospheric CO2 within the genus Brassica. *Canadian Journal of Botany-Revue Canadienne De Botanique 76(5):829-835.*

Many plants grown at elevated CO2 concentrations exhibit enhanced photosynthetic rates. However, this increase in photosynthesis is often reduced after prolonged exposure to elevated CO2. This reduction may be related to the capacity of plants to utilize the extra photosynthate produced at elevated CO2. This study examined the effect of source to sink ratio on the capacity of plants to respond to elevated CO2. Seven species or cultivars within the genus Brassica were germinated and grown at either 350 or 1000 ppm CO2. Broccoli (Brassica oleracea L.) and cauliflower (B. oleracea L.) have large carbon sinks in the reproductive structures; Chinese broccoli (Brassica campestris L.) and marrow stem kale (B. oleracea) have carbon sinks in the stem; turnip (B. campestris) stores carbon in the root; rape (Brassica napus L.) and white mustard (Brassica alba (L.) Rabenh.) have no obvious carbon storage structures and were assumed to have a lower sink strength relative to the above cultivars. Plants were harvested at three stages of development and total plant weight, leaf area ratio, and allocation to leaf, root, and stem determined. As young seedlings, all cultivars responded positively to elevated CO2. The long-term growth response of different cultivars to CO2 was independent of sink location, but was dependent on sink size. Cultivars with no obvious carbon storage structures showed no significant growth enhancement by elevated CO2 by the end of the experiment. However, neither leaf area ratio nor biomass allocation pattern were reliable predictors of response to CO2 suggesting that assessing differences in source to sink ratio is not necessarily straightforward.

KEYWORDS: ENRICHMENT, PHOTOSYNTHESIS, PINE, PLANTS, TEMPERATURE

1953

Reekie, J.Y.C., P.R. Hicklenton, and E.G. Reekie. 1994. Effects of elevated co2 on time of flowering in 4 short-day and 4 long-day species. *Canadian Journal of Botany-Revue Canadienne De Botanique 72(4):533-538.*

This study was undertaken to determine if the effect of elevated CO2 on flowering phenology is a function of the photoperiodic response of the species involved. Four long-day plants, Achillea millefolium, Callistephus chinensis, Campanula isophylla, and Trachelium caeruleum, and four short-day plants, Dendranthema grandiflora, Kalanchoe blossfeldiana, Pharbitis nil, and Xanthium pensylvanicum, were grown under inductive photoperiods (9 h for short day and 17 h for long day) at either 350 or 1000 mu L/L CO2. Time of visible flower bud formation, flower opening, and final plant biomass were assessed. Elevated CO2 advanced flower opening in all four long-day species and delayed flowering in all four short-day species. In the long-day species, the effect of CO2 was primarily on bud initiation; all four species formed buds earlier at high CO,. Bud development, the difference in time between flower opening and bud initiation, was advanced in only one long-day species, Callistephus chinensis. Mixed results were obtained for the short-day species. Elevated CO, exerted no effects on bud initiation but delayed bud development in Dendranthema and Kalanchoe. In Xanthium, bud initiation rather than bud development was delayed. Data on bud initiation and development were not obtained for Pharbitis. The negative effect of CO, upon phenology in the short-day species was not associated with negative effects on growth. Elevated CO2 increased plant size in both long-day and short-day species.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, PHARBITIS

1954

Reekie, J.Y.C., P.R. Hicklenton, and E.G. Reekie. 1997. The interactive effects of carbon dioxide enrichment and daylength on growth and development in Petunia hybrida. *Annals of Botany 80(1):57-64.*

Plants were grown at either 350 or 1000 mu l l(-1) CO2 and in one of three photoperiod treatments: continuous short days (SD), continuous long days (LD), or short switched to long days at day 41 (SD-LD). All plants received 9 h of light at 450 mu mol m(-2) s(-1) and LD plants received an additional 4 h of light at 8 mu mol m(-2) s(-1). Growth of SD plants responded more positively to elevated CO2 than did LD plants, due largely to differences in the effect of CO2 on unit leaf rate. High CO2 increased height and decreased branching under SD conditions, but had no effect under LD conditions. Elevated CO2 also increased the number of buds and open flowers, the effect for flower number being greater in short than in long days. The specific leaf area of plants grown at 1000 mu l l(-1) CO2 was reduced regardless of daylength. High CO2 also decreased leaf and increased reproductive allocation, the magnitude of these effects being greater under SD conditions. Bud formation and flower opening was advanced under high CO2 conditions in SD plants but bud formation was delayed and there was no effect on flower opening under LD conditions. The effects of CO2 on plants switched from SD to LD conditions were largely intermediate between the two continuous treatments, but for some parameters, more closely resembled one or the other. The results illustrate that daylength is an important factor controlling response of plants to elevated CO2. (C) 1997 Annals of Botany Company.

KEYWORDS: AMBIENT, C-3, ELEVATED CO2, INCREASING CO2 CONCENTRATION, IRRADIANCE, PHARBITIS, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, TEMPERATURE

1955

Reeves, D.W., H.H. Rogers, S.A. Prior, C.W. Wood, and G.B. Runion. 1994. Elevated atmospheric carbon-dioxide effects on sorghum and soybean nutrient status. *Journal of Plant Nutrition 17(11):1939-1954.*

Increasing atmospheric carbon dioxide (CO2) concentration could have significant implications on technologies for managing plant nutrition to sustain crop productivity in the future. Soybean (Glycine max [L.] Merr.) (C3 species) and grain sorghum (Sorghum bicolor [L.] Moench) (C4 species) were grown in a replicated split-plot design using open-top field chambers under ambient (357 mu mol/mol) and elevated (705 mu mol/mol) atmospheric CO2. At anthesis, leaf disks were taken from upper mature leaves of soybean and from the third leaf below the head of sorghum for analysis of plant nutrients. Leaf greenness was measured with a Minolta SPAD-502 chlorophyll meter. Concentrations of chlorophylls a and b and specific leaf weight were also measured. Above-ground dry matter and seed yield were determined at maturiry. Seed yield of sorghum increased 17.5% and soybean seed yield increased 34.7% with elevated CO2. There were no differences in extractable chlorophyll concentration or chlorophyll meter readings due to CO2 treatment, but meter readings were reduced 6% when sorghum was grown in chambers as compared in the open. Leaf nitrogen (N)

concentration of soybean decreased from 54.5 to 39.1 g/kg at the higher CO2 concentration. Neither the chambers nor CO2 had an effect on concentrations of other plant nutrients in either species. Further work under field conditions is needed to determine if current critical values for tissue N in crops, especially C3 crops, should be adjusted for future increases in atmospheric CO2 concentration.

KEYWORDS: CHLOROPHYLL METER, CO2- ENRICHMENT, EXCHANGE-RATES, FIELD, GROWTH, MAIZE, MINERAL NUTRITION, NITROGEN STATUS, RESPONSES, WHEAT

1956

Refouvelet, E., and F. Daguin. 1999. Polymorphic glutamate dehydrogenase in lilac vitroplants as revealed by combined preparative IEF and native PAGE: Effect of ammonium deprivation, darkness and atmospheric CO2 enrichment upon isomerization. *Physiologia Plantarum 105(2):199-206.*

The activity and polymorphism of glutamate dehydrogenase (GDH) were studied in basal callus of Lilac (Syringa eulgaris L.) vitroplants. Native PAGE alone revealed seven bands staggered at regular intervals. Preparative liquid-vein IEF allowed the separation of six to ten GDH fractions with charges ranging between 5.18 and 7.08. Analysis of these GDH fractions in native PAGE indicated that up to seven GDH bands can be detected for each fraction. This suggests the existence of seven isoforms of the enzyme with subunits presenting different isoelectric points. Dark- and ammonium-controlled forms were found to be the more acidic and faster migrating ones in native PAGE. The results support for the first time that atmospheric CO2 enrichment increases GDH activity dramatically and modifies isomerization of the enzyme.

KEYWORDS: ARABIDOPSIS-THALIANA, HIGHER-PLANTS, LEAF, MITOCHONDRIA, NITROGEN ASSIMILATION, SYNTHETASE, TISSUES

1957

Reich, P.B. 1995. Phenology of tropical forests - patterns, causes, and consequences. *Canadian Journal of Botany-Revue Canadienne De Botanique 73(2):164-174.*

Leaf phenology of tropical forests is distinct from other biomes. Unlike the marked temperature-related periodicity of temperate forests, development tends to be continuous in aseasonal lowland tropical rain forests and becomes more episodic in response to increasing annual drought in tropical dry forests. Hence, in tropical rain forests, foliar development (production, senescence, and longevity) is largely under internal rather than environmental control. In contrast, tropical forests with marked annual dry seasons display associated seasonality of leaf production and shedding. This developmental seasonality can be explained by overlaying the influence of seasonality on trees' internally regulated development and appears to be controlled by acclimative physiological processes and not by sensitivity to photo-, thermo-periodic, or direct environmental cues. Consequences of tropical phenology stem from both the variety of leaf and species ecophysiological types common to a given moisture regime and their relative synchrony of development, and include the following: larger diversity of ecophysiological species types in rain than dry forests; differential rates of herbivory in dry than wet seasons and for synchronous versus asynchronous leaf flushes; ecosystems with greater canopy foliar mass per hectare in rain than dry forests; and several leaf adaptations perhaps unique to tropical forests, such as delayed greening and seasonal leaf phenotypes. Tropical forests may vary in sensitivity to predicted climate change. Phenology of rain forests should change little unless water balance changes markedly, and developmental events in rain forests may be relatively insensitive to moderate changes in CO2 or temperature. Phenology of dry forests could be more sensitive, and in opposite directions, to elevated CO2 and temperatures. Elevated CO2 might delay the onset of leaf shedding and stimulate longer life span if stand level transpiration is reduced, whereas higher temperatures could lead to more rapid water depletion, longer leafless periods, and more strongly synchronized phenology.

KEYWORDS: COSTA-RICA, DECIDUOUS FOREST, DRY FOREST, HERBIVORY, LEAF LIFE-SPAN, LONGEVITY, LOWLANDS, SEASONAL DROUGHT, TREES, UNDERSTORY COMMUNITY

1958

Reich, P.B., J. Oleksyn, and M.G. Tjoelker. 1996. Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal range: A common garden test with field-grown trees. *Functional Ecology 10(6):768-776.*

1. Models of tree function and forest ecosystem carbon budgets often assume that potential global changes in temperature and/or other factors may alter tissue nitrogen (N) and dark respiration rates (R(d)). However, little is known of patterns of co-variation in tissue N and R(d) among intraspecific populations originating along climatic gradients, and of whether an N-based model of R(d) can link these two variables. To address these issues, we studied N and R(d) in fully expanded needles of 10-year-old trees of 14 Scots Pine (Pinus sylvestris) populations of wide-ranging origin (43 degrees to 60 degrees N), grown under common garden conditions. 2. For 11 lowland populations (elevation <200 m) from the contiguous part of the species range (48 degrees to 60 degrees N) grown at a field site in Kornik, western Poland (52 degrees N), there were greater needle %N in populations from increasing latitude of origin or decreasing mean annual temperature (r greater than or equal to 0.93, P<0.01). Similar %N and latitude of origin correlations were observed in another year at this site and in retrospective analyses of published data for different sets of Scots Pine populations grown in common gardens at 48 degrees, 52 degrees C and 62 degrees N latitudes. Needle R(d) rates of the 11 lowland populations growing at Kornik and measured at a common temperature (20 degrees C) were greater, by as much as 50%, for more northerly than southerly populations. Mean R(d) rates were positively correlated to latitude of origin and to mean annual temperature (P<0.05, r=0.7 to 0.8). R(d) and needle %N were positively correlated (P<0.01, r=0.75), with one relationship fitting all data. Across the entire range from 1.15 to 1.55 needle %N, R(d) increased from 4.5 to 6.9 nmol g(- 1) s(-1). 3. Mean needle %N and R(d) values for two montane southern populations (43 degrees and 44 degrees N, elevation greater than or equal to 885 m) growing in the same common garden at Kornik were consistent with the relationships between mean annual temperature, needle %N and R(d) observed for the more northerly populations but did not fit the latitudinal patterns. This suggests that temperature and/or associated climate variables are likely the driving force for observed genetic variation in Scots Pine needle %N and R(d) across latitudinal and altitudinal gradients. 4. Results of these common garden studies support the idea of a general relationship between needle dark respiration and N concentration, and indicate that there is intraspecific genetic variation in physiology that is selected by climate that persists in a common environment, resulting in higher needle %N and respiration in plants originating from colder habitats. Such patterns need to be better understood and quantified, and merit consideration in modelling of current and potential global change effects on plant function and global carbon cycles.

KEYWORDS: AIR-POLLUTION, CLIMATE CHANGE, CO2 EXCHANGE, DARK RESPIRATION, GRADIENTS, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS, PLANTS, SYLVESTRIS L, TEMPERATURE

1959

Reichenauer, T., H.R. BolharNordenkampf, U. Ehrlich, G. Soja,

W.F. Postl, and F. Halbwachs. 1997. The influence of ambient and elevated ozone concentrations on photosynthesis in Populus nigra. *Plant, Cell and Environment 20(8):1061-1069.*

Light-saturated net leaf photosynthesis (A(sat)), CO2 response curves (A/C-i), current photochemical capacity (F-v/F-m) and pigment contents were measured in leaves of Populus nigra (Clone T107) which had been exposed to ozone stress in open-top chambers for the entire growth period. Surprisingly, not only elevated (ao(+), i.e. ambient air + 50 mm(3) m(-3) ozone) but also ambient (aa) ozone concentrations led to a reduction in A(sat) in comparison with leaves exposed to air containing almost no ozone (cf(-), i.e. charcoal filtered ambient air). The very small change in leaf conductance (g(l)) indicated that the decrease in A(sat) was not due to stomatal limitation. This finding was supported by the fact that, a decrease in carboxylation efficiency (CE) correlated with a loss in A(sat). In comparison to cf-leaves, aa leaves showed no change in current photochemical capacity (F-v/F-m) throughout the whole experiment. However, a marked decline in F-v/F-m in ao(+) leaves was observed at a time when A(sat) and CE were already decreased by about 45% and 60% respectively. As the chlorophyll b content of leaves is known to correlate with the amount of LHC and PSII centres, it was used to normalize fluorescence parameters in relation to PSII centres present. The normalized values for F-m and F-O increased with the dosage of ozone in ao(+) leaves but not in aa leaves, indicating a change of the pigment content of PSII in the former, but not in the latter. These data led to the conclusion that ozone interacts primarily with components of the Calvin cycle, which results in a decrease in A(sat) with subsequent feedback on the current photochemical capacity of PSII centres.

KEYWORDS: AIR- POLLUTANTS, BISPHOSPHATE CARBOXYLASE OXYGENASE, CHLOROPHYLL FLUORESCENCE, DELTA C 13, EXPOSURE, LEAVES, NET PHOTOSYNTHESIS, PLANTS, STOMATAL CONDUCTANCE, STRESS

1960

Reicosky, D.C., D.W. Reeves, S.A. Prior, G.B. Runion, H.H. Rogers, and R.L. Raper. 1999. Effects of residue management and controlled traffic on carbon dioxide and water loss. *Soil & Tillage Research 52(3-4):153-165.*

Management of crop residues and soil organic matter is of primary importance in maintaining soil fertility and productivity and in minimizing agricultural impact on the environment. Our objective was to determine the effects of traffic and tillage on short-term carbon dioxide (CO2) and water (H2O) fluxes from a representative soil in the southeastern Coastal Plain (USA). The study was conducted on a Norfolk loamy sand (FAO classification, Luxic Ferralsols; USDA classification, fine-loamy siliceous, thermic Typic Kandiudults) cropped to a corn (Zea mays L.)- soybean (Glycine maw (L.) Merr) rotation with a crimson clover (Trifolium incarnatum L.) winter cover crop for eight years. Experimental variables were with and without traffic under conventional tillage (CT) (disk harrow twice, chisel plow, field cultivator) and no tillage (NT) arranged in a split-plot design with four replicates. A wide-frame tractive vehicle enabled tillage without wheel traffic. Short-term CO2 and H2O fluxes were measured with a large portable chamber. Gas exchange measurements were made on both CT and NT at various times associated with tillage and irrigation events. Tillage-induced COP and H2O fluxes were larger than corresponding fluxes from untilled soil. Irrigation caused the CO2 fluxes to increase rapidly from both tillage systems, suggesting that soil gas fluxes were initially limited by lack of water. Tillage-induced CO2 and H2O fluxes were consistently higher than under NT. Cumulative CO2 flux from CT at the end of 80 h was nearly three times larger than from NT while the corresponding H2O loss was 1.6 times larger. Traffic had no significant effects on the magnitude of CO:! fluxes, possibly reflecting this soil's natural tendency to reconsolidate. The immediate impact of intensive surface tillage of sandy soils on gaseous carbon loss was larger than traffic effects and suggests a need to develop new management practices for enhanced soil carbon and water management for these sensitive soils.

KEYWORDS: BIOMASS, CORN, NITROGEN, SOIL RESPIRATION, TILLAGE SYSTEM

1961

Reid, C.D., and E.L. Fiscus. 1998. Effects of elevated [CO2] and/or ozone on limitations to CO2 assimilation in soybean (Glycine max). *Journal of Experimental Botany 49(322):885-895.*

Soybean (Glycine max) was grown in open-top field chambers at ambient (360 mu mol mol(-1)) or doubled [CO2] either in charcoal-filtered air (20 nmol mol(-1) [O-3]) or in non- filtered air supplemented to 1.5 x ambient [O-3] (70 nmol mol(- 1)) to determine the major limitations to assimilation under conditions of elevated [CO2] and/or [O-3]. Through plant ontogeny, assimilation versus intercellular CO2 concentration (A/Ci) responses were measured to assess the limitations to assimilation imposed by the capacity for Rubisco carboxylation, RuBP regeneration, and stomatal diffusion. In the vegetative stages, no significant treatment effects of elevated [CO2] and/or [O-3] were observed on Rubisco carboxylation efficiency (CE), light and CO2-saturated assimilation capacity (A(max)), and chlorophyll content (Chl). However, for plants grown in elevated [CO2], the assimilation rate at growth [CO2] (A) was 60% higher than at ambient [CO2] up to the seed maturation stage, and the potential rate of assimilation by Rubisco capacity (A(p)) was increased. Also in elevated [CO2]: A was 51% of A(p); the relative stomatal limitation (%Stomata) was 5%; and the relative RuBP regeneration limitation (%RuBP) was 44%. In ambient [CO2], O-3 gradually decreased A per unit leaf area, but had little effect on A, and the relative limitations to assimilation where A remained 51% of A(p), %Stomata was 27%, and %RuBP was 22%. During reproduction, CE declined for plants grown in elevated [CO2] and/or [O-3]; A(p) was unaffected by elevated [CO2], but was reduced by [O-3] at ambient [CO2]; A increased to 72% of A(p) in elevated [CO2] and/or [O-3]- fumigated air; the %Stomata increased; and the %RuBP decreased, to become non significant in elevated [CO2] from the beginning of seed growth on, and in O-3-fumigated air at ambient [CO2] at the seed maturation stage. The decrease in %RuBP occurred concomitantly with an increase in A(max) and Chl. Significant [CO2] x [O-3] interactions support the lack of an O-3 effect on assimilation and its limitations at elevated [CO2] during seed maturation. These data suggest that elevated [CO2] alleviated some of the effects of O-3 on photosynthesis.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, LEAF PROTEINS, NET PHOTOSYNTHESIS, OPEN-TOP CHAMBERS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPRING WHEAT, STOMATAL CONDUCTANCE, TRITICUM-AESTIVUM L

1962

Reid, C.D., E.L. Fiscus, and K.O. Burkey. 1998. Combined effects of chronic ozone and elevated CO2 on Rubisco activity and leaf components in soybean (Glycine max). *Journal of Experimental Botany 49(329):1999-2011.*

Content and activity of Rubisco and concentrations of leaf nitrogen, chlorophyll and total non-structural carbohydrates (TNC) were determined at regular intervals during the 1993 and 1994 growing seasons to understand the effects and interactions of [O-3] and elevated [CO2] on biochemical limitations to photosynthesis during ontogeny. Soybean (Glycine max var. Essex) was grown in open-top field chambers in either charcoal- filtered air (CF, 20 nmol mol(-1)) or non-

filtered air supplemented with 1.5 x ambient [O-3] (c. 80 nmol mol(-1)) at ambient (AA, 360 mu mol mol(-1)) or elevated [CO2] (700 pmol mol(-1)). Sampling period significantly affected all the variables examined. Changes included a decrease in the activity and content of Rubisco during seed maturation, and increased nitrogen (N), leaf mass per unit area (LMA) and total non- structural carbohydrates (TNC, including starch and sucrose) through the reproductive phases. Ontogenetic changes were most rapid in O-3-treated plants. At ambient [CO2], O-3 decreased initial activity (14-64% per unit leaf area and 14-29% per unit Rubisco) and content of Rubisco (9-53%), and N content per unit leaf area. Ozone decreased LMA by 17-28% of plants in CF-AA at the end of the growing season because of a 24-41% decrease in starch and a 59-80% decrease in sucrose. In general, elevated [CO2] in CF or O-3-fumigated air, reduced the initial activity of Rubisco and activation state while having little effect on Rubisco content, N and chlorophyll content, per unit leaf area. Elevated CO2 decreased Rubisco activity by 14-34% per unit leaf area and 15-25% per unit Rubisco content of plants in grown CF- AA, and increased LMA by 27-74% of the leaf mass per unit area in CF-AA because of a 23-148% increase in starch. However, the data suggest that, at elevated [CO2], increases in starch and sucrose are not directly responsible for the deactivation of Rubisco. Also, there was little evidence of an adjustment of Rubisco activity in response to starch and sucrose metabolism. Significant interactions between elevated [CO2] and [O-3] on all variables examined generally resulted in alleviation or amelioration of the O-3 effects at elevated CO2. These data provide further support to the idea that elevated atmospheric CO2 will reduce or prevent damage from pollutant O-3.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, LEAVES, NET PHOTOSYNTHESIS, O-3, PHOTOSYNTHETIC APPARATUS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOMATO PLANTS, TRITICUM-AESTIVUM L, WHEAT

1963

Reid, C.D., E.L. Fiscus, and K.O. Burkey. 1999. Effects of chronic ozone and elevated atmospheric CO2 concentrations on ribulose-1,5-bisphosphate in soybean (Glycine max). *Physiologia Plantarum 106(4):378-385.*

Ribulose-1,5-bisphosphate (RuBP) pool size was determined at regular intervals during the growing season to understand the effects of tropospheric ozone concentrations, elevated atmospheric carbon dioxide concentrations and their interactions on the photosynthetic limitation by RuBP regeneration. Soybean (Glycine max [L.] Merr, cv, Essex) was grown from seed to maturity in open-top field chambers in charcoal-filtered air (CF) either without (22 nmol O-3 mol(-1)) or with added O-3 (83 nmol mol(-1)) at ambient (AA, 369 mu mol CO2 mol(-1)) or elevated CO, (710 mu mol mol(-1)). The RuBP pool size generally declined with plant age in all treatments when expressed on a unit leaf area and in all treatments but CF-AA when expressed per unit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco; EC 4,1,1,39) binding site, Although O-3 in ambient CO2 generally reduced the RuBP pool per unit leaf area, it did not change the RuBP pool per unit Rubisco binding site, Elevated CO2, in CF or O-3-fumigated air, generally had no significant effect on RuBP pool size, thus mitigating the negative O-3 effect. The RuBP pools were below 2 mol mol(-1) binding site in all treatments for most of the season, indicating limiting RuBP regeneration capacity. These low RuBP pools resulted in increased RuBP regeneration Fia faster RUBP turnover, but only in CF air and during vegetative and flowering stages at elevated CO2. Also, the low RuBP pool sizes did not always reflect RuBP consumption rates or the RuBP regeneration limitation relative to potential carboxylation (%RuBP). Rather, %RuBP increased linearly with decrease in the RuBP pool turnover lime. These data suggest that amelioration of damage from O-3 by elevated atmospheric CO2 to the RuBP regeneration may be in response to changes in the Rubisco carboxylation.

KEYWORDS: CARBOXYLASE OXYGENASE ACTIVITY, LEAVES, O-3, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PLANTS, POOL SIZES, RIBULOSE 1;5-BISPHOSPHATE, SPRING WHEAT, STATE GAS-EXCHANGE

1964

Reid, C.D., and B.R. Strain. 1994. Effects of co(2) enrichment on whole-plant carbon budget of seedlings of fagus-grandifolia and acer-saccharum in low irradiance. *Oecologia 98(1):31-39.*

Carbon exchange rates (CER) and whole-plant carbon balances of beech (Fagus grandifolia) and sugar maple (Acer saccharum) were compared for seedlings grown under low irradiance to determine the effects of atmospheric CO2 enrichment on shade-tolerant seedlings of co-dominant species. Under contemporary atmospheric CO2, photosynthetic rate per unit mass of beech was lower than for sugar maple, and atmospheric CO2 enrichment enhanced photosynthesis for beech only. Aboveground respiration per unit mass decreased with CO2 enrichment for both species while root respiration per unit mass decreased for sugar maple only. Under contemporary atmospheric CO2, beech had lower C uptake per plant than sugar maple, while C losses per plant to nocturnal aboveground and root respiration were similar for both species. Under elevated CO2, C uptake per plant was similar for both species, indicating a significant relative increase in whole-seedling CER with CO2 enrich ment for beech but not for sugar maple. Total C loss per plant to aboveground respiration was decreased for beech only because increase in sugar maple leaf mass counterbalanced a reduction in respiration rates. Carbon loss to root respiration per plant was not changed by CO2 enrichment for either species. However, changes in maintenance respiration cost and nitrogen level suggest changes in tissue composition with elevated CO2. Beech had a greater net daily C gain with CO2 enrichment than did sugar maple in contrast to a lower one under contemporary CO2. Elevated CO2 preferentially enhances the net C balance of beech by increasing photosynthesis and reducing respiration cost. In all cases, the greatest C lost was by roots, indicating the importance of belowground biomass in net C gain. Relative growth rate estimated from biomass accumulation was not affected by CO2 enrichment for either species possibly because of slow growth under low light. This study indicates the importance of direct effects of CO2 enrichment when predicting potential change in species distribution with global climate change.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CLIMATE CHANGE, ELEVATED CO2, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR- STYRACIFLUA, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RESPIRATION, WATER-STRESS

1965

Reid, C.D., D.T. Tissue, E.L. Fiscus, and B.R. Strain. 1997. Comparison of spectrophotometric and radioisotopic methods for the assay of Rubisco in ozone-treated plants. *Physiologia Plantarum 101(2):398-404.*

Radioisotopic and spectrophotometric assays for ribulose-1,5-bisphosphate carboxy lase/oxygenase (Rubisco) initial and final activities and Rubisco content were compared in plants chronically exposed to ozone (O-3) in a greenhouse and the field. In a greenhouse experiment, Glycine max was treated in exposure chambers with either charcoal-filtered air (CF air) or 100 nl O-3 l(-1) for 6 h daily during vegetative growth. Samples were collected after 7 days of exposure. In a field experiment, G. max was treated in open-top chambers with either CF air or nonfiltered air with O-3 added at 1.5 times ambient O-3 for 12 h daily. Average daily O-3 concentrations were 21 and 92 nl l(-1) in the CF and O-3 treatments, respectively samples were collected during vegetative and reproductive growth, Both assays generally yielded comparable Rubisco initial and final activities for greenhouse-grown

plants regardless of the O-3 treatment. However for field-grown plants, Rubisco initial and final activities averaged 15 and 23% lower when assayed by the spectrophotometric rather than the radioisotopic method. For Rubisco content estimated by the spectrophotometric method, lower r(2) values for the regression of Rubisco activity vs concentration of carboxyarabinitol-1,5- bisphosphate were observed in O3- than in CF-treated plants. Both assays yielded comparable Rubisco contents in the greenhouse and in the field although the variation was larger with the spectrophotometric method in field-grown plants. Growth conditions, field vs greenhouse, were more critical to the spectrophotometric assay performance than the O-3 treatments for measurement of Rubisco activity and content.

KEYWORDS: 1,5-BISPHOSPHATE, ACTIVATION, ELEVATED CO2, LIGHT-DEPENDENT REGULATION, NET PHOTOSYNTHESIS, PHASEOLUS-VULGARIS L, POOL SIZES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RUBP CARBOXYLASE

1966

Reinert, R.A., G. Eason, and J. Barton. 1997. Growth and fruiting of tomato as influenced by elevated carbon dioxide and ozone. *New Phytologist 137(3):411-420.*

'Tiny Tim' tomato plants were exposed to five CO2 treatments (375 (ambient), 450, 525, 600 or 675 mu mol mol(-1)) in combination with O-3 (O or 80 nmol mol(-1)). Biomass was evaluated following 3, 5, 7 and 13 wk exposure. Biomass following 13 wk exposure also included weekly harvests of mature tomato fruit beginning week 8. Carbon dioxide enrichment significantly enhanced total vegetative plant d. wt at each harvest, as well as cumulative yield of mature fruit, whereas O-3 significantly suppressed total Vegetative plant d. wt at each harvest and reduced total cumulative fruit yield. The magnitude of these changes varied with the development of tomato from early growth to mature fruit yield. Carbon dioxide enrichment reduced the detrimental effects of O-3 on total vegetative plant d. wt of tomato following 3, 5, 7 and 13 wk exposure. Final mature fruit yield was 24% higher under enriched CO2 treatments than in ambient CO2. Ozone suppressed final yield by 31% following exposure to 80 nmol mol(-1) O-3 when compared with exposure to charcoal-filtered (CF) air. The impacts of both CO2 and O-3 on yield were, however, dependent upon the presence or absence of the other gas. In the absence of O-3, yields were very similar for the ambient and elevated CO2 treatments, but in the presence of O-3, yields under ambient CO2 were greatly suppressed whereas yields under elevated CO2 were similar to those in the absence of O-3. Thus, enriched CO2 ameliorated most of the suppressive effect of O-3 on yield of mature fruit.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, ENVIRONMENT, EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, RADISH, RESPONSES, TEMPERATURE, VEGETATION, YIELD

1967

Reinert, R.A., and M.C. Ho. 1995. Vegetative growth of soybean as affected by elevated carbon- dioxide and ozone. *Environmental Pollution 89(1):89-96.*

The effects of elevated carbon dioxide (CO2) and ozone (O-3) on soybean (Glycine max (L.) Merr. cv. Centennial) growth and biomass partitioning were evaluated under greenhouse conditions. Soybeans were exposed to CO2 concentrations at 350 (ambient), 450, 550, and 650 mu l liter(-1) (ppm) for 24 h day(-1) for 5 weeks. Ozone treatments of 0 and 120 nl liter(-1) (ppb) for 6 h day(-1) for 5 days week-1 for 5 weeks were added in combination with the CO2 treatments. Plant dry weight and biomass partitioning were assessed each week. Dry weight of leaf, stem, and root, as well as the total plant dry weight increased with exposure to increasing levels of CO2. Dry weight of leaf, root and total plant were suppressed significantly by the O-3 treatment. Stem dry weight was not affected by O-3. Suppression of root dry weight due to O-3 at each weekly harvest was significantly dependent on the CO2 concentration. Root growth was enhanced by CO2 at 650 mu l liter(-1) compared with ambient CO2 (350 mu l liter(-1)) at 5 weeks of age. At ambient CO2 in the presence of O3 the roots were only about 63% of the weight of the root grown in the absence of O-3. At 550 and 650 mu l liter(-1) CO2 the biomass of soybean roots in the presence of 120 nl liter(-1) O-3 was 88.2 and 88.4% of the control, respectively. Thus, CO2 limited the amount of root growth suppression caused by O-3. The partitioning of leaf, stems and root dry weight in relation to total plant dry weight remained relatively constant across each CO2 concentration. Thus, CO2 did not affect biomass partitioning among leaves, stems and roots of soybean.

KEYWORDS: CO2- ENRICHMENT, COMBINATION, EXPOSURE, FIELD, NITROGEN, PHOTOSYNTHESIS, RESPONSES, SEED YIELD, SOIL-WATER DEFICIT, TEMPERATURE

1968

Reining, E. 1994. Acclimation of C-3 photosynthesis to elevated co2 - hypotheses and experimental-evidence. *Photosynthetica 30(4):519-525.*

Acclimation of the photosynthesis of C-3 plants to elevated atmospheric CO2 concentrations is frequently observed. Some hypotheses frequently proposed to explain this phenomenon are: (1) stomatal closure; (2) inhibition of photosynthesis by starch accumulation, and (3) reduced activity or concentration of ribulose-1,5-bisphosphate carboxylase/oxygenase. These hypotheses are compared with experimental evidence from the literature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CARBOHYDRATE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, STARCH

1969

Reining, F. 1995. The effect of elevated co2 concentrations on the competition between lamium-galeobdolon and stellaria-holostea. *Photosynthetica 31(4):501-508.*

The effect of enhanced air CO2 concentrations (c(520) and c(650) = 520 and 650 cm(3) m(-3)) on the growth of Lamium galeobdolon and Stellaria holostea and on the competition between the two species was examined. After five months growth under CO2 enrichment the dry masses of both species increased when the plants were grown in monoculture, but the increase in biomass was much more pronounced in Stellaria. When the plants were grown together in competition, the measured shoot masses of Stellaria were again higher under c(520) and c(650) than at ambient CO2 concentration (c(390) = 390 cm(3) m(-3)), while the shoot masses of lamium strongly decreased at c(650) The effect of CO2 enrichment on the two plant species in monoculture differed significantly from that observed in mixed cultures. In terms of plant relative yield. Stellaria benefitted slightly but insignificantly from competition, while Lamium was significantly suppressed under c(650). Total community production of the mixed culture was optimum at c(520), while that of the monocultures was highest at c(650) At c(390) and c(520), growth of Stellaria depended strongly on irradiance in all types of culture. At c(650) no such dependence could be demonstrated.

KEYWORDS: ANNUALS, ASSEMBLAGE, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, GROWTH, OLD- FIELD PERENNIALS, PLANTS

1970

Reitz, S.R., D.N. Karowe, M.M. Diawara, and J.T. Trumble. 1997. Effects of elevated atmospheric carbon dioxide on the growth and linear furanocoumarin content of celery. *Journal of Agricultural and Food Chemistry 45(9):3642-3646.*

The effects of elevated atmospheric carbon dioxide on the growth and development of celery (Apium graveolens) were examined to determine if anticipated global increases in CO2 will affect the nutritional quality and secondary chemistry of celery. The size (fresh and dry mass), nitrogen and carbon composition, and concentrations of linear furanocoumarins of celery grown under ambient (363 mu L L-1) and elevated (718 mu L L-1) carbon dioxide were analyzed. Growth under elevated CO2 resulted in larger petioles, reduced nitrogen content, and higher C:N ratios in both leaves and petioles. However, CO2 treatment did not affect plant water content or carbon content. Moreover, in contrast to the carbon-nutrient balance hypothesis, the increased C:N ratios of plants grown under elevated CO2 were not associated with increased concentrations of potentially harmful linear furanocoumarins. Levels of linear furanocoumarins in the petioles of plants from each treatment did not exceed concentrations reported to cause acute or chronic contact dermatitis.

KEYWORDS: ALLELOCHEMICALS, ALLOCATION PATTERNS, CO2 ENVIRONMENTS, ELEMENTAL ORGANIC-ANALYSIS, ENRICHMENT, INTEGRATED PEST-MANAGEMENT, NUTRIENT BALANCE, PERFORMANCE, RESISTANCE, RESPONSES

1971

Rennenberg, H., and A. Gessler. 1999. Consequences of N deposition to forest ecosystems - Recent results and future research needs. *Water, Air, and Soil Pollution 116(1-2):47-64.*

Wet and dry deposition of atmospheric nitrogen (N) compounds into forest ecosystems and their effect on physical, chemical and microbial processes in the soil has attracted considerable attention for many years. Still the consequences of atmospheric N deposition on N metabolism of trees and its interaction with soil microbial processes has only recently been studied. Atmospheric N deposited to the leaves is thought to enter the general N metabolism of the leaves, but the processes involved, the interaction with different metabolic pathways, and the connection between injury by atmospheric N and its metabolic conversion are largely unknown. Laboratory and field experiments have shown that N of atmospheric NO2 and NH3, deposited to the leaves of trees, is subject to long-distance transport in the phloem to the roots. This allocation can result in considerable decline of N uptake by the roots. Apparently, the flux of N from the soil into the roots can be down-regulated to an extent that equals N influx into the leaves. This down-regulation is not mediated by generally enhanced amino-N contents, but by elevated levels of particular amino acids. Field experiments confirm these results from laboratory studies: Nitrate (NO3) uptake by the roots of trees at a field sites exposed to high loads of atmospheric N is negligible, provided concentrations of Gln in the roots are high. At the ecosystem level, consequences of reduced N uptake by the roots of trees exposed to high loads of atmospheric N are (1) an increased availability of N for soil microbial processes, (2) enhanced emission of gaseous N-oxides from the soil, and (3) elevated leaching of NO3 into the ground water. How recent forest management practices aimed at transforming uniform monocultures to more structured species-rich forests will interact with these processes remains to be seen. Possible implications of these forest management practices on N metabolism in trees and N conversion in the soil are discussed particularly in relation to atmospheric N deposition.

KEYWORDS: AMINO-ACIDS, ATMOSPHERIC AMMONIA, DYNAMIC CHAMBER EXPERIMENTS, ELEVATED CO2, GLUTAMINE-SYNTHETASE ISOFORMS, HORDEUM VULGARE L, L KARST, NITRATE REDUCTASE, NITROGEN-DIOXIDE, SPRUCE PICEA-ABIES

1972

Repo, T., H. Hanninen, and S. Kellomaki. 1996. The effects of long-term elevation of air temperature and CO2 on the frost hardiness of Scots pine. *Plant, Cell and Environment 19(2):209-216.*

The frost hardiness of 20 to 25-year-old Scots pine (Pinus sylvestris L.) saplings was followed for 2 years in an experiment that attempted to simulate the predicted climatic conditions of the future, i,e, increased atmospheric CO2 concentration and/or elevated air temperature, Frost hardiness was determined by an electrolyte leakage method and visual damage scoring on needles, Elevated temperatures caused needles to harden later and deharden earlier than the controls, In the first year, elevated CO2 enhanced hardening at elevated temperatures, but this effect disappeared the next year, Dehardening was hastened by elevating CO2 in both springs, The frost hardiness was high (<-40 degrees C), even at elevated temperatures, in midwinter, at which time the electrolyte leakage method underestimated the frost hardiness compared with the visual scoring, In addition to the significant differences between treatments, there was also significant variation between trees in frost hardiness within treatments, These results suggest that the risks of frost damage are marked in the predicted climatic conditions in Finland, and, more specifically, they depend on how the occurrence of the frost episodes changes with respect to climatic warming during the annual cycle, especially in the autumn and spring, We also conclude that the conditions in midwinter are not critical for frost injury to trees in the future.

KEYWORDS: BUDBURST, DAMAGE, SEASONAL-CHANGES, SEEDLINGS, TREES

1973

Retamales, J., T. Cooper, J. Streif, and J.C. Kania. 1992. Preventing cold-storage disorders in nectarines. *Journal of Horticultural Science 67(5):619-626.*

A storage experiment was aimed at preventing low temperature storage disorders in nectarine fruits, of cvs July Red and Autumn Grand. Fruit was either cooled immediately after harvest or kept at 20-degrees-C for 48 h, before transfer to controlled atmosphere (CA) conditions at 0-degrees-C. Combinations of 0, 10, 15 and 20% CO2 with 8 and 16% O2 were assayed. The fruit was evaluated following cold storage, 31 days after harvest, and after four and eight days under 'shelf conditions'(ripening at 15-18-degrees-C). Warming of the fruit at 20-degrees-C before cold storage prevented woolliness in the absence of elevated CO2 levels but did not affect internal browning and increased reddish discoloration; further, it enhanced water loss and ripening, increasing fruit softening markedly. Conversely, high CO2 delayed fruit ripening in CA storage, keeping the fruit firmer, and preventing the development of woolliness, internal browning and reddish discoloration during ripening, the best results being mostly obtained with 20% CO2. O2 levels assayed did not show clear effects, but decreased O2 concentration in absence of high CO2 showed some benefit in 'July Red'. No deleterious effect of CO2 concentrations even as high as 20% could be detected. Thus, even though high CO2 in CA conditions showed promise for controlling disorders and preventing over-ripening, further work is needed on other cultivars, and lower O2 concentrations should be investigated before making a general recommendation.

KEYWORDS: INTERNAL BREAKDOWN, PEACHES, TEMPERATURES

1974

Retuerto, R., L. Rochefort, and F.I. Woodward. 1996. The influence of plant density on the responses of Sinapis alba to CO2 and windspeed. *Oecologia 108(2):241-251.*

Plants in nature live in populations of variable density, a characteristic which may influence individual plant responses to the environment. We investigated how the responses of Sinapis alba plants to different wind speeds and CO2 concentrations could be modified by plant density. In our wind- density experiment the expectation that mechanical and physiological effects of wind will be ameliorated by growing in high density, as a result of positive plant interactions, was realised. Although individual plants were smaller at higher densities, the effect of increasing windspeed was much less than at lower plant densities. A similar reduced sensitivity of individual plant growth under high densities was also observed under CO2 enrichment. When measured as a population or stand response, there was no effect of density on the CO2 responses, with all stands showing very similar increases in total biomass with CO2 enrichment. In the wind speed experiment, total biomass per stand increased significantly with density, although there was no effect of density on the wind speed response. Specific leaf area decreased with increasing wind speed and this response was significantly affected by the density at which the plants grew.

KEYWORDS: BIOMASS ALLOCATION, CANOPY STRUCTURE, CARBON DIOXIDE, GROWTH, LEAF-AREA, LIGHT, PHOTOSYNTHESIS, SIZE, WATER RELATIONS, WIND

1975

Retuerto, R., and F.I. Woodward. 1993. The influences of increased co2 and water-supply on growth, biomass allocation and water-use efficiency of sinapis-alba L grown under different wind speeds. *Oecologia 94(3):415-427.*

We examined how independent and interactive effects of CO2 concentrations, water supply and wind speed affect growth rates, biomass partitioning, water use efficiency, diffusive conductance and stomatal density of plants. To test the prediction that wind stress will be ameliorated by increased CO2 and/or by unrestricted water supply we grew Sinapis alba L. plants in controlled chambers under combinations of two levels of CO2 (350 ppmv, 700 ppmv), two water regimes and two wind speeds (0.3 ms-1, 3.7 ms-1). We harvested at ten different dates over a period of 60 days. A growth analysis was carried out to evaluate treatment effects on plant responses. Plants grown both in increased CO2 and in low wind conditions had significantly greater stem length, leaf area and dry weights of plant parts. Water supply significantly affected stem diameter, root weight and leaf area. CO2 enrichment significantly increased the rate of biomass accumulation and the relative ratio of biomass increase to leaf area expansion. High wind speed significantly reduced plant growth rates and the rate of leaf area expansion was reduced more than the rate of biomass accumulation. Regression analysis showed significant CO2 effects on the proportion of leaf and stem dry weight to total dry weight. A marked plant-age effect was dependent on water supply, wind speed and CO2 concentration. A reduced water supply significantly decreased the stomatal conductance, and water use efficiency significantly increased with a limited water supply, low wind and increased CO2. We found significant CO2 x wind effects for water diffusion resistance, adaxial number of stomata and water use efficiencies and significant wind x water effect for water use efficiency. In conclusion, wind stress was ameliorated by growing in unrestricted water but not by growing in increased CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, LEAF-AREA, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, PLANT GROWTH, STOMATAL DENSITY

1976

Reuveni, J., and B. Bugbee. 1997. Very high CO2 reduces photosynthesis, dark respiration and yield in wheat. *Annals of Botany 80(4):539-546.*

Although terrestrial CO2 concentrations, [CO2], are not expected to reach 1000 mu mol mol(-1) for many decades, CO2 levels in closed systems such as growth chambers and glasshouses, can easily exceed this concentration. CO2 levels in life support systems in space can exceed 10 000 mu mol mol(- 1) (1 %). Here we studied the effect of six CO2 concentrations, from ambient up to 10000 mu mol mol(-1), on seed yield, growth and gas exchange of two wheat cultivars (USU-Apogee and Veery- 10). Elevating [CO2] from 350 to 1000 mu mol mol(-1) increased seed yield (by 33 %), vegetative biomass (by 25 %) and number of heads m(-2) (by 34 %) of wheal plants. Elevation of [CO2] from 1000 to 10000 mu mol mol(-1) decreased seed yield (by 37 %), harvest index (by 14%), mass per seed (by 9 %) and number of seeds per head (by 29 %). This very high [CO2] had a negligible, non-significant effect on vegetative biomass, number of heads m(-2) and seed mass per head. A sharp decrease in seed yield, harvest index and seeds per head occurred by elevating [CO2] from 1000 to 2600 mu mol mol(-1). Further elevation of [CO2] from 2600 to 10000 mu mol mol(-1) caused a further but smaller decrease. The effect of CO2 on both wheal cultivars was similar for all growth parameters. Similarly there were no differences in the response to high [CO2] between wheal grown hydroponically in growth chambers under fluorescent lights and those grown in soilless media in a glasshouse under sunlight and high pressure sodium lamps. There was no correlation between high [CO2] and ethylene production by flag leaves or by wheal heads. Therefore, the reduction in seed set in wheal plants is not mediated by ethylene. The photosynthetic rate of whole wheat plants was 8 % lower and dark respiration of the wheat heads 25 % lower when exposed to 2600 mu mol mol(- 1) CO2 compared to ambient [CO2]. It is concluded that the reduction in the seed set can be mainly explained by the reduction in the dark respiration in wheat heads, when most of the respiration is functional and is needed for seed development. (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON DIOXIDE, ENHANCEMENT, ENRICHMENT, ETHYLENE PRODUCTION, GROWTH, INTACT SUNFLOWER PLANTS, LEAVES, LIGHT, PHYSIOLOGY, RELEASE

1977

Reuveni, J., J. Gale, and A.M. Mayer. 1993. Reduction of respiration by high ambient co2 and the resulting error in measurements of respiration made with o2 electrodes. *Annals of Botany 72(2):129-131.*

KEYWORDS: EFFLUX, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHESIS

1978

Reuveni, J., J. Gale, and M. Zeroni. 1997. Differentiating day from night effects of high ambient [CO2] on the gas exchange and growth of Xanthium strumarium L exposed to salinity stress. *Annals of Botany 79(2):191-196.*

Sodium chloride, at a concentration of 88 mol m(-3) in half strength Hoagland nutrient solution, increased dry weight per unit area of Xanthium strumarium L. leaves by 19%, and chlorophyll by 45% compared to plants grown without added NaCl at ambient (350 mu mol mol(-1)) CO2 concentration. Photosynthesis, per unit leaf area, was almost unaffected. Even so, over a 4-week period, growth (dry weight increment) was reduced in the salt treatment by 50%. This could be ascribed to a large reduction in leaf area (>60%) and to an approx. 20% increase in the rate of dark respiration (Rd). Raising ambient [CO2] from zero to 2000 mu mol mol(-1) decreased Rd in both control and salinized plants (by 20% at 1000, and by 50% at 2000 mu mol mol(-1) CO2 concentration) compared to Rd in the absence of ambient CO2. High night-time [CO2] had no significant effect on growth of non-salinized plants, irrespective of day-time ambient [CO2]. Growth reduction caused by salt was reduced from 51% in plants grown in 350 mu mol mol(-1) throughout the day, to 31% in those grown continuously

in 900 mu mol mol(-1) [CO2]. The effect of [CO2] at night on salinized plants depended on the daytime CO2 concentration. Under 350 mu mol mol(-1) day-time [CO2], 900 mu mol mol(-1) at night reduced growth over a 4-week period by 9% (P <0.05) and 1700 mu mol mol(-1) reduced it by 14% (P <0.01). However, under 900 mu mol mol(-1) day-time [CO2], 900 vs. 350 mu mol mol(-1) [CO2] at night increased growth by 17% (P <0.01). It is concluded that there is both a functional and an otiose (functionless) component to Rd, which is increased by salt. Under conditions of low photosynthesis (such as here, in the low day-time [CO2] regime) the otiose component is small and high night-time [CO2] partly suppresses functional Rd, thereby reducing salt tolerance. In plants growing under conditions which stimulate photosynthesis (e.g. with increased daytime [CO2]), elevated [CO2] at night suppresses mainly the otiose component of respiration, thus increasing growth. Consequently, in regions of adequate water and sunlight, the predicted further elevation of the world atmospheric [CO2] may increase plant salinity tolerance. (C) 1997 Annals of Botany Company.

KEYWORDS: DARK RESPIRATION RATE, ELEVATED CARBON-DIOXIDE, ENRICHMENT, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, MATURE LEAVES, PHOTOSYNTHESIS, PLANTS, SELECTION, TEMPERATURE

1979

Reuveni, J., A.M. Mayer, and J. Gale. 1995. High ambient carbon-dioxide does not affect respiration by suppressing the alternative, cyanide-resistant pathway. *Annals of Botany 76(3):291-295.*

Total dark respiration (v(t)), cytochrome pathway (v(eyt)), alternative pathway (v(alt)) and residual (v(res)) respiration were measured in Lemna gibba plants, by the use of pathway inhibitors. NaCN was used to inhibit v(eyt) and SHAM (salicylhydroxamic acid) to inhibit v(alt). Residual respiration (v(res)) was about 5% of v(t). The effect of high (100 Pa) and low (0 Pa) carbon dioxide partial pressure ([CO2) on v(t), v(cyt) and v(alt) was determined from both CO2 efflux and O(2)uptake measurements. The higher [CO2] suppressed v(t) by about 30%. When respiration operated through the cytochrome pathway only. in the absence of v(alt), it was suppressed by about 12% as measured by the O-2 uptake of submerged Lemna fronds or by about 40% as measured by CO2 efflux from Boating fronds. The higher [CO2] treatment had only a small effect oil respiration, when v(alt) alone operated. There was no evidence of a specific suppression of the v(alt) pathway by high [CO2]. Succinic dehydrogenase activity of the mitochondria of roots of Medicago sativum was reduced by 18%, when the mitochondria were pre-treated with 120 as compared to 34 Pa [CO2]. There was no such effect on cytochrome c oxidase activity of mitochondria under the same conditions. It is concluded that there is no evidence for the hypothesis that the high [CO2] suppression of respiration is a result of a CO2 effect on the non- phosphorylating alternative respiration pathway. (C) 1995 Annals of Botany Company

KEYWORDS: DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, GROWTH, INHIBITION, LEAVES, MITOCHONDRIA, OXIDASE, PLANT RESPIRATION, TEMPERATURE

1980

Rey, A., and P.G. Jarvis. 1997. Growth response of young birch trees (Betula pendula Roth.) after four and a half years of CO2 exposure. *Annals of Botany 80(6):809-816.*

A field experiment consisting of 18 birch trees grown in open top chambers in ambient and elevated CO2 concentrations was set up with the aim of testing whether the positive growth response observed in many short-term studies is maintained after several growing seasons. We present the results of growth and biomass after 4.5 years of CO2 exposure, one of the longest studies so far on deciduous tree species. We found that elevated CO2 led to a 58% increase in biomass at the end of the experiment. However, estimation of stem mass during the growing season showed that elevated CO2 did not affect relative growth rate during the fourth growing season, and therefore, that the large accumulation of biomass was the result of an early effect on relative growth rate in previous years. Trees grown in elevated CO2 invested more carbon into fine roots and had relatively less leaf area than trees grown in ambient CO2, In contrast with previous studies, acceleration of growth did not involve a significant decline in nutrient concentrations of any plant tissue. It is likely that increased fine root density assisted the trees in meeting their nutrient demands. Changes in the species composition of the ectomycorrhizal fungi associated with the trees grown in elevated CO2 in favour of late successional species supports the hypothesis of an acceleration of the ontogeny of the trees in elevated CO2. (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, ENRICHMENT, GAS-EXCHANGE, LEAF ANATOMY, MINERAL NUTRITION, NUTRIENT STATUS, POPLAR CLONES, SEEDLINGS, SOUR ORANGE TREES

1981

Rey, A., and P.G. Jarvis. 1998. Long-term photosynthetic acclimation to increased atmospheric CO2 concentration in young birch (Betula pendula) trees. *Tree Physiology 18(7):441-450.*

To study the long-term response of photosynthesis to elevated atmospheric CO2 concentration in silver birch (Betula pendula Roth.), 18 trees were grown in the field in open-top chambers supplied with 350 or 700 mu mol mol(-1) CO2 for four consecutive growing seasons. Maximum photosynthetic rates, stomatal conductance and CO2 response curves were measured over the fourth growing season with a portable photosynthesis system. The photosynthesis model developed by Farquhar et al. (1980) was fitted to the CO2 response curves. Chlorophyll, soluble proteins, total nonstructural carbohydrates, nitrogen and Rubisco activity were determined monthly. Elevated CO2 concentration stimulated photosynthesis by 33% on average over the fourth growing season. However, comparison of maximum photosynthetic rates at the same CO2 concentration (350 or 700 mu mol mol(-1)) revealed that the photosynthetic capacity of trees grown in an elevated CO2 concentration was reduced. Analysis of the response curves showed that acclimation to elevated CO2 concentration involved decreases in carboxylation efficiency and RuBP regeneration capacity. No clear evidence for a redistribution of nitrogen within the leaf was observed. Down-regulation of photosynthesis increased as the growing season progressed and appeared to be related to the source-sink balance of the trees. Analysis of the main leaf components revealed that the reduction in photosynthetic capacity was accompanied by an accumulation of starch in leaves (100%), which was probably responsible for the reduction in Rubisco activity (27%) and to a lesser extent for reductions in other photosynthetic components: chlorophyll (10%), soluble protein (9%), and N concentrations (12%) expressed on an area basis. Despite a 21% reduction in stomatal conductance in response to the elevated CO2 treatment, stomatal limitation was significantly less in the elevated, than in the ambient, CO2 treatment. Thus, after four growing seasons exposed to an elevated CO2 concentration in the field, the trees maintained increased photosynthetic rates, although their photosynthetic capacity was reduced compared With trees grown in ambient CO2.

KEYWORDS: ELEVATED CARBON-DIOXIDE, FOLIAR GAS-EXCHANGE, GROWTH, LEAF, PINUS TAEDA L, PLANTS, RESPONSES, RUBISCO, SINK REGULATION, STOMATAL CONDUCTANCE

1982

Rey, P., F. Eymery, and G. Peltier. 1990. Effects of CO2-enrichment and of aminoacetonitrile on growth and photosynthesis of photoautotrophic calli of Nicotiana plumbaginifolia. *Plant Physiology 93(2):549-554.*

1983

Reyenga, P.J., S.M. Howden, H. Meinke, and G.M. McKeon. 1999. Modelling global change impacts on wheat cropping in south-east Queensland, Australia. *Environmental Modelling & Software 14(4):297-306.*

The wheat module, I-WHEAT, from the APSIM cropping system model was used to investigate the impacts of changes in atmospheric CO2 concentrations on wheat crops by modifying radiation use efficiency, transpiration efficiency, specific leaf area and critical nitrogen concentrations. The effects of several combinations of atmospheric CO2, climate change and crop adaptation strategies on wheat production in the Burnett region were studied. Mean wheat yields were increased under doubled CO2, with the response relative to ambient CO2 greatest in dry years. Higher temperatures under the climate change scenarios moderated the yield gains achieved with increasing CO2 and in some instances reversed them under the reduced rainfall scenario. The status of the region as a producer of prime hard wheat may be at risk due to reduced grain protein levels under doubled CO2 and the increased likelihood of "heat shock" in the climate scenarios used.

KEYWORDS: AMBIENT ATMOSPHERE, ATMOSPHERIC CO2 CONCENTRATIONS, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, HEAT-SHOCK, PLANT GROWTH, PROTEIN ACCUMULATION, RESPONSES, TEMPERATURE, WATER-USE EFFICIENCY

1984

Reynolds, J.F., J.L. Chen, P.C. Harley, D.W. Hilbert, R.L. Dougherty, and J.D. Tenhunen. 1992. Modeling the effects of elevated co2 on plants - extrapolating leaf response to a canopy. *Agricultural and Forest Meteorology 61(1-2):69-94.*

The response of canopies to short-duration exposure to elevated CO2 was examined by using a detailed submodel of single-leaf ps exchange combined with a model of canopy structure and light penetration. The leaf model included a mechanistic ps exchange model and leaf energy balance equations, and the canopy model included a detailed description of spatial variability in environmental conditions within the canopy. The structure of the canopy model was designed to facilitate implementation of different leaf aggregation schemes. To compare six aggregation methods of increasing simplicity, daily carbon gain, and water use were simulated for Quercus coccifera under current ambient and future doubled CO2. Analyses of simulated canopy responses confirmed the importance of including (1) leaf energy balance and (2) distinguishing between sunlit and shaded leaves. A multi-layer canopy model with Gaussian integration for sunlit leaves and a single leaf class for shaded leaves in each layer gave excellent results. A multi-layer model with one shaded and one sunlit leaf class gave a reasonable approximation, and the single-layer model with one sunlit and one shaded leaf class resulted in errors of up to 15%. Vertical gradients in leaf nitrogen content and leaf and stem area index had greater effects on canopy assimilation and transpiration than did gradients of stem or leaf inclination or leaf width. However, predictions of the relative response of CO2 assimilation and transpiration to doubled CO2 are rather robust and were not greatly affected by simplifications of the canopy model.

KEYWORDS: ALLOCATION, C-3, CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, WATER-USE

1985

Rice, C.W., F.O. Garcia, C.O. Hampton, and C.E. Owensby. 1994. Soil microbial response in tallgrass prairie to elevated co2. *Plant and Soil 165(1):67-74.*

Terrestrial responses to increasing atmospheric CO2 are important to the global carbon budget. Increased plant production under elevated CO2 is expected to increase soil C which may induce N limitations. The objectives of this study were to determine the effects of increased CO2 on 1) the amount of carbon and nitrogen stored in soil organic matter and microbial biomass and 2) soil microbial activity. A tallgrass prairie ecosystem was exposed to ambient and twice-ambient CO2 concentrations in open-top chambers in the field from 1989 to 1992 and compared to unchambered ambient CO2 during the entire growing season. During 1990 and 1991, N fertilizer was included as a treatment. The soil microbial response to CO2 was measured during 1991 and 1992. Soil organic C and N were not significantly affected by enriched atmospheric CO2. The response of microbial biomass to CO2 enrichment was dependent upon soil water conditions. In 1991, a dry year, CO2 enrichment significantly increased microbial biomass C and N. In 1992, a wet year, microbial biomass C and N were unaffected by the CO2 treatments. Added N increased microbial C and N under CO2 enrichment. Microbial activity was consistently greater under CO2 enrichment because of better soil water conditions. Added N stimulated microbial activity under CO2 enrichment. Increased microbial N with CO2 enrichment may indicate plant production could be limited by N availability. The soil system also could compensate for the limited N by increasing the labile pool to support increased plant production with elevated atmospheric CO2. Longer-term studies are needed to determine how tallgrass prairie will respond to increased C input.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ENRICHMENT, GRASSLAND SOILS, MODEL, NITROGEN, ORGANIC-MATTER

1986

Riedo, M., D. Gyalistras, A. Fischlin, and J. Fuhrer. 1999. Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO2 on dry matter production and partitioning, and water use in temperate managed grasslands. *Global Change Biology 5(2):213-223.*

Local effects of climate change (CC) and elevated CO2 (2 x CO2, 660 mu mol mol(-1)) on managed temperate grasslands were assessed by forcing a dynamic ecosystem model with weather scenarios. The aims of the study were to compare the relative importance of individual and combined effects of CC, 2 x CO2, and photosynthetic acclimation, and to assess the importance of local site conditions. The model was driven by hourly means for temperature (T), precipitation (P), global radiation (G), vapour pressure (VP), and wind speed (U). Local climate scenarios were derived by statistical downscaling techniques from a 2 x CO2 simulation with the General Circulation Model of the Canadian Climate Centre (CCC-GCMII). Simulations over 14 growing seasons to account for year-to-year variability of climate were carried out for a low, relatively dry site, and a high, more humid site. At both sites, shoot dry matter responded positively to 2 x CO2 with the site at low elevation being more sensitive than the higher site. The effect of assumed changes in climate was negative at the lower, but positive at the higher site. Shoot dry matter was more sensitive to the effects of 2 x CO2 than to CC. Both effects combined increased shoot dry matter by up to 20%. This was attributed to direct effects of 2 x CO2 and increased T,and indirect stimulation via increased soil N availability. Biomass partitioning to roots increased with 2 x CO2 but decreased with CC, while an intermediate response resulted from the combination. Leaf area index (LAI) increased under 2 x CO2, but not enough to compensate fully for a decrease in leaf conductance. Under the 2 x CO2 scenario

evapotranspiration (ET) decreased, but increased under CC. Photosynthetic acclimation reduced the effect of 2 x CO2 on shoot growth, but had little effect on ET. The seasonal water use efficiency (WUE) was improved under 2 x CO2, and reduced under CC. With the combination of both factors, the change was small but still positive, especially at the high elevation site with more favourable soil water conditions. This reflects the stronger positive yield response in combination with a smaller increase in ET under cooler, more humid conditions. The results for the combination of factors suggest that except for shoot growth, effects of 2 x CO2 and CC tend to offset each other. While CC determines the sign of the ET response, the sign of the biomass response is determined by 2 x CO2. The results highlight the importance of a site-specific analysis of ecosystem responses by using a flexible approach based on a combination of state- of-the-art downscaling, spatially resolved data sets, and a mechanistic model to obtain quantitative and reproducible assessments of climate change impacts at the ecosystem level.

KEYWORDS: ATMOSPHERIC CO2, DAILY PRECIPITATION, GENERAL-CIRCULATION MODEL, GROWTH, LOLIUM-PERENNE L, RESPONSES, ROOT, SENSITIVITY ANALYSIS, SIMULATION, TRIFOLIUM-REPENS L

1987

Riedo, M., D. Gyalistras, A. Grub, M. Rosset, and J. Fuhrer. 1997. Modelling grassland responses to climate change and elevated CO2. *Acta Oecologica-International Journal of Ecology 18(3):305-311.*

A mechanistic model for productive grassland was used to simulate the annual production of above-and belowground plant biomass in relation to fluxes of C, N, and water, and to test the sensitivity of yield, shoot/root ratio, evapotranspiration, and water use efficiency (WUE) to climate change scenarios (CC) and to elevated CO2 (2 x CO2) with or without consideration oi photosynthetic acclimation of the plants. Validation with data from two Swiss sites revealed satisfactory agreement between simulation and measurement for yield, energy fluxes, and N- dynamics. Local weather scenarios were derived from the results of two General Circulation Models (GCM) for 2 x CO2 by a statistical down-scaling procedure. Biomass production changed by a maximum of 8% in response to CC without 2 x CO2 effects, by 1-17% in response to 2 x CO2 alone, and by 6-20% in response to the combination of CC and 2 x CO2. With plant acclimation, biomass Production increased only up to 8% with elevated CO2, as compared to a maximum increase of 20% in the absence of plant acclimation. Reduced yield with CC was obtained for sites with low soil water holding capacity. Decreased evapotranspiration and increased WUE with 2 x CO2 were partially offset by CC. The simulations indicated that productivity of managed grassland is sensitive to different assumptions about changes in climate, CO2 concentration, and photosynthetic acclimation, and that the effects of elevated CO2 are modified by CC and depend on local soil conditions.

KEYWORDS: CARBON, GENERAL-CIRCULATION MODEL, SOIL

1988

Righetti, B., E. Magnanini, and F. Rossi. 1993. Photosynthetic carbon-dioxide uptake and oxygen accumulation during in-vitro culture of actinidia-deliciosa CV tomuri. *Environmental and Experimental Botany 33(4):523-528.*

Proliferating cultures of Actinidia deliciosa cv Tomuri were grown in vitro under a photosynthetic photon flux density (PPFD) of 120 mumol m2/s. Some jars were daily enriched with 2000 mul/l CO2 administered at the end of the dark period. Head space analysis revealed that CO2 accumulated up to 9500 mul/l during the dark period and was drastically reduced by photosynthetic activity to 150-200 mul/l during the photoperiod without any significant difference between CO2-enriched and non-enriched cultures. Oxygen concentration assayed at the end of the photoperiod showed a steady increase during the 44 days of culture and was not reduced to atmospheric values by respiratory processes during the dark period. CO2 enrichment enhanced O2 production and accumulation to 32.5% at the end of the culture period. Oxygen photoreduction and its photo- oxidative damage to green tissue cells are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ENRICHMENT, EXCHANGE, GROWTH, LIGHT, PLANTS, STARCH, STRESS, TOXICITY

1989

Righetti, B., D.M. Reid, and T.A. Thorpe. 1996. Growth and tissue senescence in Prunus avium shoots grown in vitro at different CO2/O-2 ratios. *In Vitro Cellular & Developmental Biology-Plant 32(4):290-294.*

The rate of metabolism and biosynthetic processes make in vitro cultures very sensitive to environmental changes, and therefore subject to physiological and morphological alterations leading to senescence in the short term. The effects of three different calibrated atmospheric compositions were studied during in vitro culture of Prunus avium shoots. At 0.034% CO2-21% O-2 (vol/vol), which stimulate the natural atmosphere, the highest growth rate and chlorophyll content were recorded. When grown at 0.09% CO2-8% O-2 (vol/vol), a favorable condition for photosynthesis and growth, cultures showed a higher percentage of dry matter and elevated ethylene production, but total chlorophyll was lower. These shoots were also highly lignified and fibrous with red pigmentation along the leaves and stems. At 0% CO2-21% O-2 (vol/vol), in contrast, growth and ethylene formation were inhibited; chlorophyll content was lowest in comparison with the other two environmental conditions, hut regreening of tissues was observed after the first half of the culture period. Senescence symptoms, as indicated by decreased chlorophyll, appeared after about 18 d of culture for tissues grown in CO2-containing atmospheres. These experiments provided evidence that in CO2-enriched cultures biomass production steadily increased even when chlorophyll decreased. A possible role of CO2 in promoting tissue-senescence through activation of photooxidative events and ethylene synthesis is discussed.

KEYWORDS: ACTIVATION, BEAN-LEAVES, CARBON DIOXIDE, CO2- ENRICHMENT, CROP RESPONSES, LONG-TERM ACTION, NET PHOTOSYNTHETIC RATE, OXYGEN CONCENTRATION, PHOTORESPIRATION, TOXICITY

1990

Rigler, E., and S. Zechmeister-Boltenstern. 1998. Influence of nitrogen and carbon dioxide on ethylene and methane production in two different forest soils. *Microbiological Research 153(3):227-237.*

The impact of nitrogen and CO, on ethylene and methane production was investigated in two different forest soils. The soils were adjusted to a water tension of 30 kPa. Nitrogen was added in the form of KNO3 or (NH4)(2)SO4 and CO2 was added in 5 different concentrations. To half of the samples, C2H2 was added to inhibit ethylene uptake. After 0, 24, and 96 hours, ethylene and methane concentrations were measured by gas chromatography. Ethylene net production increased with increasing N and CO2 concentrations. In the presence of acetylene, ethylene production was unaffected by the investigated amendments. Therefore, we suppose that the increasing ethylene net production rates are due to decreasing ethylene uptake rates. In the deciduous forest soil, there was no ethylene net production rate, as uptake rates exceeded production rates. Methane net production rates in the spruce forest soil increased with increasing N additions possibly due to a lowered C:N ratio and a decreased methane oxidation. Ethylene production rates in the presence

of acetylene were slightly enhanced. In the deciduous forest soil, methane uptake rates decreased with nitrogen possibly due to the inhibition of the methanemonooxygenase. CO2 seemed to increase methane production in the presence of acetylene but had no significant effect on methane net production. Acetylene might serve as a substrate for methanogenesis.

KEYWORDS: ACCUMULATION, ACETYLENE-REDUCTION ASSAY, BIOSYNTHESIS, CONSUMPTION, FERTILIZERS, INHIBITION, MICROORGANISMS, NADH-FE(III)EDTA OXIDOREDUCTASE, NITRATE, RESPONSES

1991

Rigler, E., and S. Zechmeister-Boltenstern. 1999. Oxidation of ethylene and methane in forest soils - effect of CO2 and mineral nitrogen. *Geoderma 90(1-2):147-159.*

The influence of inorganic nitrogen and CO2 on microbial C2H4 and CH4 consumption was evaluated in two forest soils (montane spruce forest and colline deciduous forest) under laboratory conditions at 25 degrees C. The soils were adjusted to a water tension of - 30 kPa. Nitrogen was added as KNO3 or (NH4)(2)SO4, while CO2 enrichment ranged from 1-20%. At 0, 24, and 96 h, the amounts of CH4 and C2H4 consumed were determined. In both soils, we observed a parallel response of C2H4 and CH4 to all kinds and concentrations of amendments, plausibly due to co- metabolism of C2H4 by either methanotrophs or nitrifiers. Ammonium-N inhibited hydrocarbon oxidation in the deciduous forest soil, but promoted it in the acidic spruce forest soil. Ammonium addition narrowed the C:N ratio of the spruce forest soil which was characterized by low pH but high humus content. Therefore, the general living conditions for microorganisms might have been improved. Conversely, NO3- inhibited hydrocarbon oxidation in both soils, here a non-specific ion toxicity ('salt-effect') is discussed. CO2 also had an inhibitory effect on hydrocarbon microbial uptake at high concentrations, with its production increasing at elevated CO2 levels. We conclude that the impact of nitrogen inputs and of enhanced CO2 on the sink strength for hydrocarbons depends on the amount and the kind of addition as well as on soil type. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: AMMONIUM INHIBITION, ATMOSPHERIC METHANE, BACTERIA, CAPACITY, CONSUMPTION, HYDROCARBONS, METABOLISM, N-FERTILIZATION, NITRIFICATION, TEMPERATURE

1992

Riis, T., and K. SandJensen. 1997. Growth reconstruction and photosynthesis of aquatic mosses: Influence of light, temperature and carbon dioxide at depth. *Journal of Ecology 85(3):359-372.*

1 The mosses Sphagnum subsecundum and Drepanocladus exannulatus dominate the vegetation in the oligotrophic, softwater Lake Grane Langso, Denmark, even at great depths where light and temperature are low. We used seasonal changes in morphology to reconstruct the annual growth and the longevity of the mosses and measurements of photosynthesis and respiration to evaluate the importance of light, temperature and CO2 for the growth patterns at depth in the lake. 2 The reconstruction technique revealed that the mosses had a relatively fast growth rate (90- 250 mm shoot(-1) year(-1)) and were short lived (0.7-2.9 years). The shoots of both moss species grew faster in deep than in shallow water. Growth experiments in summer confirmed that Sphagnum grew more slowly and decayed more rapidly in shallow than in deep water. 3 Fast growth of mosses in deep waters can be accounted for by lower temperature, extensive CO2 supersaturation and nutrient enrichment in the hypolimnion during summer stratification. Maximum rate of light-saturated photosynthesis in July was 3.3-fold higher and of dark respiration 1.3-fold lower in Sphagnum from 9.5m incubated at the ambient 8 degrees C than in Sphagnum from 0.7m incubated at 20 degrees C. The net daily carbon fixation was greater in deep than in shallow water despite the much lower irradiance at depth. Extensive CO2 supersaturation stimulated photosynthesis several-fold relative to the rates observed in air-saturated water. Tissues of Sphagnum were richer in nitrogen in deep than in shallow water during summer, but the importance of nutrient availability to annual moss growth remains unclear. 4 Reconstruction techniques are recommended for comparative studies on annual and interannual growth patterns of mosses within lakes and among lakes of different altitude, latitude and water chemistry. This information can be based on just a single collection and can therefore include remote sites with adverse climate.

KEYWORDS: ANTARCTIC LAKES, BENTHIC PLANTS, FONTINALIS-ANTIPYRETICA, IRRADIANCE, MACROPHYTE COMMUNITIES, POPULATION-DYNAMICS, PRODUCTION ECOLOGY, STRATEGIES, SWEDISH LAPLAND, TUNDRA PLANTS

1993

Rillig, M.C., and M.F. Allen. 1998. Arbuscular mycorrhizae of Gutierrezia sarothrae and elevated carbon dioxide: Evidence for shifts in C allocation to and within the mycobiont. *Soil Biology and Biochemistry 30(14):2001-2008.*

In a complete 2 x 2 factorial greenhouse experiment we examined the responses of arbuscular mycorrhizal (AM) and non- mycorrhizal fungi to Gutierrezia sarothrae shrubs grown in elevated atmospheric carbon dioxide (750 mu l l(-1)) and fertilized with N. AM percent infection did not change significantly with elevated CO2, but arbuscular infection increased 14-fold in the low-N treatment. Extraradical hyphal length increased on an absolute basis in elevated CO2, and also per infected root length. In the high-N treatments, increasing CO2 caused a decrease in hyphal length per infected root length, and an increase in vesicular infection. There was a significant positive response of AM infection intensity to increasing CO2 for the high N treatment, and a similar trend in the low N treatment. Infection intensity was positively correlated with arbuscular infection and with vesicular infection. Nonmycorrhizal fungi did not respond to any of the treatment combinations, as measured by percent root infection and external hyphal length. Our results indicate that C allocation to the AM fungi was increased in elevated CO2, and that the mycobiont in turn increased C allocation to external hyphae. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO2, COLONIZATION, ENRICHMENT, FUNGI, HYPHAE, RESPONSES, RHIZOSPHERE, ROOTS, SOIL

1994

Rillig, M.C., and M.F. Allen. 1999. What is the role of arbuscular mycorrhizal fungi in plant-to- ecosystem responses to Elevated atmospheric CO2? *Mycorrhiza 9(1):1-8.*

We advocate the concept of an arbuscular mycorrhiza (AM) as a temporally and spatially complex symbiosis representing a suite of hosts and fungi, as against the more traditional "dual organism" view. We use the hierarchical framework presented in Fig. 1 as a basis for organizing many unanswered questions, and several questions that have not been asked, concerning the role of AM in responses to elevated atmospheric CO2. We include the following levels: plant host, plant population, plant community, functional group and ecosystem. Measurements of the contributions of AM fungi at the various levels require the use of different response variables. For example, hyphal nutrient translocation rates or percent AM root infection may be important measures at the individual plant level, but hyphal biomass or glomalin production and turnover are more relevant at the ecosystem level. There is a discrepancy

between our knowledge of the multifaceted role of AM fungi in plant and ecosystem ecology and most of the current research aimed at elucidating the importance of this symbiosis in global-change scenarios. Our framework for more integrated and multifactorial research on mycorrhizal involvement in regulating CO2 responses may also serve to enhance communication between researchers working at different scales on large global-change ecosystem projects.

KEYWORDS: BIOMASS PRODUCTION, BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, LITTER DECOMPOSITION, ROOTS, SOIL BIOTA, SYMBIOTIC N-2 FIXATION, TRIFOLIUM-REPENS L, WATER RELATIONS

1995

Rillig, M.C., M.F. Allen, J.N. Klironomos, N.R. Chiariello, and C.B. Field. 1998. Plant species-specific changes in root-inhabiting fungi in a California annual grassland: responses to elevated CO2 and nutrients. *Oecologia 113(2):252-259.*

Five co-occurring plant species from an annual mediterranean grassland were grown in monoculture for 4 months in pots inside open-top chambers at the Jasper Ridge Biological Preserve (San Mateo County, California). The plants were exposed to elevated atmospheric CO2 and soil nutrient enrichment in a complete factorial experiment. The response of root-inhabiting non- mycorrhizal and arbuscular mycorrhizal fungi to the altered resource base depended strongly on the plant species. Elevated CO2 and fertilization altered the ratio of non-mycorrhizal to mycorrhizal fungal colonization for some plant species, but not for others. Percent root infection by non-mycorrhizal fungal increased by over 500% for Linanthus parviflorus in elevated CO2, but decreased by over 80% for Bromus hordeaceus. By contrast, the mean percent infection by mycorrhizal fungi increased in response to elevated CO2 for all species, but significantly only for Avena barbata and B. hordeaceus. Percent infection by mycorrhizal fungi increased, decreased, or remained unchanged for different plant hosts in response to fertilization. There was evidence of a strong interaction between the two treatments for some plant species and non- mycorrhizal and mycorrhizal fungi. This study demonstrated plant species-and soil fertility-dependent shifts in belowground plant resource allocation to different morphogroups of fungal symbionts. This may have consequences for plant community responses to elevated CO2 in this California grassland ecosystem.

KEYWORDS: AMMONIUM-SULFATE, ARBUSCULAR MYCORRHIZAL FUNGI, ATMOSPHERIC CARBON-DIOXIDE, COLONIZATION, COMMUNITIES, ENRICHMENT, FEEDBACK, INFECTION, NITRATE, RHIZOSPHERE

1996

Rillig, M.C., M.F. Allen, J.N. Klironomos, and C.B. Field. 1998. Arbuscular mycorrhizal percent root infection and infection intensity of Bromus hordeaceus grown in elevated atmospheric CO2. *Mycologia 90(2):199-205.*

Using Bromus hordeaceus, a grass from a Mediterranean annual grassland in California, we measured changes in infection intensity, rather than the more traditional % root infection, as an indicator of response to elevated atmospheric CO2 and soil nutrient enrichment. Intensity was measured as the number of intraradical hyphae intersecting a microscope cross-hair for specific root diameter size classes. We found an increase in intensity of infection when plants were exposed to elevated CO2, and we found a decrease in infection intensity when plants were fertilized. This finding is significant in that it provides evidence for an increase in carbon allocation to the mycobiont under elevated CO2 even in the absence of change in percent infection, or mycorrhizal root length. Previous studies may therefore have overlooked an important response of arbuscular mycorrhizal fungi to this treatment, leading to an underestimation of the importance of mycorrhizae under elevated CO2. Infection intensity may also change in response to many other treatments and environmental variables that the symbiosis is exposed to, high-lighting the potential usefulness of intensity as a response variable in mycorrhizal research.

KEYWORDS: CARBON, COLONIZATION, COTTON, ENRICHMENT, PHOTOSYNTHESIS, PLANTS, RESPONSES, RHIZOSPHERE

1997

Rillig, M.C., C.B. Field, and M.F. Allen. 1999. Fungal root colonization responses in natural grasslands after long-term exposure to elevated atmospheric CO2. *Global Change Biology 5(5):577-585.*

Arbuscular mycorrhizae, ubiquitous mutualistic symbioses between plant roots and fungi in the order Glomales, are believed to be important controllers of plant responses to global change, in particular to elevated atmospheric CO2. In order to test if any effects on the symbiosis can persist after long-term treatment, we examined root colonization by arbuscular mycorrhizal (AM) and other fungi of several plant species from two grassland communities after continuous exposure to elevated atmospheric CO2 for six growing seasons in the field. For plant species from both a sandstone and a serpentine annual grassland there was evidence for changes in fungal root colonization, with changes occurring as a function of giant host species. We documented decreases in percentage nonmycorrhizal fungal root colonization in elevated CO2 for several plant species. Total AM root colonization (%) only increased significantly for one out of the five plant species in each grassland. However, when dividing AM fungal hyphae into two groups of hyphae (fine endophyte and coarse endophyte), we could document significant responses of AM fungi that were hidden when only total percentage colonization was measured. We also documented changes in elevated CO2 in the percentage of root colonized by both AM hyphal types simultaneously. Our results demonstrate that changes in fungal root colonization can occur after long-term CO2 enrichment, and that the level of resolution of the study of AM fungal responses may have to be increased to uncover significant changes to the CO2 treatment. This study is also one of the first to document compositional changes in the AM fungi colonizing roots of plants grown in elevated CO2. Although it is difficult to relate the structural data directly to functional changes, possible implications of the observed changes for plant communities are discussed.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, BOUTELOUA-GRACILIS, ENRICHMENT, GROWTH, INFECTION, SYSTEM, TREE

1998

Rillig, M.C., C.B. Field, and M.F. Allen. 1999. Soil biota responses to long-term atmospheric CO2 enrichment in two California annual grasslands. *Oecologia 119(4):572-577.*

Root, arbuscular-mycorrhizal (AM), soil faunal (protozoa and microarthropods), and microbial responses to field exposure to CO2 for six growing seasons were measured in spring 1997 in two adjacent grassland communities. The grasslands showed contrasting root responses to CO2, enrichment: whereas root length was not affected in the sandstone grassland, it was greater in the serpentine grassland, as was specific root length. AM fungal hyphal lengths were greater in the sandstone, but were unaffected in the serpentine community. This lent support to the hypothesis that there may be a tradeoff in resource allocation to more fine roots or greater mycorrhizal extraradical hyphal length. AM root infection was greater in both communities at elevated CO2, as was the proportion of roots containing arbuscules. Our data on total hyphal lengths, culturable and active fungi, bacteria, and protozoa supported the hypothesis that the fungal food chain was more strongly stimulated than the bacterial chain. This study is one of the first to test

these hypotheses in natural multi-species communities in the field.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ELEVATED CO2, GROWTH, PASTURE, RHIZOSPHERE, SYSTEMS, TALLGRASS PRAIRIE

1999

Rillig, M.C., K.M. Scow, J.N. Klironomos, and M.F. Allen. 1997. Microbial carbon-substrate utilization in the rhizosphere of Gutierrezia sarothrae grown in elevated atmospheric carbon dioxide. *Soil Biology and Biochemistry 29(9-10):1387-1394.*

Differences in rhizosphere microbial community function in response to Gutierrezia sarothrae plants grown in elevated CO2 (750 mu l l(-1)) and fertilized with nitrogen were studied using the Biolog microplate analysis of sole C substrate utilization. Compared to ambient CO2 under elevated CO2, polymers were more slowly oxidized by the microbial community, amides showed no change in usage, and all other substrate groups were more rapidly utilized, although there was no significant change in the number of viable bacteria. No microbial community responses to N fertilization were detected. The results indicate that potential functional changes in the soil microbial community in response to elevated CO2 have to be taken into account in future experiments. Differential use of rhizo-deposits in elevated CO2 may have important consequences for biogeochemistry and plant growth. (C) 1997 Elsevier Science Ltd.

KEYWORDS: CO2, COMMUNITIES, DECOMPOSITION, DIVERSITY, FEEDBACK, LEAF LITTER, PATTERNS, RESPONSES, ROOTS

2000

Ringelberg, D.B., J.O. Stair, J. Almeida, R.J. Norby, E.G. ONeill, and D.C. White. 1997. Consequences of rising atmospheric carbon dioxide levels for the belowground microbiota associated with white oak. *Journal of Environmental Quality 26(2):495-503.*

The consequences for belowground microbiota under conditions of rising atmospheric CO2 are largely unknown. In this research we examined the microbiota associated with white oak (Quercus alba L.). It was our hypothesis that an increase in CO2 level would induce a change in the rhizosphere-associated microbial abundance and community composition. To provide an in situ estimation of microbial abundance and community composition, ester-linked polar lipid fatty acid (PLFA) technology was utilized. This technology, based on the quantitative measurement of membrane lipid fatty acids, has been utilized in the accurate identification and description of bacterial isolates and communities. Initial experiments demonstrated that a clear distinction in lipid patterns and microbial biomass existed between sterile roots and those of roots containing an associated viable microbiota. Statistical approaches were then used to determine what differences existed between individual PLFA and PLFA patterns obtained from white oak fine roots and bulk soils. An analysis of variance (ANOVA) showed significant differences to exist in the relative percentages of individual prokaryotic PLFA collected under ambient vs. elevated CO2 and between those associated with fine roots and bulk soils. Multivariate statistics showed distinct differences in the patterns of prokaryotic PLFA detected in the rhizosphere vs. the surrounding bulk soil, but did not identify differences related to elevated CO2 exposures. An artificial neural network recognized PLFA patterns unique to three different CO2 exposures: similar to 35, similar to 50, and similar to 65 Pa. Results of the three statistical tests were viewed as supportive of the hypothesis describing significant differences in individual PLFA and patterns of PLFA as a result of elevated CO2 exposure.

KEYWORDS: BIOMASS, ELEVATED CO2, ENRICHMENT, FATTY-ACIDS, GROWTH, MYCORRHIZAL COLONIZATION, PLANT-RESPONSES, POLY BETA HYDROXYBUTYRATE, QUERCUS-ALBA, RHIZOSPHERE

2001

RiviereRolland, H., P. Contard, and T. Betsche. 1996. Adaptation of pea to elevated atmospheric CO2: Rubisco, phosphoenolpyruvate carboxylase and chloroplast phosphate translocator at different levels of nitrogen and phosphorus nutrition. *Plant, Cell and Environment 19(1):109-117.*

Resource allocation in high CO2 was studied with respect to plant nutrition. Pea (Pisum sativum) was grown in CO2-enriched air (1000 cm(3) m(-3) CO2) during the entire vegetative phase, or grown in ambient air (340 cm(3) m(-3) CO2), with different levels of nitrogen or phosphorus supply. Rubisco specific activity, abundance and small subunit transcript levels were unaltered at high N but declined at reduced N depending upon the degree of N deprivation. It is proposed that (a) a threshold value for the N status occurs in pea above which Rubisco is not down-regulated by high CO2 and (b) a high leaf level of soluble carbohydrates is not a sufficient condition to down-regulate Rubisco in high CO2. Phesphoenolpyruvate (PEP) carboxylase decreased, and chloroplast phosphate (P)- translocator increased, in high CO2. In contrast to Rubisco, down-regulation of PEP carboxylase was alleviated by low N and enhanced by low P. The increase in the P-translocator was little affected by N but was accentuated by low P. The increase in the P-translocator is considered to be one way of alleviating low P conditions in the chloroplast and thus re- balancing carbon partitioning between starch and soluble carbohydrates and amino acids. It is proposed that acclimation of PEP carboxylase and P-translocator reflects adaptation to metabolic perturbations caused by high CO2.

KEYWORDS: ANTISENSE RBCS, C-3 PLANTS, CARBON DIOXIDE, CELLS, GROWTH, LIGHT, OXYGENASE, PHOTOSYNTHESIS, SINK REGULATION, TRIFOLIUM-SUBTERRANEUM L

2002

Roberntz, P. 1999. Effects of long-term CO2 enrichment and nutrient availability in Norway spruce. I. Phenology and morphology of branches. *Trees-Structure and Function 13(4):188-198.*

Branches of 30-year-old Norway spruce [Picea abies (L.) Karst.] trees were enclosed in ventilated, transparent plastic bags and flushed with air containing ambient (A approximate to 370 mu mol CO2 mol(-1)) or ambient plus 340 mu mol CO2 mol(-1) (EL). Light-saturated photosynthesis was on average 56% higher in EL compared to A. Branch phenology and morphology were strongly related to nitrogen concentration (mg g(-1) dry mass) in the foliage and to elevated temperatures in the bags, but no direct effect of EL was found. In 1995, budbreak occurred on average 4 days earlier in the bags compared to the control branches, which was partly explained by the temperature elevation in the bags. No nutrient or EL effect on budbreak was found. Increases in temperature and nitrogen supply increased shoot growth: together they explained 76% of the variation in the extension rate, 63% of the variation in extension duration and 65% of the variation in final length of leading shoots. Shoot morphology was altered both by increased nitrogen availability and by the enclosure induced environmental changes inside the bags, leading to reduced mutual shading between needles. Specific needle area (SNA) was lower in EL, but this was related to lower nitrogen concentrations. Total dry mass of the branches was unaffected by EL. It is concluded that treating individual branches of Norway spruce with elevated CO2 does not increase branch growth. The nutrient status of the branch and climate determine its growth, i.e, its sink strength for carbon. Increased export of carbohydrates to the rest of the tree is probable in EL treated branches.

KEYWORDS: ABIES AMABILIS, CARBON DIOXIDE, ELEVATED CO2, GROWTH, LOBLOLLY-PINE TREES, NET PHOTOSYNTHESIS, NUTRITION, PICEA-SITCHENSIS, RESPONSES, STOMATAL CONDUCTANCE

2003

Roberntz, P., and S. Linder. 1999. Effects of long-term CO2 enrichment and nutrient availability in Norway spruce. II. Foliar chemistry. *Trees-Structure and Function 14(1):17-27.*

Branches on 30-year-old Norway spruce trees [Picea abies (L.) Karst.] were exposed to ambient (AMB) or ambient plus 350 mu mol CO2 mol(-1) (EL) for 4 years (except winters), using the branch bag technique (BB). The trees were growing on plots with low (control) and high (irrigated-fertilised) availability of soil nutrients. The seasonal variation in foliar macronutrients and non-structural carbohydrates in current and 1-year-old shoots was monitored throughout the treatment period. When the branches were harvested at the end of treatment, macronutrients were analysed in five age classes of foliage. The concentration of all elements, except magnesium, generally increased in AMB, i.e. a 'bag effect', but decreased as an effect of EL, i.e. a 'CO2 effect'. At the final harvest K, P, N and S were reduced in young needles by EL, whereas Mg was reduced in older needles on both plots. A change in needle morphology by EL possibly caused a dilution effect in irrigated-fertilised needles, but not in control needles. Reductions in K and Mg are suggested to be an effect of increased phloem transport from the branch, in consequence of higher rates of carbon fixation in EL. Foliage in BBs had higher concentration of Ca, but there was no significant effect of the EL-treatment, indicating that elevated CO2 had no effect on stomatal conductance. Quinic acid concentration decreased, but shikimic acid concentration increased in BBs, independently of CO2 treatment. Concentrations of starch and sugars increased in the EL- treatment, but pinitol decreased.

KEYWORDS: ELEVATED ATMOSPHERIC CO2, GROWTH, LEAF ANATOMY, LEAVES, NEEDLES, PLANTS, RESPONSES, SCOTS PINE, STOMATAL CONDUCTANCE, TREES

2004

Roberntz, P., and J. Stockfors. 1998. Effects of elevated CO2 concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. *Tree Physiology 18(4):233-241.*

To study the effects of elevated CO2 on gas exchange, nonstructural carbohydrate and nutrient concentrations in current-year folia,ae of 30-year-old Norway spruce (Picea abies (L.) Karst.) trees, branches were enclosed in ventilated, transparent plastic bags and flushed with ambient air (mean 370 mu mol CO2 mol(-1); control) or ambient air + 340 mu mol CO2 mol(-1) (elevated CO2) during two growing seasons. One branch bag was installed on each of 24 selected trees From control and fertilized plots. To reduce the effect of variation among trees, results from each treated branch were compared with those from a control branch on the same whorl of the same tree. Elevated CO2 increased rates of light-saturated photosynthesis on average by 55% when measured at the treatment CO2 concentration. The increase was larger in shoots with high needle nitrogen concentrations than in shoots with low needle nitrogen concentrations. However, shoots grown in elevated CO2 showed a decrease in photosynthetic capacity compared with shoots grown in ambient CO2. When measured at the internal CO2 concentration of 200 mu mol CO2 mol(-1), photosynthetic rates of branches in the elevated CO2 treatments were reduced by 8 to 32%. The elevated CO2 treatment caused a 9 to 20% reduction in carboxylation efficiency and an 18% increase in respiration rates. In response to elevated CO2, starch, fructose and glucose concentrations in the needles increased on average 33%, whereas concentrations of potassium, nitrogen, phosphorus, magnesium and boron decreased. Needle nitrogen concentrations explained 50-60% of the variation in photosynthesis and CO2 acclimation was greater at low nitrogen concentrations than at high nitrogen concentrations. We conclude that the enhanced photosynthetic rates found in shoots exposed to elevated CO2 increased carbohydrate concentrations, which may have a negative feedback on the photosynthetic apparatus and stimulate cyanide-resistant respiration. We also infer that the decrease in nutrient concentrations of needles exposed to elevated CO2 was the result of retranslocation of nutrients to other parts of the branch or tree.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ENRICHMENT, GAS-EXCHANGE, LEAVES, NITROGEN, PICEA, PINE, PLANTS, RISING CO2

2005

Roberts, S.W., W.C. Oechel, P.J. Bryant, S.J. Hastings, J. Major, and V. Nosov. 1998. A field fumigation system for elevated carbon dioxide exposure in chaparral shrubs. *Functional Ecology 12(4):708-719.*

1. Modifications and improvements in the hardware and software of a free-air CO2 enrichment (FACE) system are described. The modifications were undertaken to minimize the amount of structure required and to improve software control of CO2 set points. 2. A new low-cost CO2 flow controller which provides increased reliability is described. 3, Analysis of system performance during a 79-day evaluation period of operation (13 h day(-1)) showed that for 1 min averages, the system is capable of maintaining a 550 p.p.m. +/- 10% CO2 set point during 78% of the operating time and a 550 p.p.m. +/- 20% set point during 95% of the operating time. Ten-minute averages were within +/- 10% and 20% during 87% and 96% of the operating time, respectively. 4, Continuous measurements of the spatial variation in CO2 concentration inside the FACE ring over an 18- day period showed that of the total 16-m diameter treatment area, the central 11-m diameter portion remains within the 550 p.p.m. +/- 10% set point. 5, Daily course gas-exchange measurements in matched individuals of the chaparral shrub Adenostoma fasciculatum just prior to and following a 6-week fumigation period at 550 p.p.m. CO2 in the FACE treatment ring showed the FACE plants with reduced photosynthetic rates and higher (less stressful) water potentials compared with control A. fasciculatum plants measured at the same times and conditions, indicating the responsiveness of this species to elevated CO2 conditions.

KEYWORDS: CO2, DESIGN

2006

Robertson, E.J., and R.M. Leech. 1995. Significant changes in cell and chloroplast development in young wheat leaves (triticum-aestivum CV hereward) grown in elevated co2. *Plant Physiology 107(1):63-71.*

Cell and chloroplast development were characterized in young Triticum aestivum cv Hereward leaves grown at ambient (350 mu L L(-1)) or at elevated (650 mu L L(-1)) CO2. In elevated CO2, cell and chloroplast expansion was accelerated by 10 and 25%, respectively, in the first leaf of 7-d-old wheat plants without disruption to the leaf developmental pattern. Elevated CO2 did not affect the number of chloroplasts in relation to mesophyll cell size or the linear relationship between chloroplast number or size and mesophyll cell size. No major changes in leaf anatomy or in chloroplast ultrastructure were detected as a result of growth in elevated CO2, but there was a marked reduction in starch accumulation. In leaf sections fluorescently tagged antisera were used to visualize and quantitate the amount of cytochrome f, the alpha- and beta-subunits of the coupling factor 1 in ATP synthase, D1 protein of the photosystem II reaction center, the 33-kD protein of the extrinsic oxygen-evolving complex, subunit II of photosystem I, and ribulose-1,5-

bisphosphate carboxylase/oxygenase. A significant finding was that in 10 to 20% of the mesophyll cells grown in elevated CO2 the 33-kD protein of the extrinsic oxygen-evolving complex of photosystem II and cytochrome f were deficient by 75%, but the other proteins accumulated normally.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, LEAF, LIGHT, PHOTOSYNTHESIS, PLANTS, PROTEIN

2007

Robertson, E.J., M. Williams, J.L. Harwood, J.G. Lindsay, C.J. Leaver, and R.M. Leech. 1995. Mitochondria increase 3-fold and mitochondrial proteins and lipid change dramatically in postmeristematic cells in young wheat leaves grown in elevated co2. *Plant Physiology 108(2):469-474.*

A dramatic stimulation in mitochondrial biogenesis during the very early stages of leaf development was observed in young wheat plants (Triticum aestivum cv Hereward) grown in elevated CO2 (650 mu L L(-1)). An almost 3-fold increase in the number of mitochondria was observed in the very young leaf cells at the base of the first leaf of a 7-d-old wheat plant. In the same cells large increases in the accumulation of a mitochondrial chaperonin protein and the mitochondrial 2-oxoglutarate dehydrogenase complex and pyruvate dehydrogenase complex were detected by immunolabeling. Furthermore, the basal segment also shows a large increase in the rate of radiolabeling of diphosphatidylglycerol, a lipid confined to the inner mitochondrial membrane. This dramatic response in very young leaf cells to elevated CO2 suggests that the numerous documented positive effects of elevated CO2 on wheat leaf development are initiated as early as 12 h postmitosis.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LOCALIZATION, PHOTOSYNTHESIS, RESPIRATION

2008

Robertson, G.P. 1999. Effect on the biosphere of elevated atmospheric CO2. *Science 285(5435):1852.*

2009

Robinson, C.H., A. Michelsen, J.A. Lee, S.J. Whitehead, T.V. Callaghan, M.C. Press, and S. Jonasson. 1997. Elevated atmospheric CO2 affects decomposition of Festuca vivipara (L) Sm litter and roots in experiments simulating environmental change in two contrasting arctic ecosystems. *Global Change Biology 3(1):37-49.*

Mass loss, together with nitrogen and carbon loss, from above- ground material and roots of Festuca vivipara were followed for 13 months in a high Arctic polar semidesert and a low Arctic tree-line dwarf shrub heath. Festuca vivipara for the study was obtained from plants cultivated at two different CO2 concentrations (350 and 500 mu L L(-1)) in controlled environment chambers in the UK. Each of the four resource types (shoots or roots from plants grown in elevated or ambient CO2 concentrations) was subsequently placed in an experiment simulating aspects of environmental change in each Arctic ecosystem. Air, litter and soil temperatures were increased using open-topped polythene tents at both sites, and a 58% increase in summer precipitation was simulated at the high Arctic site. Mass loss was greatest at the low Arctic site, and from the shoot material, rather than the roots. Shoots grown under an elevated CO2 concentration decomposed more slowly at the high Arctic site, and more quickly at the low Arctic one, than shoots grown at ambient CO2. After 13 months, greater amounts of C and N remained in above-ground litter from plants grown under elevated, rather than ambient, CO2 at the polar semi-desert site, although lower amounts of C remained in elevated CO2 litter at the low Arctic ecosystem. In the high Arctic, roots grown in the 500 mu L L(-1) CO2 concentration decomposed significantly more slowly than below-ground material derived from the ambient CO2 chambers. Elevated CO2 concentrations significantly increased the initial C:N ratio, % soluble carbohydrates and alpha-cellulose content, and significantly decreased the initial N content, of the above- ground material compared to that derived from the ambient treatment. Initially, the C:N ratio and percentage N were similar in both sets of roots derived from the two different CO2 treatments, but soluble carbohydrate and or-cellulose concentrations were higher, and percentage lignin lower, in the elevated CO2 treatments. The tent treatments significantly retarded shoot decomposition in both ecosystems, probably because of lower litter bag moisture contents, although the additional precipitation treatment had no effect on mass loss from the above-ground material. The results suggest that neither additional summer precipitation (up to 58%), nor soil temperature increase of 1 degrees C, which may occur by the end of the next century as an effect of a predicted 4 degrees C rise in air temperature, had an appreciable effect on root decomposition in the short term in a high Arctic soil. However, at the low Arctic site, greater root decomposition, and a lower pool of root N remaining, were observed where soil temperature was increased by 2 degrees C in response to a 4 degrees C rise in air temperature. These results suggest that decomposition below-ground in this ecosystem would increase as an effect of predicted climate change. These data also show that there is a difference in the initial results of decomposition processes between the two Arctic ecosystems in response to simulated environmental change.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, FOREST, GRASS, LEAF LITTER, MINERALIZATION, NITROGEN, QUALITY, SOILS, TUNDRA

2010

Robinson, D., and J.P. Conroy. 1999. A possible plant-mediated feedback between elevated CO2, denitrification and the enhanced greenhouse effect. *Soil Biology and Biochemistry 31(1):43-53.*

Natural abundances (delta) of N-15 were used to detect effects of elevated atmospheric CO2 concentration ([CO2]) and soil wetness on soil N transformations in the presence or absence of plants. An elevated [CO2] of 1000 mu l l(-1) reduced water use by the perennial C-4 grass Panicum coloratum and stimulated root and whole-plant growth. Soil remained wetter between infrequent irrigations than in soil supporting P. coloratum grown in an ambient [CO2] (350 mu l l(-1)). The delta(15)N value of soil nitrate increased from -2.4 to + 9.6 parts per thousand as nitrate was depleted from the soil, but remained unchanged in unplanted soil. The change in delta(15)N of soil nitrate was greatest in frequently watered soil regardless of [CO2], and in infrequently watered soil only in elevated [CO2]. It was least in the infrequently watered, ambient [CO2] treatment. Isotope mass balances and N-15/N-14 fractionation theory identified denitrification as the most probable cause of this effect, through the effect of elevated [CO2] on soil wetness. Nitrification, nitrogen assimilation, leaching or ammonia volatilisation were unlikely causes. The data suggest a positive, plant-induced effect of elevated atmospheric [CO2] on denitrification. The possibility exists, therefore, for a positive feedback between elevated atmospheric [CO2], a greater soil-to-atmosphere N2O flux and an exacerbation of the enhanced greenhouse effect.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, GRASSLAND, ISOTOPE FRACTIONATION, N-15, NATURAL ABUNDANCE, NITRIFICATION, NITROGEN, SOIL, WATER-USE

2011

Robinson, M.F., J. Heath, and T.A. Mansfield. 1998. Disturbances in stomatal behaviour caused by air pollutants. *Journal of Experimental Botany 49:461-469.*

Many atmospheric pollutants, even when present at relatively low concentrations, may interfere with the control of stomatal aperture, and they thus have the potential to upset the water balance of the leaf or the whole plant. Although at high concentrations pollutants such as SO2 and O-3 usually cause stomatal closure, at low concentrations stomatal conductance is often increased. As well as creating a risk of loss of control of water relations, this is likely to increase the dose of the pollutant entering the mesophyll. It is, however, difficult to generalize about the nature of the physiological disturbances caused by pollutants because of variation in the responses between plants. In some cases the effects may be peculiar to one, or just a few, species. Two mechanisms underlying the interference with stomatal control have recently been identified, one involving O-3 and the other CO2. In Aster tripolium (sea aster) stomata in detached epidermal strips close as the external Na+ concentration is increased, and it has been proposed that this phenomenon is involved in the regulation of salt loading of shoot tissues. Ozone has been shown to have the capacity to interfere with Na+-induced stomatal closure, and the possibility that it therefore disrupts an aspect of salinity tolerance in this species is worthy of further research. Elevated CO2, on the other hand, has been found to interfere with the control of water relations of beech (Fagus sylvatica): for a given degree of drought, stomatal conductance and rates of soil water depletion were significantly higher in elevated CO2 than in ambient air. It is normally assumed that atmospheric CO2-enrichment will lead to increased plant productivity and improved water economy, while also providing some protection against other atmospheric pollutants through partial stomatal closure. However, the response of beech indicates that in some species there may also be detrimental effects of CO2-enrichment on plant-water relations.

KEYWORDS: ABIES L KARST, ABSCISIC- ACID, ASTER-TRIPOLIUM L, CARBON DIOXIDE, CYTOSOLIC-FREE CALCIUM, GUARD-CELLS, PLANTAGO-MAJOR L, PLASMA-MEMBRANE, SULFUR-DIOXIDE, VICIA-FABA L

2012

Rochefort, L., and F.A. Bazzaz. 1992. Growth-response to elevated CO2 in seedlings of 4 cooccurring birch species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22(11):1583-1587.*

Seedlings of four birch species were examined to evaluate the presence and extent of phylogenetic constraints on the response of species to global CO2 change. The species differ in their habitat preferences and their successional status. Seedlings were grown for 3 months at near ambient (380 muL L-1) and double (690 muL L-1) CO2 concentrations in glasshouses. We found the following: (i) yellow birch (Betula alleghaniensis Britton) was the only species whose survival differed among CO2 treatments. Survival was slightly increased by elevated CO2. (ii) All growth parameters considered in all four species were significantly stimulated by enriched CO2 Conditions, but the magnitude of response was different among species. The most shade-intolerant, fast-growing species (grey birch; Betula populifolia Marsh.) took greater advantage of the elevated CO2 resource than the more shade-tolerant, later successional species (e.g., yellow birch). (iii) Patterns of allocation, shoot architecture, and leaf nitrogen content were affected differently by CO2 concentrations for the different species. (iv) The presence and identity of a neighbor did not influence the magnitude or pattern of response to CO2 in birches of a given community. Our results suggest that congeneric species might be more similar in their response to global CO2 in comparison to unrelated species of the same ecosystem that had been studied by others, despite the fact that these closely related birch species differ in their habitat preferences and successional status.

KEYWORDS: ENRICHMENT, FOREST, LIQUIDAMBAR-STYRACIFLUA, NITROGEN, PINUS-TAEDA SEEDLINGS, PLANT, TREES

2013

Roden, J.S., and M.C. Ball. 1996. The effect of elevated [CO2] on growth and photosynthesis of two eucalyptus species exposed to high temperatures and water deficits. *Plant Physiology 111(3):909-919.*

Two species of eucalyptus (Eucalyptus macrorhyncha and Eucalyptus rossii) were grown for 8 weeks in either ambient (350 mu L L(-1)) or elevated (700 mu L L(-1)) CO2 concentrations, either well watered or without water additions, and subjected to a daily, 3-h high-temperature (45 degrees C, maximum) and high-light (1250 mu mol photons m(-2) s(-1), maximum) stress period. Water-stressed seedlings of E. macrorhyncha had higher leaf water potentials when grown in elevated [CO2]. Growth analysis indicated that increased [CO2] may allow eucalyptus species to perform better during conditions of low soil moisture. A down-regulation of photosynthetic capacity was observed for seedlings grown in elevated [CO2] when well watered but not when water stressed. Well-watered seedlings grown in elevated [CO2] had lower quantum efficiencies as measured by chlorophyll fluorescence (the ratio of variable to maximal chlorophyll fluorescence [F- v/F-m]) than seedlings grown in ambient [CO2] during the high- temperature stress period. However, no significant differences in F-v/F-m were observed between CO2 treatments when water was withheld. The reductions in dark-adapted F-v/F-m for plants grown in elevated [CO2] were not well correlated with increased xanthophyll cycle photoprotection. However, reductions in the F-v/F-m were correlated with increased levels of nonstructural carbohydrates. The reduction in quantum efficiencies for plants grown in elevated [CO2] is discussed in the context of feedback inhibition of electron transport associated with starch accumulation and variation in sink strength.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, DROUGHT, ELECTRON-TRANSPORT, LEAVES, LIGHT, PHOTOSYSTEM, SEEDLINGS, STRESS

2014

Roden, J.S., and M.C. Ball. 1996. Growth and photosynthesis of two eucalypt species during high temperature stress under ambient and elevated [CO2]. *Global Change Biology 2(2):115-128.*

Two species of eucalypt (Eucalyptus macrorhyncha and E. rossii) were grown under conditions of high temperatures (45 degrees C, maximum) and high light (1500 mu mol m(-2) s(-1), maximum) at either ambient (350 mu L L(-1)) or elevated (700 mu L L(-1)) CO2 concentrations for 8 weeks. The growth enhancement, in terms of total dry weight, was 41% and 103% for E. macrorhyncha and E. rossii, respectively, when grown in elevated [CO2]. A reduction in specific leaf area and increased concentrations of non-structural carbohydrates were observed for leaves grown in elevated [CO2]. Plants grown in elevated [CO2] had an overall increase in photosynthetic CO2 assimilation rate of 27%; however, when measured at the same CO2 concentration a down- regulation of photosynthesis was evident especially for E. macrorhyncha. During the midday period when temperatures and irradiances were maximal, photosynthetic efficiency as measured by chlorophyll fluorescence (F-v/F-m) was lower in E. macrorhyncha than in E. rossii. Furthermore, F-v/F-m was lower in leaves of E. macrorhyncha grown under elevated than under ambient [CO]. These reductions in F-v/F-m were accompanied by increases in both photochemical (q(p)) and nonphotochemical quenching (q(N) and NPQ), and by increases in the concentrations of xanthophyll cycle pigments with an increased

proportion of the total xanthophyll cycle pool comprising of antheraxanthin and zeaxanthin, Thus, increased atmospheric [CO2] may enhance photoinhibition when environmental stresses such as high temperatures limit the capacity of a plant to respond with growth to elevated [CO2].

KEYWORDS: CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, COTTON PLANTS, ELECTRON-TRANSPORT, LIGHT, MECHANISM, PHOTOINHIBITION, QUANTUM YIELD, RESPONSES, SEEDLINGS

2015

Roden, J.S., J.J.G. Egerton, and M.C. Ball. 1999. Effect of elevated [CO2] on photosynthesis and growth of snow gum (Eucalyptus pauciflora) seedlings during winter and spring. *Australian Journal of Plant Physiology 26(1):37-46.*

Snow gum (Eucalyptus pauciflora Sieb. ex Spreng.) seedlings were grown from autumn through spring in open top chambers located in a pasture naturally subject to freezing temperatures in either ambient or elevated (350 mu L L-1 above ambient) CO2 concentrations. Sustained reduction in quantum efficiency, as measured by chlorophyll fluorescence (F-v/F-m), in over- wintering leaves may be related to seasonal down-regulation of photosynthesis, combined with cumulative effects of freeze- induced damage to the photosynthetic apparatus, with the effect being greater in leaves grown under elevated [CO2]. Down-regulation of photosynthesis apparently occurred in response to seasonal limitations to growth which were not overcome by elevation of [CO2] despite temperatures being favorable for photosynthesis during most of the photoperiod. Elevated [CO2] had no effect on growth of over-wintering seedlings, but enhanced growth in spring when minimum temperatures rose consistently above freezing. As there were no effects of elevated [CO2] on allocation, the stimulation of growth in spring was attributable to increase in net assimilation rates. Thus seasonal differences in photoinhibition were consistent with seasonal differences in the capacity for growth, with plants grown under elevated [CO2] having to dissipate more excess excitation energy over-winter.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CLIMATE, COLD-INDUCED PHOTOINHIBITION, ELECTRON-TRANSPORT, LEAVES, LOW-TEMPERATURE, PERFORMANCE, QUANTUM YIELD, SCOTS PINE, WATER-STRESS

2016

Roden, J.S., D.J. Wiggins, and M.C. Ball. 1997. Photosynthesis and growth of two rain forest species in simulated gaps under elevated CO2. *Ecology 78(2):385-393.*

Two species common to the temperate rain forests of New South Wales, Australia (Doryphora sassafras and Acmena smithii) were grown for 2 wk in either ambient (350 mu L/L) or elevated (700 mu L/L) CO2 concentrations and low light (30 mu mol photons . m(-2). s(-1)) after which the seedlings were exposed for over 9 wk to a midday 2-h highlight period (1250 mu mol photons . m(- 2). s(-1), maximum) to simulate a tree fall gap. For both species, plants grown in elevated CO2 had greater biomass than plants grown in ambient CO2. However, relative increases in biomass were greater in Acmena, which is an early-successional species, than Doryphora, which is a late-successional species. Doryphora sassafras also had greater reductions in photosynthetic efficiency, as measured by chlorophyll fluorescence techniques (F-v/F-m) upon exposure to the high- light treatment than Acmena. Recovery in quantum efficiencies over time was observed for Doryphora, implying physiological acclimation to the new light environment. Plants grown in elevated CO2 had lower values of F-v/F-m than plants grown in ambient CO2, but these differences between CO2 treatments were only significant for the late-successional Doryphora. Although exposure to the simulated tree fall gap dramatically increased the conversion of pigments of the xanthophyll cycle, as well as increased the total pool size of xanthophyll cycle pigments relative to total chlorophyll concentration, there were no differences in either parameter between CO2 treatments. Leaves of Doryphora and those seedlings grown in elevated CO2 had greater starch concentrations than Acmena and those seedlings grown in ambient CO2, respectively. The reduction in quantum efficiencies for plants grown in elevated CO2 and exposed to a simulated tree fall gap is discussed in the context of the importance of gap phase regeneration for species in rain forest ecosystems and the potential effects of global change on those processes.

KEYWORDS: ACCLIMATION, ALOCASIA-MACRORRHIZA, DIVERSITY, ELECTRON-TRANSPORT, LIGHT, PHOTOINHIBITION, RESPONSES, SEEDLINGS, TOLERANT, TREES

2017

Roderick, M.L., S.L. Berry, and I.R. Noble. 1999. The relationship between leaf composition and morphology at elevated CO2 concentrations. *New Phytologist 143(1):63-72.*

The composition and morphology of leaves exposed to elevated [CO2] usually change so that the leaf nitrogen (N) per unit dry mass decreases and the leaf dry mass per unit area increases. However, at ambient [CO2], leaves with a high leaf dry mass per unit area usually have low leaf hi per unit dry mass. Whether the changes in leaf properties induced by elevated [CO2] follow the same overall pattern as that at ambient [CO2] has not previously been addressed. Here we address this issue by using leaf measurements made at ambient [CO2] to develop an empirical model of the composition and morphology of leaves. Predictions from that model are then compared with a global database of leaf measurements made at ambient [CO2]. Those predictions are also compared with measurements showing the impact of elevated [CO2]. In the empirical model both the leaf dry mass and liquid mass per unit area are positively correlated with leaf thickness, whereas the mass of C per unit dry mass and the mass of N per unit liquid mass are constant. Consequently, both the N:C ratio and the surface area:volume ratio of leaves are positively correlated with the liquid content. Predictions from that model were consistent with measurements of leaf properties made at ambient [CO2] from around the world. The changes induced by elevated [CO2] follow the same overall trajectory. It is concluded that elevated [CO2] enhances the rate at which dry matter is accumulated but the overall trajectory of leaf development is conserved.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GRADIENT, GROWTH, INSECT HERBIVORY, LEAVES, NITROGEN, PHOTOSYNTHETIC CAPACITY, RAIN-FOREST, RESPONSES

2018

Rodriguez, D., M. Van Oijen, and A.H.M.C. Schapendonk. 1999. LINGRA-CC: a sink-source model to simulate the impact of climate change and management on grassland productivity. *New Phytologist 144(2):359-368.*

A simulation model for the prediction of grassland (Lolium perenne) productivity under conditions of climate change is described and validated for grass growing in the Wageningen Rhizolab, Wageningen, The Netherlands. In this work the model was used to study the impact of different management strategies on the productivity of grassland under present and increased atmospheric CO2 concentrations. In LINGRA-CC simulated key processes are light utilization, leaf formation, leaf elongation, tillering and carbon partitioning. The daily growth rate is determined by the minimum of a sink and a source term. As in a previous model (LINGRA), the potential growth of the sink depends on the mean daily temperature, and can be modified by the effects of the availability of assimilates on tillering. The growth of roots is calculated

from the amount of carbohydrates the shoot is unable to utilize when the number or activity of the sinks is small (overflow hypothesis). The main difference between LINGRA and LINGRA-CC is the way the source of assimilates for growth is calculated. Assimilate production depends on intercepted radiation, and a photosynthetic light- use efficiency (LUE) calculated as a function of CO2, temperature, light intensity and the Rubisco concentration of upper leaves. Other differences are that in LINGRA-CC, the specific shoot area for new growth depends on the level of reserves. Data from two independent experiments with L, perenne swards, grown in enclosures at two levels of CO2 during 1994 and 1995, were used to calibrate and validate the model, respectively. The model predicted well the observed amounts of harvested biomass, and the dynamics of the leaf area index, tiller number and specific shoot area. LINGRA-CC was used to stud? the effects of different combinations of cutting interval and cutting height on biomass production, at ambient (350 mu mol mol(-1) CO2) and double (700 mu mol mol(-1) CO2) CO2 conditions. Under both ambient and doubled CO2, maximum biomass was produced with cuttings of leaf area index >1, and at cutting intervals of 20 and 17 d for ambient and increased CO2 environments, respectively. Under high CO2 conditions the curling interval for maximum yield was 15% shorter than at ambient CO2. However, the gain in harvested biomass obtained by reducing the cutting interval by 3 d under high CO2 conditions was negligible.

KEYWORDS: ELEVATED CO2, GROWTH, INCREASED CO2 CONCENTRATION, LOLIUM-PERENNE, PHOTOSYNTHESIS, PRAIRIE GRASS, RYEGRASS, TEMPERATURE, USE EFFICIENCY, WHEAT

2019

Rogers, A., B.U. Fischer, J. Bryant, M. Frehner, H. Blum, C.A. Raines, and S.P. Long. 1998. Acclimation of photosynthesis to elevated CO2 under low- nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO2 enrichment. *Plant Physiology 118(2):683-689.*

Acclimation of photosynthesis to elevated CO2 has previously been shown to be more pronounced when N supply is poor. Is this a direct effect of N or an indirect effect of N by limiting the development of sinks for photoassimilate? This question was tested by growing a perennial ryegrass (Lolium perenne) in the field under elevated (60 Pa) and current (36 Pa) partial pressures of CO2 (pCO2) at low and high levels of N fertilization. Cutting of this herbage crop at 4- to 8-week intervals removed about 80% of the canopy, therefore decreasing the ratio of photosynthetic area to sinks for photoassimilate. Leaf photosynthesis, in vivo carboxylation capacity, carbohydrate, N, ribulose-1,5-bisphosphate carboxylase/oxygenase, sedoheptulose-l,7-bisphosphatase, and chloroplastic fructose-1,6-bisphosphatase levels were determined for mature lamina during two consecutive summers. just before the cut, when the canopy was relatively large, growth at elevated pCO(2) and low N resulted in significant decreases in carboxylation capacity and the amount of ribulose- 1,5-bisphosphate carboxylase/oxygenase protein. In high N there were no significant decreases in carboxylation capacity or proteins, but chloroplastic fructose-1,6-bisphosphatase protein levels increased significantly. Elevated pCO(2) resulted in a marked and significant increase in leaf carbohydrate content at low N, but had no effect at high N. This acclimation at low N was absent after the harvest, when the canopy size was small. These results suggest that acclimation under low N is caused by limitation of sink development rather than being a direct effect of N supply on photosynthesis.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PLANTS, RISING ATMOSPHERIC CO2, SOURCE-SINK RELATIONS, TRANSCRIPT LEVELS, TRIFOLIUM-REPENS L

2020

Rogers, G.S., P.W. Gras, I.L. Batey, P.J. Milham, L. Payne, and J.P. Conroy. 1998. The influence of atmospheric CO2 concentration on the protein, starch and mixing properties of wheat flour. *Australian Journal of Plant Physiology 25(3):387-393.*

Wheat (Triticum aestivum L.) cultivars Hartog and Rosella were grown at CO2 concentrations of 280 mu L L-1 (representing the pre-industrial CO2 concentration), 350 mu L L-1 (ambient) and 900 mu L L-1 tan extreme projection of atmospheric CO2 concentration). The plants were grown in naturally lit glasshouses in 7 L pots containing soil to which basal nutrients had been added and the pH adjusted to 6.5, Hartog yielded 2.4 g of grain per plant when grown at 280 mu L CO2 L- 1. This yield was increased by 38% and 75% at CO2 concentrations of 350 mu L L-1 and 900 mu L L-1 respectively. These changes were due to increases in both grain number and individual grain weight as the level of CO2 was raised. The yield of Rosella was unaffected by altering the CO2 concentration. Increasing the CO2 concentration reduced grain protein concentration of cv. Hartog from 17.4% at 280 mu L CO2 L-1 to 16.5% and 16% at CO2 concentrations of 350 mu L L-1 and 900 mu L L-1 respectively. The grain protein concentration of cv. Rosella was reduced from 10.7% to 10.2% by increasing the CO2 concentration from 280 mu L L-1 to 350 mu L L-1; however, an additional increase in the CO2 concentration to 900 mu L L-1 had no effect on grain protein concentration. In Hartog flour, the highest proportion of polymeric protein in the flour (7.7%) occurred at 280 mu L CO2 L-1. This was reduced to 6.3% at 350 mu L CO2 L-1 but then increased again to 7.0% at 900 mu L CO2 L-1. These changes in concentration of polymeric protein were correlated (r(2)=0.58) with changes in mixing properties, The mixing time required to produce optimum dough strength was greatest at 900 mu L CO2 L-1 (181 s), then 141 s and 151 s at 350 mu L CO2 L-1 and 280 mu L CO2 L-1 respectively. These changes in mixing time could not be explained by changes in grain protein concentration. The proportion of 'B' starch granules (<10 mu m diameter) increased from 25% of total weight of starch at 280 mu L CO2 L-1 to 30% at CO2 concentrations 350 and 900 mu L L-1. There were generally no effects of CO2 concentration on dough mixing properties or starch granule size distribution for Rosella.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GENOTYPES, GRAIN QUALITY, NITROGEN, NUTRITION, STRESS, TEMPERATURE, WINTER-WHEAT, YIELD

2021

Rogers, G.S., P.J. Milham, M. Gillings, and J.P. Conroy. 1996. Sink strength may be the key to growth and nitrogen responses in N-deficient wheat at elevated CO2. *Australian Journal of Plant Physiology 23(3):253-264.*

The influence of elevated CO2 (350, 550 and 900 mu L L(-1)) and N supplies ranging from deficient to excess (0-133 mg N kg(-1) soil week(-1)) on the leaf N concentration and shoot growth of wheat (Triticum aestivum L.), cultivar Hartog, was investigated. Shoot growth was 30 % greater at 550 mu L L(-1) compared to ambient CO2 at all levels of N supply. When the CO2 concentration was increased to 900 mu L L(-1), there was no increase in shoot growth at low N supply but it more than doubled at high N supply (67 mg N kg(-1) soil week(-1)). Growth effects were closely matched by changes in sink development, suggesting that sink strength, mediated through N supply controlled the shoot growth response to elevated CO2 The shoot N concentration was lower at each level of CO2 enrichment and the greatest effect (30% reduction) occurred at 900 mu L CO2 L(-1), 33 mg N kg(-1) soil week(-1). The effect of high CO2 on shoot N concentration diminished as N supply increased and, at the highest N addition rate, there was only a 7% reduction. Changes in foliar N concentration due to CO2 enrichment were closely correlated with lower soluble protein concentration, accounting for 58 % of the total leaf N reduction. Ribulose- 1,5-

bisphosphate carboxylase/oxygenase (Rubisco) levels we:re also reduced at high CO2 and N was allocated away from Rubisco and into other soluble proteins at high CO2 when N supply was low. Nonstructural carbohydrate concentration (dry weight basis) was greatest at 900 mu L CO2 L(-1) and low N supply and may have reduced Rubisco concentration via a feed-back response. Critical foliar N concentrations (N concentration at 90 % of maximum shoot growth) were reduced from 43 mg g(-1) at ambient CO2 to 39 and 38 mg g(-1) at 550 and 900 mu L CO2 L(- 1), respectively. Elevated CO2, at N supplies of 0-17 mg N kg(- 1) soil week(-1), reduced flour protein concentration by 9-13 %.

KEYWORDS: CARBAMYLATION, CARBON DIOXIDE, ENRICHMENT, NUTRITION, PHOTOSYNTHESIS, PLANTS, PROTEIN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STRESS, TOBACCO

2022

Rogers, G.S., P.J. Milham, M.C. Thibaud, and J.P. Conroy. 1996. Interactions between rising CO2 concentration and nitrogen supply in cotton .1. Growth and leaf nitrogen concentration. *Australian Journal of Plant Physiology 23(2):119-125.*

The influence of sink development on the response of shoot growth in cotton (Gossypium hirsutum L. cv. Siokra BT1-4) was investigated by growing plants at three levels of CO2 concentration: 350 (ambient), 550 and 900 mu L L(-1) and six levels of nitrogen (N) supply ranging from deficient to excess (0-133 mg N kg(-1) soil week(-1)). Changes in leaf N concentration were also investigated. At 59 days after sowing, there was an average 63% increase in shoot growth at 550 mu L CO2 L(-1) compared with ambient CO2-grown plants, with no significant growth increase at 900 mu L CO2 L(-1) and, this response was closely matched by sink development (flower number and stem weight). Low N supply restricted the responses of both sink development and shoot growth to high CO2. At elevated CO2, leaf N concentration was reduced by an average 27% at low to adequate N supply. The high CO2-induced reduction in leaf N concentration, however, disappeared when the N supply was increased to a high level of 133 mg N kg(-1) soil week(-1). These CO2 effects on leaf N concentration were smaller when N was expressed per unit leaf area, apparently due to a combination of the effects of elevated CO2 or high N supply reducing specific leaf area and, to an N uptake limitation at low to moderate levels of N supply. The critical foliar N concentrations (leaf N concentration at 90% of maximum shoot growth) were reduced from 42 to 38 and 36 mg g(-1) when CO2 concentrations were increased from 350 to 550 and 900 mu L L(- 1) respectively, indicating that changes in fertiliser management may be required under changing CO2 concentrations.

KEYWORDS: C-3 PLANTS, CARBOHYDRATE, CARBON, LEAVES, PHOTOSYNTHESIS, WHEAT

2023

Rogers, G.S., L. Payne, P. Milham, and J. Conroy. 1993. Nitrogen and phosphorus requirements of cotton and wheat under changing atmospheric co2 concentrations. *Plant and Soil 156:231-234.*

The influence of increasing atmospheric CO2 on shoot growth, leaf nitrogen and phosphorus concentrations and carbohydrate composition was investigated in cotton and wheat. Shoot dry weight of both species was generally higher at elevated CO2, especially at high rates of available soil N and P. Critical leaf N concentration was reduced but critical P concentration was increased in both species at high CO2.

KEYWORDS: CARBOHYDRATE, ENRICHMENT, GROWTH, METABOLISM, STRESS

2024

Rogers, H.H., and R.C. Dahlman. 1993. Crop responses to co2 enrichment. *Vegetatio 104:117-131.*

Carbon dioxide is rising in the global atmosphere, and this increase can be expected to continue into the foreseeable future. This compound is an essential input to plant life. Crop function is affected across all scales from biochemical to agro-ecosystem. An array of methods (leaf cuvettes, field chambers, free-air release systems) are available for experimental studies of CO2 effects. Carbon dioxide enrichment of the air in which crops grow usually stimulates their growth and yield. Plant structure and physiology are markedly altered. Interactions between CO2 and environmental factors that influence plants are known to occur. Implications for crop growth and yield are enormous. Strategies designed to assure future global food security must include a consideration of crop responses to elevated atmospheric CO2. Future research should include these targets: search for new insights, development of new techniques, construction of better simulation models, investigation of belowground processes, study of interactions, and the elimination of major discrepancies in the scientific knowledge base.

KEYWORDS: AGRICULTURAL PRODUCTIVITY, AIR-TEMPERATURE, CLIMATIC CHANGE, ELEVATED CARBON-DIOXIDE, INCREASING ATMOSPHERIC CO2, MINERAL NUTRITION, PLANT GROWTH, SOYBEAN CANOPY, WATER-USE EFFICIENCY, WINTER-WHEAT

2025

Rogers, H.H., C.M. Peterson, J.N. McCrimmon, and J.D. Cure. 1992. Response of plant-roots to elevated atmospheric carbon-dioxide. *Plant, Cell and Environment 15(6):749-752.*

Plant root response to atmospheric CO2 enrichment can be great. Results from this controlled environment investigation demonstrate substantial effects on root system architecture, micromorphology and physiology. The most pronounced effects were an increase in root length (110%) and root dry weight (143%). Root diameter, stele diameter, cortex width, root/shoot and root weight ratios all increased; root numbers did not increase. The long-term implications for belowground processes could be enormous.

KEYWORDS: GROWTH

2026

Rogers, H.H., S.A. Prior, and E.G. Oneill. 1992. Cotton root and rhizosphere responses to free-air co-2 enrichment. *Critical Reviews in Plant Sciences 11(2-3):251-263.*

KEYWORDS: AGRICULTURE, CARBON DIOXIDE, CO2, GROWTH, INFECTION, SOIL, WHEAT, YIELD

2027

Rogers, H.H., S.A. Prior, and G.B. Runion. 1993. Effects of elevated atmospheric co2 on soybean and sorghum root-growth. *Plant Physiology 102(1):173.*

2028

Rogers, H.H., S.A. Prior, G.B. Runion, and R.J. Mitchell. 1996. Root to shoot ratio of crops as influenced by CO2. *Plant and Soil 187(2):229-248.*

Crops of tomorrow are likely to grow under higher levels of atmospheric CO2. Fundamental crop growth processes will be affected and chief

among these is carbon allocation. The root to shoot ratio (R:S, defined as dry weight of root biomass divided by dry weight of shoot biomass) depends upon the partitioning of photosynthate which may be influenced by environmental stimuli. Exposure of plant canopies to high CO2 concentration often stimulates the growth of both shoot and root, but the question remains whether elevated atmospheric CO2 concentration will affect roots and shoots of crop plants proportionally. Since elevated CO2 can induce changes in plant structure and function, there may be differences in allocation between root and shoot, at least under some conditions. The effect of elevated atmospheric CO2 on carbon allocation has yet to be fully elucidated, especially in the context of changing resource availability, Herein we review root to shoot allocation as affected by increased concentrations of atmospheric CO2 and provide recommendations for further research. Review of the available literature shows substantial variation in R:S response for crop plants. In many cases (59.5%) R:S increased, in a very few (3.0%) remained unchanged, and in others (37.5%) decreased. The explanation for these differences probably resides in crop type, resource supply, and other experimental factors. Efforts to understand allocation under CO2 enrichment will add substantially to the global change response data base.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, ELEVATED CO2, MECHANICAL IMPEDANCE, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, WATER-STRESS, YIELD RESPONSES

2029

Rogers, H.H., G.B. Runion, and S.V. Krupa. 1994. Plant-responses to atmospheric co2 enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution 83(1-2):155-189.*

Empirical records provide incontestable evidence of global changes; foremost among these changes is the rising concentration of CO2 in the earth's atmosphere. Plant growth is nearly always stimulated by elevation of CO2. Photosynthesis increases, more plant biomass accumulates per unit of water consumed, and economic yield is enhanced The profitable use of supplemental CO2 over years of greenhouse practice points to the value of CO2 for plant production. Plant responses to CO2 are known to interact with other environmental factors, e.g. light, temperature, soil water, and humidity. Important stresses including drought, temperature, salinity, and air pollution have been shown to be ameliorated when CO2 levels are elevated In the agricultural context, the growing season has been shortened for some crops with the application of more CO2; less water use has generally, but not always, been observed and is under further study; experimental studies have shown that economic yield for most crops increases by about 33% for a doubling of ambient CO2 concentration. However, there are some reports of negligible or negative effects. Plant species respond differently to CO2 enrichment, therefore, clearly competitive shifts within natural communities could occur. Though of less importance in managed agro-ecosystems, competition between crops and weeds could also be altered. Tissue composition can vary as CO2 increases (e.g. higher C:N ratios) leading to changes in herbivory, but tests of crop products (consumed by man) from elevated CO2 experiments have generally not revealed significant differences in their quality. However, any CO2-induced change in plant chemical or structural make-up could lead to alterations in the plant's interaction with any number of environmental factors- physicochemical or biological. Host-pathogen relationships, defense against physical stressors, and the capacity to overcome resource shortages could be impacted by rises in CO2. Root biomass is known to increase but, with few exceptions, detailed studies of root growth and function are lacking. Potential enhancement of root growth could translate into greater rhizodeposition, which, in turn, could lead to shifts in the rhizosphere itself. Some of the direct effects of CO2 on vegetation have been reasonably well-studied, but for others work has been inadequate. Among these neglected areas are plant roots and the rhizosphere. Therefore, experiments on root and rhizosphere response in plants grown in CO2-enriched atmospheres will be reviewed and, where possible, collectively integrated To this will be added data which have recently been collected by us. Having looked at the available data base, we will offer a series of hypotheses which we consider as priority targets for future research.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, FIELD-GROWN SOYBEANS, KUDZU PUERARIA-LOBATA, LONG-TERM EXPOSURE, OPEN-TOP CHAMBERS, PINUS-TAEDA SEEDLINGS, SOUR ORANGE TREES, SOYBEAN GLYCINE-MAX, WATER-USE EFFICIENCY

2030

Rolland, C., V. Petitcolas, and R. Michalet. 1998. Changes in radial tree growth for Picea abies, Larix decidua, Pinus cembra and Pinus uncinata near the alpine timberline since 1750. *Trees-Structure and Function 13(1):40-53.*

Changes in radial growth of the four coniferous species growing in the French Alps near the upper treeline are investigated. Thirty-seven populations of Norway spruce [Picea abies (L.) Karat.], European larch (Larix decidua Mill.), Swiss stone pine (Pinus cembra L.) and mountain pine (Pinus uncinata Mill. ex Mirb.) were sampled by taking 1320 cores and analysing treering widths. Sites were chosen in various climatic conditions (macroclimate and aspect) and on two kinds of bedrock in order to take into account the ecological be haviour of these species. Belledonne, Moyenne-Tarentaise: Haute-Maurienne and Brianconnais areas were sampled along increasing gradients of summer aridity and winter continentality. The calculation of time series after removing the age trend brings strong evidence for an increase in radial growth during the two last centuries, but with different stages and fluctuations for each species. This growth trend is significantly enhanced since 1860 for the spruce, and since 1920 for the two pine species. Furthermore, it also appears on Larix decidua with the same pattern despite periodical growth reduction due to attacks of the larch bud moth (Zeiraphera diniana Gn.). The analysis of ring-widths at a given cambial age reveals that this enhanced phenomenon is observed especially during the tree's early years (25-75 years). The analysis of four regional climatic series, and three longer series of temperature (in farther single sites) reveals synchronous decadal fluctuations and an evident secular increase in minimum temperatures (especially in January and from July to October), that may be involved in tree-growth enhancement. Thermic amplitudes are significantly reduced during the whole growing period, what is more pronounced in Belledonne, the most oceanic region. Long term growth changes are well described by stepwise regression models, especially for the pine species. These models involved both a linear trend (CO2 concentration or N-deposition) and low frequency of Turin monthly temperatures. However, they show different patterns than those observed from response functions at a yearly scale.

KEYWORDS: CARBON DIOXIDE, CO2, FOREST, FRANCE, HIGH-ELEVATION SITES, RESPONSES, SPRUCE MODEL-ECOSYSTEMS, TEMPERATURE, TRENDS

2031

Ronen-Tarazi, M., D.J. Bonfil, D. Schatz, and A. Kaplan. 1998. Cyanobacterial mutants impaired in bicarbonate uptake isolated with the aid of an inactivation library. *Canadian Journal of Botany-Revue Canadienne De Botanique 76(6):942-948.*

An inactivation library consisting of genomic fragments ligated within a modified bluescript vector was used to isolate several new high CO2 requiring mutants of Synechococcus PCC7942. The mutants described hen were impaired in the ability to accumulate C-i internally when supplied with HCO3-. The relevant genomic regions bearing novel genes

involved in the ability to transport and to accumulate Ci within the cells and thus to grow under low-CO2 conditions are presented. Some of the mutants were also impaired in ability to adjust to an elevated pH in their medium. We show that the use of inactivation libraries enabled cloning of genes encoding membrane-located proteins; we point to mutations introduced by the single cross-recombination events resulting in the formation of some of these mutants. Possible artifacts that may result in incorrect identification of genes, the inactivation of which could have led to the observed phenotype, are discussed.

KEYWORDS: CO2 CONCENTRATING MECHANISM, INORGANIC CARBON, PCC6803, PHOTOSYNTHESIS, REGION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SP STRAIN PCC-7942, SUBUNIT, SYNECHOCOCCUS, TRANSPORT

2032

Ronentarazi, M., J. Liemanhurwitz, C. Gabay, M.I. Orus, and A. Kaplan. 1995. The genomic region of rbcls in synechococcus sp pcc-7942 contains genes involved in the ability to crow under low co2 concentration and in chlorophyll biosynthesis. *Plant Physiology 108(4):1461-1469.*

Several genes involved in the ability of Synechococcus sp. PCC 7942 to grow under different CO, concentrations were mapped in the genomic region of rbcLS (the operon encoding the large and small subunits of ribulose-1,5-bisphosphate carboxylase/oxygenase). Insertion of a cartridge encoding kanamycin resistance within open reading frame (ORF) 78, designated ccmJ, located 7 kb upstream of rbcLS, resulted in a kanamycin-resistant, high-CO2-requiring mutant, M3, which does not contain normal carboxysomes. ccmJ shows significant homology to csoS1 encoding a carboxysomal shell polypeptide in Thiobacillus neopolitanus. Analysis of the polypeptide pattern of a carboxysome-enriched fraction indicated several differences between the wild type and the mutant. The amount of the ribulose-1,5-bisphosphate carboxylase/oxygenase subunits was considerably smaller in the carboxysomal fraction of the mutant when compared to the wild type. On the basis of the sequence analyses, ORF286 and ORF466, located downstream of ccmJ were identified as chit and chlN, respectively, which are involved in chlorophyll biosynthesis in the dark.

KEYWORDS: ANACYSTIS-NIDULANS, CARBOXYLASE-OXYGENASE, CARBOXYSOME, CYANOBACTERIA, INORGANIC-CARBON UPTAKE, MECHANISM, MICROALGAE, PCC7942, TRANSPORT

2033

Rosenqvist, E., H. Pedersen, and C.O. Ottosen. 1996. Effects of elevated CO2 on growth and photosynthesis in dendranthema grandiflorum. *Plant Physiology 111(2):355.*

2034

Rosenthal, Y. 1998. Variations of ecosystem gas exchange in the rain forest mesocosm at Biosphere 2 in response to elevated CO2. *Global Change Biology 4(5):539-547.*

The effects of elevated CO2 on tropical ecosystems were studied in the artificial rain forest mesocosm at Biosphere 2, a large- scale and ecologically diverse experimental facility located in Oracle, Arizona. The ecosystem responses were assessed by comparing the whole-system net gas exchange (NEE) upon changing CO2 levels from 900 to 450 ppmV. The day-NEE was significantly higher in the elevated CO2 treatment. In both experiments, the NEE rates were similar to values observed in natural analogue systems. Variations in night-NEE, reflecting both soil CO2 efflux and plants respiration, covaried with temperature but showed no clear correlation with atmospheric CO2 levels. After correcting for changes in CO2 efflux we show that the rain forest net photosynthesis increased in response to increasing atmospheric CO2. The photosynthetic enhancement was expressed in higher quantum yields, maximum assimilation rates and radiation use efficiency. The results suggest that photosynthesis in large tropical trees is CO2 sensitive, at least following short exposures of days to weeks. Taken at face value, the data suggest that as a result of anthropogenic emissions of CO2, tropical rain forests may shift out of steady state, and become a carbon sink at least for short periods. However, a better understanding of the unique conditions and phenomena in Biosphere 2 is necessary before these results are broadly useful.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, MODEL

2035

Rosenthal, Y., B. Farnsworth, F.V.R. Romo, G.H. Lin, and B.D.V. Marino. 1999. High quality, continuous measurements of CO2 in Biosphere 2 to assess whole mesocosm carbon cycling. *Ecological Engineering 13(1-4):249-262.*

Accurate measurements of atmospheric CO2 concentrations are performed routinely in a variety of experimental settings including open fields and forests, leaf gas-exchange chambers, phytotrons and specialized growth chambers. However, the accurate monitoring of large scale structurally and biologically complex experimental systems, operating as materially closed systems, is not widely reported. Here we report the design elements, material specifications and other details for high precision monitoring of CO2 in Biosphere 2, a large scale ecologically diverse experimental facility located in Oracle, AZ. The results are used to illustrate how carbon balance in a temporarily isolated sub-system of the facility is used to assess carbon dynamics under different environmental conditions such as variable atmospheric CO2 levels, temperature, light, and soil moisture. The analytical system described here should be applicable for any settings in which continuous, high accuracy measurements of CO2 in a complex system are needed for quantitative research.

KEYWORDS: ACCLIMATION, ELEVATED CO2, FOREST, GAS-EXCHANGE

2036

Rosenzweig, C., and D. Hillel. 1993. Agriculture in a greenhouse world. *Research & Exploration 9(2):208-221.*

While agriculture in some temperate regions may benefit from global climate change, tropical and subtropical regions may suffer. Even where potential production will improve, the required adjustments may disrupt ecosystems and land-use patterns. Agricultural zones will shift toward high latitudes, while heat stress and increased droughts will reduce productivity in lower latitudes. On the positive side, higher CO2 may enhance photosynthesis and water-use efficiency. Future hazards include sea-level rise, insect infestation, and greater evaporation losses. Some agricultural activities augment the greenhouse effect by releasing CO2, CH4, and N2O. Understanding the potential impacts of climate change is a prerequisite to developing societal responses.

KEYWORDS: CLIMATE CHANGE

2037

Rosenzweig, C., J. Phillips, R. Goldberg, J. Carroll, and T. Hodges. 1996. Potential impacts of climate change on citrus and potato production in the US. *Agricultural Systems 52(4):455-479.*

Potential impacts of global climate change on fruit and vegetable yield

in the US were investigated through simulations of citrus and potato. Simulated treatments included combinations of three increased temperature regimes (+1.5, +2.5 and +5.0 degrees C), and estimates of the impact of three levels of atmospheric carbon dioxide (440, 530, and 600 ppm) in addition to control runs representing current climatic conditions. Adaptive planting dates of -28, -14, +14 and +28 days were included in the potato simulations for current and increased temperature regimes. Twenty-two sites were simulated for citrus yields and 12 sites for potato, using climate records from 1951 to 1980. Response surfaces were developed for all combinations of increased temperature and CO2. Results of citrus simulations without CO2-induced yield improvement indicate that production may shift slightly northward in the southern states, but yields may decline in southern Florida and Texas due to excessive heat during the winter. CO2 effects tended to counteract the decline in simulated citrus yields. Fall potato production under current management practices appears vulnerable to an increase in temperature in the northern states; increased CO2 and changes in planting date were estimated to have minimal compensating impacts on simulated potato yields.

KEYWORDS: DARK RESPIRATION, DRY-MATTER PRODUCTION, ELEVATION, GROWTH, HEAT TOLERANCE, HIGH-TEMPERATURE, SOLANUM TUBEROSUM L, SOUR ORANGE TREES, WATER DEFICIT, YIELD PERFORMANCE

2038

Rosenzweig, C., and F.N. Tubiello. 1996. Effects of changes in minimum and maximum temperature on wheat yields in the central US - A simulation study. *Agricultural and Forest Meteorology 80(2-4):215-230.*

Recent observations and general circulation models indicate that future temperature changes linked to global warming might be characterized by a marked asymmetry between daytime maxima and nighttime minima. We investigate the importance of such a pattern in determining future wheat (Triticum aestivum) yields in the Central United States by using a dynamic crop growth model, CERES-Wheat, modified to include physiological effects of temperature and CO2 on canopy photosynthesis. Simulations are run at four sites spanning a north-south transect of the Central US; four mean temperatures increases (1-4 degrees C) are applied to baseline daily climate data (1951-1980). The effects of two different scenarios of temperature change (minimum and maximum temperatures equally raised; minima increased three times as much as maxima in agreement with recent observations) are analyzed under both current (330 ppm) and elevated (550 ppm) CO2 concentrations. The main mechanisms controlling the simulated wheat responses are direct and indirect temperature effects on wheat phenological development. Negative effects of temperature on simulated wheat yields are reduced when minima increase more than maxima. Yield changes are consistently negative under temperature change and current CO2 concentration, while they range from positive to negative under temperature change and elevated CO2 concentration. Responses vary across the transect, with larger negative effects occurring at the southernmost site.

KEYWORDS: CERES, CLIMATE CHANGE, CROP RESPONSE, MODEL

2039

Ross, D.J., S. Saggar, K.R. Tate, C.W. Feltham, and P.C.D. Newton. 1996. Elevated CO2 effects on carbon and nitrogen cycling in grass/clover turves of a Psammaquent soil. *Plant and Soil 182(2):185-198.*

Effects of elevated CO2 (525 and 700 mu L L(-1)), and a control (350 mu L L(-1) CO2), on biochemical properties of a Mollic Psammaquent soil in a well-established pasture of C3 and C4 grasses and clover were investigated with continuously moist turves in growth chambers over four consecutive seasonal temperature regimes from spring to winter inclusive. After a further 'spring' period, half of the turves under 350 and 700 mu L L(-1) were subjected to 'summer' drying and were then re-wetted before a further 'autumn' period; the remaining turves were kept continuously moist throughout these additional three consecutive 'seasons'. The continuously moist turves were then pulse-labelled with C-14-CO2 to follow C pathways in the plant/soil system during 35 days. Growth rates of herbage during the first four 'seasons' averaged 4.6 g m(-2) day(-1) under 700 mu L L(-1) CO2 and were about 10% higher than under the other two treatments. Below-ground net productivity at the end of these 'seasons' averaged 465, 800 and 824 g m(-2) in the control, 525 and 700 mu L L(-1) treatments, respectively. In continuously moist soil, elevated CO2 had no overall effects on total, extractable or microbial C and N, or invertase activity, but resulted in increased CO2-C production from soil, and from added herbage during the initial stages of decomposition over 21 days; rates of root decomposition were unaffected. CO2 produced h(-1) mg(-1) microbial C was about 10% higher in the 700 mu L L(-1) CO2 treatment than in the other two treatments. Elevated CO2 had no clearly defined effects on N availability, or on the net N mineralization of added herbage. In the labelling experiment, relatively more C-14 in the plant/soil system occurred below ground under elevated CO2, with enhanced turnover of C-14 also being suggested. Drying increased levels of extractable C and organic-N, but decreased mineral-N concentrations; it had no effect on microbial C, but resulted in lowered microbial N in the control only. In soil that had been previously 'summer'-dried, CO2 production was again higher, but net N mineralization was lower, under elevated CO2 than in the control after 'autumn' pasture growth. Over the trial period of 422 days, elevated CO2 generally appears to have had a greater effect on soil C turnover than on soil C pools in this pasture ecosystem.

KEYWORDS: BIOCIDAL TREATMENTS, EXTRACTION METHOD, GRASS, LOLIUM-PERENNE, MICROBIAL BIOMASS, PASTURE TURVES, PLANTS, RHIZOSPHERE PH, SIMULATED SEASONAL-CHANGES, TEMPERATURE

2040

Ross, D.J., K.R. Tate, and P.C.D. Newton. 1995. Elevated co2 and temperature effects on soil carbon and nitrogen cycling in ryegrass/white clover turves of an endoaquept soil. *Plant and Soil 176(1):37-49.*

Effects of elevated CO2 (700 mu L L(-1)) and a control (350 mu L L(-1) CO2) on the productivity of a 3-year-old rye- grass/white clover pasture, and on soil biochemical properties, were investigated with turves of a Typic Endoaquept soil in growth chambers. Temperature treatments corresponding to average winter, spring, and summer conditions in the field were applied consecutively to all of the turves. An additional treatment, at 700 mu L L(-1) CO2 and a temperature 6 degrees C higher throughout than in the other treatments, was included. Under the same temperature conditions, overall herbage yields in the '700 mu L L(-1) CO2' treatment were ca. 7% greater than in the control at the end of the 'summer' period. Root mass (to ca 25 cm depth) in the '700 mu L L(-1) CO2' treatment was then about 50% greater than in the control, but in the '700 mu L L(- 1) CO2 + 6 degrees C' treatment it was 6% lower than in the control. Based on decomposition results, herbage from the '700 mu L L(-1) + 6 degrees C' treatment probably contained the highest proportion of readily decomposable components. Elevated CO2 had no consistent effect on soil total C and N, microbial C and N, or extractable C concentrations in any of the treatments. Under the same temperature conditions, it did, however, enhance soil respiration (CO2-C production) and invertase activity. The effects of elevated CO2 on rates of net N mineralization were less distinct, and the apparent availability of N for the sward was not affected. Under elevated CO2, soil in the higher-temperature treatment had a higher microbial C:N ratio; it also had a greater potential to degrade plant materials. Data interpretation was

complicated by soil spatial variability and the moderately high background levels of organic matter and biochemical properties that are typical of New Zealand pasture soils. More rapid cycling of C under CO2 enrichment is, nevertheless, indicated. Futher long- term experiments are required to determine the overall effect of elevated CO2 on the soil C balance.

KEYWORDS: ATMOSPHERIC CO2, BIOCIDAL TREATMENTS, CHLOROFORM, DECOMPOSITION, DIOXIDE, DIRECT EXTRACTION METHOD, FUMIGATION, MICROBIAL BIOMASS-C, MINERALIZATION, RESIDUES

2041

RossKarstens, G.S., G. Ebert, and P. Ludders. 1996. Diurnal time courses of CO2 gas exchange in closed and open gas systems for coffee (Coffea arabica L), pomegranate (Punica granatum L), citrus (Citrus limonia Osb), grape (Vitis vinifera L), and banana (Musa x paradisiaca L) in vitro plantlets under different environment conditions. *Journal of Applied Botany-Angewandte Botanik 70(3-4):155-162.*

Continuous measurements were made of CO2 gas exchange over a period of three days on ill vitro plantlets of coffee (Coffea arabica L.), pomegranate (Punica granatum L.), citrus (Citrus limonia Osb.), grape (Vitis vinifera L.), and banana (Musa x paradisiaca L.). The gas used for measurements contained CO2 concentrations of 350, 600, 1000 or 2000 mu l l(-1). Measurements in the closed system for coffee plantlets grown in medium containing different sucrose concentrations showed a strong decrease of the CO2 concentration in the cuvette atmosphere during the light period almost reaching the CO2 compensation point (70 mu l l(-1) CO2). During the dark period a continuous increase was observed. Measured in the open system diurnal time courses of in vitro pomegranate and citrus plantlets showed that CO2 assimilation rates were strongly influenced by light intensity and temperature. A positive balance of CO2 gas exchange was found for pomegranate plantlets only with light intensities beyond 100 mu mol m(-2) s(-1) photosynthetic photon flux density (PPFD). Citrus plantlets were independent of the sucrose concentration in the medium and showed a positive CO2 balance at 350 mu l l(-1) CO2 gas concentration. Banana plantlets revealed negative balances under all conditions examined.

KEYWORDS: CULTURE, ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHETIC CHARACTERISTICS, TOBACCO

2042

RossKarstens, G.S., G. Ebert, and P. Ludders. 1996. Influence of CO2 concentration, light intensity, and sucrose concentration on net photosynthesis of citrus plantlets during in vitro propagation. *Journal of Applied Botany-Angewandte Botanik 70(5-6):188-193.*

Light curves of the CO2 gas exchange of irt vitro plantlets of citrus (Citrus limonia Osb. (Rutaceae)) were measured continuously in an open system using different CO2 concentrations (350, 1000, and 2000 mu l l(-1) CO2). The plantlets were grown in media with sucrose concentrations from 0 to 5% under light intensities of 60, 100, and 260 mu mol m(- 2) l(-1). Before starting the measurements the plantlets were pretreated with 1000 mu l l(-1) CO2 for several weeks. Control plantlets were grown for the same period in gas tight vessels. CO2 concentration of the gas atmosphere inside the plant vessels had a stronger influence on CO2 gas exchange of citrus plantlets than sucrose concentration of the medium. Net photosynthesis of plantlets grown under various light intensities differed only little when using the same CO2 concentration for measurement as used for growing. After pretreatment with 1000 mu l l(-1) CO2 during growth, net photosynthesis of plantlets measured under 350 Cll l(-1) CO2 was higher compared to control plantlets.

KEYWORDS: ASPARAGUS, CARBON DIOXIDE, CULTURE, ENRICHMENT, GROWTH, INVITRO

2043

Roth, S.K., and R.L. Lindroth. 1994. Effects of co2-mediated changes in paper birch and white-pine chemistry on gypsy-moth performance. *Oecologia 98(2):133-138.*

We examined the effects of CO2-mediated changes in the foliar chemistry of paper birch (Betula papyrifera) and white pine (Pinus strobus) on performance of the gypsy moth (Lymantria dispar). Trees were grown under ambient or enriched CO2 conditions, and foliage was subjected to plant chemical assays and insect bioassays. Enriched CO2 atmospheres reduced foliar nitrogen levels and increased condensed tannin levels in birch but not in pine. Foliar carbohydrate concentrations were not markedly altered by CO2 environment. Gypsy moth performance was significantly affected by CO2 level, species, and the CO2 x species interaction. Under elevated CO2 conditions, growth was reduced for larvae fed birch, while development was prolonged for larvae fed pine. Although gypsy moths performed better overall on birch than pine, birch-fed larvae were influenced more by CO2-mediated changes in host quality.

KEYWORDS: CARBON NUTRIENT BALANCE, CHEMICAL DEFENSE, CO2, NITROGEN, PLANTS, PROTEIN, RESOURCE AVAILABILITY, TURNOVER

2044

Roth, S.K., and R.L. Lindroth. 1995. Elevated atmospheric co2 effects on phytochemistry, insect performance and insect parasitoid interactions. *Global Change Biology 1(3):173-182.*

This study was conducted to examine the effects of CO2-mediated changes in tree chemistry on the performance of the gypsy moth (Lymantria dispar L.) and the parasitoid Cotesia melanoscela (Ratz.). We used carbon-nutrient balance theory to develop hypotheses regarding changes in tree chemistry and the performance of both insects under elevated CO2. As predicted, levels of foliar nitrogen declined and concentrations of carbon-based compounds (e.g. starch and phenolics) increased under elevated CO2. Gypsy moth performance (e.g. growth, development) was altered by CO2-mediated changes in foliar chemistry, but the magnitude was small and varied across tree species. Larvae feeding on high CO2 aspen exhibited the largest reduction in performance, relative to larvae feeding on birch, oak, or maple. Parasitism by C. melanoscela significantly prolonged gypsy moth development and reduced growth rates. Overall, the effect of parasitism on gypsy moth performance did not differ between CO2 treatments. Altered gypsy moth performance on high CO2 foliage in turn affected parasitoid performance, but the response was variable: parasitoid mortality increased and adult female size declined slightly under high CO2, while development time and adult male size were unaffected. Our results suggest that CO2-induced changes in plant chemistry were buffered to the extent that effects on third trophic level interactions were weak to non-existent for the system examined in this study.

KEYWORDS: CARBON NUTRIENT BALANCE, DEFENSE, DIET, NITROGEN, PLANTS, PROTEIN, TREES

2045

Roth, S., R.L. Lindroth, J.C. Volin, and E.L. Kruger. 1998. Enriched atmospheric CO2 and defoliation: effects on tree chemistry and insect performance. *Global Change Biology 4(4):419-430.*

We examined the effects of CO2 and defoliation on tree chemistry and performance of the forest tent caterpillar, Malacosoma disstria. Quaking aspen (Populus tremuloides) and sugar maple (Acer saccharum) trees

were grown in open-top chambers under ambient or elevated concentrations of CO2. During the second year of growth, half of the trees were exposed to free-feeding forest tent caterpillars, while the remaining trees served as nondefoliated controls. Foliage was collected weekly for phytochemical analysis. Insect performance was evaluated on foliage from each of the treatments. At the sampling date coincident with insect bioassays, levels of foliar nitrogen and starch were lower and higher, respectively, in high CO2 foliage, and this trend persisted throughout the study. CO2-mediated increases in secondary compounds were observed for condensed tannins in aspen and gallotannins in maple. Defoliation reduced levels of water and nitrogen in aspen but had no effect on primary metabolites in maple. Similarly, defoliation induced accumulations of secondary compounds in aspen but not in maple. Larvae fed foliage from the enriched CO2 or defoliated treatments exhibited reduced growth and food processing efficiencies, relative to larvae on ambient CO2 or nondefoliated diets, but the patterns were host species-specific. Overall, CO2 and defoliation appeared to exert independent effects on foliar chemistry and forest tent caterpillar performance.

KEYWORDS: BIRCH, CARBON NUTRIENT BALANCE, COVARIANCE, FOLIAGE, HERBIVORE RESPONSES, INDUCTION, MOTH, NITROGEN, PHYTOCHEMISTRY, PLANTS

2046

Roth, S., E.P. McDonald, and R.L. Lindroth. 1997. Atmospheric CO2 and soil water availability: consequences for tree-insect interactions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 27(8):1281-1290.*

The consequences of elevated CO2 for interactions between trees and associated insects will be influenced by the availability of other plant resources. We investigated the effects of CO2 and water availability on phytochemistry of quaking aspen (Populus tremuloides Michx.) and sugar maple (Acer saccharum Marsh.) and the associated performance of the forest tent caterpillar (Malacosoma disstria Hbn.). Seedlings were grown under ambient or elevated CO2 concentrations and under well-watered or drought conditions. We measured rates of gas exchange and subjected foliage to phytochemical assays. Bioassays were conducted to quantify larval performance on foliage from the various treatments. In general, elevated CO2 increased photosynthetic rates and had no effect on stomatal conductance, while drought reduced both parameters. Foliar nitrogen levels declined and secondary metabolite concentrations increased under enriched CO2, but starch and sugar levels were unaffected. All phytochemicals measured, with the exception of simple sugars, declined or did not change in response to drought. CO2- and drought-mediated changes in phytochemistry reduced forest tent caterpillar growth and food processing efficiencies, but the patterns were host-species specific. This work demonstrates that CO2 effects on forest trees will be mediated by the availability of water and that the direction and magnitude of responses will depend on the tree species involved, which will, in turn, affect patterns of host use by herbivorous insects.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GAS-EXCHANGE, GROWTH, HERBIVORE INTERACTIONS, LEPIDOPTERA, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STRESS

2047

Rothschild, L.J. 1994. Elevated co2 - impact on diurnal patterns of photosynthesis in natural microbial ecosystems. *Life Sciences and Space Research XXV (3) 14(11):285-289.*

Algae, including blue-green algae (cyanobacteria), are the major source of fixed carbon in many aquatic ecosystems. Previous work has shown that photosynthetic carbon fixation is often enhanced in the presence of additional carbon dioxide (CO2). This study was undertaken to determine if this CO2 fertilization effect extended to microbial mats, and, if so, at what times during the day might the addition of CO2 affect carbon fixation. Four microbial mars from diverse environments were selected, including mars from a hypersaline pond (area 5, Exportadora de Sal, Mexico), the marine intertidal (Lyngbya, Laguna Ojo de Liebre, Mexico), an acidic hotspring (Cyanidium, Nymph Creek, Yellowstone National Park), and an acidic stream at ambient temperature (Zygogonium, Yellowstone National Park). Carbon fixation in the absence of additional CO2 essentially followed the rising and falling sunlight levels, except that during the middle of the day there was a short dip in carbon fixation rates. The addition of CO2 profoundly enhanced carbon fixation rates during the daylight hours, including during the midday dip. Therefore, it is unlikely that the midday dip was due to photoinhibition. Surprisingly, enhancement of carbon fixation was often greatest in the early morning or late afternoon, times when carbon fixation would be most likely to be light limited.

KEYWORDS: CARBON FIXATION, MARINE MACROALGAE, MAT, MODEL, OXYGENIC PHOTOSYNTHESIS

2048

Rotter, R., and S.C. Van de Geijn. 1999. Climate change effects on plant growth, crop yield and livestock. *Climatic Change 43(4):651-681.*

A review is given of the state of knowledge in the field of assessing climate change impacts on agricultural crops and livestock. Starting from the basic processes controlling plant growth and development, the possible impacts and interactions of climatic and other biophysical variables in different agro- environments are highlighted. Qualitative and quantitative estimations of shifts in biomass production and water relations, inter-plant competition and crop species adaptability are discussed. Special attention is given to the problems encountered when scaling up physiological responses at the leaf- and plant level to yield estimates at regional to global levels by using crop simulation models in combination with geo-referenced, agro-ecological databases. Some non-linear crop responses to environmental changes and their relations to adaptability and vulnerability of agro-ecosystems are discussed.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2 ENRICHMENT, B RADIATION, ELEVATED CARBON-DIOXIDE, GLOBAL ENVIRONMENT CHANGE, LEAF-AREA, RESPONSES, TEMPERATURE-GRADIENT CHAMBERS, WATER-USE, WINTER-WHEAT

2049

Rotzel, C., P.W. Leadley, and C. Korner. 1997. Non-destructive assessment of the effects of elevated CO2 on plant community structure in a calcareous grassland. *Acta Oecologica-International Journal of Ecology 18(3):231-239.*

Calcareous grassland was exposed to ambient or elevated CO2 using a Screen-Aided CO2 Control (SACC) system starting in March 1994. The effects of elevated CO2 on plant community structure were studied using the paint intercept method. Measurements were made in March 1994 prior to the start of CO2 exposure and again in June 1994 at peak plant biomass. There were no significant differences in the initial structure of the communities based on their assigned CO2 treatments in March. After 9 weeks of exposure of the community to elevated CO2, the total number of intercepts per plot was not significantly different between CO2 treatments; however, Carex flacca and Cirsium acaule had marginally significant ($P = 0.055$ and $P = 0.06$) increases in the % sward of the community at elevated CO2 (number of intercepts for a single species divided by the total number of intercepts for all species). Measurements of leaf extension in Carex flacca showed that at least part of the increase in % sward at elevated CO2 could be explained by

greater leaf length per plant (P = 0.02). These measurements and other experiments with calcareous grassland species and communities suggest that rising atmospheric CO2 concentrations will probably alter the structure of calcareous grassland communities.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, GROWTH

2050

Rouhier, H., G. Billes, L. Billes, and P. Bottner. 1996. Carbon fluxes in the rhizosphere of sweet chestnut seedlings (Castanea sativa) grown under two atmospheric CO2 concentrations: C-14 partitioning after pulse labelling. *Plant and Soil 180(1):101-111.*

Partitioning of C-14 was assessed in sweet chestnut seedlings (Castanea sativa Mill.) grown in ambient and elevated atmospheric [CO2] environments during two vegetative cycles. The seedlings were exposed to (CO2)-C-14 atmosphere in both high and low [CO2] environments for a 6-day pulse period under controlled laboratory conditions. Six days after exposure to (CO2)-C-14, the plants were harvested, their dry mass and the radioactivity were evaluated. C-14 concentration in plant tissues, root-soil system respiratory outputs and soil residues (rhizodeposition) were measured. Root production and rhizodeposition were increased in plants growing in elevated atmospheric [CO2]. When measuring total respiration, i.e. CO2 released from the root/soil system, it is difficult to separate CO2 originating from roots and that coming from the rhizospheric microflora. For this reason a model accounting for kinetics of exudate mineralization was used to estimate respiration of rhizospheric microflora and roots separately. Root activity (respiration and exudation) was increased at the higher atmospheric CO2 concentration. The proportion attributed to root respiration accounted for 70 to 90% of the total respiration. Microbial respiration was related to the amount of organic carbon available in the rhizosphere and showed a seasonal variation dependent upon the balance of root exudation and respiration. The increased carbon assimilated by plants grown under elevated atmospheric [CO2] stayed equally distributed between these increased root activities.

KEYWORDS: DIOXIDE, ELEVATED CO2, ENRICHMENT, MICROBIAL BIOMASS, NITROGEN, RESPIRATION, ROOT, SOIL, SPRING WHEAT, TURNOVER

2051

Rouhier, H., G. Billes, A. Elkohen, M. Mousseau, and P. Bottner. 1994. Effect of elevated co2 on carbon and nitrogen distribution within a tree (castanea-sativa mill) soil system. *Plant and Soil 162(2):281-292.*

Two-year-old sweet chestnut trees were grown outside in normal or double CO2 atmospheric concentration. In spring and in autumn of two growing seasons, a six day labelling pulse of C- 14 labelled CO2 was used to follow the carbon assimilation and distribution in the plant-soil system. Doubling atmospheric CO2 had a significant effect on the tree net carbon uptake. A large proportion of the additional C uptake was 'lost' through the root system. This suggests that increased C uptake under elevated CO2 conditions increases C cycling without necessarily increasing C storage in the plant. Total root derived material represented a significant amount of the 'extra-assimilated' carbon due to the CO2 treatment and was strongly correlated with the phenological stage of the tree. Increasing root rhizodeposition led to a stimulation of microbial activity, particularly near the end of the growing season. When plant rhizodeposition was expressed as a function of the root dry weight, the effect of increasing CO2 resulted in a higher root activity. The C to N ratios were significantly higher for trees grown under elevated CO2 except for the fine root compartment. An evaluation of the plant-soil system nitrogen dynamics showed, during the second season of CO2 treatment, a decrease of soil N mineralization rate and total N uptake for trees grown at elevated CO2 levels.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ENRICHMENT, GROWTH, PLANTS, QUERCUS-ALBA, RESPIRATION, RHIZOSPHERE, SEEDLINGS, TURNOVER

2052

Rouhier, H., and D.J. Read. 1998. Plant and fungal responses to elevated atmospheric carbon dioxide in mycorrhizal seedlings of Pinus sylvestris. *Environmental and Experimental Botany 40(3):237-246.*

The effects of elevated CO2 concentration upon the mycorrhizal relationships of Scots pine (Pinus sylvestris) seedlings were investigated. Plants were grown for 4 months with their shoots exposed to ambient (C-AMB = 360 mu l l(-1)) or elevated (C-ELEV = 700 mu l l(-1)) CO2 environments while their root systems, either colonised by the mycorrhizal fungi Paxillus involutus or Suillus bovinus, or left in the non-mycorrhizal condition, were maintained in sealed dishes. In one series of these plants the effects of C-ELEV upon the extent of mycorrhizal development and upon their growth and nutrition were determined, while another series were transferred from the dishes after 1 month, to transparent observation chambers before being returned to the two CO2 environments. In these chambers, the effects of C- ELEV upon development of the external mycelial systems of the two mycorrhizal fungi was determined by measuring the advance of the hyphal fronts of the mycorrhizal fungi across non- sterile peat from the colonised plants. The dry mass and number of mycorrhizal tips were significantly higher in C-ELEV than in the C-AMB condition in plants colonised by both fungi in the dishes. Yields of whole plants and of shoots were higher in the C-ELEV treatment whether or not they were grown in the mycorrhizal condition, but the greater yields were not associated in these sealed systems with enhanced nutrient gain. The dry mass of non-mycorrhizal plants was greater than that of those colonised by mycorrhizal fungi under elevated CO2. This is thought to be attributable to the energetic cost of production of the larger mycorrhizal systems in this treatment. The extent of development of the mycorrhizal mycelial systems of both fungi was greatly increased in C-ELEV relative to that in C-AMB environments. It is hypothesised that increased allocation of carbon to mycorrhizal root systems and their associated mycelia would provide the potential for enhancement of nutrient acquisition in open systems of greater fertility.

KEYWORDS: CO2, DYNAMICS, ECTOMYCORRHIZAL COLONIZATION, GROWTH, JUVENILE PONDEROSA PINE, MYCELIUM, NITROGEN, ROOTS, SOIL N

2053

Rouhier, H., and D.J. Read. 1998. The role of mycorrhiza in determining the response of Plantago lanceolata to CO2 enrichment. *New Phytologist 139(2):367-373.*

Plantago lanceolata L. was grown for 104 d with (M) or without (NM) arbuscular mycorrhizal colonization under conditions of ambient (C-AMB = 350 mu l l(-1)) and elevated (C-ELEV = 540 mu l l(-1)) CO2. Sequential harvests (H) were taken at 41 (H-1), 76 (H-2) and 104 d (H-3) to determine the time-course of mycorrhizal influence on the response of the plant to CO2 enrichment. Total yields of M plants were greater than those of NM from H-2 onwards. Plants in the M-ELEV treatment were significantly larger than those in the M-AMB at 104 d. There were significant but much smaller differences in yield between NMELEV and NMAMB. The differences in total yield arose through impact of C-ELEV on both shoots and roots. Total root length was greater in M-ELEV than in M-AMB only at H-3, but total length of mycorrhizal root was greater at H-2 and H-3. The percentages of root length colonized and that occupied by arbuscules and vesicles were greater in M-ELEV than in M-AMB at the last two harvests, indicating increased sequestration of carbon in internal fungal structures. Though extraradical

hyphal lengths were greater in M-ELEV than in M-AMB at H-2 and H-3, the differences were not significant. Phosphorus inflow and P content of M plants were higher than those of NM plants at H-2 and H-3, and were higher in M-ELEV than in M-AMB at H-3. ANOVA revealed no significant interactions between CO2 and mycorrhizal treatment. The results are discussed in relation to carbon sequestration in mycorrhizal systems and likely impacts of CO2 enrichment on P. lanceolata grown under field conditions. The importance of sequential harvesting for realistic determination of responses to CO2 is stressed.

KEYWORDS: BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, COMMUNITY, DIVERSITY, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO2, FUNGI, RHIZOSPHERE, ROOTS

2054

Rouhier, H., and D.J. Read. 1999. Plant and fungal responses to elevated atmospheric CO2 in mycorrhizal seedlings of Betula pendula. *Environmental and Experimental Botany 42(3):231-241.*

The effects of elevated CO2 concentrations upon carbon allocation in mycorrhizal (M) and non-mycorrhizal (NM) birch (Betula pendula) seedlings were investigated. M plants, colonised by the fungus Paxillus involutus, and NM plants, were exposed for 3 months to ambient (350 mu l 1(-1)) or elevated (700 mu l 1(-1)) CO2 environments. The assimilation and distribution of carbon within the different compartments of the plant-substrate-fungal system were investigated using radioactive carbon as a tracer. In addition, the impact of elevated CO2 upon extension growth of the ectomycorrhizal mycelium of the fungus was determined in transparent observation chambers. Yields of whole plants and of shoots were significantly decreased under elevated CO2 whether they were grown with or without their fungal symbionts. Neither the dry mass production of roots of mycorrhizal plants, nor the amount of carbon allocated to shoots, roots and mycorrhizal tips were affected by elevated CO2. While the number of mycorrhizal root tips was decreased with CO2 enrichment, their relative importance in the total root system was unchanged. There was a significant increase in the extent of development of the external mycelium under elevated CO2. A greater proportion of the radioactive carbon was allocated to the soil compartment under elevated CO2. This increase, probably arising through increased rhizodeposition, was greater in NM than M plants. The responses are discussed in terms of nutrient availability in the growth media and the possible role of increased carbon allocation to mycorrhizal mycelium in nature.

KEYWORDS: ALLOCATION, AVAILABILITY, CARBON-DIOXIDE CONCENTRATION, COLONIZATION, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, PINE SEEDLINGS, ROTH

2055

Roumet, C., M.P. Bel, L. Sonie, F. Jardon, and J. Roy. 1996. Growth response of grasses to elevated CO2: A physiological plurispecific analysis. *New Phytologist 133(4):595-603.*

The effect of CO2 enrichment on the growth and the economy of carbon and nitrogen of 11 Mediterranean grass species was investigated in order to determine the underlying causes of the large variation observed between species in their responses to elevated CO2. Plants were grown for 26-43 d (depending on species growth rate) under productive conditions at ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) concentrations of CO2. Plant parameters were determined at a common biomass of 0.15 g to determine the CO2 effect independent of ontogenic effects. The effect of CO2 on RGR ranged from -6.7 to 22.5%, with a mean stimulation of 10.3%. Averaged over the 11 species, the growth enhancement resulted from an increase in net assimilation rate per unit leaf d. wt. (NAR(w)) of 10.6%. This was the result of a large increase (18.7%) in NAR per unit leaf area (NAR(a)) associated with a 8.1% decrease in the specific leaf area (SLA). This decrease in SLA was due to a large increase of the non-structural carbohydrates. The increase in shoot activity was balanced by a 7.6% increase in the specific absorption rate of nitrogen (SAR). AS a result, plant nitrogen content was not modified. Leaf nitrogen productivity was significantly increased (14.9%). Shoot vs. root allocation of biomass and nitrogen was not modified. An analysis across the 11 species of the relationships between the stimulation of RGR and the alteration in RGR components showed a significant correlation only with increases in NAR(w), SAR and nitrogen productivity. The co- ordinated increase in these three parameters constitutes a single response syndrome, whose intensity is responsible for most of the species variability.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, C-3, CARBON DIOXIDE, ENRICHMENT, NITROGEN CONCENTRATION, NUTRITION, PHOTOSYNTHESIS, PLANT GROWTH, ROOT

2056

Roumet, C., G. Laurent, and J. Roy. 1999. Leaf structure and chemical composition as affected by elevated CO2: genotypic responses of two perennial grasses. *New Phytologist 143(1):73-81.*

Genotypic variability was studied in two Mediterranean grass species, Bromus erectus and Dactylis glomerata, with regard to the response to CO2 of leaf total non-structural carbohydrate concentration ([TNC](1f)), specific leaf area (SLA), and leaf carbon and nitrogen concentrations ([C](1f) and [N](1f), respectively). Fourteen genotypes of each species were grown together on intact soil monoliths at ambient and elevated CO2 concentrations (350 and 700 mu mol mol(-1), respectively). In both species, the most consistent effect of elevated CO2 was an increase in [TNC](1f) and a decrease in leaf nitrogen concentration when expressed either as total dry mass [N- m](1f), structural dry mass [N(m)st](1f) or leaf area [N- a](1f). The SLA decreased only in D, glomerata, due to an accumulation of total nonstructural carbohydrates and to an increase in leaf density. No genotypic variability was found for any variable in B. erectus, suggesting that genotypes responded in a similar way to elevated CO2. In D. glomerata, a genotypic variability was found only for [Cst], [N-m](1f), [N(m)st](1f) and [N-a](1f). Since [N-m](1f) is related to plant growth and is a strong determinant of plant-herbivore interactions, our results suggest evolutionary consequences of elevated CO2 through competitive interactions or herbivory.

KEYWORDS: ARABIDOPSIS-THALIANA, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSE, INTRASPECIFIC VARIATION, LITTER QUALITY, NITROGEN CONCENTRATION, NUTRIENT, PLANTAGO-MAJOR

2057

Roumet, C., and J. Roy. 1996. Prediction of the growth response to elevated CO2: A search for physiological criteria in closely related grass species. *New Phytologist 134(4):615-621.*

Using 11 closely related grass species, we tested the capacity of physiological criteria to predict the growth response to elevated CO2 and to categorize the species with regard to their CO2 response. A growth analysis was conducted under productive conditions both at ambient (350 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) CO2. The relative growth rate stimulation was regressed against each of the growth rate components measured at ambient CO2. Growth response to CO2 was positively correlated with specific leaf area (SLA, the leaf surface area per unit of leaf weight), leaf area ratio (the leaf area per unit of total plant dry weight) and negatively correlated with net assimilation rate and leaf nitrogen concentration, both per unit of leaf area. We suggest that SLA has a predominant role in these relationships. Different hypotheses are proposed and discussed in order to explain why species with low

SLA are less responsive to elevated CO2. Neither biomass allocation, relative growth rate, shoot or root specific activities per unit of mass, nor chemical composition were significantly correlated with growth response to CO2. The four predictive criteria mentioned above coherently differentiate the five wild annual species (higher SLA, stronger growth response to CO2) from the four wild perennials. The two perennial crop species, with the highest SLA, were more responsive than the wild species.

KEYWORDS: AMBIENT, ARABIDOPSIS-THALIANA, ASSIMILATION RATE, BIOMASS, CARBON-DIOXIDE ENRICHMENT, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS, TEMPERATURE

2058

Roussopoulos, D., A. Liakatas, and W.J. Whittington. 1998. Cotton responses to different light-temperature regimes. *Journal of Agricultural Science 131:277-283.*

A series of experiments investigating the interactive effects of light and temperature on vegetative growth, earliness, fruiting, yield and fibre properties in three cultivars of cotton, was undertaken in growth rooms. Two constant day/night temperature regimes with a difference of 4 degrees C (30/20 and 26/16.5 degrees C) were used throughout the growing season in combination with two light intensities (75 and 52.5 W m(-2)). The results showed that significant interactions occurred for most of the characters studied. Although the development of leaf area was mainly temperature-dependent, plants at harvest had a larger leaf area when high temperature was combined with low rather than with high light intensity. Leaf area was least in the low temperature-low light regime. However, the plants grown under the high temperature-low light combination weighed the least. Variations in the number of nodes and internode length were largely dependent on temperature rather than light. Light did, however, affect the numbers of branches, sympodia and monopodia. The first two of these were highest in the high light-high temperature regime and the third in the low light- low temperature regime. All other characters, except time to certain developmental stages and fibre length, were reduced at the lower light intensity. Variation in temperature modified the light effect and vice versa, in a character-dependent manner. More specifically, square and boil dry weights, as well as seed cotton yield per plant, were highest in high light combined with low temperature, where the most and heaviest bells were produced. But flower production was favoured by high light and high temperature, suggesting increased boil retention at low temperature, especially when combined with low light. Low temperature and high light also maximized lint percentage. Fibres were shortest in the high temperature-high light regime, where fibre strength, micronaire index and maturity ratio were at a maximum. However, the finest and the most uniform fibres were produced when high light was combined with low temperature. Cultivar differences were significant mainly in leaf area and dry matter production at flowering.

KEYWORDS: AIR CO-2 ENRICHMENT, CANOPY PHOTOSYNTHESIS, FIELD, GROWTH, LEAF CONDUCTANCE, LEAVES, RESPIRATION, TRANSPIRATION, WATER-STRESS

2059

Rowlandbamford, A.J., L.H. Allen, J.T. Baker, and K.J. Boote. 1990. Carbon-dioxide effects on carbohydrate status and partitioning in rice. *Journal of Experimental Botany 41(233):1601-1608.*

The atmospheric carbon dioxide (CO2) concentration has been rising and is predicted to reach double the present concentration sometime during the next century. The objective of this investigation was to determine the long-term effects of different CO2 concentrations on carbohydrate status and partitioning in rice (Oryza sativa L. cv. IR-30). Rice plants were grown season-long in outdoor, naturally sunlit, environmentally controlled growth chambers with CO2 concentrations of 160, 250, 330, 500, 660, and 900 mu-mol CO2 mol-1 air. In leaf blades, the priority between the partitioning of carbon into storage carbohydrates or into export changed with development stage and CO2 concentration. During vegetative growth, leaf sucrose and starch concentrations increased with increasing CO2 concentration but tended to level off above 500 mu-mol mol-1 CO2. Similarly, photosynthesis also increased with CO2 concentrations up to 500 mu-mol mol-1 and then reached a plateau at higher concentrations. The ratio of starch to sucrose concentration was positively correlated with the CO2 concentration. At maturity, increasing CO2 concentration resulted in an increase in total non-structural carbohydrate (TNC) concentration in leaf blades, leaf sheaths and culms. Carbohydrates that were stored in vegetative plant parts before heading made a smaller contribution to grain dry weight at CO2 concentrations below 330 mu-mol mol-1 than for treatments at concentrations above ambient. Increasing CO2 concentration had no effect on the carbohydrate concentration in the grain at maturity.

KEYWORDS: CO2, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANTS, STARCH, YIELD

2060

Rowlandbamford, A.J., J.T. Baker, L.H. Allen, and G. Bowes. 1991. Acclimation of rice to changing atmospheric carbon-dioxide concentration. *Plant, Cell and Environment 14(6):577-583.*

The effects were studied of season-long (75 and 88 d) exposure of rice (Oryza sativa L. cv. IR-30) to a range of atmospheric CO2 concentrations in outdoor, computer-controlled, environment chambers under natural solar radiation. The CO2 concentrations were maintained at 160, 250, 330, 500, 660 and 900-mu-mol mol-1 air. Photosynthesis increased with increasing growth CO2 concentrations up to 500-mu-mol mol-1, but levelled off at higher CO2 values. Specific leaf area also increased significantly with increasing CO2. Although leaf dry weight and leaf area index increased, the overall response was not statistically significant. Leaf nitrogen content dropped slightly with elevated CO2, but the response was not statistically significant. The specific activity of ribulose bisphosphate carboxylase/oxygenase (rubisco) declined significantly over the CO2 concentration range 160 to 900-mu- mol mol-1. When expressed on a leaf area basis, rubisco activity decreased by 66%. This was accompanied by a 32% decrease in the amount of rubisco protein as a fraction of the total soluble leaf protein, and by 60% on a leaf area basis. For leaves in the dark, the total rubisco activity (CO2/Mg2+- activated) was reduced by more than 60%. This indicates that rice accumulated an inhibitor in the dark, probably 2-carboxyarabinitol 1-phosphate (CA-1-P). However, the inhibitor did not seem to be involved in the acclimation response. The degree of carbamylation of the rubisco enzyme was unchanged by the CO2 growth regime, except at 900-mu-mol mol-1 where it was reduced by 24%. The acclimation of rice to different atmospheric CO2 conditions involved the modulation of both the activity and amount of rubisco protein in the leaf.

KEYWORDS: ACTIVATION, ENRICHMENT, GROWTH, HIGH CO2, INHIBITOR, LIGHT, MONOECIOUS CUCUMBERS, PHOTOSYNTHESIS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOYBEAN LEAVES

2061

RowlandBamford, A.J., J.T. Baker, L.H. Allen, and G. Bowes. 1996. Interactions of CO2 enrichment and temperature on carbohydrate accumulation and partitioning in rice. *Environmental and Experimental Botany 36(1):111-124.*

The objective of this study was to determine the long-term effects of CO2 concentration and temperature on carbohydrate partitioning and

status in rice (Oryza sativa L. cv. IR-30). The plants were grown season-long in sunlit, controlled- environment chambers with CO2 concentrations of 330 or 660 mu mol mol(-1), and daytime air temperatures of 28, 34 or 40 degrees C. In leaf blades, the priority between partitioning of carbon into storage or into export changed with CO2 concentration and temperature. Leaf sucrose concentration increased with CO2 enrichment at all temperature regimes. Over the season, elevated CO2 resulted in an increase in total non- structural carbohydrate (TNC) concentration in leaf blades, leaf sheaths and culms at all temperature treatments. Elevated CO2 had no effect on carbohydrate concentration in the grain at maturity, however, grain TNC concentration was significantly lowered by increasing temperature. Under the highest temperature regime, the plants in the 330 mu mol mol(-1) CO2 treatment died during stem extension while the CO2 enriched plants survived but produced sterile panicles. The results suggest that CO2-enriched plants could survive and maintain carbohydrate production rates at higher temperatures than the non-enriched plants; however, the optimum temperature for TNC accumulation was 28 degrees C at both CO2 concentrations.

KEYWORDS: AIR- TEMPERATURE, CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, GROWTH, LEAVES, MODEL, OCEAN, RESPONSES

2062

Rozema, J. 1993. Plant-responses to atmospheric carbon-dioxide enrichment - interactions with some soil and atmospheric conditions. *Vegetatio 104:173-190.*

In general, C3 plant species are more responsive to atmospheric carbon dioxide (CO2) enrichment than C4-plants. Increased relative growth rate at elevated CO2 primarily relates to increased Net Assimilation Rate (NAR), and enhancement of net photosynthesis and reduced photorespiration. Transpiration and stomatal conductance decrease with elevated CO2, water use efficiency and shoot water potential increase, particularly in plants grown at high soil salinity. Leaf area per plant and leaf area per leaf may increase in an early growth stage with increased CO2, after a period of time Leaf Area Ratio (LAR) and Specific Leaf Area (SLA) generally decrease. Starch may accumulate with time in leaves grown at elevated CO2, Plants grown under salt stress with increased (dark) respiration as a sink for photosynthates, may not show such acclimation to increased atmospheric CO2 levels. Plant growth may be stimulated by atmospheric carbon dioxide enrichment and reduced by enhanced UV-B radiation but the limited data available on the effect of combined elevated CO2 and ultraviolet B (280-320 nm) (UV-B) radiation allow no general conclusion. CO2-induced increase of growth rate can be markedly modified at elevated UV-B radiation. Plant responses to elevated atmospheric CO2 and other environmental factors such as soil salinity and UV-B tend to be species-specific, because plant species differ in sensitivity to salinity and UV-B radiation, as well as to other environmental stress factors (drought, nutrient deficiency). Therefore, the effects of joint elevated atmospheric CO2 and increased soil salinity or elevated CO2 and enhanced UV-B to plants are physiologically complex.

KEYWORDS: AIR- TEMPERATURE, B RADIATION, CO2-ENRICHMENT, DIFFERENT IRRADIANCES, ELEVATED CO2, ESTUARINE MARSH, GROWTH, PHOTOSYNTHESIS, STRESS, WATER RELATIONS

2063

Rozema, J., F. Dorel, R. Janissen, G. Lenssen, R. Broekman, W. Arp, and B.G. Drake. 1991. Effect of elevated atmospheric CO2 on growth, photosynthesis and water relations of salt-marsh grass species. *Aquatic Botany 39(1-2):45-55.*

The C3 grass species Scirpus maritimus L. and Puccinellia maritima (Huds.) Parl., and the C4 grass species Spartina anglica C.E. Hubbard and Spartina patens (Ait.) Muhl. were grown at ambient (340 p.p.m. CO2) and elevated (580 p.p.m. CO2) atmospheric CO2 concentration, at low (10 mM NaCl) and high salinity (250 mM NaCl) under aerated and anaerobic conditions in the culture solution. The relative growth rate of both the C3 grass species was enhanced with atmospheric CO2 enrichment, no such increase was found in the C4 grass species. High salinity reduced growth of the C3 species tested, but this relative growth reduction was not prevented by elevated CO2 concentration. The growth increase at elevated CO2 of Scirpus maritimus and Puccinellia maritima is greater under aerated than under anaerobic solution conditions. Water-use efficiency of all species was increased by elevated CO2. In the case of Scirpus (C3), this increase was caused by increased net photosynthesis, for Spartina patens (C4) photosynthesis was not increased, but transpiration was reduced. The water potential of the shoot was less negative under conditions of CO2 enrichment, in particular at increased salinity (250 mM NaCl).

KEYWORDS: C-4 PLANTS, CARBON DIOXIDE, ENRICHMENT, ESTUARINE MARSH, NITROGEN, PLANT GROWTH, TEMPERATURE

2064

Rozema, J., G.M. Lenssen, J.W.M. vandeStaaij, M. Tosserams, A.J. Visser, and R.A. Broekman. 1997. Effects of UV-B radiation on terrestrial plants and ecosystems: Interaction with CO2 enrichment. *Plant Ecology 128(1-2):182-191.*

UV-B radiation is just one of the environmental factors, that affect plant growth. It is now widely accepted that realistic assessment of plant responses to enhanced UV-B should be performed at sufficiently high Photosynthetically Active Radiation (PAR), preferably under field conditions. This will often imply, that responses of plants to enhanced UV-B in the field will be assessed under simultaneous water shortage, nutrient deficiency and variation of temperature. Since atmospheric CO2 enrichment, global warming and increasing UV-B radiation represent components of global climatic change, interactions of UV-B with CO2 enrichment and temperature are particularly relevant. Only few relevant UV-B x CO2 interaction studies have been published. Most of these studies refer to greenhouse experiments. We report a significant CO2 x UV-B interaction for the total plant dry weight and root dry weight of the C-3-grass Elymus athericus. At elevated CO2 (720 mu mol mol(-1)), plant growth was much less reduced by enhanced UV-B than at ambient atmospheric CO2 although there were significant (positive) CO2 effects and (negative) UV-B effects on plant growth. Most other CO2 x UV-B studies do not report significant interactions on total plant biomass. This lack of CO2 x UV-B interactions may result from the fact that primary metabolic targets for CO2 and UVB are different. UV-B and CO2 may differentially affect plant morphogenetic parameters: biomass allocation, branching, flowering, leaf thickness, emergence and senescence. Such more subtle interactions between CO2 and UV-B need careful and long term experimentation to be detected. In the case of no significant CO2 x UV-B interactions, combined CO2 and UV-B effects will be additive. Plants differ in their response to CO2 and UV-B, they respond in general positively to elevated CO2 and negatively to enhanced UV-B. Moreover, plant species differ in their responsiveness to CO2 and UV-B. Therefore, even in case of additive CO2 and UV-B effects, plant competitive relationships may change markedly under current climatic change with simultaneous enhanced atmospheric CO2 and solar UV-B radiation.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ENHANCEMENT, GROWTH, PHOTOSYNTHESIS, RICE

2065

Rudorff, B.F.T., C.L. Mulchi, C.S.T. Daughtry, and E.H. Lee. 1996.

Growth, radiation use efficiency, and canopy reflectance of wheat and corn grown under elevated ozone and carbon dioxide atmospheres. *Remote Sensing of Environment 55(2):163-173.*

Estimates of increases in future agricultural production in response to increases in carbon dioxide (CO2) concentrations in the atmosphere are often based on the beneficial physiological effect of CO2 enrichment on plant growth, especially in C-3 plants. However, these estimates fail to consider the negative impact of ozone (O-3) air pollution on crop production. Increases in tropospheric concentrations of both gases, CO2 and O-3, have been observed over the past century, and both are predicted to continue to increase at even higher rates in the near future to levels when they may have a significant impact on agricultural production. Field studies with wheat (Triticum aestivum L.) in 1991 and 1992, and corn (Zea mays L.) in 1991 were conducted using open-top chambers to mimic atmospheric concentrations of CO2 (similar to 500 mu L(-1) CO2) and O-3 (similar to 40 nL L(-1) O-3 above ambient air [O-3] during 7h day(-1) 5 days week(-1)) that are predicted to occur at the Earth surface during the first half of the 21st century. Wheat and corn (C-3 vs. C-4) produced clearly different responses to CO2 enrichment, but similar responses to O-3 exposure. In wheat, O-3 exposure led to reduced grain yield, biomass, and radiation use efficiency (RUE, phytomass production per unit of energy received); in both years; but reduction in accumulated absorbed photosynthetically active radiation (AAPAR) was observed only in 1991. Conversely, CO2 enrichment produced greater grain yield, dry biomass, and RUE. With CO2 enrichment, the O-3-induced stress to wheat plants was apparently ameliorated since responses were equivalent to the control group (low O-3 and ambient CO2) for all variables. In contrast, corn demonstrated no benefit to CO2 enrichment for measured variables, and corn grain yield was the only parameter negatively influenced by O-3 exposure that is attributed to O- 3-induced damage during the flowering process. Additionally, no treatment differences were observed for leaf area index (LAI) as determined nondestructively using the LICOR LAI-2000 Plant Canopy Analyzer. Also, treatment differences for normalized difference vegetation index (ND) were only observed for wheat plants from the high-O-3 and ambient-CO2 treatment, at some growing stages. Otherwise, ND were not helpful for identifying damage due to O-3 fumigation or benefits due to CO2 enrichment. Significant interactive effects of CO2 vs. O-3 were observed only for wheat grain yield in 1991 ($p < 0.10$), indicated that the detrimental effect of O-3 air pollution was more than overcome under the CO2-enriched environment.

KEYWORDS: BIOMASS, CHAMBERS, CO2, FIELD, O-3, RESPONSES, VEGETATION

2066

Rudorff, B.F.T., C.L. Mulchi, P. Fenny, E.H. Lee, and R. Rowland. 1996. Wheat grain quality under enhanced tropospheric CO2 and O-3 concentrations. *Journal of Environmental Quality 25(6):1384-1388.*

It is expected that the progressive increase of tropospheric trace gases such as CO2 and O-3 will have a significant impact on agricultural production. The single and combined effects of CO2 enrichment and tropospheric O-3 on grain quality characteristics in soft red winter wheat (Triticum aestivum L.) were examined in held studies using 3 m in diam. open-top chambers. Wheat cultivars 'Massey' (1991) and 'Saluda' (1992) were exposed to two CO2 concentrations (350 vs. 590 mu mol CO2 mol(-1); 12 h d(-1)) in combination with two O-3 regimes (charcoal-filtered air vs. ambient air + 40 +/- 20 nmol O-3 mol(-1), 7 h d(-1) Monday to Friday) from late March until maturity in June. Grain quality characteristics investigated included: test weight, milling and baking quality, flour yield, protein content, softness equivalent, alkaline water retention capacity, and cookie diameter. In general, exposure of plants to either elevated CO2 or weekly chronic O-3 episodes caused only small changes in grain quality. Milling and baking quality score were not significantly changed in response to treatments in both years. Flour yield was increased by elevated CO2 but this increase was counteracted when elevated CO2 was combined with chronic O-3 exposure. Flour protein contents were increased by enhanced O-3 exposure and reduced by elevated CO2. Softness equivalent was increased by 2.4% by enhanced O-3 exposure but unaffected by O-3 under elevated CO2. Although the single effect of either CO2 enrichment or chronic O-3 exposure had some impact on grain quality characteristic, it was noted that the combined effect of these gases was minor. It is Likely that the concomitant increase of CO2 and O-3 in the troposphere will have no significant impact on wheat grain quality.

KEYWORDS: FIELD, OPEN-TOP CHAMBERS, OZONE, RED WINTER-WHEAT, RESPONSES, VEGETATION, YIELD

2067

Rudorff, B.F.T., C.L. Mulchi, E.H. Lee, R. Rowland, and R. Pausch. 1996. Effects of enhanced O-3 and CO2 enrichment on plant characteristics in wheat and corn. *Environmental Pollution 94(1):53-60.*

The effects of CO2 enrichment and O-3 induced stress on wheat (Triticum aestivum L.) and corn (Zea mays L.) were studied in field experiments using open-top chambers to simulate the atmospheric concentrations of these two gases that are predicted to occur during the coming century. The experiments were conducted at Beltsville, MD, during 1991 (wheat and corn) and 1992 (wheat). Crops were grown under char coal filtered (CF) air or ambient air +40 nl liter(-1) O-3 (7 h per day, 5 days per week) having ambient CO2 concentration (350 mu l liter(-1) CO2) or +150 mu l liter(-1) CO2 (12 h per day). Averaged over O-3 treatments, the CO2-enriched environment had a positive effect on wheat grain yield (26% in 1991 and 15% in 1992) and dry biomass (15% in 1991 and 9% in 1992). Averaged over CO2 treatments, high O-3 exposure had a negative impact on wheat grain yield (-15% in 1991 and -11% in 1992) and drill biomass (-11% in 1991 and -9% in 1992). Averaged over CO2 treatments, high O-3 exposure decreased corn grain yield by 9%. No significant interactive effects were observed for either crop. The results indicated that CO2 enrichment had a beneficial effect in wheat (C-3 crop) but not in corn (C-4 crop). It is likely that the O-3-induced stress will be diminished under increased atmospheric CO2 concentrations; however, maximal benefits in crop production in wheat in response to CO2 enrichment will not be materialized under concomitant increases in tropospheric O-3 concentration.

KEYWORDS: CHRONIC OZONE, CROP YIELD, DRY-MATTER, ELEVATED CARBON-DIOXIDE, GRAIN QUALITY, INCREASED ATMOSPHERIC CO2, RED WINTER-WHEAT, SPRING WHEAT, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L

2068

Rudorff, B.F.T., C.L. Mulchi, E. Lee, R. Rowland, and R. Pausch. 1996. Photosynthetic characteristics in wheat exposed to elevated O-3 and CO2. *Crop Science 36(5):1247-1251.*

Tropospheric trace gases such as CO2 and O-3 have progressively increased over the past century and are predicted to increase to levels at which they may have a significant impact on agricultural production. The effects of CO2 enrichment and O-3 air pollution on leaf photosynthesis (P-n) and stomatal conductance (g(s)) were investigated. Two soft red winter wheat (Triticum aestivum L.) cultivars, Massey in 1991 and Saluda in 1992, were studied in field experiments at Beltsville, RID, by means of open-top chambers to mimic atmospheric environments predicted for the first half of the 21st century. Plants were exposed to two levels of O-3 (charcoal filtered air and ambient air + an average of 40 nnol O-3 mol(-1) from Monday-Friday of every week). Ozone treatments were superimposed on two CO2 treatments (350 mu mol CO2 mol(-1) and 500 mu mol CO2 mol(-1)). Averaged over O-3

treatments, P-n was stimulated during the early and late growing season under enriched CO2. Averaged over CO2 treatments, high O-3 exposure had a negative impact on P-n early in the season of 1992 and a major impact late in the season of 1991 and 1992 due to premature senescence. Decreases in g(s) occurred under the enriched CO2 environment and to a lesser extent with high O-3. Interactive effects on P-n, and g(s) were mostly absent. It is likely that if CO2 and O-3 concentrations continue to increase, the beneficial effect of CO2 enrichment on P-n may be partially negated by O-3-induced stress. Conversely, damaging effects of O-3 on P-n may be compensated by elevated atmospheric CO2.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CO2, CARBON DIOXIDE, FIELD, GAS-EXCHANGE, GROWTH, OZONE, PLANTS, RADIATION, RESPONSES

2069

Rufty, T.W., R.B. Thomas, J.D. Cure, and W.W. Cure. 1994. Growth-response of cotton to co2 enrichment in differing light environments. *Physiologia Plantarum 91(3):503-509.*

Experiments were conducted to examine the growth responses of cotton (Gossypium hirsutum L. cv. Coker 315) to CO2 enrichment under different light regimes. Plants were exposed to 350 or 700 mu l(-1) CO2 and six light treatments differing in photosynthetic period length (8 or 16 h) and in photosynthetic photon flux density (PPFD) for 32 days of vegetative growth. Higher PPFD (1100 mu mol m(-2) s(-1)) was provided by a combination of high intensity discharge and incandescent lamps (HID), and lower PPFD (550 mu mol m(-2) s(-1)) was provided by fluorescent and incandescent lamps (F) or HID and incandescent lamps with shade cloth (HIDs). Growth was generally much slower with the 8-h photosynthetic periods, but the growth stimulation by CO2 enrichment was larger than with 16-h photosynthetic periods. After 28 to 32 days of treatment, the growth enhancement with CO2 enrichment was 152 and 78% for 8- and 16-h photosynthetic periods, respectively, under HID; 100 and 77% in F, and 77 and 56% in HIDs. The higher PPFD of HID positively influenced the CO2 effect only at the slower growth rate in the 8-h light period. The stimulation of leaf area expansion by CO2 enrichment was also greater with the 8-h photosynthetic period for all light sources. These results, and others on net assimilation rate, shoot to root dry weight ratios and specific leaf weights, suggest that the growth response to CO2 enrichment with the longer photosynthetic period was depressed by limiting factors, perhaps nutritional, in the growth environment. The results also show that extensive variability in CO2 response can occur under light intensities which are often used in growth chamber experiments.

KEYWORDS: DRY-MATTER, ELEVATED CARBON-DIOXIDE, EXPANSION, LEAVES, NITROGEN STRESS, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SOYBEAN PLANTS, YIELD

2070

Ruget, F., O. Bethenod, and L. Combe. 1996. Repercussions of increased atmospheric CO2 on maize morphogenesis and growth for various temperature and radiation levels. *Maydica 41(3):181-191.*

The effect of atmospheric CO2 enhancement on maize production was studied through four crops in two glasshouse compartments, with and without CO2 enrichment. Development (number of organs, duration of phenological phases) was measured during cultivation and growth (dry matter production) was measured at flowering and at final harvest. The main results were as follows: The number of initiated organs (florets and leaves) was not affected by the CO2 enrichment. According to the runs, aerial and whole plant production were significantly or not increased in the enriched compartment. The production increase was significantly different bem een treatments under poor radiation or high plant demand conditions. The balance between supply and demand enabled or not the effect of CO2 enhancement to be expressed. Among the four crops, the light conversion efficiency was significantly modified by CO2 enrichment only in one run. The dry matter increase was not equally partitioned between the organs. It was higher in stem, husks and cob than in leaves and grains. These organs have a morphogenetically limited size (through the number of grains). This controlled the expression of the effect of CO2 enhancement in these runs and explained why the conversion efficiency only increased in one run, which was not morphogenetically limited. These crops proved the interactions between CO2 concentration and the other main climatic factors (temperature and radiation) and the need to know the morphogenesis in order to be able to estimate the effects of CO2 enrichment correctly.

KEYWORDS: ACCUMULATION, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELEVATED CO2, PLANT-RESPONSES, SOIL-WATER, SOURCE-SINK RELATIONS, USE EFFICIENCY

2071

Runion, G.B., E.A. Curl, H.H. Rogers, P.A. Backman, R. Rodriguezkabana, and B.E. Helms. 1994. Effects of free-air co2 enrichment on microbial-populations in the rhizosphere and phyllosphere of cotton. *Agricultural and Forest Meteorology 70(1-4):117-130.*

Cotton (Gossypium hirsutum L.) plants were exposed to free-air CO2 enriched (FACE = 550 mumol mol-1) or ambient (CONTROL = 370 mumol mol-1) levels of atmospheric CO2 and to wet (100% of evapotranspiration replaced) or dry (67% of ET replaced) soil water content treatments. Foliar, soil and root samples were collected in June and August 1991 to determine the effects of elevated CO2 on selected groups of phyllosphere and rhizosphere microorganisms. Foliage and rhizosphere soil were analyzed for bacteria and/or fungi using dilution plating. Mycorrhizal colonization of cotton roots was assessed. Root-zone soil was analyzed for populations of nematodes, microarthropods and Rhizoctonia using various extraction methods. A dehydrogenase assay for total microbial respiration and a bioassay for cotton root infecting organisms were also conducted using root-zone soil. Populations of fungi on cotton leaves varied, by genera, in response to CO2 enrichment, but none was affected by soil water content treatments; populations of foliar bacteria were not affected by either CO2 or soil water content treatments. In August, higher total numbers of rhizosphere fungi were found under the wet compared with the dry soil water treatment, but differences related to CO2 were not detected. There was a trend for infestation by Rhizoctonia solani to be higher under FACE in the August sample, but the soil bioassay demonstrated no increase in damping-off potential. There was a significant interaction between CO2 concentration and soil water content for populations of saprophagous nematodes; populations were different between the CO2 levels in the dry soil treatment only, with higher numbers under FACE. Microarthropod numbers were low; however, there was a trend for Collembola populations to be higher under FACE in the August sample and more fungi were isolated from Collembola in June. Total microbial activity was higher under FACE at both sample dates. Effects of elevated atmospheric CO2 on plant-microbe interactions could have profound influence on the productivity of agro-ecosystems, and deserve further research.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COLLEMBOLA, GROWTH, NITROGEN, NODULATION

2072

Runion, G.B., J.A. Entry, S.A. Prior, R.J. Mitchell, and H.H. Rogers. 1999. Tissue chemistry and carbon allocation in seedlings of Pinus palustris subjected to elevated atmospheric CO2 and water stress. *Tree Physiology 19(4-5):329-335.*

Longleaf pine (Pinus palustris Mill.) seedlings were grown in 45-1 pots and exposed to ambient or elevated (365 or 730 mu mol CO2 mol(-1)) CO2 concentration in open-top chambers for 20 months. Two water-stress treatments (target values of -0.5 or - 1.5 MPa xylem pressure potential) were imposed 19 weeks after initiation of the study. At harvest, tissues (needles, stems, taproots, coarse roots, and fine roots) were analyzed for carbon (C), nitrogen (N), nonpolar extractives (fats, waxes, and oils), nonstructural carbohydrates (sugars and starch), structural components (cellulose and lignin), and tannins. The greatest dry weights and lowest N concentrations occurred in tissues of plants grown at elevated CO2 or with adequate water. Although allocation of C fractions among tissues was generally unaffected by treatments, concentrations of the analyzed compounds were influenced by treatments in needles and taproots, but not in stems and lateral roots. Needles and taproots of plants exposed to elevated CO2 had increased concentrations of nonstructural carbohydrates. Among plant tissues, elevated CO2 caused reductions in structural C concentrations and foliar concentrations of fats, waxes and oils.

KEYWORDS: ARMILLARIA-OSTOYAE, CLIMATE CHANGE, DECIDUOUS TREES, DECOMPOSITION RATES, INSECT PERFORMANCE, LEAF LITTER, LONGLEAF PINE, NUTRIENT BALANCE, SOIL CARBON, USE EFFICIENCY

2073

Runion, G.B., R.J. Mitchell, T.H. Green, S.A. Prior, H.H. Rogers, and D.H. Gjerstad. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. *Journal of Environmental Quality 28(3):880-887.*

Gas exchange responses during a drought cycle were studied in longleaf pine (Pinus palustris Mill.) seedlings after prolonged exposure to varying levels of atmospheric CO2 (approximate to 365 or approximate to 730 mu mol CO2 mol(-1)), soil N (40 or 100 kg N ha(-1) yr(-1)), and water ("adequate" and "stressed"). Elevated atmospheric CO2 concentration increased photosynthesis, tended to decrease stomatal conductance, and increased water-use efficiency (WUE). Although soil resource availability influenced gas exchange measurements, it generally did not affect the magnitude or direction of the response to CO2 concentration. However, significant interactions among treatment variables Here observed for plant xylem pressure potential. In seedlings grown with high N, a positive growth response to elevated atmospheric CO2 increased whole-plant water use resulting in more severe plant water stress, despite increased leaf-level WUE; however, under low N conditions the lark of a growth response to elevated CO2 reduced wholeplant water use, decreased water stress severity, and increased WUE. Photosynthetic response to CO2 was greatest in the high N treatment at the beginning of the drought cycle, but diminished as water stress increased: however, plants grown with low N showed greater photosynthetic responses to CO2 later in the drought cycle. Therefore, plant gas exchange rates interact with growth response in determining the severity of water stress under drought and, thus, the ability of elevated atmospheric CO2 to ameliorate the effects of drought and allow plants to maintain increased rates of photosynthesis mag be influenced bq the availability of other resources, such as N and water.

KEYWORDS: CO2- ENRICHMENT, DROUGHT STRESS, FIELD, GAS-EXCHANGE, GROWTH, LOBLOLLY-PINE, NITROGEN, PLANT-RESPONSES, SEEDLINGS, WATER-USE EFFICIENCY

2074

Running, S.W., D.D. Baldocchi, D.P. Turner, S.T. Gower, P.S. Bakwin, and K.A. Hibbard. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sensing of Environment 70(1):108-127.*

Acurrate monitoring of global seals changes in the terrestrial biosphere has become acutely important as the scope of human impacts on biological systems and atmospheric chemistry grows. For example, the Kyoto Protocol of 1997 signals some of the dramatic socioeconomic and political decisions that may lie ahead concerning CO2 emissions and global carbon cycle impacts. These decisions will rely heavily on accurate measures of global biospheric changes (Schimel 1998; IGBP TCWG, 1998). An array of national and international programs have inaugurated global satellite observations, critical field measurements of carbon and water fluxes, and global model development for the purposes of beginning to monitor the biosphere. The detection by these programs of interannual variability of ecosystem fluxes and of longer term trends will permit early indication of fundamental biospheric changes which might otherwise go undetected until major biome conversion begins. This article describes a blueprint for more comprehensive coordination of the various flux measurement and modeling activities into a global terrestrial monitoring network that will have direct relevance to the political decision making of global change. (C) Elsevier Science Inc., 1999.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, CO2, EDDY-CORRELATION, EXCHANGE, FOREST, NET PRIMARY PRODUCTION, SEASONAL-VARIATION, SPATIAL-RESOLUTION, WATER-VAPOR

2075

Rustad, L.E., and I.J. Fernandez. 1998. Experimental soil warming effects on CO2 and CH4 flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology 4(6):597-605.*

The effect of soil warming on CO2 and CH4 flux from a spruce- fir forest soil was evaluated at the Howland Integrated Forest Study site in Maine, USA from 1993 to 1995. Elevated soil temperatures (similar to 5 degrees C) were maintained during the snow-free season (May November) in replicated 15 x 15-m plots using electric cables buried 1-2 cm below the soil surface; replicated unheated plots served as the control. CO2 evolution from the soil surface and soil air CO2 concentrations both showed clear seasonal trends and significant ($P < 0.0001$) positive exponential relationships with soil temperature. Soil warming caused a 25-40% increase in CO2 flux from the heated plots compared to the controls. No significant differences were observed between heated and control plot soil air CO2 concentrations which we attribute to rapid equilibration With the atmosphere in the O horizon and minimal treatment effects in the B horizon. Methane fluxes were highly variable and showed no consistent trends with treatment.

KEYWORDS: BALANCE, CLIMATE, FLOOR, METHANE, PATTERNS, RESPIRATION, TEMPERATURE, TRACE GAS FLUXES

2076

Rusterholz, H.P., and A. Erhardt. 1998. Effects of elevated CO2 on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. *Oecologia 113(3):341-349.*

Effects of elevated CO2 on flowering phenology and nectar production were investigated in Trifolium pratense, Lotus corniculatus, Scabiosa columbaria, Centaurea jacea and Betonica officinalis, which are all important nectar plants for butterflies. In glasshouse experiments, juvenile plants were exposed to ambient (350 mu l l(-1)) and elevated (660 mu l l(- 1)) CO2 concentrations for 60-80 days. Elevated CO2 significantly enhanced the development of flower buds in C. jacea. B. officinalis flowered earlier and L. corniculatus produced more flowers under elevated CO2. In contrast, the number of flowers decreased in T. pratense. The amount of nectar per flower was not affected by elevated CO2 in the tested legumes (T. pratense and L. corniculatus), but was significantly reduced (!) in the other forbs. Elevated CO2 did not

significantly affect nectar sugar concentration and composition. However, S. columbaria and C. jacea produced significantly less total sugar under elevated CO2. The nectar amino acid concentration remained unaffected in all investigated plant species, whereas the total of amino acids produced per flower was reduced in all non-legumes. In addition, the amino acid composition changed significantly in all investigated species except for C. jacea. The observed effects are unexpected and are a potential threat to flower visitors such as most butterflies which have no alternative food resources to nectar. Changes in nectar production due to elevated CO2 could also have generally detrimental effects on the interactions of flowers and their pollinators.

KEYWORDS: ADULT DIET, AMINO-ACIDS, ATMOSPHERIC CARBON-DIOXIDE, CHROMATOGRAPHY, ENRICHMENT, GROWTH, LEPIDOPTERA, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, RESPONSES

2077

Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecological Applications 1(2):157-167.*

Plant respiration is a large, environmentally sensitive component of the ecosystem carbon balance, and net ecosystem carbon flux will change as the balance between photosynthesis and respiration changes. Partitioning respiration into the functional components of construction, maintenance, and ion uptake will aid the estimation of plant respiration for ecosystems. Maintenance respiration is the component most sensitive to changes in temperature, CO2, protein concentration and turnover, water stress, and atmospheric pollutants. For a wide variety of plant tissues, maintenance respiration, corrected for temperature, appears to be linearly related to Kjeldahl nitrogen content of live tissue. Total and maintenance respiration may decline under CO2 enrichment, but the mechanism, independence from changes in protein content, and acclimation are unknown. Response of respiration to temperature can be modelled as a Q10 relationship, if corrections for bias arising from daily and annual temperature amplitude are applied. Occurrence and control of the cyanide- resistant respiratory pathway and acclimation of respiration rates to different climates are poorly understood, but may substantially affect the reliability of model estimates of plant respiration.

KEYWORDS: CO2, CYANIDE- RESISTANT, DARK RESPIRATION, ELEVATED CARBON-DIOXIDE, GRAIN-SORGHUM, GROWTH, LOLIUM-MULTIFLORUM, MAINTENANCE RESPIRATION, ROOT RESPIRATION, WHOLE PLANTS

2078

Rygiewicz, P.T., and C.P. Andersen. 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature 369(6475):58-60.*

PLANTS and sails are a critically important element in the global carbon-energy equation. It is estimated that in forest ecosystems over two-thirds of the carbon is contained in soils and peat deposits(1). Despite the importance of forest soils in the global carbon cycle, fluxes of carbon associated with fundamental processes and soil functional groups are inadequately quantified, limiting our understanding of carbon movement and sequestration in soils. We report here the direct measurement of carbon id and through all major pools of a mycorrhizal (fungus-root) coniferous seedling (a complete carbon budget). The mycorrhizal symbiont reduces overall retention of carbon in the plant-fungus symbiosis by increasing carbon in roots and below-ground respiration and reducing its retention and release above ground. Below ground, mycorrhizal plants shifted allocation of carbon to pools that are rapidly turned over, primarily to fine roots and fungal hyphae, and host root and fungal respiration. Mycorrhizae alter the size of below-ground carbon pools, the quality and, therefore, the retention time of carbon below ground. Our data indicate that if elevated atmospheric CO2 and altered climate stressors alter mycorrhizal colonization in forests, the role of forests in sequestering carbon could be altered.

KEYWORDS: CO2, FLOW, HYPHAE, ROOTS, SEEDLINGS, SOIL

2079

Rygiewicz, P.T., M.G. Johnson, L.M. Ganio, D.T. Tingey, and M.J. Storm. 1997. Lifetime and temporal occurrence of ectomycorrhizae on ponderosa pine (Pinus ponderosa Laws) seedlings grown under varied atmospheric CO2 and nitrogen levels. *Plant and Soil 189(2):275-287.*

Climate change (elevated atmospheric CO2, and altered air temperatures, precipitation amounts and seasonal patterns) may affect ecosystem processes by altering carbon allocation in plants, and carbon flux from plants to soil. Mycorrhizal fungi, as carbon sinks, are among the first soil biota to receive carbon from plants, and thereby influence carbon release from plants to soil. One step in this carbon release is via fine root and mycorrhizal turnover. It is necessary to know the lifetime and temporal occurrence of roots and mycorrhizae to determine the capacity of the soil ecosystem to sequester carbon assimilated aboveground. In this study, ponderosa pine (Pinus ponderosa Laws) seedlings were grown under three levels of atmospheric CO2 (ambient, 525 and 700 mu mol CO2 mol(-1)) and three levels of annual nitrogen additions (0,100 and 200 kg N ha(-1)) in open-top chambers. At a two-month frequency during 18 months, we observed ectomycorrhizal root tips observed using minirhizotron tubes and camera. The numbers of new mycorrhizal root tips, the numbers of tips that disappeared between two consecutive recording events, and the standing crop of tips at each event were determined. There were more mycorrhizal tips of all three types seen during the summer compared with other times of the year. When only the standing crop of mycorrhizal tips was considered, effects of the CO2 and N addition treatments on carbon allocation to mycorrhizal tips was weakly evident. However, when the three types of tips were considered collectively, tips numbers flux of carbon through mycorrhizae was greatest in the: (1) high CO2 treatment compared with the other CO2 treatments, and (2) intermediate N addition treatment compared with the other N addition treatments. A survival analysis on the entire 18 month cohort of tips was done to calculate the median lifetime of the mycorrhizal root tips. Average median lifetime of the mycorrhizal tips was 139 days and was not affected by nitrogen and CO2 treatments.

KEYWORDS: CARBON, COMPENSATORY INCREASES, DOUGLAS-FIR STANDS, ELEVATED CO2, FINE ROOTS, FOREST, MYCORRHIZAL COLONIZATION, QUERCUS-ALBA, SEMINAL ROOT-SYSTEM, SOIL RESPIRATION

2080

Ryle, G.J.A., and C.E. Powell. 1992. The influence of elevated co2 and temperature on biomass production of continuously defoliated white clover. *Plant, Cell and Environment 15(5):593-599.*

Clonal plants of white clover (Trifolium repens L.), grown singly in pots of Perlite and solely dependent for nitrogen on root nodule N2 fixation, were maintained in controlled environments which provided four environments: 18/13-degrees-C day/night temperature at 340 and 680-mu-mol mol-1 CO2 and 20.5/15.5-degrees-C day/night temperature at 340 and 680-mu-mol mol-1 CO2. The daylength was 12h and the photon flux density 500+/-25-mu-mol m-2 s-1 (PFD). All plants were defoliated for about 80d, nominally every alternate day, to leave the youngest expanded leaf intact on 50% of stolons, plus expanding leaves (simulated grazing). Elevated CO2 increased the yield of biomass removed at defoliation by a constant 45% during the second 40d of the experiment and by a varying amount in the first half of the experiment. Elevated temperature had little effect on biomass yield. Nitrogen, as a

proportion of the harvested biomass, was only fractionally affected by elevated CO2 or temperature. In contrast, N2 fixation increased in concert with the promoting effect of elevated CO2 on biomass production. The increased yield of biomass harvested in 680 mu- mol mol-1 CO2 was primarily due to the early development and continued maintenance of more stolons. However, the stolons of plants grown in elevated CO2 also developed leaves which were heavier and slightly larger in area than their counterparts in ambient CO2. The conclusion is that, when white clover plants are maintained at constant mass by simulated grazing, they continue to respond to elevated CO2 in terms of a sustained increase in biomass production.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, ENVIRONMENTS, GROWTH, PHOTOSYNTHESIS, YIELD

2081

Ryle, G.J.A., C.E. Powell, and I.A. Davidson. 1992. Growth of white clover, dependent on n2 fixation, in elevated co2 and temperature. *Annals of Botany 70(3):221-228.*

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, RESPIRATION, STARCH

2082

Ryle, G.J.A., C.E. Powell, and V. Tewson. 1992. Effect of elevated co2 on the photosynthesis, respiration and growth of perennial ryegrass. *Journal of Experimental Botany 43(251):811-818.*

Single, seed-grown plants of ryegrass (Lolium perenne L. cv. Melle) were grown for 49 d from the early seedling stage in growth cabinets at a day/night temperature of 20/15-degrees-C, with a 12 h photoperiod, and a CO2 concentration of either 340 or 680-mu-l l-1 CO2. Following complete acclimation to the environmental regimes, leaf and whole plant CO2 effluxes and influxes were measured using infra-red gas analysis techniques. Elevated CO2 increased rates of photosynthesis of young, fully expanded leaves by 35-46% and of whole plants by more than 50%. For both leaves and whole plants acclimation to 680-mu-l l-1 CO2 reduced rates of photosynthesis in both CO2 regimes, compared with plants acclimated to 340-mu-l l-1. There was no significant effect of CO2 regime on respiration rates of either leaves or whole plants, although leaves developed in elevated CO2 exhibited generally lower rates than those developed in 340-mu-l l-1 CO2. Initially the seedling plants in elevated CO2 grew faster than their counterparts in 340-mu-l l-1 CO2, but this effect quickly petered out and final plant weights differed by only c. 10%. Since the total area of expanded and unexpanded laminae was unaffected by CO2 regime, specific leaf area was persistently 13-40% lower in elevated CO2 while, similarly, root/shoot ratio was also reduced throughout the experiment. Elevated CO2 reduced tissue nitrogen contents of expanded leaves, but had no effect on the nitrogen contents of unexpanded leaves, sheaths or roots. The lack of a pronounced effect of elevated CO2 on plant growth was primarily due to the fact that CO2 concentration did not influence tiller (branch) numbers. In the absence of an effect on tiller numbers, any possible weight increment was restricted to the c. 2.5 leaves of each tiller. The reason for the lack of an effect on tillering is not known.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, LIGHT, LOLIUM, NITROGEN, PLANTS, RESPONSES

2083

Ryle, G.J.A., and J. Stanley. 1992. Effect of elevated co2 on stomatal size and distribution in perennial ryegrass. *Annals of Botany 69(6):563-565.*

KEYWORDS: ENRICHMENT, GROWTH

2084

Ryle, G.J.A., J. Woledge, V. Tewson, and C.E. Powell. 1992. Influence of elevated co2 and temperature on the photosynthesis and respiration of white clover dependent on n2 fixation. *Annals of Botany 70(3):213-220.*

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GRASS, LEAVES, NITROGEN, PLANT GROWTH, SHORT- TERM

2085

Sa, T., and D.W. Israel. 1997. Effect of phosphorus deficiency on response of symbiotic N-2 fixation of soybean to atmospheric CO2 enrichment. *Plant Physiology 114(3):484.*

2086

Sa, T.N., and D.W. Israel. 1998. Phosphorus-deficiency effects on response of symbiotic N-2 fixation and carbohydrate status in soybean to atmospheric CO2 enrichment. *Journal of Plant Nutrition 21(10):2207-2218.*

The impact of phosphorus (P) deficiency on response of symbiotic N-2 fixation and carbohydrate accumulation in soybean (Glycine max [L.] Merr.) to atmospheric CO2 enrichment was examined. Plants inoculated with Bradyrhizobium japonicum MN 110 were grown in growth chambers with controlled atmospheres of 400 and 800 mu L CO2 L-1 and supplied either 1.0 mM-P (P- sufficient) or 0.05 mM-P (P-deficient) nitrogen (N)-free nutrient solution. When plants were supplied with sufficient P, CO2 enrichment significantly increased whole plant dry mass (83%), nodule mass (67%), total nitrogenase activity (58%), and N (35%) and P (47%) accumulation at 35 days after transplanting (DAT). Under sufficient P supply, CO2 enrichment significantly increased starch concentrations in nodules compared to the normal atmospheric CO2 treatment. Under normal CO2 levels (400 mu L L-1) nonstructural carbohydrate concentration (starch plus soluble sugar) was significantly higher in leaves of P- deficient plants than in leaves of P-sufficient plants in which nonstructural carbohydrate concentration exhibited a strong diumal pattern. Under deficient P supply whole plant dry mass, symbiotic N-2-fixation parameters, and N and P accumulation were not enhanced by atmospheric CO2 enrichment. Phosphorus deficiency decreased nonstructural carbohydrate accumulation in nodules at the end of a 10-day period in which functional activity was developing by 86% relative to P-sufficient controls. While P deficiency elicited significant increases in the nonstructural carbohydrate concentration in leaves, it caused significant decreases in the nonstructural carbohydrate concentration in nodules over the diurnal cycle from 30 to 31 DAT. Collectively, these results indicate that the lack of a symbiotic N-2-fixation response to atmospheric CO2 enrichment by P-deficient plants may be related to the decreased carbohydrate status of nodules.

KEYWORDS: ELEVATED CARBON-DIOXIDE, GLYCINE-MAX, GROWTH, NUTRITION, PLANTS, SEED YIELD, TOTAL NITROGEN

2087

Saarinen, T. 1998. Internal C : N balance and biomass partitioning of Carex rostrata grown at three levels of nitrogen supply. *Canadian Journal of Botany-Revue Canadienne De Botanique 76(5):762-768.*

The long-term effects of high nitrogen supply on the growth and partitioning of biomass in a common sedge species, Carer rostrata Stokes, were studied in a greenhouse experiment Special attention was paid to free amino acids and soluble sugars, representing biochemically

available fractions of nitrogen and carbon, respectively, in the tissues of Carer. Plants were grown in peat in buckets, and nitrogen was added as ammonium nitrate (2, 5, and 10 g N m(-2) year(-1)) five times during two growing seasons. Changes in biomass allocation patterns became evident towards the end of the second growing season. The biomass of shoots was highest in the high-N treatment, resulting in a high ratio of aboveground to belowground biomass. The high biomass of shoots was due to both the high density of current-year shoots and later senescence in the high-N treatment. No differences were observed in the belowground biomasses. Changes in allocation patterns were accompanied by changes in the soluble fractions of carbon and nitrogen. The concentration of free amino acids (FAA) was significantly higher (both shoots and roots) and the concentration of total nonstructural carbohydrates (TNC) lower (roots only) in the high-N treatment. The concentration of total nitrogen also increased with increasing supply of nitrogen. The results indicate that a high long-term supply of nitrogen may shift the internal carbon to nitrogen balance of Carer towards higher availability of nitrogen. Compared with the carbon to nitrogen ratio, the TNC:FAA ratio seems to be a better indicator of the internal carbon to nitrogen balance. A low TNC:FAA ratio may enhance the allocation of biomass to shoots and also increase the density of shoots.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CO2 ENRICHMENT, ELEVATED CO2, FLOATING FENS, FUNCTIONAL EQUILIBRIUM, MINERAL NUTRITION, ROOT, SEASONAL ALLOCATION, SHOOT, VASCULAR PLANTS

2088

Saarnio, S., J. Alm, P.J. Martikainen, and J. Silvola. 1998. Effects of raised CO2 on potential CH4 production and oxidation in, and CH4 emission from, a boreal mire. *Journal of Ecology 86(2):261-268.*

1 In a glasshouse experiment we studied the effect of raised CO2 concentration (720 p.p.m.) on CH4 emission at natural boreal peat temperatures using intact cores of boreal peat with living vascular plants and Sphagnum mosses. After the end of the growing season half of the cores were kept unnaturally warm (17-20 degrees C). The potential for CH4 production and oxidation was measured at the end of the emission experiment. 2 The vascular cores ('Sedge') consisted of a moss layer with sedges, and the moss cores ('Sphagnum') of Sphagnum mosses (some sedge seedlings were removed by cutting). Methane efflux was 6-12 times higher from the Sedge cores than from the Sphagnum cores. The release of CH4 from Sedge cores increased with increasing temperature of the peat and decreased with decreasing temperature. Methane efflux from Sphagnum cores was quite stable independent of the peat temperatures. 3 In both Sedge and Sphagnum samples, CO2 treatment doubled the potential CH4 production but had no effect on the potential CH4 oxidation. A raised concentration of CO2 increased CH4 efflux weakly and only at the highest peat temperatures (17-20 degrees C). 4 The results suggest that in cool regions, such as boreal wetlands, temperature would restrict decomposition of the extra substrates probably derived from enhanced primary production of mire vegetation under raised CO2 concentrations, and would thus retard any consequent increase in CH4 emission.

KEYWORDS: CARBON DIOXIDE, CLIMATIC CHANGE, ENRICHMENT, FEEDBACK, METHANE FLUX, PEATLANDS, PHOTOSYNTHESIS, PLANT-ROOTS, TUNDRA, VEGETATION

2089

Saarnio, S., and J. Silvola. 1999. Effects of increased CO2 and N on CH4 efflux from a boreal mire: a growth chamber experiment. *Oecologia 119(3):349-356.*

Increases in the supply of atmospheric CO2 and N are expected to alter the carbon cycle, including CH4 emissions, in boreal peatlands. These effects were studied in a glasshouse experiment with peat monoliths cored from an oligotrophic pine fen. The cores with living plants were kept in 720 ppm(v) and 360 ppm(v) CO2 atmospheres for about 6 months under imitated natural temperature cycle. Fertilisation with NH4NO3 (3 g m(-2) for 25 weeks) was applied to 18 of the 36 monoliths. The rate of CH4 flux was non-linearly dependent on the number of Eriophorum vaginatum shoots growing in the monoliths, probably due to the gas transport properties of the aerenchyma. The average CH4 efflux rate, standardised by the number of shoots, was increased by a maximum of 10-20% in response to the raised CO2 level. In the raised-NH4NO3 treatment, the increase in CH4 release was lower. The effect of combined CO2 + NH4NO3 on CH4 release was negligible and even lower than in the single treatments. Both potential CH4 production and oxidation rates at 5, 15 and 25 degrees C were higher near the surface than at the bottom of the core. As expected, the rates clearly depended on the incubation temperature, but the different treatments did not cause any consistent differences in either CH4 production or oxidation. The determination of potential CH4 production and oxidation in the laboratory is evidently too crude a method of differentiating substrate-induced differences in CH4 production and oxidation in vivo. These results indicate that an increase in atmospheric CO2 or N supply alone, at least in the short term, slightly enhances CH4 effluxes from boreal peatlands; but together their effect may even be restrictive.

KEYWORDS: BIOMASS ALLOCATION, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO2, FOREST SOILS, LEAF LITTER, LOLIUM-PERENNE, METHANE EMISSION, NITROGEN-FERTILIZATION, OLIGOTROPHIC PINE FEN, TUSSOCK TUNDRA

2090

Saccardy, K., B. Pineau, O. Roche, and G. Cornic. 1998. Photochemical efficiency of Photosystem II and xanthophyll cycle components in Zea mays leaves exposed to water stress and high light. *Photosynthesis Research 56(1):57-66.*

The effects of two light treatments (photosynthetically active photon flux density of either 650 or 1950 mu mol m(-2) s(-1)) on the photochemical efficiency of Photosystem II (PS II) (measured as variable to maximum fluorescence ratio) and on the xanthophyll cycle components was studied in wilted Zea mays leaves. For comparison, these parameters were followed under the same light conditions in well-hydrated leaves maintained either in normal or CO2-free air. The net CO2 assimilation of dehydrated leaves declined rapidly as their relative water content (RWC) decreased from 100 to 60% while the PS II efficiency measured after a prolonged dark period of 16 h declined only when RWC leaves was lower than 60%. Furthermore, drought caused an increase in the pool size of the xanthophyll cycle pigments and the presence of a sustained elevated level of zeaxanthin and antheraxanthin at the end of the long dark period. The leaf water deficit enhanced the sensitivity of PS II efficiency to light exposure. During illumination, strong inhibition of PS II efficiency and large violaxanthin deepoxidation was observed in wilted leaves even under moderate photon flux density compared to control leaves in the same conditions. After 2 h of darkness following the light treatment, the PS II efficiency that is dependent on the previous PPFD, decreased with leaf water deficit. Moreover, zeaxanthin epoxidation led to an accumulation of antheraxanthin in dehydrated leaves, All these drought effects on PS II efficiency and xanthophyll cycle components were also obtained in well-hydrated leaves by short-term CO2 deprivation during illumination. We conclude that the increased susceptibility of PS II efficiency to light in wilted maize leaves is mainly explained by the decrease of CO2 availability and the resulting low net CO2 assimilation.

KEYWORDS: CHLOROPHYLL-A FLUORESCENCE, COTTON LEAVES, DELTA, DROUGHT STRESS, ENERGY, EXCESS LIGHT, PHOTOSYNTHETIC REACTIONS, QUANTUM YIELD,

VIOLAXANTHIN CYCLE, ZEAXANTHIN EPOXIDATION

2091

Sadowsky, M.J., and M. Schortemeyer. 1997. Soil microbial responses to increased concentrations of atmospheric CO2. *Global Change Biology 3(3):217-224.*

Terrestrial ecosystems respond to an increased concentration of atmospheric CO2. While elevated atmospheric CO2 has been shown to alter plant growth and productivity, it also affects ecosystem structure and function by changing below-ground processes. Knowledge of how soil microbiota respond to elevated atmospheric CO2 is of paramount importance for understanding global carbon and nutrient cycling and for predicting changes at the ecosystem-level. An increase in the atmospheric CO2 concentration not only alters the weight, length, and architecture of plant roots, but also affects the biotic and abiotic environment of the root system. Since the concentration of CO2 in soil is already 10-50 times higher than that in the atmosphere, it is unlikely that increasing atmospheric CO2 will directly influence the rhizosphere. Rather, it is more likely that elevated atmospheric CO2 will affect the microbe-soil- plant root system indirectly by increasing root growth and rhizodeposition rates, and decreasing soil water deficit. Consequently, the increased amounts and altered composition of rhizosphere-released materials will have the potential to alter both population and community structure, and activity of soil- and rhizosphere-associated microorganisms. This occurrence could in turn affect plant health and productivity and plant community structure. This review covers current knowledge about the response of soil microbes to elevated concentrations of atmospheric CO2.

KEYWORDS: BOUTELOUA-GRACILIS, CROP RESPONSES, ELEVATED CARBON-DIOXIDE, ENRICHMENT, LOLIUM-PERENNE, MYCORRHIZAL COLONIZATION, PLANT-RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, TALLGRASS PRAIRIE

2092

Saebo, A., T. Krekling, and M. Appelgren. 1995. Light quality affects photosynthesis and leaf anatomy of birch plantlets in-vitro. *Plant Cell Tissue and Organ Culture 41(2):177-185.*

Cultures in vitro of Betula pendula Roth were subjected to light of different spectral qualities. Photosynthetic capacity was highest when the plantlets were exposed to blue light (max recorded photosynthesis, 82 mu mol CO2 dm(-2) h(-1)) and lowest when irradiated with light high in red and/or far-red wave lengths (max recorded photosynthesis, 40 mu mol CO2 dm(-2) h(- 1)). Highest chlorophyll content (2.2 mg dm(-2) leaf area) was found in cultures irradiated with blue light, which also enhanced the leaf area. Morphometric analysis of light micrographs showed that the epidermal cell areas were largest in plantlets subjected to blue light and smallest in those subjected to red light. Morphometric analysis of electron micrographs of palisade cells, showed that the functional chloroplast area was largest in chloroplasts of leaves subjected to blue light and smallest in those exposed to red light. We suggest that light quality affects photosynthesis both through effects on the composition of the photosynthetic apparatus and on translocation of carbohydrates from chloroplasts.

KEYWORDS: BLUE, CULTURED INVITRO, FLUENCE RATE, GROWTH, PHYTOCHROME, PIGMENTS, RED

2093

Saebo, A., and L.M. Mortensen. 1995. Growth and regrowth of phleum-pratense, lolium-perenne, trifolium-repens and trifolium-pratense at normal and elevated co2 concentration. *Agriculture Ecosystems & Environment 55(1):29-35.*

The effect of elevated CO2 concentration (680 +/- 52 mu mol mol(-1)) on growth of three cultivars of Phleum pratense, two of Lolium perenne and one of Trifolium repens and Trifolium pratense each, was studied during one growth season including three harvests. The study was performed in ten 9 m(2) field chamber units in a cool maritime climate under long days (15-18 h), on the southwest coast of Norway (59 degrees N, 6 degrees E). Tillering in P. pratense and L. perenne was not significantly affected in the first harvest (June/July), but was increased by 30% in the third harvest (September) in response to elevated CO2 concentrations. The plant height was reduced by 16-24% in P. pratense and by 25-29% in L. perenne at high CO2. The dry weight yield of the two grass species was negatively affected by elevated CO2 in the two first harvests, however, no effect was found in the last harvest. The total harvestable dry matter was decreased by 18% in P. pratense and 13% in L. perenne. The dry matter of the stubble was increased at elevated CO2, by 18% in P. pratense and 26% in L. perenne, leaving more of the yield in the meadow after harvest. Raising the CO2 concentration increased the dry weight by 30% in both clover species. The results are discussed in relation to the climatic conditions during the season.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DIFFERENT IRRADIANCES, ENRICHMENT, NITROGEN, TEMPERATURE, WHEAT, YIELD

2094

Saebo, A., and L.M. Mortensen. 1996. Growth, morphology and yield of wheat, barley and oats grown at elevated atmospheric CO2 concentration in a cool, maritime climate. *Agriculture Ecosystems & Environment 57(1):9-15.*

The effects of elevated CO, concentration on the growth, yield and quality of spring wheat (Triticum aestivum L., cv. 'Sport'), barley(Hordeum vulgare, cv. 'Thule') and oats(Avena sativa, cv. 'Kapp') were studied. The study was performed from 20 April to 24 August in ten field chamber units each of 9 m(2) in a cool (12.6 degrees C) maritime climate under long days (14.6-18.1 h), on the southwest coast of Norway (59 degrees N, 6 degrees E). The total biomass increased at high CO2 concentration, by 11% and 20% in wheat and barley, respectively. The proportion of small grains increased by 6% in wheat and 26% in barley, but the total grain yield was not affected. The weight of chaff increased by 9% and 19% in wheat and barley, respectively. Plant height was significantly reduced during the growing season at elevated CO2, by 8-19% in barley and by 9-25% in oats until 6 July when no significant difference in height was found. After 6 July, barley plants at elevated CO2 were significantly taller than at ambient CO2 concentration and oats were not affected. Elongation in wheat was not affected by CO2 concentration at any time in the growing season. No difference in developmental rate could be detected between plants at normal and elevated CO2 concentrations. The protein content of the grain decreased by 8% in barley, but was not significantly affected in the other species.

KEYWORDS: AIR- TEMPERATURE, AMBIENT, CARBON DIOXIDE, ENRICHMENT, INHIBITION, LEAVES

2095

Saebo, A., and L.M. Mortensen. 1996. The influence of elevated CO2 concentration on growth of seven grasses and one clover species in a cool maritime climate. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 46(1):49-54.*

The effect of elevated CO2 concentration on the growth of eight common species and cultivars in Norwegian meadows-Festuca pratensis "Salten" and "Fure", Festuca rubra "Koket" and "Leik", Festuca arundinaceae "Vantage" Festuca duruiscula "Barfina", Poa pratensis "Lavang", Agrostis capillar is "Aros", Dactylis glomerata "Apelsvoll", and Trifolium repens "Grasslands Huia"-was studied during 11 weeks

(April 26-early July). The study was performed in ten 9 m(2) large field chamber units in a cool (11.3 degrees C) maritime climate under long days (15.1-18.1 h), on the south-west coast of Norway (59 degrees N, 6 degrees E). The different species responded differently to elevated CO2 with respect to tillering, which was enhanced in A. capillaris (81%), D. glomerata (23%) and F. pratensis (36%), but was not significantly affected in the other species. The sward length was significantly decreased by high CO2 concentration, by 20% in P. pratensis, 36% in A. capillaris, 29% in D. glomerata, 26% in F. duruiscula, 36% in F. pratensis and 16% in F. rubra, but was not affected in F. arundinacea, F. pratensis "Salten" and T. repens. The dry matter was decreased at elevated CO2 concentration in A. capillaris (14%), increased in F. rubra (10%) and not significantly affected in the other plants. The results are discussed in relation to climate and interspecific responses.

KEYWORDS: AIR- TEMPERATURE, AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, NITROGEN, ORANGE TREE LEAVES, PHOSPHORUS, WHEAT, YIELD

2096

Saebo, A., and L.M. Mortensen. 1998. Influence of elevated atmospheric CO2 concentration on common weeds in Scandinavian agriculture. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science 48(3):138-143.*

This study investigated the influence of elevated CO, on three perennial weed species (Achillea millefolium, Leontodon autumnalis and Rumex acetosa) and seven annual species (Chenopodium album, Matricaria matricarioides, Poa annua, Polygonum persicaria, Senecio vulgaris, Spergula arvensis and Stellaria media). The study was carried out during the period 3 May to 5 August in ten field chamber units of 9 m(2) in a cool (12.6 degrees C) maritime climate under long days (15.8-18.1 h day(-1)) on the south-west coast of Norway (59 degrees N, 6 degrees E). Dry weights of the seven annual species were not significantly affected by the CO2 concentration. Of the three perennial species, L. autumnalis increased in dry weight by 27% and A. millefolium by 19% at elevated compared with ambient CO2 concentration. Plant height increased by 8% in L. autumnalis and decreased by 12 and 10% in M. matricarioides and P. annua, respectively. Leaf size increased by 32% and specific leaf area decreased by 23% in P. persicaria at elevated CO2, while the other species were unaffected. The results are discussed in relation to competition between species and the influence of climate on the CO2 responses.

KEYWORDS: AIR- TEMPERATURE, AMBIENT, CARBON DIOXIDE, COOL, ENRICHMENT, GROWTH, MARITIME CLIMATE, NITROGEN, WHEAT, YIELD

2097

Saetersdal, M., and H.J.B. Birks. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *Journal of Biogeography 24(2):127-152.*

Mountain plants constitute an important part of the Norwegian flora. They are also believed to be the plant group in Norway most threatened by the expected climatic warming due to an enhanced greenhouse effect in the near future. In this study the distributions of 107 mountain Norwegian vascular plants were modelled in relation to present-day climate using Gaussian legit regression. Most species are found to have a surprisingly broad amplitude to mean July and January temperatures, suggesting that a 2 degrees C increase in summer temperature and 4 degrees C increase in winter temperature (as expected with a 2 x CO2 increase) may not have a dramatic direct effect on most of the species investigated. A comparative study between estimated July and January temperature optima and tolerances and other ecological attributes such as habitat characteristics, dispersal mechanisms, range sizes and other climatic optima and tolerances was done using multivariate analysis. The results suggest that species most vulnerable to climatic warming, namely the species with narrow July and January temperature tolerances, are characterized by small range sizes and small population sizes, i.e. they are nationally rare species. Furthermore, these vulnerable species are found in all habitats along the major moisture gradient in alpine vegetation. A classification of the species into Rabinowitz's seven forms of rarity confirms that the species most vulnerable to climatic warming are characterized by being habitat specialists with a small geographic range size.

KEYWORDS: ABUNDANCE, ENVIRONMENTAL-CHANGE, FALLOPIA-JAPONICA, GRADIENT ANALYSIS, GROWTH, MODEL, NUMERICAL- ANALYSIS, PATTERNS, REPRODUCTIVE DEVELOPMENT, RESPONSES

2098

Sage, R.F. 1990. A model describing the regulation of ribulose-1,5-bisphosphate carboxylase, electron-transport, and triose phosphate use in response to light-intensity and CO2 in C3 plants. *Plant Physiology 94(4):1728-1734.*

A model of the regulation of the activity of ribulose-1,5-bis- phosphate carboxylase, electron transport, and the rate of orthophosphate regeneration by starch and sucrose synthesis in response to changes in light intensity and partial pressures of CO2 and O2 is presented. The key assumption behind the model is that nonlimiting processes of photosynthesis are regulated to balance the capacity of limiting processes. Thus, at CO2 partial pressures below ambient, when a limitation on photosynthesis by the capacity of rubisco is postulated, the activities of electron transport and phosphate regeneration are down-regulated in order that the rate of RuBP regeneration matches the rate of RuBP consumption by rubisco. Similarly, at subsaturating light intensity or elevated CO2, when electron transport or Pi regeneration may limit photosynthesis, the activity of rubisco is downregulated to balance the limitation in the rate of RuBP regeneration. Comparisons with published data demonstrate a general consistency between modelled predictions and measured results.

KEYWORDS: ELEVATED CO2, GAS-EXCHANGE, INTACT LEAVES, INVIVO, OXYGENASE, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, TEMPERATURE, WHEAT SEEDLINGS

2099

Sage, R.F. 1994. Acclimation of photosynthesis to increasing atmospheric co2 - the gas-exchange perspective. *Photosynthesis Research 39(3):351-368.*

The nature of photosynthetic acclimation to elevated CO2 is evaluated from the results of over 40 studies focusing on the effect of long-term CO2 enrichment on the short-term response of photosynthesis to intercellular CO2 (the A/C-i response). The effect of CO2 enrichment on the A/C-i response was dependent on growth conditions, with plants grown in small pots (<5 L) or low nutrients usually exhibiting a reduction of A at a given C-i, while plants grown without nutrient deficiency in large pots or in the field tended to exhibit either little reduction or an enhancement of A at a given C-i following a doubling or tripling of atmospheric CO2 during growth. Using theoretical interpretations of A/C-i curves to assess acclimation, it was found that when pot size or nutrient deficiency was not a factor, changes in the shape of A/C-i curves which are indicative of a reallocation of resources within the photosynthetic apparatus typically were not observed. Long-term CO2 enrichment usually had little effect or increased the value of A at all C-i. However, a minority of species grown at elevated CO2 exhibited gas exchange responses indicative of a reduced amount of

Rubisco and an enhanced capacity to metabolize photosynthetic products. This type of response was considered beneficial because it enhanced both photosynthetic capacity at high CO2 and reduced resource investment in excessive Rubisco capacity. The ratio of intercellular to ambient CO2 (the C-i/C-a ratio) was used to evaluate stomatal acclimation. Except under water and humidity stress, C-i/C-a, exhibited no consistent change in a variety of C-3 species, indicating no stomatal acclimation. Under drought or humidity stress, C-i/C-a declined in high-CO2 grown plants, indicating stomata will become more conservative during stress episodes in future high CO2 environments.

KEYWORDS: C-3 PLANTS, CHENOPODIUM-ALBUM L, ELECTRON-TRANSPORT, ELEVATED CARBON-DIOXIDE, INTACT LEAVES, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE-1;5- BISPHOSPHATE CARBOXYLASE ACTIVITY, STOMATAL CONDUCTANCE, ULTRAVIOLET-B RADIATION

2100

Sage, R.F. 1995. Was low atmospheric co2 during the pleistocene a limiting factor for the origin of agriculture. *Global Change Biology 1(2):93-106.*

Agriculture originated independently in many distinct regions at approximately the same time in human history. This synchrony in agricultural origins indicates that a global factor may have controlled the timing of the transition from foraging to food- producing economies. The global factor may have been a rise in atmospheric CO:! from below 200 to near 270 mu mol mol(-1) which occurred between 15,000 and 12,000 years ago. Atmospheric CO2 directly affects photosynthesis and plant productivity, with the largest proportional responses occurring below the current level of 350 mu mol mol(-1). In the late Pleistocene, CO2 levels near 200 mu mol mol(-1) may have been too low to support the level of productivity required for successful establishment of agriculture. Recent studies demonstrate that atmospheric CO2 increase from 200 to 270 mu mol mol(-1) stimulates photosynthesis and biomass productivity of C-3 plants by 25% to 50%, and greatly increases the performance of C-3 plants relative to weedy C-4 competitors. Rising CO2 also stimulates biological nitrogen fixation and enhances the capacity of plants to obtain limiting resources such as water and mineral nutrients. These results indicate that increases in productivity following the late Pleistocene rise in CO2 may have been substantial enough to have affected human subsistence patterns in ways that promoted the development of agriculture. Increasing CO2 may have simply removed a productivity barrier to successful domestication and cultivation of plants. Through effects on ecosystem productivity rising CO2 may also have been a catalyst for agricultural origins by promoting population growth, sedentism, and novel social relationships that in turn led to domestication and cultivation of preferred plant resources.

KEYWORDS: CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSE, MINERAL NUTRITION, NITROGEN-FIXATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RISING CO2, SOIL ORGANIC MATTER, WATER RELATIONS

2101

Sage, R.F., J. Santrucek, and D.J. Grise. 1995. Temperature effects on the photosynthetic response of C-3 plants to long-term CO2 enrichment. *Vegetatio 121(1-2):67-77.*

To assess the long-term effect of increased CO2 and temperature on plants possessing the C-3 photosynthetic pathway, Chenopodium album plants were grown at one of three treatment conditions: (1) 23 degrees C mean day temperature and a mean ambient partial pressure of CO2 equal to 350 mu bar; (2) 34 degrees C and 350 mu bar CO2; and (3) 34 degrees C and 750 mu bar CO2. No effect of the growth treatments was observed on the CO2 response of photosynthesis, the temperature response of photosynthesis, the content of Ribulose-1,5-bisphosphate carboxylase (Rubisco), or the activity of whole chain electron transport when measurements were made under identical conditions. This indicated a lack of photosynthetic acclimation in C. album to the range of temperature and CO2 used in the growth treatments. Plants from every treatment exhibited similar interactions between temperature and CO2 on photosynthetic activity. At low CO2 (< 300 mu bar), an increase in temperature from 25 to 35 degrees C was inhibitory for photosynthesis, while at elevated CO2 (> 400 mu bar), the same increase in temperature enhanced photosynthesis by up to 40%. In turn, the stimulation of photosynthesis by CO2 enrichment increased as temperature increased. Rubisco capacity was the primary limitation on photosynthetic activity at low CO2 (195 mu bar). As a consequence, the temperature response of A was relatively flat, reflecting a low temperature response of Rubisco at CO2 levels below its k(m) for CO2. At elevated CO2 (750 mu bar), the temperature response of electron transport appeared to control the temperature dependency of photosynthesis above 18 degrees C. These results indicate that increasing CO2 and temperature could substantially enhance the carbon gain potential in tropical and subtropical habitats, unless feedbacks at the whole plant or ecosystem level limit the long-term response of photosynthesis to an increase in CO2 and temperature.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CHENOPODIUM-ALBUM L, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, LIGHT-INTENSITY, NERIUM-OLEANDER, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS

2102

Sage, R.F., B. Schappi, and C. Korner. 1997. Effect of atmospheric CO2 enrichment on Rubisco content in herbaceous species from high and low altitude. *Acta Oecologica-International Journal of Ecology 18(3):183-192.*

Atmospheric CO2 enrichment reduces Rubisco content in many species grown in controlled environments; however, relatively few studies have examined CO2 effects on Rubisco content of plants grown in their natural habitat. We examined the response of Rubisco content to atmospheric CO2 enrichment (600-680 mu mol mol-l in place of ppm) in 5 herbaceous species growing in a low altitude grassland (550 m) near Basel, Switzerland, and 3 herbaceous species from Swiss alpine grassland at 2 470 m. At low elevation, the dominant grass Bromus erectus and the subdominant dicot Sanquisorba miller exhibited 20% to 25% reduction of Rubisco content following high CO2 exposure; no CO2 effect was observed in the subdominants Carex flacca, Lotus corniculatus and Trifolium repens. At the Alpine site, the subdominant grass Pea alpina maintained 27% less Rubisco content when grown at high CO2 while the co-dominant forb Leontodon helveticus had 19% less Rubisco in high CO2: Rubisco content was unaffected in the tundra dominant Carer curvula. Because the degree of Rubisco modulation was similar between high and low elevation sites, it does not appear that differences in local partial pressure of CO2 (altitude) or differences in stress in general induce different patterns of modulation of photosynthetic capacity in response to high CO2. In addition, the degree of Rubisco reduction (<30%) was less than might be indicated by the low biomass response to CO2 enrichment previously observed al these sites. Thus, plants in Swiss lowland and alpine grassland appear to main tain greater Rubisco concentration and photosynthetic capacity than whale plants can effectively exploit in terms of harvestable biomass.

KEYWORDS: ALPINE GRASSLAND, C-3, ELEVATED CO2, EXPRESSION, GROWTH, LEAVES, LIGHT-DEPENDENT REGULATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS

2103

Sage, R.F., T.D. Sharkey, and J.R. Seemann. 1990. Regulation of ribulose-1,5-bisphosphate carboxylase activity in response to light-intensity and CO2 in the C3 annuals Chenopodium album L and Phaseolus vulgaris L. *Plant Physiology 94(4):1735-1742.*

The light and CO2 response of (a) photosynthesis, (b) the activation state and total catalytic efficiency (K(cata)) of ribulose-1,5-bisphosphate carboxylase (rubisco), and (c) the pool sizes of ribulose 1,5-bisphosphate, (RuBP), ATP, and ADP were studied in the C3 annuals Chenopodium album and Phaseolus vulgaris at 25-degrees-C. The initial slope of the photosynthetic CO2 response curve was dependent on light intensity at reduced light levels only (less than 450 micromoles per square meter per second in C. album and below 200 micromoles per square meter per second in P. vulgaris). Modeled simulations indicated that the initial slope of the CO2 response of photosynthesis exhibited light dependency when the rate of RuBP regeneration limited photosynthesis, but not when rubisco capacity limited photosynthesis. Measured observations closely matched modeled simulations. The activation state of rubisco was measured at three light intensities in C. album (1750, 550, and 150 micromoles per square meter per second) and at intercellular CO2 partial pressures (C(i)) between the CO2 compensation point and 500 microbars. Above a C(i) of 120 microbars, the activation state of rubisco was light dependent. At light intensities of 550 and 1750 micromoles per square meter per second, it was also dependent on C(i), decreasing as the C(i) was elevated above 120 microbars at 550 micromoles per square meter per second and above 300 microbars at 1750 micromoles per square meter per second. The pool size of RuBP was independent of C(i) only under conditions when the activation state of rubisco was dependent on C(i). Otherwise, RuBP pool sizes increases as C(i) was reduced. ATP pools in C. album tended to increase as C(i) was reduced. In P. vulgaris, decreasing C(i) at a subsaturating light intensity of 190 micromoles per square meter per second increased the activation state of rubisco but had little effect on the K(cat). These results support modelled simulations of the rubisco response to light and CO2, where rubisco is assumed to be down-regulated when photosynthesis is limited by the rate of RuBP regeneration.

KEYWORDS: ABSCISIC- ACID, CHLOROPLAST PROTEIN, GAS-EXCHANGE, INTACT LEAVES, OXYGENASE, PHOTOSYNTHESIS, POOL SIZES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE, WHEAT SEEDLINGS

2104

Sagi, M., A. Dovrat, T. Kipnis, and H. Lips. 1998. Nitrate reductase, phosphoenolpyruvate carboxylase, and glutamine synthetase in annual ryegrass as affected by salinity and nitrogen. *Journal of Plant Nutrition 21(4):707-723.*

The concentration of organic acids, organic nitrogen (N), nitrate (NO3), and total cations increased in annual ryegrass (Lolium multiflorum Lam.) with salinity and N concentration in the growth medium. Increasing salinity and N in the growth medium induced changes in the level of key enzymes of N assimilation and organic acids: nitrate reductase (NR, EC 1.6.6.1), phosphoenolpyruvate carboxylase (PEPc, EC 4.1.1.31), and glutamine synthetase (GS, EC 6.3.1.2). Plants grown in pots filled with sand were irrigated with nutrient solutions with an electroconductivity of 2 or 11.2 dS m(-1) and N applied as ammonium nitrate (NH4NO3), sodium nitrate (NaNO3), or ammonium applied as ammonium nitrate (NH4NO3), sodium nitrate (NaNO3), or ammonium (NH4) as ammonium sulfate [(NH4)(2)SO4] at concentrations of 0.5, 4.5 or 9.0 mM. Nitrate reductase, PEPc, and GS increased with salinity and N level. Shoot NR was highest in the presence of NH4NO3 irrespective of salinity level, while root NR activity responded best to NO3. Enhancement of PEPc activity in both shoots and roots was highest with NH4NO3 and lowest with NH4. Nitrogen source had no significant effect on GS activity in shoots or roots of ryegrass. Shoot NR activity increased with NO3 concentration in the tissue, as calculated from repression coefficients. The PEPc activity correlated positively with total cations and NO3 concentrations in the plants, irrespective of the salinity level, suggesting that the increase in total cations and NO3 induced by salinity may have triggered the changes in enzyme activities. The concentration of organic acids in both shoots and roots correlated positively with PEPc activity irrespectively of the salinity level. The PEPc activity was higher in roots than in shoots, while organic acid concentration was higher in shoots. These results suggest that a significant part of the organic acids produced in the roots were used as carbon skeleton for transamination reactions. The increased activity of NR, PEPc, and GS in roots may constitute part of an adaptation strategy of the plant to increasing salinity in the medium. These enzymes have an important role in the metabolism of amino acids and the synthesis of organic N in annual ryegrass irrigated with saline water, and boosting them with suitable N fertilizers could increase the nutritional value and protein content of the crop.

KEYWORDS: ASSIMILATION, CARBON, ENRICHED RHIZOSPHERE CO2, GROWTH, HIGHER-PLANTS, METABOLISM, NUTRITION, SEEDLINGS, STRESS, TOMATO

2105

Saito, M., T. Homma, Y. Nemoto, and H. Matsuoka. 1993. Intracellular potential change of tradescantia-virginiana L leaf in response to co2 stress. *Bioelectrochemistry and Bioenergetics 32(2):133-143.*

The response of a Tradescantia virginiana L. leaf to CO2 stress was measured using a double-barrelled microelectrode (a potential recording electrode and an electrode carrying Lucifer yellow CH dye (LY)). After potential measurement, LY was allowed to diffuse out of the microelectrode by iontophoresis. The position of electrode tip was ascertained from the pattern of LY diffusion. The intracellular potential changed markedly in response to CO2 stress. The most typical response pattern obtained during CO2 exposure (ON response) was two-phase, initially changing in the positive direction and then in the negative direction. During the ON response, marked efflux of K+ and slight influx of Cl- occurred initially, followed by efflux of Cl- and influx of H+. On cessation of CO2 exposure, the potential showed a similar two-phase pattern (OFF response) but the ion fluxes reversed. Therefore the effect Of CO2 exposure is not just decrease in intracellular pH owing to dissolution Of CO2.

KEYWORDS: ELEVATED CO2, LEAVES, PH MICRO-ELECTRODES, PHOTOSYNTHESIS, PLANT-CELLS

2106

Sala, A., and J.D. Tenhunen. 1996. Simulations of canopy net photosynthesis and transpiration in Quercus ilex L under the influence of seasonal drought. *Agricultural and Forest Meteorology 78(3-4):203-222.*

A mechanistically based C-3 leaf photosynthesis model combined with an empirical stomatal model and a canopy model of light interception and microclimate was used to simulate Quercus ilex canopy net photosynthesis and transpiration at l'Avic watershed (NE Spain). The model takes into account the sun-shade leaf differentiation of photosynthetic characteristics as affected by depth within the canopy. Based on field studies, simulations were carried out for two locations within the watershed along a gradient in elevation, microclimate and forest structure. Effective predictions of diurnal and seasonal courses of stomatal conductance of sun and shade leaves for different days during the year were obtained by changing a single model variable termed g(F). The value of g(F) determined from least squares of observed vs. simulated time courses was linearly related to pre-dawn xylem water

potential over critical ranges of the response curve. Response to g(F) in the model may to a great extent be thought of as the integrated expression of canopy response to root system generated signals or control mechanisms. For development of predictive capability, g(F) is extremely useful because it allows seasonal assessments of water use and carbon dioxide uptake with differing patterns in water availability. Based on simulated responses on representative clear, overcast and variable days throughout the year, only small differences in annual totals for net photosynthesis and transpiration were found between the two sites, despite large differences in soil drying. Annual estimates of canopy water loss were in close agreement with independent estimates of evapotranspiration using the hydrological input/output method.

KEYWORDS: CAPACITY, CARBON GAIN, EFFICIENCY, ELEVATED CO2, EXCHANGE, FOREST, NITROGEN, OAK, STOMATAL CONDUCTANCE, WATER-USE

2107

Saleska, S.R., J. Harte, and M.S. Torn. 1999. The effect of experimental ecosystem warming on CO2 fluxes in a montane meadow. *Global Change Biology 5(2):125-141.*

Climatic change is predicted to alter rates of soil respiration and assimilation of carbon by plants. Net loss of carbon from ecosystems would form a positive feedback enhancing anthropogenic global warming. We tested the effect of increased heat input, one of the most certain impacts of global warming, on net ecosystem carbon exchange in a Rocky Mountain montane meadow. Overhead heaters were used to increase the radiative heat flux into plots spanning a moisture and vegetation gradient. We measured net whole-ecosystem CO2 fluxes using a closed-path chamber system, relatively nondisturbing bases, and a simple model to compensate for both slow chamber leaks and the CO2 concentration-dependence of photosynthetic uptake, in 1993 and 1994. In 1994, we also measured soil respiration separately. The heating treatment altered the timing and magnitude of net carbon fluxes into the dry zone of the plots in 1993 (reducing uptake by approximate to 100 g carbon m(-2)), but had an undetectable effect on carbon fluxes into the moist zone. During a strong drought year (1994), heating altered the timing, but did not significantly alter the cumulative magnitude, of net carbon uptake in the dry zone. Soil respiration measurements showed that when differences were detected in dry zone carbon Fluxes, they were caused by changes in carbon input from photosynthesis, not by temperature-driven changes in carbon output from soil respiration. When differences were detected in dry-zone carbon fluxes, they were caused by changes in carbon input from photosynthesis, not by a temperature-driven changes in carbon output from soil respiration. Regression analysis suggested that the reduction in carbon inputs from plants was due to a combination of two soil moisture effects: a direct physiological response to decreased soil moisture, and a shift in plant community composition from high-productivity species to low-productivity species that are more drought tolerant. These results partially support predictions that warming may cause net carbon losses from some terrestrial ecosystems. They also suggest, however, that changes in soil moisture caused by global warming may be as important in driving ecosystem response as the direct effects of increased soil temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC CHANGE, FEEDBACKS, MANIPULATION, PLANT-RESPONSES, SOIL MICROCLIMATE, STORAGE, TEMPERATURE, TRACE GAS FLUXES, VEGETATION

2108

Sallanon, H., B. Dimon, P. Carrier, and P. Chagvardieff. 1995. Effects of co2 concentration and irradiance on growth and photosynthesis of juglans-regia plantlets grown in-vitro. *Photosynthetica 31(2):241-249.*

Walnut (Juglans regia L.) plantlets were incubated during micropropagation in standard vessels (quasi confined vessels) or in aerated vessels flushed with 360 or 20 000 cm(3)(CO2) m(- 3) under irradiances of 70 (LI) and 250 (HI) mu mol m(-2) s(- 1). Plantlet morphology was strongly affected by the environment: leaf surface was increased, but shoot elongation and number of stems were reduced after increasing the irradiance of culture. Gross photosynthesis (P-G) capacity measured by using the O-18(2) isotope and mass-spectrometry techniques was increased by increasing photosynthetic photon flux (PPF) and CO2 concentration. Plantlets exhibited a potential for photorespiratory activity and Mehler-type reaction and a high rate of mitochondrial respiration in all vessel types and irradiances. When a long-term HI was applied, gas exchange rates (P-G and O-2 uptake) were reduced in most of the vessel and PPF conditions, except in quasi confined vessels. Under all the growth conditions, net photosynthetic rate (P-N) was zero or slightly positive and the dry matter accumulation was very similar. Changes in O-2 exchange, growth rate or enzyme activities linked to carbon fixation that were induced by changes in PFD and CO2 concentration showed that the photosynthetic characteristics of plantlets were typical for hetero-mixotrophic tissues.

KEYWORDS: ENRICHMENT, FIXATION, INVITRO, LEAVES, LIGHT, O2, RESPIRATION

2109

Sallanon, H., H. Isaka, B. Dimon, C. Ravel, and P. Chagvardieff. 1997. CO2 exchanges and nutrient uptake during multiplication and rooting of micropropagated Juglans regia plantlets. *Plant Science 124(1):107-116.*

CO2 gas exchanges in light and dark, PEPC and Rubisco activities and consumption of sugar and mineral nutrients (K+, Ca2+ Mg2+: NH4+, NO3-, PO43-, SO42-) were measured during multiplication and rooting stages of in vitro-cultivated Juglans regia. CO2 gas exchanges in light and dark, and PEPC and Rubisco activities varied with plantlet age during a growth cycle. They were higher during the first part of the exponential stage of growth (defined in terms of dry weight increase). Respiratory gas exchanges were always higher than photosynthetic ones. The differences between the two stages of growth were reflected in respiration/photosynthesis and total Rubisco activity/initial Rubisco activity ratios, which were higher in the rooting than in the multiplication stage. This work underlines the need to consider the wide variations in photosynthetic and respiratory gas exchanges related to the plantlet development stage. Mineral absorption also displayed variations, both in the quantity and selectivity of the inorganic nutrients supplied. During the multiplication stage, fast exhaustion of PO43- and NH4(+) occurred, whereas depletion of Ca2+, NH4+, PO43- and SO42- were observed throughout the rooting stage. The inhibition of photosynthetic activity may be linked to the presence of sugar in the medium and also to ion deficiencies during the multiplication stage. Hence, this work also highlights the importance of mineral elements, suggesting a need to review nutrient medium compositions. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: AERATION, ANATOMY, CULTURE, ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHESIS

2110

Salt, D.T., G.L. Brooks, and J.B. Whittaker. 1995. Elevated carbon-dioxide affects leaf-miner performance and plant-growth in docks (rumex spp). *Global Change Biology 1(2):153-156.*

Exposure of R. crispus and R. obtusifolius to elevated CO2 (600 ppm) resulted in an increased C:N ratio of leaf tissue and greater leaf areas. Larvae of P. nigritarsis mining leaves of X. obtusifolius during exposure produced significantly bigger mines in elevated than in ambient (350

ppm) conditions. There were no significant treatment effects on pupal weight although in both host species mean weight was greater in ambient than in elevated conditions. These results are consistent with the hypothesis that insect herbivores compensate for increased C:N ratios by increased food consumption This response by herbivores may partially offset predicted increases in plant biomass in a future high CO2 environment.

KEYWORDS: CO2, INSECTS, YIELD

2111
Salt, D.T., P. Fenwick, and J.B. Whittaker. 1996. Interspecific herbivore interactions in a high CO2 environment: Root and shoot aphids feeding on Cardamine. *Oikos 77(2):326-330.*

This study investigated the effects of elevated CO2 on populations of root and/or shoot aphids and their effects on partitioning in Cardamine pratensis. Total plant biomass in elevated (approximate to 600 ppm) CO2 of uninfested Cardamine plants was 52% higher than in ambient (approximate to 350 ppm) concentrations but CO2 effects were not statistically significant. In elevated CO2, feeding by shoot aphids (Aphis fabae fabae) alone and in combination with root aphids (Pemphigus populitransversus), and root aphids alone had no significant effect on plant biomass. No significant effects of elevated CO2 were detected on population size of the shoot or root-feeding species. Interspecific effects were detected between the root and shoot species. Root aphid populations were significantly smaller in the presence of shoot aphids on the same plants. In this system plant growth was unaffected by an elevated CO2 environment. Plant species which are more sensitive to elevated CO2 may show a modified response to herbivore pressure in a future atmospheric environment.

KEYWORDS: COMPETITION, FIELD, GROWTH, HOMOPTERA, INSECT HERBIVORES, PERFORMANCE, PLANT-MEDIATED INTERACTIONS, QUALITY, RESISTANCE, STRESS

2112
Samarakoon, A.B., and R.M. Gifford. 1995. Soil water content under plants at high CO2 concentration and interactions with the direct CO2 effects: A species comparison. *Journal of Biogeography 22(2-3):193-202.*

Wheat, maize and cotton, grown as spaced plants in large pots of soil, differed in the way high (2 X ambient) CO2 concentration affected the time-course of soil water use. For wheat, the tendency to conserve water owing to reduction in stomatal conductance in high CO2 was largely offset by the stimulation of leaf area development as the soil column dried. However, when the soil was maintained continuously wet, soil water conservation occurred because in the absence of water stress high CO2 did not maintain a greater leaf area. For maize, which has little or no photosynthetic response to CO2 concentrations above ambient but a strong stomatal response, water was conserved and the soil profile dried more slowly. Maize leaf area and dry matter growth increased in response to damper soil under high CO2, despite no growth response to CO2 in the absence of water stress. For cotton, which has a strong photosynthetic but weak stomatal response to CO2, the soil column dried faster under high CO2. Despite this drier soil, cotton still showed the greatest response to high CO2 of leaf area and dry matter growth of the three species compared. Under wet soil conditions, cotton exhibited a very large leaf area response to CO2 leading to much greater water use per plant. This contrasts with both wheat and maize which conserved water at high CO2 when wet. Despite these contrasting transpiration and growth responses, all three species exhibited a relatively similar increase in water use efficiency under high CO2 for both wet and dry conditions. It is concluded that the secondary effect of high CO2 on soil water content exerts a strong confounding influence on growth responses to CO2. In the longer term, the changed soil water status would influence hydrology, soil microbiology, nutrient relations and species composition. From indirect evidence it is proposed that the relative enhancement of growth owing to CO2 enrichment is greater under drought conditions than in wet soil because of the effect of water deficit on the intercellular CO2 concentration in the leaf, C-i. If water deficits cause C-i/C-a to decline then photosynthesis is operating in a more CO2-sensitive region of the CO2 response curve.

KEYWORDS: CARBON DIOXIDE, COTTON, FIELD, GROWTH, LEAF, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION, WHEAT, YIELD

2113
Samarakoon, A.B., and R.M. Gifford. 1996. Elevated CO2 effects on water use and growth of maize in wet and drying soil (vol 23, pg 53, 1996). *Australian Journal of Plant Physiology 23(3):401.*

2114
Samarakoon, A.B., and R.M. Gifford. 1996. Elevated CO2 effects on water use and growth of maize in wet and drying soil. *Australian Journal of Plant Physiology 23(1):53-62.*

It is unclear from the literature as to whether growth of C-4 species is responsive to elevated atmospheric CO2 concentration. Reports vary between no response to strong response. To explore the origin of this discrepancy, spaced plants of maize (Zea mays) were grown at atmospheric CO2 concentrations of 362 or 717 mu L L(-1) under continuously wet or drying soil regimes. The aims were to evaluate the comparative growth promotion from elevated CO2 in a C-4 plant under the two contrasting water regimes and the causes of any such promotion, and also how water-use efficiency (WUE) is influenced by high CO2 under the two water regimes. In wet soil, transpiration rate was reduced on average by 29% at high CO2 but neither total dry matter nor plant height was significantly affected by CO2 level. Leaf area was not influenced significantly, so daily water use per plant was 25% lower and WUE was increased entirely due to reduced water use at high CO2. In soil that was drying from field capacity, plants in high CO2 used about 30% less water than those in ambient CO2 while the soil was still wet. This resulted in higher soil water content at high CO2. Plant growth showed a marked response, accumulating 35% more leaf area and 50% more dry matter. Young internodes elongated up to 170% more, giving taller plants. The growth enhancement was largely due to higher average net assimilation rate indicating that C-4 photosynthesis responded to elevated CO2 during drought. In drying soil the increase in WUE was due to both increased dry matter and reduced water use, the contribution from each depending on the stage of soil drying. We hypothesise therefore that literature examples where maize growth responded to elevated CO2 may have involved (possibly unrecognised) minor water deficits.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, CARBON DIOXIDE, COMMUNITIES, ENRICHMENT, MARSH, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, YIELD

2115
Samarakoon, A.B., and R.M. Gifford. 1996. Water use and growth of cotton in response to elevated CO2 in wet and drying soil (vol 23, pg 63, 1996). *Australian Journal of Plant Physiology 23(3):401.*

2116
Samarakoon, A.B., and R.M. Gifford. 1996. Water use and growth of

cotton in response to elevated CO2 in wet and drying soil. *Australian Journal of Plant Physiology 23(1):63-74.*

Cotton (Gossypium hirsutum cv. Sicala 34) was grown at 352 ('low CO2') or 710 ('high CO2') mu L L(-1) atmospheric CO2 in continuously wet soil, or in drying soil, or in drying soil re- wetted after plant wilting. In wet soil, the approximately 15% reduction in transpiration per unit leaf area owing to high CO2 was only half that for other species, whereas effects on growth and leaf area were relatively larger. Consequently, water use per plant was 45-50% higher for high CO2 plants in contrast to other species for which the rate of water use is either the same or lower in high CO2. Greater plant water use early in a drying cycle caused the soil to dry faster under high CO2 than under low CO2. The addition of the consequential greater water stress at high CO2 in drying soil to the direct CO2 effect on stomata caused the transpiration rate of high CO2 plants to fall by up to 60% as the soil dried relative to plants drying at low CO2. After re-wetting the dry soil, the reduction in transpiration rate at high CO2 returned within hours to the value of 15% seen in wet soil. The results were inconsistent with the idea that water deficits increase the sensitivity of stomatal aperture to CO2. Other consequences of drier soil under high CO2 compared with low CO2 were: (a) unlike in many other species, in cotton, the relative growth enhancement by high CO2 is not higher under drying soil compared with wet soil owing to the opposite effect on soil water content; and (b) the increased water-use efficiency in drying soil relative to wet soil was greater in high CO2 plants than in low CO2. The confounding of indirect effects of soil water with the direct CO2 effects may explain the wide variability of literature reports about CO2 effects on stomatal conductance and water use.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO2, CARBON DIOXIDE, FIELD, LEAF, PHOTOSYNTHETIC RATE, PLANT GROWTH, STOMATAL CONDUCTANCE, TRANSPIRATION, YIELD

2117

Samarakoon, A.B., W.J. Muller, and R.M. Gifford. 1995. Transpiration and leaf-area under elevated co2 - effects of soil-water status and genotype in wheat. *Australian Journal of Plant Physiology 22(1):33-44.*

Transpiration rate, leaf area expansion, water use and water- use efficiency (WUE) of spaced plants of wheat (cvv. Matong and Quarrion), were examined at ambient and twice ambient CO2 concentrations in wet and drying soil regimes. A hypothesis tested was that both stomatal conductance (g(s)) and leaf area development are so regulated by the plant in relation to soil water status that the reduction of approximately 40% in g(s) in high CO2 has no permanent impact on whole-plant water use. Whereas, during a soil drying cycle, leaf area increase under elevated CO2 counterbalanced closely for reduced g(s) in terms of soil water depletion as reported elsewhere, this counterbalance was neither exact at all times, nor did it apply when the soil was continuously wet. In wet soil, leaf area was not enhanced much by elevated CO2, probably because, under the high radiation and nutritional conditions used, the tillering rate was almost maximal anyway. Quarrion, having a 40% lower g(s) than Matong genetically, did not counterbalance a reduced transpiration rate with a larger leaf area under either drying or wet soil conditions. These results support rejection, for wheat, of the hypothesis posed; elevated CO2 increased leaf area mainly by virtue of the direct photosynthetic increase rather than changed soil water status. In wet soil, low g(s) Quarrion had a higher CO2 effect on WUE (+ 73 to 82%) than did Matong (+ 54 to 65%). In drying soil, both cultivars had a similar increase in WUE at high CO2 (+ 60 to 68%).

KEYWORDS: AMBIENT, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, PLANT GROWTH, RESPONSES, RICE, ROOT RESTRICTION, STRESS, TERM, YIELD

2118

Sampson, D.A., E.J. Cooter, P.M. Dougherty, and H.L. Allen. 1996. Comparison of the UKMO and GFDL GCM climate projections in NPP simulations for southern loblolly pine stands. *Climate Research 7(1):55-69.*

We used the process model BIOMASS version 13.0 to simulate contemporary net primary production (NPP) and NPP response to climate projections for a doubling of atmospheric CO2 concentration from 2 general circulation models (GCMs) that vary in their CO2 sensitivity: the less sensitive GFDL and the more sensitive UKMO. Increased GCM sensitivity to CO2 is reflected in increased predictions in the magnitude, variation, and range of the climate variables. Simulations used a 40 yr historical climate record, and 2 stand and site conditions to standardize the total NPP response estimates for eighteen 1x1 degrees grid cells across the southern United States, Contemporary NPP and NPP response estimates from the 18 cells were smoothed using a cell search algorithm to obtain an NPP response index matrix for the entire loblolly pine (Pinus taeda) forest-type. We conducted a sensitivity analysis of the environmental variables projected to change in a 2xCO(2) environment to help interpret simulation output. Contemporary NPP varied from 2.5 to 8.5 Mg C ha(-1) yr(-1) over the range of loblolly pine, High leaf area index (LAI) simulations had 1.5 to 2 times the productivity of low LAI simulations, but the regional patterns were similar; NPP was correlated with regional differences in precipitation and temperature. The NPP response to future climate and atmospheric changes depended on the GCM used, and on the stand and site condition assumed. Inter-annual estimates for the 18 cell simulations resulted in a +22 to +84% NPP response for the GFDL climate projections and a -30 to +94% NPP response for the UKMO climate projections. The 40-year average NPP response for the smoothed data ranged from +43 to +65% and -1 to +94% for the GFDL and the UKMO climate projections, respectively. Consequently, the magnitude and range of the 40-year average NPP response to the climate projections was directly correlated with the GCM CO2 sensitivity. Although increased CO2 sensitivity resulted in broader extremes in the predicted temperature response, precipitation response for the 2 models was similar. The NPP response was also correlated with the patterns in predicted climate change, with regional differences coupled to local climatic conditions. Climate projections from both models produced similar NPP responses when predicted temperatures and precipitation regimes were similar. Elevated ambient CO2 had a greater effect on NPP response than temperature or precipitation in the sensitivity comparisons. Simulations indicate that a CO2 fertilizer effect, assuming no CO2 acclimation, more than compensates for declines in productivity over most of the loblolly pine forest-type associated with projected decreased precipitation and/or projected low to moderate increases in temperature and, therefore, increased maintenance respiration costs.

KEYWORDS: CO2 CONCENTRATIONS, ELEVATED CARBON-DIOXIDE, FORESTS, GROWTH, LEAF-AREA, MODEL, RADIATA, RESPONSES, SLASH PINE, WATER

2119

Sampson, R.N., M. Apps, S. Brown, C.V. Cole, J. Downing, L.S. Heath, D.S. Ojima, T.M. Smith, A.M. Solomon, and J. Wisniewski. 1993. Workshop summary statement - terrestrial biospheric carbon fluxes - quantification of sinks and sources of co2. *Water, Air, and Soil Pollution 70(1-4):3-15.*

Understanding the role of terrestrial ecosystems in the global carbon (C) cycle has become increasingly important as policymakers consider options to address the issues associated with global change, particularly climate change. Sound scientific theories are critical in predicting how these systems may respond in the future, both to climate change and human actions. In March 1993, 60 scientists from 13 nations gathered

in Bad Harzburg, Germany, to develop a state-of-the- science assessment of the present and likely future C fluxes associated with the major components of the earth's terrestrial biosphere. In the process, particular emphasis was placed on the potential for improving C sinks and managing long-term C sequestration. The majority of the week's work was conducted in eight working groups which independently considered a particular biome or subject area. The working groups considered: the Global Carbon Cycle; Boreal Forests and Tundra; Temperate Forests; Tropical Forests; Grasslands, Savannas and Deserts; Land and Water Interface Zones; Agroecosystems; and Biomass Management. This paper presents a brief overview of their major conclusions and findings. In addition, Table 1 brings together the best estimates from each group as to the current magnitude and estimated future direction of changes in the terrestrial C fluxes.

2120

Samuelson, L.J., and J.R. Seiler. 1992. Fraser fir seedling gas-exchange and growth in response to elevated co2. *Environmental and Experimental Botany 32(4):351-356.*

Growth and gas exchange characteristics were examined in Fraser fir (Abies fraseri (Pursh.) Poir.) seedlings grown from seed in elevated (713 ppm) or ambient (374 ppm) CO2 for 1 year (two artificial growing seasons) to determine the potential influence of a twice-ambient CO, concentration on this species. A subset of seedlings was transplanted from 172 cm3 pots into 1000 cm3 pots at 7 months to determine if CO2 effects were dependent on rooting volume. At 5 and 12 months, net photosynthesis (P(net)) and leaf conductance (g1) were lower in elevated CO2-grown seedlings grown in 172 cm3 pots than in ambient CO2-grown seedlings when measured at either 346 or 796 ppm CO2. For 12-month-old seedlings grown in 1000 cm3 pots, P(net) was reduced by an elevated CO2 growth environment only when measured at 346 ppm CO2, although g1 was lower in these seedlings when measured at either CO2 measurement level. Seedlings grown in both pot sizes and in elevated CO2 for 1 year had greater height, diameter, and leaf, stem, root and total dry weights than seedlings grown in ambient CO2. Specific leaf weight (SLW) was greater in elevated than in ambient CO2- grown needles only in the large pot size treatment. These results suggest that Fraser fir seedling growth will increase in a future elevated CO2 environment despite changes in gas exchange characteristics.

KEYWORDS: ATMOSPHERIC CO2, INCREASE

2121

Samuelson, L.J., and J.R. Seiler. 1993. Interactive role of elevated co2, nutrient limitations, and water-stress in the growth-responses of red spruce seedlings. *Forest Science 39(2):348-358.*

Red spruce (Picea rubens Sarg.) seedlings were grown from seed for 5 mo in ambient (362 ppm) or elevated (711 ppm) CO2 to determine the potential effect of an increase in global CO2 concentration on seedling growth and establishment. CO2 exposure treatments were crossed with two levels of soil fertility and water stress treatments to determine if seedling dry weight, size, and fixed growth responses to elevated CO2 depended on nutrient and water supply. Seedling dry weight and size responses to elevated CO2 at 5 mo did not depend on nutrient and water supply. Seedlings grown in both soil fertility treatments and water stress treatments responded similarly to CO2 treatment. Water stress and CO2 treatments did have an interactive influence on the fixed growth potential of the terminal leader. Leaf weight, leaf area, and height of the terminal leader of water-stressed seedlings were greater in seedlings exposed to elevated CO2 during budset than seedlings exposed to ambient CO2. Total new fixed growth (lateral plus terminal) and total terminal fixed growth (leaf plus stem) were greater in seedlings that formed shoot primordia in elevated CO2 than in ambient CO2. Red spruce seedlings grown in elevated CO2 for 5 mo had greater stem diameter, height, branching density, leaf weight, root weight, stem weight, total weight, and mean relative growth rate (RGR) from 3 to 5 mo than seedlings grown in ambient CO2. Red spruce seedling responses to elevated CO2 suggest that seedling establishment in natural environments may be enhanced when ambient CO2 concentrations rise even if water and nutrient availabilities are limited.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NUTRITION, PATTERNS, PINE, STANDS

2122

Samuelson, L.J., and J.R. Seiler. 1994. Red spruce seedling gas-exchange in response to elevated co2, water-stress, and soil fertility treatments. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 24(5):954-959.*

The interactive influences of ambient (374 muL.L-1) or elevated (713 muL.L-1) CO2, low or high soil fertility, well-watered or water-stressed treatment, and rooting volume on gas exchange and growth were examined in red spruce (Picea rubens Sarg.) grown from seed through two growing seasons. Leaf gas exchange throughout two growing seasons and growth after two growing seasons in response to elevated CO2 were independent of soil fertility and water-stress treatments, and rooting volume. During the first growing season, no reduction in leaf photosynthesis of seedlings grown in elevated CO2 compared with seedlings grown in ambient CO2 was observed when measured at the same CO2 concentration. During the second growing season, net photosynthesis was up to 21% lower for elevated CO2-grown seedlings than for ambient CO2-grown seedlings when measured at 358 muL.L-1. Thus, photosynthetic acclimation to growth in elevated CO2 occurred gradually and was not a function of root- sink strength or soil-fertility treatment. However, net photosynthesis of seedlings grown and measured at an elevated CO2 concentration was still over 2 times greater than the photosynthesis of seedlings grown and measured at an ambient CO2 concentration. Growth enhancement by CO2 was maintained, since seedlings grown in elevated CO2 were 40% larger in both size and weight after two growing seasons.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSES, NUTRIENT-UPTAKE, PHOTOSYNTHESIS, PHYSIOLOGY, RISING CO2, STANDS, TREES

2123

Sanders, I.R., R. Streitwolf-Engel, M.G.A. van der Heijden, T. Boller, and A. Wiemken. 1998. Increased allocation to external hyphae of arbuscular mycorrhizal fungi under CO2 enrichment. *Oecologia 117(4):496-503.*

Prunella vulgaris is was inoculated with different arbuscular mycorrhizal fungi (AMF) and grown at two concentrations of CO2 (ambient, 350 mu l l(-1), and elevated, 600 mu l l(-1)) to test whether a plants response to elevated CO2 is dependent on the species of AMF colonizing the roots. Using compartments accessible only to AMF hyphae but not to roots, we also tested whether elevated CO2 affects the growth of external AMF hyphae. Plant biomass was significantly greater at elevated than at ambient CO2; the biomass of the root system, for example, increased by a factor of 2. The colonization of AMF inside the root remained constant, indicating that the total AMF inside the root system also increased by a factor of 2. The length of external AMF hyphae at elevated CO2 was up to 5 times that at ambient CO2, indicating that elevated CO2 promoted allocation of AMF biomass to the external hyphae. The concentration and content of phosphorus in the stolons differed significantly between ambient and elevated CO2 but this resulted in either an increase or a decrease, according to which AMF isolate occupied the roots. We hypothesized that an increase in external

hyphal growth at elevated CO2 would result in increased P acquistion by the plant. To test this we supplied phosphorus, in a compartment only accessible to AMF hyphae. Plants did not acquire more phosphorus at elevated CO2 when phosphorus was added to this compartment. Large increases in AMF hyphal growth could, however? play a significant role in the movement of fixed carbon to the soil and increase soil aggregation.

KEYWORDS: CARBON DIOXIDE, COLONIZATION, ELEVATED CO2, GROWTH, ROOTS

2124

Santrucek, J., and R.F. Sage. 1996. Acclimation of stomatal conductance to a CO2-enriched atmosphere and elevated temperature in Chenopodium album. *Australian Journal of Plant Physiology 23(4):467-478.*

Acclimation of stomatal conductance to different CO2 and temperature regimes was determined in Chenopodium album L. plants grown at one of three treatment conditions: 23 degrees C and 350 mu mol CO2 mol(-1) air; 34 degrees C and 350 mu mol mol(-1); and 34 degrees C and 750 mu mol mol(-1). Stomatal conductance (g(s)) as a function of intercellular CO2 (C-i) was determined for each treatment at 25 and 35 degrees C, and these data were used to estimate gains of the feedback loops linking changes in intercellular CO2 with stomatal conductance and net CO2 assimilation. Growth temperature affected the sensitivity of stomata to measurement temperature in a pattern that was influenced by intercellular CO2. Stomatal conductance more than doubled at intercellular CO2 varying between 200 and 600 mu mol mol(-1) as leaf temperature increased from 25 to 35 degrees C for plants grown at 23 degrees C. In contrast, stomatal conductance was almost unaffected by measurement temperature in plants grown at 34 degrees C. Elevated growth CO2 attenuated the response of stomatal conductance to CO2, but growth temperature did not. Stomatal sensitivity to C-i was extended to higher C-i in plants grown in elevated CO2. As a result, plants grown at 750 mu mol mol(-1) CO2 had higher C-i/C-a at ambient CO2 values between 300 and 1200 mu mol mol(-1) than plants grown at 350 mu mol mol(-1) CO2. The gain of the stomatal loop was reduced in plants grown at elevated CO2 or at lower temperature when compared to plants grown at 350 mu mol mol(-1) and 34 degrees C. Both photosynthetic and stomatal loop gains acclimated to elevated CO2 in proportion so that their ratio, integrated over the range of C-i in which the plant operates, remained constant. Water use efficiency (WUE) more than doubled after a short-term doubling of ambient CO2. However, the WUE of plant grown and measured at elevated CO2 was only about 1.5 times that of plant transiently exposed to elevated CO2, due to stomatal acclimation. An optimal strategy of water use was maintained for all growth treatments.

KEYWORDS: C-3 PLANTS, CARBON DIOXIDE, CO2 ASSIMILATION, GAIN, HUMIDITY, LEAF CONDUCTANCE, LIGHT, PHOTOSYNTHESIS, RESPONSES, WATER-USE EFFICIENCY

2125

Santrucek, J., H. Santruckova, J. Kveton, M. Simkova, and K. Rohacek. 1994. The effect of elevated co2 concentration on photosynthetic co2 fixation, respiration and carbon economy of wheat plants. *Rostlinna Vyroba 40(8):689-696.*

Winter wheat plants were grown under controlled atmospheric and light conditions for 25 days to assess the response of photosynthesis, respiration and carbon allocation to elevated ambient CO2 concentration. Daily balance of carbon fixation and loss was measured separately for shoots and roots including root exudation. Doubled CO2 (700 mumol CO2 mol-1) stimulated photosynthetic CO2 uptake and dark respiration rate when calculated on the leaf area basis. However, total daily carbon gain per plant and total dry matter of shoot was lower for high-CO2-grown plants due to reduced leaf area. After 23 days of exposition to high CO2, photosynthesis was depressed probably due to limiting regeneration of ribulose bisphosphate. Both stomatal resistance and water use efficiency were markedly higher in high-CO2-grown plants. Higher evaporative demand in low-CO2-grown plants promoted root elongation. Total root length was 160% of that in high-CO2-grown plants. Root exudation of high-CO2-grown plants was higher in the first days of plant development, but the inhibition of net photosynthesis was followed by a decrease in exudation.

2126

Santruckova, H., J. Santrucek, J. Kveton, M. Simkova, D. Elhottova, and K. Rohacek. 1999. Carbon balance of a winter wheat-root microbiota system under elevated CO2. *Photosynthetica 36(3):341-354.*

We examined the carbon budget of young winter wheat plants and their associated microorganisms as affected by a doubling of the atmospheric CO2 concentration (700 mu mol mol(-1)). Plants were grown hydroponically in pre-sterilised sand at a controlled irradiance and temperature regime. Net photosynthesis (P-N) and respiration (R-D) rates of roots and shoots were measured continuously, plant growth and carbon distribution in the plant-root medium-associated microorganism system were determined destructively in interval-based analyses. P-N in elevated CO2 grown plants (EC) was 123 % of that in the control (AC) plants when averaged over the whole life span (39-d-old plants, 34 d in EC), but the percentage varied with the developmental stage being 115, 88, and 167 % in the pretillering, tillering, and posttillering phase, respectively. There was a transient depression of P-N, higher amplitude of day/night fluctuations of the chloroplast starch content, and depression of carbon content in rhizosphere of EC plants during the period of tillering. After 34 d in EC, carbon content in shoots,'roots, and in rhizodepositions was enhanced by the factors 1.05, 1.28, and 1.96, respectively. Carbon partitioning between above and belowground biomass was not affected by EC, however, proportionally more C in the belowground partitioning was allocated into the root biomass, Carbon flow from roots to rhizodepositions and rhizosphere microflora was proportional to P-N; its fraction in daily assimilated carbon decreased from young (17 %) to older (3-4 %) plants.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, GAS-EXCHANGE, GROWTH, NITROGEN, PHOTOSYNTHESIS, RESPONSES, RHIZOSPHERE, SOIL, TRITICUM-AESTIVUM L

2127

Santruckova, H., and M. Simek. 1997. Effect of soil CO2 concentration on microbial biomass. *Biology and Fertility of Soils 25(3):269-273.*

The effect of increasing soil CO2 concentration was studied in six different soils. The soils were incubated in ambient air (0.05 vol.% CO2) or in air enriched with CO2 (up to 5.0 vol.% CO2). Carbon dioxide evolution, microbial biomass, growth or death rate quotients and glucose decay rate were measured at 6, 12 and 24 h of CO2 exposure. The decrease in soil respiration ranged from 7% to 78% and was followed by a decrease in microbial biomass by 10-60% in most cases. High CO2 treatments did not affect glucose decay rate but the portion of C-gluc mineralized to CO2 was lowered and a larger portion of C-gluc remained in soils. This carbon was not utilized by soil microorganisms.

KEYWORDS: CARBON DIOXIDE, LAND, MICROORGANISMS, RESPIRATION

2128

Saralabai, V.C., M. Vivekanandan, and R.S. Babu. 1997. Plant responses to high CO2 concentration in the atmosphere. *Photosynthetica 33(1):7-37.*

The impact of continuous rise in ambient CO2 concentration (AC) in the atmosphere on different facets of growth of crop plants is assessed. The effects of CO2 enrichment (EC) on plant growth, C-3 and C-4 photosynthesis, source-sink ratio, partitioning and translocation of metabolites, photosynthetic enzymes, respiratory rate, leaf area index, stomatal conductance (g(s)), transpiration rate, biomass production and water use efficiency are reviewed. The CO2 fertilization effects are studied in both short-term (open top chambers) and long-term experiments. Long-term experiments suggest that ribulose-1,5-bisphosphate carboxylase is inactivated at high CO2 concentrations. Also g(s) is lowered. One of the conspicuous effects of EC is the closure of stomata in C-3 plants. Photosystem (PS) 2 electron transport is more affected than PS1. Starch is the immediate product accumulated in the leaf of C-3 plants. The "CO2 fertilization effect" does not confer any great advantage even in C-3 plants.

KEYWORDS: DARK RESPIRATION, DRY-MATTER PRODUCTION, ELEVATED CARBON-DIOXIDE, LOLIUM-PERENNE, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOYBEAN CANOPY PHOTOSYNTHESIS, SWEET-POTATO, WATER-USE EFFICIENCY

2129

Sasek, T.W., and B.R. Strain. 1990. Implications of atmospheric CO2 enrichment and climatic-change for the geographical-distribution of 2 introduced vines in the USA. *Climatic Change 16(1):31-51.*

2130

Sasek, T.W., and B.R. Strain. 1991. Effects of CO2 enrichment on the growth and morphology of a native and an introduced honeysuckle vine. *American Journal of Botany 78(1):69-75.*

Japanese honeysuckle (Lonicera japonica Thunb.), introduced to the United States, and the native coral honeysuckle (Lonicera sempervirens L.) were compared to determine how intrinsic differences in their growth characteristics would affect their response to atmospheric carbon dioxide enrichment. Plants of both species grown from cuttings were harvested after 54 days of growth in controlled environment growth chambers at 350, 675, or 1,000-mu-l/liter CO2. The biomass of Japanese honeysuckle was increased 135% at 675-mu-l/liter CO2 and 76% at 1,000-mu-l/liter CO2 after 54 days. Morphologically, the main effect of CO2 enrichment was to triple the number of branches and to increase total branch length six times. Enhanced and accelerated branching also increased total leaf area 50% at elevated CO2 concentrations. In coral honeysuckle, total biomass was only 40% greater in the elevated CO2 treatments. Branching was quadrupled but had not proceeded long enough to affect total leaf area. Main stem height was increased 36% at 1,000-mu-l/liter CO2. The much less significant height response of other woody erect growth forms suggests that vines may increase in importance during competition if atmospheric CO2 concentrations increase as predicted. The impact of Japanese honeysuckle in the United States may become more serious.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CLIMATE, KUDZU PUERARIA-LOBATA, LIQUIDAMBAR- STYRACIFLUA

2131

Sato, H., N. Sakurai, S. Sendo, H. Saneoka, H. Nobuyasu, and K. Fujita. 1997. Factors affecting leaf area development in husk leaf of flint corn. *Crop Science 37(6):1826-1831.*

Some corn (Zea mays L.) genotypes produce husk leaves (laminae extending from the husk) that on a per unit area basis, contribute more photosynthate to grain production than culm leaves. Furthermore, a high correlation between husk leaf area and dry weight has been observed, but little is known about the changes in cell components during development of husk leaves. A field experiment was conducted to quantify methanol (MeOH)- soluble fraction (cytosol) and incorporation of C-13-labeled photosynthate in cell walls from 9 d before silking (DBS) to silking. The ear leaf of flint corn (F-1 of N-19 by X-15) was subjected to (CO2)-C-13, eight DBS. Leaf area, dry weight, and photosynthetic activity of the husk leaves, and sugar content of various cell components were measured continuously during the 9-d period. The husk leaf attained one-half of its maximum apparent photosynthetic rate (P-0,) when it had 8% of its maximum leaf area at 4 DES. At 9 DBS, neutral sugars in the MeOH-soluble fraction accounted for most of nonstarch carbohydrates within the husk leaf (68%), while hemicellulose and cellulose fractions accounted for <10%. At silking, however, sugars in the hemicellulose and cellulose fractions increased by 23 and 56%, respectively. Results of (CO2)-C-13 labeling suggest that during rapid husk leaf development, MeOH- soluble fraction decreases, while the hemicellulose fraction fluctuates, and cellulose fraction increases.

KEYWORDS: DRY-MATTER, ELEVATED CO2, EXTENSION, GROWTH, HYPOCOTYLS, LEAVES, SWEET CORN, WALLS

2132

Saurer, M., S. Maurer, R. Matyssek, W. Landolt, M.S. Gunthardtgoerg, and U. Siegenthaler. 1995. The influence of ozone and nutrition on delta-C-13 in betula- pendula. *Oecologia 103(4):397-406.*

In the cellulose of stems and leaves, delta(13)C was investigated in a birch clone (Betula pendula), which was exposed throughout the growing season to either <3 (control) or 90/40 nl O-3 1(-1) (day/night). Each regime was split into plants under high or low nutrient supply. delta(13)C was increased (becoming less negative), in stems rather than leaves, by both high nutrition (+2 parts per thousand) and O-3 stress (+1 parts per thousand). Whereas high nutrition raised the water-use efficiency (WUE) while lowering the CO2 concentration in the inner leaf air space (c(i)), WUE decreased and c(i) increased under O-3 stress. Therefore, only the nutritional effect on the carbon isotope fractionation was reproduced by the model of Farquhar et al. (1982) which estimates WUE by means of delta(13)C based on C-i, C-i was not biased by 'patchiness' in respect to stomatal opening. The latter was verified by microscopical analysis and the complete water infiltration of the birch leaves through the stomata, independent of the diurnal course of the leaf conductance for water vapour. Under low nutrient supply, the activity of phosphoenol pyruvate carboxylase (PEPC) was roughly doubled by ozone to about 1.3% of the total carboxylation capacity (by PEPC + rubisco), and was increased to 1.7% under high nutrition. The fractionation model, extended to account for varying activities of the carboxylating enzymes, indicated that stimulated PEPC was the cause of elevated delta(13)C, although c(i) was increased under O-3 stress. The stimulation of PEPC and, as a consequence, elevated delta(13)C are discussed as part of a whole-plant acclimation to O-3 stress.

KEYWORDS: ABSCISIC- ACID, BIRCH LEAVES, CARBON ISOTOPE DISCRIMINATION, CO2, DECLINE, GAS-EXCHANGE, GROWTH, NET PHOTOSYNTHESIS, PLANTS, WATER-VAPOR EXCHANGE

2133

Saxe, H. 1994. Relative sensitivity of greenhouse pot plants to long-term exposures of no-containing and no2-containing air. *Environmental Pollution 85(3):283-290.*

Thirty-five cultivars of pot plants of 20 families were exposed for 50-64 days in a greenhouse facility to either 1 mul litre-1 NO with 0.5 mul litre-1 NO2, or 1 mul litre-1 NO2 with 0.1 mul litre-1 NO for 15 h each day, with air which was free from these gases as the reference. A sensitivity ranking of the pot plants was compiled, with the highest priority on visible injuries, followed by growth reductions, primarily as a response to the NO-dominated exposures, simulating the NO(x)-polluted environment in direct-fired, CO2-enriched greenhouses. This treatment reduced the leaf dry weight more than the number and area of the leaves. Twenty-two cultivars were significantly injured, while two (Hibiscus sp., Epipremnum pinnatum, green) were significantly improved. The NO(x)-sensitivity of pot plants was highest in cultivars with variegated, small or narrow leaves, and in the Moraceae family. Nine cultivars (Ficus elastica 'Robusta, F. benjamina, F. pumila 'Sonny, Dieffenbachia maculata 'Camilla', F. elastica 'Tineke, Epipremnum pinnatum 'Marble Queen', Begonia elatior 'Nelson, Cyclamen persica, Poinsettia 'Mini) were specifically sensitive to the NO-containing exposure; six were specifically sensitive to the NO2-containing exposure (F. elastica 'Robusta', Asparagus den. 'Sprengeri, Hedera helix 'Shamrock, Aspledium nidus, Aster novo-belgii, Hypoestes phyl. 'Betina); and 12 (Soleirolia soleirolii, Asparagus den. 'Sprengeri, H. helix 'Ester, Codiaeum 'Pictum, Rosa 'Minimo Red, F. benjamina 'Starlight, Saintpaulia ionantha 'light blue', F. pumila, Rhododendron simsii, H. helix 'Shamrock', Hibiscus sp., E. pinnatum) were equally sensitive to mixtures dominated by either gas, as measured by at least one response parameter.

KEYWORDS: CARBON DIOXIDE, CO2, NET PHOTOSYNTHESIS, NITROGEN-DIOXIDE, OXIDES, POLLUTION

2134

Saxe, H., D.S. Ellsworth, and J. Heath. 1998. Tree and forest functioning in an enriched CO2 atmosphere. *New Phytologist 139(3):395-436.*

Forests exchange large amounts of CO2 with the atmosphere and can influence and be influenced by atmospheric CO2. There has been a recent proliferation of literature on the effects of atmospheric CO2 on forest trees. More than 300 studies of trees on five different continents have been published in the last five years. These include an increasing number of field studies with a long-term focus and involving CO2 x stress or environment interactions. The recent data on long-term effects of elevated atmospheric CO2 on trees indicate a potential for a persistent enhancement of tree growth for several years, although the only relevant long-term datasets currently available are for juvenile trees. The current literature indicates a significantly larger average long-term biomass increment under elevated CO2 for conifers (130%) than for deciduous trees (49%) in studies not involving stress components. However, stimulation of photosynthesis by elevated CO2 in long-term studies was similar for conifers (62 %) and deciduous trees (53 %). Recent studies indicate that elevated CO2 causes a more persistent stimulation of biomass increment and photosynthesis than previously expected. Results of seedling studies, however, might not be applicable to other stages of tree development because of complications of age- dependent and size-dependent shifts in physiology and carbon allocation, which are accelerated by elevated CO2. In addition, there are many possible avenues to down-regulation, making the predicted canopy CO2 exchange and growth of mature trees and forests in a CO2-rich atmosphere uncertain. Although, physiological down-regulation of photosynthetic rates has been documented in field situations, it is rarely large enough to offset entirely photosynthetic gains in elevated CO2. A persistent growth stimulation of individual mature trees has been demonstrated although this effect is more uncertain in trees in natural stands. Resource interactions can both constrain tree responses to elevated CO2 and be altered by them. Although drought can reduce gas-exchange rates and offset the benefits of elevated CO2, even in well watered trees, stomatal conductance is remarkably less responsive to elevated CO2 than in herbaceous species. Stomata of a number of tree species have been demonstrated to be unresponsive to elevated CO2. We conclude that positive effects of CO2 on leaf area can be at least as important in determining canopy transpiration as negative, direct effects of CO2 on stomatal aperture. With respect to nutrition, elevated CO2 has the potential to alter tree-soil interactions that might influence future changes in ecosystem productivity. There is continued evidence that in most cases nutrient limitations diminish growth and photosynthetic responses to elevated CO2 at least to some degree, and that elevated CO2 can accelerate the appearance of nutrient limitations with increasing time of treatment. In many studies, tree biomass responses to CO2 are artefacts in the sense that they are merely responses to CO2-induced changes in internal nutritional status of the tree. There are numerous interactions between CO2 and factors of the biotic and abiotic environment. The importance of increasing atmospheric CO2 concentrations for productivity is likely to be overestimated if these are not taken into account. Many interactions, however, are simply additive rather than synergistic or antagonistic. This appears to hold true for many parameters under elevated CO2 in combination with temperature, elevated O- 3, and other atmospheric pollutants. However, there is currently little evidence that elevated CO2 will counteract O-3 damage. When the foliage content of C, mineral nutrients and secondary metabolites is altered by elevated CO2, tree x insect interactions are modified. In most trees, mycorrhizal interactions might be less important for direct effects of CO2 than for alleviating general nutrient deficiencies. Since many responses to elevated CO2 and their interactions with stress show considerable variability among species/genotypes, one principal research need is for comparative studies of a large variety of woody species and ecosystems under realistic conditions. We still need more long-term experiments on mature trees and stands to address critical scaling issues likely to advance our understanding of responses to elevated CO2 at different stages of forest development and their interactions with climate and environment. The only tools available at present for coping with the consequences of rising CO2 are management of resources and selection of genotypes suitable for the future climate and environment.

KEYWORDS: BEECH FAGUS- SYLVATICA, BETULA-PENDULA ROTH, CO2-INDUCED GROWTH ENHANCEMENTS, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE RESPONSES, LONG-TERM EXPOSURE, PICEA-ABIES L, PONDEROSA PINE- SEEDLINGS, SITCHENSIS BONG CARR, WATER-LOSS REGULATION

2135

ScarasciaMugnozza, G., P. DeAngelis, G. Matteucci, and R. Valentini. 1996. Long-term exposure to elevated [CO2] in a natural Quercus ilex L community: Net photosynthesis and photochemical efficiency of PSII at different levels of water stress. *Plant, Cell and Environment 19(6):643-654.*

Naturally grown trees of Mediterranean evergreen oak (Quercus ilex L.), representing the climax species of the region, were enclosed in six large open-top chambers and exposed to ambient and elevated CO2 concentrations during a 3 year period, Maximum daily net photosynthetic rates measured at the two different CO2 concentrations were from 30 to 100% higher in elevated than in ambient [CO2] throughout the experimental period, The increase in maximum daily photosynthesis was also accompanied by a 93% rise in the apparent quantum yield of CO2 assimilation, measured during periods of optimum soil moisture conditions, Hence, no clear evidence of downregulation of net photosynthetic activity was found, Interactions between atmospheric CO2 concentration and plant water stress were studied by following the natural evolution of drought in different seasons and years, At each level of water stress, the maximum rate of carbon assimilation was higher in elevated than in ambient [CO2] by up to 100%. Analysis of in vivo chlorophyll fluorescence parameters in normal (21%) and low (2%) oxygen concentrations provided useful insights into

the functioning and stability of the photosynthetic processes, The photochemical efficiency of PSII (F-v/F-m) progressively decreased as drought conditions became more evident; this trend was accentuated under elevated [CO2]. Thermal de-excitation processes were possibly more significant under elevated than under ambient [CO2], in a combination of environmental stresses. This research suggests two possible conclusions: (i) a 'positive' interaction between elevated [CO2] and carbon metabolism can be obtained through relief of water stress limitation in the summer months, and (ii) elevated [CO2], under drought conditions, may also enhance the significance of slow- relaxing quenching.

KEYWORDS: CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, O-2 EVOLUTION, PHOTON YIELD, PHOTOSYSTEM, QUANTUM YIELDS, VASCULAR PLANTS

2136

Schaffer, B., C. Searle, A.W. Whiley, and R.J. Nissen. 1996. Effects of atmospheric CO2 enrichment and root restriction on leaf gas exchange and growth of banana (Musa). *Physiologia Plantarum 97(4):685-693.*

The effects of atmospheric CO2 enrichment and root restriction on photosynthetic characteristics and growth of banana (Musa sp, AAA cv. Gros Michel) plants were investigated. Plants were grown aeroponically in root chambers in controlled environment glasshouse rooms at CO2 concentrations of 350 or 1000 mu mol CO2 mol(-1). At each CO2 concentration, plants were grown in large (200 l) root chambers that did not restrict root growth or in small (20 l) root chambers that restricted root growth. Plants grown at 350 pmol CO2 mol(-1) generally had a higher carboxylation efficiency than plants grown at 1 000 mu mol CO2 mol(-1), although actual net CO2 assimilation (A) was higher at the higher ambient CO2 concentration due to increased intercellular CO2 concentrations (Ci) resulting from CO2 enrichment. Thus, plants grown at 1 000 mu mol CO2 mol(-1) accumulated more leaf area and dry weight than plants grown at 350 mu mol CO2 mol(-1). Plants grown in the large root chambers were more photosynthetically efficient than plants grown in the small root chambers. At 350 mu mol CO2 mol(-1), leaf area and dry weights of plant organs were generally greater for plants in the large root chambers compared to those in the small root chambers. Atmospheric CO2 enrichment may have compensated for the effects of root restriction on plant growth since at 1 000 mu mol CO2 mol(-1) there was generally no effect of root chamber size on plant dry weight.

KEYWORDS: AAA, CAVENDISH SUBGROUP, ELEVATED CARBON-DIOXIDE, LEAVES, LIGHT, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGICAL-RESPONSES, PLANTS, STRESS, SUBTROPICS

2137

Schaffer, B., A.W. Whiley, and C. Searle. 1999. Atmospheric CO2 enrichment, root restriction, photosynthesis, and dry-matter partitioning in subtropical and tropical fruit crops. *Hortscience 34(6):1033-1037.*

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GENE-EXPRESSION, GROWTH, LEAF GAS- EXCHANGE, LEAVES, NET PHOTOSYNTHESIS, NITROGEN, PLANTS, SOUR ORANGE TREES

2138

Schaffer, B., A.W. Whiley, C. Searle, and R.J. Nissen. 1997. Leaf gas exchange, dry matter partitioning, and mineral element concentrations in mango as influenced by elevated atmospheric carbon dioxide and root restriction. *Journal of the American Society for Horticultural Science 122(6):849-855.*

The effects of atmospheric CO2 enrichment and root restriction on net CO2 assimilation (A), dry mass partitioning, and leaf mineral element concentrations in 'Kensington' and 'Tommy Atkins' mango (Mangifera indica L.) were investigated. Trees were grown in controlled-environment glasshouse rooms at ambient CO2 concentrations of 350 or 700 mu mol.mol(-1). At each CO2 concentration, trees were grown in 8-L containers, which restricted root growth, or grown aeroponically in 200-L root mist chambers, which did not restrict root growth. Trees grown in 350 mu mol.mol(-1) CO2 were more efficient at assimilating CO2 than trees grown in 700 mu mol.mol(-1) CO2. However, total plant and organ dry mass was generally higher for plants grown at 700 mu mol.mol(-1) CO2 due to increased A as a result of a greater internal partial pressure of CO2 (Ci) in leaves of plants in the CO2 enriched environment. Root restriction reduced A resulting in decreased organ and plant dry mass. In root-restricted plants, reduced A and dry matter accumulation offset the increases in these variables resulting from atmospheric CO2 enrichment. Atmospheric CO2 enrichment and root restriction did not affect dry mass partitioning. Leaf mineral element concentrations were generally lower for trees grown at the higher ambient CO2 concentration, presumably due to a dilution effect from an increased growth rate.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, WHEAT

2139

Schapendonk, A.H.C.M., P. Dijkstra, J. Groenwold, C.S. Pot, and S.C. vandeGeijn. 1997. Carbon balance and water use efficiency of frequently cut Lolium perenne L swards at elevated carbon dioxide. *Global Change Biology 3(3):207-216.*

The impact of doubled atmospheric [CO2] on the carbon balance of regularly cut Lolium perenne L. swards was studied for two years under semi-field conditions in the Wageningen Rhizolab. CO2 and H2O vapour exchange rates of the swards were measured continuously for two years in transparent enclosures. The light utilization efficiencies of the swards ranged between 1.5 g CO2 MJ(-1) global radiation (high light, ambient [CO2]) and 2.8 g CO2 MJ(-1) (low light, doubled [CO2]). The above-ground net primary productivity (NPP) in the enclosures was greater by 29% in 1994 and 43% in 1995 in the doubled [CO2] treatments, but only 20% and 25% more carbon was recovered in the periodical cuts. Thus, NPP increased significantly more than did the harvested aboveground biomass. The positive [CO2] effect on net carbon assimilation is therefore associated with a preferential allocation of extra carbon to the roots and soil. In addition to higher canopy photosynthesis and leaf elongation rates, a small part of the positive [CO2] effects on NPP could be attributed to a decrease of the specific respiration of the shoots. On a canopy basis however, respiration was equal or slightly higher at doubled [CO2] due to the higher amount of standing biomass. Comparison of NPP and carbon recovered in different harvests showed that allocation to roots and soil was highest in spring, it was low in early summer and increased again in late summer and autumn. The total gross amount of carbon partitioned to the roots and soil during the two year period was 57% more at doubled [CO2]. The total amount of carbon that was sequestered in the soil after subtraction of the respiratory losses was 458 g m(-2) and 779 g m(-2) in the ambient and doubled [CO2] treatments, respectively. The average water use efficiency (WUE) of the swards was increased by a factor 1.5 at doubled [CO2]. Both WUE and its positive interaction with [CO2] varied between years and were positively correlated with global irradiance. At doubled [CO2], the higher WUE was fully compensated for by a higher leaf area index. Therefore, total transpiration on a canopy basis was equal for the ambient and the doubled [CO2] concentrations in both years.

KEYWORDS: ATMOSPHERIC CO2, BIOSPHERE, CONDUCTANCE, CYCLE, GRASSLAND, IMPACT, PHOTOSYNTHESIS, RESPIRATION, RYEGRASS, TEMPERATURE

2140

Schapendonk, A.H.C.M., W. Stol, D.W.G. van Kraalingen, and B.A.M. Bouman. 1998. LINGRA, a sink/source model to simulate grassland productivity in Europe. *European Journal of Agronomy 9(2-3):87-100.*

A simulation model for the prediction of the productivity of Lolium perenne L. grasslands is described and validated. Simulated key processes are light utilization, leaf formation, leaf elongation, tillering, and carbon partitioning (storage, shoot, root). Source- and sink-limited growth are simulated independently. Sink-limited growth is characterized by temperature-dependent leaf expansion and tiller development, whereas source-limited growth is determined by photosynthetic light-use-efficiency of the canopy and the remobilization of stored carbohydrates in the stubble. At each integration step, commonly 1 day, the available amount of carbon from the source is compared with the carbon required by the sink. The actual growth is determined by the minimum value of either the sink or the source. If the source is in excess of the sink, the surplus is allocated to storage carbohydrates in the stubble. This storage carbon is available for remobilization at times that the sink requires more carbohydrates than are available from photosynthesis. In contrast to previous grassland models, LINGRA describes regrowth after defoliation in a mechanistic way, balanced by temperature-driven remobilization of stored carbohydrates. In order to validate LINGRA, an extensive set of experimental data was used, derived from measurements at 35 sites in Europe. The average error between the observed and predicted yields was 14% at the level of irrigated, and 19% at the level of non-irrigated, treatments for the whole of Europe. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON BALANCE, CLIMATE, CO2- ENRICHMENT, EFFICIENCY, GROWTH, SENESCENCE, SWARD, TEMPERATURE INCREASE, WATER

2141

Schappi, B. 1996. Growth dynamics and population development in an alpine grassland under elevated CO2. *Oecologia 106(1):93-99.*

Leaf expansion, population dynamics and reproduction under elevated CO2 were studied for two dominant and four subdominant species in a high alpine grassland (2500 above sea level, Swiss Central Alps). Plots of alpine heath were exposed to 335 mu l l(-1) and 680 mu l l(-1) CO2 in open-top chambers over three growing seasons. Treatments also included natural and moderately improved mineral nutrient supply (40 kg N ha(-1) year(-1) in an NPK fertilizer mix). Seasonal dynamics of leaf expansion, which was studied for the dominant graminoid Carer curvula only, were not affected by elevated CO2 during two warm seasons or during a cool season. Improved nutrient supply increased both the expansion rate and the duration of leaf growth but elevated CO2 did not cause any further stimulation. Plant and tiller density (studied in all species) increased under elevated CO2 in the codominant Leontodon helveticus and the subdominant Trifolium alpinum, remained unchanged in two other minor species Poa alpina and Phyteuma globulariifolium, and decreased in Carex curvula. In Potentilla aurea elevated CO2 compensated for a natural decline in shoot number. By year 3 the number of fertile shoots in Leontodon and individual seed weight in Carex were slightly increased under elevated CO2, indicating CO2 effects on sexual reproduction in these two dominant species. The results suggest that the effects of elevated CO2 on the population dynamics of the species studied were not general, but species-specific and rather moderate effects. However, the reduction of tiller density in Carex curvula, in contrast to the increases observed in Leontodon helveticus and Trifolium alpinum, indicates that elevated CO2 may negatively affect the abundance of the species most characteristic of this alpine plant community.

KEYWORDS: ANNUALS, CARBON DIOXIDE, PLANT, REPRODUCTION, TEMPERATURE, TUSSOCK TUNDRA, WHITE CLOVER

2142

Schappi, B., and C. Korner. 1996. Growth responses of an alpine grassland to elevated CO2. *Oecologia 105(1):43-52.*

Alpine plant species have been shown to exhibit a more pronounced increase in leaf photosynthesis under elevated CO2 than lowland plants. In order to test whether this higher carbon fixation efficiency will translate into increased biomass production under CO2 enrichment we exposed plots of narrow alpine grassland (Swiss Central Alps, 2470 m) to ambient (355 mu l l(-1)) and elevated (680 mu l l(-1)) CO2 concentration using open top chambers. Part of the plots received moderate mineral nutrient additions (40 kg ha(-1) year(-1) of nitrogen in a complete fertilizer mix). Under natural nutrient supply CO2 enrichment had no effect on biomass production per unit land area during any of the three seasons studied so far. Correspondingly, the dominant species Carex curvula and Leontodon helveticus as well as Trifolium alpinum did not show a growth response either at the population level or at the shoot level. However, the subdominant generalistic species Poa alpina strongly increased shoot growth (+47%). Annual root production (in ingrowth cores) was significantly enhanced in C. curvula in the 2nd and 3rd year of investigation (+43%) but was not altered in the bulk samples for all species. Fertilizer addition generally stimulated above-ground (+48%) and below-ground (+26%) biomass production right from the beginning. Annual variations in weather conditions during summer also strongly influenced above-ground biomass production (19-27% more biomass in warm seasons compared to cool seasons). However, neither nutrient availability nor climate had a significant effect on the CO2 response of the plants. Our results do not support the hypothesis that alpine plants, due to their higher carbon uptake efficiency, will increase biomass production under future atmospheric CO2 enrichment, at least not in such late successional communities. However, as indicated by the response of P. alpina, species-specific responses occur which may lead to altered community structure and perhaps ecosystem functioning in the long-term. Our findings further suggest that possible climatic changes are likely to have a greater impact on plant growth in alpine environments than the direct stimulation of photosynthesis by CO2. Counter-intuitively, our results suggest that even under moderate climate warming or enhanced atmospheric nitrogen deposition positive biomass responses to CO2 enrichment of the currently dominating species are unlikely.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, BALANCE, NITROGEN, PLANT GROWTH, TEMPERATURE, TUSSOCK TUNDRA, WHITE CLOVER

2143

Schappi, B., and C. Korner. 1997. In situ effects of elevated CO2 on the carbon and nitrogen status of alpine plants. *Functional Ecology 11(3):290-299.*

1. The effect of elevated CO2 on tissue composition in an alpine grassland (Swiss Central Alps, 2500m) under both natural and increased nutrient supply (NPK) is summarized. 2. During 3 years of CO2 enrichment the concentration of total non- structural carbohydrates (TNC) in leaves increased by 32% in Leontodon helveticus (largely sugar) and by 56% in Trifolium alpinum (largely starch) but did not

change significantly in the dominant sedge Carex curvula and in Poa alpina, currently a rare species at this site. 3. Enhanced mineral nutrient supply (unlike elevated CO2) greatly stimulated growth but did not reduce the CO2-induced TNC accumulation, 4. Under elevated CO2 nitrogen concentrations (per g TNC-free dry matter) of green leaves decreased in Leontodon (-21%) and in Trifolium (-24%) but not or only slightly in Carer and in Pea. NPK addition compensated this CO2 effect an nitrogen concentration in Trifolium bur not in the other species. 5. In below-ground tissue neither TNC nor nitrogen concentration responded to CO2 fertilization. 6. The nitrogen pool per unit land area at peak season biomass remained unaffected by the CO2 treatment. 7. Overall our results suggest that the late successional dominant sedge Carex curvula remains unaffected by elevated CO2, independently of mineral nutrient supply, whereas the co- dominant and sub-dominant forbs Leontodon helveticus and Trifolium alpinum show both an increase of TNC as well as N depletion under elevated CO2. 8. None of these changes in active plant tissue translate into compositional changes in naturally senesced litter suggesting caution with predictions of CO2 effects on decomposition based on data from green plant material.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO2, DIOXIDE, ESTUARINE MARSH, GROWTH, HIGH- ALTITUDES, LONG-TERM EXPOSURE, LOW-TEMPERATURE, PHOTOSYNTHETIC INHIBITION, TUSSOCK TUNDRA

2144

Schenk, U., H.J. Jager, and H.J. Weigel. 1996. Nitrogen supply determines responses of yield and biomass partitioning of perennial ryegrass to elevated atmospheric carbon dioxide concentrations. *Journal of Plant Nutrition 19(10-11):1423-1440.*

Perennial ryegrass (Lolium perenne L. cv. Parcour) grown at eight levels of nitrogen (N) fertilization (0-765 mg/pot) was exposed to ambient (390 ppm) and elevated (690 ppm) carbon dioxide (CO2) concentrations for 83 days. Plants were cut three times and dry matter yields determined for each harvest. At final harvest, dry weight of root and stubble biomass was determined, as N concentrations of all plant fractions were determined. Carbon dioxide enrichment effects on yield and total plant biomass increased with increasing N fertilization. The weaker CO2-related yield enhancement at low N supply was due to the plants inability to increase tiller number. Root fraction of total plant biomass at final harvest was increased by high CO2 and decreased by N supply. Root biomass was significantly increased by CO2 enrichment and for both CO2 treatments the N supply for maximum root mass coincided with the N supply for reaching maximum total plant biomass. A significant correlation between root fraction of total plant dry matter and N concentration of total plant biomass, which was not changed by CO2 enrichment, indicates that biomass partitioning between shoot and root is controlled by the internal N status of the plant.

KEYWORDS: CO2- ENRICHMENT, GRASSLANDS, GROWTH-RESPONSE, MOBILIZATION, PLANT-RESPONSES, ROOTS, SOIL, STORAGE, STUBBLE, WHITE CLOVER

2145

Schenk, U., H.J. Jager, and H.J. Weigel. 1997. The response of perennial ryegrass white clover mini-swards to elevated atmospheric CO2 concentrations: effects on yield and fodder quality. *Grass and Forage Science 52(3):232-241.*

In order to assess the effects of future elevated atmospheric CO2 concentrations on yield, mineral content and the nutritive value of mixed swards of perennial ryegrass (Lolium perenne L.) and white clover (Trifolium repens L.). both species were grown as monocultures and as different mixtures and were exposed season-long to ambient (380 p.p.m.) and elevated (670 p.p.m.) CO2 concentrations in open-top chambers. Mini-swards were cut four times at about monthly intervals at a height of 5 cm, dry- matter yields were determined and content of macroelements (N, P, K, S, Mg, Ca, Na) and crude fibre, crude protein and ash content were measured. The CO2-related increase in seasonal yield amounted to 16-38% for white clover monocultures, 12-29% for mixed swards and 5-9% for ryegrass monocultures. The white clover content of all swards was significantly enhanced by elevated CO2. The K and Na content of total yield was decreased by high CO2 but did not fall below the minimum requirements for ruminants. As the Ca content of total yield was increased by elevated CO2 and the P content was not changed, the Ca/P ratio of total yield was increased and exceeded values required for animal nutrition. The crude protein content of total yield was reduced by high CO2 at thr beginning of the growing season only and was increased by elevated CO2 in the course of the experiment, whereas crude fibre content was decreased through out the season, sometimes falling below the minimum requirement for ruminants. Removal of N, P, S, Mg and Ca by cutting was significantly enhanced because of CO2 enrichment, The results show that, besides the positive effect of rising atmospheric CO2 on dry-matter yield of white clover/ryegrass swards, impacts on the nutritive value should be expected. Possible changes in species composition and implications for grassland management are briefly discussed.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GROWTH-RESPONSE, LOLIUM-PERENNE, NITROGEN, PASTURE TURVES, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, TRIFOLIUM- REPENS

2146

Schenk, U., H.J. Jager, and H.J. Weigel. 1997. The response of perennial ryegrass/white clover swards to elevated atmospheric CO2 concentrations .1. Effects on competition and species composition and interaction with N supply. *New Phytologist 135(1):67-79.*

The effects of long-term carbon dioxide enrichment on competition for nutrients and light in a ryegrass/clover association were determined for simulated swards of perennial ryegrass (Lolium perenne L. cv. Parcour) and white clover (Trifolium repens L. cv. Karina), which were grown as monocultures and in three mixtures (25/75, 50/50, 75/25), according to the replacement design, at two levels of nitrogen (N) supply (no additional N and 200 kg N ha(-1)) and at season- long ambient (380 ppm) and elevated (670 ppm) CO2 concentrations, in open-top chambers. Stands were cut four times, at about monthly intervals, to a height of 5 cm. Plant material was separated into different species, fresh and dry weights were determined and the content of macroelements (N, P, K, S, Mg) in both species was measured. In addition, plant height of both species at harvest dates and during several regrowth periods was monitored. Results indicate that both species made demand on different resources and profited from growth in a mixed sward. CO2-related yield increase amounted to 16-42% for white clover whereas the effect of high CO2 on ryegrass yield ranged between -33% and +9% depending on N supply, mixture and year. As a result the contribution of white clover to total yield in mixed swards was significantly enhanced by CO2 enrichment at many harvests in both N supply treatments. Without additional N supply, shoot competition for light was intensified by CO2 enrichment to the disadvantage of ryegrass, since clover petioles grew longer and ryegrass was shorter at elevated CO2. With N fertilization, no marked effect of CO2 enrichment on interspecific competition could be observed. Since clover and total yield were increased by CO2 enrichment, nutrient requirements were also increased and potassium deficiency and increased intraspecific competition of clover for K was observed in the mixtures under elevated CO2 which had the highest nutrient withdrawal. Although white clover profited much more from CO2 enrichment in both N fertilization treatments, the suppression of ryegrass in mixed swards could only be observed under low N conditions. Generally, the effect of N fertilization on competitive interference between both species was much greater than the effect of

CO2 enrichment and it is suggested that the effect of elevated CO2 on the balance of species and the outcome of competition in a grass/clover sward is mainly dependent on the N status.

KEYWORDS: CARBON DIOXIDE, GROWTH-RESPONSE, LOLIUM-PERENNE, MINERAL NUTRITION, MODEL-ECOSYSTEMS, PASTURE TURVES, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, TRIFOLIUM-REPENS L, WHITE CLOVER

2147

Schenk, U., R. Manderscheid, J. Hugen, and H.J. Weigel. 1995. Effects of co2 enrichment and intraspecific competition on biomass partitioning, nitrogen-content and microbial biomass carbon in soil of perennial ryegrass and white clover. *Journal of Experimental Botany 46(289):987-993.*

Seedlings of perennial ryegrass (Lolium perenne L. cv. Parcour) and white clover (Trifolium repens L. cv. Karina) grown at five different plant densities were exposed to ambient (390 ppm) and elevated (690 ppm) CO2 concentrations, After 43 d the effects of CO2 enrichment and plant density on growth of shoot and root, nitrogen concentration of tissue, and microbial biomass carbon (C-mic) in soil were determined, CO2 enrichment of Lolium perenne increased shoot growth on average by 17% independent of plant density, while effects on root biomass ranged between -4% and +107% due to an interaction with plant density, Since tiller number per plant was unaffected by elevated CO2, the small response of shoot growth to CO2 enrichment was attributed to low sink strength. A significant correlation between nitrogen concentration of total plant biomass and root fraction of total plant dry matter, which was not changed by CO2 enrichment, indicates that nitrogen status of the plant controls biomass partitioning and the effect of CO2 enrichment on root growth. Effects of elevated CO2( )and plant density on shoot and root growth of Trifolium repens were not significantly interacting and mean CO2 related increase amounted to 29% and 66%, respectively, However, growth enhancement due to elevated CO2 was strongest when leaf area index was lowest. Total amounts of nitrogen in shoots and roots were bigger at 690 ppm than at 390 ppm CO2. There was a significant increase in C-mic in experiments with both species whereas plant density had no substantial effect.

KEYWORDS: DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO2, ENVIRONMENTS, GROWTH, LEAF, PHOTOSYNTHESIS, PLANT, RESPIRATION, TEMPERATURE, TRIFOLIUM- REPENS

2148

Scherzer, A.J., J. Rebbeck, and R.E.J. Boerner. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. *Forest Ecology and Management 109(1-3):355-366.*

Yellow-poplar (Liriodendron tulipifera L.) and eastern white pine (Pinus strobus L.) seedlings growing in two plantations were fumigated from 1992 to 1995 in open-top chambers with charcoal-filtered air (CF), ambient air (chamberless), one time ambient ozone (1X), twice ambient ozone (2X), or twice ambient ozone+twice ambient CO2 (2X+CO2). Across all treatments and years, concentrations of foliar nitrogen (N) in yellow-poplar averaged 26.3 mg g(-1) in June and decreased to 13.8 mg g(-1) just prior to leaf senescence. While leaves from all treatments exhibited similar seasonal reductions, actual N concentrations were greatly affected by treatment. Ozone (O-3) alone did not significantly alter foliar N concentrations; however, 2X+CO2 decreased N concentrations by 18-40% depending on time of sampling. After one season of fumigation, 2X+CO2-exposed leaves of yellow-poplar decayed significantly more slowly than leaves from all other treatments. In contrast, white pine needles demonstrated few differences in N concentrations or decomposition during the first 3 years of fumigation. By the forth season, 2X-CO2-air significantly reduced N concentrations of current year needles. In needles grown in CF air N concentrations ranged from 14.8 mg g(-1) in June to 17.2 mg g(- 1) in October. 2X+CO2-air reduced N levels in white pine by 10- 23% depending on time of sampling. For both species, significant differences in N due to leaf age and canopy position must be taken into consideration when evaluating the data. Our experiments indicate that elevated CO2 in the presence of elevated O-3 can reduce foliar N concentrations and reduce litter decay, thus affecting nutrient cycling. (C) 1998 Elsevier Science B.V.

KEYWORDS: CLIMATE CHANGE, CO2, FIELD, GROWTH, L SEEDLINGS, LEAF LITTER, NUTRITION, PLANTS, SIMULATED ACID-RAIN, SPRUCE PICEA-ABIES

2149

Schier, G.A., and C.J. McQuattie. 1998. Effects of carbon dioxide enrichment on response of mycorrhizal pitch pine (Pinus rigida) to aluminum: growth and mineral nutrition. *Trees-Structure and Function 12(6):340-346.*

Carbon dioxide enrichment may increase the Al tolerance of trees by increasing root growth, root exudation and/or mycorrhizal colonization. The effect of elevated CO2 on the response of mycorrhizal pitch pine (Pinus rigida Mill.) seedlings to Al was determined in two experiments with different levels of nutrients, 0.1- or 0.2-strength Clark solution. During each experiment, seedlings inoculated with the ectomycorrhizal fungus Pisolithus tinctorius (Pers.) Coker & Couch were grown 13 weeks in sand irrigated with nutrient solution (pH 3.8) containing 0, 6.25, 12.5, or 25 mg/l Al (0, 232, 463, or 927 mu M Al) in growth chambers fumigated with 350 (ambient) or 700 (elevated) mu l/l CO2. At ambient CO2 in the absence of Al, mean total dry weights (DW) of seedlings at the high nutrient level were 164% higher than those at the low level. Total DW at elevated CO2, in the absence of Al, was significantly greater than that in ambient CO2 at the low (+34%) and high (+16%) nutrient levels. Root and shoot DW at both nutrient levels decreased with increasing Al concentrations with Al reducing root growth more than shoot growth. Although visible symptoms of Al toxicity in roots and needles were reduced by CO2 enrichment, there were no significant CO2 x Al interactions for shoot or root DW. The percentage of seedling roots that became mycorrhizal was negatively related to nutrient level and was greater at elevated than at ambient CO2 levels. Generally, elevated CO2 had little effect on concentration of mineral nutrients in roots and needles. Aluminum reduced concentrations of most nutrients by inhibiting uptake.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, COLONIZATION, ELEVATED CO2, NUTRIENT, PHOSPHORUS, PICEA-RUBENS, QUERCUS-ALBA, ROOTS, SEEDLING GROWTH, SOIL N

2150

Schimel, D.S. 1995. Terrestrial biogeochemical cycles - global estimates with remote-sensing. *Remote Sensing of Environment 51(1):49-56.*

The carbon rand nitrogen cycles are crucial for understanding the changing Earth system, influencing atmospheric concentrations of greenhouse gases, primary productivity of the biosphere, and biogenic emissions of reactive trace species. The carbon budget of the terrestrial biosphere has attracted special attention because of its role in atmospheric changes in carbon dioxide. The terrestrial biosphere influences atmospheric CO2 through three main modes: First, large, nearly balanced fluxes of CO2 in photosynthesis and respiration exhibit a degree of interannual variability which can influence atmospheric CO2, at feast on annual to decadal time scales. Second, land use changes release CO2 to the atmosphere. Third, poorly understood processes are

likely resulting in enhanced uptake of CO2 in certain ecosystems, acting as a sink in the global carbon cycle. This sink may result from forest demographics, atmospheric N deposition, or direct CO2 fertilizatian, or some synergistic combination of those processes. Global estimates of terrestrial carbon cycle components requires the use of remote observations; however, the appropriate remote sensing strategies are quite different for the various components.

KEYWORDS: ATMOSPHERIC CO2, BIOSPHERE, CARBON DIOXIDE, FOREST ECOSYSTEMS, HIGH-RESOLUTION RADIOMETER, MODEL, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TALLGRASS PRAIRIE

2151

Schimel, D.S. 1995. Terrestrial ecosystems and the carbon-cycle. *Global Change Biology 1(1):77-91.*

The terrestrial biosphere plays an important role in the global carbon cycle. In the 1994 Intergovernmental Panel Assessment on Climate Change (IPCC), an effort was made to improve the quantification of terrestrial exchanges and potential feedbacks from climate, changing CO2, and other factors; this paper presents the key results from that assessment, together with expanded discussion. The carbon cycle is the fluxes of carbon among four main reservoirs: fossil carbon, the atmosphere, the oceans, and the terrestrial biosphere. Emissions of fossil carbon during the 1980s averaged 5.5 Gt y(-1). During the same period, the atmosphere gained 3.2 Gt C y(-1), and the oceans are believed to have absorbed 2.0 Gt C y(-1). The regrowing forests of the Northern Hemisphere may have absorbed 0.5 Gt C y(-1) during this period. Meanwhile, tropical deforestation is thought to have released an average 1.6 Gt C y(-1) over the 1980s. While the fluxes among the four pools should balance, the average 1980s values lead to a 'missing sink' of 1.4 Gt C y(-1). Several processes, including forest regrowth, CO2 fertilization of plant growth (c. 1.0 Gt C y(-1)), N deposition (c. 0.6 Gt C y(-1)), and their interactions, may account for the budget imbalance. However, it remains difficult to quantify the influences of these separate but interactive processes. Uncertainties in the individual numbers are large, and are themselves poorly quantified. This paper presents detail beyond the IPCC assessment on procedures used to approximate the flux uncertainties. Lack of knowledge about positive and negative feedbacks from the biosphere is a major limiting factor to credible simulations of future atmospheric CO2 concentrations. Analyses of the atmospheric gradients of CO2 and (CO2)-C-13 concentrations provide increasingly strong evidence for terrestrial sinks, potentially distributed between Northern Hemisphere and tropical regions, but conclusive detection in direct biomass and soil measurements remains elusive. Current regional-to-global terrestrial ecosystem models with coupled carbon and nitrogen cycles represent the effects of CO2 fertilization differently, but all suggest long-term responses to CO2 that are substantially smaller than potential leaf- or laboratory whole plant-level responses. Analyses of emissions and biogeochemical fluxes consistent with eventual stabilization of atmospheric CO2 concentrations are sensitive to the way in which biospheric feedbacks are modeled by c. 15%. Decisions about land use can have effects of 100s of Gt C over the next few centuries, with similarly significant effects on the atmosphere. Critical areas for future research are continued measurements and analyses of atmospheric data (CO2 and (CO2)-C-13) to serve as large-scale constraints, process studies of the scaling from the photosynthetic response to CO2 to whole-ecosystem carbon storage, and rigorous quantification of the effects of changing land use on carbon storage.

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, DIOXIDE, ELEVATED CO2, FOREST ECOSYSTEMS, GLOBAL CLIMATE-CHANGE, GROWTH-RESPONSE, NITROGEN DEPOSITION, STORAGE, TREE GROWTH

2152

Schindler, D.W., and S.E. Bayley. 1993. The biosphere as an increasing sink for atmospheric carbon - estimates from increased nitrogen deposition. *Global Biogeochemical Cycles 7(4):717-733.*

Estimates of carbon uptake and storage based on global nitrogen deposition, C:N ratios for typical terrestrial ecosystems, and recent ecosystem-scale nutrient studies indicate that 1.0-2.3 Gt C yr-1 of carbon storage may be stimulated by anthropogenically caused increases in nitrogen deposition in the past century. Sixty four to eighty four percent of global nitrogen uptake appears to occur on northern continents, with the remainder largely in northern coastal oceans. Increased nitrogen input by terrestrial ecosystems causes increased accumulation of carbon as plant tissue, with C:N ratios generally 50 to 200:1. Calculations suggest that northern continents are a major sink for carbon and that nitrogen- stimulated carbon uptake may more or less balance global carbon losses to the atmosphere from deforestation and agriculture. Much of the uptake appears to occur in aggrading forests, and the question of how long it can continue has important consequences for global carbon budgets.

KEYWORDS: ACIDIFICATION, BUDGET, CO2, CYCLE, DECOMPOSITION, ECOSYSTEMS, FOREST, GLOBAL CHANGE, OCEANIC UPTAKE, SPHAGNUM

2153

Schlesinger, W.H. 1993. Response of the terrestrial biosphere to global climate change and human perturbation. *Vegetatio 104:295-305.*

Despite 20 years of intensive effort to understand the global carbon cycle, the budget for carbon dioxide in the atmosphere is unbalanced. To explain why atmospheric CO2 is not increasing as rapidly as it should be, various workers have suggested that land vegetation acts as a sink for carbon dioxide. Here, I examine various possibilities and find that the evidence for a sink of sufficient magnitude on land is poor. Moreover, it is unlikely that the land vegetation will act as a sink in the postulated warmer global climates of the future. In response to rapid human population growth, destruction of natural ecosystems in the tropics remains a large net source of CO2 for the atmosphere, which is only partially compensated by the potential for carbon storage in temperate and boreal regions. Direct and inadvertent human effects on land vegetation might increase the magnitude of regional CO2 storage on land, but they are unlikely to play a significant role in moderating the potential rate of greenhouse warming in the future.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, FOREST ECOSYSTEMS, LAND-USE, NITROGEN, NO-TILLAGE, ORGANIC-CARBON, SOIL PROPERTIES, STORAGE, TUSSOCK TUNDRA

2154

Schmid, R., R. Forster, and M.J. Dring. 1992. Circadian-rhythm and fast responses to blue-light of photosynthesis in ectocarpus (phaeophyta, ectocarpales) .2. Light and co2 dependence of photosynthesis. *Planta 187(1):60-66.*

Photosynthesis of Ectocarpus siliculosus (Dillwyn) Lyngb. under continuous saturating red irradiation follows a circadian rhythm. Blue-light pulses rapidly stimulate photosynthesis with high effectiveness in the troughs of this rhythm but the effectiveness of such pulses is much lower at its peaks. In an attempt to understand how blue light and the rhythm affected photosynthesis, the effects of inorganic carbon on photosynthetic light saturation curves were studied under different irradiation conditions. The circadian rhythm of photosynthesis was apparent only at irradiances which were not limiting for photosynthesis. The same was found for blue- light-stimulated photosynthesis, although

stimulation was observed also under very low red-light irradiances after a period of adaptation, provided that the inorganic-carbon concentration was not in excess. Double-reciprocal plots of light-saturated photosynthetic rates versus the concentration of total inorganic carbon (up to 10 mM total inorganic carbon) were linear and had a common constant for half-saturation (3.6 mM at pH 8) at both the troughs and the peaks of the rhythm and before and after blue-light pulses. Only at very low carbon concentrations was a clear deviation found from these lines for photosynthesis at the rhythm maxima (red and blue light), which indicated that the strong carbon limitation specifically affected photosynthesis at the peak phases of the rhythm. Very high inorganic carbon concentrations (20 mM) in the medium diminished the responses to blue light, although they did not fully abolish them. The kinetics of the stimulation indicate that the rate of photosynthesis is affected by two blue-light- dependent components with different time courses of induction and decay. The faster component seemed to be at least partially suppressed at red-light irradiances which were not saturating for photosynthesis. Lowering the pH of the medium had the same effects as an increase of the carbon concentration to levels of approx. 10 mM. This indicates that Ectocarpus takes up free CO2 only and not bicarbonate, although additional physiological mechanisms may enhance the availability of CO2.

KEYWORDS: CHLAMYDOMONAS-SEGNIS, DIOXIDE, INORGANIC CARBON-SOURCES

2155

Schmitt, V., A. Kussmaul, and A. Wild. 1999. Interaction of elevated CO2 and ozone concentrations and irrigation regimes on leaf anatomy and carbohydrate status of young oak (Quercus petraea) trees. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 54(9-10):812-823.*

Young sessile oak (Quercus petraea) trees were exposed for one vegetation period in closed environmental chambers in a crossed factorial study on effects to varied CO2 concentrations, ozone concentrations and irrigation treatments. Elevated CO2 concentrations (ambient + 350 mu mol mol(-1)) caused a significant increase in biomass production, alterations in leaf anatomy and chloroplast ultrastructure as well as an increase in leaf starch content, as compared to ambient CO2 concentrations. The effects of elevated O-3 concentrations and drought stress were far less distinct. The leaf starch content was influenced by CO2 and O-3 in a synergistic manner.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PLANTS, SOURCE-SINK RELATIONS, STARCH, ULTRASTRUCTURE

2156

Schneider, S.H., and T.L. Root. 1996. Ecological implications of climate change will include surprises. *Biodiversity and Conservation 5(9):1109-1119.*

In addition to assessing the impacts of CO2 doubling on environment and society, more consideration is needed to estimate extreme events or 'surprises'. This is particularly important at the intersection of disciplines like climate and ecology because the potential for large discontinuities is high given all the possible climate/biota interactions. The vast disparities in scales encountered by those working in traditional ecology (typically 20 m) and climatology (typically 200 km) make diagnoses of such interactions difficult, but these can be addressed by an emerging research paradigm we call strategic cyclical scaling (SCS). The need to anticipate outlier events and assign them subjective probabilities suggests emphasis on interdisciplinary research associations. The desire to reduce societal vulnerability to such events suggests the need to build adaptive management and diverse economic activities into social organizations. The effectiveness of adaptation responses to anticipated climatic changes is complicated when consideration of transient changes, regional disturbances, large unforseeable natural fluctuations and surprises are considered. Slowing down the rate of disturbances and decreasing vulnerability are advocated as the most prudent responses to the prospect of human-induced climatic changes.

KEYWORDS: CO2, SCALE

2157

Scholes, M.C., D. Powlson, and G.L. Tian. 1997. Input control of organic matter dynamics. *Geoderma 79(1-4):25-47.*

The amount and quality of inputs into soil organic matter will be altered by both climate and landuse change. The increase in growth of plants caused by increasing CO2 concentration implies not only potential increases in yields but also increases in plant residues. Simulation models using doubled CO2 levels predict global net primary productivity (NPP) to increase by 16.3%, over half of which will occur in the tropics. For tropical ecosystems increases in NPP will be dominated by the effects of elevated CO2, with water and nitrogen availability and temperature playing a less significant role. Phosphorus limitation may determine whether the potential for increased plant growth will be realized. The distribution of C3 and C4 species in the tropics could be affected by landuse change and estimates of yield increases will be dependent on their proportions. The allocation of photosynthate to the root will increase under elevated CO2, resulting in increased fine root dry weight and root length. Root sink strength and the turnover of roots and associated symbionts are critical knowledge gaps. Carbon:nitrogen ratios in tissues will increase resulting in decreased decomposition rates. The concentration of secondary compounds will be affected more by nitrogen limitations than a direct CO2 effect. Changes in lignin, tannin and polyphenol levels are more important in the decomposability of tropical liners than changes in the C:N ratios. Decomposition models will have to be altered to take into account changes in plant composition. The role of models in predicting the effects of management practice on long-term fertility is addressed. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, C-13 NATURAL ABUNDANCE, CHEMICAL-COMPOSITION, ELEVATED CARBON-DIOXIDE, NITROGEN MINERALIZATION, NUTRIENT RELEASE, ROOT-GROWTH, SIZE-FRACTIONS, SOIL MICROBIAL BIOMASS, TROPICAL CONDITIONS

2158

Scholes, R.J., and N. vanBreemen. 1997. The effects of global change on tropical ecosystems. *Geoderma 79(1-4):9-24.*

Alteration of land use will continue to be the dominant driver of environmental change in the tropics for the next several decades. It can take the form of fundamental vegetation cover transformation, or of intensification of existing land use without substantial change in cover type. Atmospheric composition changes and resultant climate changes could become ecologically significant within the next century. Changes in atmospheric composition in the tropics are essentially the same as those in higher latitudes, despite differences in the source and sink strengths for trace gases. Such changes can affect the functioning of tropical ecosystems through several processes, principally those related to carbon and nutrient assimilation and their interactions. Atmospheric composition may also have an indirect affect on tropical ecosystems via its effects on the climate. Predicted temperature increases in the tropics are less extreme than at high latitudes, but could still be biologically significant, especially at the tropical margins. The structure and productivity of ecosystems of the subhumid and dry tropics are very sensitive to changes in water balance, which could be caused by a combination of changes in precipitation and temperature. It is presently not possible to predict rainfall changes at ecologically meaningful scales

with any confidence. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO2, DECOMPOSITION, DEFORESTATION, GRASSLANDS, MODEL, NITROGEN, SOIL ORGANIC MATTER, TURNOVER

2159

Schortemeyer, M., O.K. Atkin, N. McFarlane, and J.R. Evans. 1999. The impact of elevated atmospheric CO2 and nitrate supply on growth, biomass allocation, nitrogen partitioning and N-2 fixation of Acacia melanoxylon. *Australian Journal of Plant Physiology 26(8):737-747.*

The interactive effects of nitrate supply and atmospheric CO2 concentration on growth, N-2 fixation, dry matter and nitrogen partitioning in the leguminous tree Acacia melanoxylon R. Br. were studied. Seedlings were grown hydroponically in controlled-environment cabinets for 5 weeks at seven N-15- labelled nitrate levels, ranging from 3 to 6400 mmol m(-3). Plants were exposed to ambient (similar to 350 mu mol mol(-1)) or elevated (similar to 700 mu mol mol(-1)) atmospheric CO2 for 6 weeks. Total plant dry mass increased strongly with nitrate supply. The proportion of nitrogen derived from air decreased with increasing nitrate supply. Plants grown under either ambient or elevated CO2 fixed the same amount of nitrogen per unit nodule dry mass (16.6 mmol N per g nodule dry mass) regardless of the nitrogen treatment. CO2 concentration had no effect on the relative contribution of N2 fixation to the nitrogen yield of plants. Plants grown with greater than or equal to 50 mmol m(-3) N and elevated CO2 had approximately twice the dry mass of those grown with ambient CO2 after 42 days. The rates of net CO2 assimilation under growth conditions were higher per unit leaf area for plants grown under elevated CO2. Elevated CO2 also decreased specific foliage area, due to an increase in foliage thickness and density. Dry matter partitioning between plant organs was affected by ontogeny and nitrogen status of the plants, but not by CO2 concentration. In contrast, plants grown under elevated CO2 partitioned more of their nitrogen to roots. This could be attributed to reduced nitrogen concentrations in foliage grown under elevated CO2.

KEYWORDS: ALNUS-GLUTINOSA, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ENRICHMENT, GAS-EXCHANGE, MODULATION, PLANTAGO-MAJOR, SEEDLINGS, TRIFOLIUM-REPENS L

2160

Schortemeyer, M., U.A. Hartwig, G.R. Hendrey, and M.J. Sadowsky. 1996. Microbial community changes in the rhizospheres of white clover and perennial ryegrass exposed to free air carbon dioxide enrichment (FACE). *Soil Biology and Biochemistry 28(12):1717-1724.*

Increases in the global atmospheric concentration of CO2 will not only directly affect the growth of plants, but might also alter the living conditions for soil biota. This could lead to shifts in the size and composition of the soil microbial communities. In this study we investigated the response of heterotrophic bacteria, NH4+-oxidising bacteria, and Rhizobium leguminosarum by. trifolii populations to elevated atmospheric CO2 concentrations in a model field-scale grassland ecosystem. The Free Air CO2 Enrichment (FACE) facility in Eschikon, Switzerland, releases CO2-enriched air into three large circular areas, each of 18 m dia, to a final CO2 concentration of 600 mu mol mol(-1), while three control areas of the same size receive ambient CO2 concentrations (similar to 350 mu mol mol(-1)). For this study, white clover (Trifolium repens L.) and perennial ryegrass (Lolium perenne L.) were grown as replicated monocultures within the FACE rings. Soil samples were taken from 0-10 cm depth in May and November 1994 (the second year of CO2-enrichment), and rhizosphere soil was obtained from clover and ryegrass roots for enumeration of bacteria. While the total numbers of culturable heterotrophic bacteria (determined by plate counts) in the rhizospheres of both plant species were little affected by CO2-enrichment, the populations of R. leguminosarum by. trifolii (enumerated by MPN) were increased two-fold in the rhizospheres of white clover exposed to elevated atmospheric CO2. There was no effect of the CO2 concentration on the populations of R. leguminosarum by. trifolii in the rhizospheres of perennial ryegrass, indicating that the increase of Rhizobium numbers is a host-related response to elevated atmospheric CO2. The numbers of autotrophic NH4+-oxidizing bacteria in the rhizospheres (enumerated by MPN) were unaffected by the atmospheric CO2 concentration. There was also no effect of the CO2 concentration on the amount of microbial biomass C in the bulk, non-rhizosphere soils in white clover or perennial ryegrass plots. These data indicate that under a legume crop, at least in terms of inoculum quality in the rhizosphere soil, symbiotic nitrogen-fixing organisms might be favoured by elevated atmospheric CO2 concentrations. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BIOMASS-C, COMPETITION, DECOMPOSITION, ELEVATED CO2, GROWTH, HETEROTROPHIC BACTERIA, LEGUMES, RESPONSES, ROOT

2161

Schrope, M.K., J.P. Chanton, L.H. Allen, and J.T. Baker. 1999. Effect of CO2 enrichment and elevated temperature on methane emissions from rice, Oryza sativa. *Global Change Biology 5(5):587-599.*

Methane emissions from rice grown within Temperature Gradient Greenhouse Tunnels under doubled CO2 concentrations were 10-45 times less than emissions from control plants grown under ambient CO2. For two cultivars of rice (cvs. Lemont and IR-72), methane emissions increased with a temperature increase of 2 degrees, from outdoor ambient temperatures to the first cell of the ambient CO2 tunnel (ambient temperature + 2 degrees C). Within both tunnels and for both cultivars methane emissions decreased with further temperature increases (from 2 degrees to 5 degrees C above ambient). Carbon dioxide enrichment stimulated both above- and below-ground production. Our original hypothesis was that increased CO2 would stimulate plant productivity and therefore stimulate methane emission, since direct linkages between these parameters have been observed. We hypothesize that CO2 enrichment led to the attenuation of methane production due to increased delivery of oxygen to the rhizosphere because of increased root biomass and porosity. The increased root biomass due to elevated CO2 may have more effectively aerated the soil, suppressing methane production. However, this study may be unique because the low organic content (<1%) of the sandy soils in which the rice was grown created very little oxygen demand.

KEYWORDS: ATMOSPHERIC METHANE, BACTERIA, CARBON DIOXIDE, EXCHANGE, GROWTH RATE, METHANOGENESIS, METHYL-FLUORIDE, OXIDATION, SEASONAL-VARIATION, STABLE ISOTOPES

2162

Schulte, M., C. Herschbach, and H. Rennenberg. 1998. Interactive effects of elevated atmospheric CO2, mycorrhization and drought on long-distance transport of reduced sulphur in young pedunculate oak trees (Quercus robur L.). *Plant, Cell and Environment 21(9):917-926.*

Pedunculate oak (Quercus robur L.) was germinated and grown under nutrient non-limiting conditions for a total of 10-15 weeks at ambient CO2 concentration and 1100 mu mol mol(-1) CO2 either in the presence or the absence of the mycorrhizal fungus Laccaria laccata. Half of the oak trees of these treatments were exposed to drought during final growth by suspending the water supply for 21 d. Mycorrhization and elevated atmospheric CO2 each enhanced total plant biomass per tree. Whereas additional biomass accumulation of trees grown under elevated

CO2 was mainly attributed to increased growth of lateral roots, mycorrhization promoted shoot growth. Water deficiency reduced biomass accumulation without affecting relative water content, but this effect was more pronounced in mycorrhizal as compared to non-mycorrhizal trees. Elevated CO2 partially prevented the development of drought stress, as indicated by leaf water potential, but did not counteract the negative effects of water deficiency on growth during the time studied. Enhanced biomass accumulation requires adaption in protein synthesis and, as a consequence, enhanced allocation of reduced sulphur produced in the leaves to growing tissues. Therefore, allocation of reduced sulphur from oak leaves was studied by flap-feeding radiolabelled GSH, the main long-distance transport form of reduced sulphur, to mature oak leaves. Export of radiolabel proceeded almost exclusively in basipetal direction to the roots. The rate of export of radioactivity out of the fed leaves was significantly enhanced under elevated CO2, irrespective of mycorrhization. A higher proportion of the exported GSH was transported to the roots than to basipetal stem sections under elevated CO2 as compared to ambient CO2. Mycorrhization did not affect S-35 export out of the fed leaves, but the distribution of radiolabel between stem and roots was altered in preference of the stem. Trees exposed to drought did not show appreciable export of the S-35 radioactivity fed to the leaves when grown under ambient CO2. Apparently, drought inhibited basipetal transport of reduced sulphur at the level of phloem loading and/or phloem transport. Elevated CO2 seemed to counteract this effect of drought stress to some extent, since higher leaf water potentials and improved S-35 export out of the fed leaves was observed in oak trees exposed to drought and elevated CO2 as compared to trees exposed to drought and ambient CO2.

KEYWORDS: ABIES KARST L, CARBON DIOXIDE, ENRICHMENT, FAGUS-SYLVATICA, GAS-EXCHANGE, GROWTH, PLANTS, SEEDLINGS, SULFUR NUTRITION, WATER-STRESS

2163

Schwanz, P., K.H. Haberle, and A. Polle. 1996. Interactive effects of elevated CO2, ozone and drought stress on the activities of antioxidative enzymes in needles of Norway spruce trees (Picea abies, [L] Karsten) grown with luxurious N- supply. *Journal of Plant Physiology 148(3-4):351-355.*

The aim of the present study was to address the complex interactions of environmental constraints, ozone and drought stress, with elevated atmospheric CO2 on the activities of antioxidative enzymes and soluble protein contents in needles of Norway spruce trees (Picea abies L.). Five-year-old spruce trees were kept from bud break in June until January of the following year in phytochambers under climatic conditions similar to those of a natural site in the Bavarian forest. The trees were well-supplied with nitrogen and exposed to either elevated CO2 (ambient + 200 mu LL(-1)), elevated ozone (80 nLL(-1), from June to October) or to a combination of both factors. Controls were grown with 20 nLL(-1) O-3 and ambient CO2 levels. In each chamber, a subset of trees was subjected to episodical drought stress in summer. Needles from controls investigated in October (summer conditions) and January (winter conditions) showed little seasonal variation of superoxide dismutase (SOD), an approximately 2-fold reduction in catalase (CAT), and a 2-fold increase in guaiacol peroxidase (POD) activity. Exposure to elevated CO2 did not affect the activities of any of these enzymes in October and January, respectively, but caused a significant reduction in soluble protein. Ozone had no significant effect. Drought stress caused memory effects. In January, needles from trees drought-stressed in summer contained higher activities of defence enzymes and soluble protein contents than needles from well-watered trees. Three weeks after the end of a drought episode in summer, needles from spruce trees grown at elevated CO2 contained increased CAT and POD activities as compared to needles from trees grown at ambient CO2. This response was increased, if elevated ozone was present as an additional stress factor. These observations suggest that Norway spruce trees grown under elevated atmospheric CO2 concentrations might better be able to compensate environmental stresses than trees grown at ambient atmospheric CO2 concentrations.

KEYWORDS: GAS-EXCHANGE, PLANTS, SUPEROXIDE-DISMUTASE ACTIVITY

2164

Schwanz, P., B.A. Kimball, S.B. Idso, D.L. Hendrix, and A. Polle. 1996. Antioxidants in sun and shade leaves of sour orange trees (Citrus aurantium) after long-term acclimation to elevated CO2. *Journal of Experimental Botany 47(305):1941-1950.*

Antioxidative systems and the contents of pigments, malondialdehyde, soluble protein, and carbohydrate were investigated in sun- and shade-acclimated leaves of sour orange (Citrus aurantium) trees that had been grown for 7.5 years under ambient and elevated (+300 mu mol mol(-1)) atmospheric CO2 concentrations. Sun-acclimated leaves contained higher ascorbate, glutathione and soluble carbohydrate contents and higher catalase activities than shade-acclimated leaves. The activities of superoxide dismutases, which belonged to the family of Cu/Zn-isozymes, were similar in sun- and shade- acclimated leaves and decreased in response to enhanced CO2. In shade-acclimated leaves, none of the other parameters studied was affected by elevated CO2. In sun-acclimated leaves elevated CO2 caused increases in carbohydrate and ascorbate contents. There was no evidence for enhanced lipid peroxidation as assessed from the determination of the malondialdehyde contents under either conditions.

KEYWORDS: CARBON-DIOXIDE CONCENTRATIONS, CUZN-SUPEROXIDE, GLUTATHIONE-REDUCTASE, HIGH LIGHT, NEEDLES, NORWAY SPRUCE, PHOTOOXIDATIVE STRESS, PICEA-ABIES L, RISING ATMOSPHERIC CO2, SUPEROXIDE-DISMUTASE

2165

Schwanz, P., C. Picon, P. Vivin, E. Dreyer, J.M. Guehl, and A. Polle. 1996. Responses of antioxidative systems to drought stress in pendunculate oak and maritime pine as modulated by elevated CO2. *Plant Physiology 110(2):393-402.*

The aim of the present study was to investigate the effects of an enhanced CO2 concentration alone or in combination with drought stress on antioxidative systems of a deciduous (oak; Quercus robur) and an evergreen (pine; Pious pinaster) tree species. The seedlings were grown for one season in a greenhouse in tunnels supplied with 350 or 700 mu L L(-1) CO2. The experiment was repeated in a second year. Antioxidants, protective enzymes, soluble protein, and pigments showed considerable fluctuations in different years. Elevated CO2 caused significant reductions in the activities of superoxide dismutases in both oak and pine. The activities of ascorbate peroxidase and catalase were also reduced in most cases. The activities of dehydroascorbate reductase, monodehydroaseorbate radical reductase, glutathione reductase, and guaiacol peroxidase were affected little or not at all by elevated CO2. When the trees were subjected to drought stress by withholding water, the activities of antioxidative enzymes decreased in leaves of pine and oak grown at ambient CO2 and increased in plants grown at elevated CO2 concentrations. The present results suggest that growth in elevated CO2 might reduce oxidative stress to which leaf tissues are normally exposed and enhance metabolic flexibility to encounter increased stress by increases in antioxidative capacity.

KEYWORDS: ASCORBATE, CLIMATE CHANGE, GLUTATHIONE, LEAVES, NEEDLES, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PICEA-ABIES L, QUERCUS-ROBUR L, WATER-STRESS

2166

Schwanz, P., and A. Polle. 1998. Antioxidative systems, pigment and protein contents in leaves of adult Mediterranean oak species (Quercus pubescens and Q- ilex) with lifetime exposure to elevated CO2. *New Phytologist 140(3):411-423.*

The aim of the present study was to investigate the effects of elevated CO2 on the antioxidative systems and the contents of pigments, soluble protein and lipid peroxidation in leaves of adult oaks, Quercus pubescens and Quercus ilex, grown at naturally enriched CO2 concentrations. For this purpose, a field study was conducted at two CO2 springs in Central Italy. Measurements of the pre-dawn water potentials indicated less drought stress in trees close to CO2 springs than in those grown at ambient CO2 concentrations. Most leaf constituents investigated showed significant variability between sampling dates, species and sites. The foliar contents of protein and chlorophylls were not affected in trees grown close to the CO2 vents compared with those in ambient conditions. Increases in glutathione and other soluble thiols were observed, but these responses might have been caused by a low pollution of the vents with sulphurous gases. At CO2 vents, glutathione reductase was unaffected, and superoxide dismutase activity was significantly diminished, in both species. Generally, the activities of catalase, guaiacol peroxidase and ascorbate peroxidase as well as the sum of dehydroascorbate and ascorbate were decreased in leaves from trees grown in naturally CO2- enriched environments compared with those grown at ambient CO2 concentrations. The reduction in protective enzymes did not result in increased lipid peroxidation, but increased monodehydroascorbate radical reductase and dehydroascorbate reductase activities found in leaves of Q. pubescens suggest that the smaller pool of ascorbate was subjected to higher turnover rates. These data show that changes in leaf physiology persist, even after lifetime exposure to enhanced atmospheric CO2. The results suggest that the down-regulation of protective systems, which has also previously been found in young trees or seedlings under controlled exposure to elevated CO2 concentrations, might reflect a realistic response of antioxidative defences in mature trees in a future high-CO2 world.

KEYWORDS: ASCORBATE, CARBON DIOXIDE, DROUGHT STRESS, ENHANCED OZONE, ENZYMES, NEEDLES, PICEA-ABIES L, RESPONSES, RISING ATMOSPHERIC CO2, TREES

2167

Schwartz, M.W. 1992. Potential effects of global climate change on the biodiversity of plants. *The Forestry Chronicle 68(4):462-471.*

Climatologists have observed a consistent increase in atmospheric CO2 over the past 30 years. It is predicted that CO2 levels could double the pre-industrial level of 280 ppm by the year 2100, perphaps much earlier. Climate models of doubled atmospheric CO2 predict that mean temperatures will increase between 1.5 and 4.5-degrees-C globally; these temperature changes will be greater at high latitudes. Mid-continental regions will experience lower rainfall. Predictions of species northward range shifts in response to climate change vary from 100 km to over 500 km. Historical evidence of species range movements following the Pleistocene indicate that tree species typically migrated at rates of 10 km to 40 km per century. A simulation model that predicts the migration response of trees through modem fragmented landscapes predicts migration rates much lower than Pleistocene observations. Thus migration response is likely to lag far behind rates of climatic change, potentially threatening narrowly distributed species whose predicted future ranges do not overlap with their current range. Insect pests and microbial pathogens should respond to climatic warming faster than long-lived trees. Predicted increased drought frequency may increase plant stress and thereby increase the frequency of insect outbreaks and disease. Predictions of species responses are complicated by direct effects of increased CO2, such as increased water-use. efficiency. However, response to elevated CO2 vanes among species. Thus, shifts in composition within plant communities are also likely, but are, as yet, unpredictable.

2168

Scurlock, J.M.O., and D.O. Hall. 1998. The global carbon sink: a grassland perspective. *Global Change Biology 4(2):229-233.*

The challenge to identify the biospheric sinks for about half the total carbon emissions from fossil fuels must include a consideration of below-ground ecosystem processes as well as those more easily measured above-ground. Recent studies suggest that tropical grasslands and savannas may contribute more to the 'missing sink' than was previously appreciated, perhaps as much as 0.5 Pg (= 0.5 Gt) carbon per annum. The rapid increase in availability of productivity data facilitated by the Internet will be important for future scaling-up of global change responses, to establish independent lines of evidence about the location and size of carbon sinks.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, CONIFEROUS FORESTS, CYCLE, ECOSYSTEMS, PRODUCTIVITY, SOIL CARBON, STORAGE, TEMPERATE, WORLDWIDE

2169

Seaton, K.A., and D.C. Joyce. 1993. Effects of low-temperature and elevated co2 treatments and of heat-treatments for insect disinfestation on some native- australian cut flowers. *Scientia Horticulturae 56(2):119-133.*

For bioassay insects, 14 days storage at 1-degrees-C was required for 100% kill of adult flour beetles (Tribolium confusum Koch.), and 10 days at 1-degrees-C killed 100% of Mediterranean fruit fly larvae (Ceratitis capitata Wied.). A CO2 enriched atmosphere of between 45% and 60% (11% and 8% O2, respectively) reduced the time required to achieve 100% mortality of these bioassay insects to 7 days at 1-degrees-C. Increasing the CO2 content of the atmosphere to 80% (4% O2) did not further reduce the time to achieve 100% mortality. Vase life of red kangaroo paw (Anigozanthos rufus) was reduced below that of the unstored control after just 3.5 days at 1-degrees- C. Geraldton wax (Chamelaucium uncinatum) cultivar 'Newmarracarra' was similarly affected after 14 days, and acorn banksia (Banksia prionotes) after 28 days. Vase lives of Geraldton wax cultivar 'Newmarracarra' and of red kangaroo paw were not reduced following 7 days storage at 1-degrees-C in 15% CO2, compared with controls stored in air. However, Geraldton wax and red kangaroo paw vase lives were shortened and flower colour was altered after storage for 7 days in 30% CO2 (15% O2). Geraldton wax and red kangaroo paw had no vase lives following storage in 80% CO2 (4% O2) at 1-degrees-C for 3. 5 days. Heat treatments of hot water dips (46-degrees-C for 30 min or 56-degrees-C for 10 min) and vapour heat (66-degrees-C for 10 min) killed 100% of adult flour beetles and Mediterranean fruit fly larvae, but damaged and shortened the vase lives of Geraldton wax and banksia.

KEYWORDS: COLD-STORAGE, INFLORESCENCES TELOPEA-SPECIOSISSIMA, PHYSIOLOGY, PROTEACEAE, QUARANTINE PROCEDURE, VASE LIFE

2170

Seegmuller, S., and H. Rennenberg. 1994. Interactive effects of mycorrhization and elevated carbon- dioxide on growth of young pedunculate oak (quercus-robur L) trees. *Plant and Soil 167(2):325-329.*

Pedunculate oak (Quercus robur L.) was germinated and grown at ambient CO2 level and 650 ppmv CO2 in the presence and absence of the ectomycorrhizal fungus Laccaria laccata for a total of 6 month under

nutrient non-limiting conditions. Mycorrhization and elevated atmospheric CO2 each supported the growth of the trees. Stem height, stem diameter, and dry matter accumulation of pedunculate oak were increased by mycorrhization. Elevated atmospheric CO2 enhanced stem height, stem diameter, fresh weight and dry weight, as well as lateral root formation of the trees. In combination, mycorrhization and elevated atmospheric CO2 had a more than additive, positive effect on tree height and biomass accumulation, and further improved lateral root formation of the trees. From these findings it is suggested that the efficiency of the roots in supporting the growth of the shoot is increased in mycorrhized oak trees at elevated atmospheric CO2.

KEYWORDS: CO2- ENRICHMENT, MINERAL NUTRITION, SEEDLINGS

2171

Seegmuller, S., M. Schulte, C. Herschbach, and H. Rennenberg. 1996. Interactive effects of mycorrhization and elevated atmospheric CO2 on sulphur nutrition of young pedunculate oak (Quercus robur L) trees. *Plant, Cell and Environment 19(4):418-426.*

Pedunculate oak (Quercus robur L.) was germinated and grown at ambient CO2 concentration and 650 mu mol mol(-1) CO2 in the presence and absence of the ectomycorrhizal fungus Laccaria laccata for a total of 22 weeks under non-limiting nutrient conditions. Sulphate uptake, xylem loading and exudation were analysed in excised roots. Despite a relatively high affinity for sulphate (K-M = 1.6 mmol m(-3)), the rates of sulphate uptake by excised lateral roots of mycorrhizal oak trees were low as compared to herbaceous plants. Rates of sulphate uptake were similar in mycorrhizal and non-mycorrhizal roots and were not affected by growth of the trees at elevated CO2. However, the total uptake of sulphate per plant was enhanced by elevated CO2 and further enhanced by elevated CO2 and mycorrhization. Sulphate uptake seemed to be closely correlated with biomass accumulation under the conditions applied. The percentage of the sulphate taken up by mycorrhizal oak roots that was loaded into the xylem was an order of magnitude lower than previously observed for herbaceous plants. The rate of xylem loading was enhanced by mycorrhization and, in roots of mycorrhizal trees only, by growth at elevated CO2. On a whole-plant basis this increase in xylem loading could only partially be explained by the increased growth of the trees. Elevated CO2 and mycorrhization appeared to increase greatly the sulphate supply of the shoot at the level of xylem loading. For all treatments, calculated rates of sulphate exudation were significantly lower than the corresponding rates of xylem loading of sulphate. Radiolabelled sulphate loaded into the xylem therefore seems to be readily diluted by unlabelled sulphate during xylem transport. Allocation of reduced sulphur from oak leaves was studied by flap-feeding radiolabelled GSH to mature oak leaves. The rate of export of radioactivity from the fed leaves was 4.5 times higher in mycorrhizal oak trees grown at elevated CO2 than in those grown at ambient CO2. Export of radiolabel proceeded almost exclusively in a basipetal direction to the roots. From these experiments it can be concluded that, in mycorrhizal oak trees grown at elevated CO2, the transport of sulphate to the shoot is increased at the level of xylem loading to enable increased sulphate reduction in the leaves. Increased sulphate reduction seems to be required for the enhanced allocation of reduced sulphur to the roots which is observed in trees grown at elevated CO2. These changes in sulphate and reduced sulphur allocation may be a prerequisite for the positive effect of elevated CO2 on growth of oak trees previously observed.

KEYWORDS: CELLS, EFFICIENCY, GROWTH, LONG-DISTANCE TRANSPORT, PLANTS, ROOTS, SEEDLINGS, SULFATE TRANSPORT, SULFUR, TRANSLOCATION

2172

Segal, M., P. Alpert, U. Stein, M. Mandel, and M.J. Mitchell. 1994. Some assessments of the potential 2 X co2 climatic effects on water-balance components in the eastern mediterranean. *Climatic Change 27(4):351-371.*

General circulation model (GCM) coarse evaluations of the climatological impact in the Eastern Mediterranean due to global doubling of the atmospheriC CO2 concentration were used as input for a preliminary estimation of modifications in local processes affecting the water balance in this region. It is suggested that: (i) in the 2 x CO2 climate the average regional change of precipitation associated with typical mid-winter cyclonic systems is relatively small, however, it is associated with redistribution of the regional rainfall; (ii) in the elevated terrain in the northern part of the region, daytime snowmelt due to warm air advection may be enhanced, as much as 2.8 cm per day; and (iii) transpiration in the coastal area of the Eastern Mediterranean may increase by approximately 13% of its current level in the summer and somewhat more in the winter.

KEYWORDS: HEAT-STORAGE, LAYER, MODEL, OCEAN, PRECIPITATION, SENSITIVITY

2173

Seginer, I., C. Gary, and M. Tchamitchian. 1994. Optimal temperature regimes for a greenhouse crop with a carbohydrate pool - a modeling study. *Scientia Horticulturae 60(1-2):55-80.*

A simple crop model with two state variables, namely structural biomass and carbohydrate pool, was used to explore the effect of alternative temperature regimes on greenhouse crop production, Assuming a repeated environmental cycle, certain qualitative predictions could be made. (1) The smaller the plants and the higher the light integral and CO2 enrichment, the higher are the temperatures which lead to maximum production. (2) Day temperatures higher than night temperatures usually lead to higher production. On winter days, however, an inverse temperature regime may result in energy saving without loss of production. (3) Temperature variations may often be tolerated, provided that the mean temperature (temperature integral) is maintained at the level appropriate for maximum production. A limited amount of published experimental data was used to fit the model, leading to a satisfactory agreement.

KEYWORDS: ENRICHMENT, GROWTH, LEAVES, LEVEL, RESPIRATION, TOMATO PLANTS, TOMGRO, YIELD

2174

Sehmer, L., V. Fontaine, F. Antoni, and P. Dizengremel. 1998. Effects of ozone and elevated atmospheric carbon dioxide on carbohydrate metabolism of spruce needles. Catabolic and detoxification pathways. *Physiologia Plantarum 102(4):605-611.*

We have studied the effects of ozone, carbon dioxide and ozone combined with carbon dioxide fumigations on catabolic and detoxification pathways in spruce (Picea abies [L.] Karst.) needles. The results obtained showed an increase in the activities of three enzymes involved in the detoxification pathway, superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (AscPOD, EC 1.11.1.11) and glutathione reductase (GR, EC 1.6.4.2) when trees were exposed to ozone and to ozone- carbon dioxide treatments. In these two treatments, the fraction of SOD activity due to the chloroplastic isoform was increased (1.5-fold). In the needles of trees exposed to ozone and to ozone-carbon dioxide fumigation, an increase in the activities of glucose-6-phosphate dehydrogenase (G-6-PDH, EC 1.1.1.49) showed that the cell had the capacity to produce more NADPH necessary for the detoxification. Stimulation of other enzymes of catabolic pathways (fumarase [EC 4.2.1.2], phosphofructokinase [PFK, EC 7.1.1] and

phosphoenolpyruvate carboxylase [PEPC, EC 4.1.1.31]), was also observed making it possible for the cell to provide the reducing power necessary for detoxification as well as energy and carbon skeletons involved in the repair processes. When carbon dioxide alone was applied, no effects could be detected on these enzyme activities. However, when carbon dioxide was combined with ozone, the effect of ozone on trees was less than that induced by ozone alone, suggesting that elevated atmospheric carbon dioxide concentrations may to some extent protect plants from ozone injury.

KEYWORDS: AIR- POLLUTANTS, ASSAY, CO2, ENZYMES, HYDROGEN- PEROXIDE, NORWAY SPRUCE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PINE, PLANTS, SUPEROXIDE-DISMUTASE

2175

Seko, Y., and M. Nishimura. 1996. Effect of CO2 and light on survival and growth of rice regenerants grown in vitro on sugar-free medium. *Plant Cell Tissue and Organ Culture 46(3):257-264.*

Rice (Oryza sativa L.) plantlets regenerated from callus (rice regenerants) were grown in vitro during the preparation stage either on a 1/4 strength N6 gellan gum (4 g 1(-1)) medium without sucrose (SFM) or with 30 g 1(-1) sucrose (SCM), and under CO2 concentrations of 0.4, 2, 10, 50 or 100 mmol mol(-1), a photoperiod of 24 h and a photosynthetic photon flux density (PPFD) of 125 mu mol m(-2) s(-1). Rice regenerants were also grown in vitro on SFM or SCM under CO2 concentration of 50 mmol mol(-1), a photoperiod of 12 or 24 h and a PPFD of 80 or 125 mu mol m(-2) s(-1). All rice regenerants grew successfully on SFM under CO2 concentrations of 50 or 100 mmol mol(-1). Increasing the CO2 concentration increased the survival percentage, shoot length and shoot and root dry weights of rice regenerants grown on SFM. Increasing CO2 concentration had no significant effect on the survival or growth of rice regenerants grown on SCM. Survival percentages of rice regenerants grown on SCM were less than 80% for each of the CO2 concentrations. A photoperiod of 24 h under CO2 enrichment improved the survival and growth of rice regenerants grown on SFM, and increased the survival percentage and shoot dry weight of rice regenerants grown on SCM.

KEYWORDS: CARBON DIOXIDE, CULTURE, ENRICHMENT, INVITRO, SUCROSE CONCENTRATION

2176

Seligman, N.G., and T.R. Sinclair. 1995. Global environment change and simulated forage quality of wheat .2. Water and nitrogen stress. *Field Crops Research 40(1):29-37.*

Forage crops are frequently subjected to stress conditions resulting from inadequate supplies of water and N. Because forages grown under these stress conditions constitute an important resource in animal agriculture, this study was undertaken to assess possible changes in the nutritive value and productivity of forage crops as a consequence of global environment change. A relatively simple, mechanistic model of wheat was extended to simulate growth and important determinants of feed quality ([N], leaf:stem, dry matter digestibility) in an annual, temperate climate C-3 forage grass. Weather data for a semiarid region and different levels of applied N were used to examine the response of forage productivity to various levels of water and N availability. Not surprisingly, responses to global environment change were highly dependent on the availability of both water and N. When either resource was available at low levels, production of digestible dry matter was nearly unchanged by elevated [CO2] or increased temperature. When compared at equivalent development stages, small increases in forage quality were simulated, mainly because higher temperature resulted in achievement of the initiation of grain fill at an earlier date. As N availability increased, differences in forage characteristics and productivity became more prominent. Elevated ambient [CO2] increased vegetative mass, digestible dry matter, and concentration of digestible dry matter but decreased leaf:stem and [N]. Increased temperature generally had an effect on forage traits that was opposite to the elevated [CO2] response. The combined effects of both factors sometimes cancelled each other, but usually one of the factors was dominant. Negative effects of temperature tended to be aggravated by dry conditions. At crop maturity, positive effects of elevated atmospheric [CO2] on forage productivity and quality were severely decreased by nutrient and physiological constraints. These simulations indicate that when forage crops are grown under irrigation in semiarid regions, there may be substantial and complex changes in productivity and feed quality as a consequence of warmer temperature and elevated atmospheric [CO2]. Under rainfed conditions, these differences could be quite erratic and virtually unpredictable within the current range of interannual variation in forage productivity and quality.

KEYWORDS: CARBOHYDRATE, CARBON DIOXIDE, CO2-ENRICHMENT, DIGESTIBILITY, DRY-WEIGHT, GROWTH, PLANT, TEMPERATURE, YIELD

2177

Sellers, P.J., F.G. Hall, R.D. Kelly, A. Black, D. Baldocchi, J. Berry, M. Ryan, K.J. Ranson, P.M. Crill, D.P. Lettenmaier, H. Margolis, J. Cihlar, J. Newcomer, D. Fitzjarrald, P.G. Jarvis, S.T. Gower, D. Halliwell, D. Williams, B. Goodison, D.E. Wickland, and F.E. Guertin. 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. *Journal of Geophysical Research-Atmospheres 102(D24):28731-28769.*

The goal of the Boreal Ecosystem-Atmosphere Study (BOREAS) is to improve our understanding of the interactions between the boreal forest biome and the atmosphere in order to clarify their roles in global change. This overview paper describes the science background and motivations for BOREAS and the experimental design and operations of the BOREAS 1994 and BOREAS 1996 field years. The findings of the 83 papers in this journal special issue are reviewed, In section 7, important scientific results of the project to date are summarized and future research directions are identified.

KEYWORDS: AMAZONIAN FOREST, ATMOSPHERIC CO2, CANOPY, CARBON DIOXIDE, ENERGY, EXCHANGE, FIELD EXPERIMENT FIFE, GENERAL-CIRCULATION MODEL, LAND-SURFACE, WATER-VAPOR

2178

Sellers, P., F. Hall, H. Margolis, B. Kelly, D. Baldocchi, G. Denhartog, J. Cihlar, M.G. Ryan, B. Goodison, P. Crill, K.J. Ranson, D. Lettenmaier, and D.E. Wickland. 1995. The boreal ecosystem-atmosphere study (boreas) - an overview and early results from the 1994 field year. *Bulletin of the American Meteorological Society 76(9):1549-1577.*

The Boreal Ecosystem Atmosphere Study (BOREAS) is a large-scale international field experiment that has the goal of improving our understanding of the exchanges of radiative energy, heat, water, CO2, and trace gases between the boreal forest and the lower atmosphere. An important objective of BOREAS is to collect the data needed to improve computer simulation models of the processes controlling these exchanges so that scientists can anticipate the effects of global change. From August 1993 through September 1994, a continuous set of monitoring measurements-meteorology, hydrology, and satellite remote sensing-were gathered over the 1000 x 1000 km BOREAS study region that covers most of Saskatchewan and Manitoba, Canada. This monitoring program was punctuated by six campaigns that saw the

deployment of some 300 scientists and aircrew into the field, supported by 11 research aircraft. The participants were drawn primarily from U.S. and Canadian agencies and universities, although there were also important contributions from France, the United Kingdom, and Russia. The field campaigns lasted for a total of 123 days and saw the compilation of a comprehensive surface-atmosphere flux dataset supported by ecological, trace gas, hydrological, and remote sensing science observations. The surface-atmosphere fluxes of sensible heat, latent heat, CO2, and momentum were measured using eddy correlation equipment mounted on a surface network of 10 towers complemented by four flux-measurement aircraft. All in all, over 350 airborne missions (remote sensing and eddy correlation) were flown during the 1994 field year. Preliminary analyses of the data indicate that the area-averaged photosynthetic capacity of the boreal forest is much less than that of the temperate forests to the south. This is reflected in very low photosynthetic and carbon drawdown rates, which in turn are associated with low transpiration rates (less than 2 mm day-1 over the growing season for the coniferous species in the area). The strong sensible fluxes generated as a result of this often lead to the development of a deep dry planetary boundary layer over the forest, particularly during the spring and early summer. The effects of frozen soils and the strong physiological control of evapotranspiration in the biome do not seem to be well represented in most operational general circulation models of the atmosphere. Analyses of the data will continue through 1995 and 1996. Some limited revisits to the field are anticipated.

KEYWORDS: CARBON, DYNAMICS, FIFE, MODEL

2179

Seneweera, S.P., A.S. Basra, E.W. Barlow, and J.P. Conroy. 1995. Diurnal regulation of leaf blade elongation in rice by co2 - is it related to sucrose-phosphate synthase activity. *Plant Physiology 108(4):1471-1477.*

The relationship between leaf blade elongation rates (LER) and sucrose-phosphate synthase (SPS) activity was investigated at different times during ontogeny of rice (Oryza safiva L. cv Jarrah) grown in flooded soil at either 350 or 700 mu L CO2 L(- 1). High CO2 concentrations increased LER of expanding blades and in vivo activity (V-limiting) SPS activity of expanded blades during the early vegetative stage (21 d after planting [DAP]), when tiller number was small and growing blades were strong carbohydrate sinks. Despite a constant light environment, there was a distinct diurnal pattern in LER, V- limiting SPS activity, and concentration of soluble sugars, with an increase in the early part of the light period and a decrease later in the light period. The strong correlation (r = 0.65) between LER and V-limiting SPS activity over the diurnal cycle indicated that SPS activity played an important role in controlling blade growth. The higher V-limiting SPS activity at elevated CO, at 21 DAP was caused by an increase in the activation state of the enzyme rather than an increase in V- max. Fructose and glucose accumulated to a greater extent than sucrose at high CO2 and may have been utilized for synthesis of cell-wall components, contributing to higher specific leaf weight. By the mid-tillering stage (42 DAP), CO2 enrichment enhanced V-limiting and V-max activities of source blades. Nevertheless, LER was depressed by high CO2, probably because tillers were stronger carbohydrate sinks than growing blades.

KEYWORDS: CARBON, GROWTH, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS

2180

Seneweera, S., A. Blakeney, P. Milham, A.S. Basra, E.W.R. Barlow, and J. Conroy. 1996. Influence of rising atmospheric CO2 and phosphorus nutrition on the grain yield and quality of rice (Oryza sativa cv. Jarrah). *Cereal Chemistry 73(2):239-243.*

Raising the atmospheric CO2 concentration from 350 mu l of CO2 per liter to a level expected by the end of the next century (700 mu l/L) influenced both the grain yield and quality of the short-duration rice (Oryza sativa) cultivar, Jarrah. Yield was enhanced by up to 58%, primarily due to an increase in grain number, although grain size was also greater at high CO2. Varying the supply of phosphorus influenced the magnitude of the CO2 response with greatest responses occurring at medium rather than luxury or low phosphorus supplies. However, yield enhancement by high CO2 was observed even when phosphorus supply was severely growth limiting. Chemical (amylose and nutrient concentration) and physical (relative paste viscosity) measurements made on the ground grain indicated that cooked rice grain from plants grown under high levels of CO2 would be firmer. The nutritive value of grain was also changed at high CO2 due to a reduction in grain nitrogen and, therefore, protein concentration. However, total nitrogen content per grain was unaffected by high CO2. In contrast, phosphorus content per grain was greater at high CO2 and there was a strong correlation between magnesium and phosphorus concentrations. These results indicate that there is a need to plan for the inevitable rise in atmospheric CO2 concentrations by selecting genotypes that will maintain suitable quality characteristics under global change.

KEYWORDS: CARBON DIOXIDE, GROWTH, STARCH

2181

Seneweera, S.P., and J.P. Conroy. 1997. Growth, grain yield and quality of rice (Oryza sativa L.) in response to elevated CO2 and phosphorus nutrition (Reprinted from Plant nutrition for sustainable food production and environment, 1997). *Soil Science and Plant Nutrition 43:1131-1136.*

The influence of rising atmospheric CO2 concentrations and phosphorus nutrition on growth, grain yield and quality of a early maturing rice cultivar (Oryza sativa L. cv. Jarrah) was investigated by growing plants in a range of phosphorus levels at tither 350 or 700 mu L CO2 L-1 in the growth chambers. Total above ground biomass and grain yield were greater at elevated CO2 concentrations and with increasing phosphorus supply. The CO2 response was evident at all but the lowest phosphorus treatments but its magnitude was greater at moderate phosphorus supplies. The increase in grain yield at high CO2 was due mainly to an enhancement of tiller number. The phosphorus concentration in the foliage was unaffected by CO2 enrichment and the critical concentration of 1.8 g kg(-1) dwt was the same as reported for field-grown rice. The concentration of calcium in the foliage was increased by high CO2 and the nitrogen concentration was reduced, Chemical analysis (amylose and mineral concentration) indicated that cooked rice grain from high-CO2-grown plants would be firmer and that concentrations of Zn and Fe, which are important in the diet of humans, will be lower. These results indicate that there is a need to plan for the inevitable rise in global CO2 concentrations by selecting cultivars which will be more productive and yet maintain suitable quality characteristics under elevated CO2 levels.

KEYWORDS: CARBON DIOXIDE, DURATION, ENRICHMENT, NITROGEN, TEMPERATURE, WHEAT

2182

Seneweera, S.P., O. Ghannoum, and J. Conroy. 1998. High vapour pressure deficit and low soil water availability enhance shoot growth responses of a C-4 grass (Panicum coloratum cv. Bambatsi) to CO2 enrichment. *Australian Journal of Plant Physiology 25(3):287-292.*

The hypothesis that shoot growth responses of C-4 grasses to elevated CO2 are dependent on shoot water relations was tested using a C-4 grass, Panicum coloratum (NAD-ME subtype). Plants were grown for 35 days at CO2 concentrations of 350 or 1000 mu L CO2 L-1. Shoot water relations were altered by growing plants in soil which was brought daily

to 65, 80 or 100% field capacity (FC) and by maintaining the vapour pressure deficit (VPD) at 0.9 or 2.1 kPa. At 350 mu L CO2 L-1, high VPD and lower soil water content depressed shoot dry mass, which declined in parallel at each VPD with decreasing soil water content. The growth depression at high VPD was associated with increased shoot transpiration, whereas at low soil water, leaf water potential was reduced. Elevated CO2 ameliorated the impact of both stresses by decreasing transpiration rates and raising leaf water potential. Consequently, high CO2 approximately doubled shoot mass and leaf length at a VPD of 2.1 kPa and soil water contents of 65 and 80% FC but had no effect on unstressed plants. Water use efficiency was enhanced by elevated CO2 under conditions of stress but this was primarily due to increases in shoot mass. High CO2 had a greater effect on leaf growth parameters than on stem mass. Elevated CO2 increased specific leaf area and leaf area ratio, the latter at high VPD only. We conclude that high CO2 increases shoot growth of C-4 grasses by ameliorating the effects of stress induced by either high VPD or low soil moisture. Since these factors limit growth of field-grown C-4 grasses, it is likely that their biomass will be enhanced by rising atmospheric CO2 concentrations.

KEYWORDS: ELEVATED CO2, HUMIDITY

2183

Seneweera, S., P. Milham, and J. Conroy. 1994. Influence of elevated co2 and phosphorus-nutrition on the growth and yield of a short-duration rice (oryza-sativa L CV jarrah). *Australian Journal of Plant Physiology 21(3):281-292.*

The growth and development of a short-duration rice cultivar (Oryza sativa L. cv. Jarrah), grown in flooded soil with a range of phosphorus (P) levels and exposed to atmospheric CO2 concentrations of either 350 or 700 mu L L(-1) was followed for 146 days after planting (DAP). Development (estimated by rate of tiller production and time to flowering) was faster with higher soil P levels and CO2 enrichment, the effect being more pronounced with CO2 enrichment. During the early vegetative phase (up to 35 DAP), when rates of tiller production were low, shoot growth and rates of leaf expansion were faster at elevated CO2 concentrations and high soil P levels. Rates of tiller production were greater with these treatments during the 35-56 DAP period, when tillering was at a maximum. Shoot elongation was reduced at elevated CO2 levels and at high soil P levels during this period. By 146 DAP leaf weight was greater at high P levels, but CO2 enrichment accelerated tiller production to such an extent that final leaf weight was lower at high CO2, probably because there were fewer, and smaller, leaves on each tiller. Despite this, grain yield was increased by up to 58% by CO2 enrichment, with increases occurring even at low soil P levels. This was due mainly to an increase in grain number per panicle, although panicle number also increased. Higher soil P levels also increased grain number and yield. The P concentration in the foliage was unaffected by the CO2 treatments and the concentration required to produce maximum yield was 0.18% (dry wt basis) at both CO2 levels. Greater starch accumulation in the stems of high-CO2-grown plants may have accounted for the higher number of grains in each panicle.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, CARBON DIOXIDE, NITROGEN, PLANT GROWTH

2184

Senock, R.S., J.M. Ham, T.M. Loughin, B.A. Kimball, D.J. Hunsaker, P.J. Pinter, G.W. Wall, R.L. Garcia, and R.L. LaMorte. 1996. Sap flow in wheat under free-air CO2 enrichment. *Plant, Cell and Environment 19(2):147-158.*

The effects of elevated carbon dioxide (CO2) concentration on plant water use are best evaluated on plants grown under field conditions and with measurement techniques that do not disturb the natural function of the plant, seat balance sap flow gauges were used on individual main stems of wheat (Triticum aestivun L. cv Yecora rojo) grown under normal ambient conditions (control) and in a free-air CO2 enrichment (FACE) system in Arizona with either high (control+high H2O=CW; FACE+high H2O=FW) or low (control+low H2O=CD; FACE+low H2O=FD) irrigation regimens, Over a 30d period (stem elongation to anthesis), combinations of treatments were monitored with 10-40 gauges per treatment, The effects of increased CO2 on tiller water use were inconsistent in both the diurnal patterns of sap flow and the statistical analyses of daily sap flow (F-tot), Initial results suggested that the reductions in F-tot from CO2 enrichment were small (0-10%) in relation to the H2O treatment effect (20-30%), For a 3d period, F-tot of FW was 19-26% less than that of CW (P=0.10). Examination of the different sources of variation in the study revealed that the location of gauges within the experimental plots influenced the variance of the sap flow measurements, This variation was probably related to positional variation in subsurface drip lines used to irrigate plots, A sampling design was proposed for use of sap flow gauges in FACE systems with subsurface irrigation that takes into account the main treatment effects of CO2 enrichment and the other sources of variation identified in this study, Despite the small and often statistically non-significant differences in F-tot between the CW and FW treatments, cumulative water use of the FW treatment at the end of the first three test periods ranged from 7 to 23% lower than that of the CW treatment, Differences in sap flow between FW and CW compared well with treatment differences in evapotranspiration. The results of the study, based on the first reported sap flow measurements of wheat, suggest that irrigation requirements for wheat production, in the present climatic regimen of the south- western US, may be predicted to decreases lightly because of increasing atmospheric CO2.

KEYWORDS: BALANCE, CARBON DIOXIDE, COTTON, GROWTH, RESPONSES, TRANSPIRATION, WATER-USE

2185

Serraj, R., L.H. Allen, and T.R. Sinclair. 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology 5(3):283-291.*

This study was conducted to determine the response in leaf growth and gas exchange of soybean (Glycine man: Merr.) to the combined effects of water deficits and carbon dioxide (CO2) enrichment. Plants grown in pots were allowed to develop initially in a glasshouse under ambient CO2 and well-watered conditions. Four-week old plants were transferred into two different glasshouses with either ambient (360 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2. Following a 2-day acclimation period, the soil of the drought-stressed pots was allowed to dry slowly over a 2-week period. The stressed pots were watered daily so that the soil dried at an equivalent rate under the two CO2 levels. Elevated [CO2] decreased water loss rate and increased leaf area development and photosynthetic rate under both well-watered and drought-stressed conditions. There was, however, no significant effect of [CO2] in the response relative to soil water content of normalized leaf gas exchange and leaf area. The drought response based on soil water content for transpiration, leaf area, and photosynthesis provide an effective method for describing the responses of soybean physiological processes to the available soil water, independent of [CO2].

KEYWORDS: CO2 EXPOSURE, PHOTOSYNTHESIS, PHYSIOLOGY, RICE, SOIL, STAGE, TEMPERATURE, TRANSPIRATION, WATER-STRESS, WHEAT

2186

Serraj, R., T.R. Sinclair, and L.H. Allen. 1998. Soybean nodulation and N-2 fixation response to drought under carbon dioxide enrichment.

Plant, Cell and Environment 21(5):491-500.

The combined effects of carbon dioxide (CO2) enrichment and water deficits on nodulation and N-2 fixation were analysed in soybean [Glycine max (L.) Merr.]. Two shortterm experiments were conducted in greenhouses with plants subjected to soil drying, while exposed to CO2 atmospheres of either 360 or 700 mu mol CO2 mol(-1). Under drought-stressed conditions, elevated [CO2] resulted in a delay in the decrease in Nz fixation rates associated,vith drying of the soil used in these experiments. The elevated [CO2] also allowed the plants under drought to sustain significant increases in nodule number and mass relative to those under ambient [CO2], The total non-structural carbohydrate (TNC) concentration was lower in the shoots of the plants exposed to drought; however, plants under elevated CO2 had much higher TNC levels than those under ambient CO2. For both [CO2] treatments, drought stress induced a substantial accumulation of TNC in the nodules that paralleled N-2 fixation decline, which indicates that nodule activity under drought may not be carbon limited. Under drought stress, ureide concentration increased in all plant tissues. However, exposure to elevated [CO2] resulted in substantially less drought-induced ureide accumulation in leaf and petiole tissues. A strong negative correlation was found between ureide accumulation and TNC levels in the leaves. This relationship, together with the large effect of elevated [CO2] on the decrease of ureide accumulation in the leaves, indicated the importance of ureide breakdown in the response of N-2 fixation to drought and of feedback inhibition by ureides on nodule activity. It is concluded that an important effect of CO2 enrichment on soybean under drought conditions is an enhancement of photoassimilation, an increased partitioning of carbon to nodules and a decrease of leaf ureide levels, which is associated with sustained nodule growth and N-2 rates under soil water deficits. We suggest that future [CO2] increases are likely to benefit soybean production by increasing the drought tolerance of N-2 fixation.

KEYWORDS: AMINO-ACID, GAS-EXCHANGE, GROWTH, NITROGENASE ACTIVITY, OXYGEN PERMEABILITY, REDUCTION ACTIVITY, ROOT NODULE ACTIVITY, STRESS, WATER DEFICIT, WHITE CLOVER

2187

Sgherri, C.L.M., M.F. Quartacci, M. Menconi, A. Raschi, and F. Navari-Izzo. 1998. Interactions between drought and elevated CO2 on alfalfa plants. *Journal of Plant Physiology 152(1):118-124.*

Alfalfa (Medicago sativa L.) plants were grown in open top chambers at ambient (340 ppm) and high (600 ppm) CO2 concentrations. Twenty-five days after the first cutting one set of both plants was subjected to water deficit conditions by withholding water for 5 days. A chamber effect on proteolytic activity, monogalactosyl diacylglycerol to digalactosyl diacylglycerol molar ratio, total non-structural carbohydrates and soluble protein contents occurred. In contrast, no change in leaf water potential was observed between plants grown outdoors and inside the chambers. Plants grown at high CO2 concentration showed a lower decrease in leaf water potential in comparison with plants grown at atmospheric CO2 when subjected to water stress. Under high CO2 concentration leaf nitrogen content decreased whereas starch accumulation and a higher proteolytic activity were recorded. Following water depletion, CO2-enriched plants showed a decrease in total non- structural carbhydrates and soluble proteins. In thylakoid membranes high CO2 caused an increase in chlorophyll and lipid contents and a degradation of monogalactosyl diacylglycerol. A higher degree of unsaturation in the main thylakoid lipids was also observed. CO2-enriched plants were less affected by water stress as shown by reduced chlorophyll degradation and a higher membrane stability.

KEYWORDS: ACIDS, ATMOSPHERIC CARBON-DIOXIDE, FIELD, GROWTH, LIPIDS, PROTEIN, WATER-STRESS

2188

Shafer, S.R., U. Blum, S.J. Horton, and D.L. Hesterberg. 1998. Biomass of tomato seedlings exposed to an allelopathic phenolic acid and enriched atmospheric carbon dioxide. *Water, Air, and Soil Pollution 106(1-2):123-136.*

Increased atmospheric CO2 can affect plant growth, so competition among plants may be influenced. Allelopathy is one mechanism involved in plant competition. Experiments were conducted in a controlled-environment chamber to determine if the concentration of atmospheric CO2 altered the dose-response relationship between an allelopathic phenolic acid and tomato seedling biomass. Seeds of Lycopersicon lycopersicum were planted in quartz sand in styrofoam cups and allowed to germinate and grow for 15-17 days. During the next 14 days, seedlings were watered twice daily with nutrient solution amended with p-coumaric acid (4-hydroxycinnamic acid, HOC6H4CH = CHCO2H; ranging 0-0.85 mg mL(-1); 5 concentrations in each experiment) and exposed 24 hr day(-1) in continuous-stirred tank reactors (CSTRs) to ambient air (335-375 ppm CO2) or ambient air to which 350 ppm CO2 was added (i.e., approximately twice-ambient CO2; two CSTRs per CO2 concentration in each experiment). Dose-response data relating p-coumaric acid concentration and shoot, root, and total biomass were fit to a flexible decay function. In all three experiments, twice- ambient CO2 significantly increased the y-intercept for the dose-response model for the p-coumaric acid effect on shoot biomass by 25-50% but had negligible effects on other aspects of the models. Results suggest that if CO2 affects plant competition, mechanisms involving allelopathic phenolic acids may not be involved.

KEYWORDS: ANNUALS, CO2- ENRICHMENT, CUCUMBER LEAF EXPANSION, ELEVATED CO2, FERULIC ACID, GROWTH, INHIBITION, NUTRIENT CULTURE, PLANT-RESPONSES, RESOURCE USE

2189

Shainsky, L.J., and S.R. Radosevich. 1992. Mechanisms of competition between douglas-fir and red alder seedlings. *Ecology 73(1):30-45.*

Mechanisms of interactions between Douglas-fir (Pseudotsuga menziesii) and red alder (Alnus rubra) seedlings were assessed in experimentally manipulated stands. The density of each species was varied systematically, creating a matrix of competitive regimes that consisted of five monoculture densities and 25 mixtures of all possible pairwise combinations of the monoculture densities. Response surfaces for growth rates, leaf area, photon flux density, soil moisture content and depletion, and plant water potential were generated within the matrix. Regression coefficients quantified the effects of species densities on response variables, and correlation analysis yielded insight into interrelationships between variables. Tree performance, leaf area per square metre of ground surface area, resources, and physiological variables were all quantitatively altered by alder density, Douglas-fir density, and the interaction between species densities. Alder was the dominant competitor and overtopped the Douglas-fir. Competition for light was mediated by density effects on the leaf area of each species per square metre of ground surface area. Increasing alder leaf area reduced the light reaching the understory Douglas-fir. In contrast, increasing Douglas-fir leaf areas increased the light penetrating through to the understory conifers, due to Douglas-fir's suppression of alder leaf area per square metre. Soil moisture limitations were also created by increasing the density of both species and resulted in increasingly negative leaf water potentials for both species. Growth rates concurrently declined as plant water stress increased. Response variables were assembled into a conceptual modeling proposing how species density

regulated growth through the interactions between resource limitations and impairment of physiological function.

KEYWORDS: CANOPY LEAF-AREA, CARBON RELATIONS, CENTRAL EUROPEAN HEDGEROW, ELEVATED CO2, GROWTH, INTERFERENCE, PLANTATIONS, PLANTS, PRODUCTIVITY, WATER RELATIONS

2190
Sharma, A., and U.K. Sengupta. 1997. Carbon allocation and partitioning in Vigna radiata (L.) Wilczek as affected by additional carbon gain. *Photosynthetica 34(3):419-426.*

Carbon allocation to the source leaf export and partitioning to the sink were studied in mungbean supplied by additional carbon from the source leaves subjected to high CO2 concentrations (600 and 900 cm(3) m(-3)) in three metabolic and functional source-sink combinations. The plants were pruned to a source- path-sink system. With CO2 enrichment there was an appreciable increase in net photosynthetic CO2 uptake in earlier formed and physiologically younger leaves. Most of the carbon fixed as a result of enrichment was translocated out of the source leaf within one diurnal cycle. The carbon remaining in the source leaf was unchanged. Partitioning of extra carbon into starch or sugar depended upon the amount of extra carbon synthesized. The unloading of the extra carbon into sinks depended on whether it was used for growth or stored. Under increased carbon content, the leaf as a sink was able to reorganize its metabolic reactions more rapidly to maintain the required gradient for unloading than the pod acting as the sink.

KEYWORDS: CO2 EXCHANGE, DIOXIDE ENRICHMENT, LEAF, LEAVES, METABOLISM, PHOTOSYNTHESIS, RATES, TRANSLOCATION

2191
Sharma-Natu, P., F.A. Khan, and M.C. Ghildiyal. 1997. Photosynthetic acclimation to elevated CO2 in wheat cultivars. *Photosynthetica 34(4):537-543.*

Wheat (T. aestivum) cvs. Kalyansona and Kundan grown under atmospheric (CA) and elevated CO2 concentrations (650-150 cm(3) m(-3) - CE) in open top chambers were examined for net photosynthetic rate (P-N), stomatal limitation (l(S)) of P-N, ribulose-1,5-bisphosphate carboxylase (RuBPC) activity, and saccharide content of the leaves. The P-N values of both CA- and CE-grown plants compared at the same CO2 concentration showed a down regulation under CE at the post-anthesis stage. The negative acclimation of P-N appeared to be due to both stomatal and mesophyll components, and the RuBPC activity got also adjusted. There was a decrease in activation state of RuBPC under CE. In connection with this, an increased accumulation of saccharides in wheat leaf under CE was observed. Kalyansona, owing to its larger sink potential in terms of the number of grains, showed a greater enhancement under CE in both post-ear emergence dry matter production and grain yield. Under CE, this cultivar also showed a lower down regulation of P-N than Kundan.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, CARBOXYLASE ACTIVITY, DIURNAL CHANGES, ENHANCED CO2, EXCHANGE, GROWTH, LEAVES, LONG-TERM, PLANTS

2192
Shaver, G.R., W.D. Billings, F.S. Chapin, A.E. Giblin, K.J. Nadelhoffer, W.C. Oechel, and E.B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. *BioScience 42(6):433-441.*

KEYWORDS: ACCUMULATION, ALASKAN TUSSOCK TUNDRA, BOREAL FORESTS, CLIMATE, CO2, DIOXIDE, ERIOPHORUM VAGINATUM, GROWTH, NITROGEN, NUTRIENT

2193
Sheehy, J.E., F. Gastal, P.L. Mitchell, J.L. Durand, G. Lemaire, and F.I. Woodward. 1996. A nitrogen-led model of grass growth. *Annals of Botany 77(2):165-177.*

This model is built by considering the utilization rate of nitrogen as the first step in calculating the rate of growth of the various organs of a grass crop. The amount of carbohydrate determines whether there are sufficient carbon skeletons and sufficient energy available to support synthesis of new material. Growth of roots, tillers/stems and leaves is simulated with leaf divided into photosynthetic and non- photosynthetic structures. The model keeps account of soluble carbohydrate and nitrogen pools in each of the organs and storage pools of carbohydrate in the leaves and roots. The modelled crop has an age structure so that each plant organ has an age profile describing daily changes in growth; when the oldest tissue becomes senescent a fraction of its nitrogen is recycled. Seasonal changes in the percentage nitrogen content of the crop, when large amounts of soil nitrogen are available, are shown to be a consequence of changes in both soluble and stored carbohydrate. The contrast between high and low nitrogen treatments is shown to be a consequence of different allocation priorities for nitrogen. The model demonstrates that considering nitrogen as the primary element of synthesis provides an approach that predicts dry matter production successfully, as well as giving a different perspective of the growth processes, and suggesting that the capacity of the enzymatic processes governing synthesis ultimately limits crop yields. This different perspective may be most useful when trying to understand what controls growth and the relative influence of environmental changes on the physiology and morphology of the crop. (C) 1996 Annals of Botany Company

KEYWORDS: CO2- ENRICHMENT, CROPS, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, LEAF, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PLANT GROWTH, RESPONSES

2194
Sheppard, M.I., L.L. Ewing, and J.L. Hawkins. 1994. Soil processes and chemical-transport - soil degassing of C-14 dioxide - rates and factors. *Journal of Environmental Quality 23(3):461-468.*

Soil air normally contains elevated levels of CO2 relative to the atmosphere. The primary source of soil C is plant-root and microbial respiration. The exchange of soil and atmospheric CO2 is important to many environmental concerns, such as acid rain, global warming and waste management. Proposed disposal of high- level nuclear wastes containing primarily inorganic C-14 may provide a source of (CO2)-C-14 to the atmosphere. Field and laboratory experiments show that (CO2)-C-14 Soil degassing rate constants, the flux density (Bq.M2.s-1) divided by soil inventory (Bq-m-2), range from -10(-7) to -10(-2) S-1, and that the loss of inorganic C-14 is driven primarily by gaseous diffusion. These constants are affected by soil pH and porosity, with smaller influences of soil temperature, moisture and organic matter content. Degassing rate constants derived through mass balance calculations to estimate loss differ only by 20% from direct trapping methods. Frozen soil degassing rate constants were up to 25 times smaller than lab values, indicating that annual C-14 loss rates in northern climates would be lower because of reduced gaseous diffusion during the winter months. Using our field data, we recommend an annual C- 14 soil degassing rate constant of -1 x 10(-6) s-1 for acidic soils and a value of -5 x 10(-7) S-1 for calcareous soils. For probabilistic assessment modelling, we recommend a geometric mean degassing constant of -4.3 X 10(-7) S-1 with a geometric standard deviation of 3.26 for three different soils. This indicates the median half-life of C-14

in surface soils is 18 d, with a 99% confidence interval of 13 h and 640 d.

KEYWORDS: CO2, GAS-TRANSPORT, LAW, MODEL, NUCLEAR-FUEL WASTE, UNSATURATED ZONE, VADOSE ZONE

2195

Sheu, B.H., and C.K. Lin. 1999. Photosynthetic response of seedlings of the sub-tropical tree Schima superba with exposure to elevated carbon dioxide and temperature. *Environmental and Experimental Botany 41(1):57-65.*

Seedlings of Schima superba were exposed to both ambient (375 ppm) and 720 ppm levels of CO2 in combination with two incubation temperatures (25/20, 30/25 degrees C, day/night) for a six-month period. Net height growth of seedlings was enhanced in the early period of exposure to high levels of CO2. However, when seedlings were exposed for a longer period of time to this high concentration, net height growth was inhibited. Decreased photosynthetic rate with elevated CO2 was observed when measured in the ambient CO2 over a long-term exposure of 6 months. In contrast, a significant increase in photosynthesis was noted for seedlings exposed to higher incubation temperature in either ambient or 720 ppm CO2 concentrations. The response of CO2 assimilation to internal Ci was indicated by the lower sensitivity in seedlings grown in elevated CO2 concentration. Though this response could also be found in a higher sensitivity in seedlings grown at higher temperature, the seedlings grown in normal conditions (ambient CO2 and temperature) were still more sensitive to CO2 assimilation response to internal Ci. This experiment suggests that: (1) exposure of seedlings to higher CO2 levels for longer periods may lead to a decrease in seedling height growth and photosynthetic rate, as well as decreasing sensitivity to changing internal CO2 concentrations; (2) the optimum temperature for photosynthesis of seedlings grown in an elevated CO2 concentration was higher than that for seedlings grown in ambient concentration. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCLIMATION, ALLOCATION, CARBOXYLASE, GROWTH, HIGH ATMOSPHERIC CO2, PERSPECTIVE, PLANTS, PRODUCTIVITY, SOURCE-SINK RELATIONS

2196

Shipley, B., M. Lechowicz, S. Dumont, and W.H. Hendershot. 1992. Interacting effects of nutrients, ph-al and elevated co2 on the growth of red spruce (picea-rubens sarg) seedlings. *Water, Air, and Soil Pollution 64(3-4):585-600.*

A 4 mo growth chamber experiment was conducted to evaluate the presence and importance of interactions between nutrient supply, atmospheric CO2 concentration, and four different combinations of pH - Al concentration on the growth, vitality, and tissue element concentrations of 1-yr-old red spruce seedlings. Solution chemistry was chosen to simulate soil conditions at a red spruce dic-back site at Roundtop Mountain (Quebec) that has high acid loadings. CO2 levels were chosen to simulate ambient levels and those expected in the next century. All three experimental factors affected growth and all factors except CO2 affected the visual symptoms of die-back. There was an important interaction between nutrient levels and the different pH - Al combinations, indicating that the response of red spruce to various pH and Al concentrations changes with soil fertility. The positive growth response to enriched CO2 was not sufficient to offset the negative effects of the acid rain induced stresses. A principal component analysis showed that multivariate functions of foliar element concentrations could clearly distinguish plants from different experimental regimes.

KEYWORDS: ACID-RAIN, ALUMINUM, CARBON DIOXIDE, CLIMATE, FORESTS, INCREASING CO2, LOBLOLLY-PINE, OZONE, RESPONSES, TREE SEEDLINGS

2197

Shugart, H.H., T.M. Smith, and W.M. Post. 1992. The potential for application of individual-based simulation- models for assessing the effects of global change. *Annual Review of Ecology and Systematics 23:15-38.*

KEYWORDS: BOREAL FORESTS, CO2-INDUCED CLIMATE CHANGE, COMPUTER-MODEL, ENVIRONMENTAL-FACTORS, EVALUATING PERFORMANCE, FOREST SUCCESSION MODELS, INTERIOR ALASKA, PLANT- COMMUNITIES, STAND DEVELOPMENT, VEGETATION DYNAMICS

2198

Sicher, R. 1995. Diurnal amylolytic activity in soybean leaves grown at ambient and elevated co2. *Plant Physiology 108(2):55.*

2199

Sicher, R.C. 1997. Irradiance and spectral quality affect chlorosis of barley primary leaves during growth in elevated carbon dioxide. *International Journal of Plant Science 158(5):602-607.*

The development of chlorosis was studied in primary leaves of barley plants (Hordeum vulgare L. cv. Brant) grown at ambient and twice-ambient CO, partial pressures. Leaf yellowing was observed 17 d after sowing when plants were grown in controlled environment chambers equipped with high-intensify discharge lamps at an irradiance of 800 mu mol quanta m(-2) s(-1). The extent of leaf yellowing, measured as changes of total chlorophyll, increased when the CO, partial pressure was raised from 37 to 70 Pa. Chlorosis was increased further by increasing the irradiance from 800 to 1100 mu mol quanta m(-2) s(-1). Rates of photosynthetic O-2 evolution by primary leaves,measured 17 d after sowing, were 20% lower for elevated compared with ambient CO2-grown plants. This result agreed with the level of chlorosis. However soluble protein, Rubisco protein (ribulose, 1,5-bisphosphate carboxylase/oxygenase), and initial and total Rubisco activity 17 d after sowing were unaffected by CO2 enrichment and the extent of chlorosis. Leaf starch, sucrose, and glucose were increased by elevated CO2 treatment at almost every sampling. However,only glucose was correlated with leaf damage. Leaf yellowing also was observed on primary leaves of plants grown under microwave-powered sulfur lamps at 800 but not at 550 mu mol quanta m(-2) s(-1). The extent of leaf yellowing on plants grown under microwave- powered sulfur lamps was unaffected by CO2 enrichment. It was concluded that leaf yellowing was influenced by irradiance, photoquality, and CO2 enrichment. Photobleaching of antenna chlorophyll, rather than premature senescence, was the most Likely cause of visible leaf injury in barley.

KEYWORDS: ACCUMULATION, CARBOHYDRATE, CHLOROPHYLL CONTENT, CO2 CONCENTRATION, ENRICHMENT, FOLIAR DEFORMATION, FRUIT PRODUCTION, HIGH-PRESSURE SODIUM, PLANTS, TOMATO GENOTYPES

2200

Sicher, R.C. 1998. Yellowing and photosynthetic decline of barley primary leaves in response to atmospheric CO2 enrichment. *Physiologia Plantarum 103(2):193-200.*

The photosynthetic response of barley (Hordeum vulgare L. cv. Brant) primary leaves was studied as a function of chlorosis induced by CO2 enrichment. Leaf yellowing; measured as changes of chlorophyll a and b, was more extensive in controlled environments at elevated (680 +/- 17

mu l l(-1)) than at ambient (380 +/- 21 mu l l(-1)) CO2. Stomatal conductance of primary leaves was decreased by growth in elevated CO2 between 11 and 18 days after sowing (DAS) when measured at both 380 and 680 mu l l(-1) CO2. Internal leaf CO2 concentration (C-i) was also lower for elevated- compared to ambient-CO2-grown primary leaves between 11 and 14 DAS. Results suggest that non-stomatal factors were responsible for the decreased photosynthetic rates of elevated- compared to ambient-CO2-grown primary leaves 18 DAS. Various photochemical measurements, including quantum absorptance (alpha), minimal (F-0), maximal (F-m), and variable (F-v) chlorophyll fluorescence, as well as the F-v/F-m ratio, were significantly decreased 18 DAS in the elevated- compared to ambient-CO2 treatment. Photochemical (q(P)) and nonphotochemical (q(N)) chlorophyll fluorescence quenching: coefficients of 18-day-old primary leaves did not differ between CO2 treatments. Photosynthetic electron transport rates of photosystem II were slightly lower for elevated- compared to ambient-CO2-grown primary leaves 18 DAS. Concentrations of alpha-amino N (i.e. free amino acids) in barley primary leaves were increased by CO2 enrichment 10 DAS, but subsequently, alpha-amino N decreased in association with photosynthetic decline. Total acid protease activity was greater in elevated- than in ambient-CO2-grown leaves 18 DAS. The above findings suggest that photoinhibition and premature senescence were factors in the CO2-dependent yellowing of barley primary leaves.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL FLUORESCENCE, FOLIAR DEFORMATION, FRUIT PRODUCTION, GROWTH, LEAF, LONG-TERM EXPOSURE, TOMATO, WHEAT, YIELD

2201

Sicher, R.C. 1999. Photosystem-II activity is decreased by yellowing of barley primary leaves during growth in elevated carbon dioxide. *International Journal of Plant Science 160(5):849-854.*

Leaf yellowing was studied in 10-18-d-old barley seedlings (Houdeum vulgare L. cv. Brant) grown at ambient (38 Pa) and at elevated (68, 100, and 140 Pa) CO2 partial pressures in controlled-environment chambers. Maximal total chlorophyll (Chl) concentrations of primary leaves from all four CO2 growth treatments were 0.36 +/- 0.01 g m(-2), and these concentrations were observed 10-12 d after sowing (DAS). Total Chi levels in primary leaves were 35%, 64%, and 78% below maximal levels in the 38, 68, and 100 Pa CO2 growth treatments, respectively, when measured 18 DAS. Losses of Chi in 18-d-old primary leaves were similar in the 100 and 140 Pa CO2 treatments. Decreases of Chi d and Chi b in response to CO2 enrichment were comparable in isolated chloroplast preparations and in intact 18-d-old barley primary leaves of plants grown at 38 and 68 Pa CO2. Total thylakoid membrane proteins, the Chi alb binding protein (LHC-II), and D1 protein levels were also lower in chloroplast preparations from plants grown in the elevated compared to the ambient CO2 treatment. Both ferricyanide reduction and whole- chain electron-transport rates (H2O --> methylviologen) were significantly lower for chloroplasts from plants grown at 68 Pa CO2 compared with those grown at 38 Pa CO2. However, photosystem-I-dependent chloroplast photoreductions did not differ between CO2 treatments. The results indicated that the CO2-dependent yellowing of barley primary leaves adversely affected photosystem-II activity. Growth in elevated CO2 may have increased the susceptibility of photosystem-II to light damage.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CHLOROPHYLL, CHLOROSIS, EXCHANGE, FOLIAR DEFORMATION, IRRADIANCE, PHOTOSYNTHESIS, PLANTS, PROTEINS, TOMATO

2202

Sicher, R.C., and J.A. Bunce. 1997. Relationship of photosynthetic acclimation to changes of Rubisco activity in field-grown winter wheat and barley during growth in elevated carbon dioxide. *Photosynthesis Research 52(1):27-38.*

The responses of photosynthesis, Rubisco activity, Rubisco protein, leaf carbohydrates and total soluble protein to three carbon dioxide treatments were studied in winter wheat [Triticum aestivum (L.)] and barley [Hordeum vulgare (L.)]. Barley and wheat plants were grown in small field plots during 1995 and 1996 in clear, acrylic chambers (1.2-2.4 m(2)) and were provided with continuous carbon dioxide fertilization at concentrations of 350, 525 and 700 mu mol mol(-1). Photosynthetic rates of barley penultimate leaves and wheat flag leaves measured at growth carbon dioxide concentrations decreased with leaf age in all three CO2 treatments during 1995 and 1996. Photosynthetic acclimation to elevated CO2 was observed on seven of eight measurement dates for barley and ten of eleven measurement dates for wheat over both years. Initial Rubisco activity, total soluble protein and Rubisco protein in barley penultimate leaves and wheat flag leaves also decreased with leaf age. Total Rubisco activity was not used because of enzyme degradation. There was a significant CO2 treatment effect on initial Rubisco activity, total soluble protein and Rubisco protein for wheat in 1995 and 1996 and for barley in 1995. Responses of barley penultimate leaf Rubisco activity and leaf protein concentrations to elevated carbon dioxide were nonsignificant in 1996. A significant CO2 treatment effect also was detected when means of Rubisco activity, soluble protein and Rubisco protein for wheat flag leaves were combined over harvests and years. These three flag leaf parameters were not significantly different in the 350 and 525 mu mol mol(-1) CO2 treatments but were decreased during growth in 700 mu mol mol(- 1) CO2 relative to the other two CO2 treatments. Ratios of photosynthesis at 700 and 350 mu mol mol(-1) were compared to ratios of Rubisco activity at 700 and 350 mu mol mol(-1) using wheat flag leaf data from 1995 and 1996. Regression analysis of these data were linear [y = 0.586 + 1.103x(r(2) = 0.432)] and were significant at P less than or equal to 0.05. This result indicated that photosynthetic acclimation was positively correlated with changes of initial Rubisco activity in wheat flag leaves in response to CO2 enrichment. Effects of elevated CO2 on wheat leaf proteins during 1995 and 1996 and on barley during 1995 were consistent with an acceleration of senescence.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, PLANTS, PROTEINS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, YIELD

2203

Sicher, R.C., and J.A. Bunce. 1998. Evidence that premature senescence affects photosynthetic decline of wheat flag leaves during growth in elevated carbon dioxide. *International Journal of Plant Science 159(5):798-804.*

Net CO2 exchange (NCE) rates and various flag leaf constituents were measured in wheat plants (Triticum aestivum L.) grown in field chambers at either 350 or 700 mu L L-1 CO2. Rates of NCE decreased with leaf age in both CO2 treatments during 1997. A stimulation of NCE initially occurred in response to CO2 enrichment, but this was not observed on the final eight of 33 experimental days. Net photosynthetic rates in response to growth at elevated CO2 were decreased ca. 22% on average for all measurement dates in 1997 and when all NCE rates measured at elevated CO2 for 1995-1997 were averaged (P less than or equal to 0.0001). Soluble protein, alpha-amino nitrogen, and Chi a + b concentrations were significantly lower (P less than or equal to 0.0001) in elevated compared with ambient CO2-grown wheat flag leaves in 1997. The treatment by date interactions for these Rag leaf constituents were nonsignificant (P greater than or equal to 0.05). Flag leaf storage carbohydrates were measured on 10 dates in 1997, but only starch and sucrose were affected by the elevated CO2 treatment. An increase of acid proteinase activity was observed on the last two measurement dates of this study. However, changes of acid proteinase activity were unaffected

by CO2 enrichment (P greater than or equal to 0.05) and only occurred during late stages of senescence. These findings supported the suggestion that premature senescence contributed to the photosynthetic decline observed in wheat flag leaves during growth at elevated CO2. Changes of alpha-amino nitrogen were correlated with photosynthetic decline, but acid proteinase activity probably was under endogenous control.

KEYWORDS: ACCLIMATION, ACCUMULATION, CARBOXYLASE, ENRICHMENT, GRAIN-GROWTH, INCREASING ATMOSPHERIC CO2, LEAF, NITROGEN REDISTRIBUTION, PROTEINS, TRITICUM-AESTIVUM L

2204

Sicher, R.C., and D.F. Kremer. 1994. Responses of nicotiana-tabacum to co2 enrichment at low-photon flux-density. *Physiologia Plantarum 92(3):383-388.*

Effects of CO2 enrichment on photosynthesis and on dry matter allocation were examined in two tobacco (Nicotiana tabacum L.) genotypes, Samsun and W38. Plants were grown from seed in controlled environment chambers at a photosynthetic photon flux density of 450 mu mol m(-2) s(-1). Averaged over the 9 day study, net photosynthesis rates were 14.2 +/- 0.5 and 13.0 +/- 0.4 mu mol m(-2) s(-1) in elevated (70 Pa) and in ambient (35 Pa) CO2 air, respectively, when measured at the irradiance and CO2 partial pressure employed for plant growth. However, photosynthesis rates of plants grown in elevated CO2 were 50% less than those of the ambient controls on the last day of treatment, when measured at 70 Pa CO2 air and an irradiance of 900 mu mol m(-2) s(-1). Total plant dry weight and specific leaf weight were greater (P<0.05) in enriched-CO2-grown than in ambient-CO2-grown plants. Leaf starch, measured during the first hour of the photoperiod, increased over 7 days of treatment in elevated-CO2-grown but not in ambient-CO2-grown plants. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) activities of tobacco plants grown at 35 and 70 Pa CO2 air were 58.5 +/- 4.5 and 48.5 +/- 3.7 mu mol m(-2) s(-1), respectively, between days 0 and 9 of the study. Rubisco activation stale, Rubisco protein concentration, soluble protein and total chlorophyll were unaffected by CO2 enrichment. The above findings demonstrated that photosynthesis was down regulated in tobacco plants after 7 to 9 days of CO2 enrichment at low photosynthetic photon flux density, but less than at moderate irradiances.

KEYWORDS: ACCLIMATION, ANTISENSE RBCS, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, LEAVES, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

2205

Sicher, R.C., and D.F. Kremer. 1996. Rubisco activity is altered in a starchless mutant of Nicotiana sylvestris grown in elevated carbon dioxide. *Environmental and Experimental Botany 36(4):385-391.*

Dry matter and net photosynthesis of a wild type and a starchless mutant NS 458 of Nicotiana sylvestris (Speg. et Comes) were studied after 25 d of CO2 enrichment. Plants were grown from seed in controlled environment chambers and treatments of either ambient (35 Pa) or twice ambient (70 Pa) CO2 were initiated when plants were 3-4 weeks old. Photosynthetic rates measured at 35 and 70 Pa CO2 and at 900 mu mole quanta m(-2) s(-1) were unaffected (P>0.05) by 25 d of CO2 enrichment. However, a CO2-by-genotype interaction was observed indicating that photosynthetic rates of the wild type but not the mutant at 35 Pa CO2 differed in response to CO2 enrichment. Photosynthetic enhancement was greater (P < 0.001) in the wild type than in the mutant when the measurement CO2 was doubled. Total biomass and leaf areas of the mutant and wild type also were unaffected by CO2 enrichment, although specific leaf weight increased 27% and 13% (P<0.001) for the wild type and mutant lines, respectively. Neither chlorophyll nor soluble leaf protein were affected by CO, enrichment. Starch, sucrose, glucose and fructose in wild type and mutant leaf samples were also unaffected by CO2 enrichment. Rubisco protein levels of the wild type and mutant were about 20% lower in elevated compared to ambient CO2-grown plants. Initial and total Rubisco activities of wild type and mutant leaf samples were not significantly different (P>0.05) between CO2 environments. However, initial Rubisco activity was more than 30% lower in mutant than than in wild type samples when results from ambient and elevated CO2-grown plants were combined. Ribulose 1,5-bisphosphate and 3-phosphoglycerate were 280% and 28% greater in the mutant than in the wild type, respectively. These findings suggested that photosynthesis rates of the mutant were limited by Rubisco activity at 35 Pa CO2 and that end product synthesis rates limited photosynthesis of the mutant at 70 Pa CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, C-3 PLANTS, CARBOXYLASE, ENZYME, LEAVES, PHOSPHOGLUCOMUTASE, PHOTOSYNTHESIS, STEADY-STATE

2206

Sicher, R.C., D.F. Kremer, and J.A. Bunce. 1995. Photosynthetic acclimation and photosynthate partitioning in soybean leaves in response to carbon dioxide enrichment. *Photosynthesis Research 46(3):409-417.*

Photosynthetic rates and photosynthate partitioning were studied in three-week-old soybean [Glycine max (L.) Merr. cv. Williams] plants exposed to either ambient (35 Pa) or elevated (70 Pa) CO2 in controlled environment chambers. Ambient CO2- grown plants also were given a single 24 h treatment with 70 Pa CO2 1 d prior to sampling. Photosynthetic rates of ambient CO2- grown plants initially increased 36% when the measurement CO2 was doubled from 35 to 70 Pa. Photosynthetic rates of the third trifoliolate leaf, both after 1 and 21 d of elevated CO2 treatment, were 30 to 45% below those of ambient CO2-grown plants when measured at 35 Pa CO2. These reduced photosynthetic rates were not due to increased stomatal resistance and were observed for 2 to 8 h after plants given 1 d of CO2 enrichment were returned to ambient CO2. Initial and total ribulose 1,5- bisphosphate carboxylase/oxygenase (Rubisco) activities, percent activation, Rubisco protein, soluble protein and leaf chlorophyll content were similar in all CO2 treatments. Quantum yields of photosynthesis, determined at limiting irradiances and at 35 Pa CO2, were 0.049 +/- 0.003 and 0.038 +/- 0.005 mol CO2 fixed per mol quanta for ambient and elevated CO2-grown plants, respectively (p < 0.05). Leaf starch and sucrose levels were greater in plants grown at 70 than at 35 Pa CO2. Starch accumulation rates during the day were greater in ambient CO2- grown plants than in plants exposed to elevated CO2 for either 1 or 21 d. However, the percentage of C partitioned to starch relative to total C fixed was unaffected by 1 d of CO2 enrichment. The above results showed that both photosynthetic and starch accumulation rates of soybean leaflets measured at 35 Pa CO2 were temporarily reduced after 1 and 21 d of CO2 enrichment. The biochemical mechanism affecting these responses was not identified.

KEYWORDS: CARBOHYDRATE, ELEVATED ATMOSPHERIC CO2, EXPOSURE, GROWTH, LIGHT, RIBULOSE BISPHOSPHATE CARBOXYLASE, SEEDLINGS, STARCH, SUCROSE SYNTHESIS, TEMPERATURE

2207

Sicher, R.C., D.F. Kremer, and S.R. Rodermel. 1993. Role of rubisco during acclimation of transformed tobacco to co2 enriched atmospheres. *Plant Physiology 102(1):88.*

2208

Sicher, R.C., D.F. Kremer, and S.R. Rodermel. 1994. Photosynthetic acclimation to elevated co2 occurs in transformed tobacco with decreased ribulose-1,5-bisphosphate carboxylase/oxygenase content. *Plant Physiology 104(2):409-415.*

Inhibition of net carbon assimilation rates during growth at elevated CO2 was studied in transgenic tobacco (Nicotiana tabacum L.) plants containing zero to two copies of antisense DNA sequences to the small subunit polypeptide (rbcS) gene of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). High- and low-Rubisco tobacco plants were obtained from the selfed progeny of the original line 3 transformant (S.R. Rodermel, M.S. Abbott, L. Bogorad [1988] Cell 55: 673-681). Assimilation rates of high- and low-Rubisco tobacco plants increased 22 and 71%, respectively, when transferred from 35- to 70-Pa CO2 chamber air at 900 mu mol m(-2) s(-1) photon flux density. However, CO2-dependent increases of net carbon assimilation rates of high- and low-Rubisco plants virtually disappeared after 9 d of growth in elevated CO2 chamber air. Total above-ground dry matter production of high- and low- Rubisco plants was 28 and 53% greater, respectively, after 9 d of growth at 70 Pa compared with 35 Pa CO2. Most of this dry weight gain was due to increased specific leaf weight. Rubisco activity, Rubisco protein, and total chlorophyll were lower in both high- and low-Rubisco plants grown in enriched compared with ambient CO2 chamber air. Soluble leaf protein also decreased in response to CO2 enrichment in high- but not in low-Rubisco tobacco plants. Decreased Rubisco activities in CO2-adapted high- and low-Rubisco plants were not attributable to changes in activation state of the enzyme. Carbonic anhydrase activities and subunit levers measured with specific antibodies were similar in high- and low-Rubisco tobacco plants and were unchanged by CO2 enrichment. Collectively, these findings suggested that photosynthetic acclimation to enriched CO2 occurred in tobacco plants either with or without transgenically decreased Rubisco levels and also indicated that the down-regulation of Rubisco in CO2-adapted tobacco plants was related to decreased specific activity of this enzyme.

KEYWORDS: ANHYDRASE, ANTISENSE RBCS, CARBON DIOXIDE, GROWTH, HIGH ATMOSPHERIC CO2, LIGHT, OXYGENASE, PLANTS, PROTEIN, RIBULOSE BISPHOSPHATE CARBOXYLASE

2209

Siebke, K., and E. Weis. 1995. Imaging of chlorophyll-a-fluorescence in leaves: Topography of photosynthetic oscillations in leaves of Glechoma hederacea. *Photosynthesis Research 45(3):225-237.*

Images of chlorophyll-alpha-fluorescence oscillations were recorded using a camera-based fluorescence imaging system. Oscillations with frequencies around 1 per min were initiated by a transient decrease in light intensity during assimilation at an elevated CO2-concentration. The oscillation was inhomogenously distributed over the leaf. In cells adjacent to minor veins, frequency and damping rate was high, if there was any oscillation. In contrast, the amplitude was highest in cells most distant from phloem elements (maximal distance about 300 mu m). The appearance of minor veins in oscillation images is explained by a gradient in the metabolic control in the mesophyll between minor veins and by transport of sugar from distant cells to phloem elements. The potential of fluorescence imaging to visualize 'microscopic' source-sink interactions and metabolic domains in the mesophyll is discussed.

KEYWORDS: CALVIN-CYCLE, CARBON METABOLISM, CO2 FIXATION, ELECTRON-TRANSPORT, FRUCTOSE 2;6-BISPHOSPHATE, INVIVO, LIMITATION, PHOSPHORYLATION, SPINACH LEAF-DISKS, SUCROSE PHOSPHATE SYNTHASE

2210

Signora, L., N. Galtier, L. Skot, H. Lucas, and C.H. Foyer. 1998. Over-expression of sucrose phosphate synthase in Arabidopsis thaliana results in increased foliar sucrose/starch ratios and favours decreased foliar carbohydrate accumulation in plants after prolonged growth with CO2 enrichment. *Journal of Experimental Botany 49(321):669-680.*

Arabidopsis thaliana ecotype Columbia was transformed with a maize sucrose phosphate synthase (SPS) cDNA under the control of the promoter for the small subunit of ribulose-l,5- bisphosphate carboxylase from tobacco (rbcS). The effects of SPS over-expression were compared in plants of the T-2 and T-3 generations grown either in air or with CO2 enrichment (700 mu l l(-1)) for either 4 or 10 weeks. Maximal extractable foliar SPS activities were three times those of the untransformed controls in the highest rbcS-SPS expressing line. In untransformed Arabidopsis leaves SPS activity was not subject to light/dark regulation, but was modified by incubation with either the inhibitor, orthophosphate, or the activator, mannose. Photosynthesis (A(max)) values were similar in all lines grown in air. After 10 weeks of CO, enrichment a decrease in A,,, in the untransformed controls, but not in the high SPS expressors, was observed. There was a strong correlation between the sucrose-to-starch ratio of the leaves and their SPS activity in both growth conditions. The total foliar carbohydrate contents of 4-week-old plants was similar in all lines whether plants were grown in air or with CO2 enrichment, After 10 weeks growth the leaves of the high rbcS-SPS expressors accumulated much less total carbohydrate than untransformed control leaves in both growth conditions. It was concluded that SPS overexpression causes increased foliar sucrose/starch ratios in Arabidopsis leaves and favours decreased foliar carbohydrate contents when plants are grown for long periods with CO2 enrichment.

KEYWORDS: ATMOSPHERIC CO2, ELECTRON-TRANSPORT, ENZYME-ACTIVITIES, INORGANIC- PHOSPHATE, KINETIC-PROPERTIES, LIGHT-MODULATION, SINK REGULATION, SPINACH LEAVES, TRANSCRIPT LEVELS, TRANSGENIC PLANTS

2211

Sild, E., S. Younis, H. Pleijel, and G. Sellden. 1999. Effect of CO2 enrichment on non-structural carbohydrates in leaves, stems and ears of spring wheat. *Physiologia Plantarum 107(1):60-67.*

Field-grown spring wheat (Triticum aestivum L, cv, Dragon) was exposed to ambient and elevated CO2 concentrations (15 and 2 times ambient) in open-top chambers. Contents of non-structural carbohydrates mere analysed enzymatically in leaves, stems and ears six times during the growing season. The impact of elevated CO2 on wheat carbohydrates was non-significant in most harvests. However, differences in the carbohydrate contents due to elevated CO2 were found in all plant compartments. Before anthesis, at growth stage (GS) 30 (the stem is 1 cm to the shoot apex), the plants grown in elevated CO2 contained significantly more mater soluble carbohydrates (WSC), fructans, starch and total non-structural carbohydrates (TNC) in the leaves in comparison with the plants groan in ambient CO2. It is hypothesised that the plants from the treatments with elevated CO2 were sink-limited at GS30, After anthesis, the leaf WSC and TNC contents of the plants from elevated CO2 started to decline earlier than those of the plants from ambient CO2. This may indicate that the leaves of plants grown in the chambers with elevated CO2 senesced earlier. Elevated CO2 accelerated grain development: 2 weeks after anthesis, the plants groan in elevated CO2 contained significantly more starch and significantly less fructans in the ears compared to the plants grown in ambient CO2. Elevated CO2 had no effect on ear starch and TNC contents at the final harvest. Increasing the CO2 concentration from 360 to 520 mu mol mol(-1) had a larger effect on wheat nonstructural carbohydrates than the further increase from 520 to 680 mu mol mol(-1). The results are discussed in relation to the effects of elevated CO2 on yield and yield components.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, FRUCTAN ACCUMULATION, GRAIN-YIELD, GROWTH, LONG-TERM, PHOTOSYNTHESIS, RESPONSES, TRITICUM-AESTIVUM L, WINTER-WHEAT

2212

Silver, W.L. 1998. The potential effects of elevated CO2 and climate change on tropical forest soils and biogeochemical cycling. *Climatic Change 39(2-3):337-361.*

Tropical forests are responsible for a large proportion of the global terrestrial C flux annually for natural ecosystems. Increased atmospheric CO2 and changes in climate are likely to affect the distribution of C pools in the tropics and the rate of cycling through vegetation and soils. In this paper, I review the literature on the pools and fluxes of carbon in tropical forests, and the relationship of these to nutrient cycling and climate. Tropical moist and humid forests have the highest rates of annual net primary productivity and the greatest carbon flux from soil respiration globally. Tropical dry forests have lower rates of carbon circulation, but may have greater soil organic carbon storage, especially at depths below 1 meter. Data from tropical elevation gradients were used to examine the sensitivity of biogeochemical cycling to incremental changes in temperature and rainfall. These data show significant positive correlations of litterfall N concentrations with temperature and decomposition rates. Increased atmospheric CO2 and changes in climate are expected to alter carbon and nutrient allocation patterns and storage in tropical forest. Modeling and experimental studies suggest that even a small increase in temperature and CO2 concentrations results in more rapid decomposition rates, and a large initial CO2 efflux from moist tropical soils. Soil P limitation or reductions in C:N and C:P ratios of litterfall could eventually limit the size of this flux. Increased frequency of fires in dry forest and hurricanes in moist and humid forests are expected to reduce the ecosystem carbon storage capacity over longer time periods.

KEYWORDS: AMAZONIAN RAINFOREST, GLOBAL CARBON-CYCLE, LITTER DECOMPOSITION, LOA ENVIRONMENTAL MATRIX, LUQUILLO EXPERIMENTAL FOREST, MULU NATIONAL PARK, NUTRIENT AVAILABILITY, ORGANIC-MATTER, PUERTO-RICO, TERRESTRIAL ECOSYSTEMS

2213

Silvola, J., and U. Ahlholm. 1993. Effects of co2 concentration and nutrient status on growth, growth rhythm and biomass partitioning in a willow, salix- phylicifolia. *Oikos 67(2):227-234.*

Cuttings of the willow Salix phylicifolia were grown in pots containing moist organic-rich soil for four months in closed chambers at 4 CO2 concentrations (300). 500, 700, 1000 ppm) and 4 nutrient levels (fertilization of 0, 100, 500, 1000 kg ha-1 monthly). The plants received natural light, but the average temperature was 3-6-degrees-C higher than out of doors. Both CO2 concentration and fertilization affected biomass production. the average increase caused by CO2 enhancement being approx. 100%. Nutrient level had a considerable effect on the increased biomass production achieved by CO2 enhancement, since the increase was minimal at lower nutrient levels. At the same time the effect of fertilization was dependent on the CO2 concentration, the production increase caused by fertilization being much less at 300 ppm than at the other CO2 concentrations. CO2 concentration and fertilization had the opposite effects on biomass partitioning, a higher nutrient level increasing the proportion of the biomass located in the stems and a higher CO2 concentration that in the roots. Both fertilization and CO2 concentration affected the growth rhythm, a high CO2/nutrient ratio leading to a shorter growing season and a low ratio to a longer one.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-MATTER PRODUCTION, ELEVATED CO2, ENRICHMENT, INCREASE, NITROGEN, PHOTOSYNTHETIC RATE, SEEDLINGS, SENESCENCE, TREES

2214

Silvola, J., and U. Ahlholm. 1995. Combined effects of co2 concentration and nutrient status on the biomass production and nutrient-uptake of birch seedlings (betula-pendula). *Plant and Soil 169:547-553.*

Birch seedlings (Betula pendula) were grown for four months in a greenhouse at three nutrient levels (fertilization of 0, 100 and 500 kg ha(-1) monthly) and at four CO2 concentrations (350, 700, 1050 and 1400 ppm). The effect of CO2 concentration on the biomass production depended on the nutrient status. When mineralization of the soil material was the only source of nutrients (0 kg ha(-1)), CO2 enhancement reduced the biomass production slightly, whereas the highest production increase occurred at a fertilization of 100 kg ha(-1), being over 100% between 350 and 700 ppm CO2. At 500 kg ha(-1) the production increase was smaller, and the production decreased beyond a CO2 concentration of 700 ppm. The CO2 concentration had a slight effect on the biomass distribution, the leaves accounting for the highest proportion at the lowest CO2 concentration (350 ppm). An increase in nutrient status led to a longer growth period and increased the nutrient concentrations in the plants, but the CO2 concentration had no effect on the growth rhythm and higher CO2 reduced the nutrient concentrations.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, GROWTH, MARSH, NUTRITION, PHOTOSYNTHESIS, RESPONSES, SIZE, TEMPERATURE

2215

Simard, S.W., D.M. Durall, and M.D. Jones. 1997. Carbon allocation and carbon transfer between Betula papyrifera and Pseudotsuga menziesii seedlings using a C-13 pulse-labeling method. *Plant and Soil 191(1):41-55.*

Here we describe a simple method for pulse-labeling tree seedlings with (CO2(gas)-C-13), and then apply the method in two related experiments: (i) comparison of carbon allocation patterns between Betula papyrifera Marsh. and Pseudotsuga menziesii (Mirb.) France, and (ii) measurement of one-way belowground carbon transfer from B. papyrifera to Fl menziesii. Intraspecific carbon allocation patterns and interspecific carbon transfer both influence resource allocation, and consequently development, in mixed communities of B. papyrifera and P. menziesii. In preparation for the two experiments, we first identified the appropriate (CO2(gas)-C-13) pulse-chase regime for labeling seedlings: a range of pulse (100-mL and 200-mL 99 atom% (CO2(gas)-C-13)) and chase (0, 3 and 6 d) treatments were applied to one year-old B. papyrifera and P. menziesii seedlings. The amount of (CO2)-C-13 fixed immediately after 1.5 h exposure was greatest for both B. papyrifera (40.8 mg excess C-13) and P. menziesii (22.9 mg excess C-13) with the 200-mL pulse, but higher C-13 loss and high sample variability resulted in little difference in excess C-13 content between pulse treatments after 3 d for either species. The average excess C-13 root/shoot ratio of B. papyrifera and P. menziesii changed from 0.00 immediately following the pulse to 0.61 and 0.87 three and six days later, which reflected translocation of 75% of fixed isotope out of foliage within 3 d following the pulse and continued enrichment in fine roots over 6 d. Based on these results, the 100-mL CO2(gas) and 6-d chase were considered appropriate for the carbon allocation and belowground transfer experiments. In the carbon allocation experiment, we found after 6 d that B. papyrifera allocated 49% (average 9.5 mg) and P. menziesii 41% (average 5.8 mg) of fixed isotope to roots, of which over 55% occurred in fine roots in both species. Species differences in isotope allocation patterns paralleled differences in tissue biomass distribution. The greater pulse labeling

efficiency of B. papyrifera compared to P. menziesii was associated with its two-fold and 13-fold greater leaf and whole seedling net photosynthetic rates, respectively, 53% greater biomass, and 35% greater root/shoot ratio. For the carbon transfer experiment, B. papyrifera and P. menziesii were grown together in laboratory rootboxes, with their roots intimately mingled. A pulse of 100 mL (CO2(gas)-C- 13) was applied to paper birch and one-way transfer to neighboring P. menziesii was measured after 6 d. Of the excess C-13 fixed by B. papyrifera, 4.7% was transferred to neighboring P. menziesii, which distributed the isotope evenly between roots and shoots. Of the isotope received by P. menziesii, we estimated that 93% was taken up through belowground pathways, and the remaining 7% taken up by foliage as (CO2(gas)-C-13) respired by B. papyrifera shoots. These two experiments indicate that B. papyrifera fixes more total carbon and allocates a greater proportion to its root system than does Il menziesii, giving it a competitive edge in resource gathering; however, below-ground carbon sharing is of sufficient magnitude that it may help ensure co-existence of the two species in mixed communities.

KEYWORDS: BIRCH, CO2, GROWTH, HYPHAE, PHOTOSYNTHESIS, PLANTS

2216

Simola, L.K., J. Lemmetyinen, and A. Santanen. 1992. Lignin release and photomixotrophism in suspension-cultures of picea-abies. *Physiologia Plantarum 84(3):374-379.*

The effect of different concentrations of sucrose (0-4%) and of two growth regulators (0-50-mu-M 2,4-D and 0-25-mu-M kinetin) was tested on growth and chlorophyll content of suspension cultures of Picea abies (L.) Karst. originating from chlorophyllous embryo callus in an elevated CO2 (2%) atmosphere. A continuous chlorophyllous suspension culture was achieved on a medium containing 2% sucrose and a low level of organic nitrogen (0.25 mM arginine and 0.5 mM glutamine) supplemented with 2,4-D (0.5-mu-M) and kinetin (2.5-mu-M). The same medium with 4% sucrose gave the best growth response, but a negative correlation between chlorophyll level and growth was observed. The chlorophyllous cultures grew slowly in a medium with low (0.5%) sucrose or without any carbohydrate source, suggesting photomixotrophism. A high concentration of kinetin inhibited both growth and chlorophyll synthesis. Release of lignin into the nutrient medium was observed in several experiments, especially in slow-growing cultures supplemented with sucrose. Only a few successive passages of suspensions that produced lignin could be cultured before cell death. The cultures releasing lignin may be unique for studies on synthesis and biodegradation of this very complex compound.

KEYWORDS: CALLUS LINES, CELL-CULTURES, DIFFERENTIATION, ESTABLISHMENT, FINE-STRUCTURE, GROWTH, LIGNIFICATION, MEGAGAMETOPHYTE, NICOTIANA-TABACUM, SPRUCE

2217

Simon, J.P. 1996. Molecular forms and kinetic properties of pyruvate, P-i dikinase from two populations of barnyard grass (Echinochloa crus-galli) from sites of contrasting climates. *Australian Journal of Plant Physiology 23(2):191-199.*

Plants from two populations of the C-4 barnyard grass (Echinochloa crus-galli (L.) Beauv.) from Quebec (QUE) and Mississippi (MISS) were acclimated under controlled conditions to 26/20 and 14/8 degrees C day/night. The apparent energy of activation (E(a)), K-m for pyruvate, V-max/K-m ratios, K-cat (substrate turnover number) and specific activity of pyruvate, P-i dikinase (PPDK, EC 2.7.9.1) were analysed from partially purified Sephadex G-25 extracts of PPDK from leaves and from highly purified PPDK. PPDK from both populations consisted of one isomorph with the same electrophoretic mobility in polyacrylamide gels and similar molecular weights for the native enzyme (385 kDa) and for the subunit of the tetramer (94.8 kDa). No significant differences were observed for any of the kinetic properties of partially purified or purified PPDK or for the specific activity per mg protein of purified PPDK extracted from plants of the two populations and acclimated to the two thermoperiods. Net photosynthetic rates (Ps) were positively correlated with PPDK activity levels (E) but E/Ps ratios were lower than 1.0, ranging from 0.43 to 0.67. Results indicate that differences in activity levels, thermal properties and in the kinetics of light activation and dark inactivation of PPDK extracted from cold-acclimated MISS and QUE plants, as reported in earlier studies, are due to causes other than kinetic properties or electrophoretic characteristics of PPDK.

KEYWORDS: C-4 PHOTOSYNTHESIS, CO2- ENRICHMENT, CRUSGALLI L BEAUV, ECOTYPES, ENZYME LEVEL, HIGHER-PLANTS, NADP+-MALATE DEHYDROGENASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PURIFICATION, TEMPERATURE

2218

Sims, D.A., W.X. Cheng, Y.Q. Luo, and J.R. Seemann. 1999. Photosynthetic acclimation to elevated CO2 in a sunflower canopy. *Journal of Experimental Botany 50(334):645-653.*

Sunflower canopies were grown in mesocosom gas exchange chambers at ambient and elevated CO2 concentrations (360 and 700 ppm) and leaf photosynthetic capacities measured at several depths within each canopy. Elevated [CO2] had little effect on whole-canopy photosynthetic capacity and total leaf area, but had marked effects on the distribution of photosynthetic capacity and leaf area within the canopy. Elevated [CO2] did not significantly reduce the photosynthetic capacities per unit leaf area of young leaves at the top of the canopy, but it did reduce the photosynthetic capacities of older leaves by as much as 40%. This effect was not dependent on the canopy light environment since elevated [CO2] also reduced the photosynthetic capacities of older leaves exposed to full sun on the south edge of the canopy. In addition to the effects on leaf photosynthetic capacity, elevated [CO2] shifted the distribution of leaf area within the canopy so that more leaf area was concentrated near the top of the canopy. This change resulted in as much as a 50% reduction in photon flux density in the upper portions of the elevated [CO2] canopy relative to the ambient [CO2] canopy, even though there was no significant difference in the total canopy leaf area. This reduction in PFD appeared to account for leaf carbohydrate contents that were actually lower for many of the shaded leaves in the elevated as opposed to the ambient [CO2] canopy. Photosynthetic capacities were not significantly correlated with any of the individual leaf carbohydrate contents, However, there was a strong negative correlation between photosynthetic capacity and the ratio of hexose sugars to sucrose, consistent with the hypothesis that sucrose cycling is a component of the biochemical signalling pathway controlling photosynthetic acclimation to elevated [CO2].

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, GAS-EXCHANGE, GENE-EXPRESSION, GROWTH, LEAF, LIGHT, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SOYBEAN LEAVES

2219

Sims, D.A., Y. Luo, and J.R. Seemann. 1998. Comparison of photosynthetic acclimation to elevated CO2 and limited nitrogen supply in soybean. *Plant, Cell and Environment 21(9):945-952.*

Plants grown at elevated CO2 often acclimate such that their photosynthetic capacities are reduced relative to ambient CO2- grown plants. Reductions in synthesis of photosynthetic enzymes could result

either from reduced photosynthetic gene expression or from reduced availability of nitrogen-containing substrates for enzyme synthesis. Increased carbohydrate concentrations resulting from increased photosynthetic carbon fixation at elevated CO2 concentrations have been suggested to reduce the expression of photosynthetic genes. However, recent studies have also suggested that nitrogen uptake may be depressed by elevated CO2, or at least that it is not increased enough to keep pace with increased carbohydrate production. This response could induce a nitrogen limitation in elevated-CO2 plants that might account for the reduction in photosynthetic enzyme synthesis. If CO2 acclimation were a response to limited nitrogen uptake, the effects of elevated CO2 and limiting nitrogen supply on photosynthesis and nitrogen allocation should be similar. To test this hypothesis we grew non- nodulating soybeans at two levels each of nitrogen and CO2 concentration and measured leaf nitrogen contents, photosynthetic capacities and Rubisco contents. Both low nitrogen and elevated CO2 reduced nitrogen as a percentage of total leaf dry mass but only low nitrogen supply produced significant decreases in nitrogen as a percentage of leaf structural dry mass. The primary effect of elevated CO2 was to increase non-structural carbohydrate storage rather than to decrease nitrogen content. Both low nitrogen supply and elevated CO2 also decreased carboxylation capacity (V-cmax) and Rubisco content per unit leaf area. However, when V-cmax and Rubisco content were expressed per unit nitrogen, low nitrogen supply generally caused them to increase whereas elevated CO2 generally caused them to decrease. Finally, elevated CO2 significantly increased the ratio of RuBP regeneration capacity to V-cmax whereas neither nitrogen supply nor plant age had a significant effect on this parameter. We conclude that reductions in photosynthetic enzyme synthesis in elevated CO2 appear not to result from limited nitrogen supply but instead may result from feedback inhibition by increased carbohydrate contents.

KEYWORDS: ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PARTIAL-PRESSURE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, SMALL-SUBUNIT

2220

Sims, D.A., Y. Luo, and J.R. Seemann. 1998. Importance of leaf versus whole plant CO2 environment for photosynthetic acclimation. *Plant, Cell and Environment 21(11):1189-1196.*

The reduction of photosynthetic capacity in many plants grown at elevated CO2 is thought to result from a feedback effect of leaf carbohydrates on gene expression, Carbohydrate feedback at elevated CO2 could result from limitations on carbohydrate utilization at many different points, for example export of triose phosphates from the chloroplast, sucrose synthesis and phloem loading, transport in the phloem, unloading of the phloem at the sinks, or utilization for growth of sinks. To determine the relative importance of leaf versus whole plant level limitations on carbohydrate utilization at elevated CO2, and the possible effects on the regulation of photosynthetic capacity, we constructed a treatment system in which we could expose single, attached, soybean leaflets to CO2 concentrations different from those experienced by the rest of the plant. The single leaflet treatments had dramatic effects on the carbohydrate contents of the treated leaflets. However, photosynthetic capacity and rubisco content were unaffected by the individual leaflet treatment and instead were related to the whole plant CO2 environment, despite the fact that the CO2 environment around the rest of the plant had no significant affect on the total non-structural carbohydrate (TNC) contents of the treated leaflets. These results necessitate a re- evaluation of the response mechanisms to CO2 as well as some of the methods used to test these responses. We propose mechanisms by which sink strength could influence leaf physiology independently of changes in carbohydrate accumulation.

KEYWORDS: CARBON ASSIMILATION, ELEVATED CO2, GAS-EXCHANGE, GENE-EXPRESSION, IN-BAG EXPERIMENT, LEAVES, PHLOEM TRANSPORT, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, SCOTS PINE, SINK REGULATION

2221

Sims, D.A., J.R. Seemann, and Y. Luo. 1998. The significance of differences in the mechanisms of photosynthetic acclimation to light, nitrogen and CO2 for return on investment in leaves. *Functional Ecology 12(2):185-194.*

1. We report changes in photosynthetic capacity of leaves developed in varying photon flux density (PFD), nitrogen supply and CO2 concentration. We determined the relative effect of these environmental factors on photosynthetic capacity per unit leaf volume as well as the volume of tissue per unit leaf area. We calculated resource-use efficiencies from the photosynthetic capacities and measurements of leaf dry mass, carbohydrates and nitrogen content. 2. There were clear differences between the mechanisms of photosynthetic acclimation to PFD, nitrogen supply and CO2. PFD primarily affected volume of tissue per unit area whereas nitrogen supply primarily affected photosynthetic capacity per unit volume. CO2 concentration affected both of these parameters and interacted strongly with the PFD and nitrogen treatments. 3. Photosynthetic capacity per unit carbon invested in leaves increased in the low PFD, high nitrogen and low CO2 treatments. Photosynthetic capacity per unit nitrogen was significantly affected only by nitrogen supply. 4. The responses to low PFD and low nitrogen appear to function to increase the efficiency of utilization of the limiting resource. However, the responses to elevated CO2 in the high PFD and high nitrogen treatments suggest that high CO2 can result in a situation where growth is not limited by either carbon or nitrogen supply. Limitation of growth at elevated CO2 appears to result from internal plant factors that limit utilization of carbohydrates at sinks and/or transport of carbohydrates to sinks.

KEYWORDS: ALOCASIA-MACRORRHIZA, C-3 PLANTS, CARBON BALANCE, ELEVATED CO2, ENRICHMENT, GROWTH, LEAF ANATOMY, PHOTON FLUX DENSITIES, SCALING SUN, WHOLE-PLANT PERFORMANCE

2222

Sims, D.A., J.R. Seemann, and Y.Q. Luo. 1998. Elevated CO2 concentration has independent effects on expansion rates and thickness of soybean leaves across light and nitrogen gradients. *Journal of Experimental Botany 49(320):583-591.*

The rate and extent of leaf thickness and development are important determinants of plant photosynthetic capacity, The interactive effects of photon flux density (PFD), nitrogen supply and CO2 concentration on leaf expansion rate were measured as well as final leaf size and thickness of soybean, Leaf thickness and final area were not correlated with leaf relative expansion rate (RER) suggesting that these parameters are controlled by different mechanisms and that final leaf dimensions are determined by the duration rather than the rate of leaf expansion, Carbohydrate supply did not explain the variation ii? leaf RER since RER increased with increasing CO2 concentration, but decreased with increasing PFD. Leaf thickness and final area were related to resource supply but not in a simple fashion, Both positive and negative correlations between leaf thickness and carbohydrate and nitrogen concentrations were obtained depending on the environmental variable responsible for the variation. In contrast, there was a simple proportional relationship between whole plant relative growth rate and a correlate of leaf thickness (leaf water content per unit area), suggesting that leaf thickness responds to the balanced supply of all resources, in the same fashion as RGR, rather than to any individual resource.

KEYWORDS: ACCLIMATION, ANATOMY, CARBON, ENRICHMENT,

LEAF GROWTH, PHASEOLUS-VULGARIS, PHOTOSYNTHESIS, PLANTS, TEMPERATURE, WATER RELATIONS

2223

Sinclair, T.R. 1992. Mineral-nutrition and plant-growth response to climate change. *Journal of Experimental Botany 43(253):1141-1146.*

The limiting factor concept has often been used to describe plant growth responses to altered availability of resources. However, even preliminary experiments, where atmospheric CO2 concentrations and solution mineral concentrations were varied, demonstrated that a more complex concept was required to interpret the potential effects of climate change and mineral availability on plant growth. It is proposed that these resources for plant growth may be better viewed as simultaneously limiting. Further, in considering the limitation in plant growth to mineral nutrition it is important to consider both the solution concentration and the total amount of the individual minerals available to the plant. Sustaining a positive response to increased CO2 concentration, for example, requires an increase in plant uptake of the total amount of minerals. Consequently, it is very difficult to predict the plant growth response to climate change because of the large uncertainty about mineral availability. On the one hand, increased CO2 concentrations should stimulate nitrogen fixation by both free-living organisms and symbiotic systems, and improve soil properties for mineral availability as a result of increased organic matter deposition in the soil. On the other hand, increased temperature and altered rainfall patterns may result in increased losses of soil minerals. Even the direction in the net change in available soil minerals is unclear. Realistic evaluations of the effects of climate change on plant growth will be challenged to contend with the large uncertainty and complexities in understanding mineral availability and plant mineral nutrition.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHMENT, NET NITROGEN MINERALIZATION, ROOT NODULE ACTIVITY, SEED YIELD, SOILS

2224

Sinclair, T.R., and N.G. Seligman. 1995. Global environment change and simulated forage quality of wheat .1. Nonstressed conditions. *Field Crops Research 40(1):19-27.*

Projected changes in the global environment may affect both the quantity and quality of grain and forage mass produced and harvested in that environment. Quality is a major factor in determining the value of a forage crop as feed for ruminants. The objective of this study was to make a preliminary assessment of potential changes in the quantity and quality of forage as measured by [N] and leaf:stem of an annual, temperate climate C-3 forage crop grown under nonstressed conditions. Starting with a relatively simple, well-checked mechanistic model of wheat, adaptations were added to estimate changes in forage attributes. Increased temperature influenced both yield and nutritive value, mainly through changes in ontological development rates. Elevated,atmospheric [CO2] resulted in greater mass accumulation, but with lower leaf:stem and [N]. The combined effect of increased temperature and elevated [CO2] was to decrease slightly forage yield and to increase the forage nutritive value. These compensating effects of higher temperature and elevated [CO2] could be modified by interactions between [CO2] and the chemical composition and cell wall structure of forage plants. Analysis of such subtle interaction requires considerable experimental amplification.

KEYWORDS: CARBON DIOXIDE, CO2- ENRICHMENT, DRY-MATTER, ELEVATED CO2, GROWTH, NITROGEN, SPRING WHEAT, TEMPERATURE, WINTER-WHEAT, YIELD

2225

Singer, A., A. Eshel, M. Agami, and S. Beer. 1994. The contribution of aerenchymal co2 to the photosynthesis of emergent and submerged culms of scirpus-lacustris and cyperus- papyrus. *Aquatic Botany 49(2-3):107-116.*

In this work it was investigated whether sediment-derived aerenchymal CO2 could be utilized for photosynthesis in the culms of the two emergent aquatic macrophytes Scirpus lacustris L. (a C-3 plant) and Cyperus papyrus L. (a C-4 plant). Aerenchymal CO2 concentrations within the submerged parts of the culms were found to be 30 000-50 000, mu l l(-1), and ca. 800 mu l l(-1) in the emergent parts of Scirpus lacustris and 2000 mu l l(-1) in Cyperus papyrus. These concentrations tended to be lower during the day in Cyperus, while no dear diurnal pattern was observed for Scirpus. Photosynthetic rates based on fixation of external or internal CO2 were measured in situ by providing (CO2)-C-14 either externally or from the aerenchyma (by supplying C-14-labelled CO2 through test-tubes attached to excised culms). The results showed that the contribution of aerenchymal CO2 to the total photosynthesis of emergent culms was less than 0.25% in both species. This has a rationale in that photosynthetic rates of both species were saturated at the ambient air CO2 concentration, but it remains unclear why CO2 does not diffuse towards the photosynthesizing tissues. By contrast, internal CO2 appeared to be the only source of inorganic carbon used for photosynthesis of young submerged green culms. It is thus suggested that the aerenchyma, in addition to other functions, is important in providing sediment-derived CO2 for photosynthesis in young shoots or culms if growing submerged, before they reach the water surface.

KEYWORDS: CARBON, ELEVATED ATMOSPHERIC CO2, FLOW, TRIN EX STEUD

2226

Singh, B., and R.B. Stewart. 1991. Potential impacts of a CO2-induced climate change using the GISS scenario on agriculture in quebec, canada. *Agriculture Ecosystems & Environment 35(4):327-347.*

This study examines the potential impacts of a climate change resulting from an effective doubling of atmospheric CO2 on the potential and anticipated yields of a variety of agricultural crops including corn, soya, potatoes, wheat, phaseolus beans, sorghum, barley, oats, rapeseed and sunflowers and two horticultural crops namely apples and grapes, for southern Quebec. The GISS climate change scenario is used. Our results show that yields would increase for some crops such as corn, soybeans, potatoes, phaseolus beans and sorghum and would decrease for the cereal and oilseed crops, namely wheat, barley, oats, sunflowers and rapeseed. Production opportunities for apples and grapes are enhanced. Also it would seem that the more northerly regions of Abitibi-Temiscamingue and Lac St-Jean would benefit most, in terms of agriculture, from a CO2-induced climate change.

KEYWORDS: BALANCE, CARBON DIOXIDE, CO2, COMPONENTS, CROP, CYCLE, GENERAL-CIRCULATION MODEL, SENSITIVITY, WHEAT, YIELD

2227

Singh, T., and E.E. Wheaton. 1991. Boreal forest sensitivity to global warming - implications for forest management in western interior canada. *The Forestry Chronicle 67(4):342-348.*

Unmitigated global warming due to the enhanced greenhouse effect could have significant impacts on the boreal forest in interior western Canada. Increases in annual temperature of 3 to 7-degrees-C are projected for Alberta under a 2 x CO2 scenario by 2030-2050 A.D. Such an unprecedented rate of change has many short- and long-term

implications for forest management and for industries. As the boreal forest is highly sensitive to climatic changes, foresters need to develop a set of safe strategies to minimize the negative impacts and maximize the benefits of these changes.

2228

Slafer, G.A. 1995. Wheat development as affected by radiation at two temperatures. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 175(4):249-263.*

A wheat cultivar (Condor) was grown in two experiments (thermal regimes 18/13 and 21/16 degrees C) under low (298 mu E m(-2) s(-1)) radiation regimes during either an early phase from seedling emergence to terminal spikelet initiation (S-1), a late phase from terminal spikelet initiation to anthesis (S-2), or for the full period from seedling emergence to anthesis (S- 12), or high (560 mu E m(-2) s(-1)) radiation throughout the growing period (S-0) to determine whether developmental events are affected by radiation. The main developmental events considered in this study were the timing of terminal spikelet initiation and anthesis, the final number of leaf and spikeler primordia initiated in the apex and the rare of leaf appearance. Number of grains per spike and culm height were also measured. The duration of each phenophase was not affected by radiation intensity. Temperature affected the rate of wheat development, but the acceleration of development due to temperature during the seedling emergence-terminal spikelet initiation phase only slightly reduced (from 24.8 to 23.2 days). Differences in time from terminal spikelet initiation to anthesis were greater than in the earlier phases, having been the duration reduced from 24.6 to 20.0 days due to high temperature. Associated with the lack of effect of radiation on phasic development and the negligible effect of temperature on the duration of the early phases of development, final leaf number was practically unchanged in this study by either the radiation level or the growing temperature. Thus, radiation did not affect the rate of leaf initiation. The number of spikelets was affected by neither the treatments nor the thermal environment. The rates of leaf appearance were accelerated by temperature. Radiation, on the other hand, did nor significantly alter the rates of leaf appearance in any of the treatments. As expected from many sources in the literature, the number of grains per spike was significantly affected by radiation during the phase from terminal spikelet initiation to anthesis. Due to the lack of significant effects of radiation on the developmental patterns of wheat, the changes in number of grains per spike were due to changes in the number of grains born in each spikelet. The results of the present study were compared with others available in the literature on the effects (or lack of them) of radiation and CO2 concentration on phasic development, plastochron and phyllochron in wheat to reach the general conclusion that the rate of developmental events in wheat, in contrast to other plants, is almost completely independent of the availability of assimilates, with a possible exception for the Equatorial latitudes.

KEYWORDS: BASE TEMPERATURE, CARBON-DIOXIDE ENRICHMENT, CO2- ENRICHMENT, GRAIN-YIELD, GROWTH, PHOTOPERIOD, SPIKELET NUMBER, SPRING WHEAT, WATER-STRESS, WINTER-WHEAT

2229

Slafer, G.A., and H.M. Rawson. 1997. CO2 effects on phasic development, leaf number and rate of leaf appearance in wheat. *Annals of Botany 79(1):75-81.*

It has been predicted that the concentration of CO2 in the air could double during the 21st century. Though it is recognized that CO2-doubling could increase yield through its effects on plant photosynthesis and stomatal behaviour, it is unclear whether CO2-doubling will change phasic development in wheat. A phytotron study was conducted with two contrasting cultivars of wheat, Condor (spring) and Cappelle Desprez (winter), to determine whether development is affected by a season-long exposure to 360 and 720 ppmv CO2. Plants were vernalized for 50 d (8/4 degrees C, s h photoperiod) before their exposure to the CO2 treatments. There were significant differences between cultivars in the duration of different phenophases as well as in the final number of leaves. However, CO2 concentration had no effect in either cultivar on the duration of the early developmental phase to terminal spikelet initiation, or on the final number of leaves, though CO2-doubling did slightly increase the later phase from terminal spikelet initiation to heading in Cappelle Desprez. Condor and Cappelle Desprez also differed markedly in the dynamics of leaf appearance. While the former had a constant rate of leaf appearance throughout development, the latter had a fast rate initially (between leaves 1 and 7), similar to that of Condor, which was followed by a slower rate after the appearance of leaf 7. Overall, CO2- doubling did not significantly affect the rates of leaf appearance nor the shape of the relationship. Phyllochron for the first seven leaves was the same for both CO2 concentrations. However, the change in phyllochron associated with CO2-doubling for leaves 7-12 in Cappelle Desprez, although quite small (4%), accounts for part of the slightly increased duration of the phase from terminal spikelet initiation to heading under high CO2 concentration in that cultivar. We conclude that CO2 concentration does not influence development in wheat to a degree relevant to agronomy. (C) 1997 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO2, BASIC DEVELOPMENT RATE, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, PHOTOPERIOD, SOWING DATE, SPRING WHEAT, TEMPERATURE, WINTER-WHEAT

2230

Smart, D.R., N.J. Chatterton, and B. Bugbee. 1994. The influence of elevated co2 on nonstructural carbohydrate distribution and fructan accumulation in wheat canopies. *Plant, Cell and Environment 17(4):435-442.*

We grew 2.4 m2 wheat canopies in a large growth chamber under high photosynthetic photon flux (1000 mumol m-2 s-1) and using two CO2 concentrations, 360 and 1200 mumol mol-1. Photosynthetically active radiation (400-700 nm) was attenuated slightly faster through canopies grown in 360 mumol mol-1 than through canopies grown in 1200 mumol mol-1, even though high- CO2 canopies attained larger leaf area indices. Tissue fractions were sampled from each 5-cm layer of the canopies. Leaf tissue sampled from the tops of canopies grown in 1200 mumol mol-1 accumulated significantly more total non-structural carbohydrate, starch, fructan, sucrose, and glucose (p less- than-or-equal-to 0-05) than for canopies grown in 360 mumol mol-1. Non-structural carbohydrate did not significantly increase in the lower canopy layers of the elevated CO2 treatment. Elevated CO2 induced fructan synthesis in all leaf tissue fractions, but fructan formation was greatest in the uppermost leaf area. A moderate temperature reduction of 10-degrees-C over 5 d increased starch, fructan and glucose levels in canopies grown in 1200 mumol mol-1, but concentrations of sucrose and fructose decreased slightly or remained unchanged. Those results may correspond with the use of fructosyl-residues and release of glucose when sucrose is consumed in fructan synthesis.

KEYWORDS: CARBON DIOXIDE, LEAVES, LOLIUM-TEMULENTUM L, METABOLISM, PHOTOSYNTHESIS, PLANTS, RESPIRATION, SUCROSE, TEMPERATURES

2231

Smart, D.R., K. Ritchie, A.J. Bloom, and B.B. Bugbee. 1998. Nitrogen balance for wheat canopies (Triticum aestivum cv. Veery 10) grown under elevated and ambient CO2 concentrations. *Plant, Cell and Environment 21(8):753-763.*

We examined the hypothesis that elevated CO2 concentration would increase NO3- absorption and assimilation using intact wheat canopies (Triticum aestivum cv, Veery 10), Nitrate consumption, the sum of plant absorption and nitrogen loss, was continuously monitored for 23 d following germination under two CO2 concentrations (360 and 1000 mu mol mol(-1) CO2) and two root zone NO3- concentrations (100 and 1000 mmol m(3) NO3-). The plants were grown at high density (1780 m(-2)) in a 28 m3 controlled environment chamber using solution culture techniques. Wheat responded to 1000 mu mol mol(-1) CO2 by increasing carbon allocation to root biomass production. Elevated CO2 also increased root zone NO3- consumption, but most of this increase did not result in higher biomass nitrogen. Rather, nitrogen loss accounted for the greatest part of the difference in NO3- consumption between the elevated and ambient [CO2] treatments. The total amount of NO3--N absorbed by roots or the amount of NO3--N assimilated per unit area did not significantly differ between elevated and ambient [CO2] treatments. Instead, specific leaf organic nitrogen content declined, and NO3- accumulated in canopies growing under 1000 mu mol mol(-1) CO2. Our results indicated that 1000 mu mol mol(-1) CO2 diminished NO3- assimilation. If NO3- assimilation were impaired by high [CO2], then this offers an explanation for why organic nitrogen contents are often observed to decline in elevated [CO2] environments.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, BARLEY, CARBON-DIOXIDE ENRICHMENT, LEAVES, NITRATE REDUCTASE-ACTIVITY, PLANT GROWTH, TEMPERATURE, TOMATO, WINTER-WHEAT

2232

Smart, D.R., K. Ritchie, J.M. Stark, and B. Bugbee. 1997. Evidence that elevated CO2 levels can indirectly increase rhizosphere denitrifier activity. *Applied and Environmental Microbiology 63(11):4621-4624.*

We examined the influence of elevated CO2 concentration on denitrifier enzyme activity in wheat rhizoplanes by using controlled environments and solution culture techniques. Potential denitrification activity was from 3 to 24 times higher on roots that were grown under an elevated CO2 concentration of 1,000 mu mol of CO2 mol(-1) than on roots grown under ambient levels of CO2. Nitrogen loss, as determined by a nitrogen mass balance, increased with elevated CO2 levels in the shoot environment and with a high NO3- concentration in the rooting zone. These results indicated that aerial CO2 concentration can play a role in rhizosphere denitrifier activity.

KEYWORDS: AMMONIA, ENVIRONMENT, EXCHANGE, PLANTS, RICE, SOIL DENITRIFICATION, WHEAT

2233

Smeekens, S. 1998. Sugar regulation of gene expression in plants. *Current Opinion in Plant Biology 1(3):230-234.*

The molecular details of sugar sensing and sugar-mediated signal transduction pathways are unclear but recent results suggest that hexokinase functions as an important plant sugar sensor in a way that is similar to that found in yeast. The use of mutants in Arabidopsis defective in specific signaling steps is of particular importance because these give access to the genes encoding components in the signaling pathways. In addition, the physiological analysis of such mutants may reveal the interaction of sugar-induced signaling pathways and those induced by other stimuli such as environmental or biotic stress.

KEYWORDS: ARABIDOPSIS-THALIANA, BETA-AMYLASE, CHENOPODIUM-RUBRUM, ELEVATED CO2, GLUCOSE, INVERTASE, SACCHAROMYCES- CEREVISIAE, SIGNAL-TRANSDUCTION, SUCROSE EXPORT, TISSUE-SPECIFIC EXPRESSION

2234

Smernoff, D.T., J. Gale, B.A. Macler, and J. Reuveni. 1993. Inhibition of photosynthesis in duckweed by elevated co2 concentration is rapid and is not offset by a temperature- induced increase in metabolic-rate. *Photosynthetica 28(1):17-28.*

The rates of net photosynthesis (P(N)), respiration and growth of Lemna gibba L. were measured as functions of time across ranges of temperature, irradiance and carbon dioxide concentrations. P(N) on an area basis increased with temperature up to 30-degrees-C but decreased dramatically with a few hours of exposure to elevated CO2, when reported on a dry mass basis. Reductions in the apparent quantum efficiency, photosynthetic capacity and the affinity of ribulose- 1,5-bisphosphate carboxylase/oxygenase for CO2 were observed for plants grown at elevated CO2. Starch concentration was not significantly affected by elevated CO2. Although elevated temperature increased metabolic activity, it only partially alleviated the inhibition of P(N). L. gibba exhibits a characteristic C3-type response to elevated CO2 and the methodology described is useful for further elucidating the mechanism of photosynthetic acclimation to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, CULTIVATION, DESERT CONDITIONS, ENRICHMENT, GROWTH, HIGH ATMOSPHERIC CO2, LEMNA-GIBBA, PHOTORESPIRATION

2235

Smit, B., and Y.L. Cai. 1996. Climate change and agriculture in China. *Global Environmental Change-Human and Policy Dimensions 6(3):205-214.*

The implications of climate change for agriculture and food are global concerns, and they are very important for China, The country depends on an agricultural system which has evolved over thousands of years to intensively exploit environmental conditions. The pressures on the resource base are accentuated by the prospect of climate change, This paper synthesizes information from a variety of studies on Chinese agriculture and climate. Historical studies document the impacts of past climate changes and extremes, and the types of adjustments which have occurred, the vulnerability of Chinese agriculture to climate change, Climate change scenarios are assessed relative to the current distribution of agro-climatic regions and systems, Notwithstanding the enhancing effects of warming and elevated CO2 levels, expected moisture deficits and uncertain changes in the timing and frequency of critical conditions indicate that there are serious threats to the stability and adaptability of China's food production system. Copyright (C) 1996 Elsevier Science Ltd

2236

Smith, P.H.D., and T.H. Jones. 1998. Effects of elevated CO2 on the chrysanthemum leafminer, Chromatomyia syngenesiae: a greenhouse study. *Global Change Biology 4(3):287-291.*

Although feeding behaviour of Chromatomyia syngenesiae on plants grown in elevated CO2 (ambient + 200ppm) was unaffected, leaf-miner development was slower in elevated compared to ambient CO2 atmospheres. Pupal weight was lower at high CO2 and correlated with the area of leaf mined; no such correlation existed in ambient CO2. There appears to be no compensatory feeding by the leaf-miner for the reduced food quality of plants growing in elevated CO2. The implications of these findings are discussed.

KEYWORDS: HERBIVORE INTERACTIONS

2237

Smith, R.B. 1992. Controlled-atmosphere storage of redcoat strawberry fruit. *Journal of the American Society for Horticultural Science 117(2):260-264.*

Strawberries (Fragaria x ananassa Duch.) cv. Redcoat were stored at several temperatures and for various intervals in controlled atmospheres (CA) containing 0% to 18% CO2 and 15% to 21% O2. Bioyield point forces recorded on the CA-stored fresh fruit indicated that the addition of CO2 to the storage environment enhanced fruit firmness. Fruit kept under 15% CO2 for 18 hours was 48% firmer than untreated samples were initially. Response to increasing CO2 concentrations was linear. There was no response to changing O2 concentrations. Maximum enhancement of firmness was achieved at a fruit temperature of 0C; there was essentially no enhancement at 21C. In some instances, there was a moderate firmness enhancement as time in storage increased. Carbon dioxide acted to reduce the quantity of fruit lost due to rot. Fruit that was soft and bruised after harvest became drier and firmer in a CO2-enriched environment.

KEYWORDS: DECAY, QUALITY

2238

Smith, R.B., and L.J. Skog. 1992. Postharvest carbon-dioxide treatment enhances firmness of several cultivars of strawberry. *Hortscience 27(5):420-421.*

Various cultivars of strawberry (Fragaria xananassa Duch.) were stored for 42 h under an atmosphere of 15% CO2 to determine whether their firmness would be enhanced. Compared to initial samples and stored control samples, enhanced firmness was found in 21 of the 25 cultivars evaluated. The CO2 had no effect on color, as measured by Hunter 'L', 'a' and 'b', or on soluble solids concentration (SSC) or pH. There were significant differences among cultivars in firmness; Hunter color 'L', 'a', and 'b'; SSC; and pH.

KEYWORDS: ATMOSPHERES, QUALITY

2239

Smith, T.M., W.P. Cramer, R.K. Dixon, R. Leemans, R.P. Neilson, and A.M. Solomon. 1993. The global terrestrial carbon-cycle. *Water, Air, and Soil Pollution 70(1-4):19-37.*

There is great uncertainty with regard to the future role of the terrestrial biosphere in the global carbon cycle. The uncertainty arises from both an inadequate understanding of current pools and fluxes as well as the potential effects of rising atmospheric concentrations of CO2 on natural ecosystems. Despite these limitations, a number of studies have estimated current and future patterns of terrestrial carbon storage. Future estimates focus on the effects of a climate change associated with a doubled atmospheric concentration of CO2. Available models for examining the dynamics of terrestrial carbon storage and the potential role of forest management and landuse practices on carbon conservation and sequestration are discussed.

KEYWORDS: CLIMATE CHANGE, ECOSYSTEMS, ELEVATED CO2 CONCENTRATIONS, ESTUARINE MARSH, FORESTS, GENERAL-CIRCULATION MODEL, INCREASE, SENSITIVITY, SOILS, STORAGE

2240

Smith, T.M., R. Leemans, and H.H. Shugart. 1992. Sensitivity of terrestrial carbon storage to co2-induced climate change - comparison of 4 scenarios based on general- circulation models. *Climatic Change 21(4):367-384.*

The potential impacts of CO2-induced climate change on terrestrial carbon storage was estimated using the Holdridge Life-Zone Classification and four climate change scenarios derived from general circulation models. Carbon values were assigned to life-zones and their associated soils from published studies. All four scenarios suggest an increase in area occupied by forests although details of predicted patterns vary among the scenarios. There is a poleward shift of the forested zones, with an increase in the areal extent of tropical forests and a shift of the boreal forest zone into the region currently occupied by tundra. Terrestrial carbon storage increased from 0.4% (8.5 Gt) to 9.5% (180.5 Gt) above estimates for present conditions. These changes represent a potential reduction of 4 to 85 ppm on elevated atmospheric CO2 levels.

KEYWORDS: CO2, INCREASE

2241

Smith, W.K., and R.A. Donahue. 1991. Simulated influence of altitude on photosynthetic CO2 uptake potential in plants. *Plant, Cell and Environment 14(1):133-136.*

A simulation of the quantitative influence of altitude on photosynthetic CO2 uptake capability (A(P)) included the effects of predicted changes (1) in air temperature (lapse rate) and (2) leaf temperature, (3) ambient pressure and CO2 concentration, and (4) the diffusion coefficient for CO2 in air. When a dry lapse rate (0.01-degrees-C m-1) in air temperature was simulated, significant declines (up to 14%) in A(P) were predicted from sea level to 4km altitude. A moist lapse rate of 0.003-degrees-C m-1 resulted in less than a 4% decrease in A(P) over the same altitude range. When natural leaf temperatures (predicted from heat balance analyses) were simulated, A(P) was significantly greater (almost-equal-to 20%) than when leaf temperatures were considered equal to air temperature for all lapse conditions. There was virtually no change in A(P) with altitude when predicted leaf temperatures and moist lapse conditions were simulated. There was a significant (almost-equal-to 10%) increase in A(P) with altitude when leaf temperature was held constant at 30-degrees- C (regardless of altitude) under moist lapse conditions. Future studies evaluating the effects of elevation on photosynthesis could benefit from the above considerations of the effects of natural leaf temperature regimes and prevailing lapse conditions on CO2 uptake potential.

KEYWORDS: CONDUCTANCE, LEAF ANATOMY

2242

Socias, F.X., H. Medrano, and T.D. Sharkey. 1993. Feedback limitation of photosynthesis of phaseolus-vulgaris L grown in elevated co2. *Plant, Cell and Environment 16(1):81-86.*

The capacity for photosynthesis is often affected when plants are grown in air with elevated CO2 partial pressure. We grew Phaseolus vulgaris L. in 35 and 65Pa CO2 and measured photosynthetic parameters. When assayed at the growth CO2 level, photosynthesis was equal in the two CO2 treatments. The maximum rate of ribulose-1,5-bisphosphate (RuBP) consumption was lower in plants grown at 65Pa, but the CO2 partial pressure at which the maximum occurred was higher in the high-CO2-grown plants, indicating acclimation to high CO2. The acclimation of RuBP consumption to CO2 involved a reduction of the activity of RuBP carboxylase which resulted from reduced carbamylation, not a loss of protein. The rate of RuBP consumption declined with CO2 when the CO2 partial pressure was above 50Pa in plants grown under both CO2 levels. This was caused by feedback inhibition as judged by a lack of response to removing O2 from the air stream. The rate of photosynthesis at high CO2 was lower in the high-CO2-grown plants and this was correlated with reduced activity of sucrose-phosphate synthase. This is only the second report Of O2-insensitive

photosynthesis under growth conditions for plants grown in high CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, GAS-EXCHANGE, ISOPRENE EMISSION, LEAVES, PHOTORESPIRATION, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, SUCROSE PHOSPHATE SYNTHASE

2243

Solarova, J., and J. Pospisilova. 1997. Effect of carbon dioxide enrichment during in vitro cultivation and acclimation to ex vitro conditions. *Biologia Plantarum 39(1):23-30.*

Tobacco and carnation plantlets were grown in vitro on Murashige and Skoog's medium with 2% saccharose. Carnation plantlets were also grown fully photoautotrophically on a medium without saccharose. The ambient CO2 concentration was increased from 0.6 to 10 or 40 g m(-3) during the last 3 weeks of in vitro cultivation or during the first 3 weeks of acclimation to ex vitro condition (plantlets transplanted to pots with sand and nutrient solution) or during both growth phases. CO2 enrichment during in vitro cultivation markedly stimulated growth of tobacco plantlets, and also of carnation plantlets, both with and without saccharose. CO2 enrichment during the acclimation period promoted plant growth more effectively in plantlets grown in vitro at a CO2 concentration of 0.6 g m(-3) than in plantlets grown in either growth phase at higher CO2 concentrations.

KEYWORDS: CO2- ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHESIS, PLANTLETS, RASPBERRY, STRAWBERRY

2244

Sombroek, W.G., F.O. Nachtergaele, and A. Hebel. 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. *Ambio 22(7):417-426.*

The organic carbon pool in the upper 1 m of the world's soils contains 1220 Gt organic carbon, 1.5 times the total for the standing biomass. In the widespread deep soils in the tropics the carbon stored below 1 m may add about 50 Gt C. The contributions of charcoal, roots and soil fauna should be added to these totals. The much less dynamic carbonate-carbon pool amounts to 720 Gt C. Changes in land use, particularly by clearing of forests, reduce organic carbon by 20 to 50% in the upper soil layers, but little in deeper layers. On the other hand, there are indications that a human-induced enrichment of soil organic matter can be maintained over centuries. Research on the causative soil processes should be supported, because an improved understanding of this phenomenon might lead to better management strategies and sound programs to stimulate organic carbon storage and fertility levels in tropical and subtropical soils. Recent research data on the CO2 fertilization effect and the associated antitranspiration effect due to an increase of CO2 in the atmosphere indicate that a positive influence on soil organic carbon levels can be expected.

KEYWORDS: AMAZON, BIOMASS, BIOSPHERE, CYCLE, FORESTS, STORAGE

2245

Sommerfeld, R.A., W.J. Massman, R.C. Musselman, and A.R. Mosier. 1996. Diffusional flux of CO2 through snow: Spatial and temporal variability among alpine-subalpine sites. *Global Biogeochemical Cycles 10(3):473-482.*

Three alpine and three subalpine sites were monitored for up to 4 years to acquire data on the temporal and spatial variability of CO2 flux through snowpacks. We conclude that the snow formed a passive cap which controlled the concentration of CO2 at the snow-soil interface, while the flux of CO2 into the atmosphere was controlled by CO2 production in the soil. Seasonal variability in the flux at all sites was characterized by early winter minima followed by a rise in flux that averaged 70% above the minima over about a I-month period. The seasonal variability was not related to soil temperatures which remained relatively constant. Interannual variability was small, and spatial variability was smaller than previously reported. Spatial variability on a scale of 1 to 10 m was less than 30% of the average fluxes and not significantly greater than estimated error in most cases. Spatial variability on a scale of 10- to 100-m was about a factor of 2 and on a scale of 100 to 1000 m was about a factor of 4. The 100- to 1000-m variability was complicated by the fact that the sites were in different ecosystems, alpine and subalpine, and at different elevations. We attribute the small variability at the 1- to 10- m scale to the deep snow cover, from 1.4 to 5 m. We hypothesize that horizontal diffusion under the snow cover reduced small- scale horizontal gradients, while the insulating effect of the deep snow cover kept the soil temperature and moisture relatively constant. Equivalent annual wintertime flux averaged about 95 g C m(-2) yr(-1) in the alpine and about 232 g C m(-2) yr(-1) in the subalpine sites. Measurements of CO2 concentrations at 0.2 and 0.5 m in the soil of one of the subalpine sites indicated that production early in the snow season occurred at or below 0.5 m while production between 0.5 m, and the surface became important after the start of the melt season.

KEYWORDS: SOILS

2246

Sonesson, M., T.V. Callaghan, and L.O. Bjorn. 1995. Short-term effects of enhanced UV-B and CO2 on lichens at different latitudes. *Lichenologist 27:547-557.*

Interaction effects of UV-B and CO2 on three lichens species, Cladonia arbuscula, Cetraria islandica and Stereocaulon paschale, from two latitudinal sites, 68 degrees N and 56 degrees N, were studied in a laboratory experiment. The response of the plants was recorded by measuring their chlorophyll fluorescence. All species had a similar response to enhanced UV-B depending on the latitude from which the population came and the time of the season when they were sampled. Overall, there was a significant increase in photosystem II yield (as measured by a fluorescence technique) due to UV-B and no separate effect due to enhanced CO2, although there was a significant interaction between CO2 and UV-B. The increase due to UV-B was at the low CO2 level. There were also significant differences in response due to latitude. The results contradict our hypotheses that negative effects of UV-B would be larger in the North than in the South and that a negative response should be especially large during the early season. (C) 1995 The British Lichen Society

KEYWORDS: ALPINE LIFE ZONE, BLUE-GREEN PHYCOBIONTS, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GROWTH, MARINE DIATOMS, PHOTOSYNTHETIC CHARACTERISTICS, PLANTS, RADIATION, STRATOSPHERIC OZONE

2247

Sonesson, M., T.V. Callaghan, and B.A. Carlsson. 1996. Effects of enhanced ultraviolet radiation and carbon dioxide concentration on the moss Hylocomium splendens. *Global Change Biology 2(1):67-73.*

In a laboratory experiment interaction effects of UV-B and CO2 on photosynthesis and growth of the moss Hylocomium splendens were studied. The plants were exposed to two CO2 levels (350 ppm and 600 ppm) and three UV-B levels (no UV-B, ambient UV-B and that corresponding to 20% ozone depletion) for 5 months. The effects were recorded by measuring the photosynthetic response and growth of the plants. There was a statistically significant change in photosynthetic

efficiency and maximum photosynthetic rates due to time and to enhanced CO2 concentration, whereas there was no effect due to UV-B. There was a decreased growth due to both UV-B and CO2 and an interaction effect on growth (in length). The UV-B dose corresponding to the ambient level had a larger reducing effect on growth than the highest UV-B dose. This was a counter- intuitive result and the following tentative interpretation was made: differences in the measured UV-A/UV-B/PAR ratios between the treatments could explain the result provided there was a non-linear response to UV over the range of irradiance levels used.

KEYWORDS: ACTION SPECTRUM, CO2, DAMAGE, GROWTH, IRRADIATION, LIGHT, MARINE DIATOMS, PHOTOSYNTHETIC CHARACTERISTICS, PLANTS, UV-B RADIATION

2248

Soule, P.T., and P.A. Knapp. 1999. Western juniper expansion on adjacent disturbed and near-relict sites. *Journal of Range Management 52(5):525-533.*

We determined rates of western juniper (Juniperus occidentalis spp. occidentalis Hook.) density and cover change during the period 1951 to 1994 at 3 adjacent sites with nearly identical elevation, slope, aspect, soils, plant communities, and climate, but different land-use histories. The 3 sites are located in central Oregon at the confluence of the Deschutes and Crooked Rivers. Two of the sites are typical of central Oregon rangelands in that they have a history of anthropogenic disturbance including active fire suppression and domestic livestock grazing. The third site is a relict mesa that is a protected Research Natural Area and has experienced minimal anthropogenic impacts. We used large scale aerial photography to determine cover and density of western juniper in 1951, 1956, 1961, 1972, 1982, and 1994. We found that western juniper density and cover during the last 4 decades increased at all sites, with changes on the relict site similar to those on one of the disturbed sites. We suggest that even though 2 of the traditionally cited causes of western juniper expansion since the late 1800s (altered fire regimes, domestic livestock grazing) may have contributed to expansion on our disturbed sites, these mechanisms can not explain expansion on the near- relict mesa. Further, we examined climatic changes since 1900 in the region and concluded that the data did not fully support a climate-driven mechanism for the expansion. In seeking to explain western juniper expansion on semiarid rangelands, we suggest that all potential causal mechanisms (e.g., fire history, biological inertia, climate, domestic grazing, atmospheric CO2 enrichment) be considered.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, CENTRAL OREGON, GROWTH, OCCIDENTALIS, TRENDS, UNITED-STATES, VEGETATION CHANGE

2249

Soussana, J.F., E. Casella, and P. Loiseau. 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward .2. Plant nitrogen budgets and root fraction. *Plant and Soil 182(1):101-114.*

Perennial ryegrass swards were grown in large containers on a soil and were exposed during two years to elevated (700 mu L L(-1)) or ambient atmospheric CO2 concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO2. The nitrogen nutrition of the grass sward was studied at two sub-optimal (160 and 530 kg N ha(-1) y(-1)) and one non-limiting (1000 kg N ha(-1) y(-1)) N fertilizer supplies. At cutting date, elevated CO2 reduced by 25 to 33%, on average, the leaf N concentration per unit mass. Due to an increase in the leaf blade weight per unit area in elevated CO2, this decline did not translate for all cuts in a lower N concentration per unit leaf blade area. With the non-limiting N fertilizer supply, the leaf N concentration (% N) declined with the shoot dry-matter (DM) according to highly significant power models in ambient (% N=4.9 DM(-0.38)) and in elevated (% N=5.3 DM(-0.52)) CO2. The difference between both regressions was significant and indicated a lower critical leaf N concentration in elevated than in ambient CO2 for high, but not for low values of shoot biomass. With the sub-optimal N fertilizer supplies, the nitrogen nutrition index of the grass sward, calculated as the ratio of the actual to the critical leaf N concentration, was significantly lowered in elevated CO2. This indicated a lower inorganic N availability for the grass plants in elevated CO2, which was also apparent from the significant declines in the annual nitrogen yield of the grass sward and in the nitrate leaching during winter. For most cuts, the harvested fraction of the plant dry-matter decreased in elevated CO2 due, on average, to a 45-52% increase in the root phytomass. In the same way, a smaller share of the plant total nitrogen was harvested by cutting, due, on average, to a 25-41% increase in the N content of roots. The annual means of the DM and N harvest indices were highly correlated to the annual means of the nitrogen nutrition index. Changes in the harvest index and in the nitrogen nutrition index between ambient and elevated CO2 were also positively correlated. The possible implication of changes in the soil nitrogen cycle and of a limitation in the shoot growth potential of the grass in elevated. CO2 is discussed.

KEYWORDS: CANOPY, CARBON-DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO2, GROWTH, LEAF, NUTRITION, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, TALL FESCUE

2250

Soussana, J.F., and U.A. Hartwig. 1996. The effects of elevated CO2 on symbiotic N-2 fixation: A link between the carbon and nitrogen cycles in grassland ecosystems. *Plant and Soil 187(2):321-332.*

The response of plants to elevated CO2 is dependent on the availability of nutrients, especially nitrogen. It is generally accepted that an increase in the atmospheric CO2 concentration increases the C:N ratio of plant residues and exudates. This promotes temporary N-immobilization which might, in turn, reduce the availability of soil nitrogen. In addition, both a CO2 stimulated increase in plant growth (thus requiring more nitrogen) and an increased N demand for the decomposition of soil residues with a large C:N will result under elevated CO2 in a larger N-sink of the whole grassland ecosystem. One way to maintain the balance between the C and N cycles in elevated CO2 would be to increase N-import to the grassland ecosystem through symbiotic N-2 fixation. Whether this might happen in the context of temperate ecosystems is discussed, by assessing the following hypothesis: i) symbiotic N-2 fixation in legumes will be enhanced under elevated CO2, ii) this enhancement of N- 2 fixation will result in a larger N-input to the grassland ecosystem, and iii) a larger N input will allow the sequestration of additional carbon, either above or below- ground, into the ecosystem. Data from long-term experiments with model grassland ecosystems, consisting of monocultures or mixtures of perennial ryegrass and white clover, grown under elevated CO2 under free-air or field-like conditions, supports the first two hypothesis, since: i) both the percentage and the amount of fixed N increases in white clover grown under elevated CO2 ii) the contribution of fixed N to the nitrogen nutrition of the mixed grass also increases in elevated CO2. Concerning the third hypothesis? an increased nitrogen input to the grassland ecosystem from N-2 fixation usually promotes shoot growth (above-ground C storage) in elevated CO2. However, the consequences of this larger N input under elevated CO2 on the belowground carbon fluxes are not fully understood. On one hand, the positive effect of elevated CO2 on the quantity of plant residues might be overwhelming and lead to an increased long-term below-ground C storage; on the other hand, the enhancement of the decomposition process by the N-rich legume material might favour carbon turn-over and, hence, limit the storage of below-ground carbon.

KEYWORDS: ACETYLENE-REDUCTION ACTIVITY, ATMOSPHERIC CO2, BIRDSFOOT-TREFOIL, CLOVER TRIFOLIUM-REPENS, HYDROGEN EVOLUTION, LEGUME NODULES, MEDICAGO-SATIVA, NITRATE INHIBITION, ROOT NODULE ACTIVITY, WHITE CLOVER

2251

Sozzi, G.O., G.D. Trinchero, and A.A. Fraschina. 1999. Controlled-atmosphere storage of tomato fruit: low oxygen or elevated carbon dioxide levels alter galactosidase activity and inhibit exogenous ethylene action. *Journal of the Science of Food and Agriculture 79(8):1065-1070.*

The effects of 3% O-2 and 20% CO2, both alone and together with 100 mu g g(-1) C2H4, on ethylene production, chlorophyll degradation, carotenoid biosynthesis and alpha- and beta- galactosidase activity in breaker tomato (Lycopersicon esculentum Mill) fruit were investigated. The low O-2 and high CO2 atmospheres prevented the rise in ethylene production, total carotenoid and lycopene biosynthesis and alpha- and beta- galactosidase activity and slowed down chlorophyll degradation and loss of firmness (P<0.05). These suppressive effects were not reversed, or only in part - in the case of chlorophyll breakdown - by addition of 100 mu g g(-1) C2H4 to said controlled atmospheres. After transfer from the various atmospheres to air, flesh firmness decreased and ethylene production, total carotenoids, lycopene and beta-galactosidase II activity increased but these parameters were, in all cases, still significantly different from those of fruit held in air. Keeping tomatoes in controlled atmospheres, even in the presence of ethylene, had marked residual effects. Results suggest an antagonism between elevated CO2/low O-2 and exogenous ethylene which could determine most of the ripening parameter behaviour under controlled-atmosphere storage, though a direct regulatory mechanism by O-2 and/or CO2 should not be discarded. (C) 1999 Society of Chemical Industry.

KEYWORDS: BIOSYNTHESIS, CELL-WALL POLYSACCHARIDES, CELLULASE, DEGRADATION, POLYGALACTURONASE, PROTEIN, RNA, STRESS

2252

Spring, G.M., G.H. Priestman, and J.P. Grime. 1996. A new field technique for elevating carbon dioxide levels in climate change experiments. *Functional Ecology 10(4):541-545.*

1. A compact, low-cost, free-air carbon dioxide enrichment system for use in climate change experiments is described, The system has been used in a small-scale study of the effects of an enriched carbon dioxide atmosphere on the growth and functioning of a natural plant community, 2. The experiment ran for 4 months in summer on a nutrient-poor limestone grassland in Derbyshire, The study examined the separate and combined effects of elevated CO2, temperature and soil nutrient status on the growth of seedlings of obligate mycorrhizal and non- mycorrhizal plant species native to the site. 3. It was demonstrated that the CO2 elevation could be controlled within the limits set for 64% of the time. Significant effects of elevated CO2 on the growth and recruitment of seedlings were found in the presence of added nutrients and elevated temperatures.

KEYWORDS: CO2- ENRICHMENT, GROWTH, LIGHT, NUTRIENTS, PLANTS, RESPONSES

2253

Spunda, V., J. Kalina, M. Cajanek, H. Pavlickova, and M.V. Marek. 1998. Long-term exposure of Norway spruce to elevated CO2 concentration induces changes in photosystem II mimicking an adaptation to increased irradiance. *Journal of Plant Physiology 152(4-5):413-419.*

Fifteen-year-old Norway spruces (Picea abies [L.] Karst.) were grown in open top chambers (OTC) at ambient (A) and elevated (i.e. ambient + 350 mu mol(CO2)mol(-1)) concentrations of CO2 (E) for four growing seasons (1992-1995). During this time period several examples of the depression of photosynthetic activities were observed for E needles. In order to better characterize the nature of this depression the gas exchange and fluorescence parameters were analyzed on current year needles during the last season (July 1995). The photon flux density response curves of CO2 uptake (P-N) revealed a significantly reduced stimulation of P-N for E needles as compared with short-term exposure to doubled CO2. Moreover, the sudden exposure of E shoots to 350 mu mol(CO2)mol(-1) at saturating irradiance revealed a depression of both P-Nmax (by 20 %) and quantum yield of PS II (by 32 %) compared with A shoots measured at 350 mu mol(CO2)mol(-1). The data supporting the diminished light harvesting system of photosystem II (PS II) in E shoots compared with A shoots were obtained from pigment analysis, low temperature fluorescence spectra and Chl a fluorescence induction kinetics. The relative proportion of inactive reaction centres of PS II determined from F-pl of the fluorescence induction was 20 % higher for E needles. These changes found for E needles mimicked an adaptation of PS II to increased irradiance compared with A needles. As the irradiance exposure was the same for the examined needles from both E and A spruces we suggest that these changes reported for E needles resulted from the feed-back limitation of photochemical reactions due to suppressed electron transport through the plastoquinone pool.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWTH, LEAVES, PHOTOINHIBITION, PHOTOSYNTHESIS, TOMATO PLANTS

2254

Sritharan, R., H. Caspari, and F. Lenz. 1992. Influence of co2 enrichment and phosphorus supply on growth, carbohydrates and nitrate utilization of kohlrabi plants. *Gartenbauwissenschaft 57(5):246-251.*

Kohlrabi (Brassica oleracea var. gongylodes (L.) cv. Express Forcer) plants were grown in sand with adequate nutrient supply. From two weeks after germination until harvest they were treated with two levels of phosphorus supply (1.0 or 0.005 mM P). Four weeks after introducing the P supply regimes the plants were exposed to either a low (300 muL CO2 L-1) or high (900 muL CO2 L-1) CO2 concentration in growth chambers for three weeks. At elevated CO2 concentration plants with 1.0 mM phosphorus produced a larger leaf area and dry matter than those grown at low CO2. At reduced P supply CO2 enrichment promoted leaf senescence and did not increase growth and dry matter. Phosphorus deficiency resulted in increased accumulation of starch in leaves, tuber, and roots and reduced NO3-N concentrations in all plant parts. The CO2 enrichment reduced N and NO3 concentration and increased nitrate utilization efficiency at both P levels. Phosphorus deficiency decreased nitrogen, potassium, calcium, and magnesium concentrations in leaves particularly at high CO2.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, EXCHANGE, LEAVES, NITROGEN, NUTRITION, PHOSPHATE STATUS, PHOTOSYNTHESIS, REDUCTASE-ACTIVITY, STARCH

2255

Sritharan, R., and F. Lenz. 1992. Effects of carbon-dioxide enrichment and nitrogen supply on kohlrabi (brassica-oleracea var gongylodes L) .1. Water-use, gas-exchange, and carbohydrate partitioning. *Gartenbauwissenschaft 57(3):138-145.*

Six weeks old kohlrabi plants (Brassica oleracea var, gongylodes [L.] cv.

Express Forcer) were grown in growth chambers for three weeks at two levels of CO2 concentration (300-mu-l CO2 l-1-low or 900-mu-l CO2 l-1-high) and three levels of N-nutritional regimes (0.1, 1.0 or 6.0 mM nitrate supply). Carbon dioxide enrichment significantly increased total water uptake of plants at all N supply levels. Water use efficiency, photosynthesis and stomatal conductance were increased by high CO2 only at 1.0 and 6.0 mM supply and reduced at the lowest N level. Photosynthetic efficiency (mu-Mol CO2 fixed m-2 s-1 per mu-l intercellular CO2 l-1) was reduced by both low N supply and CO2 enrichment. Intercellular CO2 concentration was not affected by N deficiency at both CO2 levels. Low NO3 had a lesser effect on photosynthesis than on leaf area growth; photosynthetic rates of mature leaves at both CO2 levels were lowered by about 30 % as compared to the respective controls, after seven weeks of reduction in NO3 supply. In leaves lowest NO3 treatment increased starch and sucrose and in roots starch glucose, fructose, and sucrose and in tuber starch concentrations. Photosynthetic reduction at low N supply showed a significant correlation with leaf starch concentration at both CO2 levels indicating that the inhibition is a result of feed back inhibition. Carbohydrate partitioning within the plant organs were predominantly governed by N supply levels than CO2 treatments.

KEYWORDS: ACCUMULATION, CO2, CONDUCTANCE, COTTON, LEAVES, PHOTOSYNTHESIS, STRESS, TRANSPIRATION

2256

Staddon, P.L. 1998. Insights into mycorrhizal colonisation at elevated CO2: a simple carbon partitioning model. *Plant and Soil 205(2):171-180.*

A simulation model was used to investigate the effect of an increased rate of plant photosynthesis at enhanced atmospheric CO2 concentration on a non-leguminous plant-mycorrhizal fungus association. The model allowed the user to modify carbon allocation patterns at three levels: (1) within the plant (shoot-root), (2) between the plant and the mycorrhizal fungus and (3) within the mycorrhizal fungus (intraradical- extraradical structures). Belowground (root and fungus) carbon losses via respiration (and turnover) could also be manipulated. The specific objectives were to investigate the dynamic nature of the potential effects of elevated CO2 on mycorrhizal colonisation and to elucidate some of the various mechanisms by which these effects may be negated. Many of the simulations showed that time (i.e. plant age) had a more significant effect on the observed stimulation of mycorrhizal colonisation by elevated CO2 than changes in carbon allocation patterns or belowground carbon losses. There were two main mechanisms which negated a stimulatory effect of elevated CO2 on internal mycorrhizal colonisation: an increased mycorrhizal carbon allocation to the external hyphal network and an increased rate of mycorrhizal respiration. The results are discussed in relation to real experiments. The need for studies consisting of multiple harvests is emphasised, as is the use of allometric analysis. Implications at the ecosystem level are discussed and key areas for future research are presented.

KEYWORDS: ATMOSPHERIC CO2, BOUTELOUA-GRACILIS, CLIMATE CHANGE, DIOXIDE, GROWTH, INFECTION UNITS, PLANTS, RESPONSES, ROOTS, TRIFOLIUM-SUBTERRANEUM L

2257

Staddon, P.L., and A.H. Fitter. 1998. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution 13(11):455-458.*

It is well established that an increase in the concentration of atmospheric CO2 stimulates plant growth. Recently, many researchers have concluded that elevated CO2 concentrations also stimulate mycorrhizal colonization. However, new evidence suggests that the observed CO2 effects on arbuscular mycorrhizal fungi are indirect and are a result of faster plant growth at higher CO2 concentrations. Potential changes to species assemblages of mycorrhizal fungi could affect soil carbon storage and, consequently, the feedback effects of terrestrial soil-vegetation systems on global environmental change.

KEYWORDS: BOUTELOUA-GRACILIS, CO2- ENRICHMENT, COLONIZATION, GROWTH, INFECTION, QUERCUS-ALBA, RESPONSES, ROOT, SEEDLINGS, SOIL

2258

Staddon, P.L., A.H. Fitter, and J.D. Graves. 1999. Effect of elevated atmospheric CO2 on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in Plantago lanceolata and Trifolium repens in association with the arbuscular mycorrhizal fungus Glomus mosseae. *Global Change Biology 5(3):347-358.*

Plantago lanceolata and Trifolium repens were grown under ambient (400 mu mol. mol(-1)) and elevated (650 mu mol mol(-1)) atmospheric CO2 conditions. Plants were inoculated with the arbuscular mycorrhizal fungus Glomus mosseae and given a phosphorus supply in the form of bonemeal. Six sequential harvests were taken in order to determine whether the effect of elevated CO2 on internal mycorrhizal colonization and external hyphal production was independent of the stimulatory effect of elevated CO2 on plant growth. At a given time, elevated CO2 increased the percentage of root length colonized (RLC), the total length of colonized root and the external mycorrhizal hyphal (EMH) density and decreased the ratio of EMH to total length of colonized root. When plant size was taken into account, the CO2 effect on RLC and total length of colonized roof was greatly reduced land only apparent for early harvests in T. repens) and the effects on the EMH parameters disappeared. Root tissue P concentration was unchanged at elevated CO2, but there was a decrease in shoot P at the later harvests. There was no direct effect of elevated CO2 on P inflow for the earlier period (< 50 d) of the experiment. However, over the last period, there was a significant negative effect of elevated CO2 on P inflow for both species, independent of plant size. It is concluded that elevated CO2 had no direct effect on mycorrhizal colonization or external hyphal production, and that any observed effects on a time basis were due to faster growing plants at elevated CO2. However, for older plants, elevated CO2 had a direct negative effect on P inflow This decrease in P inflow coincides with the observed decrease in shoot P concentration. This is discussed in terms of downregulation of photosynthesis often seen in elevated CO2 grown plants, and the potential for mycorrhizas (via external hyphal turnover to alleviate the phenomenon. The direction for future research is highlighted, especially in relation to carbon flow to and storage in the soil.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, QUERCUS-ALBA, ROOT, SINK ACTIVITY, SOIL, SUBTERRANEUM L

2259

Staddon, P.L., A.H. Fitter, and D. Robinson. 1999. Effects of mycorrhizal colonization and elevated atmospheric carbon dioxide on carbon fixation and below-ground carbon partitioning in Plantago lanceolata. *Journal of Experimental Botany 50(335):853-860.*

Plantago lanceolata with or without the mycorrhizal fungus Glomus mosseae were grown over a 100 d period under ambient (380 +/- 50 mu mol mol(-1)) and elevated (600 +/- 150 mu mol mol(-1)) atmospheric CO2 conditions. To achieve similar growth, non-mycorrhizal plants received phosphorus in solution whereas mycorrhizal plants were supplied with bonemeal. Measures of plant growth, photosynthesis and carbon input to the soil were obtained, Elevated CO2 stimulated plant growth to the same extent in mycorrhizal and non-mycorrhizal plants,

but had no effect on the partitioning of carbon between shoots and roots or on shoot tissue phosphorus concentration. Mycorrhizal colonization was low, but unaffected by CO2 treatment. Net photosynthesis was stimulated both by mycorrhizal colonization and elevated CO2, and there was a more than additive effect of the two treatments on net photosynthesis. Colonization by mycorrhizal fungi inhibited acclimation, in terms of net carbon assimilation, of plants to elevated CO2. C-13 natural abundance techniques were used to measure carbon input into the soil, although the results were not conclusive. Direct measurements of below-ground root biomass showed that elevated CO2 did stimulate carbon flow below-ground and this was higher in mycorrhizal than non-mycorrhizal plants. For the four treatment combinations, the observed relative differences in amount of below-ground carbon were compared with those expected from the differences in net photosynthesis. A considerable amount of the extra carbon fixed both as a result of mycorrhizal colonization and growth in elevated CO2 did not reveal itself as increased plant biomass, As there was no evidence for a substantial increase in soil organic matter, most of this extra carbon must have been respired by the mycorrhizal fungus and the roots or by the the plants as dark-respiration. The need for detailed studies in this area is emphasized.

KEYWORDS: CO2- ENRICHMENT, GLOMUS-MOSSEAE, GROWTH, NATURAL ECOSYSTEMS, PHOTOSYNTHESIS, RESPONSES, SOIL, SOURCE-SINK RELATIONS, TRIFOLIUM- REPENS, USE EFFICIENCY

2260

Staddon, P.L., J.D. Graves, and A.H. Fitter. 1998. Effect of enhanced atmospheric CO2 on mycorrhizal colonization by Glomus mosseae in Plantago lanceolata and Trifolium repens. *New Phytologist 139(3):571-580.*

Plantage lanceolata L. and Trifolium repens L. were grown for 16 wk in ambient (360 mu mol mol(-1)) and elevated (610 mu mol mol(-1)) atmospheric CO2. Plants were inoculated with the arbuscular mycorrhizal (AM) fungus Glomus mosseae (Nicol. & Gerd.) Gerdemann & Trappe and given a phosphorus supply in the form of bonemeal, which would not be immediately available to the plants. Seven sequential harvests were taken to determine whether the effect of elevated CO2 on mycorrhizal colonization was independent of the effect of CO2 on plant growth. Plant growth analysis showed that both species grew faster in elevated CO2 and that P. lanceolata had increased carbon allocation towards the roots. Elevated CO, did not affect the percentage of root length colonized (RLC); although total colonized root length was greater, when plant size was taken into account this effect disappeared. This finding was also true for root length colonized by arbuscules. No CO2 effect was found on hyphal density (colonization intensity) in roots. The P content of plants was increased at elevated CO2, although both shoot and root tissue P concentration were unchanged. This was again as a result of bigger plants at elevated CO2. Phosphorus inflow was unaffected by CO2 concentrations. It is concluded that there is no direct permanent effect of elevated CO2, on mycorrhizal functioning, as internal mycorrhizal development and the mycorrhizal P uptake mechanism are unaffected. The importance of sequential harvests in experiments is discussed. The direction for future research is highlighted, especially in relation to C storage in the soil.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ELEVATED CO2, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, QUERCUS-ALBA, RESPONSES, ROOTS, SINK

2261

Staddon, P.L., J.D. Graves, and A.H. Fitter. 1999. Effect of enhanced atmospheric CO2 on mycorrhizal colonization and phosphorus inflow in 10 herbaceous species of contrasting growth strategies. *Functional Ecology 13(2):190-199.*

1, Ten herbaceous species were grown over a 4-month period under ambient (360 mu mol mol(-1)) and elevated (610 mu mol mol(-1)) atmospheric CO2 conditions. Plants were inoculated with the arbuscular mycorrhizal (AM) fungus Glomus mosseae and given a phosphorus (P) supply which was not immediately available to the plants. 2. Multiple harvests were taken in order to determine whether the effect of elevated CO2 on mycorrhizal colonization and phosphorus inflow was independent of its effect on plant growth. 3, All species grew faster under elevated CO2 and carbon partitioning was altered, generally in favour of the shoots. All species responded similarly to elevated CO2. 4. Elevated CO2 did not affect the percentage of root length colonized by AM fungi, but the total amount of colonized root length was increased, because the plants were bigger. 5. Elevated CO2 increased total P content, but had little or no effect on P concentration. At a given age, P inflow was stimulated by elevated CO2, but when root length was taken into account the CO2 effect disappeared. 6. In these host species there is no evidence for a direct effect of elevated CO2 on mycorrhizal functioning, because both internal mycorrhizal colonization and P inflow are unaffected. 7. Future research should concentrate on the potential for carbon flow to the soil via the external mycelial network.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, ENRICHMENT, NUTRITION, PLANTAGO-LANCEOLATA, QUERCUS-ALBA, RESPONSES, ROOT, TRIFOLIUM- REPENS

2262

Stange, G. 1997. Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, Cactoblastis cactorum. *Oecologia 110(4):539-545.*

Sensory organs that detect CO2 are common in herbivorous moths and butterflies, but their function has been unclear until now. As the CO2 gradients in the vicinity of a host plant depend on its physiological condition, CO2 could provide a sensory cue for the suitability of the plant as a larval food source. This study investigated whether changing the atmospheric CO2 concentration affected oviposition by Cactoblastis cactorum on its host, the cactus Opuntia stricta. On host plants exposed to rapid fluctuations in CO2 concentration, the frequency of oviposition was reduced by a factor of 3.2 compared to the control. As the fluctuations mask the much smaller CO2 signals generated by the plants, this suggests that those signals constitute an important component of the host identification process. On host plants exposed to a constant background of doubled CO2, oviposition was also reduced, by a factor of 1.8. An increased background reduces host signal detectability, partially as a consequence of a general principle of sensory physiology (Weber-Fechner's law), and partially due to other factors specific to CO2-receptor neurons.

KEYWORDS: AUSTRALIA, BIOLOGICAL-CONTROL, ELEVATED CO2, LEPIDOPTERA, NOCTUIDAE, OPEN-TOP CHAMBERS, OPUNTIA-STRICTA, PIT ORGAN, RECEPTORS, SELECTION

2263

Stanghellini, C., and J.A. Bunce. 1993. Response of photosynthesis and conductance to light, co2, temperature and humidity in tomato plants acclimated to ambient and elevated co2. *Photosynthetica 29(4):487-497.*

In tomato (Lycopersicon esculentum L.) plants, net carbon dioxide exchange rate (P(N)) response curves to both irradiance (I) and short-term [CO2] were similar for plants grown at both 350 and 700 cm3(CO2) m-3. However, water vapor conductance (gH2O) of plants grown at high [CO2] was less sensitive to short term [CO2] variations,

when measured at low vapor pressure difference, and was larger than the conductance of "ambient [CO2]" plants when both were exposed to high [CO2]. P(N) and g(H2O) under high I increased with temperature over the range 18 to 32-degrees-C. P(N) of plants grown in both [CO2] treatments increased at most about 25 % from 350 to 700 cm3 m-3 at 18 and 25-degrees-C, and decreased when exposed to 1000 cm3 m-3 at these temperatures. Thus increasing atmospheric [CO2] might not increase P(N) by as much as expected and water use of crops might not decrease.

KEYWORDS: C-3, CARBON DIOXIDE, CARBOXYLASE, FIELD-GROWN TOMATO, HIGH ATMOSPHERIC CO2, INHIBITION, O2, SENSITIVITY, STOMATAL CLOSURE, TERM

2264

Steffen, W.L., W. Cramer, M. Plochl, and H. Bugmann. 1996. Global vegetation models: Incorporating transient changes to structure and composition. *Journal of Vegetation Science 7(3):321-328.*

We describe an approach for developing a Dynamic Global Vegetation Model (DGVM) that accounts for transient changes in vegetation distribution over a decadal time scale. The DGVM structure is based on a linkage between an equilibrium global vegetation model and smaller scale ecosystem dynamics modules that simulate the rate of vegetation change. Vegetation change is classified into four basic types, based largely on the projected change in above-ground biomass of the vegetation. These four types of change are: (1) dieback of forest, shrubland or grassland; (2) successional replacement within forest, shrubland or grassland; (3) invasion of forest, shrubland or grassland; (4) change in tree/grass ratio. We then propose an approach in which the appropriate ecosystem dynamics module for each type of change is applied and the grid cells of the global model updated accordingly. An approach for accounting for fire, as an example of a disturbance which may strongly influence the rate and spatial pattern of forest dieback, is incorporated. We also discuss data needs for the development, calibration and validation of the model.

KEYWORDS: ATMOSPHERE, CO2, CO2-INDUCED CLIMATE CHANGE, DEFORESTATION, ECOSYSTEMS, FORESTS, IMPACT, SIMULATION-MODEL, SOIL, TERRESTRIAL CARBON STORAGE

2265

Steffen, W.L., and J.S.I. Ingram. 1995. Global change and terrestrial ecosystems: An initial integration. *Journal of Biogeography 22(2-3):165-174.*

We present a framework for integrating GCTE's research programme based on three interacting axes-time, space and applicability. We use the contributed papers from the First GCTE Science Conference to undertake an initial integration of GCTE-type research using this three-axis structure. We assess where progress is being made, where progress is likely to be made in the near future, and where critical gaps exist which require a major effort to eliminate. Elevated CO2 research is one of the most mature areas within GCTE, and provides scope for initial integration along all three axes. Soils, being key to the functioning of all terrestrial ecosystems, provide another excellent opportunity to integrate research along all three axes. A major obstacle to further integration is our lack of understanding of landscape-scale processes, particularly disturbances, and our ability to simulate global change impacts on them. GCTE's Focus 2, Change in Ecosystem Structure, is perhaps best placed to attack many of the gaps that prevent this further integration along space and time scales, and is now entering a rapid development phase; the other Foci also have a major role to play. Integration specifically along the applicability axis is being developed in some areas but requires an enhanced effort to achieve its potential to increase scientific efficiency and effectiveness. The emerging field of global ecology, i.e. ecology at very large space and time scales, is progressing rapidly on the basis of linkages to more traditional ecological research at smaller scales, but requires further interaction with work along the applicability axis.

2266

Steinger, T., C. Lavigne, A. Birrer, K. Groppe, and B. Schmid. 1997. Genetic variation in response to elevated CO2 in three grassland perennials - a field experiment with two competition regimes. *Acta Oecologica-International Journal of Ecology 18(3):263-268.*

Intraspecific Variation in the response to increased concentrations of atmospheric CO2 was investigated in three plant species (Bromus erectus, Prunella vulgaris, P. grandiflora) in a calcareous grass land. Genotypes of each species were grown both in multispecies communities and under reduced competition pressure in tubes buried in the soil. Plant growth was reduced in the artificial communities but no significant effect of CO2 was observed on any of the measured traits. Significant genotype by-CO2 interactions were found in two species when plants were grown under reduced competition in the tubes. No genotype-by-CO2 interactions were found for the same genotypes grown in the multispecies communities indicating that genetic variation was swamped by large environmental variation. Furthermore, no correlations were observed between CO2 responses of identical genotypes grown individually in tubes and in multispecies communities. This result cautions about the ability to predict CO2-induced evolutionary changes from data of individually-grown plants.

KEYWORDS: ENVIRONMENTS, PLANTS

2267

Stekiel, T.A., W.J. Stekiel, M. Tominaga, A. Stadnicka, Z.J. Bosnjak, and J.P. Kampine. 1996. Effect of halothane and isoflurane on in situ diameter responses of small mesenteric veins to acute graded hypercapnia. *Anesthesia and Analgesia 82(2):349-357.*

The purpose of the present study was to quantify the inhibitory effect of inhaled halothane and isoflurane on acute hypercapnia-induced responses of capacitance-regulating veins and related cardiovascular variables in response to sequential 40-s periods of 5%, 10%, 15%, and 20% inspired CO2 (FICO2). Measurements were made in normoxic alpha-chloralose- anesthetized rabbits before, during, and after either 0.75 minimum alveolar anesthetic concentration inhaled halothane or isoflurane. The graded hypercapnia caused graded venoconstriction and bradycardia but minimal presser responses. Hypercapnia-induced venoconstriction was blocked by prior local superfusion of the exposed veins with 3 x 10(-6) M tetrodotoxin. Both the hypercapnia-induced venoconstriction and bradycardia responses were significantly attenuated by halothane or isoflurane and did not fully recover af ter removal of the anesthetics from the circulation. Both anesthetics produced a significant baseline (i.e., prehypercapnia) hypotension and a tendency toward a resultant tachycardia. The baseline hypotension did not recover completely after elimination of the anesthetic. Neither anesthetic altered baseline vein diameter. These results agree with previous studies demonstrating that hypercapnic acidosis :produces mesenteric venoconstriction by elevating excitatory sympathetic efferent neural input via activation of peripheral and central chemoreceptors and that bradycardia results from activation of compensatory baroreflexes. The neural components of these reflexes are possible primary sites for attenuation of these cardiovascular responses by halothane and isoflurane.

KEYWORDS: ANESTHESIA, ANESTHETIZED DOGS, BARORECEPTOR, CARBON DIOXIDE, CIRCULATION, HYPOXIC HYPERCAPNIA, RABBITS, REFLEX CONTROL, SYMPATHETIC-NERVE ACTIVITY, VASCULAR CAPACITANCE

2268

Sternberg, M., V.K. Brown, G.J. Masters, and I.P. Clarke. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. *Plant Ecology 143(1):29-37.*

This study investigates the effects of field manipulations of local climate to determine the potential impact of climate change on plant community dynamics in a calcareous grassland. The experimental site is located in a grassland at the Wytham estate, Oxfordshire, UK. The one hectare study area is within a 10 ha abandoned arable field on Jurassic corallian limestone. Two climate change scenarios were used: warmer winters with increased summer rainfall and warmer winters with summer drought. Plant cover and species richness were significantly increased in plots receiving supplemented summer rainfall, while the amount of litter was significantly reduced. Litter formation was significantly increased by winter warming and drought. The responses of the plant community to the climate manipulations were related to the life-history attributes of the dominant species. Seedling recruitment was limited by microsite availability, which also varied in the different climate manipulations. The results are discussed in terms of successional dynamics. They suggest that warmer winters may delay succession, as gap formation in the sward will provide sites for colonisation of annuals, thereby enabling their persistence in the sward. Under wetter conditions during summer, perennial grasses tend to close the sward, thereby inhibiting the establishment of later successional species.

KEYWORDS: ELEVATED CO2, GROWTH, INSECT HERBIVORE INTERACTIONS, LITTER DECOMPOSITION, MECHANISMS, NITROGEN, RESPONSES, SEEDLING ESTABLISHMENT, TEMPERATURE, TUNDRA

2269

Stewart, J.D., and J. Hoddinott. 1993. Photosynthetic acclimation to elevated atmospheric carbon- dioxide and uv irradiation in pinus-banksiana. *Physiologia Plantarum 88(3):493-500.*

Pinus banksiana seedlings were grown for 9 months in enclosures in greenhouses at CO2 concentrations of 350 or 750 mumol mol-1 with either low (0.005 to 0.3 W M-2) or high (0.25 to 0.90 W M- 2) ultraviolet-B (UV-B) irradiances. Total seedling dry weight decreased with high UV treatment but was unaffected by CO2 enrichment. High UV treatment also shifted biomass partitioning in favor of leaf production. Both CO2 and UV treatments decreased the dark respiration rate and light compensation point. High UV light inhibited photosynthesis at 350 but not at 750 mumol mol-1 CO2 due to a UV induced increase in ribulose- 1,5-bisphosphate carboxylase/oxygenase efficiency and ribulose- 1,5-bisphosphate regeneration. Stomatal density was increased by high UV irradiance but was unchanged by CO2 enrichment.

KEYWORDS: ABSCISIC- ACID, C-3, CO2, GAS-EXCHANGE, GROWTH, LEAVES, PLANTS, SEEDLINGS, STOMATAL CLOSURE, ULTRAVIOLET-B RADIATION

2270

Stewart, J., and C. Potvin. 1996. Effects of elevated CO2 on an artificial grassland community: Competition, invasion and neighbourhood growth. *Functional Ecology 10(2):157-166.*

1. We analysed the effect of CO2 enrichment on plant-plant interactions in an artificial community dominated by Trifolium repens and Poa pratensis. Plants were enriched either in open- tops or growth chambers. 2. Our main hypotheses were supported, i.e. elevated CO2 increased the strength and number of plant- plant interactions and Trifolium benefited more than Poa from a high CO2 concentration. However, responses differed depending on whether plants were enriched in open-top or in growth chambers. These differences are discussed regarding possible density dependence. 3. This study emphasizes the importance of invasions in the dynamics of our artificial community. Invasiveness was best predicted by traits pertaining to space acquisition. 4. To provide insights into evolutionary processes, phenotypic plasticity and genetic correlation of individual traits were analysed across environments. Our results suggest that little opportunity had occurred for adaptive plasticity to evolve for most characters.

KEYWORDS: ABILITY, EVOLUTIONARY-THEORY, PLANTS

2271

Stiling, P., A.M. Rossi, B. Hungate, P. Dijkstra, C.R. Hinkle, W.M. Knott, and B. Drake. 1999. Decreased leaf-miner abundance in elevated CO2: Reduced leaf quality and increased parasitoid attack. *Ecological Applications 9(1):240-244.*

Most studies on the effects of elevated CO2 have focused on the effects on plant growth and ecosystem processes. Fewer studies have examined the effects of elevated CO2 on herbivory, and of these, most have examined feeding rates in laboratory conditions. Our study takes advantage of an open-top CO2 fertilization study in a Florida scrub-oak community to examine the effects of elevated CO2 on herbivore densities, herbivore feedings rates, and levels of attack of herbivores by natural enemies. Higher atmospheric CO2 concentration reduced plant foliar nitrogen concentrations, decreased abundance of leaf- mining insect herbivores, increased per capita leaf consumption by leafminers, and increased leaf miner mortality. As suggested by other authors, reduced foliar quality contributed to the increase in herbivore mortality, but only partly. The major factor increasing mortality was higher attack rate by parasitoids. Thus increasing CO2 concentrations may reduce the survivorship of insect herbivores directly, by reducing plant quality, but also indirectly, by changing herbivore feeding and eliciting greater top-down pressure from natural enemies.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECIDUOUS TREES, DENSITY, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, PERFORMANCE, PHYTOCHEMISTRY, PLANTS, POPULATION

2272

Stirling, C.M., P.A. Davey, T.G. Williams, and S.P. Long. 1997. Acclimation of photosynthesis to elevated CO2 and temperature in five British native species of contrasting functional type. *Global Change Biology 3(3):237-246.*

Acclimation of photosynthesis to growth at elevated CO2 concentration varies markedly between species. Species functionally classified as stress-tolerators (S) and ruderals (R), are thought to be incapable, or the least capable, of responding positively in terms of growth to elevated [CO2]. Is this pattern of response also apparent in leaf photosynthesis of wild S- and R-strategists? Acclimatory loss of a photosynthetic and growth response to elevated [CO2] is assumed to reflect limitation on capacity to utilize additional photosynthate. The doubling of pre-industrial global [CO2] is expected to coincide with a 3 degrees C increase in mean temperature which could stimulate growth; will photosynthetic capacity at elevated [CO2] be greater when the concurrent temperature increase is simulated? Five species from natural grassland of NW Europe and of contrasting ecological strategy were grown in hemispherical greenhouses, environmentally controlled to track the external microclimate. Within a replicated design, plants were grown at (i) current ambient [CO2] and temperature, (ii) elevated [CO2] (ambient + 340 mu mol mol(-1)) and ambient temperature, (iii) ambient [CO2] and elevated temperature (ambient + 3 degrees C), or (iv) elevated [CO2] and elevated temperature. After 75-104 days, the CO2

response of light-saturated rates of photosynthesis (A(sat)) was analysed in controlled-environment cuvettes in a field laboratory. There was no acclimatory loss of photosynthetic capacity with growth in elevated [CO2] or elevated temperature over this period in Poa alpina (S), Bellis perennis (R) or Plantago lanceolata (mixed C-S-R strategist), and a significant (P < 0.05) increase in capacity in Helianthemum nummularium (S) and Poa annua (R). Photosynthetic rates of leaves grown and measured in elevated [CO2] were therefore significantly higher than rates for leaves grown and measured in ambient [CO2], for all species. With the exception of Poa alpina, stomatal conductance and stomatal limitation on A(sat) showed no acclimatory response to growth in elevated [CO2]. Carboxylation efficiency, determined from the initial slope of the response of A(sat) to intercellular CO2 concentration was significantly increased by elevated [CO2] and elevated temperature in H. nummularium, implying a possible increase in in vivo RubisCO activity. Increased carboxylation efficiency of this species was also reflected by an increase in the CO2- and light- saturated rates of photosynthesis, indicating an increased capacity for regeneration of the primary CO2 acceptor in photosynthesis. The results show that R-strategists and slow- growing S-strategists, are inherently capable of large increases in leaf photosynthetic capacity with growth in elevated [CO2] in contrast to expectations from growth studies. With the exception of P. annua, where there was a significant negative interaction between CO2 and temperature, concurrent increase in growth temperature had little effect on this pattern of response.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, EXPOSURE, GAS-EXCHANGE, GROWTH, PARTIAL-PRESSURE, PLANTS, RESPONSES

2273

Stirling, C.M., M. Heddell-Cowie, M.L. Jones, T.W. Ashenden, and T.H. Sparks. 1998. Effects of elevated CO2 and temperature on growth and allometry of five native fast-growing annual species. *New Phytologist 140(2):343-354.*

Whereas much is known of the short-term growth response to elevated atmospheric CO2 concentrations, [CO2](elev), there is relatively little information on how the response of native species is modified by temperature, despite the fact that an increase in global mean temperature is expected to accompany the rise in [CO2]. In this study, five functionally related annual native species were exposed to different combinations of ambient and elevated [CO2] and temperatures in order to assess their response in terms of growth and allometry. Fast-growing annuals were selected for the study because their growth responses could be assessed over a major portion of the plant's life cycle and in as short a period as 8 wk. Plants were grown in eight hemi-spherical glasshouses, programmed to track outside ambient conditions and provide a replicated experimental design. Treatments comprised (i) current ambient [CO2] and temperature, (ii) elevated [CO2] (ambient + 34 kPa), and ambient temperature (iii) ambient [CO2] and elevated temperature (ambient + 3 degrees C) and (iv) elevated [CO2] and elevated temperature (T degrees C-elev). All five species responded positively to [CO2](elev), although the response was statistically significant for only one, Poa annua L. Averaged over all five species, [CO2](elev) increased total plant biomass by 25 % (P = 0.005) at 56 d, reflecting a proportionally greater increase in leaf and stem mass relative to root weight. Elevated [CO2] had no effect on leaf area, either at the individual species level or overall. Elevated T degrees C, by contrast, had little effect on shoot growth but increased root mass on average by 43 % and leaf area by 22 %. Few interactions between elevated [CO2] and T degrees C were observed, with the CO2 response generally greater at elevated than ambient T degrees C. Both [CO2](elev) and T degrees C-elev resulted in a transient increase in relative growth rate, (RGR), during the first 14 d exposure and a 3 degrees C increase in temperature had no effect on the duration of the response. CO2 stimulation of growth operated through a sustained increase in net assimilation rate. (NAR), although the potential benefit to RGR was offset by a concurrent decline in leaf area ratio (LAR), as a result Of a decrease in leaf area per unit leaf mass (SLA). The response to T degrees C-elev was generally opposite of that to [CO2](elev). For example, T degrees C-elev increased LAR through an increase in SLA and this, rather than any effect on NAR, was the major factor responsible for the stimulation of RGR. Allometric analysis of CO2 effects revealed that changes in allocation observed at individual harvests were due solely to changes associated with plant size. Elevated T degrees C, by contrast, had a direct effect on allocation patterns to leaves, with an increase in leaf area expansion relative to whole plant mass during the initial stages of growth and subsequent increased allocation of biomass away from leaves to other regions of the plant. No change in the allometric relation between roots and shoots were observed at either elevated [CO2] or T degrees C. We conclude, therefore, that allocation of biomass and morphological characteristics such as SLA, are relatively insensitive to [CO2], at least when analysed at the whole-plant level, and where changes have been observed, these are the product of comparing plants of the same age but different size.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, ENRICHMENT, GRASSES, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RESPIRATION, RESPONSES, SINK

2274

Stitt, M. 1991. Rising CO2 levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment 14(8):741-762.*

In the first part of this review, I discuss how we can predict the direct short-term effect of enhanced CO2 on photosynthetic rate in C3 terrestrial plants. To do this, I consider: (1) to what extent enhanced CO2 Will stimulate or relieve demand on partial processes like carboxylation, light harvesting and electron transport, the Calvin cycle, and end-product synthesis; and (2) the extent to which these various processes actually control the rate of photosynthesis. I conclude that control is usually shared between Rubisco (which responds sensitively to CO2) and other components (which respond less sensitively), and that photosynthesis will be stimulated by 25- 75% when the CO2 concentration is doubled from 35 to 70 Pa. This is in good agreement with the published responses. In the next part of the review, I discuss the evidence that most plants undergo a gradual inhibition of photosynthesis during acclimation to enhanced CO2. I argue that this is related to an inadequate demand for carbohydrate in the remainder of the plant. Differences in the long-term response to CO2 may be explained by differences in the sink-source status of plants. depending upon the species, the developmental stage, and the developmental conditions. In the third part of the review, I consider the biochemical mechanisms which are involved in 'sink' regulation of photosynthesis. Accumulating carbohydrate could lead to a direct inhibition of photosynthesis, involving mechanical damage by large starch grains or Pi-limitation due to inhibition of sucrose synthesis. I argue that Pi is important in the short-term regulation of partitioning to sucrose and starch, but that its contribution to 'sink' regulation has not yet been conclusively demonstrated. Indirect or 'adaptive' regulation of photosynthesis is probably more important, involving decreases in amounts of key photosynthetic enzymes, including Rubisco. This decreases the rate of photosynthesis, and potentially would allow resources (e.g. amino acids) to be remobilized from the leaves and reinvested in sink growth to readjust the sink-source balance. In the final part of the review, I argue that similar changes of Rubisco and, possibly, other proteins are probably also involved during acclimation to high CO2.

KEYWORDS: CALVIN CYCLE ENZYMES, DRY-MATTER PRODUCTION, FLUX-CONTROL COEFFICIENTS, HIGH ATMOSPHERIC CO2, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE,

ROOTED SOYBEAN LEAVES, SOURCE SINK BALANCE, SUCROSE PHOSPHATE SYNTHASE

2275

Stitt, M., and A. Krapp. 1999. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant, Cell and Environment 22(6):583-621.*

This review first summarizes the numerous studies that have described the interaction between the nitrogen supply and the response of photosynthesis, metabolism and growth to elevated [CO2]. The initial stimulation of photosynthesis in elevated [CO2] is often followed by a decline of photosynthesis, that is typically accompanied by a decrease of ribulose-1,5- bisphosphate carboxylase/oxygenase (Rubisco), an accumulation of carbohydrate especially starch, and a decrease of the nitrogen concentration in the plant. These changes are particularly marked when the nitrogen supply is low, whereas when the nitrogen supply is adequate there is no acclimation of photosynthesis, no major decrease in the internal concentration of nitrogen or the levels of nitrogen metabolites, and growth is stimulated markedly. Second, emerging evidence is discussed that signals derived from nitrate and nitrogen metabolites such as glutamine act to regulate the expression of genes involved in nitrate and ammonium uptake and assimilation? organic acid synthesis and starch accumulation, to modulate the sugar-mediated repression of the expression of genes involved in photosynthesis, and to modulate whole plant events including shoot-root allocation, root architecture and flowering. Third, increased rates of growth in elevated [CO2] will require higher rates of inorganic nitrogen uptake and assimilation. Recent evidence is discussed that an increased supply of sugars can increase the rates of nitrate and ammonium uptake and assimilation, the synthesis of organic acid accepters, and the synthesis of amino acids. Fourth, interpretation of experiments in elevated [CO2] requires that the nitrogen status of the plants is monitored, The suitability of different criteria to assess the plant nitrogen status is critically discussed. Finally the review returns to experiments with elevated [CO2] and discusses the following topics: is, and if so how, are nitrate and ammonium uptake and metabolism stimulated in elevated [CO2], and does the result depend on the nitrogen supply? Is acclimation of photosynthesis the result of sugar- mediated repression of gene expression, end-product feedback of photosynthesis, nitrogen-induced senescence, or ontogenetic drift? Is the accumulation of starch a passive response to increased carbohydrate formation, or is it triggered by changes in the nutrient status? How do changes in sugar production and inorganic nitrogen assimilation interact in different conditions and at different stages of the life history to determine the response of whole plant growth and allocation to elevated [CO2]?

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, ARABIDOPSIS-THALIANA L, ATMOSPHERIC CO2 ENRICHMENT, CALVIN CYCLE ENZYMES, DEPENDENT GLUTAMATE SYNTHASE, NITRATE REDUCTASE-ACTIVITY, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE PHOSPHATE SYNTHASE, TRANSGENIC TOBACCO PLANTS

2276

Stitt, M., W.P. Quick, U. Schurr, E.D. Schulze, S.R. Rodermel, and L. Bogorad. 1991. Decreased ribulose-1,5-bisphosphate carboxylase-oxygenase in transgenic tobacco transformed with antisense rbcs .2. Flux- control coefficients for photosynthesis in varying light, CO2, and air humidity. *Planta 183(4):555-566.*

Transgenic tobacco (Nicotiana tabacum L.) plants transformed with 'antisense' rbcS to produce a series of plants with a progressive decrease in the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) have been used to investigate the contribution of Rubsico to the control of photosynthesis at different irradiance, CO2 concentrations and vapour-pressure deficits. Assimilation rates, transpiration, the internal CO2 concentration and chlorophyll fluorescence were measured in each plant. (i) The flux-control coefficient of Rubisco was estimated from the slope of the plot of Rubisco content versus assimilation rate. The flux-control coefficient had a value of 0.8 or more in high irradiance, (1050 mumol m-2 s-1), low-vapour pressure deficit (4 mbar) and ambient CO2 (350-mu-bar). Control was marginal in enhanced CO2 (450-mu-bar) or low light (310 mumol m-2 s-1) and was also decreased at high vapour- pressure deficit (17 mbar). No control was exerted in 5% CO2. (ii) The flux-control coefficients of Rubisco were compared with the fractional demand placed on the calculated available Rubisco capacity. Only a marginal control on photosynthetic flux is exerted by Rubisco until over 50% of the available capacity is being used. Control increases as utilisation rises to 80%, and approaches unity (i.e. strict limitation) when more than 80% of the available capacity is being used. (iii) In low light, plants with reduced Rubisco have very high energy-dependent quenching of chlorophyll fluorescence (qE) and a decreased apparent quantum yield. It is argued that Rubisco still exerts marginal control in these conditions because decreased Rubisco leads to increased thylakoid energisation and high-energy dependent dissipation of light energy, and lower light-harvesting efficiency. (iv) The flux-control coefficient of stomata for photosynthesis was calculated from the flux-control coefficient of Rubisco and the internal CO2 concentration, by applying the connectivity theorem. Control by the stomata varies between zero and about 0.25. It is increased by increased irradiance, decreased CO2 or decreased vapour-pressure deficit. (v) Photosynthetic oscillations in saturating irradiance and CO2 are suppressed in decreased- activity transformants before the steady-state rate of photosynthesis is affected. This provides direct evidence that these oscillations reveal the presence of "excess" Rubisco. (vi) Comparison of the flux-control coefficients of Rubisco with mechanistic models of photosynthesis provides direct support for the reliability of these models in conditions where Rubisco has a flux-control coefficient approach unity (i.e. "limits" photosynthesis), but also indicates that these models are less useful in conditions where control is shared between Rubisco and other components of the photosynthetic apparatus.

KEYWORDS: C-3 PLANTS, FIXATION, LEAVES, LIMITATIONS, METABOLISM, NITROGEN, PHOSPHATE

2277

Stocker, R., C. Korner, B. Schmid, P.A. Niklaus, and P.W. Leadley. 1999. A field study of the effects of elevated CO2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology 5(1):95-105.*

The relationship between plant species diversity and ecosystem CO2 and water vapour fluxes was investigated for planted calcareous grassland communities composed of 5, 12, or 32 species assembled from the native plant species pool. These diversity manipulations were done in factorial combination with a CO2 enrichment experiment in order to investigate the degree to which ecosystem responses to elevated CO2 are altered by a loss of plant diversity. Ecosystem CO2 and H2O fluxes were measured over several 24-h periods during the 1994 and 1995 growing seasons. Ecosystem CO2 assimilation on a ground area basis decreased with decreasing plant diversity in the first year and this was related to a decline in above-ground plant biomass. In the second year, however, CO2 assimilation was not affected by diversity, and this corresponded to the disappearance of a diversity effect on above-ground biomass. Irrespective of diversity treatment, CO2 assimilation on a ground area basis was linearly related to peak aboveground biomass in both years. Elevated CO2 significantly increased ecosystem CO2 assimilation in both years with no interaction between diversity and CO2 treatment, and no corresponding increase in above-ground biomass. There were no significant effects of diversity on water vapour nux, which was measured only in the second year. There were indications of a small CO2 effect on

water vapour flux (3-9% lower at elevated CO2 depending on the light level). Our findings suggest that decreasing plant species diversity may substantially decrease ecosystem CO2 assimilation during the establishment of such planted calcareous grassland communities, but also suggest that this effect may not persist. In addition, we find no evidence that plant species diversity alters the response of ecosystem CO2 assimilation to elevated CO2.

KEYWORDS: ALTER, BIODIVERSITY, CARBON, ECOLOGY, PERFORMANCE, PRODUCTIVITY, STOMATAL RESPONSES, TRANSPIRATION

2278

Stocker, R., P.W. Leadley, and C. Korner. 1997. Carbon and water fluxes in a calcareous grassland under elevated CO2. *Functional Ecology 11(2):222-230.*

1. As part of a long-term study of the effects of elevated CO2 on biodiversity and ecosystem function in a calcareous grassland, we measured ecosystem carbon dioxide and water- vapour fluxes over 24-h periods during the 1994 and 1995 growing seasons. Data were used to derive CO2 and H2O gas- exchange response functions to quantum flux density (QFD). 2. The relative increase in net ecosystem CO2 flux (NEC) owing to CO2 enrichment increased as QFD rose. Daytime NEC at high QFD under elevated CO2 increased by 25% to 60%, with the greatest increases in the spring and after mowing in June when above-ground biomass was lowest. There was much less stimulation of NEC in early June and again in October when the canopy was fully developed. Night-time NEC was not significantly altered under elevated CO2. 3. Short-term reversal of CO2 concentrations between treatments after two seasons of CO2 exposure provided evidence for a 50% downward adjustment of NEC expressed per unit above-ground plant dry weight. However, when expressed on a land area basis, this difference disappeared because of a c. 20% increase in above-ground biomass under elevated CO2. 4. Ecosystem evapotranspiration (ET) was not significantly altered by elevated CO2 when averaged over all measurement dates and positions. However, ET was reduced 3-18% at high QFD in plots at the top of the slope at our study site. In summary, CO2 enrichment resulted in a large stimulation of ecosystem CO2 capture, especially during periods of a large demand of carbon in relationship to its supply, and resulted in a relatively small and variable effect on ecosystem water consumption.

KEYWORDS: ATMOSPHERIC CO2, CARBOXYLASE ACTIVITY, DIOXIDE, GAS-EXCHANGE, GROWTH, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANT, RISING CO2, TUSSOCK TUNDRA

2279

Stocklin, J., and C. Korner. 1999. Interactive effects of elevated CO2, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. *Functional Ecology 13(2):200-209.*

1, We investigated the interactive effects of elevated CO2, supply of phosphorus (P) and legume presence in model communities of calcareous grassland. Half of the communities contained six graminoids and eight nan-legume forb species, In the other half, four non-legume forbs were replaced by legumes. 2, Ecosystem responses. Above-ground phytomass (>5 cm) hardly responded to elevated CO2 alone. However, when P and legumes were combined. the CO2 effect on above-ground community phytomass in year two was a stimulation of 45% (P < 0.001). Below-ground community dry matter was stimulated by elevated CO2 alone by + 36% (P < 0.01), but was only + 20% (P < 0.05) when legumes were present and P was added, At the final (late season) harvest the mean effect of elevated CO2 on total above- and below-ground phytomass was + 23% (P < 0.001) and revealed no significant interactions among treatment combinations, because above- and belowground effects of CO2 enrichment had opposite directions. 3, Functional group responses. When legumes were absent, graminoids increased their total above- and below-ground phytomass in elevated CO2 by 60% (P < 0.001) but there was no increase when legumes were present. The response of forbs to CO2 was nor significant, irrespective of co-treatment. Legumes. however, were significantly stimulated by P supply and their CO2 response was much larger when P was added (+ 55%, P < 0.01 vs + 25%, NS). 4, Species responses. CO2 effects on species ranged from highly positive (+ 143%) to moderately negative (- 43%). 5, Our results demonstrate that the effect of CO2 enrichment in such natural grassland communities will be low on above-ground phytomass and largely below-ground if no additional nutrients are provided. N-2- fixing legumes appear to be crucial for the community response to elevated CO2 but legume responsiveness is largely controlled by P availability.

KEYWORDS: CARBON BALANCE, CHALK GRASSLAND, GROWTH-RESPONSE, LEVEL RESPONSES, LOLIUM-PERENNE L, NITROGEN-FIXATION, OLD-FIELD MICROCOSMS, PLANTS, STOMATAL RESPONSES, TRIFOLIUM-REPENS L

2280

Stocklin, J., P.W. Leadley, and C. Korner. 1997. Community and species level responses to elevate CO2 in designed calcareous grassland communities. *Acta Oecologica-International Journal of Ecology 18(3):241-248.*

We present a synthesis of two independent glasshouse experiments in which we investigated the short term response of model communities of calcareous grassland species to CO2- enrichment. Communities consisted of six species in the first study and of 14 species in-the second study. Communities were grown in containers filled with ca. 20 liters of natural soil. Total aboveground biomass production was increased by 14% (n.s., p=0.21) in the first study and by 8.5% (p=0.03) in the second study. This community level response was due to a significant stimulation of growth in 2 and 5 species, respectively. In each of the experiments, one species responded negatively to CO2-enrichment. The remaining species, including all legumes, remained unaffected by CO2-enrichment. Positive or negative responding species did not belong to specific functional groups, hence responses could not have been predicted from a priori knowledge of individual plant traits. Bromus erectus, which is the dominant species in calcareous grasslands of the Jura mountains, did not exhibit a CO2- response at the species level, but genotype-specific responses in this species varied significantly and included positive as well as negative responses. No such genotypic differentiation of CO2-response was observed in Fes tuca ovina. In the long term, we expect directional selection of positively responding genotypes and shifts in species composition to alter both population and community structure of calcareous grass lands - a conclusion that may also hold for other diverse plant communities.

KEYWORDS: ABANDONMENT, GROWTH, UNFERTILIZED MOWN MEADOWS

2281

Stocklin, J., K. Schweizer, and C. Korner. 1998. Effects of elevated CO2 and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. *Oecologia 116(1-2):50-56.*

We investigated the effects of elevated CO2 (600 mu l 1(-1) vs 350 mu l 1(-1)) and phosphorus supply (1 g P m(-2) year(-1) vs unfertilized) on intact monoliths from species-rich calcareous grassland in a greenhouse. Aboveground community dry mass remained almost unaffected by elevated CO2 in the first year(+ 6%, n.s.), but was significantly stimulated by CO2 enrichment in year two (+26%. P<0.01). Among

functional groups, only graminoids contributed significantly to this increase. The effect of phosphorus alone on community biomass was small in both years and marginally significant only when analyzed with MANOVA (+6% in year one, +9% in year two, 0.1 greater than or equal to P > 0.05). Belowground biomass and stubble after two seasons were not different in elevated CO2 and when P was added. The small initial increase in aboveground community biomass under elevated CO2 is explained by the fact that some species, in particular Carex flacca, responded very positively right from the beginning, while others, especially the dominant Bromus erectus, responded negatively to CO2 enrichment. Shifts in community composition towards more responsive species explain the much larger CO2 response in the second year. These shifts, i.e., a decline in xerophytic elements (B. erectus) and an increase in mesophytic grasses and legumes occurred independently of treatments in all monoliths but were accelerated significantly by elevated CO2. The difference in average biomass production at elevated compared to ambient CO2 was higher when P was supplied (at the community level the CO2 response was enhanced from 20% to 33% when P was added, in graminoids from 17% to 27%, in legumes from 4% to 60%? and in C. flacca from 120% to 298% by year two). Based on observations in this and similar studies, we suggest that interactions between CO2 concentration, species presence, and nutrient availability will govern community responses to elevated CO2.

KEYWORDS: BIOMASS, CHALK GRASSLAND, ECOSYSTEMS, ENRICHMENT, GROWTH, LEVEL RESPONSES, PLANTS

2282

Stoffella, P.J., Y.C. Li, R.R. Pelosi, and A.M. Hamner. 1995. Citrus rootstock and carbon-dioxide enriched irrigation influence on seedling emergence, growth, and nutrient content. *Journal of Plant Nutrition 18(7):1439-1448.*

Seeds of Carrizo citrange (Citrus senensis (L.) Osb. X Poncirus trifolliata (L.), Cleopatra mandarin (C. reticulata Bianco), Sour orange (C. aurantium L.), and Rough lemon (C. limon (Burm f.) were sown in trays, irrigated without or with enriched Carbon dioxide (CO2) (1,362 mg L(-1)) and evaluated for seedling emergence, growth, and nutrient contents. Rough lemon had a faster rate and higher percent emergence than the other rootstocks. Carrizo citrange had thicker stem diameters and taller seedlings than other rootstocks. Cleopatra mandarin had the smallest seedling shoot and root weights and larger shoot:root ratios than Rough lemon and Sour orange. Carrizo citrange and Cleopatra mandarin had higher leaf chlorophyll-a and total chlorophyll content than Rough lemon or Sour orange. Carbon dioxide enriched irrigation had no effects on emergence or seedling growth variables except lower root weight. Lower media pH (6.90 versus 5.65), attributed to CO2 enriched irrigation, may have adversely affected root growth as compared to shoot characteristics. Leaf nutrient contents generally differed between rootstocks but were not affected by CO2 enriched water except for higher Zn and lower Mn contents. These results indicate that citrus seedling emergence, subsequent growth and leaf nutrient content differred between rootstocks but there are no beneficial effect from CO2 enriched irrigation.

KEYWORDS: CO2, FIELD, ROOT ZONE, TOMATO, WATER

2283

Storlie, C.A., and J.R. Heckman. 1996. Bell pepper yield response to carbonated irrigation water. *Journal of Plant Nutrition 19(10-11):1477-1484.*

Field studies were conducted to determine the influence of carbonated irrigation water on bell pepper (Capsicum annuum L.) yield, plant nutrient status, canopy carbon dioxide (CO2) concentration, and soil pH. Marketable yield, early yield, marketable fruit size distribution, and plant nutrient status were unaffected by carbonated irrigation water. Air CO2 concentration in the lowest portion of the canopy increased during irrigation events, but returned to the ambient CO2 concentration shortly after irrigation ceased. The effect of carbonated irrigation water on soil pH was marginal and unpredictable.

KEYWORDS: CO2, DIOXIDE ENRICHMENT, FIELD, FIXATION, GROWTH, POTATO PLANTS, ROOT ZONE, TOMATO

2284

Strain, B.R., and R.B. Thomas. 1992. Field-measurements of co2 enhancement and climate change in natural vegetation. *Water, Air, and Soil Pollution 64(1-2):45-60.*

It is generally assumed that healthy, natural ecosystems have the potential to sequester carbon under favorable environmental conditions. There is also evidence that CO2 acts as a plant fertilizer. It is of interest to know if these assumptions are valid and how natural systems might respond under future scenarios of CO2 increase and possible climate changes. Few measurements of the effects of CO2 and global climate change have been made on "natural" ecosystems under realistic field conditions. Most measurements have been conducted in the synthetic environments of totally controlled greenhouses and growth chambers. Several lines of evidence indicate that controlled environment studies using plants growing in pots induce experimental artifacts that reduce confidence in the use of results for prediction of future global responses. Open top chambers are being used in several autecological field studies in an attempt to obtain more realistic field environments. A few field microcosm studies have been completed and a system for the free air release of CO2 has been applied in cotton fields. Unfortunately, the requirement of large amounts of CO2 and financial restrictions have precluded the initiation of larger scale field studies in natural vegetation. This paper lists and summarizes the best field studies available but draws heavily on studies from artificial environments and conditions in an attempt to summarize knowledge of global environmental change on forests and other non-agricultural ecosystems. Finally the paper concludes that there is a need for the development and application of equipment for field measurements in several representative natural ecosystems and makes specific recommendation of the creation of a tropical research center.

KEYWORDS: ALASKAN TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ELEVATED CO2, ESTUARINE MARSH, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, PINUS-TAEDA SEEDLINGS, TUSSOCK TUNDRA, WATER-STRESS

2285

Strand, M., D.A. Herms, M.P. Ayres, M.E. Kubiske, M.G. Kaufman, E.D. Walker, K.S. Pregitzer, and R.W. Merritt. 1999. Effects of atmospheric CO2, light availability and tree species on the quality of leaf detritus as a resource for treehole mosquitoes. *Oikos 84(2):277-283.*

Elevated CO2 could alter the productivity of heterotrophic aquatic ecosystems through effects on allochthonous litter inputs. The effects of atmospheric CO2 concentration, light availability to trees and tree species, on leaf detritus quality as a food resource for eastern treehole mosquitoes (Aedes triseriatus) were examined. Larvae were reared in laboratory microcosms (simulated treeholes) with naturally- senesced, abscised foliage from seedlings of red oak (Quercus rubra) and paper birch (Betula papyrifera) grown in ambient and elevated atmospheric CO2 environments. Elevated CO2 did not have significant effects on any measure of mosquito performance. In contrast, host species and light availability had dramatic effects on mosquito development time and survival; light availability had additional effects on adult size. Mosquito reproductive potential (+/- SE) averaged 8.4 +/- 1.5 females female(-1)

generation(-1) when litter input was from birch-sun leaves, but was 19.6 +/- 1.8 when the litter was from birch-shade leaves and 13.0 +/- 1.8 when from oak-sun leaves. Mosquito development time was nearly halved when the litter input was from oak-sun leaves versus birch-sun leaves, suggesting a potential for even greater demographic effects (e.g. two generations per year instead of one could yield a 20- fold increase in annual growth rate). Trophic transfer rates (mg insect detritivore g litter(-1) d(-1)) were 3-fold greater on birch-shade leaves than on birch-sun leaves. Changes in insolation and tree species composition can have important consequences for forest ecosystems, because of effects on litter quality that impact microbial saprobes and, ultimately, invertebrate detritivores.

KEYWORDS: AEDES-TRISERIATUS DIPTERA, BETULA-PENDULA ROTH, CARBON NUTRIENT BALANCE, CONDENSED TANNINS, DECOMPOSITION RATES, ELEVATED CO2, HOLE ECOSYSTEMS, LITTER QUALITY, SECONDARY METABOLITES, TERRESTRIAL ECOSYSTEMS

2286

Street-Perrott, F.A., Y.S. Huang, R.A. Perrott, G. Eglinton, P. Barker, L. BenKhelifa, D.D. Harkness, and D.O. Olago. 1997. Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science 278(5342):1422-1426.*

Carbon-isotope values of bulk organic matter from high-altitude lakes on Mount Kenya and Mount Elgon, East Africa, were 10 to 14 per mil higher during glacial times than they are today. Compound-specific isotope analyses of leaf waxes and algal biomarkers show that organisms possessing CO2-concentrating mechanisms, including C-4 grasses and freshwater algae, were primarily responsible for this large increase. Carbon limitation due to lower ambient CO2 partial pressures had a significant impact on the distribution of forest on the tropical mountains, in addition to climate. Hence, tree line elevation should not be used to infer palaeotemperatures.

KEYWORDS: CO2, HYDROCARBONS, ICE CORE, ISOTOPE FRACTIONATION, ORGANIC-MATTER, PHYTOPLANKTON, PLANTS, QUATERNARY, SACRED-LAKE, SEDIMENTS

2287

Stronach, I.M., S.C. Clifford, A.D. Mohamed, P.R. Singletonjones, S.N. Azamali, and N.M.J. Crout. 1994. The effects of elevated carbon-dioxide, temperature and soil- moisture on the water-use of stands of groundnut (arachis- hypogaea L). *Journal of Experimental Botany 45(280):1633-1638.*

Stands of groundnut (Arachis hypogaea L. cv. Kadiri 3) were grown in controlled environment glasshouses at two mean air temperatures (28 degrees C and 32 degrees C), two atmospheric CO2 concentrations (375 ppmv and 700 ppmv) and two soil moisture treatments (irrigated weekly to field capacity or allowed to dry from 22 d after sowing). The transpiration equivalent, Omega(W) (g kPa kg(-1))-the product of the accumulated biomass/transpired water ratio and the saturation deficit-was calculated for all the treatments using aboveground harvest, root core and neutron probe measurements. Neither temperature nor soil moisture treatment was found to have an effect on Omega(W). Increased CO2 concentration raised Omega(W) from 6.21 +/- 0.30 to 7.67 +/- 0.29 g kPa kg(-1), an increase of 24% (P < 0.005). The importance of accounting for root material and pod composition when calculating Omega(W) was highlighted.

KEYWORDS: CO2, CROPS, USE EFFICIENCY

2288

Stryiewski, E.C., and D.A. Vieglais. 1995. Changes in leaf structure of 3 native florida plant-species grown in elevated co2 concentrations. *Plant Physiology 108(2):63.*

2289

Stuhlfauth, T., and H.P. Fock. 1990. Effect of whole season CO2 enrichment on the cultivation of a medicinal plant, digitalis-lanata. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 164(3):168-173.*

2290

Stulen, I., and J. Denhertog. 1993. Root-growth and functioning under atmospheric co2 enrichment. *Vegetatio 104:99-115.*

This paper examines the extent to which atmospheric CO2 enrichment may influence growth of plant roots and function in terms of uptake of water and nutrients, and carbon allocation towards symbionts. It is concluded that changes in dry matter allocation greatly depend on the experimental conditions during the experiment, the growth phase of the plant, and its morphological characteristics. Under non-limiting conditions of water and nutrients for growth, dry matter partitioning to the root is not changed by CO2 enrichment. The increase in root/shoot ratio, frequently observed under limiting conditions of water and/or nutrients, enables the plant to explore a greater soil volume, and hence acquire more water and nutrients. However, more data on changes in dry matter allocation within the root due to atmospheric CO2 are needed. It is concluded that nitrogen fixation is favored by CO2 enrichment since nodule mass is increased, concomitant with an increase in root length. The papers available so far on the influence of CO2 enrichment on mycorrhizal functioning suggest that carbon allocation to the roots might be increased, but also here more experiments are needed.

KEYWORDS: CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, NUTRIENT CONCENTRATION, PINUS-TAEDA SEEDLINGS, PISUM-SATIVUM, PLANT GROWTH, SOYBEAN PLANTS, WATER-STRESS

2291

Stutte, G.W., N.C. Yorio, and R.M. Wheeler. 1996. Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *Journal of the American Society for Horticultural Science 121(2):264-268.*

The effect of photoperiod (PP) on net carbon assimilation rate (A(net)) and starch accumulation in newly mature canopy leaves of 'Norland) potato (Solanum tuberosum L.) was determined under high (412 proportional to mol .(m-)2 . s(-1)) and low (263 proportional to mol . m(-2). s(-1)) photosynthetic photon flux (PPF) conditions. The A(net) decreased from 13.9 to 11.6 and 9.3 mu mol . m(-2). s(-1), and leaf starch increased from 70 to 129 and 118 mg . g(-1) drymass (DM) as photoperiod (PP) was increased from 12/12 to 18/6, and 24/0, respectively. Longer PP had a greater effect with high PPF conditions than with low PPF treatments, with high PPF showing greater decline in A(net). Photoperiod did not affect either the CO2 compensation point (50 mu mol . mol(-1)) or CO2 saturation point (1100-1200 mu mol . mol(-1)) for A(net). These results show an apparent limit to the amount of starch that can be stored (approximate to 15% DM) in potato leaves. An apparent feedback mechanism exists for regulating A(net) under high PPF, high CO2 and long PP, but there was no correlation between A(net) and starch concentration in individual leaves. This suggests that maximum A(net) cannot be sustained with elevated CO2 conditions under long PP (greater than or equal to 12 hours) and high PPF

conditions. If a physiological limit exists for the fixation and transport of carbon, then increasing photoperiod and light intensity under high CO2 conditions Is not the most appropriate means to maximize the yield of potatoes.

KEYWORDS: GROWTH, LIFE SUPPORT SYSTEMS, LIGHT, PLANTS, SOLANUM TUBEROSUM L, SPACE

2292

Sukumar, R., H.S. Suresh, and R. Ramesh. 1995. Climate change and its impact on tropical montane ecosystems in southern India. *Journal of Biogeography 22(2-3):533-536.*

The montane regions (>2000 m MSL) of the Western Ghats in southern India feature stunted evergreen forests (C3 plant type) interspersed with extensive grasslands (C3 or C4 plant types). We have studied the vegetational history of this ecosystem in relation to climate change during the late Quaternary through stable-carbon isotope analysis of peat deposits as indicators of C3 or C4 plant types. Grasslands (of C4 type) were predominant during the last glacial maximum (20- 18 kyr sp) and again during 6-3.5 kyr sp, while forest and possibly C3 grassland expanded during the deglaciation, attaining their peak distribution at 10 kyr sp. The shift in C3 and C4 plant types seems related to changes in moisture and atmospheric CO2, with lower moisture and CO2 levels favouring the latter plant types. The oscillating climate and vegetation has influenced the structure and composition of the montane ecosystem. Plant diversity of the near-pristine montane forests is relatively lower than other comparable sites in the neotropics. The implications of global change on the tropical montane ecosystem, in particular the composition of the angiosperm and vertebrate communities, are discussed. In particular, an expansion of montane forest and replacement of C4 with C3 grassland can be expected. Human impact on the natural vegetation, such as conversion of grasslands to monoculture plantations of wattle and eucalypts may, however, interfere with natural succession caused by global climate change. Endemic mammals such as the Nilgiri tahr would face increased risk of extinction.

KEYWORDS: ICE-AGE, ISOTOPE EVIDENCE, KENYA, POLLEN, RECORD

2293

Sullivan, J.H. 1997. Effects of increasing UV-B radiation and atmospheric CO2 on photosynthesis and growth: Implications for terrestrial ecosystems. *Plant Ecology 128(1-2):194-206.*

Increases in UV-B radiation reaching the earth as a result of stratospheric ozone depletion will most likely accompany increases in atmospheric CO2 concentrations. Many studies have examined the effects of each factor independently, but few have evaluated the combined effects of both UV-B radiation and elevated CO2. In general the results of such studies have shown independent effects on growth or seed yield. Although interspecific variation is large, high levels of UV-B radiation tends to reduce plant growth in sensitive species, while CO2 enrichment tends to promote growth in most C-3 species. However, most previous studies have not looked at temporal effects or at the relationship between photosynthetic acclimation to CO2 and possible photosynthetic limitations imposed by UV-B radiation. Elevated CO2 may provide some protection against UV-B for some species. In contrast, UV-B radiation may limit the ability to exploit elevated CO2 in other species. Interactions between the effects of CO2 enrichment and UV-B radiation exposure have also been shown for biomass allocation. Effects on both biomass allocation and photosynthetic acclimation may be important to ecosystem structure in terms of seedling establishment, competition and reproductive output. Few studies have evaluated ecosystem processes such as decomposition or nutrient cycling. Interactive effects may be subtle and species specific but should not be ignored in the assessment of the potential impacts of increases in CO2 and W-B radiation on plants.

KEYWORDS: BARLEY PRIMARY LEAVES, ELEVATED CARBON-DIOXIDE, HERBIVORE INTERACTIONS, LEAF EXPANSION, LIQUIDAMBAR- STYRACIFLUA, OZONE DEPLETION, PHOTON FLUX- DENSITY, PINUS-TAEDA SEEDLINGS, PLANT COMPETITION, SCIRPUS- OLNEYI

2294

Sullivan, J.H., and A.H. Teramura. 1994. The effects of uv-b radiation on loblolly-pine .3. Interaction with co2 enhancement. *Plant, Cell and Environment 17(3):311-317.*

Projected depletions in the stratospheric ozone layer will result in increases in solar ultraviolet-B radiation (290- 320nm) reaching the earth's surface, These increases will likely occur in concert with other environmental changes such as increases in atmospheric carbon dioxide concentrations. Currently very little information is available on the effectiveness of UV-B radiation within a CO2-enriched atmosphere, and this is especially true for trees. Loblolly pine (Pinus taeda L.) seedlings were grown in a factorial experiment at the Duke University Phytotron with either 0, 8.8 or 13.8 kJ m(-2) of biologically effective UV-B radiation (UV- B-BE) The CO2 concentrations used were 350 and 650 mu mol mol(- 1). Measurements of chlorophyll fluorescence were made at 5- week intervals and photosynthetic oxygen evolution and leaf pigments were measured after 22 weeks, prior to harvest. The results of this study demonstrated a clear growth response to CO2 enrichment but neither photosynthetic capacity nor quantum efficiency were altered by CO2. The higher UV-B irradiance reduced total biomass by about 12% at both CO2 levels but biomass partitioning was altered by the interaction of CO2 and UV-B radiation. Dry matter was preferentially allocated to shoot components by UV-B radiation at 350 mu mol mol(-1) CO2 and towards root components at 650 mu mol mol(-1) CO2. These subtle effects on biomass allocation could be important in the future to seedling establishment and competitive interactions in natural as well as agricultural communities.

KEYWORDS: COMPETITION, ENRICHMENT, GROWN SEEDLINGS, HIGHER-PLANTS, IRRADIANCE, LIQUIDAMBAR- STYRACIFLUA, PHOTOSYNTHESIS, TAEDA SEEDLINGS, ULTRAVIOLET-B, VISIBLE-LIGHT

2295

Sultemeyer, D. 1997. Changes in the CO2 concentrating mechanism during the cell cycle in Dunaliella tertiolecta. *Botanica Acta 110(1):55-61.*

Synchronised cells of Dunaliella tertiolecta were used to investigate the expression of the CO2 concentrating mechanism over the cell cycle during growth in either ambient air (low Ci cells) or air enriched with 5% CO2 (high Ci cells). The cultures were analysed for extracellular carbonic anhydrase activity, affinity of photosynthesis for inorganic carbon (Ci) and the ability to accumulate Ci. In high Ci cells, carbonic anhydrase activity changed between 2-4 units mg(-1) Chl during the light-dark rhythm showing no clear periodicity. Similarly, the apparent affinity for Ci remained rather constant over the cell cycle. This was judged from the Ci concentrations required for half maximum rate of photosynthesis (K-1/2(Ci)) of 72-80 mu M. In the same cells the accumulation ratio of internal Ci versus external Ci ranged between 5 and 9.5 without a clear rhythm. In contrast, these parameters showed distinct periodical changes in synchronised low Ci cells. Carbonic anhydrase activity changed from 10 to 350 units mg(-1) Chl with maximum and minimum activities occurring in the middle and at the end of the light period, respectively. The K-1/2(Ci) values showed similar periodicity ranging between 13-36 mu M. In addition the

accumulation ratio increased up to 30 in the middle of illumination and decreased to its lowest level of 12 at the end of the light period. These results indicate the presence of a common step in regulating the induction of the measured parameters and that light is not an absolute requirement for the induction of the CO2 concentrating mechanism in synchronous low CO2 grown cells of Dunaliella tertiolecta.

KEYWORDS: ADAPTATION, BICARBONATE, CARBONIC-ANHYDRASE ACTIVITY, CARBOXYLASE, CHLAMYDOMONAS-REINHARDTII, CI CELLS, INDUCTION, INORGANIC CARBON, PHOTOSYNTHESIS, TRANSPORT

2296

Sultemeyer, D., and K.A. Rinast. 1996. The CO2 permeability of the plasma membrane of Chlamydomonas reinhardtii: Mass-spectrometric O-18-exchange measurements from (CO2)-C-13-O-18 in suspensions of carbonic anhydrase-loaded plasma-membrane vesicles. *Planta 200(3):358-368.*

The unicellular green alga Chlamydomonas reinhardtii possesses a CO2-concentrating mechanism. In order to measure the CO2 permeability coefficients of the plasma membranes (PMs), carbonic anhydrase (CA)-loaded vesicles were isolated from C. reinhardtii grown either in air enriched with 50 mL CO2 . L(-1) (high-C-i cells) or in ambient air (350 mu L CO2 . L(-1); low- C-i cells). Marker-enzyme measurements indicated less than 1% contamination with thylakoid and mitochondrial membranes, and that more than 90% of the PMs from high- and low-C-i cells were orientated right-side-out. The PMs appeared to be sealed as judged from the ability of vesicles to accumulate [C-14]acetate along a proton gradient for at least 10 min. Carbonic anhydrase-loaded PMs from high- and low-C-i cells of C. reinhardtii were used to measure the exchange of O-18 between doubly labelled CO2((CO2)-C-13-O-18) and H2O in stirred suspensions by mass spectrometry. Analysis of the kinetics of the O-18 depletion from (CO2)-C-13-O-18 in the external medium provides a powerful tool to study CO2 diffusion across the PM to the active site of CA which catalyses O-18 exchange only inside the vesicles but not in the external medium (Silverman et al., 1976, J Biol Chem 251: 4428-4435). The activity of CA within loaded PM vesicles was sufficient to speed-up the O-18 loss to H2O to 45360-128800 times the uncatalysed rate, depending on the efficiency of CA-loading and PM isolation. From the O-18-depletion kinetics performed at pH 7.3 and 7.8, CO2 permeability coefficients of 0.76 and 1.49 . 10(-3) cm . s(-1), respectively, were calculated for high- C-i cells. The corresponding values for low-C-i cells were 1.21 and 1.8 . 10(- 3)cm . s(-1). The implications of the similar and rather high CO2 permeability coefficients (low CO2 resistance) in high- and low-C-i cells for the CO2-concentrating mechanism of C. reinhardtii are discussed.

KEYWORDS: CHLOROPLASTS, CI CELLS, CONCENTRATING MECHANISM, CYANOBACTERIA, DIOXIDE, HCO3, IDENTIFICATION, INORGANIC CARBON, PHOTOSYNTHESIS, TRANSPORT

2297

Sulzman, E.W., K.A. Poiani, and T.G.F. Kittel. 1995. Modeling human-induced climatic-change - a summary for environmental managers. *Environmental Management 19(2):197-224.*

The rapid increase in atmospheric concentrations of greenhouse gases has caused concern because of their potential to alter the earth's radiation budget and disrupt current climate patterns. While there are many uncertainties associated with use of general circulation models (GCMs), GCMs are currently the best available technology to project changes in climate associated with elevated gas concentrations. Results indicate increases in global temperature and changes in global precipitation patterns are likely as a result of doubled CO2. GCMs are not reliable for use at the regional scale because local scale processes and geography are not taken into account. Comparison of results from five GCMs in three regions of the United States indicate high variability across regions and among models depending on season and climate variable. Statistical methods of scaling model output and nesting finer resolution models in global models are two techniques that may improve projections. Despite the many limitations in GCMs, they are useful tools to explore climate-earth system dynamics when used in conjunction with water resource and ecosystem models. A variety of water resource models showed significant alteration of regional hydrology when run with both GCM-generated and hypothetical climate scenarios, regardless of region or model complexity. Similarly, ecological models demonstrate the sensitivity of ecosystem production, nutrient dynamics, and distribution to changes in climate and CO2 levels. We recommend the use of GCM-based scenarios in conjunction with water resource and ecosystem models to guide environmental management and policy in a "no-regrets" framework or as part of a precautionary approach to natural resource protection.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, CHANGE IMPACTS, DELAWARE RIVER BASIN, ELEVATED CO2, GENERAL-CIRCULATION MODEL, GREAT-LAKES, THORNTHWAITE MOISTURE INDEX, TROPICAL DEFORESTATION, WATER-BALANCE

2298

Sun, J.D., G.E. Edwards, and T.W. Okita. 1999. Feedback inhibition of photosynthesis in rice measured by O-2 dependent transients. *Photosynthesis Research 59(2-3):187-200.*

The kinetic properties of photosynthesis (both transient and steady-state) were monitored using three non-invasive techniques to evaluate limitations on triose-phosphate (triose- P) conversion to carbohydrate in rice. These included analyzing the O-2 sensitivity of CO2 fixation and the assimilatory charge (AC) using gas exchange (estimate of the ribulose 1,5- bisphosphate pool) and measuring Photosystem II activity by chlorophyll fluorescence analysis under varying light, temperature and CO2 partial pressures. Photosynthesis was inhibited transiently upon switching from 20 to 2 kPa O-2 (reversed O-2 sensitivity), the degree of which was correlated with a terminal, steady-state suppression of low O-2 enhancement of photosynthesis. Under current ambient levels of CO2 and moderate to high light, the transient pattern was more obvious at 18 degrees C than at 26 degrees C while at 34 degrees C no transient response was observed. The transient inhibition at 18 degrees C ranged from 15% to 31% depending on the pre-measurement temperature. This pattern, symptomatic of feedback, was observed with increasing light and CO2 partial pressures with the degree of feedback decreasing from moderate (18 degrees C) up to high temperature (34 degrees C). Under feedback conditions, the rate of assimilation is shifted from being photorespiration limited to being triose-P utilization limited. Transitory changes in CO2 assimilation rates (A) under low O-2 indicative of feedback coincided with a transitory drop in assimilatory charge (AC) and inhibition of electron transport. In contrast to previous studies with many C-3 species, our studies indicate that rice shows susceptibility to feedback inhibition under moderate temperatures and current atmospheric levels of CO2.

KEYWORDS: CARBON METABOLISM, CHILLING INJURY, CHLOROPHYLL FLUORESCENCE, CO2 FIXATION, ELECTRON-TRANSPORT, LOW-TEMPERATURE, MATURE LEAVES, PHOTOSYSTEM, QUANTUM YIELD, VARIETAL DIFFERENCES

2299

Sung, F.J.M., and J.J. Chen. 1991. Gas-exchange rate and yield response of strawberry to carbon- dioxide enrichment. *Scientia Horticulturae 48(3-4):241-251.*

Short-term carbon dioxide (CO2) enrichment (1000-mu-l l-1 for 10 days), starting 2 weeks after initial bloom, enhanced the leaf CO2 exchange rate (CER) in rockwool-cultured strawberry (Fragaria x ananassa). CO2 enrichment throughout the fruiting period stimulated canopy CER, decreased chlorophyll and leaf protein loss, and enhanced fruit set and consequent fruit production.

KEYWORDS: ATMOSPHERES, ELEVATED CO2, GROWTH, PHOTOSYNTHESIS, PLANTS

2300

Suzuki, K. 1995. Phosphoglycolate phosphatase-deficient mutants of chlamydomonas-reinhardtii capable of growth under air. *Plant and Cell Physiology 36(1):95-100.*

Mutants deficient in phosphoglycolate phosphatase (PGPase) require elevated levels of CO2 for growth in the light and cannot grow when photorespiration occurs. Revertants, namely, double mutants capable of growth under air without restoration of the missing PGPase activity, might be expected to have secondary mutations that reduce or eliminate photorespiration. Nineteen revertants were selected from a culture of a PGPase- deficient mutant of Chlamydomonas reinhardtii (pgp-1-18-7F) after a second mutagenesis that involved treatment with 5-fluorodeoxyuridine and ethyl methanesulfonate. There were significant differences in the photosynthetic affinity for CO2 among revertant cells grown under 5% CO2. Eight revertants had five times higher photosynthetic affinity for CO2 than that of wild type 2137 cells grown under 5% CO2, resembling air-adapted wild-type cells, whereas four revertants had less than half the affinity for CO2 of the wild type. In all of the revertant cells with higher affinity grown in 5% CO2, the rates of photosynthesis under levels of CO2 below those in air were apparently higher than that of the wild type, whereas the rates under CO2-saturating conditions were lower than that of wild type, indicating that the efficiency of photosynthesis under air was significantly improved in these revertants. In addition, some revertants had a photosynthetic capacity and a growth rate higher than those of the wild type, without any increased photosynthetic affinity for CO2.

KEYWORDS: LIMITING CO2, PHOTORESPIRATORY MUTANT

2301

Suzuki, T., K. Ohtaguchi, and K. Koide. 1991. Effects of gas-flow rate of co2-enriched air, high co2 concentration, and anaerobic atmosphere on the growth of blue- green-alga anacystis-nidulans. *Journal of Chemical Engineering of Japan 24(6):797-798.*

2302

Svedang, M.U. 1992. Carbon-dioxide as a factor regulating the growth dynamics of juncus-bulbosus. *Aquatic Botany 42(3):231-240.*

The unusual growth pattern exhibited by Juncus bulbosus L. in a slightly acidic Swedish brown-water lake is due to a CO2 deficit. Decrease in growth rate during the summer can be avoided through CO2 addition in July when CO2 availability is low and epiphytes are thriving. Growth of J. bulbosus in the laboratory is stimulated by CO2 addition up to a concentration somewhat higher than in air (500 ppm). while higher CO2 pressure restrains growth. Root growth reflects the leaf biomass development, but is favoured by elevated CO2 levels even more than the leaves.

KEYWORDS: ACIDIFICATION, EUTROPHICATION, IMPACT, MACROPHYTE COMMUNITIES, PHOTOSYNTHESIS, PLANTS, SOFT WATERS

2303

Svensson, B.H., T.R. Christensen, E. Johansson, and M. Oquist. 1999. Interdecadal changes in CO2 and CH4 fluxes of a subarctic mire: Stordalen revisited after 20 years. *Oikos 85(1):22-30.*

The first subarctic wetland CO2 and CH4 Aux measurements were made at Stordalen in the beginning of the 1970s in connection with the IBP study. A return to this area in 1994-95 offered a unique opportunity to study possible interdecadal changes in northern wetland CO2 and CH4 emissions. Measurements of CO2 and CH4 fluxes were carried out in similar habitats as those investigated in 1974. The mire distribution of wet minerotrophic areas relative to the elevated ombrotrophic areas had changed dramatically over the twenty years. There were no significant differences between the CH4-flux in 1974. 1994, and 1995. However, the CO2 fluxes were significantly higher in 1995 than in 1974. Since differences in climatic conditions gave no cause for such a change it suggests a possible increase in decomposition rate to be due ro other factors. We suggest changes in vegetation composition, altered mineralization pathways and disintegration of permafrost as causes for the interdecadal increase in decomposition rates.

KEYWORDS: ALASKA, ARCTIC TUNDRA, CARBON DIOXIDE, CLIMATE CHANGE, METHANE EMISSIONS, PEAT, PEATLANDS, WETLANDS

2304

Swift, M.J., O. Andren, L. Brussaard, M. Briones, M.M. Couteaux, K. Ekschmitt, A. Kjoller, P. Loiseau, and P. Smith. 1998. Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies. *Global Change Biology 4(7):729-743.*

The relative contribution of different soil organism groups to nutrient cycling has been quantified for a number of ecosystems. Some functions, particularly within the N-cycle, are carried out by very specific organisms. Others, including those of decomposition and nutrient release from organic inputs are, however, mediated by a diverse group of bacteria, protozoa, fungi and invertebrate animals. Many authors have hypothesized that there is a high degree of equivalence and flexibility in function within this decomposer community and thence a substantial extent of redundancy in species richness and resilience in functional capacity. Three case studies are presented to examine the relationship between soil biodiversity and nitrogen cycling under global change in ecosystem types from three latitudes, i.e. tundra, temperate grassland and tropical rainforest. In all three ecosystems evidence exists for the potential impact of global change factors (temperature change, COP enrichment, land-use-change) on the composition and diversity of the soil community as well as on various aspects of the nitrogen and other cycles. There is, however, very little unequivocal evidence of direct causal linkage between species richness and nutrient cycling efficiency. Most of the changes detected are shifts in the influence of major functional groups of the soil biota (e.g. between microflora and fauna in decomposition). There seem to be few data, however, from which to judge the significance of changes in diversity within functional groups. Nonetheless the soil biota are hypothesized to be a sensitive link between plant detritus and the availability of nutrients to plant uptake. Any factors affecting the quantity or quality of plant detritus is likely to change this link. Rigorous experimentation on the relationships between soil species richness and the regulation or resilience of nutrient cycles under global change thus remains a high priority.

KEYWORDS: ATMOSPHERIC CO2, CARBON BALANCE, CO2-ENRICHMENT, COMMUNITY STRUCTURE, ELEVATED CO2, ENCHYTRAEIDAE OLIGOCHAETA, FERTILIZER APPLICATION, FOREST SOIL, MOWN GRASSLAND, TEMPERATE GRASS SWARD

2305

Sykes, M.T., I.C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography 23(2):203-233.*

A bioclimatic model based on physiological constraints to plant growth and regeneration is used here in an empirical way to describe the present natural distributions of northern Europe's major trees. Bioclimatic variables were computed from monthly means of temperature, precipitation and sunshine (%) interpolated to a 10' grid taking into account elevation. Minimum values of mean coldest-month temperature (T-c) and 'effective' growing degree days (GDD*) were fitted to species' range limits. GDD* is total annual growing degree days (GDD) minus GDD to budburst (GDD(o)). Each species was assigned to one of the chilling-response categories identified by Murray, Cannell & Smith (1989) to calculate GDD(o). Maximum T-c values were fitted to continental species' mild-winter limits and other deciduous species' warm-winter limits. Minimum values of relative growing-season moisture availability (alpha*) were estimated from silvics. Growth indices were calculated based on potential net assimilation (a quadratic in daily temperature) and alpha*. Growth can be rapid near a range limit, e.g. Picea abies (L.) Karsten in southern Sweden. Climate changes expected for CO2 doubling were projected on to the grid. Simulated distribution changes reflected interspecific differences in response to changing seasonality. Chilling responses proved important, e.g. the predicted range limit of Fagus sylvatica L. contracts in the west while expanding northwards as winters warm more than summers. Transient responses to climate change can be modelled using the same information provided that fundamental and realized niche limitations are distinguished-a caveat that underlines the dearth of experimental information on the climatic requirements for growth, and especially regeneration, of many important trees.

KEYWORDS: AMERICA, BUDBURST, FORESTS, FROST DAMAGE, PICEA-SITCHENSIS, RESPONSES, VEGETATION

2306

Syvertsen, J., and J.H. Graham. 1997. Carbon budgets of two Citrus sp. in response to elevated CO2 VA mycorrhizae and phosphorus status. *Plant Physiology 114(3):111.*

2307

Syvertsen, J.P., and J.H. Graham. 1999. Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two Citrus spp. grown at elevated [CO2]. *Plant and Soil 208(2):209-219.*

We hypothesized that greater photosynthate supply at elevated [CO2] could compensate for increased below-ground C demands of arbuscular mycorrhizas. Therefore, we investigated plant growth, mineral nutrition, starch, and net gas exchange responses of two Citrus spp. to phosphorus (P) nutrition and mycorrhizas at elevated atmospheric [CO2]. Half of the seedlings of sour orange (C. aurantium L.) and `Ridge Pineapple' sweet orange (C. sinensis L. Osbeck) were inoculated with the arbuscular mycorrhizal (AM) fungus, Glomus intraradices Schenck and Smith and half were non-mycorrhizal (NM). Plants were grown at ambient or 2X ambient [CO2] in unshaded greenhouses for 11 weeks and fertilized daily with nutrient solution either without added P or with 2 mM P in a low-P soil. High P supply reduced AM colonization whereas elevated [CO2] counteracted the depressive effect of P on intraradical colonization and vesicle development. Seedlings grown at either elevated [CO2], high P or with G. intraradices had greater growth, net assimilation of CO2 (A(CO2)) in leaves, leaf water-use efficiency, leaf dry wt/area, leaf starch and carbon/nitrogen (C/N) ratio. Root/whole plant dry wt ratio was decreased by elevated [CO2], P, and AM colonization. Mycorrhizal seedlings had higher leaf-P status but lower leaf N and K concentrations than nonmycorrhizal seedlings which was due to growth dilution effects. Starch in fibrous roots was increased by elevated [CO2] but reduced by G. intraradices, especially at low-P supply. In fibrous roots, elevated [CO2] had no effect on C/N, but AM colonization decreased C/N in both Citrus spp. grown at low-P supply. Overall, there were no species differences in growth or A(CO2). Mycorrhizas did not increase plant growth at ambient [CO2]. At elevated [CO2], however, mycorrhizas stimulated growth at both P levels in sour orange, the more mycorrhiza-dependent species, but only at low- P in sweet orange, the less dependent species. At low-P and elevated [CO2], colonization by the AM fungus increased A(CO2) in both species but more so in sour orange than in sweet orange. Leaf P and root N concentrations were increased more and root starch level was decreased less by AM in sour orange than in sweet orange. Thus, the additional [CO2] availability to mycorrhizal plants increased CO2 assimilation, growth and nutrient uptake over that of NM plants especially in sour orange under P limitation.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COLONIZATION, DEPENDENCY, ENRICHMENT, NITROGEN, PLANTAGO-LANCEOLATA, ROOT, SOUR ORANGE, TREES

2308

Szente, K., Z. Nagy, and Z. Tuba. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO2 concentration. *Photosynthetica 35(4):637-640.*

Net CO2 assimilation rate (P-N), Stomatal conductance (g(s)), transpiration rate (E), and water use efficiency (WUE) in four perennial C-3 species (grasses: Dactylis glomerata, Festuca rupicola, dicots: Filipendula vulgaris, Salvia nemorosa) grown for 231 d in open-top chambers at ambient (CA, 350 mu mol mol(- 1)) or elevated (CE, 700 mu mol mol(-1)) CO2 concentrations were compared. When measured at CE, PN was significantly higher in CE plants of all four species than in the CA ones. The increase in P-N was less prominent in the two grasses than in the two dicots. The E was significantly higher in the CE-grass F. rupicola and CE-dicot F. vulgaris than in the CA plants. There was no change in E owing to CE in the other grass and dicot. The g(s) in F. vulgaris and F. rupicola increased, while there was a decrease in D. glomerata and no change in S. nemorosa. WUE increased in all species grown in CE: four- to five-fold in the dicots and less than two-fold in the grasses. The increase in WUE was primarily due to an increase in P-N and not to a decrease in E.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, LONG-TERM, PHOTOSYNTHESIS, PLANTS, RESPONSES, STEPPE, STOMATAL CONDUCTANCE, TRANSPIRATION

2309

Tajiri, T. 1997. Studies on the cultivation and storage quality of bean sprouts .13. Growth and quality of thick bean sprouts cultivated with a CO2-enriched rotary method. *Journal of the Japanese Society for Food Science and Technology-Nippon Shokuhin Kagaku Kogaku Kaishi 44(4):332-339.*

Thick bean sprouts cultivated using a rotary box (rotary cultivation, RC) have a decreased yield and inferior quality, although the growth of sprouts from the beans is promoted and the nutrient content of the sprouts is improved(1)2)). Because exposure to high levels of carbon dioxide was useful for promoting the growth of the hypocotyl and increasing the quantity of harvested sprouts(3)), we combined the rotary box method with the CO2-enriched method(1)). Herein the usefulness of this combination method for improving the physical properties and the yield of bean sprouts by controlling hypocotyl growth were

examined.

2310

Takagi, M., K. Gyokusen, and A. Saito. 1998. Increase in the CO2 exchange rate of leaves of Ilex rotunda with elevated atmospheric CO2 concentration in an urban canyon. *International Journal of Biometeorology 42(1):16-21.*

It was found that the atmospheric carbon dioxide (CO2) concentration in an urban canyon in Fukuoka city, Japan during August 1997 was about 30 mu mol mol(-1) higher than that in the suburbs. When fully exposed to sunlight, in situ the rate of photosynthesis in single leaves of Ilex rotunda planted in the urban canyon was higher when the atmospheric CO2 concentration was elevated. A biochemically based model was able to predict the in situ rate of photosynthesis well. The model also predicted an increase in the daily CO2 exchange rate for leaves in the urban canyon with an increase in atmospheric CO2 concentration. However, in situ such an increase in the daily CO2 exchange rate may be offset by diminished sunlight, a higher air temperature and a lower relative humidity. Thus, the daily CO2 exchange rate predicted using the model based soleley on the environmental conditions prevailing in the urban canyon was lower than that predicted based only on environmental factors found in the suburbs.

KEYWORDS: BOUNDARY-LAYER, CANOPY PHOTOSYNTHESIS, CARBON DIOXIDE, CITY, CONDUCTANCE, LEAF PHOTOSYNTHESIS, MODEL, TEMPERATURE, TRANSPIRATION

2311

Takle, E.S., D.J. Bramer, W.E. Heilman, and M.R. Thompson. 1994. A synoptic climatology for forest-fires in the ne US and future implications from gcm simulations. *International Journal of Wildland Fire 4(4):217-224.*

We studied surface-pressure patterns corresponding to reduced precipitation, high evaporation potential, and enhanced forest- fire danger for West Virginia, which experienced extensive forest-fire damage in November 1987. From five years of daily weather maps we identified eight weather patterns that describe distinctive flow situations throughout the year. Map patterns labeled extended-high, back-of-high, and pre-high were the most frequently occurring patterns that accompany forest fires in West Virginia and the nearby four-stare region. Of these, back- of-high accounted for a disproportionately large amount of fire-related damage. Examination of evaporation acid precipitation data showed that these three patterns and high- to-the-south patterns ail led to drying conditions and all other patterns led to moistening conditions. Surface-pressure fields generated by the Canadian Climate Centre global circulation model for simulations of the present (1xCO(2)) climate and 2xCO(2) climate were studied to determine whether forest-fire potential would change under increased atmospheric CO2. The analysis showed a tendency for increased frequency of drying in the NE US, but the results were not statistically significant.

2312

Talbott, L.D., A. Srivastava, and E. Zeiger. 1996. Stomata from growth-chamber-grown Vicia faba have an enhanced sensitivity to CO2. *Plant, Cell and Environment 19(10):1188-1194.*

Abaxial stomata from Vicia faba leaves grown in a growth chamber under constant light, temperature and humidity showed an elaborate pattern of aperture changes over the course of a light cycle. These aperture changes, were tightly correlated with changes in chamber COL concentration (r(2)=0.83). Changes in chamber [CO2] resulted, in turn, from substantial daily fluctuations in ambient [CO2], typical of the Los Angeles environment, with a constant offset caused by photosynthesis and respiration of the plants within the chamber, The dominant role of the stomatal response to CO2 in the control of aperture tvas confirmed by manipulation of chamber [CO2]. Fast (15 min) increases and decreases in [CO2] caused rapid decreases and increases in aperture, while constant [CO2] resulted in constant aperture. In contrast, aperture changes in comparable plants grown under greenhouse conditions were tightly correlated with changes in incident solar radiation (r(2)=0.80), and poorly correlated with changes in [CO2] (r(2)=0.09). Greenhouse-grown plants transferred to growth chamber conditions showed no apparent response to CO2. These data indicate that growth-chamber-grown V. faba leaves provide an experimental system optimally suited for the study of the stomatal response to CO2, and suggest that acclimation to environmental conditions alters the sensitivity of stomata to CO2.

KEYWORDS: ABSCISIC- ACID, BEHAVIOR, BLUE-LIGHT, CARBON DIOXIDE, CONDUCTANCE, GUARD-CELLS, IRRADIANCE, PLANTS, RED, SUGAR

2313

Talkkari, A., S. Kellomaki, and H. Peltola. 1999. Bridging a gap between a gap model and a physiological model for calculating the effect of temperature on forest growth under boreal conditions. *Forest Ecology and Management 119(1-3):137-150.*

The applicability of the parabolic function of the Jabowa gap model for the relationship between tree growth and temperature sum for aggregating short-term temperatures responses was investigated by determining parameter values for the temperature function in a gap model from material generated by means of a physiological model (Kellomaki et al,, 1993; Kellomaki and Vaisanen, 1997), in which the growth and development of a tree stand is linked with the climate and soil through photosynthesis, respiration, transpiration and the uptake of water and nitrogen. Predictions of stand volume and total stand production were compared using the following functions for Scots pine (Pinus sylvestris L.): (i) the original parabolic function of the Jabowa model with parameter values based on the geographical distribution of trees (TO), (ii) the same parabolic function with parameter values obtained by fitting data generated using the physiological model (T1), and (iii) a fit of a truncated parabolic function to data generated using the physiological model (T2). The differences in volume and total production between the functions were greater at the site in northern Finland than at the sites in southern and central Finland, although absolute timber production was lowest at the northern site. The stand volume and timber production were highest at all three sites with the truncated parabola (T2) under conditions of climate change. Total production following climate change (average of TO, T1, and T2) was an average of 104% of that observed under current climatic conditions at the southern site, 105% at the central site and 121% at the northern site. The gap model was not found to be sensitive to the growing degree-days (gdd) response curve when the model was applied to Finnish conditions, and thus appeared to be satisfactory for aggregating the short-term physiological responses of Scots pine to temperature. The situation would be more problematic, however, if the model were applied under the conditions prevailing near the southern or northern edge of the geographical distribution of Scots pine.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATION, CO2-INDUCED CLIMATE CHANGE, COMPUTATIONS, ELEVATED CO2, FINLAND, PHOTOSYNTHESIS, SCOTS PINE, SIMULATION-MODEL, SOIL MOISTURE, TRANSIENT RESPONSES

2314

Tanaka, M., T. Takamura, H. Watanabe, M. Endo, T. Yanagi, and K. Okamoto. 1998. In vitro growth of Cymbidium plantlets cultured under superbright red and blue light-emitting diodes (LEDs). *Journal of Horticultural Science & Biotechnology 73(1):39-44.*

The effects of light generated by superbright blue and red LEDs on the growth of Cymbidium plantlets cultured in vitro have been studied. Leaf growth, chlorophyll content and shoot and root weights were affected by different LED irradiations. Red light promoted leaf growth but decreased chlorophyll content. This was reversed by blue Light. The growth of Cymbidium plantlets in terms of increase in total shoot and root weights was comparable under red plus blue LEDs and the fluorescent systems. Generally, the response to different LED was similar for plantlets grown on sugar-free medium with or without CO2 enrichment and sugar-containing medium but without CO2 enrichment. The growth of Cymbidium plantlets was enhanced by CO2 enrichment. Our study demonstrates the effectiveness of a total irradiation system for Cymbidium plantlets growth in vitro. The significance of our findings in relation to the development of a suitable lighting system for plant tissue culture is discussed.

KEYWORDS: LETTUCE, PEPPER, PHOTOSYNTHESIS, QUALITY

2315

Tanaka, M., D.C.H. Yap, C.K.Y. Ng, and C.S. Hew. 1999. The physiology of Cymbidium plantlets cultured in vitro under conditions of high carbon dioxide and low photosynthetic photon flux density. *Journal of Horticultural Science & Biotechnology 74(5):632-638.*

Cymbidium plantlets were grown in vitro under conditions of high CO2 and low photosynthetic photon flux density using the Miracle Pack(R) culture system. Shoots and roots of plantlets showed differential growth characteristics. Shoot growth was not different in plantlets cultured under CO2-enriched (CDE) and non-enriched (NCDE) conditions. Root growth was promoted in plantlets cultured under CDE in the presence or absence of 2% sucrose (S) with rockwool (R) as the supporting material. Growth was poor in plantlets cultured in 1% agar, Root growth was best in plantlets cultured under CDE R;S. Sucrose is still an important component for root growth under CDE conditions even though CO2 can be used as an alternative carbon source. Photosynthetic measurements (CO2 uptake and total Rubisco activity) showed the presence of active and operational photosynthetic machinery in plantlets cultured under CDE and NCDE conditions. The apparent lack of photoautotrophy (as evident from the lack of starch grains in chloroplasts) in plantlets cultured under NCDE conditions is not the result of a lesser potential for photoautotrophy; rather it is a consequence of sub-optimal CO2 concentrations within the culture vessels.

KEYWORDS: ACCLIMATION, ACCUMULATION, CO2-ENRICHMENT, ETHYLENE, INVITRO

2316

Tang, K.L., X.H. Feng, and G. Funkhouser. 1999. The delta C-13 of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology 5(1):33-40.*

Dendrochronological work at Sheep Mountain in the White Mountains, CA has demonstrated that bristlecone pine trees in two forms, full-bark and strip-bark, have experienced different cambial growth rates over the past century or longer. The strip-bark trees showed a greater growth increase than the full-bark ones. A calculation of the plant water-use efficiency (W) in response to anthropogenic CO2 released into the atmosphere shows that W of trees in both forms has increased for the past 200 years. However, there is no significant difference between the two tree forms in the rate of increase in W. This implies at least two possibilities with respect to the CO2 fertilization effect. First, the biomass in both tree forms might have increased, but carbon distribution among different parts of a tree was different. Second, the biomass may increase without causing any corresponding change in the plant water-use efficiency.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON ISOTOPE DISCRIMINATION, DIOXIDE, ECOSYSTEMS, ELEVATED CO2, FERTILIZATION, NITROGEN, PHOTOSYNTHESIS, RESPONSES, WATER-USE

2317

Tanigawa, T., Y. Kobayashi, H. Matsui, and Y. Sakai. 1995. Effects of co2 enrichment on growth and vase life of cut flowers of dendranthema-grandiflorum (ramat) kitamura. *Journal of the Japanese Society for Horticultural Science 64(2):417-424.*

The effects of CO2 enrichment of chrysanthemum (Dendranthema grandiflorum) on the subsequent growth and mineral and carbohydrate contents of the plant and on CO2 and C2H4 production and vase life of cut flowers were investigated. By enriching the atmosphere with 1,000 and 2,000 ppm CO2 for 2-1/2 hours each morning, stem length, fresh weight, and leaf number of cut flowers were increased by 3 to 11%, and vase life was extended 3 days compared with flowers grown in ambient CO2 concentration of 350 ppm. N, K, Mg, and Na concentrations, especially in the lower leaves were lower, whereas P and Ca concentrations were either the same or higher in the CO2 treatment than they were in leaves of plants grown in the ambient CO2. Starch and sugar contents in the leaves and stem were increased under CO2 enriched condition. CO2 production in the leaves was significantly reduced by the CO2 treatments; C2H4 production was unaffected. From these data, we propose that the decline of [N+K]/Ca ratio (Funakoshi, 1984) and the increase in starch and sugar contents in the leaves and seem as a result of the CO2 enriched atmosphere effectively prolonged vase life of the cut flowers.

KEYWORDS: ACCLIMATION, ETHYLENE

2318

Tanigawa, T., M. Nagaoka, H. Ikeda, and A. Shimizu. 1993. Effects of co-2 enrichment on growth, photosynthesis and physiological-activity of roots of dendranthema X grandiflorum (ramat) kitamura. *Journal of the Japanese Society for Horticultural Science 61(4):873-878.*

To assess the effect of CO2 enrichment on growth of greenhouse chrysanthemum, the plants were cultivated in the phytotron with 300, 600 and 1,200 ppm CO2. i. CO2 enriched plants showed a significant increase in stem length, number of leaves, leaf area, and fresh and dry weights. The greatest rate of increase after 60 days of CO2 enrichment was observed in the dry weight of roots (39%). Flower bud formation was delayed 3 days under CO2 enriched condition. 2. No difference in photosynthetic rates of whole plants measured in 400 and 800 ppm CO2 was observed among those grown under high CO2 (600 or 1,200 ppm) and those grown in ambient air (300 ppm). After 60 days of exposure to ambient and high CO2, the photosynthetic rate measured in 800 PPM CO2 declined markedly compared to the rate at the beginning of the treatment. 3. TTC (2, 3, 5-triphenyl tetrazolium chloride) reductive activity of roots decreased under CO2 enriched atmosphere, but it increased on a per plant basis because fresh weight of the roots increased. There was a high positive correlation between TTC reduction per plant and the fresh weight of the top (aerial part).

KEYWORDS: CHRYSANTHEMUM-MORIFOLIUM RAMAT, CO2-ENRICHMENT, ENVIRONMENT, GREENHOUSE PLANTS, LIGHT, RESPONSES

2319

Tanimoto, H., T. Kagi, and S. Morita. 1993. Relationship between the utilization of sugars by cultured petiole segments of begoniaxhiemalis and the optimum time for co2 enrichment. *Journal of the Japanese Society for Horticultural Science 62(2):437-441.*

By monitoring the utilization of sugars by petiole segments of Begonia X hiemalis cultured in medium containing the plant grwoth regulators, kinetin (1 PPM), NAA (1 ppm), the optimum time for beginning the CO2 enrichment treatment was established. The total sugar concentration in the medium decreased rapidly after 40 days of culturing. The cessation of sugar depletion by the tissues after 60 days is attributed to the onset of photosynthesis by the plantlets. CO2 administration at this time promoted leaf development, whereas CO2 enrichment 10 to 20 days earlier halted the development of adventitious shoots. These observations suggest that the optimum period to begin CO2 enrichment to promote shoot growth and to enhance photosynthesis is about 60 days after the culturing the petiole segments.

2320

Tarnawski, M.G., T.G.A. Green, B. Buedel, A. Meyer, H. Zellner, and O.L. Lange. 1994. Diel changes of atmospheric co2 concentration within, and above, cryptogam stands in a new-zealand temperate rain-forest. *New Zealand Journal of Botany 32(3):329-336.*

Atmospheric CO2 levels were determined (at 2m height) in the rainforest and in a clearing outside the forest, during spring (November) 1991, Urewera National Park, New Zealand. CO2 levels within the forest were 30 ppm higher and showed a more variable diel pattern (range up to 70 ppm) than outside the forest. CO2 levels were generally higher at night than during the day. Detailed measurements were made at several sites at a depth of 25 mm in the phylloplane of three moss species and under, or between, the thalli of four lichen species. Mean levels were 50% (moss phylloplane) and 10% (lichen thalli) higher than the levels in the clearing and, in 80% of sites, also higher than air within the rainforest. The diel pattern of the CO2 concentration at each of the sites was not predictable from measurements of CO2 in the bulk air of the forest. High levels of CO2 may be important in elevating photosynthetic rates of mosses and, to a lesser extent, lichens in the field.

KEYWORDS: FIELD, FOREST, LICHENS, MICROCLIMATE, PHOTOSYNTHESIS, PSEUDOCYPHELLARIA, THALLUS WATER-CONTENT

2321

Tate, K.R. 1992. Assessment, based on a climosequence of soils in tussock grasslands, of soil carbon storage and release in response to global warming. *Journal of Soil Science 43(4):697-707.*

A soil climosequence in tussock grasslands in South Island, New Zealand, encompassing climates ranging from cold to warm temperate provided a spatial analogue of climate change for investigating the effects of global warming on soil C contents and turnover. Mean annual temperature (T) and annual precipitation (P) ranged from 2 to 10-degrees-C, and 350 to 5000 mm, respectively. Soil C contents were curvilinearly related to T/P across the sequence (r = -0.95, significant at P < 0.01), indicating that east of the Southern Alps, increased decomposition of organic matter with global warming would provide a positive feedback to further increase atmospheric CO2. This decrease in New Zealand's soil C, estimated to be up to 10% of the current content for a global temperature rise of 0.03 K a-1 to 2050, could contribute about 0.5 x 10(15) g C to the atmosphere over the next 60 years. These conclusions were generally supported by changes in soil C turnover estimated from 'bomb' C-14 enrichment. The unexpectedly slow turnover found for two soils was explained by a 'memory' effect from the former southern beech forest that grew on these soils in prehistoric times. Accumulation of Al-humus under the forest may be responsible for the slow C turnover observed.

KEYWORDS: ALUMINUM, ANDOSOLS, CO2, EMISSIONS, FRACTIONS, MICROBIAL BIOMASS, MINERALIZATION, NEW-ZEALAND, ORGANIC-MATTER, VEGETATION

2322

Tate, K.R., and D.J. Ross. 1997. Elevated CO2 and moisture effects on soil carbon storage and cycling in temperate grasslands. *Global Change Biology 3(3):225-235.*

In grassland ecosystems, most of the carbon (C) occurs below- ground. Understanding changes in soil fluxes induced by elevated atmospheric CO2 is critical for balancing the global C budget and for managing grassland ecosystems sustainably. In this review, we use the results of short-term (1-2 years) studies of below-ground processes in grassland communities under elevated CO2 to assess future prospects for longer-term increases in soil C storage. Results are broadly consistent with those from other plant communities and include: increases in below-ground net primary productivity and an increase in soil C cycling rate, changes in soil faunal community, and generally no increase in soil C storage. Based on other experimental data, future C storage could be favoured in soils of moderate nutrient status, moderate-to-high clay content, and low (or moderately high) soil moisture status. Some support for these suggestions is provided by preliminary results from direct measurements of soil C concentrations near a New Zealand natural CO2-venting spring, and by simulations of future changes in grassland soils under the combined effects of CO2 fertilization and regional climate change. Early detection of any increase in soil C storage appears unlikely in complex grassland communities because of (a) the difficulty of separating an elevated CO2 effect from the effects of soil factors including moisture status, (b) the high spatial variability of soil C and (c) the effects of global warming. Several research imperatives are identified for reducing the uncertainties in the effects of elevated atmospheric CO2 on soil C.

KEYWORDS: AGGREGATE STABILITY, ATMOSPHERIC CO2, CLIMATE CHANGE, DIOXIDE, ENRICHMENT, LONG-TERM RESPONSE, MICROBIAL BIOMASS, NITROGEN, PLANT-RESPONSES, TALLGRASS PRAIRIE

2323

Tateno, M., and F.S. Chapin. 1997. The logic of carbon and nitrogen interactions in terrestrial ecosystems. *The American Naturalist 149(4):723-744.*

Simple ecosystem models of carbon (C) and nitrogen (N) interactions between plants and soil show that differences in N-use efficiency cause convergence of plant growth in ecosystems with a closed N cycle because rapid growth associated with high N-use efficiency results in litter with a high C:N ratio and a low N mineralization rate, whereas slow growth associated with low N-use efficiency leads to a low C:N ratio and a high N mineralization rate. This plant-induced negative feedback on production contrasts with the positive feedback that had previously been hypothesized. Our model explains the causes and results of several important ecological patterns. First, all ecosystems with a fixed N pool will show a small increase in C storage (especially in soils) in response to elevated CO2 despite constraints by litter-quality feedbacks to N mineralization rate. Second, the decreased N-use efficiency and plateauing of primary production in forest ecosystems with a high N supply reflect saturation of photosynthetic rate with high plant N pools. Finally, the addition of inorganic N to ecosystems induces a quick increase in productivity and N supply. However, these increases disappear if N additions are not sustained. These findings suggest that

those global changes that alter N input to or output from ecosystems are likely to have larger long-term impact on biomass, productivity, and C storage of ecosystems with a tightly closed N cycle than would changes in plant N-use efficiency.

KEYWORDS: ELEVATED CO2, GLOBAL CHANGE, GRASSES, NUTRIENT, PATTERNS, PHOTOSYNTHESIS, PLANTS, POLYGONUM-CUSPIDATUM, RESPONSES, USE EFFICIENCY

2324

Taulavuori, E., K. Taulavuori, K. Laine, T. Pakonen, and E. Saari. 1997. Winter hardening and glutathione status in the bilberry (Vaccinium myrtillus) in response to trace gases (CO2, O-3) and nitrogen fertilization. *Physiologia Plantarum 101(1):192-198.*

Bilberry plants (Vaccinium myrtillus L.) at a field site in northern Finland (65 degrees N) were subjected to nitrogen fertilization [6.5 mmol m(-2) NH4NO3 x Ca(OH)(2)] at the beginning of 3 growing seasons in late May and to trace gas fumigation (CO2 and O-3) for 5 months (May-September) in 1993- 1995 in order to investigate frost resistance and glutathione concentrations during the winter hardening period, and to assess the correlation between these variables. Harvesting was performed twice in the autumn of both 1994 and 1995, and the two-year data for each harvest were pooled. The frost resistance of the bilberry stems increased by about 10 degrees C during the hardening period between the two harvests. Nitrogen fertilization increased the frost resistance towards late autumn. The fumigation treatments had no marked effect on it. The combination of elevated CO2 and nitrogen fertilization induced a decrease in frost resistance. Increases in total glutathione concentrations and the proportion of reduced glutathione (GSH) in the stems were evident during hardening. Nitrogen fertilization positively affected the total glutathione concentration and the proportion of GSH at the beginning of the hardening period but the effect disappeared during the hardening process. Trace gas fumigation as such had no marked effect on glutathione concentration. Increases in glutathione concentrations during hardening did not correlate with frost resistance, possibly due to different timing of the appearence of the response to fertilization treatment, i.e., glutathione responded in the beginning of hardening while frost resistance at the end. The lack of correlation with frost resistance, and especially the different responses to nitrogen fertilization, may reflect the indirect role of glutathione in the development of winter hardening, as a transport and storage form of reduced nitrogen and sulphur. In conclusion, winter hardening and glutathione status in the bilberry seems to be sensitive to nitrogen fertilization, and not affected by elevated CO2 and O-3.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CO2, CARBON DIOXIDE, FREEZING-INJURY, FROST HARDINESS, PICEA-ABIES L, PINE NEEDLES, RED SPRUCE, RUBENS SARG, SEASONAL-VARIATION

2325

Tausz, M., L.J. DeKok, I. Stulen, and D. Grill. 1996. Physiological responses of Norway spruce trees to elevated CO2 and SO2. *Journal of Plant Physiology 148(3-4):362-367.*

Young Norway spruce (Picea abies (L.) Karst.) trees were exposed to elevated CO2 (0.8 mL L(-1)), SO2 (0.06 mu L L(-1)), and elevated CO2 and SO2 (0.8 mL L(-1) and 0.06 mu L L(-1), respectively) for three months. Exposure to elevated CO2 resulted in an increased biomass production of the needles, while the pigment content was decreased. Exposure to SO2 hardly affected growth and pigment contents. Chlorophyll/carotenoid- and chlorophyll a/chlorophyll b-ratios were not affected by either CO2 or SO2. The epoxidation state of the xanthophyll-cycle was changed upon SO2-exposure, due to a higher zeaxanthin and a lower violaxanthin content. Chlorophyll fluorescence measurements showed F-v/F-m-ratios of 0.7 or higher for all needles, which indicated a healthy photosynthetic apparatus. Exposure to SO2 resulted in increased foliar contents of sulfate, total glutathione (reduced and oxidized form), cyst(e)ine, and a slightly more reduced redox state of glutathione. Exposure to elevated CO2 resulted in a slight decrease in glutathione contents, but it did not affect sulfate or cyst(e)ine contents of the spruce needles. Neither ascorbic acid content nor its redox state were affected by CO2 or SO2. The effects of CO2 and SO2 were independent from each other, since significant interactions CO(2)xSO(2) were not observed.

KEYWORDS: AIR- POLLUTANTS, CARBON DIOXIDE, LEAVES, O-3, OZONE

2326

Taylor, G., S.D.L. Gardner, C. Bosac, T.J. Flowers, M. Crookshanks, and L. Dolan. 1995. Effects of elevated co2 on cellular mechanisms, growth and development of trees with particular reference to hybrid poplar. *Forestry 68(4):379-390.*

Growth is often stimulated when C-3 plants, including trees, are exposed to elevated CO2, although evidence from the literature suggests that the responsiveness of trees to CO2 varies, depending on species. This paper explores some of the cellular mechanisms which underlie increased growth, using both the authors' own data and information from the literature. Mechanisms include photosynthetic fixation of CO2 and the role of Rubisco, the link between carbon fixation and growth, in particular, how increased carbon is thought to influence the process of plant cell expansion and cell production and finally the consequences of cellular effects for the growth and development of whole planes. Data are presented for the growth and development of hybrid poplars in elevated CO2, following both field (open-top chambers) and laboratory experiments which suggest that this type of tree with indeterminate, rapid growth may be favoured by the CO2 concentrations of the next century.

KEYWORDS: ACCLIMATION, BETULA-PENDULA ROTH, CARBON DIOXIDE, EFFICIENCY, PHOTOSYNTHESIS, PLANTS, RESPONSES, ROOT

2327

Taylor, G., S. Ranasinghe, C. Bosac, S.D.L. Gardner, and R. Ferris. 1994. Elevated co2 and plant-growth - cellular mechanisms and responses of whole plants. *Journal of Experimental Botany 45(280):1761-1774.*

Much research has focused on the photosynthetic responses of plants to elevated CO2, with less attention given to the post- photosynthetic events which may lead to changes in the growth of tissues, organs and whole plants. The aim of this review is to identify how plant growth is altered in elevated CO2 and to determine which growth processes or cellular mechanisms are sensitive to carbon supply. For leaves, both the expansion of individual leaves and the initiation of leaf primordia are stimulated in elevated CO2. When lamina growth is promoted, this is usually associated with increased leaf cell expansion rather than increased leaf cell production. Using several clones of hybrid poplar (Populus euramericana, P. interamericana) two native herbs (Plantago media, Sanguisorba minor) and bean (Phaseolus vulgaris) we have identified the mechanism through which leaf cell expansion is promoted in elevated CO2. Changes in the water relations, turgor pressure (P) and yield turgor (Y) of growing leaves cannot explain increased cell expansion; this appears to occur because cell wall loosening is promoted, as suggested by three pieces of evidence. (i) The rate of decline of water potential (psi) with time is accelerated when growing leaves are placed in psychrometers and allowed to relax, (ii) Instron-measured cell wall extensibility (WEX), is greater for leaves exposed to elevated CO2 and

(iii) the activity of the putative wall loosening enzyme, XET is increased for leaves of P. vulgaris exposed to elevated CO2. Species differences do, however, exist; in the herb Lotus corniculatus small stimulations of leaf growth in elevated CO2 are due to increased leaf cell production and decreased cell size in elevated CO2. These results are discussed in relation to the concept of functional types. There is evidence to suggest that both cell production and cell expansion are promoted in roots of plants exposed to elevated CO2. For native herbs (Anthyllis vulneraria, Lotus corniculatus, P. media and S. minor), increased root growth in elevated CO2 is due to increased cell elongation. In contrast to leaves, this appears to occur because both root cell turgor pressure (P) and root cell wall extensibility (WEX) are promoted by exposure of shoots to elevated CO2. In longer-term studies on root growth, the effects of additional carbon on the production of root primordia and root branching are of overriding importance, suggesting that carbon supply may influence some aspect of the cell cycle, when effects on the extension of individual roots may not be apparent.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, LEAF GROWTH, PHOTOSYNTHESIS, ROOT-GROWTH, SOURCE-SINK RELATIONS, WALL EXTENSIBILITY, WATER POTENTIALS, XYLOGLUCAN ENDOTRANSGLYCOSYLASE, YIELD THRESHOLD

2328

Taylor, J., and A.S. Ball. 1994. The effect of plant-material grown under elevated co2 on soil respiratory activity. *Plant and Soil 162(2):315-318.*

The biodegradability of aerial material from a C4 plant, sorghum grown under ambient (345 mu mol mol(-1)) and elevated (700 mu mol mol(-1)) atmospheric CO2 concentrations were compared by measuring soil respiratory activity. Initial daily respiratory activity (measured over 10 h per day) increased four fold from 110 to 440 cm(3) CO2 100g dry weight soil(-1) in soils amended with sorghum grown under either elevated or ambient CO2. Although soil respiratory activity decreased over the following 30 days, respiration remained significantly higher (t-test; p>0.05) in soils amended with sorghum grown under elevated CO2 concentrations. Analysis of the plant material revealed no significant differences in C:N ratios between sorghum grown under elevated or ambient CO2. The reason for the differences in soil respiratory activity have yet to be elucidated. However if this trend is repeated in natural ecosystems, this may have important implications for C and N cycling.

KEYWORDS: CARBON DIOXIDE, ESTUARINE MARSH, LITTER, NITROGEN

2329

Taylor, J.A., and J. Lloyd. 1992. Sources and sinks of atmospheric co2. *Australian Journal of Botany 40(4-5):407-418.*

The biosphere plays an important role in determining the sources, sinks, levels and rates of change of atmospheric CO2 concentrations. Significant uncertainties remain in estimates of the fluxes of CO2 from biomass burning and deforestation, and uptake and storage of CO2 by the biosphere arising from increased atmospheric CO2 concentrations. Calculation of probable rates of carbon sequestration for the major ecosystem complexes and global 3-D tracer transport model runs indicate the possibility that a significant net CO2 uptake (> 1 Pg C yr-1), a CO2 'fertilisation effect', may be occurring in tropical rainforests, effectively accounting for much of the 'missing sink'. This sink may currently balance much of the CO2 added to the atmosphere from deforestation and biomass burning. Interestingly, CO2 released from biomass burning may itself be playing an important role in enhanced carbon storage by tropical rainforests. This has important implications for predicting future CO2 concentrations. If tropical rainforest destruction continues then much of the CO2 stored as a result of the CO2 'fertilisation effect' will be rereleased to the atmosphere and much of the 'missing sink' will disappear. These effects have not been considered in the IPCC (Intergovernmental Panel on Climate Change) projections of future atmospheric CO2 concentrations. Predictions which take account of the combined effects of deforestation, the return of carbon previously stored through the CO2 'fertilisation effect' and the loss of a large proportion of the 'missing sink' as a result of deforestation, would result in much higher predicted concentrations and rates of increase of atmospheric CO2 and, as a consequence, accelerated rates of climate change.

KEYWORDS: BIOSPHERE, BUDGET, CARBON DIOXIDE, EMISSIONS

2330

Taylor, K., and C. Potvin. 1997. Understanding the long-term effect of CO2 enrichment on a pasture: the importance of disturbance. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(10):1621-1627.*

This study is part of a research program examining the effects of elevated atmospheric carbon dioxide on a pasture. It was designed to examine (i) the interaction between disturbance and the atmospheric CO2 concentration at the community level, and (ii) the response of a major weed Chenopodium album to CO2 enrichment in a natural field situation. Although both the total number of species and Simpson's index increased upon disturbance, these traits did not respond to CO2 fertilization. Counter to our expectation, we found no significant interaction between disturbance and CO2. The composition of the community that established in the open, disturbed spaces was a function of seed availability and as such independent of the atmospheric CO2 concentration. Using height of the background vegetation to assess the impact of elevated CO2, we found some evidence for density dependence in the undisturbed quadrats but not in the disturbed ones. For C. album, the disturbance regimes outweigh the CO2 increase in importance. Neighboring plants have a strong influence on C. album growth, this even though the C. album photosynthetic mechanisms are potentially responsive to elevated CO2. The present study highlights the complex feed- back interactions occurring when a community is exposed to elevated CO2 concentration.

KEYWORDS: C-3, CHENOPODIUM-ALBUM L, COMMUNITY, COMPETITION, ELEVATED CO2, GROWTH, LIGHT, PHYTOCHROME, PLANTS, RESPONSES

2331

Teese, P. 1995. Intraspecific variation for co2 compensation point and differential growth among variants in a C-3-C-4 intermediate plant. *Oecologia 102(3):371-376.*

CO2 compensation point (Gamma), the concentration of CO2 at which photosynthesis and respiration are at equilibrium, is a commonly used diagnostic for the C-4 photosynthetic pathway, since it reflects the reduced photorespiration that is a property of C-4 photosynthesis. Geographic variation for Gamma was examined within Flaveria linearis, a C-3-C-4 intermediate species. Collections from four widely separated Floridian populations were propagated in a greenhouse and measured for Gamma. Little differentiation among populations was found, but significant within-population variation was present. Temperature is a hypothesized selective agent for the C-4 photosynthetic pathway. To test this hypothesis, plants exhibiting a range of Gamma were cloned and placed in growth chambers at 25 degrees C and 40 degrees C. After 7 weeks, Gamma valves were remeasured and plants were harvested and weighed. There was a poor correlation between initial and final measures of Gamma for a given genotype ($r = 0.38$, $P > 0.1$). Broad sense heritability for Gamma was computed to be 0.10. At 25 degrees C, there was no relationship between final size and Gamma. At 40 degrees C,

more C,like plants, as indicated by their low Gamma, had grown larger. Differences in relative growth rate were attributable more to differences in net assimilation rate than in leaf area ratio. Taken together, these results demonstrate that although significant plasticity exists in the amount of photorespiration in this C-3-C-4 species, high temperature appears to be an effective selective agent for the reduction of photorespiration and the enhancement of C-4-like traits.

KEYWORDS: ASSIMILATION, C-4 PHOTOSYNTHESIS, C3-C4, EVOLUTION, FLAVERIA, LEAF ANATOMY, PATHWAYS, QUANTITATIVE GENETICS, ULTRASTRUCTURE

2332

Telewski, F.W., R.T. Swanson, B.R. Strain, and J.M. Burns. 1999. Wood properties and ring width responses to long-term atmospheric CO2 enrichment in field-grown loblolly pine (Pinus taeda L.). *Plant, Cell and Environment 22(2):213-219.*

Loblolly pine (Pinus taeda L.) were grown in the field, under non-limiting nutrient conditions, in open-top chambers for 4 years at ambient CO2 partial pressures (pCO(2)) and with a CO2- enriched atmosphere (+ 30 Pa pCO(2) compared to ambient concentration). A third replicate of trees were grown without chambers at ambient pCO(2). Wood anatomy, wood density and tree ring width were analysed using stem wood samples. No significant differences were observed in the cell wall to cell lumen ratio within the latewood of the third growth ring formed in 1994. No significant differences were observed in the density of resin canals or in the ratio of resin canal cross- sectional area to xylem area within the same growth ring. Ring widths were significantly wider in the CO2-enrichment treatment for 3 of 4 years compared to the ambient chamber control treatment. Latewood in the 1995 growth ring was significantly wider than that in the ambient control and represented a larger percentage of the total growth-ring width. Carbon dioxide enrichment also significantly increased the total wood specific gravity (determined by displacement). However, when determined as total sample wood density by X-ray densitometry, the density of enriched samples was not significantly higher than that of the ambient chamber controls. Only the 1993 growth ring of enriched trees had a significantly higher maximum latewood density than that of trees grown on non-chambered plots or ambient chambered controls. No significant differences were observed in the minimum earlywood density of individual growth rings between chambered treatments. These results show that the most significant effect of CO2 enrichment on wood production in loblolly pine is its influence on radial growth, measured as annual tree ring widths. This influence is most pronounced in the first year of growth and decreases with age.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, CLIMATE, ELEVATED CO2, FOREST, INCREASING CO2, MECHANICAL PERTURBATION, PHOTOSYNTHESIS, TREE GROWTH, TRENDS

2333

Teramura, A.H., and J.H. Sullivan. 1994. Effects of uv-b radiation on photosynthesis and growth of terrestrial plants. *Photosynthesis Research 39(3):463-473.*

The photosynthetic apparatus of some plant species appears to be well-protected from direct damage from UV-B radiation. Leaf optical properties of these species apparently minimizes exposure of sensitive targets to UV-B radiation. However, damage by UV-B radiation to Photosystem II and Rubisco has also been reported. Secondary effects of this damage may include reductions in photosynthetic capacity, RuBP regeneration and quantum yield. Furthermore, UV-B radiation may decrease the penetration of PAR, reduce photosynthetic and accessory pigments, impair stomatal function and alter canopy morphology, and thus indirectly retard photosynthetic carbon assimilation. Subsequently, UV-B radiation may limit productivity in many plant species. In addition to variability in sensitivity to UV- B radiation, the effects of UV-B radiation are further confounded by other environmental factors such as CO2, temperature, light and water or nutrient availability. Therefore, we need a better understanding of the mechanisms of tolerance to UV-B radiation and of the interaction between UV-B and other environmental factors in order to adequately assess the probable consequences of a change in solar radiation.

KEYWORDS: CUCUMBER SEEDLINGS, ELEVATIONAL GRADIENT, FIELD CONDITIONS, LOBLOLLY-PINE, OZONE DEPLETION, PHOTON FLUX- DENSITY, PISUM-SATIVUM, REACTION CENTER PROTEIN, ULTRAVIOLET-B, VISIBLE-LIGHT

2334

Teramura, A.H., J.H. Sullivan, and L.H. Ziska. 1990. Interaction of elevated ultraviolet-b radiation and CO2 on productivity and photosynthetic characteristics in wheat, rice, and soybean. *Plant Physiology 94(2):470-475.*

2335

Teskey, R.O. 1995. A field-study of the effects of elevated co2 on carbon assimilation, stomatal conductance and leaf and branch growth of pinus-taeda trees. *Plant, Cell and Environment 18(5):565-573.*

A study was conducted in 21-year-old loblolly pine (Pinus taeda L.) trees growing in plantation in north central Georgia, USA, The experiment used branch chambers to impose treatments of ambient, ambient+165 and ambient+ 330 mu mol mol(-1) CO2. After one growing season there was no indication of acclimation to elevated CO2. In August and September, carbon assimilation, measured by two different methods, was twice as high at ambient +330 mu mol mol(-1) CO2 than at ambient, Dark respiration was suppressed by 6% at ambient+l65 and by 14% at ambient+330 mu mol mol(-1) CO2. This suppression was immediate, and not an effect of exposure to elevated CO2 during growth, since respiration was reduced by the same amount in all treatments when measured at a high CO2 concentration, Elevated CO2 increased the growth of foliage and woody tissue, It also increased instantaneous transpiration efficiency, but it had no effect on stomatal conductance, Since the soil at the study site had low to moderate fertility, these results suggest that the growth potential of forests on many sites may be enhanced by global increases in atmospheric CO2 concentration.

KEYWORDS: COOCCURRING BIRCH, DIOXIDE ENRICHMENT, GAS-EXCHANGE, LIRIODENDRON-TULIPIFERA L, LONG-TERM EXPOSURE, PHOTOSYNTHESIS, RESPIRATION, RESPONSES, SCIRPUS- OLNEYI, SEEDLINGS

2336

Teskey, R.O. 1997. Combined effects of elevated CO2 and air temperature on carbon assimilation of Pinus taeda trees. *Plant, Cell and Environment 20(3):373-380.*

Branches of 22-year-old loblolly pine (Pinus taeda, L.) trees growing in a plantation were exposed to ambient CO2, ambient + 165 mu mol mol(-1) CO2 or ambient + 330 mu mol mol(-1) CO2 concentrations in combination with ambient or ambient + 2 degrees C air temperatures for 3 years. Field measurements in the third year indicated that net carbon assimilation was enhanced in the elevated CO2 treatments in all seasons. On the basis of A/C-i curves, there was no indication of photosynthetic down-regulation. Branch growth and leaf area also increased significantly in the elevated CO2 treatments. The imposed 2 degrees C increase in air temperature only had slight effects on net assimilation and growth. Compared with the ambient CO2 treatment, rates of net

assimilation were approximate to 1.6 times greater in the ambient + 165 mu mol mol(-1) CO2 treatment and 2.2 times greater in the ambient + 330 mu mol mol(-1) CO2 treatment. These ratios did not change appreciably in measurements made in all four seasons even though mean ambient air temperatures during the measurement periods ranged from 12.6 to 28.2 degrees C. This indicated that the effect of elevated CO2 concentrations on net assimilation under field conditions was primarily additive. The results also indicated that the effect of elevated CO2 (+ 165 or + 330 mu mol mol(-1)) was much greater than the effect of a 2 degrees C increase in air temperature on net assimilation and growth in this species.

KEYWORDS: ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, LEAF, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, SENSITIVITY

2337

Teughels, H., I. Nijs, P. VanHecke, and I. Impens. 1995. Competition in a global change environment: The importance of different plant traits for competitive success. *Journal of Biogeography 22(2-3):297-305.*

Plant traits of both structural and physiological nature have been reported to play an important role in the outcome of a competitive interaction. In this experiment a survey of the importance of characteristics such as height, leaf area and vertical distribution, leaf inclination, light transmission through a leaf and through the canopy together with leaf photosynthesis rates, was made for two grasses: Lolium perenne L. and Festuca arundinacea Schreb. Both species were grown in a competitive set-up with minimal belowground interactions under four different global change conditions of CO2 concentration and air temperature (ambient, elevated CO2 concentration 700 mu mol mol(-1), increased air temperature+4 degrees C, combined) in naturally sunlit air-conditioned half-open plastic greenhouses. Plants were grown for a whole growing season with regular (every 4 weeks) clippings at 3.5 cm height. Results demonstrate that Lolium has a much greater competitive ability when compared to Festuca (aggressivity = 0.465). This may be a consequence of the slightly higher leaf photosynthesis rates (+15%) in combination with a larger amount of foliage area, which could result in a higher canopy photosynthesis. The greater leaf area remaining after mowing may lead to an additional advantage for Lolium. Height, leaf inclination, optical properties and the vertical distribution of leaf area seem to be of minor importance in this experiment. Global change treatments (elevated CO2 concentration and increased temperature) influence leaf photosynthesis rates predominantly and have little or no direct effect on structural traits such as height, leaf angles and vertical leaf distribution; nor do they exert an influence on light transmission through a leaf or through the canopy. However, treatment effects on leaf area can add to explain differences in canopy photosynthesis. In this competition experiment, focused on above-ground interactions, both a structural (leaf area) and a physiological feature (leaf photosynthesis) contribute to the competitive success of a species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CANOPY, ELEVATED CO2, LIGHT, LOLIUM-PERENNE, MODEL, PHOTOSYNTHESIS, RESPONSES, SHOOT COMPETITION, TEMPERATURE

2338

Theobald, J.C., R.A.C. Mitchell, M.A.J. Parry, and D.W. Lawlor. 1998. Estimating the excess investment in ribulose-1,5-bisphosphate carboxylase/oxygenase in leaves of spring wheat crown under elevated CO2. *Plant Physiology 118(3):945-955.*

Wheat (Triticum aestivum L.) was grown under CO2 partial pressures of 36 and 70 Pa with two N-application regimes. Responses of photosynthesis to varying CO2 partial pressure were fitted to estimate the maximal carboxylation rate and the nonphotorespiratory respiration rate in flag and preceding leaves. The maximal carboxylation rate was proportional to ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content, and the light-saturated photosynthetic rate at 70 Pa CO2 was proportional to the thylakoid ATP-synthase content. Potential photosynthetic rates at 70 Pa CO2 were calculated and compared with the observed values to estimate excess investment in Rubisco. The excess was greater in leaves grown with high N application than in those grown with low N application and declined as the leaves senesced. The fraction of Rubisco that was estimated to be in excess was strongly dependent on leaf N content, increasing from approximately 5 % in leaves with 1 g N m(-2) to approximately 40 % in leaves with 2 g N m(-2). Growth at elevated CO2 usually decreased the excess somewhat but only as a consequence of a general reduction in leaf N, since relationships between the amount of components and N content were unaffected by CO2. We conclude that there is scope for improving the N-use efficiency of C-3 crop species under elevated CO2 conditions.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELECTRON-TRANSPORT, GAS-EXCHANGE, LIGHT, MESOPHYLL CONDUCTANCE, PHASEOLUS-VULGARIS L, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RISING ATMOSPHERIC CO2, WINTER-WHEAT

2339

Thibaud, M.C., N. Cortez, H. Riviere, and T. Betsche. 1995. Photorespiration and related enzymes in pea (pisum-sativum) grown in high co2. *Journal of Plant Physiology 146(5-6):596-603.*

The adaptation of pea (Pisum sativum L. cv. Douce Provence) to the low photorespiratory conditions imposed by high CO2 was investigated at the level of enzymes and gas exchange. Seedlings were CO2-enriched (1000 and 4800 mu L CO(2)L(-1)) during most of the vegetative period, yielding <<acclimated leaves>>. Alternatively, young plants were pre-grown in ambient CO2 and then CO2-enriched, yielding <<transferred leaves>>. The level of nutrient supply was high. High CO2 did not significantly alter the specific activities of the photorespiratory enzymes glycolate oxidase, NADH- and NADPH- hydroxypyruvate reductase and glutamine synthetase in either of the experiments. Moreover, no significant effect of high CO2 on specific carboxylase activity and relative abundance of ribulose bisphosphate carboxylase-oxygenase (Rubisco) was observed. In contrast, high CO2 markedly affected the photorespiratory enzymes catalase (Cat) and phosphoglycolate phosphatase, the activity of the latter being increased. Decline of Cat activity was detected 1 day after transfer to high CO2 and in the course of 7 days, the inhibition reached values of 33% (1000 mu L CO(2)L(-1)) and 50% (4800 mu L CO(2)L(-1)). The relative abundance of Cat protein also declined, but no change in the isoform pattern was observed. Photorespiratory O-2 uptake, determined with O-18(2), decreased by 54% in an atmosphere containing 1000 mu L CO(2)L(-1). This suggests that Rubisco-oxygenase activity occurred at a substantial rate at threefold that of the current atmospheric CO2 concentration. CO2 enrichment to 4000 mu L CO(2)L(-1) further inhibited photorespiratory O-2, uptake. The decline of Cat was thus positively correlated with the inhibition of light O-2 uptake. In <<acclimated leaves>>, Cat inhibition was slight or absent, depending on the level of CO2 enrichment. This suggests that Cat inhibition in <<transferred leaves>> is a transient response that can be overcome by yet unidentified adaptative mechanisms.

KEYWORDS: CARBON DIOXIDE, CATALASE, GENE-EXPRESSION, GLUTAMINE-SYNTHETASE, GLYCINE DECARBOXYLASE, HYDROXYPYRUVATE REDUCTASE, LEAVES, LIGHT, PHOTORESPIRATION, TRIFOLIUM-SUBTERRANEUM L

2340

Thom, R.M. 1996. CO2-enrichment effects on eelgrass (Zostera marina

L) and bull kelp (Nereocystis luetkeana (Mert) P & R). *Water, Air, and Soil Pollution 88(3-4):383-391.*

I investigated the effect of CO2-enrichment on productivity of two aquatic plant species [Zostera marina L., Nereocystis luetkeana (Mert.) P. & R.] that form significant components of coastal ecosystems in the Pacific Northwest. Short-term (i.e., 2-hr) experiments showed that doubling CO2 resulted in up to a 2.5-fold increase in Zostera net apparent productivity (NAP). Nereocystis NAP was increased 2.2 - 2.8 fold. In experiments involving seven enrichment treatments, NAP increased with increasing CO2 between ambient (1.0x) and 2.5x CO2 in both Zostera and Nereocystis. Nereocystis acid Zostera NAP was lowest at highest (i.e., 5x) CO2 concentrations. In growth experiments, mean growth rate of Zostera increased with increasing CO2 during one of the two trials. I conclude that increasing CO2 in the surface waters of the coastal ocean would predictably result in increased NAP of these two species. These results supplement limited published data showing that shallow estuarine and marine systems are vulnerable to increased carbon dioxide.

KEYWORDS: DYNAMICS, METABOLISM, NITROGEN, PATTERNS, PLANTS

2341

Thomas, R.B., and K.L. Griffin. 1994. Direct and indirect effects of atmospheric carbon-dioxide enrichment on leaf respiration of glycine-max (L) merr. *Plant Physiology 104(2):355-361.*

Long-term and short-term effects of CO2 enrichment on dark respiration were investigated using soybean (Glycine max [L.] Merr.) plants grown at either 35.5 or 71.0 Pa CO2. Indirect effects, or effects of growth in elevated CO2, were examined using a functional model that partitioned respiration into growth and maintenance components. Direct effects, or immediate effects of a short-term change in CO2, were examined by measuring dark respiration, first, at the CO2 partial pressure at which plants were grown, and second, after equilibration in the reciprocal CO2 partial pressure. The functional component model indicated that the maintenance coefficient of respiration increased 34% with elevated CO2, whereas the growth coefficient was not significantly affected. Changes in maintenance respiration were correlated with a 33% increase in leaf total nonstructural carbohydrate concentration, but leaf nitrogen content of soybean leaves was not affected by CO2 enrichment. Thus, increased maintenance respiration may be a consequence of increased nonstructural carbohydrate accumulation. When whole soybean plants were switched from low CO2 to high CO2 for a brief period, leaf respiration was always reduced. However, this direct effect of CO2 partial pressure was approximately 50% less in plants grown in elevated CO2. We conclude from this study that there are potentially important effects of CO2 enrichment on plant respiration but that the effects are different for plants given a short-term increase in CO2 partial pressure versus plants grown in elevated CO2.

KEYWORDS: ELEVATED CO2, FIELD, FRUIT, GROWTH, MAINTENANCE RESPIRATION, METABOLISM, PHOSPHOENOLPYRUVATE, PLANTS, SOYBEAN LEAVES, TERM

2342

Thomas, R.B., J.D. Lewis, and B.R. Strain. 1994. Effects of leaf nutrient status on photosynthetic capacity in loblolly-pine (pinus-taeda L) seedlings grown in elevated atmospheric co2. *Tree Physiology 14(7-9):947-960.*

We measured needle photosynthesis of loblolly pine seedlings grown in a factorial experiment with two CO2 partial pressures (35 and 65 Pa) and three nutrient treatments (7 mM NH4NO3 + 1 mM PO4; 7 mM NH4NO3 + 0.2 mM PO4; 1 mM NH4NO3 + 1 mM PO4). The data were used to parameterize a physiologically based photosynthetic model that included limitations imposed by ribulose-1,5-bisphosphate carboxylase/oxygenase activity, electron transport capacity and inorganic phosphate availability. With nonlimiting nutrients, seedlings grown at 65 Pa CO2 had significantly higher net photosynthesis and lower stomatal conductance than seedlings grown at 35 Pa CO2. Nutrient limitations by either N or P significantly reduced photosynthetic capacity. When either N or P was limiting, there was no effect of growth CO2 partial pressure on photosynthesis, but stomatal conductance was significantly lower for seedlings grown at 65 Pa CO2. Modeled biochemical parameters suggest that, in all cases, photosynthesis was co-limited by carboxylation, electron transport and phosphate regeneration. Acclimation to growth in elevated CO2 involved a reduction in leaf N content. In the low-N and low-P treatments, modeled parameters indicated that the biochemical processes of photosynthesis were down regulated to the point that there was no effect of increasing CO2 partial pressure. The capacity to regenerate phosphate was reduced in both low nutrient treatments, but was only reduced by elevated C02 when seedlings were grown under low soil P conditions. Increased photosynthetic water use efficiency and nutrient use efficiency in response to CO2 enrichment occurred in all three nutrient treatments and have important implications for whole-plant water and nutrient balance. These data support the contention that soil nutrient status in forest ecosystems will be a critical influence on tree seedling response to increasing atmospheric CO2 partial pressures.

2343

Thomas, R.B., C.D. Reid, R. Ybema, and B.R. Strain. 1993. Growth and maintenance components of leaf respiration of cotton grown in elevated carbon-dioxide partial-pressure. *Plant, Cell and Environment 16(5):539-546.*

Elevated atmospheric carbon dioxide partial pressures have been shown to have variable direct and indirect effects on plant respiration rates. In this study, growth, leaf respiration, and leaf nitrogen and carbohydrate partitioning were measured in Gossypium hirsutum L. grown in 35 and 65Pa CO2 for 30 d. Growth and maintenance coefficients of leaf respiration were estimated using gas exchange techniques both at night and during the day. Elevated CO2 stimulated biomass production (107%) and net photosynthetic rates (35-50%). Total day-time respiration (R(d)) was not significantly affected by growth CO2 partial pressure. However, night respiration (R(n)) of leaves grown in 65 Pa CO2 Was significantly greater than that of plants grown in 35 Pa CO2. Correlation of R(d) and R(n) with leaf expansion rates indicated that plants in both CO2 treatments had equivalent growth respiration coefficients but maintenance respiration was significantly greater in elevated CO2. Increased maintenance coefficients in elevated CO2 appeared to be related to increased starch accumulation rather than to changes in leaf nitrogen.

KEYWORDS: CARBOHYDRATE CONTENT, CO2- ENRICHMENT, DARK RESPIRATION, EFFLUX, GAS-EXCHANGE, LEAVES, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, SHORT- TERM

2344

Thomas, R.B., D.D. Richter, H. Ye, P.R. Heine, and B.R. Strain. 1991. Nitrogen dynamics and growth of seedlings of an n-fixing tree (Gliricidia sepium (jacq) walp) exposed to elevated atmospheric carbon-dioxide. *Oecologia 88(3):415-421.*

Seeds of Gliricidia sepium (Jacq.) Walp., a tree native to seasonal tropical forests of Central America, were inoculated with N-fixing Rhizobium bacteria and grown in growth chambers for 71 days to investigate interactive effects of atmospheric CO2 and plant N status on early seedling growth, nodulation, and N accretion. Seedlings were

grown with CO2 partial pressures of 350 and 650-mu-bar (current ambient and a predicted partial pressure of the mid-21st century) and with plus N or minus N nutrient solutions to control soil N status. Of particular interest was seedling response to CO2 when grown without available soil N, a condition in which seedlings initially experienced severe N deficiency because bacterial N-fixation was the sole source of N. Biomass of leaves, stems, and roots increased significantly with CO2 enrichment (by 32%, 15% and 26%, respectively) provided seedlings were supplied with N fertilizer. Leaf biomass of N-deficient seedlings was increased 50% by CO2 enrichment but there was little indication that photosynthate translocation from leaves to roots or that plant N (fixed by Rhizobium) was altered by elevated CO2. In seedlings supplied with soil N, elevated CO2 increased average nodule weight, total nodule weight per plant, and the amount of leaf nitrogen provided by N-fixation (as indicated by leaf delta-N-15). While CO2 enrichment reduced the N concentration of some plant tissues, whole plant N accretion increased. Results support the contention that increasing atmospheric CO2 partial pressures will enhance productivity and N-fixing activity of N-fixing tree seedlings, but that the magnitude of early seedling response to CO2 will depend greatly on plant and soil nutrient status.

KEYWORDS: ALLOCATION, CO2- ENRICHMENT, FIXATION, NODULATION, PHYSIOLOGY, PINE, PISUM-SATIVUM, PLANTS, QUERCUS-ALBA, WATER

2345

Thomas, R.B., and B.R. Strain. 1991. Root restriction as a factor in photosynthetic acclimation of cotton seedlings grown in elevated carbon-dioxide. *Plant Physiology 96(2):627-634.*

Interactive effects of root restriction and atmospheric CO2 enrichment on plant growth, photosynthetic capacity, and carbohydrate partitioning were studied in cotton seedlings (Gossypium hirsutum L.) grown for 28 days in three atmospheric CO2 partial pressures (270, 350, and 650 microbars) and two pot sizes (0.38 and 1.75 liters). Some plants were transplanted from small pots into large pots after 20 days. Reduction of root biomass resulting from growth in small pots was accompanied by decreased shoot biomass and leaf area. When root growth was less restricted, plants exposed to higher CO2 partial pressures produced more shoot and root biomass than plants exposed to lower levels of CO2. In small pots, whole plant biomass and leaf area of plants grown in 270 and 350 microbars Of CO2 were not significantly different. Plants grown in small pots in 650 microbars Of CO2 produced greater total biomass than plants grown in 350 microbars, but the dry weight gain was found to be primarily an accumulation of leaf starch. Reduced photosynthetic capacity of plants grown at elevated levels Of CO2 was clearly associated with inadequate rooting volume. Reductions in net photosynthesis were not associated with decreased stomatal conductance. Reduced carboxylation efficiency in response to CO2 enrichment occurred only when root growth was restricted suggesting that ribulose-1,5- bisphosphate carboxylase/oxygenase activity may be responsive to plant source-sink balance rather than to CO2 concentration as a single factor. When root-restricted plants were transplanted into large pots, carboxylation efficiency and ribulose-1, 5-bisphosphate regeneration capacity increased indicating that acclimation of photosynthesis was reversible. Reductions in photosynthetic capacity as root growth was progressively restricted suggest sink-limited feedback inhibition as a possible mechanism for regulating net photosynthesis of plants grown in elevated CO2.

KEYWORDS: BEAN-PLANTS, CARBOXYLASE, ENRICHMENT, EXCHANGE, HIGH ATMOSPHERIC CO2, INHIBITION, LEAVES, LONG-TERM EXPOSURE, SOYBEANS, TEMPERATURE

2346

Thomas, S.C., and F.A. Bazzaz. 1996. Elevated CO2 and leaf shape: Are dandelions getting toothier? *American Journal of Botany 83(1):106-111.*

Heteroblastic leaf development in Taraxacum officinale is compared between plants grown under ambient (350 ppm) vs. elevated (700 ppm) CO2 levels. Leaves of elevated CO2 plants exhibited more deeply incised leaf margins and relatively more slender leaf laminae than leaves of ambient CO2 plants. These differences were found to be significant in allometric analyses that controlled for differences in leaf size, as well as analyses that controlled for leaf developmental order. The effects of elevated CO2 on leaf shape were most pronounced when plants were grown individually, but detectable differences were also found in plants grown at high density. Although less dramatic than in Taraxacum, significant effects of elevated CO2 on leaf shape were also found in two other weedy rosette species, Plantago major and Rumex crispus. These observations support the long-standing hypothesis that leaf carbohydrate level plays an important role in regulating heteroblastic leaf development, though elevated CO2 may also affect leaf development through direct hormonal interactions or increased leaf water potential. In Taraxacum, pronounced modifications of leaf shape were found at CO2 levels predicted to occur within the next century.

KEYWORDS: ALLOMETRY, AMBIENT, CARBON-DIOXIDE ENRICHMENT, COMPETITION, GROWTH, KUDZU PUERARIA-LOBATA, MORPHOLOGY, PLANTS, SYSTEM, TEMPERATURE

2347

Thomas, S.M., D. Whitehead, J.A. Adams, J.B. Reid, R.R. Sherlock, and A.C. Leckie. 1996. Seasonal root distribution and soil surface carbon fluxes for one-year-old Pinus radiata trees growing at ambient and elevated carbon dioxide concentration. *Tree Physiology 16(11-12):1015-1021.*

The increase in number of fine (< 0.5 mm diameter) roots of one-year-old clonal Pinus radiata D. Don trees grown in large open-top field chambers at ambient (362 mu mol mol(-1)) or elevated (654 mu mol mol(-1)) CO2 concentration was estimated using minirhizotron tubes placed horizontally at a depth of 0.3 m. The trees were well supplied with water and nutrients. Destructive harvesting of roots along an additional tube showed that there was a linear relationship between root number estimated from the minirhizotron and both root length density, L(v), and root carbon density, C-v, in the surrounding soil. Root distribution decreased with horizontal distance from the tree. At a depth of 0.3 m, 88% of the total C-v was concentrated within a 0.15-m radius from tree stems in the elevated CO2 treatment, compared with 35% for trees in the ambient CO2 treatment. Mean C-v along the tubes ranged up to 5 x 10(-2) mu g mm(-3) and tended to be greater for trees grown at elevated CO2 concentration, although the differences between CO2 treatments were not significant. Root growth started in spring and continued until late summer. There was no significant difference in seasonal rates of increase in C-v between treatments, but roots were observed four weeks earlier in the elevated CO2 treatment. No root turnover occurred at a depth of 0.3 m during the first year after planting. Mean values of carbon dioxide flux density at the soil surface, F, increased from 0.02 to 0.13 g m(-2) h(-1) during the year, and F was 30% greater for trees grown at elevated CO2 concentration than at ambient CO2. Diurnal changes in F were related to air temperature. The seasonal increase in F continued through the summer and early autumn, well after air temperature had begun to decline, suggesting that the increase was partly caused by increase in C-v as the roots colonized the soil profile.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, NITROGEN, PLANTATIONS, RESPIRATION, RESPONSES, TURNOVER

2348

Thomas, S.M., D. Whitehead, J.B. Reid, F.J. Cook, J.A. Adams, and A.C. Leckie. 1999. Growth, loss, and vertical distribution of Pinus radiata fine roots growing at ambient and elevated CO2 concentration. *Global Change Biology 5(1):107-121.*

Increased below-ground carbon allocation in forest ecosystems is a likely consequence of rising atmospheric CO2 concentration. If this results in changes to fine root growth, turnover and distribution long-term soil carbon cycling and storage could be altered. Bi-weekly measurements were made to determine the dynamics and distribution of fine roots (<1 mm diameter) for Pinus radiata trees growing at ambient (350 mu mol mol(-1)) and elevated (650 mu mol mol(-1)) CO2 concentration in large open-top chambers. Measurements were made using minirhizotrons installed horizontally at depths of 0.1, 0.3, 0.5 and 0.9 m. During the first year, at a depth of 0.3 m, the increase in relative growth rate of roots occurred 6 weeks earlier in the elevated CO2 treatment and the maximum rate was reached 10 weeks earlier than for trees in the ambient treatment. After 2 years, cumulative fine root growth (P-t) was 36% greater for trees growing at elevated CO2 than at ambient CO2 concentration, although this difference was not significant. A model of root growth driven by daily soil temperature accounted for between 43 and 99% of root growth variability. Total root loss (L-t) was 9% in the ambient and 14% in the elevated CO2 treatment, although this difference was not significant. Root loss was greatest at 0.3 m. In the first year, 62% of fine roots grown between mid-summer and late-autumn disappeared within a year in the elevated CO2 treatment, but only 18% in the ambient CO2 treatment (P < 0.01). An exponential model relating L-t to time accounted for between 74 and 99% of the variability. Root cohort half-lives were 951 d for the ambient and 333 d for the elevated treatment. Root length density decreased exponentially with depth in both treatments, but relatively more fine roots grown in the elevated CO2 treatment tended to occur deeper in the soil profile.

KEYWORDS: ATMOSPHERIC CO2, BELOWGROUND RESPONSES, BETULA- PAPYRIFERA, CARBON-DIOXIDE CONCENTRATION, COTTON ROOT, FORESTS, KIWIFRUIT ACTINIDIA-DELICIOSA, N-AVAILABILITY, NITROGEN, PONDEROSA PINE

2349

Thompson, G.B., J.K.M. Brown, and F.I. Woodward. 1993. The effects of host carbon-dioxide, nitrogen and water-supply on the infection of wheat by powdery mildew and aphids. *Plant, Cell and Environment 16(6):687-694.*

In two experiments, winter wheat (Triticum aestivum cv. Cerco) was grown in 350 (ambient) and 700 mumol mol-1 (elevated) atmospheric CO2 concentrations. In the first experiment, plants were grown at five levels of nitrogen fertilization, and in the second experiment, plants were grown at three levels of water supply. All plants were infected with powdery mildew, caused by the fungus Erysiphe graminis. Plants grown in elevated atmospheric CO2 concentrations had significantly reduced % shoot nitrogen contents and significantly increased % shoot water contents. At elevated atmospheric CO2 concentrations, where plant nitrogen content was significantly reduced, the severity of mildew infection was significantly reduced, and where host water content was significantly increased, the severity of mildew infection was significantly increased. In a moderate water supply treatment, the plants grown in elevated atmospheric CO2 concentrations had significantly reduced nitrogen contents (9.9%) and significantly increased water content (4%), the amount of mildew infection was unchanged. The severity of mildew infection appeared to be more sensitive to host water content than to host nitrogen content.

KEYWORDS: ATMOSPHERIC CO2, BARLEY, CO2- ENRICHMENT, FERTILIZATION, GRAIN-YIELD, INSECT HERBIVORE, PLANT GROWTH, SEEDLING GROWTH, WINTER-WHEAT

2350

Thompson, G.B., and B.G. Drake. 1994. Insects and fungi on a C-3 sedge and a C-4 grass exposed to elevated atmospheric co2 concentrations in open-top chambers in the field. *Plant, Cell and Environment 17(10):1161-1167.*

The effects of elevated atmospheric CO2 concentration on plant- fungi and plant-insect interactions were studied in an emergent marsh in the Chesapeake Bay. Stands of the C-3 sedge Scirpus olneyi Grey. and the C-4 grass Spartina patens (Ait.) Muhl. have been exposed to elevated atmospheric CO2 concentrations during each growing season since 1987. In August 1991 the severities of fungal infections and insect infestations were quantified. Shoot nitrogen concentration ([N]) and water content (WC) were determined. In elevated concentrations of atmospheric CO2, 32% fewer S. olneyi plants were infested by insects, and there was a 37% reduction in the severity of a pathogenic fungal infection, compared with plants grown in ambient CO2 concentrations. S. olneyi also had reduced [N], which correlated positively with the severities of fungal infections and insect infestations. Conversely, S. patens had increased WC but unchanged [N] in elevated concentrations of atmospheric CO2 and the severity of fungal infection increased. Elevated atmospheric CO2 concentration increased or decreased the severity of fungal infection depending on at least two interacting factors, [N] and WC; but it did not change the number of plants that were infected with fungi. In contrast, the major results for insects were that the number of plants infected with insects decreased, and that the amount of tissue that each insect ate also decreased.

KEYWORDS: BARLEY, CARBON DIOXIDE, GROWTH, NITROGEN-FERTILIZATION, PHOTOSYNTHESIS, POWDERY MILDEW, RESISTANCE, WATER-STRESS, WHEAT, YIELD

2351

Thompson, G.B., and F.I. Woodward. 1994. Some influences of co2 enrichment, nitrogen nutrition and competition on grain-yield and quality in spring wheat and barley. *Journal of Experimental Botany 45(276):937-942.*

Spring wheat and spring barley were grown in elevated atmospheric CO2 in controlled environments. Wheat was grown in monoculture and in competition with three weed species. In monoculture, wheat had 30% more grain yield and 28% less grain nitrogen in elevated compared to ambient atmospheric CO2. In competition, wheat had no significant increase in yield with elevated atmospheric CO2. In competition, grain nitrogen concentration was reduced in response to CO2 with the largest reduction occurring with the smallest competitor and the smallest reduction occurring with the largest competitor. Spring barley was grown in monoculture at three nitrogen fertilizer supplies. In elevated atmospheric CO2 there were significant increases in grain yield and reductions in grain nitrogen concentration at all levels of nitrogen supply. In both species the reductions in grain nitrogen concentration were large enough to affect current bread making processes.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, ELEVATED CO2, GENOTYPES, GROWTH, PARTITIONING EFFICIENCY, PLANTS, TRITICUM-AESTIVUM L, WINTER-WHEAT

2352

Thornley, J.H.M. 1998. Dynamic model of leaf photosynthesis with acclimation to light and nitrogen. *Annals of Botany 81(3):421-430.*

A simple model of photosynthesis in a mature C-3 leaf is described, based on a non-rectangular hyperbola: the model allows the high-light asymptote of that equation (P-max) to respond dynamically to light and nitrogen. This causes the leaf light response equation to acclimate continuously to the current conditions of light and N nutrition, which

can vary greatly within a crop canopy, and through a growing season, with important consequences for gross production. Predictions are presented for the dynamics of acclimation, acclimated and non-acclimated photosynthetic rates are compared, and the dependence of leaf properties on light and N availability is explored. There is good correspondence of predictions with experimental results at the leaf level. The model also provides a mechanism for a down regulation of photosynthesis in response to increased carbon dioxide concentrations, whose magnitude will depend on conditions, particularly of nitrogen nutrition. (C) 1998 Annals of Botany Company.

KEYWORDS: ALLOCATION, DAILY CANOPY PHOTOSYNTHESIS, ELEVATED CO2, FERTILIZATION, GRASSLAND, GROWTH, LEAVES, NET PHOTOSYNTHESIS, PLANTS, WATER

2353

Thornley, J.H.M., and M.G.R. Cannell. 1996. Temperate forest responses to carbon dioxide, temperature and nitrogen: A model analysis. *Plant, Cell and Environment 19(12):1331-1348.*

The ITE Edinburgh Forest Model, which describes diurnal and seasonal changes in the pools and fluxes of C, N and water in a fully coupled forest-soil system, was parametrized to simulate a managed conifer plantation in upland Britain, The model was used to examine (i) the transient effects on forest growth of an IS92a scenario of increasing [CO2] and temperature over two future rotations, and (ii) the equilibrium (sustainable) effects of all combinations of increases in [CO2] from 350 to 550 and 750 mu mol mol(-1), mean annual temperature from 7.5 to 8.5 and 9.5 degrees C and annual inputs of 20 or 40 kg N ha(- 1), Changes in underlying processes represented in the model were then used to explain the responses, Eight conclusions were supported by the model for this forest type and climate. (1) Increasing temperatures above 3 degrees C alone may cause forest decline owing to water stress. (2) Elevated [CO2] can protect trees from water stress that they may otherwise suffer in response to increased temperature. (3) In N-limiting conditions, elevated [CO2] can increase allocation to roots with little increase in leaf area, whereas in N-rich conditions elevated [CO2] may not increase allocation to roots and generally increases leaf area. (4) Elevated [CO2] can decrease water use by forests in N-limited conditions and increase water use in N-rich conditions. (5) Elevated [CO2] can increase forest productivity even in N-limiting conditions owing to increased N acquisition and use efficiency. (6) Rising temperatures (along with rising [CO2]) may increase or decrease forest productivity depending on the supply of N and changes in water stress. (7) Gaseous losses of N from the soil can increase or decrease in response to elevated [CO2] and temperature. (8) Projected increases in [CO2] and temperature (IS92a) are likely to increase net ecosystem productivity and hence C sequestration in temperate forests.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, CLIMATE CHANGE, ELEVATED CO2, GROWTH-RESPONSE, INCREASING CO2, NORTHERN FINLAND, NUTRIENT-UPTAKE, SCOTS PINE, SHORT- TERM, SOUR ORANGE TREES

2354

Thornley, J.H.M., and M.G.R. Cannell. 1997. Temperate grassland responses to climate change: An analysis using the Hurley pasture model. *Annals of Botany 80(2):205-221.*

The Hurley Pasture Model is process-based and couples the carbon, nitrogen and water cycles in the soil-grass-animal system. It was used to examine the responses of grasslands in southern, lowland and northern, upland climates in Britain. Short-term response to step-wise increases in CO2 concentration (350 to 700 mu mol mol(-1)) and temperature (5 degrees C) were contrasted with long-term equilibrium (the term 'equilibrium' is equivalent to 'steady state' throughout this paper) responses and with responses to gradually increasing [CO2] and temperature. Equilibrium responses to a range of climate variables were also examined. Three conclusions were drawn regarding the interpretation of experiments: (1) initial ecosystem responses to stepwise changes can be different in both magnitude and sign to equilibrium responses, and this can continue for many years; (2) grazing can drastically alter the magnitude and sign of the response of grasslands to climate change, be highly site-specific. It was concluded that experiments should try to lessen uncertainty about processes within models rather than try to predict ecosystem responses directly. Three conclusions were also drawn about the operation of grasslands as carbon sinks: (1) increasing [CO2] alone will produce a carbon sink, as long as it continues to accelerate photosynthesis and increase net primary productivity; (2) by contrast, increasing temperatures alone are likely to produce a carbon source, because soil respiration is accelerated more than net primary productivity, even when assuming the same temperature function for most soil and plant biochemical processes; and (3) the net effect of projected increases in [CO2] and temperature is likely to be a carbon sink of 5-15 g C m(-2) yr(-1) in humid, temperate grasslands for several decades, which is consistent with the magnitude of the hypothesized current global terrestrial carbon sink. (C) 1997 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS, CARBON-CYCLE, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NITROGEN-CONTENT, ORGANIC-MATTER DYNAMICS, SOIL, STORAGE

2355

Thron, C., K. Hahn, and C. Lutz. 1997. In situ effects of elevated CO2 on chlorophyll fluorescence and chloroplast pigments of alpine plants. *Acta Oecologica-International Journal of Ecology 18(3):193-200.*

Alpine vegetation responds to elevated CO2 with downward adjustment of photosynthesis. The experiments should show if doubling of ambient CO2 reduces the maximum quantum yield and the chlorophylls thus altering the pigment composition of the thylakoid membranes in typical species of an alpine grassland (Caricetum curvulae). The studies were part of a CO2 enrichment experiment with open-top chambers in the Swiss Central Alps in 2 470 m altitude over a period of four years. The leaves of Carer curvula and Trifolium alpinum were analysed ill situ under ambient (355 mu l/l) or elevated (680 mu l/l) CO2 and at two different nutrient levels. In each vegetation period both species showed a tendency to lower ratios of variable to maximum fluorescence (F-v/F-m) in plants with elevated CO2 treatment compared to the ambient variants. These reductions in F-v/F-m were statistically different only for Carer curvula in 1993 and 1995. CO2 enrichment caused reductions of leaf pigment concentrations of 10-30% especially far Trifolium alpinum whereas Carer curvula was less affected. The lower pigment contents per leaf were probably due to reductions of thylakoid membranes. In most cases, the influences of elevated CO2 or of nutrient treatments on pigment composition and primary photochemistry were very small. This indicates that the downward regulation begins at early stages in the photosynthetic process. Some changes of the photosynthetic apparatus are species-specific and possibly reflect different strategies of protective acclimation processes of alpine vegetation.

KEYWORDS: ALTITUDES, AVOIDANCE, CARBON DIOXIDE, EXPOSURE, FIELD, LEAVES, PHOTOINHIBITION, PHOTOSYNTHESIS, SEASON

2356

Tian, H., C.A.S. Hall, and Y. Qi. 1998. Modeling primary productivity of the terrestrial biosphere in changing environments: Toward a dynamic biosphere model. *Critical Reviews in Plant Sciences 17(5):541-557.*

There is a widespread perception that the atmosphere and the climate are

beginning to change, and that these changes could have profound impacts on the primary productivity of the terrestrial biosphere. The terrestrial biosphere is a dynamic system that interacts with the atmosphere and climate principally through the exchanges of energy, water, and elements. Due to the limitations of equilibrium terrestrial biosphere models, new generation models - dynamic biosphere models, are critically needed for assessing and predicting the primary production and biogeochemical cycles of the terrestrial biosphere in changing global environment. The goal of dynamic biosphere modeling is to model terrestrial ecosystem dynamics induced by natural and anthropogenic disturbances, as well as the interactions of energy, water, and carbon cycles within the terrestrial biosphere and between the terrestrial biosphere and the atmosphere. The critical gaps in developing such a terrestrial biosphere model are not our inability to construct model code but instead the poorly developed links between empiricism and the concepts we used to construct our models, especially a lack of data that would help to make our models mechanistic, an incomplete fundamental knowledge about how complex terrestrial ecosystems work, a poor understanding of how to scale up what we do know and of how to validate such a model. The interaction among data, model structure, parameter sets, and predictive uncertainty will Bead to important progress in the development of dynamic biosphere models.

KEYWORDS: ATMOSPHERIC CO2, CLIMATE CHANGE, EASTERN NORTH-AMERICA, ECOSYSTEM PROCESSES, GLOBAL CARBON-CYCLE, LAND-USE CHANGE, MISSING CO2 SINK, NET PRIMARY PRODUCTION, TRANSIENT-RESPONSE, TROPICAL DEFORESTATION

2357

Ticha, I. 1996. Optimization of photoautotrophic tobacco in vitro culture: Effect of suncaps closures on plantlet growth. *Photosynthetica 32(3):475-479.*

Maintenance of high carbon dioxide concentration during in vitro culture of tobacco plantlets by using suncaps closures (Sigma) and CO2 enrichment in the cultivation chamber increased dramatically the growth of plantlets measured as total dry matter accumulation and total leaf area production. The effect was enhanced with duration of culture. Photomixotrophically grown plantlets with 3 % saccharose in the Murashige-Skoog medium accumulated more dry matter and developed a larger total leaf area than plantlets grown strictly photoautotrophically without saccharose but the effect of better CO2 supply (suncaps) was seven (dry matter) to ten (leaf area) times higher in photoautotrophic plantlets as compared with photomixotrophic ones.

KEYWORDS: ACCLIMATIZATION, AGROBACTERIUM, CO2 CONCENTRATION, DEPENDENCE, GAS-EXCHANGE, INVITRO, PHOTOSYNTHESIS, REGENERANTS, STRAWBERRY PLANTLETS

2358

Tingey, D.T., M.G. Johnson, D.L. Phillips, D.W. Johnson, and J.T. Ball. 1996. Effects of elevated CO2 and nitrogen on the synchrony of shoot and root growth in ponderosa pine. *Tree Physiology 16(11-12):905-914.*

We monitored effects of elevated CO2 and N fertilization on shoot and fine root growth of Pinus ponderosa Dougl. ex P. Laws. and C. Laws. grown in native soil in open-top field- exposure chambers at Placerville, CA, over a 2-year period. The experimental design was a replicated 3 x 3 factorial with the center treatment missing; plants were exposed to ambient (similar to 365 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 in combination with one of three rates of N addition (0, 100 or 200 kg ha(-1) year(-1)). All CO2 by N interactions were nonsignificant. Both the CO2 and N treatments increased plant height, stem diameter and leaf area index (LAI). Elevated CO2 increased fine root area density and the occurrence of mycorrhizae, whereas N fertilization increased coarse root area density but had no effect on fine root area density. Spring flushes of shoot height and diameter growth were initiated concurrently with the increase in new root area density but height and diameter growth reached their maxima before that of fine roots. The temporal patterns of root and shoot growth were not altered by providing additional CO2 or N. Greatest root loss occurred in the summer, immediately following the period of greatest new fine root growth. Elevated N initially reduced the fine root area density/LAI ratio independently of CO2 treatment, indicating that the relationship between fine roots and needles was not changed by CO2 exposure.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, FINE ROOTS, MYCORRHIZAL, QUERCUS-ALBA, RESPONSES, SEEDLINGS, SITKA SPRUCE PLANTATION, SOIL N

2359

Tingey, D.T., M.G. Johnson, D.L. Phillips, and M.J. Storm. 1995. Effects of elevated CO2 and nitrogen on ponderosa pine fine roots and associated fungal components. *Journal of Biogeography 22(2-3):281-287.*

The effects of CO2 and nitrogen treatments on ponderosa pine (Pinus ponderosa Dougl. ex P. Laws. & C. Laws.) fine roots and associated fungal structures were monitored for a year (October 1992 to October 1993) using a minirhizotron camera system. The trees were grown in native soil in open-top field-exposure chambers at PlacerviUe, CA and exposed to ambient (similar to 350 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 and three levels of nitrogen addition (0, 100 and 200 kg ha(-1)); however, the 100 kg ha(-1) N treatment at ambient plus 175 mu mol mol(-1) CO2 treatment was omitted from the experimental design. Roots were classified as new, white, brown, decaying or missing and their lengths and diameters measured. The occurrence of mycorrhizae and fungal hyphae was also recorded. The majority (>90%) of roots observed were smaller than 2 mm and the mean diameter decreased during the study. None of the root parameters measured showed a significant response to elevated CO2. The elevated CO2 treatments consistently showed an increase in root area density averaging 50% larger compared to ambient CO2, but this response was not statistically significant due to the high spatial variability of root distribution. Only new root area density showed a significant nitrogen response. The most new roots were initiated between April and June and the highest level of root loss occurred between June and August. The occurrence of mycorrhizae and fungal hyphae increased in response to CO2 treatment but not the nitrogen. Their highest levels of occurrence were during August and October 93.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ECOSYSTEMS, FORESTS, MYCORRHIZAL, PHOTOSYNTHETIC ACCLIMATION, PRODUCTIVITY, QUERCUS-ALBA, SEEDLINGS, SOIL

2360

Tingey, D.T., B.D. McVeety, R. Waschmann, M.G. Johnson, D.L. Phillips, P.T. Rygiewicz, and D.M. Olszyk. 1996. A versatile sun-lit controlled-environment facility for studying plant and soil processes. *Journal of Environmental Quality 25(3):614-625.*

A new environmental-tracking, sun-lit controlled-environment facility (terracosm) that can control and manipulate climatic and edaphic factors while maintaining natural environmental variability was developed to study the effects of environmental stresses on a model ecosystem (i.e., plant and soil processes). An analysis of terracosm performance data indicates that the terracosms simulated natural seasonal and diurnal changes in atmospheric CO2, air and soil temperatures, vapor pressure

deficit (VPD), and soil moisture. The terracosm performance data indicate that between 92 and 100% of the hourly CO2 concentrations are within +/-50 mu mol mol(-1) of the target concentrations for both ambient and elevated treatments (1 Nov. 1993 through 30 Nov. 1994). Air temperatures are within 2 degrees C of the target temperature between 85 and 100% of the hours for both ambient and elevated temperature treatments. The VPD was approximately the same (0.09 kPa difference between treatments) in the ambient and elevated temperature treatments. Distributed process control was implemented to minimize down- time. Terracosm downtime, periods when terracosm environmental conditions could not be reliably controlled, varied between 2.4 and 2.8% of all hours, and was equally distributed between biological sampling and equipment problems.

KEYWORDS: CO2, ECOSYSTEMS, FIELD, PHOTOSYNTHESIS

2361

Tingey, D.T., D.L. Phillips, D.G. Johnson, D.W. Johnson, and J.A. Weber. 1997. Elevated CO2 increases fine root growth and fine root turnover in Pinus ponderosa. *Plant Physiology 114(3):1358.*

2362

Tingey, D.T., D.L. Phillips, M.G. Johnson, M.J. Storm, and J.T. Ball. 1997. Effects of elevated CO2 and N fertilization on fine root dynamics and fungal growth in seedling Pinus ponderosa. *Environmental and Experimental Botany 37(2-3):73-83.*

The effects of elevated CO2 and N fertilization on fine root growth of Pinus ponderosa Dougl. ex P. Laws. C. Laws., grown in native soil in open-top held-exposure chambers at Placerville, CA, were monitored for a 2-year period using minirhizotrons. The experimental design was a replicated 3 x 3 factorial with a treatment missing; plants were exposed to ambient (approximate to 365 mu mol mol(-1)) air or ambient air plus either 175 or 350 mu mol mol(-1) CO2 and three levels of N addition (0, 100 and 200 kg ha(-1) year(-1)). By the second year, elevated CO2 increased fine root occurrence and root length while N fertilization had no effect. The CO2 x N interactions were not significant. Neither elevated CO2 nor N fertilization altered fine root diameter. Fine root mortality was increased by increasing soil N but was reduced in elevated CO2. Highest fine root mortality occurred during summer and was lowest during winter. Elevated CO2 increased mycorrhizal and fungal occurrence earlier than N fertilization. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ENRICHMENT, LOBLOLLY-PINE, MYCORRHIZAL COLONIZATION, NITROGEN, QUERCUS-ALBA, SOIL RESPIRATION, TEMPERATURE, TURNOVER

2363

Tinker, B., and H. Mooney. 1996. Plant-soil carbon belowground: The effects of elevated CO2 selected papers from an International GCTE Workshop, 20-23 September 1995, Mansfield College, University of Oxford, UK - Introduction. *Plant and Soil 187(2):107.*

2364

Tischler, C.R., H.W. Polley, H.B. Johnson, and H.S. Mayeux. 1998. Environment and seedling age influence mesquite response to epicotyl removal. *Journal of Range Management 51(3):361-365.*

Herbivory by small mammals is a major factor controlling survival of honey mesquite (Prosopis glandulosa Torr. var, glandulosa) seedlings. Clipping below the cotyledons is lethal; removal of the epicotyl may not be lethal but can severely limit seedling growth. Seedlings of other woody species sometimes compensate for epicotyl removal by prolonging the life of cotyledons. Also, projected future increases in atmospheric CO2 concentration could influence survival and growth after epicotyl removal. Objectives of this study were to determine effects of epicotyl removal at various seedling ages, atmospheric CO2 concentrations, and soil fertility, on (1) seedling survival, (2) cotyledonary leaf longevity, and (3) shoot and root growth of young seedlings. Mesquite seedlings were grown at 350, 700, and 1,000 mu L liter(-1) atmospheric CO2 concentration in nutrient poor and nutrient rich soils. All ages of seedlings survived epicotyl removal. Cotyledonary leaf fresh mass and chlorophyll content were higher in plants where epicotyls were clipped. Root and shoot mass of both clipped and unclipped plants generally increased at higher CO2 concentrations when mineral nutrition was adequate, but responded less to CO2 when soil fertility was low. Responses to epicotyl clipping in mesquite seedlings are complex, being strongly influenced by soil fertility, atmospheric CO2 concentration, seedling age at clipping, and interactions between these factors.

KEYWORDS: ENRICHMENT, ESTABLISHMENT, GROWTH, INCREASING CO2, PLANT, PROSOPIS, RATES

2365

Tissue, D.T., K.L. Griffin, and J.T. Ball. 1999. Photosynthetic adjustment in field-grown ponderosa pine trees after six years of exposure to elevated CO2. *Tree Physiology 19(4-5):221-228.*

Photosynthesis of tree seedlings is generally enhanced during short-term exposure to elevated atmospheric CO2, but longer- term photosynthetic responses are often more variable because they are affected by morphological, biochemical and physiological feedback mechanisms that regulate carbon assimilation to meet sink demand. To examine biochemical and morphological factors that might regulate the long-term photosynthetic response of field-grown trees to elevated CO2, we grew ponderosa pine (Pinus ponderosa Dougl. ex Laws.) trees in open-top chambers for six years in native soil at ambient CO2 (35 Pa) and elevated CO2 (70 Pa) at a site near Placerville, CA. Trees were well watered and exposed to natural light and ambient temperature. At the end of the sixth growing season at elevated CO2, net photosynthesis was enhanced 53%, despite reductions in photosynthetic capacity. The positive net photosynthetic response to elevated CO2 reflected greater relative increases in Rubisco sensitivity compared with the decreases resulting from biochemical adjustments. Analyses of net photosynthetic rate versus internal CO2 partial pressure curves indicated that reductions in photosynthetic capacity in response to elevated CO2 were the result of significant reductions in maximum photosynthetic rate (20%), Rubisco carboxylation capacity (36%), and electron transport capacity (21%). Decreased photosynthetic capacity was accompanied by reductions in various photosynthetic components, including total chlorophyll (24%), Rubisco protein content (38%), and mass-based leaf nitrogen concentration (14%). Net photosynthesis was unaffected by morphological adjustments because there was no change in leaf mass per unit area at elevated CO2. An apparent positive response of photosynthetic adjustment in the elevated CO2 treatment was the redistribution of N within the photosynthetic system to balance Rubisco carboxylation and electron transport capacities. We conclude that trees, without apparent limitations to root growth, may exhibit photosynthetic adjustment responses in the field after long-term exposure to elevated CO2.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, FOLIAR GAS-EXCHANGE, LEAF, LONG-TERM, PHASEOLUS-VULGARIS, PLANTS, RISING ATMOSPHERIC CO2, STOMATAL CONDUCTANCE

2366

Tissue, D.T., K.L. Griffin, R.B. Thomas, and B.R. Strain. 1995. Effects of low and elevated co2 on C-3 and C-4 annuals .2. Photosynthesis and leaf biochemistry. *Oecologia 101(1):21-28.*

Abutilon theophrasti (C-3) and Amaranthus retroflexus (C-4), were grown from seed at four partial pressures of CO2: 15 Pa (below Pleistocene minimum), 27 Pa (pre-industrial), 35 Pa (current), and 70 Pa (future) in the Duke Phytotron under high light, high nutrient, and well-watered conditions to evaluate their photosynthetic response to historic and future levels of CO2. Net photosynthesis at growth CO2 partial pressures increased with increasing CO2, for C-3 plants, but not C-4 plants. Net photosynthesis of Abutilon at 15 Pa CO2 was 70% less than that of plants grown at 35 Pa CO2, due to greater stomatal and biochemical limitations at 15 Pa CO2. Relative stomatal limitation (RSL) of Abutilon at 15 Pa CO2 was nearly 3 times greater than at 35 Pa CO2. A photosynthesis model was used to estimate ribulose-1,5-bisphosphate carboxylase (rubisco) activity (Vc(max)), electron transport mediated RuBP regeneration capacity (J(max)), and phosphate regeneration capacity (PiRC) in Abutilon from net photosynthesis versus intercellular CO2 (A-C-i) curves. All three component processes decreased by approximately 25% in Abutilon grown at 15 Pa compared with 35 Pa CO2. Abutilon grown at 15 Pa CO2 had significant reductions in total rubisco activity (25%), rubisco content (30%), activation state (29%), chlorophyll content (39%), N content (32%), and starch content (68%) compared with plants grown at 35 Pa CO2. Greater allocation to rubisco relative to light reaction components and concomitant decreases in J(max) and PiRC suggest co-regulation of biochemical processes occurred in Abutilon grown at 15 Pa CO2. There were no significant differences in photosynthesis or leaf properties in Abutilon grown at 27 Pa CO2 compared with 35 Pa CO2, suggesting that the rise in CO2 since the beginning of the industrial age has had little effect on the photosynthetic performance of Abutilon. For Amaranthus, limitations of photosynthesis were balanced between stomatal and biochemical factors such that net photosynthesis was similar in all CO2 treatments. Differences in photosynthetic response to growth over a wide range of CO2 partial pressures suggest chang es in the relative performance of C-3 and C-4 annuals as atmospheric CO2 has fluctuated over geologic time.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELECTRON-TRANSPORT, ENRICHMENT, GROWTH, LEAVES, LIGHT-INTENSITY, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, STOMATAL CONDUCTANCE

2367

Tissue, D.T., J.P. Megonigal, and R.B. Thomas. 1997. Nitrogenase activity and N-2 fixation are stimulated by elevated CO2 in a tropical N-2-fixing tree. *Oecologia 109(1):28-33.*

Seeds of Gliricidia sepium, a fast-growing woody legume native to seasonal tropical forests of Central America, were inoculated with N-2-fixing Rhizobium bacteria and grown in environmentally controlled glasshouses for 67-71 days under ambient CO2 (35 Pa) and elevated CO2 (70 Pa) conditions. Seedlings were watered with an N-free, but otherwise complete, nutrient solution such that bacterial N-2 fixation was the only source of N available to the plant. The primary objective of our study was to quantify the effect of CO2 enrichment on the kinetics of photosynthate transport to nodules and determine its subsequent effect on N-2 fixation. Photosynthetic rates and carbon storage in leaves were higher in elevated CO2 plants indicating that more carbon was available for transport to nodules. A (CO2)-C-14 pulse-chase experiment demonstrated that photosynthetically fixed carbon was supplied by leaves to nodules at a faster rate when plants were grown in elevated CO2. Greater rates of carbon supply to nodules did not affect nodule mass per plant, but did increase specific nitrogenase activity (SNA) and total nitrogenase activity (TNA) resulting in greater N-2 fixation. In fact, a 23% increase in the rate of carbon supplied to nodules coincided with a 23% increase in SNA for plants grown in elevated CO2, suggesting a direct correlation between carbon supply and nitrogenase activity. The improvement in plant N status produced much larger plants when grown in elevated CO2. These results suggest that Gliricidia, and possibly other N-2-fixing trees, may show an early and positive growth response to elevated CO2, even in severely N- deficient soils, due to increased nitrogenase activity.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DEFOLIATION, ECOSYSTEMS, ENRICHMENT, GROWTH, NODULATION, PISUM-SATIVUM, SEEDLINGS, WHITE CLOVER, WOODY-PLANTS

2368

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1993. Long-term effects of elevated co2 and nutrients on photosynthesis and rubisco in loblolly-pine seedlings. *Plant, Cell and Environment 16(7):859-865.*

The effects of long-term CO2 enhancement and varying nutrient availability on photosynthesis and ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) were studied on loblolly pine (Pinus taeda L.) seedlings grown in two atmospheric CO2 partial pressures (35 and 65 Pa) and three nutrient treatments (low N, low P, and high N and P). Measurements taken in late autumn (November) after 2 years Of CO2 enrichment and nutrient addition showed that photosynthetic rates were higher for plants grown at elevated CO2 only when they received supplemental N. Total rubisco activity and rubisco content decreased at elevated CO2, but there was an increase in activation state. At elevated CO2, proportionately less N was found in rubisco and more N was found in the light reaction components. These results demonstrate acclimation of photosynthetic processes to elevated CO2 through reallocation of N. Loblolly pine grown in nutrient conditions similar to native soils (low N availability) had lower needle N and chlorophyll content, lower total rubisco activity and content, and lower photosynthetic rates than plants grown at high N and P. This suggests that the magnitude of the photosynthetic response to a future, high-CO2 environment will be dependent on soil fertility in the system.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-3, CHLOROPHYLL, ELECTRON-TRANSPORT, LEAVES, NITROGEN-USE EFFICIENCY, PHASEOLUS-VULGARIS L, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE

2369

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1996. Growth and photosynthesis of loblolly pine (Pinus taeda) after exposure to elevated CO2 for 19 months in the field. *Tree Physiology 16(1-2):49-59.*

To detect seasonal and long-term differences in growth and photosynthesis of loblolly pine (Pinus taeda L.) exposed to elevated CO2 under ambient conditions of precipitation, light, temperature and nutrient availability, seedlings were planted in soil representative of an early, abandoned agricultural field and maintained for 19 months in the field either in open- top chambers providing one of three atmospheric CO2 partial pressures (ambient, ambient +15 Pa, and ambient +30 Pa) or in unchambered control plots. An early and positive response to elevated CO2 substantially increased total plant biomass. Peak differences in relative biomass enhancement occurred after 11 months of CO2 treatment when biomass of plants grown at +15 and +30 Pa CO2 was 111 and 233% greater, respectively, than that of plants grown at ambient CO2. After 19 months, there was no significant difference in biomass between +15 Pa CO2-treated plants and ambient CO2-treated plants, whereas biomass of +30 Pa CO2-treated plants was 111% greater than that of ambient CO2-treated plants. Enhanced rates of leaf-level photosynthesis were maintained in plants in the elevated CO2 treatments throughout the 19-month exposure period despite reductions in both

leafN concentration and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity during the first 11 months of CO2 exposure. Reductions in Rubisco activity indicated photosynthetic adjustment to elevated CO2, but Rubisco-mediated control of photosynthesis was small. Seasonal shifts in sink strength affected photosynthetic rates, greatly magnifying the positive effects of elevated CO2 on photosynthesis during periods of rapid plant growth. Greater carbon assimilation by the whole plant accelerated plant development and thereby stimulated new sinks for carbon through increased plant biomass, secondary branching and new leaf production. We conclude that elevated CO2 will enhance photosynthesis and biomass accumulation in loblolly pine seedlings under high nutrient conditions; however, reductions over time in the relative biomass response of plants to elevated CO2 complicate predictions of the eventual magnitude of carbon storage in this species under future CO2 conditions.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, NITROGEN, RESPONSES, SEEDLINGS, SOUR ORANGE TREES, UNITED-STATES

2370

Tissue, D.T., R.B. Thomas, and B.R. Strain. 1997. Atmospheric CO2 enrichment increases growth and photosynthesis of Pinus taeda: a 4 year experiment in the field. *Plant, Cell and Environment 20(9):1123-1134.*

Forest trees are major components of the terrestrial biome and their response to rising atmospheric CO2 plays a prominent role in the global carbon cycle. In this study, loblolly pine seedlings were planted in the field in recently disturbed soil of high fertility, and CO2 partial pressures were maintained at ambient CO2 (Amb) and elevated CO2 (Amb + 30 Pa) for 4 years. The objective of the study was to measure seasonal and long- term responses in growth and photosynthesis of loblolly pine exposed to elevated CO2 under ambient field conditions of precipitation, light, temperature and nutrient availability. Loblolly pine trees grown in elevated CO2 produced 90% more biomass after four growing seasons than did trees grown in ambient CO2. This large increase in final biomass was primarily due to a 217% increase in leaf area in the first growing season which resulted in much higher relative growth rates for trees grown in elevated CO2. Although there was not a sustained effect of elevated CO2 on relative growth rate after the first growing season, absolute production of biomass continued to increase each year in trees grown in elevated CO2 as a consequence of the compound interest effect of increased leaf area on the production of more new leaf area and more biomass. Allometric analyses of biomass allocation patterns demonstrated size-dependent shifts in allocation, but no direct effects of elevated CO2 on partitioning of biomass. Leaf photosynthetic rates were always higher in trees grown in elevated CO2, but these differences were greater in the summer (60-130% increase) than in the winter (14-44% increase), reflecting strong seasonal effects of temperature on photosynthesis. Our results suggest that seasonal variation in the relative photosynthetic response to elevated CO2 will occur in natural ecosystems, but total non-structural carbohydrate (TNC) levels in leaves indicate that this variation may not always be related to sink activity. Despite indications of canopy-level adjustments in carbon assimilation, enhanced levels of leaf photosynthesis coupled with increased total leaf area indicate that net carbon assimilation for the whole tree was greater for trees grown under elevated CO2 compared with ambient CO2. If the large growth enhancement observed in loblolly pine were maintained after canopy closure, then these trees could be a large sink for fossil carbon emitted to the atmosphere and produce a negative feedback on atmospheric CO2.

KEYWORDS: BIOMASS ALLOCATION, COMPENSATORY RESPONSES, ELEVATED CARBON-DIOXIDE, FOLIAR GAS-EXCHANGE, LOBLOLLY-PINE, PLANT-RESPONSES, PONDEROSA PINE, SOIL FERTILITY, SOUR ORANGE TREES, WATER-STRESS

2371

Titus, J.E. 1992. Submersed macrophyte growth at low ph .2. Co2 X sediment interactions. *Oecologia 92(3):391-398.*

The submersed macrophyte Vallisneria americana was grown for seven weeks in a greenhouse to test for differences in the ability of three different sediments to support growth stimulation in response to CO2 enrichment at low pH. Plants accumulated 21- to 24-fold greater biomass at 10 x ambient CO2 concentrations than at ambient CO2 on all sediments. At both CO2 levels, plants grown on sediment from an acidified lake accumulated ca. 81%, and those grown on oligotrophic lake sediment ca. 47% as much biomass as plants grown on alkaline lake sediment. Despite striking CO2 and sediment effects on biomass accumulation, there was no significant interaction (using log-transformed data) between CO2 and sediment effects, indicating that all sediments allowed similar proportionate growth responses to CO2 enrichment. Plants grown on the less fertile sediments showed greater relative allocation to horizontal versus vertical growth by producing more rosette- bearing stolons in relation to plant height (leaf length) than plants grown on relatively fertile, alkaline lake sediment. Tissue analysis suggested that sediment effects on Vallisneria growth could be attributed neither to mineral nutrient (nitrogen and phosphorus) limitation nor to aluminum toxicity in these low pH treatments. In any case, CO2 availability can be an important regulator of submersed macrophyte growth at low pH on a variety of sediment types, including those from oligotrophic and acidic lakes.

KEYWORDS: AQUATIC MACROPHYTES, ATMOSPHERIC CO2, ENRICHMENT, LAKE ACIDIFICATION, NATURAL SEDIMENTS, NITROGEN, RESPONSES, TISSUE CHEMISTRY, VALLISNERIA-AMERICANA, WATER

2372

Titus, J.E., and J.H. Andorfer. 1996. Effects of CO2 enrichment on mineral accumulation and nitrogen relations in a submersed macrophyte. *Freshwater Biology 36(3):661-671.*

1. Six- to eight-week greenhouse experiments with independent control of pH and dissolved CO2 evaluated the potential for CO2 enrichment to stimulate the accumulation of Al, Fe, P and N in shoots of Vallisneria americana, particularly at pH 5. These minerals were provided only as they occurred in natural lake sediments. 2. The effect of CO2 enrichment at pH 5 v pH 7.3 on growth and tissue N concentration was also determined. 3. CO2 enrichment at pH 5 effected 5.5- and 7-fold increases in total shoot accumulation of Al and Fe, respectively. In a two-way factorial experiment, CO2 enrichment yielded 6- to 11-fold greater total shoot P accumulation in plants grown on less and more fertile sediments, respectively. 4. In a three-way factorial experiment, CO2 enrichment stimulated Vallisneria growth, especially at pH 5, and resulted in a 31-58% reduction in tissue [N] for different pH x sediment combinations. These are greater reductions than previously reported. It also increased total shoot N accumulation up to 6-fold, and there were significant interactions with pH and sediment source: the CO2 enrichment effect on shoot N accumulation was greater at pH 5 than at pH 7.3, and it was greater with the more fertile sediment at pH 5. 5. Water chemistry (pH and/or [CO2]) and sediment fertility thus both indirectly influenced the accumulation of sediment-derived minerals in macrophyte shoots within the water column.

KEYWORDS: AQUATIC MACROPHYTES, DISSOLVED INORGANIC CARBON, FRESH-WATER MACROPHYTES, INSECT HERBIVORE, MYRIOPHYLLUM- SPICATUM, NATURAL SEDIMENTS, SEDIMENT INTERACTIONS, SOIL EXTRACTS, TISSUE CHEMISTRY, VALLISNERIA-AMERICANA

2373

Titus, J.E., R.S. Feldman, and D. Grise. 1990. Submersed macrophyte growth at low ph .1. CO2 enrichment effects with fertile sediment. *Oecologia 84(3):307-313.*

2374

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO2 and temperature. *Tree Physiology 18(11):715-726.*

Biochemical models of photosynthesis suggest that rising temperatures will increase rates of net carbon dioxide assimilation and enhance plant responses to increasing atmospheric concentrations of CO2. We tested this hypothesis by evaluating acclimation and ontogenetic drift in net photosynthesis in seedlings of five boreal tree species grown at 370 and 580 mu mol mol(-1) CO2 in combination with day/night temperatures of 18/12, 21/15, 24/18, 27/21, and 30/24 degrees C. Leaf-area-based rates of net photosynthesis increased between 13 and 36% among species in plants grown and measured in elevated CO2 compared to ambient CO2. These CO2-induced increases in net photosynthesis were greater for slower-growing Picea mariana (Mill.) B.S.P., Pinus banksiana Lamb., and Larix laricina (Du Roi) K. Koch than for faster-growing Populus tremuloides Michx. and Betula papyrifera Marsh., paralleling longer-term growth differences between CO2 treatments. Measures at common CO2 concentrations revealed that net photosynthesis was down-regulated in plants grown at elevated CO2. In situ leaf gas exchange rates varied minimally across temperature treatments and, contrary to predictions, increasing growth temperatures did not enhance the response of net photosynthesis to elevated CO2 in four of the five species. Overall, the species exhibited declines in specific leaf area and leaf nitrogen concentration, and increases in total nonstructural carbohydrates in response to CO2 enrichment. Consequently, the elevated CO2 treatment enhanced rates of net photosynthesis much more when expressed on a leaf area basis (25 %) than when expressed on a leaf mass basis (10%). In all species, rates of leaf net CO2 exchange exhibited modest declines with increasing plant size through ontogeny. Among the conifers, enhancements of photosynthetic rates in elevated CO2 were sustained through time across a wide range of plant sizes. In contrast, for Populus tremuloides and B. papyrifera, mass-based photosynthetic rates did not differ between CO2 treatments. Overall, net photosynthetic rates were highly correlated with relative growth rate as it varied among species and treatment combinations through time. We conclude that interspecific variation may be a more important determinant of photosynthetic response to CO2 than temperature.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSE, LEAF, NITROGEN-USE, PLANT-TISSUE, PRODUCTIVITY, SOURCE-SINK RELATIONS, STARCH

2375

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1998. Temperature and ontogeny mediate growth response to elevated CO2 in seedlings of five boreal tree species. *New Phytologist 140(2):197-210.*

We tested the extent to which growth responses to elevated carbon dioxide (CO2) are temperature-dependent and change through early seedling ontogeny among boreal tree species of contrasting relative growth rates (RGR). Populus tremuloides Michx, Betula papyrifera Marsh, Larix laricina (Du Roi) K. Koch, Pinus banksiana Lamb., and Picea mariana (Mill.) B.S.P. were grown from seeds for 3 months in controlled-environment chambers at two CO2 concentrations (370 and 580 mu mol mol-L) and five temperature regimes of 18/12, 21/15, 24/18, 27/21 and 30/24 degrees C (light/dark). Growth increases in response to CO2 enrichment were minimal at the lowest temperature and maximal at 21/15 OC for the three conifers and at 24/18 degrees C or higher for the two broadleaved species, corresponding with differences in optimal temperatures for growth. In both CO2 treatments, RGR among species and temperatures correlated positively with leaf area ratio (LAR) (r greater than or equal to 0.90, P < 0.0001). However, at a given LAR, RGR was higher in elevated CO2, owing to enhanced whole-plant net assimilation rate. On average in all species and temperatures at a common plant mass, CO2 enrichment increased RGR (9 %) through higher whole-plant net assimilation rate (22 %), despite declines in LAR in high CO2 (11 %). Reductions in LAR are thus an important feedback mechanism reducing positive plant growth responses to CO2. Proportional allocation of dry mass to roots did not vary between CO2 treatments. Early in the experiment, proportional increases in plant dry mass in elevated CO2 were larger in faster-growing Populus tremuloides and B. papyrifera than in the slower-growing conifers. However, growth increases in response to CO2 enrichment fell with time for broadleaved species and increased for the conifers. With increasing plant size over time, compensatory adjustments to CO2 enrichment in the factors that determine RGR, such as LAR, were much larger in broadleaves than in conifers. Thus, the hypothesis that faster-growing species are more responsive to elevated CO2 was not supported, given contrasting patterns of growth response to CO2 with increasing plant size and age.

KEYWORDS: ATMOSPHERIC CO2, BIOMASS ALLOCATION, CARBON DIOXIDE, COMPENSATORY RESPONSES, GAS-EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, PLANTS, PONDEROSA PINE, RESPIRATION, SOURCE-SINK RELATIONS

2376

Tjoelker, M.G., J. Oleksyn, and P.B. Reich. 1999. Acclimation of respiration to temperature and CO2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology 5(6):679-691.*

The role of acclimation of dark respiration to temperature and CO2 concentration and its relationship to growth are critical in determining plant response to predicted global change. We explored temperature acclimation of respiration in seedlings of tree species of the North American boreal forest. Populus tremuloides, Betula papyrifera, Larix laricina, Pinus banksiana, and Picea mariana plants were grown from seed in controlled-environments at current and elevated concentrations of CO2 (370 and 580 mu mol mol(-1)) in combination with three temperature treatments of 18/12, 24/18, and 30/24 degrees C (light/dark period). Specific respiration rates of roots and shoots acclimated to temperature, damping increases in rates across growth-temperature environments compared to short-term temperature responses. Compared at a standard temperature, root and shoot respiration rates were, on average, 40% lower in plants grown at the highest compared to lowest growth temperature. Broad-leaved species had a lower degree of temperature acclimation of respiration than did the conifers. Among species and treatment combinations, rates of respiration were linearly related to size and relative growth rate, and relationships were comparable among growth environments. Specific respiration rates and whole-plant respiratory CO2 efflux as a proportion of daily net CO2 uptake increased at higher growth temperatures, but were minimally affected by CO2 concentration. Whole-plant specific respiration rates were two to three times higher in broad-leaved than coniferous species. However, compared to faster-growing broad-leaved species, slower-growing conifers lost a larger proportion of net daily CO2 uptake as respiratory CO2 efflux, especially in roots. Interspecific variation in acclimation responses of dark respiration to temperature is more important than acclimation of respiration to CO2 enrichment in modifying tree seedling growth responses to projected increases in CO2 concentration and temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CONSTRUCTION, ELEVATED CO2, ENRICHMENT, LEAF DARK RESPIRATION,

LEAVES, MAINTENANCE RESPIRATION, NITROGEN, RESPONSES, ROOT RESPIRATION

2377

Tjoelker, M.G., P.B. Reich, and J. Oleksyn. 1999. Changes in leaf nitrogen and carbohydrates underlie temperature and CO2 acclimation of dark respiration in five boreal tree species. *Plant, Cell and Environment 22(7):767-778.*

We tested the hypothesis that acclimation of foliar dark respiration to CO2 concentration and temperature is associated with adjustments in leaf structure and chemistry. Populus tremuloides Michx, Betula papyrifera Marsh, Larix laricina (Du Roi) K, Koch, Pinus banksiana Lamb., and Picea mariana (Mill,) B.S.P. were grown from seed in combined CO2 (370 or 580 mu mol mol(-1)) and temperature treatments (18/12, 24/18, or 30/24 degrees C), Temperature and CO2 effects were predominately independent. Specific respiration rates partially acclimated to warmer thermal environments through downward adjustment in the intercept, but not Q(10) of the temperature-response functions. Temperature acclimation of respiration was larger for conifers than broad-leaved species and was associated with pronounced reductions in leaf nitrogen concentrations in conifers at higher growth temperatures. Shortterm increases in CO2 concentration did not inhibit respiration. Growth in the elevated CO2 concentration reduced leaf nitrogen and increased non-structural carbohydrate concentrations. However, for a given nitrogen concentration, respiration was higher in leaves grown in the elevated CO2 concentration, as rates increased with increasing carbohydrates, Across species and treatments, respiration rates were a function of both leaf nitrogen and carbohydrate concentrations (R-2 = 0.71, P < 0.0001). Longterm acclimation of foliar dark respiration to temperature and CO2 concentration is largely associated with changes in nitrogen and carbohydrate concentrations.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, ENRICHMENT, GAS-EXCHANGE, GROWTH TEMPERATURE, LEAVES, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS, PLANT RESPIRATION, RESPONSES

2378

Tognetti, R., A. Giovannelli, A. Longobucco, F. Miglietta, and A. Raschi. 1996. Water relations of oak species growing in the natural CO2 spring of Rapolano (central Italy). *Annales Des Sciences Forestieres 53(2-3):475-485.*

The effect of elevated atmospheric carbon dioxide on water relations was examined on downy oak (Quercus pubescens) and helm oak (Q ilex) trees. The study was conducted on trees growing in a naturally enriched CO2 spring. Sap velocity and sap flow were measured by the heat pulse technique. On the same trees, daily courses of xylem water potential, leaf conductance and transpiration were monitored. Plant water relations were evaluated by pressure-volume analysis method on shoots; on the same branches, relative conductivity of xylem was measured. Both species exhibited increased osmotic potential and decreased symplasmic fraction of water in trees adapted to increased CO2. Downy oak showed lower stomatal conductance under elevated CO2, but helm oak did not. Both species displayed higher sap flow in control trees. In both species, increased carbon dioxide did not influence xylem embolism formation.

KEYWORDS: DROUGHT, EFFICIENCY, ELEVATED CO2, FORESTS, PRESSURE, RESPONSES, TEMPERATE

2379

Tognetti, R., and J.D. Johnson. 1999. The effect of elevated atmospheric CO2 concentration and nutrient supply on gas exchange, carbohydrates and foliar phenolic concentration in live oak (Quercus virginiana Mill.) seedlings. *Annals of Forest Science 56(5):379-389.*

We determined the direct effects of atmospheric CO2 concentration ([CO2]) on leaf gas exchange, phenolic and carbohydrate allocation in live oak seedlings (Quercus virginiana Mill.) grown at present (370 mu mol.mol(-1)) or elevated (520 mu mol.mol(-1)) [CO2] for 6 months in open-top chambers. Two soil nitrogen (N) treatments (20 and 90 mu mol.mol(-1) total N, low N and high N treatments, respectively) were imposed by watering the plants every 5 d with modified water soluble fertilizer. Enhanced rates of leaf-level photosynthesis were maintained in plants subjected to elevated [CO2] over the 6-month treatment period in both N treatments. A combination of increased rates of photosynthesis and decreased stomatal conductance was responsible for nearly doubling water use efficiency under elevated [CO2]. The sustained increase in photosynthetic rate was accompanied by decreased dark respiration in elevated [CO2]. Elevated [CO2] led to increased growth rates; while total non-structural carbohydrate (sugars and starch) concentrations were not significantly Affected by elevated [CO2] treatment. The concentration of phenolic compounds increased significantly under elevated [CO2]. ((C) Inra/Elsevier, Paris.).

KEYWORDS: BETULA-PENDULA ROTH, CARBON-DIOXIDE ENRICHMENT, CO2-ENRICHED ATMOSPHERES, GROWTH DYNAMICS, MINERAL NUTRITION, PHOTOSYNTHETIC ACCLIMATION, ROBUR PLANTS, STOMATAL CONDUCTANCE, TREE SEEDLINGS, WATER-USE EFFICIENCY

2380

Tognetti, R., and J.D. Johnson. 1999. Responses of growth, nitrogen and carbon partitioning to elevated atmospheric CO2 concentration in live oak (Quercus virginiana Mill.) seedlings in relation to nutrient supply. *Annals of Forest Science 56(2):91-105.*

Live oak (Quercus virginiana Mill.) seedlings were exposed at two concentrations of atmospheric carbon dioxide ([CO2], 370 or 520 mu mol.mol(-1)) in combination with two soil nitrogen (N) treatments (20 and 90 mu mol.mol(-1) total N) in open-top chambers for 6 months. Seedlings were harvested at 5-7 weeks interval. CO2 treatment had a positive effect on seedling growth. Differences in biomass between elevated and ambient CO2-treated plants increased over the experimental period. Soil N availability did not significantly affect growth. Nevertheless, growth in elevated [CO2] in combination with high N levels led to a consistently higher accumulation of total biomass by the end of the experiment (30-40 %). Biomass allocation between plant parts was similar for seedlings in all treatments, but was significantly different between harvests. The N regimes did not result in different relative growth rate (RGR) and net assimilation rate (NAR), while CO2 treatment had an overall significant effect. Across all [CO2] and N levels, there was a positive relationship between plant mass and subsequent RGR, and this relationship did not differ between treatments. Overall, specific leaf area (SLA) dl:creased in CO2-enriched air. Fine root-foliage mass ratio was increased by elevated [CO2] and decreased by high N. High CO2- and high N- treated plants had the greatest height and basal stem diameter. The allometric relationships between shoot and root dry weight and between height and basal stem diameter were not significantly affected by elevated [CO2]. Leaf N concentrations were reduced by low soil N. Plant N concentrations decreased with time. Elevated [CO2] increased the C/N ratio of all plant compartments, as a result of decreasing N concentrations. High CO2-grown plants reduced N concentrations relative to ambient CO2-grown plants when compared at a common time, but similar when compared at a common size. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, BETULA-PENDULA ROTH, DIOXIDE, ENRICHMENT, EXPOSURE, LOBLOLLY-PINE, MINERAL NUTRITION, PINUS-TAEDA, PLANT-RESPONSES, SOURCE-SINK RELATIONS

2381

Tognetti, R., and J.D. Johnson. 1999. Responses to elevated atmospheric CO2 concentration and nitrogen supply of Quercus ilex L-seedlings from a coppice stand growing at a natural CO2 spring. *Annals of Forest Science 56(7):549-561.*

Quercus ilex acorns were collected from a population of trees with a lifetime exposure to elevated atmospheric CO2 concentration (CO2), and after germination seedlings were exposed at two [CO2] (370 or 520 mu mol mol(-1)) in combination with two soil N treatments (20 and 90 mu mol mol(-1) total N) in open-tap chambers for 6 months. Increasing [CO2] stimulated photosynthesis and leaf dark respiration regardless of N treatment. The increase in photosynthesis and leaf dark respiration was associated with a moderate reduction in stomatal conductance, resulting in enhanced instantaneous transpiration efficiency in leaves of seedlings in CO2-enriched air. Elevated [CO2] increased biomass production only in the high-N treatment. Fine root/foliage mass ratio decreased with high-N treatment and increased with CO2 enrichment. There was evidence of a preferential shift of biomass to below-ground tissue at a low level of nutrient addition. Specific leaf area (SLA) and leaf area ratio (LAR) decreased significantly in leaves of seedlings grown in elevated [CO2] irrespective of N treatment. Leaf N concentration decreased significantly in elevated [CO2] irrespective of N treatment. As a result of patterns of N and carbon concentrations, C/N ratio generally increased with elevated [CO2] treatment and decreased with high nutrient supply. Afternoon starch concentrations in leaves did not increase significantly with increasing [CO2], as was the case for morning starch concentrations at low-N supply. Starch concentrations in leaves, stem and roots increased with elevated [CO2] and decreased with nutrient addition. The concentration of sugars was not significantly affected by either CO2 or N treatments. Total foliar phenolic concentrations decreased in seedlings grown in elevated [CO2] irrespective of N treatment, while nutrient supply had less of an effect. We conclude that available soil N will be a major controlling resource for the establishment and growth of Q. ilex in rising [CO2] conditions. (C) 1999 Editions scientifiques et medicales Elsevier SAS.

KEYWORDS: CARBON NUTRIENT BALANCE, DIOXIDE ENRICHMENT, FOLIAR GAS-EXCHANGE, GROWTH, LOBLOLLY-PINE, PLANT-RESPONSES, PONDEROSA PINE, RISING CO2, SOIL NUTRIENT, TREE SEEDLINGS

2382

Tognetti, R., J.D. Johnson, M. Michelozzi, and A. Raschi. 1998. Response of foliar metabolism in mature trees of Quercus pubescens and Quercus ilex to long-term elevated CO2. *Environmental and Experimental Botany 39(3):233-245.*

Long-term effects on and adaptations of the carbon physiology of long-lived trees exposed to increasing atmospheric levels of CO2 are unknown. We compared two indigenous Quercus species, Q. ilex and Q. pubescens, growing in a natural CO2 spring located in central Italy and at a nearby control site. In May, 1995 photosynthetic rate at least doubled when measured with supplemental CO2 in both species and sites. Dark respiration was much higher at the CO2 spring site in both species. Foliar sugar and starch concentrations in Q. ilex exhibited significant site and diurnal differences (May and September). In July, 1995 there was little difference in the water potential values of the measured trees at the different sites over the diurnal period. Photosynthetic rate was higher for both species in the CO2 spring, particularly in the early morning and late afternoon. Mid-day stomatal closure reduced photosynthesis to similar levels. In the morning leaf conductance and transpiration were generally lower in the CO2 spring trees, contributing to higher instantaneous water use efficiency for both species. Isoprene emission rates were higher in Q. pubescens trees growing in the CO2 spring. The maximum difference between control and CO2 spring trees occurred in late afternoon. In contrast, Q. ilex exhibited isoprene emission near background level. Foliage and branch carbon and nitrogen status showed increased concentrations of starch and tannins in Q. ilex and of soluble sugars in Q. pubescens in the elevated CO2 environment, while nitrogen concentration decreased in both species. Wood gravity increased 6 and 3% in Q. ilex and Q. pubescens, respectively, growing in the CO2 spring. Q. ilex exhibited afternoon recovery of water potential compared to Q. pubescens which had better night-time recovery. Q. ilex and e. pubescens exposed to elevated CO2 for prolonged periods exhibit different mechanisms for dealing with additional reduced carbon and do maintain an altered carbon physiology, even in midst of the region's characteristic summer drought. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, ISOPRENE EMISSION, LIQUIDAMBAR-STYRACIFLUA, LIVE OAK, LOBLOLLY-PINE SEEDLINGS, PHOTOSYNTHESIS, TAEDA SEEDLINGS, TEMPERATURE

2383

Tognetti, R., A. Longobucco, F. Miglietta, and A. Raschi. 1998. Transpiration and stomatal behaviour of Quercus ilex plants during the summer in a Mediterranean carbon dioxide spring. *Plant, Cell and Environment 21(6):613-622.*

Variations in the water relations and stomatal response of Quercus ilex were analysed under field conditions by comparing trees at two locations in a Mediterranean environment during two consecutive summers (1993 and 1994), We used the heat-pulse velocity technique to estimate transpirational water use of trees during a 5 month period from June to November 1994, At the end of sap flow measurements, the trees were harvested, and the foliage and sapwood area measured, A distinct environmental gradient exists between the two sites with higher atmospheric CO2 concentrations in the proximity of a natural CO, spring. Trees at the spring site have been growing for generations in elevated atmospheric CO2 concentrations. At both sites, maximum leaf conductance was related to predawn shoot water potential. The effects of water deficits on water relations and whole- plant transpiration during the summer drought were severe. Leaf conductance and water potential recovered after major rainfall in September to predrought values. Sap flow leaf conductance and predawn water potential decreased in parallel with increases in hydraulic resistance, reaching a minimum in mid-summer. These relationships are in agreement with the hypothesis of the stomatal control of transpiration to prevent desiccation damage but also to avoid 'runaway embolism'. Trees at the CO2 spring underwent less reduction in hydraulic resistance for a given value of predawn water potential. The decrease in leaf conductance caused by elevated CO2 was limited and tended to be less at high than at low atmospheric vapour pressure deficit. Mean land diurnal) sap flux were consistently higher in the control site trees than in the CO2 spring trees. The degree of reduction in water use between the two sites varied among the summer periods. The control site trees had consistently higher sap flow at corresponding values of either sapwood cross-sectional area or foliage area, Larger trees displayed smaller differences than smaller trees, between the control and the CO2 spring trees. A strong association between foliage area and sapwood cross-sectional area was found in both the control and the CO2 spring trees, the latter supporting a smaller foliage area at the corresponding sapwood stem cross- sectional area. The specific leaf area (SLA) of the foliage was not influenced by site. The results are discussed in terms of the effects of elevated CO2 on plant water use at the organ and whole-tree scale.

KEYWORDS: AIR CO-2 ENRICHMENT, ARBUTUS-UNEDO L, ATMOSPHERIC CO2, COMPUTER-TOMOGRAPHY, ELEVATED CO2, FOREST TREES, GAS-EXCHANGE, LONG-TERM EXPOSURE, SAP FLOW, WATER RELATIONS

2384

Tognetti, R., A. Longobucco, F. Miglietta, and A. Raschi. 1999. Water relations, stomatal response and transpiration of Quercus pubescens trees during summer in a Mediterranean carbon dioxide spring. *Tree Physiology 19(4-5):261-270.*

Variations in water relations and stomatal response of Quercus pubescens Willd. were analyzed under Mediterranean field conditions during two consecutive summers (1993 and 1994) at two locations characterized by different atmospheric CO2 concentrations because of the presence at one of them of a CO2 spring. Trees at the CO2 spring site have been growing for generations in elevated atmospheric CO2 concentrations. The heat-pulse velocity technique was used to estimate water use of trees during a 5-month period from June to November 1994. At the end of the sap flow measurements, the trees were harvested and foliage and sapwood area measured. At both sites, maximum leaf conductance was related to predawn shoot water potential. Effects of summer drought on plant water relations, including whole-plant transpiration, were severe, but leaf conductance and water potential recovered to predrought values after major rainfall in September. Leaf conductance, predawn water potential, and sometimes sap flow, decreased in parallel with increases in hydraulic resistance, reaching a minimum in midsummer. Hydraulic resistance was higher in trees at the control site than in trees at the CO2 spring site. The effect of elevated CO2 concentration on leaf conductance was less at high leaf-to-air water vapor pressure difference than at low leaf-to-air water vapor pressure difference. Mean and diurnal sap fluxes were consistently higher in trees at the control site than in trees at the CO2 spring site. During the summer period, plant water use varied between the two sites. Trees at the control site had consistently higher sap flow at corresponding values of sapwood cross-sectional area than trees at the CO2 spring site. Because trees at the CO2 spring site supported a smaller foliage area for a corresponding sapwood cross-sectional area than trees at the control site, the overall mean sap flux/foliage area ratio did not differ between sites. The results are discussed in terms of effects of elevated CO2 concentration on plant water use at the organ and whole-tree scale.

KEYWORDS: AIR CO-2 ENRICHMENT, ARBUTUS-UNEDO L, ATMOSPHERIC CO2, BIOMASS ALLOCATION, COMPUTER-TOMOGRAPHY, ELEVATED CO2, FOREST TREES, GAS-EXCHANGE, PINUS-CONTORTA, WOODY-PLANTS

2385

Tognetti, R., A. Longobucco, and A. Raschi. 1999. Seasonal embolism and xylem vulnerability in deciduous and evergreen Mediterranean trees influenced by proximity to a carbon dioxide spring. *Tree Physiology 19(4-5):271-277.*

We investigated how proximity to natural CO2 springs affected the seasonal patterns of xylem embolism in Quercus ilex L., Quercus pubescens Willd., Fraxinus ornus L., Populus tremula L. and Arbutus unedo L., which differ in leaf phenology and wood anatomy. Xylem embolism was evaluated in both artificially dehydrated branches and in hydrated apical branches collected at monthly intervals during a 20-month sampling period. Initial specific hydraulic conductivity was also evaluated. We found species-dependent differences in xylem hydraulic properties in response to elevated CO2 concentration. Populus tremula was the most embolized and A. unedo was the least embolized of the species examined. Effects of elevated CO2 were significant in Q. pubescens, P. tremula and A. unedo, whereas the overall response to elevated CO2 was less evident in F, ornus and Q. ilex. Specific hydraulic conductivity differed among species but not between sites, although. the interaction between species and site was significant. Differences in xylem vulnerability between trees growing near to the CO2 spring and those growing in control areas were small. Although differences in hydraulic properties in response to elevated CO2 concentration were small, they may be of great importance in determining future community composition in Mediterranean-type forest ecosystems. The possible causes and ecological significance of such differences are discussed in relation to elevated CO2 concentration and other environmental conditions.

KEYWORDS: ATMOSPHERIC CO2, CAVITATION, ELEVATED CO2, FAGUS-SYLVATICA, FOREST TREES, GROWTH, HYDRAULIC CONDUCTIVITY, QUERCUS, STOMATAL CONDUCTANCE, WATER-STRESS

2386

Tognetti, R., A. Longobucco, A. Raschi, F. Miglietta, and I. Fumagalli. 1999. Responses of two Populus clones to elevated atmospheric CO2 concentration in the field. *Annals of Forest Science 56(6):493-500.*

Two poplar clones, hybrid Populus deltoides Bartr. Ex Marsh x Populus nigra L. (Populus x euramericana), clone I-214, and Populus deltoides, clone Lux, were grown from clonal hardwood cuttings for one growing season in either ambient (360 mu mol mol(-1)) or elevated (560 mu mol mol(-1)) [CO2] in FACE-system rings at Rapolano Terme (Siena, Italy). Both clones I-214 and Lux exhibited a higher above-ground biomass, photosynthesis at light saturation and instantaneous transpiration efficiency (ITE) in CO2-enriched air. The elevated [CO2]-induced responses of clone I-214 included increased investment in branch and leaf biomass, and enhanced stem volume. The elevated [CO2]-induced responses of clone Lux included an increase in the number of branches and leaf area (which might result in a higher leaf area index, LAI). Photosynthetic acclimation under elevated [CO2] was found only during the early morning and only in clone I-214. Stomatal conductance and transpiration ton a leaf area basis) decreased under elevated [CO2] particularly in clone Lux and at the end of the experiment. The effects of elevated [CO2] on leaf osmotic potential were limited, at least in conditions of non-limiting water availability. Clonal differences in response to elevated [CO2] should be taken in account when planning future poplar plantations in the forecast warmer and drier Mediterranean sites. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ALLOCATION, CARBON DIOXIDE, DROUGHT, ENRICHMENT, GROWTH, PHOTOSYNTHETIC ACCLIMATION, POPLAR CLONES, PRESSURE-VOLUME, SEEDLINGS, WATER RELATIONS

2387

Tomlinson, P.T., and P.D. Anderson. 1995. Elevated co2 compensates for water-stress in red oak. *Plant Physiology 108(2):36.*

2388

Tomlinson, P.T., and P.D. Anderson. 1998. Ontogeny affects response of northern red oak seedlings to elevated CO2 and water stress - II. Recent photosynthate distribution and growth. *New Phytologist 140(3):493-504.*

Northern red oak in the western Lake States area of the USA exists on the most xeric edge of its distribution range. Future climate-change scenarios for this area predict decreased water availability along with increased atmospheric CO2. We examined recent photosynthate distribution and growth in seedlings as a function of CO2 mole fraction (400, 530 and 700 mu mol mol(-1) CO2), water regime (well watered and water-stressed), and ontogenic stage. Water stress effects on growth were largely offset by elevated CO2. Water stress increased root mass ratio without concurrently increasing allocation of recent photosynthate to the roots. However, apparent sink strength of water-stressed seedlings at the completion of the third growth stage tended to be greater than that

of well watered seedlings, as shown by continued high export, which may contribute carbon reserves to support preferential root growth under water- stressed conditions. Elevated CO2 decreased apparent shoot sink strength associated with the rapid expansion of the third flush. Carbon resources for the observed enhanced growth under elevated CO2 could be provided by enhanced photosynthetic rate over an increased leaf area (Anderson & Tomlinson, 1998, this volume). Increased sink strength of LG seedlings under water- stressed conditions, together with decreased apparent shoot sink strength associated with growth in elevated CO2 provide mechanisms for offsetting water stress effects by growth in elevated CO2. Careful control of ontogeny was necessary to discern these changes and provides further evidence of the need for such careful control in mechanistic studies.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2, CACAO SEEDLINGS, CARBON DIOXIDE, CASTANEA-SATIVA, ENRICHMENT, GAS-EXCHANGE, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, QUERCUS-ROBUR

2389

Topp, C.F.E., and C.J. Doyle. 1996. Simulating the impact of global warming on milk and forage production in Scotland .2. The effects on milk yields and grazing management of dairy herds. *Agricultural Systems 52(2-3):243-270.*

The potential impact of global warming and the enhanced atmospheric CO2 concentration on grassland management on dairy farms within the UK requires assessment. This has led to the development of a mathematical model of the grazing dairy cow. The model, that embraces grass and grass-white clover swards, has been used to assess the effects that the projected increases in temperature and rainfall under global warming and the increased levels of CO2 might have on milk production and on silage conservation for a typical dairy farm. The results suggest that the impact on milk production for grass-based systems will vary depending on the locality. On the other hand, for herds grazed on grass-white clover swards milk output might increase regardless of site, when the concentration of CO2 is enhanced. As regards silage production from grass-white clover swards, under global warming and at current levels of CO2 there is an apparent tendency to increase the percentage of total silage yield obtained from the first cut, although this does nor occur for grass swards. At the same time, there are also indications that global warming will increase the percentage of clover in the herbage cut for conservation. Copyright (C) 1996 Published by Elsevier Science Ltd

KEYWORDS: CLIMATE, GRASS-CLOVER LEYS, GROWTH, HERBAGE INTAKE, MODEL, NUTRITIONAL-VALUE, PARAMETERS, RYEGRASS, SCENARIOS, VALIDATION

2390

Torbert, H.A., S.A. Prior, and H.H. Rogers. 1995. Elevated atmospheric carbon-dioxide effects on cotton plant residue decomposition. *Soil Science Society of America Journal 59(5):1321-1328.*

Assessing the impact of elevated atmospheric CO2 concentration on the global environment is hampered due to a lack of understanding of global C cycling. Carbon fixed within plant biomass ultimately enters the soil via plant residues, but the effects of elevated-CO2-grown plant material on decomposition rates and long-term soil C storage are unknown. The objective of this study was to determine the decomposition rate of plant residues grown under an elevated CO2 environment as affected by soil type. Cotton (Gossypium hirsuturn L. 'Delta Pine 77') samples were collected from a free-air CO2 enrichment (550 mu L L(-1)) experiment. The plant residues were incubated under ambient CO2 conditions to determine decomposition rates of leaves, stems, and roots and potential N and P mineralization- immobilization in three soil series: a Blanton loamy sand (loamy siliceous, thermic Grossarenic Paleudult), a Decatur silt loam (clayey, kaolinitic, thermic Rhodic Paleudult), and a Houston clay loam (very fine, montmorillonitic Typic Chromudert). No significant difference was observed between plant residue grown under CO2 enrichment vs. ambient CO2 conditions for soil respiration or P mineralization- immobilization. Significantly greater net N immobilization was observed during the incubation in all soil types for plant residue grown at elevated CO2. These results indicate that while decomposition of plant residue may not be reduced by CO2 enrichment, N dynamics may be markedly changed.

KEYWORDS: CO2- ENRICHMENT, NITROGEN

2391

Torbert, H.A., S.A. Prior, H.H. Rogers, and G.B. Runion. 1998. Crop residue decomposition as affected by growth under elevated atmospheric CO2. *Soil Science 163(5):412-419.*

Increasing atmospheric CO2 level has led to concerns about process changes in the biosphere. Elevated atmospheric CO2 concentration has been Shown to increase plant biomass, resulting in greater amounts of residue returned to soil. However, the effects on long-term storage of C in soil are highly debated. Changes in both quantity and quality of plant residue, as well as residue management, may alter soil C and N dynamics that will, in turn, affect the ability of soil to store C. Plant residues were collected from an experiment using open top chambers to increase CO2 levels under field conditions. A soil incubation study was conducted with a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults) to examine the effect of residue additions to two crop species (soybean, Glycine max (L.) Merr. and grain sorghum, Sorghum bicolor (L.) Moench), grown at two CO2 concentrations (ambient and twice ambient), and two incorporation treatments (incorporated or surface placement) on potential C and N mineralization. The difference in biomass inputs between plants grown in ambient and elevated atmospheric CO2 was also considered. Simulated residue incorporation reduced inorganic N concentration but had no effect on C mineralization. Both inorganic N content and C mineralization were higher with soybean than with grain sorghum. Although changes to both plant residue quality and quantity caused by elevated CO2 concentration affected C cycling in soil, residue quality may be more important for determining C storage. Nitrogen cycling in soil may be a controlling factor for C storage in terrestrial ecosystems.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LITTER QUALITY, NITROGEN, SORGHUM

2392

Torbert, H.A., S.A. Prior, H.H. Rogers, W.H. Schlesinger, G.L. Mullins, and G.B. Runion. 1996. Elevated atmospheric carbon dioxide in agroecosystems affects groundwater quality. *Journal of Environmental Quality 25(4):720-726.*

Increasing atmospheric carbon dioxide (CO2) concentration has led to concerns about global changes to the environment, One area of global change that has not been addressed is the effect of elevated atmospheric CO2 on ground water quality below agroecosystems, Elevated CO2 concentration alterations of plant growth and C/N ratios may modify C and N cycling in soil and affect nitrate (NO3-) leaching to groundwater. This study was conducted to examine the effects of a legume soybean [Glycine max (L.) Merr.] and a nonlegume grain sorghum [Sorghum bicolor (L.) Moench] CO2-enriched agroecosystems on NO3- movement below the root zone in a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults). The study was a split-plot design replicated three times with plant species (soybean and grain sorghum) as the main plots and CO2 concentration (approximate to 360 and similar to 720 mu L L(-1) CO2) as subplots using open-top held chambers. Fertilizer

application was made with N-15-depleted NH4NO3 to act as a fertilizer tracer, Soil solution samples were collected weekly at 90-cm depth for a 2-yr period arid monitored for NO3-N concentrations. Isotope analysis of soil solution indicated that the decomposition ol organic matter was the primary source of NO3--N in soil solution below the root zone through most of the monitoring period. Significant differences were observed for NO3--N concentrations between soybean and grain sorghum, with soybean having the higher NO3--N concentrations. Elevated CO2 increased total dry weight, total N content, and C/N ratio of residue returned to soil in both years. Elevated CO2 significantly decreased NO3--N concentrations below the root zone in both soybean and grain sorghum. The results of this study indicate that retention of N in organic pools because of elevated atmospheric CO2 could reduce the nitrate concentration in groundwater beneath agroecosystems as indicated by NO3- movement.

KEYWORDS: CO2, DECOMPOSITION, LITTER QUALITY, LOSSES, NITRATE, NITROGEN

2393

Torbert, H.A., H.H. Rogers, S.A. Prior, W.H. Schlesinger, and G.B. Runion. 1997. Effects of elevated atmospheric CO2 in agro-ecosystems on soil carbon storage. *Global Change Biology 3(6):513-521.*

Increasing global atmospheric CO2 concentration has led to concerns regarding its potential effects on the terrestrial environment. Attempts to balance the atmospheric carbon (C) budget have met with a large shortfall in C accounting (approximate to 1.4 x 10(15) g C y(-1)) and this has led to the hypothesis that C is being stored in the soil of terrestrial ecosystems. This study examined the effects of CO2 enrichment on soil C storage in C3 soybean (Glycine max L.) Merr. and C4 grain sorghum (Sorghum bicolor L.) Moench. agroecosystems established on a Blanton loamy sand (loamy siliceous, thermic, Grossarenic Paleudults). The study was a split-plot design replicated three times with two crop species (soybean and grain sorghum) as the main plots and two CO2 concentration (ambient and twice ambient) as subplots using open top field chambers. Carbon isotopic techniques using delta(13)C were used to track the input of new C into the soil system. At the end of two years, shifts in delta(13)C content of soil organic matter carbon were observed to a depth of 30 cm. Calculated new C in soil organic matter with grain sorghum was greater for elevated CO2 vs. ambient CO2 (162 and 29 g m(-2), respectively), but with soybean the new C in soil organic matter was less for elevated CO2 vs. ambient CO2 (120 and 291 g m(-2), respectively). A significant increase in mineral associated organic C was observed in 1993 which may result in increased soil C storage over the long-term, however, little change in total soil organic C was observed under either plant species. These data indicate that elevated atmospheric CO2 resulted in changes in soil C dynamics in agro-ecosystems that are crop species dependent.

KEYWORDS: CONSERVATION, COTTON, ENRICHMENT, FIELD, NITROGEN, ORGANIC-MATTER, PLANT-RESPONSES, RESIDUE DECOMPOSITION, RHIZOSPHERE, TURNOVER

2394

Torres, M.P., J.L.J. Houpis, and J.C. Pushnik. 1995. The effects of long-term co2 enrichment on photosynthesis, stomatal conductance and internal/external co2 concentrations in pinus-ponderosa. *Plant Physiology 108(2):113.*

2395

Townend, J. 1993. Effects of elevated carbon-dioxide and drought on the growth and physiology of clonal sitka spruce plants (picea-sitchensis (bong) carr). *Tree Physiology 13(4):389-399.*

Two-year-old Sitka spruce (Picea sitchensis (Bong.) Carr.) plants from four clones were grown in naturally lit growth chambers for 6 months at either ambient (350 ppm) or ambient + 250 ppm (600 ppm) CO2 concentration. Plants were grown in large boxes filled with peat, in a system that allowed the roots of individual plants to be harvested easily at the end of the growing season. Half of the boxes were kept well watered and half were allowed to dry out slowly over the summer. Plants growing in elevated CO2 showed a 6.9% increase in mean relative growth rate compared to controls in the drought treatment and a 9.8% increase compared to controls in the well-watered treatment, though there was considerable variation in response among the different clones and water treatments. Rates of net CO2 assimilation were higher and stomatal conductances were lower in plants grown in elevated CO2 than in ambient CO2 in both the well-watered and drought treatments. Both of these factors contributed to the doubling of instantaneous water use efficiency. The partitioning of biomass to roots was unaffected by elevated CO2, but the ratio of needle mass/stems + branches mass decreased. Together with reduced stomatal conductance, this probably caused the observed increases in xylem pressure potentials with elevated CO2.

2396

Townend, J. 1995. Effects of elevated co2, water and nutrients on picea- sitchensis (bong) carr seedlings. *New Phytologist 130(2):193-206.*

Sitka spruce (Picea sitchensis (Pong.) Carr.) seedlings were grown from seed for one year in naturally lit growth chambers with either ambient or ambient + 250 ppm concentrations of CO2. In the following year the plants were grown in the same CO2 treatments for the whole growing season at two concentrations of nutrients and were either well-watered or subjected to a long-term, gradually increasing drought. Elevated CO2 increased significantly growth in all treatments except the well-watered, unfertilized treatment. The relative increases in end-of-year biomass in the elevated CO2 treatment compared with the ambient treatment were: well-watered, fertilized + 52%, well-watered, unfertilized + 19%, droughted, fertilized + 44%, and droughted, unfertilized + 49%. Growth analysis revealed that treatment effects on both unit leaf rates and leaf area duration were important in determining the final masses of the plants. Plants growing in elevated CO2 had increased relative growth rates in the first half of the growing season but only slightly increased or even slightly decreased relative growth rates in the later part of the growing season in all water x nutrient treatments. Overall there was a significant CO2 x water x nutrient interaction on end-of-year biomass. A combination of small nutrient concentration and adequate water supply led to the smallest growth response to elevated CO2.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, COOCCURRING BIRCH, GROWTH-RESPONSE, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, NITROGEN CONCENTRATION, PINUS-TAEDA SEEDLINGS, SHOOT GROWTH, SOURCE-SINK RELATIONS

2397

Townend, J., and A.L. Dickinson. 1995. A comparison of rooting environments in containers of different sizes. *Plant and Soil 175(1):139-146.*

Experiments on plants are often carried out in growth chambers or greenhouses which necessitate the use of an artificial rooting environment, though this is seldom characterized in detail. Measurements were made to compare the rooting environment in large boxes (0.25 m(3)) with that in small pots (0.19, 0.55 and 1.90 dm(3)) in naturally lit chambers. Diurnal temperature fluctuations of 14.6, 11.6 and 7.7 degrees C occurred in the pots compared with only 1.9 degrees

C in the boxes. Soil drying to a matric potential of -50 kPa was approximately 25 times faster in the pots. The mean heights of 2 year old Sitka spruce (Picea sitchensis (Bong.) Carr.) seedlings grown throughout their second growing season in the three sizes of pots were 38, 62 and 92% of the mean height of those grown in the boxes. Soil solution nutrient concentrations in the boxes were considerably increased by soil drying, an aspect which seems to have received little attention in experiments involving artificially imposed drought. An alternative system of constraining the roots of individual plants within nylon fabric bags, embedded in larger volumes of soil, to facilitate harvesting of complete root systems is described. The importance of the rooting environment in determining the outcome of physiological experiments is also briefly discussed.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SHOOT, SOIL TEMPERATURES, SPRUCE, WATER-STRESS

2398

Traw, M.B., R.L. Lindroth, and F.A. Bazzaz. 1996. Decline in gypsy moth (Lymantria dispar) performance in an elevated CO2 atmosphere depends upon host plant species. *Oecologia 108(1):113-120.*

Plant species differ broadly in their responses to an elevated CO2 atmosphere, particularly in the extent of nitrogen dilution of leaf tissue. Insect herbivores are often limited by the availability of nutrients, such as nitrogen, in their host plant tissue and may therefore respond differentially on different plant species grown in CO2-enriched environments. We reared gypsy moth larvae (Lymantria dispar) in situ on seedlings of yellow birch (Betula allegheniensis) and gray birch (B. populifolia) grown in an ambient (350 ppm) or elevated (700 ppm) CO2 atmosphere to test whether larval responses in the elevated CO2 atmosphere were species- dependent. We report that female gypsy moths (Lymantria dispar) reared on gray birch (Betula populifolia) achieved similar pupal masses on plants grown at an ambient or an elevated CO2 concentration. However, on yellow birch (B. allegheniensis), female pupal mass was 38% smaller on plants in the elevated-CO2 atmosphere. Larval mortality was significantly higher on yellow birch than gray birch, but did not differ between the CO2 treatments. Relative growth rate declined more in the elevated CO2 atmosphere for larvae on yellow birch than for those on gray birch. In preference tests, larvae preferred ambient over elevated CO2-grown leaves of yellow birch, but showed no preference between gray birch leaves from the two CO2 atmospheres. This differential response of gypsy moths to their host species corresponded to a greater decline in leaf nutritional quality in the elevated CO2 atmosphere in yellow birch than in gray birch. Leaf nitrogen content of yellow birch dropped from 2.68% to 1.99% while that of gray birch leaves only declined from 3.23% to 2.63%. Meanwhile, leaf condensed tannin concentration increased from 8.92% to 11.45% in yellow birch leaves while gray birch leaves only increased from 10.72% to 12.34%. Thus the declines in larval performance in a future atmosphere may be substantial and host-species-specific.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ENRICHMENT, GROWTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEPIDOPTERA, NITROGEN-CONTENT, PAPER BIRCH, RESPONSES, SEEDLINGS

2399

Tremblin, G., P. Jolivet, and A. Coudret. 1993. Light quality effects on subsequent dark 14co2-fixation in fucus-serratus. *Hydrobiologia 261:471-475.*

The intensity and fate Of (CO2)-C-14-fixation in the dark are studied on Fucus serratus apices previously maintained under low illumination conditions using white, blue, red or yellow isoquantic lights. In the case of a 180 s pulse, light quality affected dark carbon-fixation, with a higher level of incorporation into ethanol-soluble organic matter in the case of yellow light cultivated apices. After a 30 s pulse C-14 was mainly fixed into glycerate and aspartate-malate pools whatever the pre-treatment light conditions, with a higher level into glycerate when apices were pre-illuminated with blue or yellow light. After a 180 s pulse, C-14 was mainly transferred into amino acids (glutamate and alanine) at the expense of aspartate and malate in red and yellow pre-illumination conditions, as found in the white light reference experiment, and only at the expense of glycerate in blue light pre-illumination conditions. The metabolic pathway of glycerate formation, principally enhanced by blue light preillumination, remains unexplained under these non-photosynthetic conditions. Results are discussed with reference to CO2-fixation via phosphoenolpyruvate carboxykinase and light quality effects on its in vitro activity.

KEYWORDS: CARBON FIXATION, CYSTOSEIRA-ELEGANS SAUVAGEAU, METABOLISM, PATHWAY

2400

Tremmel, D.C., and D.T. Patterson. 1993. Responses of soybean and 5 weeds to co2 enrichment under 2 temperature regimes. *Canadian Journal of Plant Science 73(4):1249-1260.*

Rising atmospheric CO2 levels could affect plant growth both directly, through effects on physiology, and indirectly, through the effects of possible CO2-induced temperature increases. In this study we examined the interacting effects of CO2 enrichment and temperature on the growth and allocation of soybean and five weeds. individual plants of soybean [Glycine max (L.) Merr. 'Braxton'], johnsongrass [Sorghum halepense (L.) Pers. quackgrass [Elytrigia repens (L.) Nevski], redroot pigweed (Amaranthus retroflexus L.), sicklepod (Cassia obtusifolia L.). and velvetleaf (Abutilon theophrasti Medic.) were grown in growth chambers in all combinations of two temperatures (avg. day/night of 26/19-degrees-C and 30/23- degrees-C) and two CO2 concentrations (350 and 700 ppm) for 35 d. Leaf area and plant biomass were greater at higher temperatures, regardless of CO2 level, in all species except quackgrass. Quackgrass (C3) produced its greatest leaf area and biomass at elevated CO2, whereas johnsongrass (C4) showed little response. Redroot pigweed (C4) and the C3 dicotyledenous species (soybean, sicklepod, velvetleaf) produced their greatest biomass at high CO2, though effects on leaf area were less consistent or absent. In general, when significant CO2 by temperature interactions were found, CO2 responses were smallest at higher temperatures. These differential responses to elevated CO2 concentrations may cause changes in the relative importance of competitive pressure from these weeds.

KEYWORDS: AIR- TEMPERATURE, ANNUALS, ATMOSPHERIC CO2, C-4 GRASS, CARBON-DIOXIDE CONCENTRATION, COMPETITION, ELEVATED CO2, GROWTH, NITROGEN, YIELD

2401

Tremmel, D.C., and D.T. Patterson. 1994. Effects of elevated co2 and temperature on development in soybean and 5 weeds. *Canadian Journal of Plant Science 74(1):43-50.*

Developmental rates of soybean [Glycine max (L.) Merr. 'Braxton'],johnsongrass [Sorghum halepense (L.) Pers.], quackgrass [Elytrigia repens (L.) Nevski], redroot pigweed (Amaranthus retroflexus L.), sicklepod (Cassia obtusifolia L.), and velvetleaf (Abutilon theophrasti Medic.) were compared among plants grown in all combinations of two temperature levels (avg. day/night of 26/19 degrees C and 30/23 degrees C) and two CO2 levels (350 and 700 ppm). Neither temperature nor CO2 affected johnsongrass tillering rate, but plants began tillering earlier at higher temperatures. Adverse effects of higher temperatures on quackgrass development were alleviated by elevated

CO2 conditions. Plastochron rate was higher at higher temperatures in all dicot species (soybean, redroot pigweed, sicklepod, and velvetleaf), and was higher at elevated CO2 in all dicots except velvetleaf. Calculating plastochron rates on a degree day basis removed differences between temperature treatments, but did not affect responses to CO2. Responses of dicot branch and branch leaf production to treatments varied among species. Branch production per day increased with higher temperatures in redroot pigweed, decreased with higher temperatures in sicklepod, and was unaffected by temperature in soybean. The relationship between main axis and branch developmental rates was altered by temperature in soybean, and by both temperature and CO2 in sicklepod, but was unaffected by either treatment in redroot pigweed. These results indicate that developmental responses to temperature and CO2 depend on both the species and the aspect of development being considered.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, GLYCINE-MAX, GROWTH, PHOTOSYNTHESIS, WHEAT, YIELD

2402

Trenberth, K.E. 1999. Conceptual framework for changes of extremes of the hydrological cycle with climate change. *Climatic Change 42(1):327-339.*

A physically based conceptual framework is put forward that explains why an increase in heavy precipitation events should be a primary manifestation of the climate change that accompanies increases in greenhouse gases in the atmosphere. Increased concentrations of greenhouse gases in the atmosphere increase downwelling infrared radiation, and this global heating at the surface not only acts to increase temperatures but also increases evaporation which enhances the atmospheric moisture content. Consequently all weather systems, ranging from individual clouds and thunderstorms to extratropical cyclones, which feed on the available moisture through storm- scale moisture convergence, are likely to produce correspondingly enhanced precipitation rates. Increases in heavy rainfall at the expense of more moderate rainfall are the consequence along with increased runoff and risk of flooding. However, because of constraints in the surface energy budget, there are also implications for the frequency and/or efficiency of precipitation. It follows that increased attention should be given to trends in atmospheric moisture content, and datasets on hourly precipitation rates and frequency need to be developed and analyzed as well as total accumulation.

KEYWORDS: CO2, DAILY PRECIPITATION, FREQUENCY, MODEL, NORTH-AMERICA, SENSITIVITY, TRENDS, UNITED-STATES, VARIABILITY, WATER-VAPOR

2403

Treonis, A.M., and J.F. Lussenhop. 1997. Rapid response of soil protozoa to elevated CO2. *Biology and Fertility of Soils 25(1):60-62.*

Short-term changes in bacterial and protozoan populations from the soil of plants grown under elevated atmospheric CO2 were quantified. We grew Brassica nigra at either ambient or twice- ambient CO2 levels within open-top chambers in the field for 4 weeks. Plant biomass, above- and belowground, was unaffected by elevated CO2. Direct count bacterial density was unchanged under elevated CO2. Flagellate density tended to increase, whereas amoebal density significantly declined under elevated CO2. This change in protozoan community structure suggests trophic transfer of the elevated CO2 fertilization effect through the soil food chain.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, FEEDBACK, POPULATIONS, RHIZOSPHERE

2404

Tripp, K.E., W.K. Kroen, M.M. Peet, and D.H. Willits. 1992. Fewer whiteflies found on co2-enriched greenhouse tomatoes with high C-n ratios. *Hortscience 27(10):1079-1080.*

Eight tomato (Lycopersicon esculentum) cultivars were grown for 16 weeks in greenhouses enriched for an average of 8.1 hours daily to 1000 mul CO2/liter of air or in greenhouses maintained at ambient CO2. Carbon dioxide enrichment significantly decreased the mean number of greenhouse whiteflies [Trialeurodes vaporariorum (Westward), Homoptera: Aleyrodidae] as measured by counts from commercial yellow sticky traps. The number of whiteflies present was negatively correlated with both seasonal foliar C:N ratio and percent C but positively correlated with percent N in the foliage. Thus, CO2 enrichment apparently alters plant composition in such a way as to reduce significantly the population growth of greenhouse whiteflies.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, INSECT HERBIVORE, LEPIDOPTERA, NITROGEN-CONTENT, NOCTUIDAE, PLANTS

2405

Tripp, K.E., M.M. Peet, D.M. Pharr, D.H. Willits, and P.V. Nelson. 1991. CO2-enhanced yield and foliar deformation among tomato genotypes in elevated CO2 environments. *Plant Physiology 96(3):713-719.*

Yield increases observed among eight genotypes of tomato (Lycopersicon esculentum Mill.) grown at ambient CO2 (about 350) or 1000 microliters per liter CO2 were not due to carbon exchange rate increases. Yield varied among genotypes while carbon exchange rate did not. Yield increases were due to a change in partitioning from root to fruit. Tomatoes grown with CO2 enrichment exhibited nonepinastic foliar deformation similar to nutrient deficiency symptoms. Foliar deformation varied among genotypes, increased throughout the season, and became most severe at elevated CO2. Foliar deformation was positively related to fruit yield. Foliage from the lower canopy was sampled throughout the growing season and analysed for starch, K, P, Ca, Mg, Fe, and Mn concentrations. Foliar K and Mn concentrations were the only elements correlated with deformation severity. Foliar K decreased while deformation increased. In another study, foliage of half the plants of one genotype received foliar applications of 7 millimolar KH2PO4. Untreated foliage showed significantly greater deformation than treated foliage. Reduced foliar K concentration may cause CO2-enhanced foliar deformation. Reduced K may occur following decreased nutrient uptake resulting from reduced root mass due to the change in partitioning from root to fruit.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FRUITS, GREENHOUSES, RESPONSES, STORAGE

2406

Tripp, K.E., M.M. Peet, D.H. Willits, and D.M. Pharr. 1991. CO2-enhanced foliar deformation of tomato-relationship to foliar starch concentration. *Journal of the American Society for Horticultural Science 116(5):876-880.*

Two cultivars of greenhouse tomato (Lycopersicon esculentum Mill.) were grown with ambient or 1000-mu-l CO2/liter during Jan.-June 1987 and 1988. In both years, CO2-enrichment increased foliar deformation and foliar starch, but during the season, foliar starch levels decreased while deformation increased. 'Laura' had more deformation, while 'Michigan-Ohio' had higher foliar starch concentration. During an entire season, there was no significant relationship between foliar starch concentration and deformation severity. Foliar C exchange rates in the

lower canopy were not affected by severity of deformation. Data from these experiments do not support the hypothesis that excess foliar starch is responsible for foliar deformation at elevated CO2.

KEYWORDS: CO2- ENRICHMENT, LONG-TERM EXPOSURE, PHOTOSYNTHETIC INHIBITION, RESPONSES

2407

Tschaplinski, T.J., R.J. Norby, and S.D. Wullschleger. 1993. Responses of loblolly-pine seedlings to elevated co2 and fluctuating water-supply. *Tree Physiology 13(3):283-296.*

Osmotic adjustment of loblolly pine (Pinus taeda L.) seedlings to fluctuating water supply in elevated CO2 was investigated. Seedlings were grown in controlled-environment chambers in either 350 or 700 mul l-1 CO2 with weekly watering for four months, after which they were either watered weekly (well- watered treatment) or every two weeks (water-stress treatment) for 59 days. Osmotic adjustment was assessed by pressure-volume analysis of shoots and by analysis of soluble carbohydrates and free amino acids in roots during the last drying cycle. In well-watered seedlings, elevated CO2 increased the concentration of soluble sugars in roots by 68%. Water stress reduced the soluble sugar concentration in roots of seedling growing in ambient CO2 to 26% of that in roots of well-watered seedlings. Elevated CO2 mitigated the water stress-induced decrease in the concentration of soluble sugars in roots. However, this was probably due, in part, to carbohydrate loading during the first four months when all seedlings were grown in the presence of a high water supply, rather than to osmotic adjustment to water stress. Water stress caused a doubling in the concentration of free primary amino acids in roots, whereas elevated CO2 reduced primary amino acid and nitrogen concentrations to 32 and 74%, respectively, of those in roots of seedlings grown in ambient CO2. There was no indication of large-scale osmotic adjustment to water stress or that elevated CO2 enhanced osmotic adjustment in loblolly pine.

2408

Tschaplinski, T.J., D.B. Stewart, P.J. Hanson, and R.J. Norby. 1995. Interactions between drought and elevated co2 on growth and gas-exchange of seedlings of 3 deciduous tree species. *New Phytologist 129(1):63-71.*

Interactions between elevated atmospheric CO2 and drought on growth and gas exchange of American sycamore (Platanus occidentalis L.), sweetgum (Liquidambar styraciflua L.) and sugar maple (Acer saccharum Marsh.) were investigated using 1- yr-old seedlings, planted in 81 pots and grown in four open-top chambers, containing either ambient air or ambient air enriched with 300 mu mol mol(-1) CO2. Two soil moisture regimes were included within each chamber: a 'well-watered' treatment with plants watered daily and a 'drought' treatment in which plants were subjected to a series of drought cycles. Duration and depth of the drought cycles were determined by soil matric potential. Mean soil water potential at rewatering for the water-stressed seedlings under ambient CO2 for sugar maple, sweetgum and sycamore was -0.5, -0.7 and -1.8 MPa, respectively, compared with > -0.1 MPa for all well-watered plants. Elevated CO2 increased relative growth rate of well-watered sugar maple by 181%, resulting in a 4.3-fold increase in total plant dry weight after 81 d, compared with 1.4 and 1.6-fold increases for sweetgum and sycamore, respectively, after 69 d. Although elevated CO2 increased net CO2 assimilation rate of sugar maple by 115 %, there was a 10-fold increase in leaf area which contributed to the growth response. Although drought did not eliminate a growth response of sugar maple to elevated CO2, it greatly reduced the elevated CO2- induced enhancement of relative growth rate. In contrast, relative growth rates of sweetgum and sycamore were not significantly increased by elevated CO2. Drought, under elevated CO2, reduced leaf area of all three species to a greater extent than it reduced net CO2 assimilation rate. The response ranged from no effect in sugar maple to a 40 % reduction in sycamore, with sweetgum exhibiting an intermediate response. Results indicate that drought may alter the growth response, gas exchange and water relations of tree species growing in an elevated CO2 atmosphere. Under high nutrient and water availability, sugar maple may benefit the most (of the three species studied) from a CO2-enriched atmosphere, but productivity gains will be limited if frequent drought is prevalent.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ENRICHMENT, LIQUIDAMBAR-STYRACIFLUA, PHOSPHORUS DEFICIENCY, PINUS-TAEDA SEEDLINGS, RESPONSES, STOMATAL CONDUCTANCE, WATER-STRESS

2409

Tschaplinski, T.J., D.B. Stewart, and R.J. Norby. 1995. Interactions between drought and elevated co2 on osmotic adjustment and solute concentrations of tree seedlings. *New Phytologist 131(2):169-177.*

Although drought tolerance of tree species is a critical determinant of forest composition, how elevated CO2 affects drought tolerance is uncertain. Interactions between elevated CO2 and drought on osmotic potential and osmotic adjustment of American sycamore (Platanus occidentalis L.), sweetgum (Liquidambar styraciflua L.), and sugar maple (Acer saccharum Marsh.) were investigated using l-yr-old seedlings, planted in 81 pots and grown in four open-top chambers, containing either ambient air or ambient air enriched with 300 mu mol mol(-1) CO2. A well-watered treatment with plants watered daily and a droughted treatment in which plants were subjected to a series of drought cycles were included within each chamber. Sugar maple and sweetgum seedlings completed a total of seven drying cycles, whereas sycamore seedlings, because of their greater leaf area and plant size, completed 11 cycles. The mean soil water potential at re-watering for droughted seedlings in ambient CO2 was -0.5, -0.7, and -1.8 MPa for sugar maple, sweetgum and sycamore, respectively, compared with -0.2, -0.7, and -1.2 MPa, respectively, under elevated CO2. By contrast, all well-watered plants were maintained at soil water potential >-0.1 MPa. Drought under ambient CO2 reduced osmotic potential at saturation for leaves of sycamore and sweetgum by 0.30 MPa and 0.61 MPa, respectively, but leaves of sugar maple did not display osmotic adjustment to drought. Elevated CO2 increased osmotic potential at turgor loss for leaves of sugar maple by 0.33 MPa under well-watered conditions, and 0.48 MPa under drought. This response was not evident in the other species and might be related to the rapid growth of sugar maple causing a depletion of solutes. Whereas drought reduced the total solute concentration in roots of sugar maple, primarily the result of a reduction in K, elevated CO2 did not alter the concentration of total solutes in roots of any of the three species. Elevated CO2 has differing effects on drought tolerance among tree species, and thus might alter the competitive relations between species.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, FORESTS, NITROGEN RESPONSE, PHYSIOLOGICAL INDICATORS, ROTATION SYCAMORE PLANTATION, STRESS, WATER RELATIONS

2410

Tsygankov, A.A., L.T. Serebryakova, K.K. Rao, and D.O. Hall. 1998. Acetylene reduction and hydrogen photoproduction by wild-type and mutant strains of Anabaena at different CO2 and O-2 concentrations. *Fems Microbiology Letters 167(1):13-17.*

Hydrogen photoproduction by growing cultures of Anabaena variabilis and A. azollae did not occur under air+CO2 or argon+CO2 atmospheres at saturating light but did take place under argon alone. It was shown that CO2 inhibited photoproduction of H-2 as a result of the

photosynthetic production of O-2 whereas photoreduction of C2H2 by these cyanobacteria was not inhibited by O-2 concentrations up to 20% in the assay gas phase. In contrast to the wild type of A. variabilis and of A. azollae, H-2 photoproduction by the hydrogenase-impaired mutant A. variabilis PK84 showed only a slight dependence on O-2 concentration. Thus, in the wild-type Anabaena the decrease in the observed rate of H-2 evolution at elevated O-2 concentrations could be the result of an increase in hydrogenase-mediated uptake of H-2 via an oxyhydrogen reaction. (C) 1998 Federation of European Microbiological Societies. Published by Elsevier Science B.V. All rights reserved.

KEYWORDS: BLUE GREEN ALGA, FIXATION, NITROGEN, OXYGEN, VARIABILIS

2411

Tuba, Z., Z. Csintalan, K. Szente, Z. Nagy, and J. Grace. 1998. Carbon gains by desiccation-tolerant plants at elevated CO2. *Functional Ecology 12(1):39-44.*

1. There have been no reports of the long-term responses of the desiccation-tolerant (DT) plants to elevated CO2. Xerophyta scabrida is a DT woody shrub, which loses chlorophylls and thylakoids during desiccation: a so-called poikilochlorophyllous desiccation-tolerant species (PDT), When the leaves of X. scabria are allowed to desiccate, the species shows many of the normal features of (P)DT plants. 2. However, the duration of:photosynthesis in X. scabria is prolonged by 300% when the measurements are: made at 700 as opposed to 350 p.p.m. CO2. The implication is that the carboxylating enzymes must still have been active at this time to enable appreciable photosynthetic activity, This response could have far-reaching implications for the success of such species in a future climate. 3. Lichens and mosses, representing the homoiochlorophyllous DTs (HDT), retain their chlorophyll content and photosynthetic apparatus during desiccation, We show the desiccation responses of two common HDT species (Cladonia convoluta and Tortula ruralis) to elevated CO2 for comparison, Both HDT species showed increased net CO2 uptake in the material grown at high CO2 by more than 30% in moss and by more than 50% in lichen. It is concluded that desiccation- tolerant plants will be among the main beneficiaries of a high CO2 future.

KEYWORDS: ATMOSPHERIC CO2, BORYA-NITIDA LABILL, CHLOROPHYLLS, LEAVES, PHOTOSYNTHESIS, RECONSTITUTION, REHYDRATION, RESPIRATION, WATER-CONTENT, XEROPHYTA-SCABRIDA

2412

Tuba, Z., M.B. Jones, K. Szente, Z. Nagy, L. Garvey, and R. Baxter. UNKNOWN YEAR. Some ecophysiological and production responses of grasslands to long-term elevated CO2 under continental and atlantic climates. *Stress of Life :241-250.*

KEYWORDS: INCOMPLETE, ATMOSPHERIC CO2, C-3 PLANTS, CARBON DIOXIDE, COMMUNITIES, CROP RESPONSES, GROWTH, LEAVES, PHOTOSYNTHETIC CAPACITY, TRANSPIRATION, WATER-USE EFFICIENCY

2413

Tuba, Z., M.C.F. Proctor, and Z. Takacs. 1999. Desiccation-tolerant plants under elevated air CO2: A review. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences 54(9-10):788-796.*

This article summarises present knowledge of the ecophysiological responses to elevated atmospheric CO2 of desiccation tolerant (DT) plants. It deals primarily with lichens and bryophytes, as the most prominent groups of DT photosynthetic organisms, but includes some comment on algae and vascular DT plants. Results of research on DT plants are compared with those on desiccation sensitive vascular Cg plants, the most widely investigated group in the field of global change. Both DT and non-DT plants show an immediate positive response of photosynthesis to elevated CO2, but in both groups the longer term effect is generally reduced (or even reversed) by down-regulation or feedback inhibition of photosynthesis, or other limitations on production and growth. In bryophytes and lichens, enhanced short-term photosynthesis may or may not be reflected in increased production; bryophytes have limited source-sink differentiation, and lichens invest excess photosynthate in secondary metabolites. DT plants may gain some advantage from elevated CO2 at both low and excessive water contents. Neither theoretical considerations nor experimental results suggest that elevated atmospheric CO2 will lead to any substantial shift in the balance of advantage between DT and non-DT plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE CONCENTRATION, GREEN-ALGAL, GROWTH, LICHENS, PHOTOSYNTHESIS, RESPONSES, SOIL RESPIRATION, VEGETATION, WATER-CONTENT

2414

Tuba, Z., K. Szente, and J. Koch. 1994. Response of photosynthesis, stomatal conductance, water-use efficiency and production to long-term elevated co2 in winter- wheat. *Journal of Plant Physiology 144(6):661-668.*

Responses of photosynthesis, stomatal conductance, water use efficiency (at the beginning of flowering) and production allocation (at full ear/grain ripening) to long-term elevated CO2 were assessed in winter wheat (Triticum aestivum L. cv. MV16). Plants were grown in open top chambers under a temperate-continental climate from germination at ambient (350 mu molmol(-1)) and elevated (700 mu molmol(-1)) CO2 concentrations. High CO2 plants displayed a decreased initial slope of the A/C-i response curve, with the assimilation rate (A) continuing to increase above 400 mu molmol(-1) internal CO2 concentration (C-i). A in the ambient plants showed P regeneration limitation while RuBP regeneration appeared to be limiting A in the high CO2 treatment. Variable fluorescence ratios (Rfd 690) were lower in the high CO2 plants indicating a lower potential photochemical activity. The increase in the values for the chlorophyll fluorescence ratio F690/F735 in the high CO2 plants was in agreement with the lower chlorophyll a+b concentrations. The high CO2 plants had higher concentrations of starch in their leaves and roots that the ambient plants. Stomatal conductance (g(s)) was lower in the high CO2 plants at every CO2 concentration (C-a) and C-i and the C-i-dependent g(s) response had a large influence on the A/g(s), function. The higher water use efficiency (WUE) values (at C-a's > 350 mu molmol(-1)) in the high CO2 wheat plants were the result of a larger decrease in transpiration rate (E) in the high CO2 plants than in the ambient plants, and of a simultaneous larger increase in A in the range of C-a above 350 mu molmol(-1) COP. The integrated and combined effect of the photosynthetic and stomatal acclimation to elevated CO2 produced a higher C- assimilation in high CO2 plants at elevated CO2 than in the ambient plants, however, this was not followed by an acclimation in C-allocation. These were reflected in a slightly increased (6.7%) overall dry matter production and lower reproductive allocation (RA).

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, C-3 PLANTS, CHLOROPHYLL CONTENT, ENRICHMENT, EXPOSURE, INHIBITION, LEAVES, NITROGEN, PHYSIOLOGY

2415

Tuba, Z., K. Szente, Z. Nagy, Z. Csintalan, and J. Koch. 1996. Responses of CO2 assimilation, transpiration and water use efficiency to long-term elevated CO2 in perennial C-3 xeric loess steppe species.

Journal of Plant Physiology 148(3-4):356-361.

CO2 assimilation (A), transpiration (E), water use efficiency (WUE), leaf-nitrogen and carbohydrate responses to 11 months elevated (700 mu mol mol(-1)) CO2 exposure in four perennial C- 3 species (Festuca rupicola, Dactylis glomerata, Filipendula vulgaris, Salvia nemorosa) from a xeric temperate loess steppe are reported. The responses in the species varied greatly owing to their differing acclimation. The acclimation of photosynthesis was somewhat downward in F. rupicola, fully downward in D. glomerata, and upward in S. nemorosa and F. vulgaris. The reduction in the initial slope of the A/c(i) response curve in E rupicola and D. glomerata suggested a decrease in Rubisco capacity. Net CO2 assimilation at 700 mu mol mol(-1) CO2 c(a) in the high CO2 F. rupicola was higher than in those grown at present (350 mu mol mol(-1)) CO2; there was no difference in D. glomerata. The initial slope of the A/c(i) curve indicated an increased Rubisco capacity in high CO2 F. vulgaris and S. nemorosa. Their net CO2 assimilation was higher in the plants grown in the high CO2 treatment at c(i)'s over 200 mu mol mol(-1) than that in the plants grown at present CO2. The A/c(i) response curves, which were saturated in all species grown at present CO2, did not reach saturation in the plants grown at elevated CO2, reflecting that the Pi limitation of CO2 assimilation was alleviated in the plants grown at high CO2. Transpiration decreased with an increase in c(i) in both the present and elevated CO2 F. rupicola and D. glomerata. In F. vulgaris, an increase in ci caused a reduction in transpiration in the plants grown at high CO2 only. Transpiration rate in both the present and elevated CO2 S. nemorosa was not affected by any change in c(i). It is suggested then that long-term exposure to high CO2 causes a similar acclimation of stomatal regulation and transpiration to that of photosynthesis. High CO2 caused a significant decrease in protein-nitrogen content only in D. glomerata. Starch increased in F. rupicola and D. glomerata and soluble sugar content was higher in all species grown at high CO2 than at ambient. Instantaneous WUE significantly increased in ail species grown at elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, COMMUNITIES, EXCHANGE, EXPOSURE, GROWTH, INHIBITION, LEAVES, PHOTOSYNTHETIC CAPACITY, PLANTS

2416

Tubiello, F.N., G. Lin, J.W. Druitt, and B.D.V. Marino. 1999. Ecosystem-level evapotranspiration and water-use efficiency in the desert biome of Biosphere 2. *Ecological Engineering 13(1-4):263-271.*

We estimate whole-system water and carbon fluxes for the desert biome of Biosphere 2 under two different daily-mean CO2 concentrations: 450 ppmv and 850 ppmv. The desert mesocosm occupies an area of approximately 1500 m(2), has a total atmospheric Volume of about 25000 m(3) and contains a heterogeneous distribution of plants and soils. Atmospheric water content and CO2 concentrations were measured continuously using a variety of sensors, including a Li-cor 6262 for CO2 deployed within the experimental area. Daily carbon and water budgets were calculated in the desert biome, isolated from the rest of Biosphere 2 by deploying isolation curtains for 24-h periods. Data collected for six closure periods suggest that elevated CO2 concentration increased whole-system carbon uptake, while evapotranspiration remained constant. As a result, whole-system water-use efficiency (WUE, defined as net ecosystem carbon uptake per unit water transpired) in the Biosphere 2 desert increased by more than 40%. Our measurements investigate soil-plant processes at a medium scale, ideally bridging the gap between traditional controlled-environment growth chambers and open-held studies. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON, CO2, RESPONSES

2417

Tubiello, F.N., T. Mahato, T. Morton, J.W. Druitt, T. Volk, and B.D.V. Marino. 1999. Growing wheat in Biosphere 2 under elevated CO2: Observations and modeling. *Ecological Engineering 13(1-4):273-286.*

Spring wheat (Triticum aestivum L., cv. Yecora Rojo) was grown in the intensive agricultural biome (IAB) of Biosphere 2 during the 1995-1996 winter/spring season. Environmental conditions were characterized by a day/night temperature regime of 27/17 degrees C, relative humidity (RH) levels around 45%, mean atmospheric CO2 concentration of 450 ppmv, and natural light conditions with mean intensities about half of outside levels. Weekly samples of above-ground plant matter were collected throughout the growing season and phenological events recorded. A computer model, CERES-Wheat, previously tested under both field and controlled conditions, was used to simulate the observed crop growth and to help in data analysis. We found that CERES-Wheat simulated the data collected at Biosphere 2 to within 10% of observed, thus suggesting that wheat growth inside the IAB was comparable to that documented in other environments. The model predicts phenological stages and final dry matter (DM) production within 10% of the observed data. Measured DM production rates, normalized for light absorbed by the crop, suggested photosynthetic efficiencies intermediate between those observed under optimal field conditions and those recorded in NASA-Controlled Ecological Life-Support Systems (CELSS). We suggest that such a difference can be explained primarily in terms of low light levels inside the IAB, with additional effects due to elevated CO2 concentrations and diffuse light fractions. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, CROP PRODUCTIVITY, EFFICIENCY, ENRICHMENT, GROWTH, RADIATION, RESPONSES, TEMPERATURE, WINTER-WHEAT

2418

Tubiello, F.N., C. Rosenzweig, B.A. Kimball, P.J. Pinter, G.W. Wall, D.J. Hunsaker, R.L. LaMorte, and R.L. Garcia. 1999. Testing CERES-wheat with free-air carbon dioxide enrichment (FACE) experiment data: CO2 and water interactions. *Agronomy Journal 91(2):247-255.*

Dynamic crop-growth models are used to project the effects of rising atmospheric CO2 concentration and associated climate change on crop yields. Such model predictions are largely untested in the field, for lack of experimental data. We tested the CERES-Wheat model, modified to include leaf-level photosynthesis response to elevated CO2, using field data from 2 yr of Free-Air Carbon Dioxide Enrichment (FACE) experiments with spring wheat (Triticum aestivum L. cv. Yecora Rojo) in Mariclopa, AZ. Two irrigation treatments (well-watered, WW; water-deficit stressed, WS) and two atmospheric CO2 concentrations (ambient, 350 mu mol mol(-1); elevated, 550 mu mol mol(-1)) were simulated. The model was evaluated using measurements of crop phenology, aboveground dry matter (DM) production, grain yield, and evapotranspiration (ET). Model calculations of crop phenology were within 2 to 3 d of observed values under WW, ambient CO2 conditions in both years. The model did not simulate the accelerated crop phenology (5-8 d at physiological maturity) observed in the WW and elevated CO2 treatments, indicating the need to include effects of increased stomatal resistance on canopy temperature. Simulations of DM and grain yield were within 10% of measured values, except for a tendency to overcalculate DM response to CO2 by 10 to 15% in Year 1 for WS treatments. The model undercalculated cumulative ET under WW conditions by 15%; model sensitivity analyses suggest that simulation of potential evapotranspiration (PET) was too low for this arid site. The model reproduced measured dynamics of CO2-water interactions. Simulated reductions in water loss due to elevated CO2 were about 4%, in agreement with measurements. The model simulated

larger increases in DM production and yield due to elevated CO2 under WS than under WW conditions. In Year 1, simulated crop response to CO2 was 2% larger (measured: 3%) under WS than under WW conditions; in Year 2, it was 11% larger (measured: 9%). The ability to simulate CO2-water interactions, though it needs to be further evaluated with additional experimental datasets, is an important attribute of models used to project crop yields under elevated CO2 and climate change.

KEYWORDS: CLIMATE CHANGE, ECOSYS, GROWTH, RESPONSES, SIMULATIONS, TEMPERATURE, USE EFFICIENCY, WINTER-WHEAT, YIELD

2419

Tubiello, F.N., C. Rosenzweig, and T. Volk. 1995. Interactions of co2, temperature and management-practices - simulations with a modified version of ceres-wheat. *Agricultural Systems 49(2):135-152.*

A new growth subroutine was developed for CERES-Wheat, a computer model of wheat (Triticum aestivum) growth and development. The new subroutine simulates canopy photosynthetic response to CO2 concentrations and light levels, and includes the effects of temperature on canopy light-use effciency. Its performance was compared to the original CERES-Wheat V-2.10 in 30 different cases. Biomass and yield predictions of the two models were well correlated (correlation coefficient r > 0.95). As an application, summer growth of spring wheat was simulated at one site. Modeled crop responses to higher mean temperatures, different amounts of minimum and maximum warming, and doubled CO2 concentrations were compared to observations. The importance of irrigation and nitrogen fertilization in modulating the wheat crop climatic responses were also analyzed. Specifically, in agreement with observations, rainfed crops were found to be more sensitive to CO2 increases than irrigated ones. On the other hand, low nitrogen applications depressed the ability of the wheat crop to respond positively to CO2 increases. In general, the positive effects of high CO2 grain yield were found to be almost completely counterbalanced by the negative effects of high temperatures. Depending on how temperature minima and maxima were increased, yield changes averaged across management practices ranged from -4% to 8%.

KEYWORDS: CARBON DIOXIDE, CLIMATE, CROP, ENRICHMENT, LEAF-AREA, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, YIELD

2420

Turnbull, M.H., D.T. Tissue, K.L. Griffin, G.N.D. Rogers, and D. Whitehead. 1998. Photosynthetic acclimation to long-term exposure to elevated CO2 concentration in Pinus radiata D. Don. is related to age of needles. *Plant, Cell and Environment 21(10):1019-1028.*

The effects of CO2 enrichment on photosynthesis and ribulose- 1,5-bisphosphate carboxylase/oxygenase (Rubisco) in current year and 1-year-old needles on the same branch were studied on Pinus radiata D. Don. trees growing for 4 years in large, open- top chambers at ambient (36 Pa) and elevated (65 Pa) CO2 partial pressures. At this age trees were 3.5-4 m tall. Measurements made late in the growing cycle (March) showed that photosynthetic rates at the growth CO2 concentration [(pCO(2))(a)] were lower in 1-year-old needles of trees grown at elevated CO2 concentrations than in those of trees grown at ambient (pCO(2))(a). At elevated CO2 concentrations V-cmax (maximum carboxylation rate) was reduced by 13% and J(max) (RuBP regeneration capacity mediated by maximum electron transport rate) by 17%. This corresponded with photosynthetic rates at the growth (pCO(2))(a) of 4.68 +/- 0.41 mu mol m(-2) s(-1) and 6.15 +/- 0.46 mu mol m(-2) s(-1) at 36 and 65 Pa, respectively (an enhancement of 31%). In current year needles photosynthetic rates at the growth (pCO(2))(a) were 6.2 +/- 0.72 mu mol m(-2) s(-1) at 36 Pa and 10.15 +/- 0.64 mu mol m(- 2) s(-1) at 65 Pa (an enhancement of 63%). The smaller enhancement of photosynthesis in 1-year-old needles at 65 Pa was accompanied by a reduction in Rubisco activity (39%) and content (40%) compared with that at 36 Pa. Starch and sugar concentrations in 1-year-old needles were not significantly different in the CO2 treatments. There was no evidence in biochemical parameters for down-regulation at elevated (pCO(2))(a) in fully fexpanded needles of the current year cohort. These data show that enhancement of photosynthesis continues to occur in needles after 4 years' exposure to elevated CO2 concentrations. Photosynthetic acclimation reduces the degree of this enhancement, but only in needles after 1 year of growth. Thus, responses to elevated CO2 concentration change during the lifetime of needles, and acclimation may not be apparent in current year needles. This transitory effect is most probably attributable to the effects of developmental stage and proximity to actively growing shoots on sink strength for carbohydrates. The implications of such age-dependent responses are that older trees, in which the contribution of older needles to the photosynthetic biomass is greater than in younger trees, may become progressively more acclimated to elevated CO2 concentration.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, CARBOXYLASE ACTIVITY, GAS-EXCHANGE, NOTHOFAGUS-FUSCA, NUTRIENT STATUS, PHASEOLUS-VULGARIS, RISING ATMOSPHERIC CO2, RUBISCO ACTIVITY, SOUR ORANGE TREES, STOMATAL CONDUCTANCE

2421

Tyree, M.T., and J.D. Alexander. 1993. Plant water relations and the effects of elevated co2 - a review and suggestions for future-research. *Vegetatio 104:47-62.*

Increased ambient carbon dioxide (CO2) has been found to ameliorate water stress in the majority of species studied. The results of many studies indicate that lower evaporative flux density is associated with high CO2-induced stomatal closure. As a result of decreases in evaporative flux density and increases in net photosynthesis, also found to occur in high CO2 environments, plants have often been shown to maintain higher water use efficiencies when grown at high CO2 than when grown in normal, ambient air. Plants grown at high CO2 have also been found to maintain higher total water potentials, to increase biomass production, have larger root-to-shoot ratios, and to be generally more drought resistant (through avoidance mechanisms) than those grown at ambient CO2 levels. High CO2- induced changes in plant structure (i.e., vessel or tracheid anatomy, leaf specific conductivity) may be associated with changes in vulnerability to xylem cavitation or in environmental conditions in which runaway embolism is likely to occur. Further study is needed to resolve these important issues. Methodology and other CO2 effects on plant water relations are discussed.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-MATTER PRODUCTION, HYDRAULIC ARCHITECTURE, INDUCED XYLEM EMBOLISM, LIQUIDAMBAR- STYRACIFLUA, OLD- FIELD PERENNIALS, PINUS-TAEDA SEEDLINGS, RADIATA D-DON, SUB-STOMATAL CAVITIES, WOODY-PLANTS

2422

Ueda, Y., and J.H. Bai. 1993. Effect of short-term exposure of elevated co2 on flesh firmness and ester production of strawberry. *Journal of the Japanese Society for Horticultural Science 62(2):457-464.*

Strawberry fruits (Fragaria X ananasa cv. Hokowase) were treated with 20% CO2 for 12 to 48 hr at 1-degrees-C and then stored at the same temperature for an additional 24 to 48 hr; subsequently they were transferred to 20-degrees-C and held for 8 hours. 1. Berries exposed to CO2, including those stored for 8 hr at 20-degrees-C were firmer than the control berries exposed to air. 2. The CO2 treatment had a little

effect on the evolution of methyl acetate and methyl butyrate, the predominant volatiles. However, the evolution of ethyl acetate and ethyl butyrate, the minor volatiles, was increased sharply by the CO2 treatment. These changes in the concentration of volatiles gave the berries an unnatural aroma. 3. In berries given the same CO2 treatment for 24 hr but stored longer period at 1-degrees-C, the abnormal aroma formation persisted for at least 5 days.

KEYWORDS: ATMOSPHERES, DECAY, METHYLESTERASE, QUALITY

2423
Uprety, D.C. 1998. Carbon dioxide enrichment technology: Open top chambers a new tool for global climate research. *Journal of Scientific & Industrial Research 57(5):266-270.*

There are many technical difficulties in conducting crop response studies for elevated carbon dioxide. Available facilities include green house, leaf cuvettes, phytotron, and air exclusion systems. The environmental control on these systems induces uncertainity in the extrapolation of results to the variable natural environments. However, open top chamber technology does not modify the micro-climate and induces realistic natural conditions. Open top chambers are cylindrical, aluminium frames with clear flexible covering and frustrum to reduce the incursion of external air. CO2 enriched air is introduced into the chamber through a perforated spurt with the help of a blower to distribute CO2 uniformly. A relatively simpler design and construction of open top chambers make them the most likely method to be used in the near future for long-term elevated CO2 exposures of crops and other ecosystems.

2424
Uprety, D.C., N. Dwivedi, and R. Mohan. 1998. Characterization of CO2 responsiveness in a Brassica oxycamp interspecific hybrid. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 180(1):7-13.*

A study of the characterization of CO2 responsiveness in Brassica oxycamp and its parents Brassica oxyrrhina and Brassica campestris was done using open top chamber technology. The response of the X. B. oxycamp (hybrid) to elevated CO2 was significantly positive in respect of photosynthesis and growth and similar to that of its parent B. campestris is. X B. oxycamp and B. campestris with greater sink potential responded significantly, whereas B. oxyrrhina with a poor sink did not respond to CO2 enrichment. Photosynthetic changes at elevated CO2 levels in the hybrid and parents are partially attributed to the CO2 effects on stomatal conductance and chlorophyll fluorescence.

KEYWORDS: GROWTH, PHOTOSYNTHESIS, RESPONSES

2425
Uprety, D.C., R.S. Mishra, and Y.P. Abrol. 1995. Effect of elevated CO2 on the photosynthesis, growth and water relation of Brassica species under moisture stress. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau 175(4):231-237.*

An attempt has been made to study the interactive effect of elevated CO2 and moisture stress on photosynthesis, growth and water relations of Brassica species using open top chambers. It was observed that plants responded to elevated CO2 significantly under moisture stress condition mitigating the adverse effects on photosynthesis and growth of Brassica species. Relatively drought susceptible species, viz. B. campestris and B. nigra, responded to elevated CO2 markedly as compared to less sensitive B. carinata and B. juncea plants. The water status of plants significantly improved under elevated CO2 concentration possibly by increasing stomatal resistance and/or by increased root growth.

KEYWORDS: C-3, LEAVES, TERM, WHEAT

2426
Uprety, D.C., and B.K. Rabha. 1999. Effect of elevated CO2 and moisture stress on the carbon and nitrogen contents in Brassica juncea. *Biologia Plantarum 42(1):133-136.*

The responses of Brassica juncea cv, Pusa Bold to elevated CO2 was studied under water stress. Carbon accumulation in leaves, stem and roots was significantly higher at elevated CO2 concentration, The water stress decreased the carbon content in these plant parts and this adverse effect was reduced by CO2 enrichment. On the contrary nitrogen content of leaves, stem and roots was significantly reduced at elevated CO2. Water stress caused reduction in nitrogen content in these plant parts, similar at ambient as well as elevated CO2 concentration.

KEYWORDS: C-3, GROWTH, PHOTOSYNTHESIS, PLANTS, ROOT FRACTION

2427
Uselman, S.M., R.G. Qualls, and R.B. Thomas. 1999. A test of a potential short cut in the nitrogen cycle: The role of exudation of symbiotically fixed nitrogen from the roots of a N-fixing tree and the effects of increased atmospheric CO2 and temperature. *Plant and Soil 210(1):21-32.*

N-fixing trees facilitate the growth of neighboring trees of other species. These neighboring species benefit from the simple presence of the N fixation symbiosis in their surroundings. Because of this phenomenon, it has been hypothesized that a change in atmospheric CO2 concentration may alter the role of N-fixing trees in their environment. It is thought that the role of N-fixing trees in ecosystems of the future may be more important since they may help sustain growth increases due to increased CO2 concentration in nitrogen limited forests. We examined: (1) whether symbiotically fixed N was exuded from roots, (2) whether a doubled atmospheric CO2 concentration would result in increased organic N exudation from roots, and (3) whether increased temperature or N availability affected N exudation from roots. This study analyzed exudation of dissolved organic N from the roots of seedlings of the N-fixing tree Robinia pseudoacacia L. in a full factorial design with 2 CO2 (35.0 and 70.0 Pa) x 2 temperature (26 or 30 degrees C during the day) x 2 N fertilizer (0 and 10.0 mM N concentration) levels. Trees with no other source of N except N fixation exuded about 1% to 2% of the fixed N through their roots as dissolved organic N. Increased atmospheric CO2 concentrations did not, however, increase N exudation rates on a per gram belowground biomass basis. A 4 degrees C increase in temperature and N fertilization did, however, significantly increase N exudation rates. These results suggest that exudation of dissolved organic N from roots or nodules of N-fixing trees could be a significant, but minor, pathway of transferring N to neighboring plants in a much more rapid and direct way than cycling through death, decomposition and mineralization of plant residues. And, while exudation rates of dissolved organic N from roots were not significantly affected by atmospheric CO2 concentration, the previously observed 'CO2 fertilization effect' on N-fixing trees suggests that N exudation from roots could play a significant but minor role in sustaining increases in forest growth, and thus C storage, in a CO2 enriched atmosphere.

KEYWORDS: BLACK LOCUST, CARBON DIOXIDE, ELEVATED CO2, FOREST, GROWTH, N2 FIXATION, NODULATION, SOUTHERN APPALACHIANS, TRIFOLIUM-REPENS L, WOODY-PLANTS

2428

Usuda, H., and K. Shimogawara. 1998. The effects of increased atmospheric carbon dioxide on growth, carbohydrates, and photosynthesis in radish, Raphanus sativus. *Plant and Cell Physiology 39(1):1-7.*

The effects of sink capacity on the regulation of the acclimation of photosynthetic capacity to elevated levels of carbon dioxide are important from a global perspective. We investigated the effeocts of elevated (750 mu mol mol(-1)) and ambient (350 mu mol mol(-1)) atmospheric CO2 on growth, carbohydrate levels, and photosynthesis in radish seedlings from 15 to 46 d after planting. In radish, a major sink is the storage root, and its thickening is initiated early. Elevated CO2 increased the accumulation of dry matter by 111% but had no effect on the acclimation of the rate of photosynthesis or on the levels of carbohydrates in leaves at dawn, Elevated CO2 increased the dry weight in storage roots by 105% by 46 d after planting, apparently enhancing the sink capacity, This enhanced capacity seemed to be responsible for absorption of elevated levels of photosynthate and to result in the absence of any over-accumulation of carbohydrates in source leaves and the absence of negative acclimation of photosynthetic capacity at the elevated level of CO2.

KEYWORDS: CO2- ENRICHMENT, ELEVATED CO2, GAS-EXCHANGE, PLANT GROWTH, SINK STRENGTH, TEMPERATURE, WHEAT, YIELD

2429

Utriainen, J., and T. Holopainen. 1998. Ultrastructural and growth responses of young Scots pine seedlings (Pinus sylvestris) to increasing carbon dioxide and ozone concentrations. *Chemosphere 36(4-5):795-800.*

Three-year-old Scots pine seedlings were exposed to ambient or elevated (2 x ambient) O-3 and CO2 levels, singly and in combination, during one growth period in open-top field chambers. Growth measurements showed increased shoot length and needle width in response to CO2 enrichment, whereas O-3 exposure resulted in visible injury (chlorotic mottling and increased yellowing of previous year needles). At the ultrastructural level, O-3 caused increased electron density of chloroplast stroma and increased number of cytoplasmic ribosomes at both CO2 levels. CO2 enrichment also resulted in an increase in the size of starch grains in chloroplasts. In general, simultaneous exposure to elevated O-3 reduced the impact of elevated CO2. (C)1998 Elsevier Science Ltd.

KEYWORDS: ELEVATED CO2, EXPOSURE, L KARST, LEAF, NEEDLES, NORWAY SPRUCE, O-3, PICEA-ABIES L, TROPOSPHERIC OZONE

2430

Vadstrup, M., and T.V. Madsen. 1995. Growth limitation of submerged aquatic macrophytes by inorganic carbon. *Freshwater Biology 34(3):411-419.*

1. This study determined the effects of CO2 and HCO3- enrichment on in situ growth of two submerged macrophytes, Elodea canadensis and Callitriche cophocarpa, in two Danish lakes: Lake Hampen and Lake Vaeng. Lake Hampen is an oligotrophic low-alkaline lake (0.4 meg 1(-1)) and Lake Vaeng is mesotrophic with an alkalinity of 1.1 meg 1(-1). In Lake Hampen experiments were carried out throughout the growth season, whereas experiments in Lake Vaeng were restricted to late summer. The CO2 and HCO3- enrichment procedures used increased the concentration of free-CO2 by 500-1000 mu M and the concentration of HCO3- by about 80 CIM. 2. The concentration of free-CO2 in Lake Hampen was about five times atmospheric equilibrium concentration (55 mu M) in early summer declining to virtually zero at the end of summer. 3. Under ambient conditions Callitriche, which is restricted to CO2 use, was unable to grow and survive in both lakes. In contrast, Elodea, which has the potential to use HCO3- in photosynthesis, grew at rates varying from 0.046 to 0.080 day(-1) over the season. 4. Under CO2 enrichment the growth rate of Callitriche varied from 0.089 to 0.124 day-l and for Elodea from 0.076 to 0.117 day(-1) over the season. Enrichment with HCO3- affected Elodea only and only to a limited extent. This may be a result of insufficient increase in [HCO3-] upon enrichment or to a limited capacity of the plants to take up HCO3-. 5. The substantial stimulation of in situ growth of Elodea and Callitriche by enhanced concentrations of free-CO2 shows that inorganic carbon is an important determinant of growth of submerged macrophytes and that inorganic carbon limitation of in situ growth may be a common phenomenon in nature, even in lakes with an alkalinity as high a 1 meg 1(-1). Inorganic carbon, however, is only one of many parameters important for growth, and the growth rates of Elodea at both ambient and high free-CO2 were closely coupled to day length and photon irradiance, indicating that light had an ultimate control on growth.

KEYWORDS: BICARBONATE, COMMUNITIES, DIOXIDE, FRESH-WATER MACROPHYTES, LIGHT, PH, PHOTOSYNTHESIS, TEMPERATURE

2431

Vaisanen, H., H. Standman, and S. Kellomaki. 1994. A model for simulating the effects of changing climate on the functioning and structure of the boreal forest ecosystem - an approach based on object-oriented design. *Tree Physiology 14(7-9):1081-1095.*

We have developed a forest ecosystem model to assess the effects of climate change on the functioning and structure Of boreal coniferoUS forests assuming that temperature and precipitation are the major variables of the niche occupied by a tree species. We specified weather patterns to a level representing the time constant of different physiological and ecological processes relevant to the survival, growth and death of trees. We thereby coupled the long-term dynamics of the forest ecosystem with climate through physiological mechanisms such as photosynthesis and respiration in terms of energy flow through the ecosystem. The hydrological and nutrient cycles couple the dynamics of the forest ecosystem with climate change through soil processes, which represent the thermal and hydraulic properties of the soil, and the decomposition of litter and humus with mineralization of nutrients. Simulations for southern Finland (62-degrees-N) indicated that an increase in temperature of 5-degrees-C over one hundred years could reduce soil water in Scots pine-dominated forest ecosystems. At the same time, the temperature increase could enhance photosynthesis up to 6-8% under current CO2 concentrations (330 ppm) and up to 8-10% under elevated CO2 concentrations (660 ppm). Because the elevated temperature and CO2 concentration caused an increase in respiration (12-14% more than under the current climate), total stem production increased only up to 4% with a 5-degrees-C increase in temperature and up to 6% when temperature and atmospheric CO2 concentration were increased simultaneously. Because transpiration only increased up to 5% in response to elevated temperature and C02 Concentration, the water use efficiency of Scots-pine dominated forest ecosystems increased up to 3%, particularly during the late rotation.

2432

van Breemen, N., A. Jenkins, R.F. Wright, D.J. Beerling, W.J. Arp, F. Berendse, C. Beier, R. Collins, D. van Dam, L. Rasmussen, P.S.J. Verburg, and M.A. Wills. 1998. Impacts of elevated carbon dioxide and temperature on a boreal forest ecosystem (CLIMEX project). *Ecosystems 1(4):345-351.*

To evaluate the effects of climate change on boreal forest ecosystems,

both atmospheric CO2 (to 560 ppmv) and air temperature (by 3 degrees-5 degrees C above ambient) were increased at a forested headwater catchment in southern Norway. The entire catchment (860 m(2)) is enclosed within a transparent greenhouse, and the upper 20% of the catchment area is partitioned such that it receives no climate treatment and serves as an untreated control. Both the control and treatment areas inside the greenhouse receive deacidified rain. Within 3 years, soil nitrogen (N) mineralization has increased and the growing season has been prolonged relative to the control area. This has helped to sustain an increase in plant growth relative to the control and has also promoted increased N export in stream water. Photosynthetic capacity and carbon-nitrogen ratio of new leaves of most plant species did not change. While the ecosystem now loses N, the long-term fate of soil N is a key uncertainty in predicting the future response of boreal ecosystems to climate change.

KEYWORDS: ATMOSPHERIC CO2, LEAF LITTER, MODEL, NITROGEN

2433

Vandasselaar, A.V., and E.A. Lantinga. 1995. Modeling the carbon-cycle of grassland in the netherlands under various management strategies and environmental-conditions. *Netherlands Journal of Agricultural Science 43(2):183-194.*

A simulation model of the carbon cycle of grassland (CCGRASS) was developed to evaluate the long-term effects of different management strategies and various environmental conditions on carbon sequestration in the soil. The results presented here refer to permanent grassland on a young sedimentary loam soil in the Netherlands. The model predicted that the rate of increase in the amount of soil organic carbon will be highest at low to moderate application rates of nitrogen (100 - 250 kg N ha(-1) yr(-1)). This is due to the fact that the annual gross photosynthetic uptake of CO2 in permanent grassland is hardly influenced by the level of N supply. Since N shortage stimulates the growth of the unharvested plant parts (roots and stubble) the carbon supply to the soil is highest at low to moderate N application rates. The rate of increase in the amount of soil organic carbon will be higher under grazing than under mowing as a result of a greater amount of carbon added to the soil. Increase of atmospheric CO2 concentration may induce an increase in decomposition rate of soil organic matter due to simultaneously increased temperatures. At the same time: plant productivity and thus carbon supply to the soil will be stimulated due to the CO2-fertilization effect. Under the assumption of a temperature increase of 3 degrees C if the present atmospheric CO2 concentration doubles, the model predicted that the combined effect of elevated CO2 and temperature will slightly reduce the rate of increase in the amount of organic carbon in grassland soils compared to that under unchanged environmental conditions. There was 2% less carbon sequestration by grassland at the end of a period of 100 years as a result of these changes in environmental conditions. The separate effects of increased temperature or elevated CO2 were 10% less and 10% more carbon storage at the end of a period of 100 years, respectively.

KEYWORDS: BIOSPHERE, CROP RESIDUES, DYNAMICS, ECOSYSTEMS, MINERALIZATION, NITROGEN, ORGANIC-MATTER, SIMULATION, SOILS, TEMPERATURE

2434

Vandegeijn, S.C., J. Vos, J. Groenwold, J. Goudriaan, and P.A. Leffelaar. 1994. The wageningen rhizolab - a facility to study soil-root-shoot- atmosphere interactions in crops .1. Description of main functions. *Plant and Soil 161(2):275-287.*

A research facility is described for the integrated study of soil-root-shoot-atmosphere relationships in crops. The Wageningen Rhizolab has been in use since 1990, and consists of two rows, each with eight below-ground compartments aligned along a corridor. A rain shelter automatically covers the experimental area at the start of rainfall. Compartments are 125 cm x 125 cm and 200 cm deep. Each compartment has a separate drip irrigation system. Crop canopy photosynthesis, respiration, and transpiration can be measured simultaneously and continuously on four out of eight compartments at a time. Each compartment can be filled with a selected soil material (repacked soil) and is accessible from the corridor over its full depth. Multiple sensors for measuring soil moisture status, electrical conductivity, temperature, soil respiration, trace gases and oxygen are installed in spatial patterns in accordance with the requirements of the experiments. Sensors are connected to control and data-acquisition devices. Likewise, provisions have been made to sample manually the soil solution and soil atmosphere. Root observation tubes (minirhizotrons) are installed horizontally at depth intervals ranging from 5 cm (upper soil layers) to 25 cm (below 1 m). The facility is at present in use to study growth and development of vegetation (crops) in relation to drought, nutrient status, soil-borne diseases, and underground root competition. One important application is the study of elevated CO2 concentration and climate change and the way they affect crops and their carbon economy. Growth and development of field grown vegetables and winter cover crops are also evaluated. The common aspect of those studies is to gain a better understanding of crop growth under varying environmental conditions, and to collect datasets that may help to improve mechanistic crop growth simulation models that can address suboptimal growth conditions.

KEYWORDS: GROWTH, MINIRHIZOTRON, WATER

2435

VanderKooij, T.A.W., and L.J. DeKok. 1996. Impact of elevated CO2 on growth and development of Arabidopsis thaliana L. *Phyton-Annales Rei Botanicae 36(2):173-184.*

After germination, Arabidopsis thaliana L (cv. Landsberg) was grown at 350 mu l l(-1) (control) or 700 mu l l(-1) (elevated) CO2. Total shoot biomass at the end of the vegetative growth period was increased by 56% due to a short transient stimulation of the relative growth rate by elevated CO2 at the onset of the exposure. Thereafter the relative growth rate was comparable for both CO2 levels during the remaining vegetative part of the life cycle (0.42 g g(-1) day(-1)). Flowering architecture was not affected by elevated CO2, but seed production was 51% higher. Starch content of the shoot was substantially increased upon exposure to elevated CO2, while the soluble sugar content remained unaffected. Total nitrogen content, on a dry mass basis, was decreased at elevated CO2 mainly as a result of the increased starch content. Photosynthesis wag stimulated at elevated CO2 and no acclimation of the photosynthesis at elevated CO2 was observed. Even though the stimulation of relative growth rate was only temporary, elevated CO2 resulted in an increased fitness of Arabidopsis thaliana by an increased reproductive output.

KEYWORDS: ACCLIMATION, ALLOCATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RESPIRATION, RESPONSES, SHOOTS

2436

Van der Kooij, T.A.W., L.J. De Kok, and I. Stulen. 1999. Biomass production and carbohydrate content of Arabidopsis thaliana at atmospheric CO2 concentrations from 390 to 1680 mu l l(-1). *Plant Biology 1(4):482-486.*

The concentration dependency of the impact of elevated atmospheric CO2 concentrations on Arabidopsis thaliana L. was studied. Plants were exposed to nearly ambient (390), 560, 810, 1240 and 1680 mu l l(-1)

CO2 during the vegetative growth phase for 8 days. Shoot biomass production and dry matter content were increased upon exposure to elevated CO2. Maximal increase in shoot fresh and dry weight was obtained at 560 mu l l(-1) CO2, which was due to a transient stimulation of the relative growth rate for up to 3 days. The shoot starch content increased with increasing CO2 concentrations up to two-fold at 1680 mu l l(-1) CO2, whereas the contents of soluble sugars and phenolic compounds were hardly affected by elevated CO2. The chlorophyll and carotenoid contents were not substantially affected at elevated CO2 and the chlorophyll a/b ratio remained unaltered. There was no acclimation of photosynthesis at elevated CO2; the photosynthetic capacity of leaves, which had completely developed at elevated CO2 was similar to that of leaves developed in ambient air. The possible consequences of an elevated atmospheric CO2 concentration to Arabidopsis thaliana in its natural habitat is discussed.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, METABOLISM, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RISING CO2, STARCH, TOMATO

2437

van der Westhuizen, M.M., and M.D. Cramer. 1998. The influence of elevated rhizosphere dissolved inorganic carbon concentrations on respiratory O-2 and CO2 flux in tomato roots. *Journal of Experimental Botany 49(329):1977-1985.*

Respiratory CO2 and O-2 flux were measured in hydroponically grown Lycopersicon esculentum (L.) Mill. cv. F144 plants at either low (0 mu mol mol(-1)) or elevated CO2 concentrations (>2000 mu mol mol-1) supplied to the roots. In NO3--fed plants the consumption of O-2 and the engagement of the alternative pathway were increased by elevated dissolved inorganic carbon (DIC=CO2+ HCO3-) concentrations. This was ascribed to the influence of organic acids on the ICA cycle and electron transport pathways. Inhibition of O-2 consumption by elevated DIC in NH4+-fed plants may be due to the reduction requirements of anaplerotic carbon entering the TCA cycle or the removal of carbon from the TCA cycle for amino acid synthesis. In both NO3- and NH4+-fed plants elevated DIC inhibited root CO2 release due to high rates of DIC incorporation by phosphoenolpyruvate carboxylase (PEPc) activity. Transient net CO2 consumption due to the inhibition of respiration by salicylhydroxamic acid and KCN, together with high respiratory quotients after the addition of inhibitors of carbonic anhydrase (CA) activity, were also ascribed to high rates of DIC incorporation at elevated DIC concentrations. Ethoxyzolamide, an inhibitor of CA activity, inhibited both D[C-14 incorporation into organic products and NO3- uptake by 81% and 40%, respectively. This, together with a 32% increase in (DIC)-C-14 accumulation and inhibition of NO3- uptake upon inhibition of anion transport by diisothiocyanato-stilbene- 2,2'-disulphonic acid (DIDS) may indicate the exchange of HCO3- for NO3- across the root plasmalemma. It was concluded that dark incorporation of HCO3- by PEPc increased at elevated rhizosphere DIC concentrations and that the products of DIC incorporation may stimulate respiratory electron transport. Additional reducing energy and carbon skeletons from the tricarboxylic acid (TCA) cycle would therefore be available for respiration and the reduction and incorporation of NO3- into amino acids.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO2, DIOXIDE, LEAF RESPIRATION, LONG-TERM EXPOSURE, METABOLISM, NUTRITION, PLANTS, RESPONSES, TRANSPORT

2438

vandeStaaij, J.W.M., E. Bolink, J. Rozema, and W.H.O. Ernst. 1997. The impact of elevated UV-B (280-320 nm) radiation levels on the reproduction biology of a highland and a lowland population of Silene vulgaris. *Plant Ecology 128(1-2):172-179.*

A highland (altitude 1600 m) and a lowland (altitude -2 m) population of the perennial herb Silene vulgaris were tested on the effects of elevated levels of UV-B radiation on their reproductivity. Highland populations receive higher natural UV- B doses than lowland populations. Therefore adaptation to high W-B levels of the highland population is to be expected. The lowland population showed a decrease in the number of seed producing flowers and the number of seeds produced per plant under elevated UV-B levels. The highland population increased the number of seeds per plant under elevated UV-B levels. In both populations individual seed mass as well as seed germination percentages were unaffected by the UV-B flux received by the parental plant. Possible effects of UV-B induced alterations in reproductivity on the geographical distribution of the different populations are discussed.

KEYWORDS: ALPINE LIFE ZONE, CARBON-DIOXIDE CO2, ELEVATIONAL GRADIENT, GREENHOUSE, GROWTH, INHIBITION, PHOTOSYNTHESIS, PLANTS, SENSITIVITY, ULTRAVIOLET-RADIATION

2439

Vandestaaij, J.W.M., R. Huijsmans, W.H.O. Ernst, and J. Rozema. 1995. The effect of elevated uv-b (280-320 nm) radiation-levels on silene vulgaris - a comparison between a highland and a lowland population. *Environmental Pollution 90(3):357-362.*

Highland (altitude 1600 m above sea level) and lowland (altitude -2 m below sea level) populations of the perennial herb Silene vulgaris (Moench) Garcke, were tested on their response to elevated levels of UV-B radiation. Highland populations typically receive high natural UV-B fluxes, whereas lowland populations receive a lower natural UV-B dose. Adaptation to high UV-B levels of the highland population is to be expected. Experimental comparison of growth rates, gas exchange rates, transpiration and biochemical parameters using adult plants as well as seedlings did not show a difference in the response to elevated UV-B levels between the two populations. Individuals of both populations were relatively insensitive to elevated UV-B radiation. The response of alpine and lowland populations of Silene vulgaris is discussed in relation to the dispersal of this species after the last ice age.

KEYWORDS: ACCLIMATION, ALPINE LIFE ZONE, CARBON-DIOXIDE CO2, GRADIENT, GROWTH, INHIBITION, MECHANISMS, PLANTS, RESPONSES, VEGETATION

2440

Vandestaaij, J.W.M., G.M. Lenssen, M. Stroetenga, and J. Rozema. 1993. The combined effects of elevated co2 levels and uv-b radiation on growth-characteristics of elymus-athericus (= e-pycnanathus). *Vegetatio 104:433-439.*

Elymus athericus (Link) Kerguelen, a C3 grass, was grown in a greenhouse experiment to determine the effect of enhanced atmospheric CO2 and elevated UV-B radiation levels on plant growth. Plants were subjected to the following treatments; a) ambient CO2-Control UV-B, b) ambient CO2-elevated UV-B, c) double CO2-control UV-B, d) double CO2-elevated UV-B. Elevated CO2 concentrations stimulated plant growth, biomass production was 67% higher than at ambient CO2. Elevated UV-B radiation had a negative effect on growth, biomass production was depressed by 31%. Enhanced CO2 combined with elevated UV-B levels caused a biomass depression of 8% when compared with the control plants. UV-B induced growth depression can be modified by a growth stimulus caused by high CO2 concentrations. Growth analysis has been performed and possible physiological mechanisms behind changing growth parameters are discussed.

KEYWORDS: CARBON DIOXIDE, INHIBITION, PLANTS

2441

Vangardingen, P.R., J. Grace, D.D. Harkness, F. Miglietta, and A. Raschi. 1995. Carbon-dioxide emissions at an italian mineral spring - measurements of average co2 concentration and air-temperature. *Agricultural and Forest Meteorology 73(1-2):17-27.*

Emissions of carbon dioxide from vents at the Bossoleto mineral spring in Central Italy have been calculated to exceed 12 t day(-1), This emission leads to enhanced atmospheric concentrations of CO2 over an area of more than 3000 m(2). The vent gas is over 99% pure CO2, with a characteristic isotopic signature that is totally depleted in C-14. At night, concentrations at the bottom of the bowl-like depression can increase to levels approaching 75%. In the morning, this high concentration of CO2 is associated with a rapid temperature increase of over 10 degrees C before the CO2 disperses. This site is being used in a number of studies of the response of plant communities to long-term enhanced CO2 concentrations. The problem of defining CO2 concentrations in these studies was approached by comparing estimates determined by gas analysis measurements and isotopic analysis of leaf material, The isotopic method used C-14 as a tracer, integrating effective concentration over the life of a leaf by calculating from the ratio of C-14 measurements of plant material growing near the spring and at a control site. The estimates obtained using isotopic analysis of leaf material were similar to gas analysis measurements obtained during the day. This suggests that plants at this site are responding to the concentrations during the day, rather than the much higher night-time concentrations, making the system useful for biological research.

KEYWORDS: ENVIRONMENT, FORESTS

2442

van Ginkel, J.H., and A. Gorissen. 1998. In situ decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Soil Science Society of America Journal 62(4):951-958.*

The effects of elevated CO2 on belowground C input, on decomposition of roots in situ vs. decomposition of disturbed roots, and on soil microbial biomass were investigated in a perennial grass species. Forty ryegrass (Lolium perenne L.) plants were homogeneously C-14-labeled in two controlled environments for 115 d in a continuous (CO2)-C-14 atmosphere at 350 and 700 mu L CO2 L-1 and two soil N levels (low, LN, and high, HN). Thereafter, some of the plants were destructively harvested, Undisturbed root systems of the remaining plants were incubated in situ (IRS) for comparison with a disturbed incubation of the dried and ground roots (DRS) in their original soils. At the start of the incubation, elevated CO2 had increased total C-14-labeled soil C input by 44 and 27% at LN and HN, respectively, compared with input at ambient CO2, After incubation for 230 d, 40% of C-14 soil content was mineralized to (CO2)-C-14 in the disturbed system and 52% in the intact system. Native soil organic matter (SOM) decomposition of the DRS was lower than the SOM decomposition of the IRS, The formation of C-14-labeled soil microbial biomass (C-14-SMB) in the soil with DRS was 130% higher than in the soil with the IRS. Elevated CO2 decreased the decomposition of roots and root-derived products by 10% and increased the size of the C-14-SMB by 28% for both IRS and DRS, whereas the decomposition of SOM was not affected by CO2 at either LN or HN, After plant growth and in situ incubation, the C-14-labeled C in the soil solution showed a highly positive correlation with the amount of C-14-SMB, The ratio between C-14-labeled microorganisms and total (CO2)-C-14 evolved was not affected by elevated CO2, It seems that micrroorganisms adapt to changing soil C input under elevated CO2 and there is no effect on their turnover and behavior.

KEYWORDS: BETULA-PENDULA ROTH, CO2 CONCENTRATIONS, FINE ROOTS, LITTER DECOMPOSITION, LOLIUM-PERENNE, MICROBIAL BIOMASS, NITROGEN, PLANT MATERIALS, SOIL, TURNOVER

2443

vanGinkel, J.H., A. Gorissen, and J.A. vanVeen. 1996. Long-term decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Journal of Environmental Quality 25(5):1122-1128.*

Carbon input into the soil and decomposition professes under elevated CO2 are highly relevant for C sequestering in the soil. Plant growth and decomposition of root material under ambient and elevated atmospheric CO2 concentrations were monitored in wind tunnels. Grass roots (Lolium perenne L.) were homogeneously C-14-labeled at 350 and 700 mu L L(-1) CO2 and at two N levels to obtain roots of different qualities. This root material was mixed with fresh loamy sand and transferred to four wind tunnels to observe its decomposition in bare soil and as affected by plant growth (L. perenne) at ambient CO2 and elevated CO2 for two growing seasons. After the second growing season, elevated CO2 had stimulated shoot and root growth by 13 and 92%, respectively. The CO2 and N concentrations at which the grass roots had been grown affected the decomposition rate. After the first growing season, the overall decomposition of 700 roots was 19% loner than that of 350 roots. The C-14- labeled microbial biomass in the soil with 700 roots was higher (44%) compared with 350 roots. After the second growing season, the decomposition of 700 low N roots was 14% lower than that of 350 low N roots, whereas the decomposition of the high N roots was unaffected. The C-14-labeled microbial biomass in the soil with 700 roots was still higher (30%) than with 350 roots. The combination of higher root yields at elevated Co-2 combined with a decrease in root decomposition will lead to a longer residence Lime of C in the soil and probably to a higher C storage.

KEYWORDS: CO2- ENRICHMENT, LEAF LITTER, LITTER DECOMPOSITION, MINERALIZATION, NITROGEN, PLANT, QUALITY, RESPONSES, RHIZOSPHERE, SOIL ORGANIC MATTER

2444

vanGinkel, J.H., A. Gorissen, and J.A. vanVeen. 1997. Carbon and nitrogen allocation in Lolium perenne in response to elevated atmospheric CO2 with emphasis on soil carbon dynamics. *Plant and Soil 188(2):299-308.*

The effect of elevated CO2 on the carbon and nitrogen distribution within perennial ryegrass (L. perenne L.) and its influence on belowground processes were investigated. Plants were homogeneously C-14-labelled in two ESPAS growth chambers in a continuous C-14-CO2 atmosphere of 350 and 700 mu L L-1 CO2 and at two soil nitrogen regimes, in order to follow the carbon flow through all plant and soil compartments. After 79 days, elevated CO2 increased the total carbon uptake by 41 and 21% at low (LN) and high nitrogen (HN) fertilisation, respectively. Shoot growth remained unaffected, whereas CO2 enrichment stimulated root growth by 46% and the root/soil respiration by 111%, irrespective of the nitrogen concentration. The total C- 14-soil content increased by 101 and 28% at LN and HN, respectively. The decomposition of the native soil organic matter was not affected either by CO2 or by the nitrogen treatment. Elevated CO2 did not change the total nitrogen uptake of the plant either at LN or at HN. Both at LN and HN elevated CO2 significantly increased the total amount of nitrogen taken up by the roots and decreased the absolute and relative amounts translocated to the shoots. The amount of soil nitrogen immobilised by micro-organisms and the size of the soil microbial biomass were not affected by elevated CO2, whereas both were significantly increased at the higher soil N content. Most striking was the 88% increase in net carbon input into the soil expressed as: C-14-roots plus total C-14-soil content minus the C-12-carbon released by decomposition of native soil organic matter. The net carbon input into the soil at ambient CO2 corresponded with 841 and 1662 kg ha(-1) at LN and HN, respectively. Elevated CO2 increased these amounts with an extra carbon input of 950 and 1056 kg ha(-1). Combined with a reduced decomposition rate of

plant material grown at elevated CO2 this will probably lead to carbon storage in grassland soils resulting in a negative feed back an the increasing CO2 concentration of the atmosphere.

KEYWORDS: DIOXIDE, ENRICHMENT, FEEDBACK, GROWTH, MICROBIAL BIOMASS, PLANT, RHIZOSPHERE, TEMPERATURE, TURNOVER, WHEAT

2445

van Ginkel, J.H., A.P. Whitmore, and A. Gorissen. 1999. Lolium perenne grasslands may function as a sink for atmospheric carbon dioxide. *Journal of Environmental Quality 28(5):1580-1584.*

Model calculations and scenario studies suggest the existence of a considerable positive feedback between temperature and CO2 levels in the atmosphere. Rising temperatures are supposed to increase decomposition of soil organic C leading to increased production of CO2 and this extra CO2 induces a positive feedback by raising the temperature still further. Evidence was found that negative feedback mechanisms also exist: more primary production is allocated to roots as atmospheric CO2 rises and these roots decompose more slowly than roots grown at ambient CO2 levels. Experimental data partly obtained with C- 14-techniques were applied in a grassland C model. The model results show that at an atmospheric CO2 concentration of 700 mu L L-1 increased belowground C storage will be more than sufficient to balance the increased decomposition of soil organic C in a ryegrass (Lolium perenne L.) grassland soil. Once a doubling of the present atmospheric CO2 concentration has been reached, C equivalent to 55% of the annual CO2 increase above 1 ha ryegrass can be withdrawn from the atmosphere. This indicates that grassland soils represent a significant sink for rising atmospheric CO2.

KEYWORDS: CLIMATE CHANGE, DECOMPOSITION, DYNAMICS, ELEVATED CO2, EMISSIONS, MICROBIAL BIOMASS, MODEL, NET PRIMARY PRODUCTION, PLANT, SOIL ORGANIC MATTER

2446

VanHenten, E.J., J. Bontsema, and G. VanStraten. 1997. Improving the efficiency of greenhouse climate control: an optimal control approach. *Netherlands Journal of Agricultural Science 45(1):109-125.*

In this paper a method to improve the efficiency of greenhouse climate control is described. This method is based on the framework of optimal control theory. By exploiting a dynamic model of the greenhouse crop production process, information of the auction price, the operating costs of the climate conditioning equipment and the outdoor climate conditions, the optimal greenhouse climate control scheme balances on a purely objective basis costs against revenues of operating the climate conditioning equipment. Though optimal control of greenhouse climate has received considerable attention in the literature, until now little evidence supported by experimental work has been reported as to the possible improvement in efficiency which can be realised using this approach during a whole growing period. This paper reports a first exploration of this matter for a lettuce crop. In a greenhouse experiment the behaviour of conventional greenhouse climate control supervised by the grower was measured. Then, in simulation experiments, optimal control strategies were calculated for the same conditions (outdoor climate, auction price, energy price). The results obtained support the conclusion that a considerable improvement in the efficiency of greenhouse climate management is possible. This improvement may well exceed 15%.

KEYWORDS: CO2- ENRICHMENT, CROP, FORECAST WIND-SPEED, GROWTH-MODEL, LETTUCE

2447

Vanhinsberg, N., and R.F. Horton. 1992. Ethylene metabolism in pulvini of phaseolus-vulgaris L. *Biochemie Und Physiologie Der Pflanzen 188(1):51-55.*

The ability of leaf blade, pulvinar and petiolar tissue from primary leaves of Phaseolus vulgaris to release ethylene when incubated in a 1 mM solution of the ethylene-biosynthesis precursor, 1-aminocyclopropane-1-carboxylic acid, was determined over a 6h period. Ethylene release was measured under CO2-enriched and CO2-depleted conditions in the light and dark. In contrast to blade and petiolar tissue, the pulvini released more ethylene in the light than in the dark when held in sealed flanks. The amount of the gas released is largely independent of external levels of carbon dioxide.

KEYWORDS: ABSCISSION, ACID, COCCINEUS-L, LEAVES, MOVEMENT, RELEASE

2448

Van Labeke, M.C., and P. Dambre. 1998. Effect of supplementary lighting and CO2 enrichment on yield and flower stem quality of Alstroemeria cultivars. *Scientia Horticulturae 74(4):269-278.*

The effects of CO2 enrichment and supplementary lighting on the production and Rower stem quality of five Alstroemeria cultivars ('Barbara', 'Fiona', 'Helios', 'Mona Lisa' and 'Tiara') were studied. CO2 enrichment up to 900 mu l l(-1) alone was beneficial for an increase in the number of flower stems and flower stem quality regardless of the use of supplementary lighting. Supplementary lighting alone enhanced flower stem production and quality to a lower extent than CO2 enrichment. The combination of both supplementary lighting and CO2 enrichment resulted in superior flower stem production for Alstroemeria 'Fiona', 'Helios' and 'Mona Lisa', and flower stem quality for Alstroemeria 'Barbara', 'Fiona' and 'Mona Lisa'. (C) 1998 Elsevier Science B.V.

KEYWORDS: AIR, CHRYSANTHEMUM-MORIFOLIUM RAMAT, ENVIRONMENT, GREENHOUSE PLANTS, GROWTH-RESPONSES, PHOTOPERIOD, REGINA, TEMPERATURES

2449

vanMinnen, J.G., K.K. Goldewijk, and R. Leemans. 1995. The importance of feedback processes and vegetation transition in the terrestrial carbon cycle. *Journal of Biogeography 22(4-5):805-814.*

The Integrated Model to Assess the Greenhouse Effect (IMAGE 2) is developed to simulate dynamically the global society- biosphere-climate system. The terrestrial C cycle model is an important component of this model. It is implemented on a grid, runs on a annual time step and simulates the major C fluxes between the atmosphere and the biosphere and controls the storage capacity of C in different compartments. The C fluxes are influenced by the direct and indirect response of ecosystems to changing atmospheric CO2 concentrations and climates. Each ecosystem is characterized by its NPP, which depends on environmental conditions. Incorporation of grid cell specific feedback processes is an innovation in this model. Implemented feedback processes are CO2 fertilization, effects of climate change on photosynthesis, plant respiration and decomposition and shifts in vegetation patterns due to climate change and changes in water use efficiency. This paper presents an evaluation of the importance of feedback processes on global and regional scales. Temperature feedback on plant growth is the most important feedback process at the global scale, while CO? fertilization is of lesser importance. However, CO2 fertilization is the most significant feedback in low latitudes, while temperature change most strongly influences the C cycle in the high latitudes. The C dynamics of land cover change, including feedbacks, depend on characteristics of the

former and actual land cover type. The shifts in land cover are parameterized so that they mimic succession. The course and duration of the transitional phase strongly affect the C fluxes. We applied both an equilibrium approach with instantaneous transitions and dynamic approaches with gradual type-dependent transitions. Transitions in natural vegetation between 1990 and 2050 involve about one-third of all grid cells, especially in the higher latitudes. The impact of vegetation transitions on C fluxes differs depending on the instantaneous or gradual transition strategy. The latter results in higher and delayed NEP fluxes, resulting in significantly different atmospheric CO2 concentrations. The dynamic approach is more realistic and should be included in integrated assessment models that project future atmospheric CO2 levels.

KEYWORDS: BIOSPHERE, CLIMATIC CHANGE, CO2-ENRICHMENT, ECOSYSTEMS, NITROGEN, PLANT GROWTH, STORAGE, TEMPERATURE, TRANSIENT-RESPONSE

2450

van Noordwijk, M., P. Martikainen, P. Bottner, E. Cuevas, C. Rouland, and S.S. Dhillion. 1998. Global change and root function. *Global Change Biology 4(7):759-772.*

Global change includes land-use change, elevated CO2 concentrations, increased temperature and increased rainfall variability. All four aspects by themselves and in combination will influence the role of roots in linking below- and above- ground ecosystem function via organic and inorganic resource flows. Root-mediated ecosystem functions which may be modified by global change include below-ground resource (water, nutrients) capture, creation and exploitation of spatial heterogeneity, buffering of temporal variations in above-ground factors, supply and storage of C and nutrients to the belowground ecosystem, mobilization of nutrients and C from stored soil reserves, and gas exchange between soil and atmosphere including the emission from soil of greenhouse gases. The theory of a functional equilibrium between root and shoot allocation is used to explore predicted responses to elevated CO2 in relation to water or nutrient supply as limiting root function. The theory predicts no change in root:shoot allocation where water uptake is the limiting root function, but substantial shifts where nutrient uptake is (or becomes) the limiting function. Root turnover will not likely be influenced by elevated CO2, but by changes in regularity of water supply. A number of possible mechanisms for root-mediated N mineralization is discussed in the light of climate change factors. Rhizovory (root consumption) may increase under global change as the balance between plant chemical defense and adapted root. consuming organisms may be modified during biome shifts in response to climate change. Root-mediated gas exchange allows oxygen to penetrate into soils and methane (CH4) to escape from wetland soils of tundra ecosystems as well as tropical rice production systems. The effect on net greenhouse gas emissions of biome shifts (fens replacing bogs) as well as of agricultural land management will depend partly on aerenchyma in roots.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO2, METHANE EMISSION, MYCORRHIZAL COLONIZATION, NITROUS-OXIDE, NORTHERN PEATLANDS, ORGANIC-MATTER, PLANTAGO-MAJOR, TEMPERATE GRASS SWARD, WETLAND PLANTS

2451

van Oene, H., F. Berendse, and C.G.F. de Kovel. 1999. Model analysis of the effects of historic CO2 levels and nitrogen inputs on vegetation succession. *Ecological Applications 9(3):920-935.*

(S)imulation models are useful to analyze and predict the effects of changes in atmospheric CO2 concentration and N deposition on terrestrial ecosystems. The effects of such abiotic changes on ecosystem variables such as nitrogen mineralization and carbon accumulation can affect plant species composition, which in turn may affect various ecosystem processes. However, these interacting effects of plant species composition on ecosystem processes and vice versa are often not included in simulation models. In this paper, a model is developed that includes both plant competition and the flows of nutrients, carbon, and water through the ecosystem. Direct effects of changing atmospheric CO2 on biomass, plant nitrogen concentrations, and litter quantity and quality are simulated together with indirect effects through changes in plant species composition. This model is validated against data from a primary succession chronosequence sere of Dutch inland dunes. For this validation, historical N deposition and atmospheric CO2 concentration records are used. Simulated plant species biomass, organic matter C and N, and total C and N accumulation were found to correspond to measured data. The model simulated plant species replacement well at the different sites of the chronosequence even though the historic conditions differed much between the sites. Additional analyses of the effect of N deposition (preindustrial to present-day) and elevated CO2 (preindustrial to present-day) in this ecosystem showed that N deposition had a strong effect both on vegetation development and on C and N accumulation. Compared to this, the stimulating effects of elevated CO2 on vegetation development were relatively small. Elevated CO2 affected early vegetation development, but the long-term response of vegetation development is dependent on N availability. In old mature forest, N deposition had only small effects while elevated CO2 delayed forest aging. Indirect effects of CO2 on C and N accumulation through changing plant competitive relations may ultimately be larger than direct CO2 effects.

KEYWORDS: CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ELEVATED CO2, FOREST, GROWTH, MINERALIZATION, NET PRIMARY PRODUCTION, ROOT DISTRIBUTIONS, SCENARIOS

2452

van Oijen, M., and F. Ewert. 1999. The effects of climatic variation in Europe on the yield response of spring wheat cv. Minaret to elevated CO2 and O-3: an analysis of open-top chamber experiments by means of two crop growth simulation models. *European Journal of Agronomy 10(3-4):249-264.*

In the ESPACE-Wheat programme, 25 open-top chamber experiments were carried out in 1994, 1995 and 1996, on nine locations, divided over eight European countries. In most experiments, spring wheat cv. Minaret was subjected to two levels of atmospheric CO2 and two levels of ozone. Grain yields in the control treatments (ambient levels of CO2 and O-3) varied strongly between sites. Also, yield response to elevated CO2 and O-3 showed great variation. The present study was conducted to determine whether climatic differences between sites could account for the observed variation. Two simulation models were used for the analysis: AFRCWHEAT2-O3 and LINTULCC. AFRCWHEAT2- O3 simulates phenology, canopy development and photosynthesis in greater detail than LINTULCC. Both models account for the effects of radiation and temperature on crop growth. New algorithms were developed to simulate the effects of CO2 and O- 3. Weather data that were measured in the experiments were used as input, and simulated growth responses to CO2 and O-3 were compared with measurements. No attempt was made to merge the two models. Thus two independent tools for analysis of data related to climate change were developed and applied. The average measured grain yield in the control treatment, across all 25 experiments, was 5.9 tons per hectare (t ha(-1)), with a standard deviation (SD) of 1.9 t ha(-1). The models predicted similar average yields (5.5 and 5.8 t ha(-1) for AFRCWHEAT2-O3 and LINTULCC, respectively), but smaller variation (SD for both models: 1.2 t ha(-1)). Average measured yield increase due to CO2-doubling was 30% (SD 22%). AFRCWHEAT2-O3 expected a slightly lower value (24%, SD 9%), whereas LINTULCC overestimated the response (42%, SD 11%). The average measured yield decrease due to nearly-doubled O-3 levels was 9% (SD 11%). Both models showed similar results, albeit at lower

variation (7% yield decrease at SDs of 6 and 4%). Simulations accounted well for the observation that, at elevated CO2, the percentage yield loss due to O-3 was lower than at ambient CO2. The models predicted lower variation among sites and years than was measured. Yield response to CO2 and O-3 was predicted to depend on the climate, with a predominant effect of temperature on the response to CO2. In the measurements, these climatic effects were indeed observed, but a greater part of the variation was not related to light intensity, temperature, CO2, or O-3. This unexplained variability in the measured dataset was probably caused by factors not accounted for in the models, possibly related to soil characteristics. We therefore conclude that even perfect information on the climate variables examined in ESPACE-Wheat, i.e. light intensity and temperature, by itself would be insufficient for accurate prediction of the response of spring wheat to future elevated levels of CO2 and O-3. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON DIOXIDE, PLANT-RESPONSES

2453

Van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, and R. Maciorowski. 1999. Do open-top chambers overestimate the effects of rising CO2 on plants? An analysis using spring wheat. *Global Change Biology 5(4):411-421.*

The microclimate in facilities for studying effects of elevated CO2 on crops differs from ambient conditions. Open-top chambers (OTCs) increase temperature by 1-3 degrees C. If temperature and CO2 interact in their effect on crops, this would limit the value of OTC experiments. Furthermore, interaction of CO2 and temperature deserves study because increases in atmospheric CO2 concentration are expected to cause global warming. This paper describes two experiments in which a recently developed cooling system for OTCs was used to analyse the effects of temperature on photosynthesis, growth and yield of spring wheat (Triticum nestivum L., cv. Minaret). Two levels of CO2 were used (350 and 700 ppm), and two levels of temperature, with cooled OTCs being 1.6-2.4 degrees C colder than noncooled OTCs. Photosynthetic rates were increased by elevated CO2, but no effect of temperature was found. Cross-switching CO2 concentrations as well as determination of A-Ci curves showed that plant photosynthetic capacity after anthesis acclimated to elevated CO2. The acclimation may be related to the effects of CO2 on tissue composition: elevated CO2 decreased leaf nitrogen concentrations and increased sugar content. Calculations of the seasonal mean crop light-use efficiency (LUE) were consistent with the photosynthesis data in that CO2 increased LUE by 20% on average whereas temperature had no effect. Both elevating CO2 and cooling increased grain yield, by an average of 11% and 23%, respectively. CO2 and temperature stimulated yield via different mechanisms: CO2 increased photosynthetic rate, but decreased crop light interception capacity (LAI), whereas cooling increased grain yield by increasing LAI and extending the growing season with 10 days. The effects of CO2 and temperature were not additive: the CO2 effect was about doubled in the noncooled open-top chambers. In most cases, effects on yield were mediated through increased grain density rather than increased individual grain weights. The higher growth response to elevated CO2 in noncooled vs. cooled OTCs shows that a cooling system may remove a bias towards overestimating crop growth response to CO2 in open-top chambers.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, LEAVES, NITROGEN, PHOTOSYNTHESIS, RESPONSES, RUBISCO, TEMPERATURE, WINTER-WHEAT

2454

van Oijen, M., A.H.C.M. Schapendonk, M.J.H. Jansen, C.S. Pot, J. van Kleef, and J. Goudriaan. 1998. Effects of elevated CO2 on development and morphology of spring wheat grown in cooled and non-cooled open-top chambers. *Australian Journal of Plant Physiology 25(5):617-626.*

Facilities for studying effects of elevated CO2 on crops affect the microclimate in the crop. Open-top chambers may increase temperature by 1-3 degrees C compared to ambient conditions. This paper describes a newly developed cooling system for open- top chambers. In 1995 and 1996, experiments were carried out to test the system and analyse the effects of temperature on crop phenological and morphological response to elevated CO2. Spring wheat (Triticum aestivum L. cv. Minaret) was subjected to ambient and doubled CO2 concentration in both cooled and non- cooled chambers. The cooling system reduced temperature by 1.6-2.4 degrees C, and this delayed maturity by 10 days. In contrast, elevated CO2 did not affect phenological development. Elevated CO2 reduced tiller density, green leaf number per tiller and specific leaf area, thereby reducing the capacity for light interception of the crop. Crop height growth before anthesis mainly responded to temperature, but after anthesis it was only affected by CO2, indicating a shift from sink- to source-limited growth. For none of the parameters studied, a significant statistical interaction of CO2 and temperature was found. The cooling system proved effective. A temperature difference of about 2 degrees C affected crop development and morphology more strongly than CO2 doubling. However, the absence of CO2-temperature interaction suggests that CO2 effects may validly be investigated even without a cooling system.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, ENVIRONMENT, FIELD, PLANT-RESPONSES, POLLUTANTS, SORGHUM, TEMPERATURE, TRITICUM-AESTIVUM L, YIELD

2455

Vanoosten, J.J., D. Afif, and P. Dizengremel. 1992. Long-term effects of a co-2 enriched atmosphere on enzymes of the primary carbon metabolism of spruce trees. *Plant Physiology and Biochemistry 30(5):541-547.*

The long-term effects of an enriched CO2 atmosphere on the primary carbon metabolism of 4-year-old spruce trees (Picea abies L. Karst) were examined. Eight key enzymes were studied in 1-year-old needles of trees submitted for two years in open- top chambers to three CO2 levels (350, 480 and 570 ppm V). The specific activity and quantity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO, EC 4.1.1.39), and the specific activities of photorespiratory enzymes, glycolate oxidase (EC 1.1.3.15) and hydroxypyruvate reductase (HPR, EC 1.1.1.29) showed a significant decrease in the CO2-enriched atmospheres. By contrast, a net increase was found for the specific activities of the mitochondrial enzymes, NAD-malic enzyme (NAD- ME, EC 1.1.1.39) and especially fumarase (EC 4.2.1.2). The specific activity of phosphofructophosphotransferase (PFP, EC 2.7.1.90), a glycolytic enzyme, did not change while a slight decrease of the activity of glucose 6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49), a pentose phosphate pathway enzyme, was observed. The carboxylating enzyme, phosphoenolpyruvate carboxylase (PEPC, EC 4.1.1.31) showed a marked decrease in activity. These results clearly demonstrate both increases in enzyme activities linked to the respiratory process and decreases in activities of CO2-fixing enzymes as a result of long-term exposure to less than twice the ambient level of CO2.

KEYWORDS: ACCLIMATION, DIOXIDE, ELEVATED CO2, GROWTH, INCREASES, MITOCHONDRIA, PHOSPHOENOLPYRUVATE CARBOXYLASE, PHOTOSYNTHETIC INHIBITION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECTROPHOTOMETRIC ASSAY

2456

Vanoosten, J.J., and R.T. Besford. 1994. Sugar feeding mimics effect of acclimation to high co2-rapid down-regulation of rubisco small-subunit transcripts but not of the large subunit transcripts. *Journal of Plant Physiology 143(3):306-312.*

The abundance of rbcS transcripts, derived from the nuclear gene-family coding for the small subunit of RuBisCO, was dramatically reduced in tomato plants exposed to high CO2 for 4 days or more whereas the decline in the rbcL RNA transcripts, from the chloroplast gene coding for the large subunit of RuBisCO, was less pronounced. The rate of decline in the abundance of the rbcs transcripts was enhanced when leaves were detached and supplied with water so as to deprive them of any major sink and simultaneously exposed to high CO2. The reduction in the abundance of rbcS mRNA, but nor rbcL, was mimicked when sucrose or glucose was supplied to leaf tissue, whereas acetate or sorbitol had no effect. Based on these and other published data a molecular model involving the repression of transcription of nuclear-encoded genes for chloroplast proteins by photosynthetic end-products is proposed to account for photosynthetic acclimation to high CO2 in tomato and other species.

KEYWORDS: CALVIN CYCLE ENZYMES, EXPRESSION, GENES, HIGH ATMOSPHERIC CO2, LEAVES, PHOTOSYNTHESIS, PLANTS, PROTEIN, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE

2457

Vanoosten, J.J., and R.T. Besford. 1995. Some relationships between the gas-exchange, biochemistry and molecular-biology of photosynthesis during leaf development of tomato plants after transfer to different carbon-dioxide concentrations. *Plant, Cell and Environment 18(11):1253-1266.*

Tomato plants were exposed to four concentrations of CO2 (350, 700, 1050 or 1400 mu mol CO2 mol(-1)) for 31 d. The light- saturated rate of photosynthesis (A) of the unshaded fifth leaf was measured at either an ambient CO2 concentration of 350 mu mol CO2 mol(-1) [A (350)] or at the level of CO2 at which the plants were grown. The chloroplast protein composition and the level of transcripts of nuclear or plastid photosynthesis- associated genes (PAGs), as well as the main carbohydrate content of the fifth leaf maintained horizontal and unshaded, were also measured during leaf development. At 60 and 95 % leaf expansion, the A of high CO2-grown plants measured at growth CO2 was higher than the A (350) of the plants grown at ambient CO2. However, in the fully mature leaves, A (growth CO2) declined linearly as growth CO2 concentration increased. The A (350) of plants exposed to elevated CO2 up to 60% leaf expanion had not acclimated to high CO2. At 95% leaf expansion, A (350) was lower in plants grown at high CO2. A versus CO2 (C-i) for mature leaves showed that A of the plants grown at high CO2 was lower over the entire range than that for plants grown at present ambient CO2 concentration. Lines fitted to the linear part of the A/C-l curves were concurrent at a C-i of 49 mu mol CO2 mol(-1) and A=-1.21 mu mol CO2 m(-2)s(-1). This C-i value is close to Gamma* (46 mu mol CO2 mol(-1)), the compensation point at 27 degrees C calculated from the equation described in Brooks & Farquhar (1985, Planta 165, 397-406). This A is an estimate of respiration in the light (R(1)) and was not affected by acclimation to elevated CO2. Thylakoid proteins (photosystem I core protein, D-1 and D-2 of the photosystem II core complex, cytochrome f) were all reduced by elevated CO2 only in the fully mature leaves (310 exposure), whereas the large and small subunits of Rubisco and Rubisco activase proteins had already declined after 22 d exposure. Transcript levels of the plastid-encoded FAG (rbcL, psbA, psaA-B) were reduced in the mature leaves by elevated CO2 when expressed on a total RNA basis, but they were not sensitive to elevated CO2 when expressed on a chloroplast 16S rRNA basis. However, rbcS, rca and cab mRNA transcripts were lower in the plants grown at high CO2 than in control plants after 22 d exposure when expressed on a nuclear rRNA basis. The loss of these nuclear PAGs was correlated with an accumulation of soluble sugars and starch.

KEYWORDS: ACCLIMATION, ELEVATED CO2, EXPRESSION, GENES, HIGH ATMOSPHERIC CO2, LEAVES, RESPIRATION, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO ACTIVASE

2458

VanOosten, J.J., and R.T. Besford. 1996. Acclimation of photosynthesis to elevated CO2 through feedback regulation of gene expression: Climate of opinion. *Photosynthesis Research 48(3):353-365.*

Although down-regulation of photosynthesis in higher C-3 plants exposed to long-term elevated CO2 has been recognized in plants with low sink activity or poor nutrient status, the underlying molecular mechanisms remain unclear. This review covers aspects of rising CO2 on plant productivity in general, and then focuses on photosynthesis, biochemistry (stroma and thylakoid proteins, Rubisco activities and metabolites), and gene expression in tomato plants grown under ambient or elevated CO2. Taking into account these data and the recent discovery that glucose triggers repression of photosynthetic gene transcription, a molecular mechanism is proposed for feedback regulation of photosynthesis under high CO2. Different living organisms such as bacteria, yeast, and mammals have been investigated for the sensing mechanisms of the carbohydrate status of their cells, and this information is used together with some recent data obtained for plants to propose how hexose levels might be sensed in higher plant cells.

KEYWORDS: CALVIN CYCLE ENZYMES, CARBON-DIOXIDE CONCENTRATIONS, GAS-EXCHANGE, GLUCOSE REPRESSION, LEAF DEVELOPMENT, PAST 2 CENTURIES, PROTEIN-KINASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RISING ATMOSPHERIC CO2, TOMATO PLANTS

2459

Vanoosten, J.J., D. Wilkins, and R.T. Besford. 1994. Regulation of the expression of photosynthetic nuclear genes by co2 is mimicked by regulation by carbohydrates - a mechanism for the acclimation of photosynthesis to high co2. *Plant, Cell and Environment 17(8):913-923.*

The abundance of transcripts of cab-7 and cab-3C, which code for the chlorophyll a/b binding proteins of the light- harvesting complexes I and II, respectively, and the abundance of transcripts of Rca, which encodes Rubisco activase, were reduced in tomato plants exposed to high CO2 for up to 9d, whereas the abundance of mRNA from psa A-psa B and psb A, which encode the proteins of the core complex of PSI and the D1 protein of PSII, respectively, and the abundance of glycolate oxidase, which is involved in photorespiration, were not affected. However, the abundance of the transcript for the B subunit of ADP-glucose pyrophosphorylase was increased after 1 d at elevated CO2. The chlorophyll am ratio decreased significantly over 9 d of exposure to elevated CO2. The responses of the nuclear genes to high CO2 were enhanced when leaves were detached so as to deprive them of any major sink. The responses of these transcripts to high CO2 were mimicked when sucrose or glucose was supplied to the leaf tissue, whereas acetate or sorbitol had no effect. Carbohydrate analyses of leaves grown in high CO2 or supplied with sucrose revealed that major increases occurred in the amount of glucose and fructose. Based on these and other published data, a molecular model involving the repression or activation of the transcription of nuclear genes coding for chloroplast proteins by photosynthetic end-products is proposed to account for photosynthetic acclimation to high CO2 in tomato plants and other species.

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, CALVIN

CYCLE ENZYMES, CARBON-DIOXIDE CONCENTRATION, CDNA CLONE, ELEVATED LEVELS, HIGH ATMOSPHERIC CO2, MESSENGER-RNA LEVELS, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOMATO

2460

Vanoosten, J.J., D. Wilkins, and R.T. Besford. 1995. Acclimation of tomato to different carbon-dioxide concentrations - relationships between biochemistry and gas- exchange during leaf development. *New Phytologist 130(3):357-367.*

Tomato plants were transferred to different CO2 mole fractions (350, 700, 1050 and 1400 mu mol CO2 mol(-1)) 31 d after sowing (2% of full expansion) and the light saturated rate of photosynthesis (P-max) of the unshaded 5th leaf was measured at either an ambient CO2 mole fraction, C-a of 350 mu mol CO2 mol(-1) [P-max (350)] or at the mole fraction of CO2 at which the plants were grown. At 60% and 95% leaf expansion, P-max of high CO2 grown plants measured at growth CO2, was greater than the P-max (350) of the ambient CO2 grown plants. However, by leaf maturity, P-max (growth CO2) declined linearly as growth CO2 concentration increased. P-max (350) of plants exposed to elevated CO2 up to 60% leaf expansion had not acclimated to high CO2. At 95% leaf expansion, P-max (350) was smaller in the high CO2 grown plants. P-max (350) was predicted from Rubisco in vitro carboxylation capacity using tomato Rubisco kinetic constants. By 95% leaf expansion, high CO2 grown plants showed similarities to the response of plants to low nitrogen supply, in terms of Rubisco and chlorophyll content. The observed and theoretical relationships between the initial slopes of the P- max/C-i responses and Rubisco activity were statistically equivalent. Both short-term and long-term effects of elevated CO2 on dark respiration (R(n)) were also investigated at two stages of leaf development (50 and 100% expansion). R(a) (growth CO2) was smaller for the high CO2 grown plants compared with the control plants, whereas R(n) (350) was either equal or greater for the plants grown in high CO2.

KEYWORDS: ANTISENSE RBCS, CALVIN CYCLE ENZYMES, ELEVATED CO2, HIGH ATMOSPHERIC CO2, NITROGEN NUTRITION, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SHORT- TERM

2461

Vantelgen, H.J., A. Vanmil, and B. Kunneman. 1992. Effect of propagation and rooting conditions on acclimatization of micropropagated plants. *Acta Botanica Neerlandica 41(4):453-459.*

Plantlets of Calathea ornata rooted at frequencies varying between 75 and 100% irrespective of the presence of 6- benzylaminopurine (BAP) or indolebutyric acid (IBA). After transfer to soil all plants grew rapidly with the exception of BAP-rooted plants, probably because these plants lacked lateral roots. Plantlets of Malus showed slightly improved rooting and considerably improved survival at increasing sucrose concentration from 20 to 30 g l(-1) during multiplication. Their survival and performance after planting in soil depended upon the number of roots formed in rooting medium. Elevated CO2-levels (800 ml m-3) during acclimatization increased survival rate and plant height of rooted and non-rooted plantlets.

KEYWORDS: STRAWBERRY PLANTLETS

2462

Vanveen, J.A., E. Liljeroth, L.J.A. Lekkerkerk, and S.C. Vandegeijn. 1991. Carbon fluxes in plant-soil systems at elevated atmospheric CO2 levels. *Ecological Applications 1(2):175-181.*

The flow of carbon from photosynthesizing tissues of higher plants, through the roots and into the soil is one of the key processes in terrestrial ecosystems. An increased level of CO2 in the atmosphere will likely result in an increased input of organic carbon into the soil due to the expected increase in primary production. Whether this will lead to accumulation of greater amounts of organic carbon in soil depends on the flow of carbon through the plant into the soil and its subsequent transformation in the soil by microorganisms. In this paper the major controls of carbon translocation via roots into the soil as well as the subsequent microbial turnover of root-derived carbon are reviewed. We discuss possible consequences of an increased CO2 level in the atmosphere on these processes.

KEYWORDS: AMMONIUM-ENRICHED RAINWATER, DRY-MATTER, MAIZE, MICROBIAL BIOMASS, NITROGEN, ORGANIC-MATTER, ROOT-DERIVED MATERIAL, TURNOVER, WHEAT ROOTS, YOUNG CONIFEROUS TREES

2463

VanVuuren, M.M.I., D. Robinson, A.H. Fitter, S.D. Chasalow, L. Williamson, and J.A. Raven. 1997. Effects of elevated atmospheric CO2 and soil water availability on root biomass, root length, and N, P and K uptake by wheat. *New Phytologist 135(3):455-465.*

We investigated interactions between the effects of elevated atmospheric carbon dioxide concentrations ([CO2]) and soil water availability on root biomass, root length and nutrient uptake by spring wheat (Triticum aestivum cv. Tonic). We grew plants at 350 and 700 mu mol mol(-1) CO2 and with frequent and infrequent watering ('wet' and 'dry' treatments, respectively). Water use per plant was 1.25 times greater at 350 than at 700 mu mol CO2 mol(-1), and 1.4 times greater in the 'wet' than in the 'dry' treatment. Root biomass increased with [CO2] and with watering frequency. Elevated [CO2] changed the vertical distribution of the roots, with a greater stimulation of root growth in the top layers of the soil. These data were confirmed by the video data of root lengths in the 'dry' treatment, which showed a delayed root development at depth under elevated [CO2]. The apparent amount of N mineralized appeared to be equal for all treatments. Nutrient uptake was affected by [CO2] and by watering frequency, and there were interactions between these treatments. These interactions were different for N, K and P, which appeared to be related to differences in nutrient availability and mobility in the soil. Moreover, these interactions changed with time as the root system became larger with [CO2] and with watering frequency, and as fluctuations in soil moisture contents increased. Elevated [CO2] affected nutrient uptake in contrasting ways. Potassium uptake appeared to be reduced by the smaller mass how of water reaching the root surface. However, this might be countered with time by the greater root biomass at elevated [CO2], by the greater soil moisture contents at elevated [CO2], enabling faster diffusion, or both. Phosphorus uptake appeared to be increased by the greater root biomass at elevated [CO2]. We conclude that plant nutrient uptake at elevated [CO2] is affected by interactions with water availability, though differences between nutrients preclude generalizations of the response.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, FIELD, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANT-RESPONSES, WINTER-WHEAT

2464

VargasSuarez, M., A. RinconGuzman, C. MujicaJimenez, R.A. MunozClares, and E.S. deJimenez. 1996. Influence of carbon source and CO2-enrichment on biochemical parameters associated with photomixotrophia in maize callus cultures. *Journal of Plant Physiology 149(5):585-591.*

To learn about the biochemical processes underlying the induction of

photomixotrophia in maize cell culture, maize calli were cultured in medium containing either glucose or starch as the carbon source. The effect of a CO2-enriched atmosphere on different parameters was tested. Levels of chlorophyll and CO2 fixing enzymes were measured to assess the greening process concomitant to histological observations of chloroplast development. Both starch and glucose promoted higher chlorophyll accumulation in callus cultured under light than sucrose. Histological analysis of green callus grown on glucose-containing medium revealed the formation of poorly developed chloroplasts containing starch grains, whereas in starch medium a large number of elongated chloroplasts containing thylakoids were observed. Exposure of these calli to a CO2-enriched atmosphere enhanced the plastid differentiation process up to mature chloroplasts with grana and intergranal thylakoids. Western-blot analysis demonstrated the presence of CO2-fixing enzymes, Rubisco (EC 4.1.1.39) and PEP carboxylase (EC 4.1.1.31), as well as Rubisco activase in greening callus. Rubisco and PEP carboxylase activities showed large values when starch was me carbon source in the medium. Results of histological analysis and a/b chlorophyll ratios indicated that the chloroplasts formed were of the C-3-type. PEP carboxylase kinetic properties were also consistent with a C-3-type enzyme involved in anaplerotic functions. It is concluded that under the experimental conditions tested, starch plus CO2-enriched atmosphere are the best carbon source for inducing and supporting photomixotrophia in maize cultures, as indicated by several biochemical parameters.

KEYWORDS: BINDING, C-3, CHLOROPLASTS, EXPRESSION, LEAVES, PHOSPHOENOLPYRUVATE CARBOXYLASE, PLANT, POPULATIONS, YIELD, ZEA-MAYS

2465

Varoquaux, P., J. Mazollier, and G. Albagnac. 1996. The influence of raw material characteristics on the storage life of fresh-cut butterhead lettuce. *Postharvest Biology and Technology 9(2):127-139.*

The physiological characteristics of 5 butterhead lettuce cultivars (Lactuca sativa L.) were investigated using etiolated leaves. Their storage life under modified and controlled atmospheres was assessed. When prepacked butterhead lettuce was maintained under a low oxygen atmosphere to prevent enzymatic browning, high CO2 content was the main factor increasing the rate of decay. Shelf life was negatively correlated with respiration rate and susceptibility to CO2. Potassium leakage was a good indicator of physiological disorders. High oxygen and low CO2 enhanced enzymatic browning, while low oxygen and, more significantly, high carbon dioxide enhanced CO2 injury (brown stain). Maintaining CO2 concentration within the packs below 5% resulted in an improved preservation of the lettuce leaves. Practical means for obtaining modified atmospheres which were in equilibrium yet were low in both O-2 and CO2 are discussed.

KEYWORDS: CO2, CRISPHEAD LETTUCE, GROWTH-CONDITIONS, NITROGEN, PLANT-AGE, QUALITY

2466

Vasseur, L., and C. Potvin. 1998. Natural pasture community response to enriched carbon dioxide atmosphere. *Plant Ecology 135(1):31-41.*

We examined the response of a pasture community in southern Quebec (Canada) to long-term exposure of enriched atmospheric CO2 conditions. The study was conducted using open-top growth chambers directly placed on top of the natural pasture community. To investigate the change in the overall species composition in time and space, we used canonical correspondence analysis, a direct ordination method. Over the three years, the overall community responded significantly to enriched CO2. The analyses show that, after three years, CO2 was the most important environmental variable affecting the species composition. Initially the presence of the wall of the chambers influenced the composition but CO2 became more important by the third year. Soil and air temperatures only slightly influenced the community composition. The first two axes of the canonical correspondence analysis explained a large proportion of the variation in the three years and these trends appeared to increase with time. Species such as Agropyron repens appeared to be positively influenced by the presence of the wall (slightly warmer conditions). However, the analyses suggest that Phleum pratense and Trifolium repens, for example, were favored by the increase in atmospheric CO2. The variation in species composition in enriched versus ambient CO2 chambers suggests that the effect of the environmental factors, particularly CO2, were important in affecting the rate and pattern of succession. Furthermore, the temporal increase in importance of the variable CO2 in the present analyses indicates that there might be a time-lag in response to atmospheric enrichment.

KEYWORDS: COMPETITION, ECOSYSTEMS, ELEVATED CO2, GROWTH, LOLIUM-PERENNE, NITROGEN, PHENOTYPIC PLASTICITY, PLANTS, TRIFOLIUM- REPENS

2467

Veisz, O., N. Harnos, L. Szunics, and T. Tischner. 1996. Overwintering of winter cereals in Hungary in the case of global warming. *Euphytica 92(1-2):249-253.*

Under phytotronic conditions investigations were made on the effect of important environmental factors, such as temperature, water and an increasing concentration of atmospheric CO2, on the hardening of young cereal plants. In all the varieties derived from the major wheat growing regions of the world the hardening process was favourably influenced by a doubling of atmospheric CO2 content, so that a significantly larger number of plants survived the frost test than for plants of the same variety raised under normal conditions. A reduction in freezing temperature and an increase in soil moisture content caused a slight reduction in survival % for varieties with excellent frost resistance and a great reduction for those with medium or poor frost resistance. Predictions suggest that in Central Europe, as the result of global climatic changes, there will be a reduction in the quantity of winter precipitation, a considerable rise in winter temperatures and an increase in atmospheric CO2 concentration. Judging by the experimental results, these changes could improve the overwintering of winter cereals; at the same time, however, a number of factors (mainly the reduction of precipitation) leading to yield losses must be expected during the vegetation period.

KEYWORDS: COLD HARDINESS, ELEVATED CO2, GROWTH, TEMPERATURE, WHEAT, YIELD

2468

Velikova, V., T. Tsonev, and I. Yordanov. 1999. Light. and CO2 responses of photosynthesis and chlorophyll fluorescence characteristics in bean giants after simulated acid rain. *Physiologia Plantarum 107(1):77-83.*

The effects of simulated acid rain on some chlorophyll fluorescence characteristics and photosynthetic gas exchange at different light intensities and CO2 concentrations of bean plants were investigated. Measurements were carried out 3, 5 and 24 h after spraying. The results showed that a single acid rain (pH 1.8) treatment of bean plants reduced gas exchange, the maximal carboxylating efficiency and photochemical quenching, This treatment led also to increased CO2 compensation point and non-photochemical quenching and changed the shape of CO2 and light curves of photosynthesis, Both stomatal and non-stomatal factors contributed to the decreased photosynthetic rate, but their proportion changed with time of recovery of the photosynthetic apparatus. Three hours after the treatment, the stomatal factors predominated in

photosynthesis reduction, while during the next experimental period (5-24 h), mainly non-stomatal factors determined the decreased photosynthetic rate, It is suggested that the effects observed in consequence of acid rain treatment could be due to an increased intracellular accumulation of H+ and harmful ions contained in the cocktail, This probably led to impaired membrane permeability, enhancement of stroma acidity, uncoupled electron transport and insufficient accumulation of ATP and NADPH, which affected carbon metabolism.

KEYWORDS: CHLOROPLASTS, DAMAGE, ELECTRON-TRANSPORT, GAS-EXCHANGE, GROWTH, LEAVES, OZONE, PHASEOLUS-VULGARIS, STRESS, TEMPERATURE

2469

Ver, L.M.B., F.T. Mackenzie, and A. Lerman. 1999. Biogeochemical responses of the carbon cycle to natural and human perturbations: Past, present, and future. *American Journal of Science 299(7-9):762-801.*

In the past three centuries, human perturbations of the environment have affected the biogeochemical behavior df the global carbon cycle and that of the other three nutrient elements closely coupled to carbon: nitrogen, phosphorus, and sulfur. The partitioning of anthropogenic CO2 among its various sinks in the past, for the present, and for projections into the near future is controlled by the interactions of these four elemental cycles within the major environmental domains of the land, atmosphere, coastal oceanic zone, and open ocean. We analyze the past, present, and future behavior of the global carbon cycle using the Terrestrial-Ocean-aTmosphere Ecosystem Model (TOTEM), a unique process-based model of the four global coupled biogeochemical cycles of carbon, nitrogen, phosphorus, and sulfur. We find that during the past 300 yrs, anthropogenic CO2 was mainly stored in the atmosphere and in the open ocean. Human activities on land caused an enhanced loss of mass from the terrestrial organic matter reservoirs (phytomass and humus) mainly through deforestation and consequently increased humus remineralization, erosion, and transport to the coastal margins by rivers and runoff. Photosynthetic uptake by the terrestrial phytomass was enhanced owing to fertilization by increasing atmospheric CO2 concentrations and supported by nutrients remineralized from organic matter. TOTEM results indicate that through most of the past 300 yrs, the loss of C from deforestation and other land-use activities was greater than the gain from the enhanced photosynthetic uptake. During the decade of the 1980s, the terrestrial organic reservoirs were in rough carbon balance. Organic and carbonate carbon accumulating in coastal marine sediments is a small but significant sink for anthropogenic CO2. Increasing inputs of terrestrial organic matter and its subsequent oxidation in the coastal margin (increasing heterotrophy) were significant sources of CO2 in coastal waters in the 20th century. However, the coastal ocean did not evolve into a greater net source of CO2 to the atmosphere during this period because of the opposing pressure from rising atmospheric CO2. Since pre-industrial time (since 1700), the net nux of CO2 from the coastal waters has decreased by 40 percent, from 0.20 Gt C/yr to 0.12 Gt C/yr. TOTEM analyses of atmospheric CO2 concentrations for the 21st century were based on the fossil-fuel emission projections of IPCC ("business as usual" scenario) and of the more restrictive UN 1997 Kyoto Protocol. By the mid-21st century, the projected atmospheric CO2 concentrations range from about 550 ppmv (TOTEM,based on IPCC projected emissions) to 510 ppmv (IPCC projection) and to 460 ppmv (TOTEM, based on the Kyoto Protocol reduced emissions). The difference of about 40 ppmv between the IPCC and TOTEM estimates by the year 2050 reflects the different mechanisms within the C-N-P-S cycles on land that are built into our model. The effects of the reduced emissions prescribed by the Kyoto Protocol begin to show in the atmospheric CO2 concentrations by the mid-21st century, when our model projects a rise to 460 (year 2050) and 490 ppmv (2075), relative to about 360 ppmv in 1995. However, these projected increases assume no major changes in the present biogeochemical feedback mechanisms within the system of the coupled C-N-P-S cycles, no global changes in the kind and distribution of ecosystems in response to the rising CO2 and possibly temperature, and no changes in the mechanisms of CO2 exchange between the atmosphere and the ocean, such as could be induced by changes in the intensity of oceanic thermohaline circulation.

KEYWORDS: ATMOSPHERIC CO2, C-13/C-12 RATIO, GLOBAL CLIMATE-CHANGE, ICE CORE, NET PRIMARY PRODUCTION, ORGANIC-CARBON, PRECIPITATION FLUCTUATIONS, SULFUR-OXIDES, TERRESTRIAL ECOSYSTEMS, TROPICAL DEFORESTATION

2470

Verburg, P.S.J., A. Gorissen, and W.J. Arp. 1998. Carbon allocation and decomposition of root-derived organic matter in a plant-soil system of Calluna vulgaris as affected by elevated CO2. *Soil Biology and Biochemistry 30(10-11):1251-1258.*

The effect of elevated CO2 on C allocation in plant and soil was assessed using soil cores planted with 1-y-old heather (Calluna vulgaris (L.) Hull). Plants were pulse-labeled with (CO2)-C-14 at ambient and elevated CO2 and two nitrogen regimes (low and high). After harvesting the plants, the soil was incubated to monitor total respiration and decomposition of C- 14-labeled rhizodeposits. Total and shoot biomass increased at high N but were not affected by CO2. Root biomass was not affected by either N or CO2 treatments. Total C-14 uptake and shoot-C-14 increased upon adding N and elevating CO2 but the N effect was strongest. Total C-14 uptake per unit shoot mass decreased with N, but increased with CO2. Root-C-14 content was not significantly affected by the N or CO2 treatment. Total soil-C-14 slightly increased at elevated CO2 whereas microbial C-14 increased due to high N. C allocation to shoots increased at the expense of roots, soil and respiration at high N but was not affected by the CO2 treatment. Variation in C-14 distribution within each treatment was small compared to variation in total C-14 amounts in each plant-soil compartment. Initially, C-14 respiration from rhizodeposits correlated well with root-C-14, total soil-C-14, soil solution-C-14 and microbial C-14, at harvest time and was increased by elevated CO2. By the end of the incubation, however, decomposition of labeled organic matter was not affected by the treatments whereas total (=C-12+C-14) respiration was lowest for the elevated-CO2 soils. We speculate that initially, respiration is dominated by decomposition of fresh root exudates whereas in the longer term, respiration originates from decomposition of more recalcitrant root material that had been formed during the entire experiment. The increased net C-14 uptake and unchanged distribution pattern, combined with an increased decomposition of easily-decomposable compounds and a decreased decomposition of more recalcitrant root-derived material indicated a small sink function of a Calluna plant-soil system under elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, DIOXIDE, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, RESPIRATION, RESPONSES, RHIZOSPHERE, TURNOVER

2471

Verburg, P.S.J., W.K.P. Van Loon, and A. Lukewille. 1999. The CLIMEX soil-heating experiment: soil response after 2 years of treatment. *Biology and Fertility of Soils 28(3):271-276.*

Most model predictions concerning the response of boreal forest ecosystems to climate change are inferred from small-scale experiments on artificial, simplified systems. Whole-ecosystem experiments designed to validate these models are scarce. We experimentally manipulated a small forested catchment in southern Norway by increasing soil temperature (+3 degrees C in summer to +5 degrees C in winter) using

heating cables installed at 1 cm depth in the litter layer. Especially nitrification in the 0 to 10-cm soil layer increased as a result of the climate manipulation. Betula litter, produced after exposing trees for 2 years to ambient and elevated CO2 in greenhouses, was incubated for 1 year in the manipulated catchment. Exposure to elevated CO2 did not affect the C/N ratio or decomposition of the Betula litter, but lignin content decreased by 10%. We found no effect of elevated temperature on litter decomposition, probably due to desiccation of the litter. The heating cables caused a permanent increase in soil temperature in this soil layer, but when soils were dry, the temperature difference between control and heated plots decreased with increasing distance from the cables. When soils were wet, no gradients in temperature increase occurred.

KEYWORDS: C STORAGE, DISTURBANCE, ELEVATED CO2, LEAF LITTER, LITTER DECOMPOSITION, NITROGEN MINERALIZATION, QUALITY, TEMPERATURE, TERRESTRIAL, WET HEATHLAND ECOSYSTEMS

2472

Vervuren, P.J.A., S.M.J.H. Beurskens, and C.W.P.M. Blom. 1999. Light acclimation, CO2 response and long-term capacity of underwater photosynthesis in three terrestrial plant species. *Plant, Cell and Environment 22(8):959-968.*

To characterize underwater photosynthetic performance in some terrestrial plants, we determined (i) underwater light acclimation (ii) underwater photosynthetic response to dissolved CO2, and (iii) underwater photosynthetic capacity during prolonged submergence in three species that differ in submergence tolerance: Phalaris arundinacea, Rumex crispus (both submergence-tolerant) and Arrhenatherum elatius (submergence-intolerant). None of the species had adjusted to low irradiance after 1 week of submergence. Under non-submerged (control) conditions, only R. crispus displayed shade acclimation, Submergence increased the apparent quantum yield in this species, presumably because of the enhanced CO2 affinity of the elongated leaves, In control plants of the grass species II arundinacea and A. elatius, CO2 affinities were higher than for R, crispus. The underwater photosynthetic capacity of R. crispus increased during 1 month of submergence. In P. arundinacea photosynthesis remained constant during 1 month of submergence at normal irradiance; at low irradiance a reduction in photosynthetic capacity was observed after 2 weeks, although there was no tissue degeneration, In contrast, underwater photosynthesis of the submergence-intolerant species A, elatius collapsed rapidly under both irradiances, and this was accompanied by leaf decay, To describe photosynthesis versus irradiance curves, four models were evaluated, The hyperbolic tangent produced the best goodness-of-fit, whereas the rectangular hyperbola (Michaelis-Menten model) gave relatively poor results.

KEYWORDS: AQUATIC MACROPHYTES, ASSIMILATION, GROWTH, HCO3, INORGANIC CARBON, PHYTOPLANKTON, RICE, SUBMERGENCE, TOLERANCE

2473

Vidal, R., A. Gerbaud, and D. Vidal. 1996. Short-term effects of high light intensities on soybean nodule activity and photosynthesis. *Environmental and Experimental Botany 36(3):349-357.*

There is little information available on the effects of highlight intensity (HLI) on nitrogenase activity in legume nodules. Inhibitory as well as stimulatory effects have been described. The hypothesis that an increase in carbohydrate production is involved in these effects was tested by comparing the effects of high light, high CO2, or low O-2 exposure of the shoot. The HLI treatment consisted of tripling the light intensity to 1200 mu E m(-2) s(-1), compared with the growth intensity of 400 mu E m(-2) s(-1). Acetylene reduction activity (ARA) measuring nitrogenase activity was studied in relation to shoot CO:! exchange. HLI stimulated ARA. The stimulation was progressive and reached 17% after 10 hr of treatment. Photosynthesis (P) was initially doubled, but photoinhibition appeared after about 8 hr of HLI. Under HLI, P became limited by N fixation. Other treatments increasing photosynthesis were compared with HLI: elevating the ambient CO2 concentration around the shoot to 900 ppm, or lowering the O-2 concentration to 2%, increased photosynthesis, respectively, by 55% and 70% without effect on ARA. It is concluded that ARA was not regulated by the availability of carbon assimilates and that specific factors promoting or inhibiting ARA are produced by leaves under HLI.

KEYWORDS: ACETYLENE, ACTIVITY C2H2 REDUCTION, CO2-ENRICHMENT, LEGUME NODULES, NITROGEN-FIXATION, OXYGEN, PHOTOINHIBITION, PHOTORESPIRATION, ROOT-NODULES

2474

Viil, J., and T. Parnik. 1992. Fast regulation of ribulose-1,5-bisphosphate carboxylase oxygenase activity during light dark light transitions. *Soviet Plant Physiology 39(4):483-487.*

On the basis of estimates of rubisco activity in leaves of barley (Hordeum vulgare L.), we established that it declined by 30-50% in 3-4 sec following disconnection of light in the presence of CO2. In a medium without CO2, rubisco activity did not change in this time. Keeping leaves at elevated CO2 concentration lowered rubisco activity. This effect had a lasting aftereffect. With a sharp change of CO2 concentration, the rate of assimilation in the first second was proportional to the increase of CO2 concentration up to at least 1000 mul- liter-1. It is recorded that CO2 binds directly with the enol form of ribulose-1,5-bisphosphate (RuBP) without preliminary binding with the enzyme molecule.

KEYWORDS: CO2, LEAVES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE

2475

Visser, A.J., M. Tosserams, M.W. Groen, G. Kalis, R. Kwant, G.W.H. Magendans, and J. Rozema. 1997. The combined effects of CO2 concentration and enhanced UV-B radiation on faba bean .3. Leaf optical properties, pigments, stomatal index and epidermal cell density. *Plant Ecology 128(1-2):208-222.*

Seedlings of Vicia faba L. (cv. Minica) were grown in a factorial experiment in a greenhouse. The purpose of the study was to determine whether CO2 enrichment and supplemental UV-B radiation affect leaf optical properties and whether the combined effects differ from single factor effects. Seedlings were grown at either 380 mu mol mol(-1) 750 mu mol mol(-1) CO2 and at four levels of W-B radiation. After 20 and 40 days of treatment, absorptance, transmittance and reflectance of photosynthetically active radiation (PAR) were measured on the youngest fully developed leaf. On the same leaf, the specific leaf area on a fresh weight basis (SLA(fw)), chlorophyll content, UV-B absorbance, transmittance of UV light and stomatal index were measured. W-B radiation significantly increased PAR absorptance and decreased PAR transmittance. The increased PAR absorptance can be explained by an increased chlorophyll content in response to W-B radiation. Leaf transmittance of UV radiation decreased with increasing UV-B levels mainly caused by increased absorbance of UV absorbing compounds. UV-B radiation decreased both the stomatal density and epidermal cell density of the abaxial leaf surface, leaving the stomatal index unchanged. Effects of CO2 enrichment were less pronounced than those of W-B radiation. The most important CO2 effect was an increase in stomatal density and epidermal cell density of the adaxial leaf surface.

The stomatal index was not affected. No interaction between CO2 and UV-B radiation was found. The results are discussed in relation to the internal light environment of the leaf.

KEYWORDS: 280-320 NM, ATMOSPHERIC CARBON-DIOXIDE, CROP PLANTS, ELEVATED CO2, GROWTH, RICE ORYZA-SATIVA, STARCH CONTENT, STRATOSPHERIC OZONE, TERRESTRIAL PLANTS, ULTRAVIOLET-RADIATION

2476

Visser, A.J., M. Tosserams, M.W. Groen, G.W.H. Magendans, and J. Rozema. 1997. The combined effects of CO2 concentration and solar UV-B radiation on faba bean grown in open-top chambers. *Plant, Cell and Environment 20(2):189-199.*

The response of faba bean seedlings to the combined effects of increased atmospheric CO2 concentrations ([CO2]) and solar UV-B irradiance was studied using open-top chambers transparent to W-B radiation. The purpose of the study was to determine whether effects of increased [CO2] on growth and physiology are modified by the present solar UV-B fluence rate in the Netherlands. Seedlings were exposed to 350 or 700 mu mol mol(- 1) CO2. At both [CO2], solar UV-B irradiance was either present or reduced using polyester foil opaque to UV-B radiation. To obtain information on the time dependence of increased [CO2] and UV-B radiation effects, three harvests were performed during the experiment, CO2 enrichment resulted in increased biomass production at all harvests. At the final harvest, UV-B radiation did not affect biomass production but a significant decrease was observed after 14 d of treatment. A reduction of the UV-B fluence increased shoot length at both [CO2] throughout the experiment, UV-B radiation slightly altered biomass allocation. Plants grown at reduced levels of UV-B radiation invested less biomass in flowers and more in stem material compared to plants grown at ambient UV-B levels. CO2 enrichment resulted in a stimulation of net photosynthesis after 26 and 38 d of treatment. UV-B reduction did not alter this response. After 26 d of treatment, photosynthetic acclimation to CO2 enrichment was observed, which was probably the result of accumulation of carbohydrates in the leaves. After 38 d, photosynthetic acclimation was no longer present. The UV absorbance of methanolic leaf extracts was increased by CO2 enrichment only. Both CO2 enrichment and solar UV-B reduced the transmittance of radiation through intact attached leaves. Interaction between [CO2] and UV-B radiation was limited to UV- A transmittance of leaves. Under prevalent experimental conditions, UV-B radiation did not affect the measured physiological parameters. Most open-top chambers used for climate change research are constructed of materials which do not transmit UV-B radiation. Our results indicate that part of the 'chamber effects' on plant height often described in the literature might be explained by the absence of solar UV-B radiation in these chambers.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, CROP RESPONSES, ELEVATED CO2, ENHANCEMENT, IRRADIANCE, PHOTOSYNTHESIS, TERRESTRIAL PLANTS, ULTRAVIOLET-B

2477

Vitousek, P.M. 1994. Beyond global warming - ecology and global change. *Ecology 75(7):1861-1876.*

While ecologists involved in management or policy often are advised to learn to deal with uncertainty, there are a number of components of global environmental change of which we are certain-certain that they are going on, and certain that they are human-caused. Some of these are largely ecological changes, and all have important ecological consequences. Three of the well-documented global changes are: increasing concentrations of carbon dioxide in the atmosphere; alterations in the biogeochemistry of the global nitrogen cycle; and ongoing land use/land cover change. Human activity-now primarily fossil fuel combustion-has increased carbon dioxide concentrations from similar to 280 to 355 mu L/L since 1800; the increase is unique, at least in the past 160 000 yr, and several lines of evidence demonstrate unequivocally that it is human-caused. This increase is likely to have climatic consequences-and certainly it has direct effects on biota in all Earth's terrestrial ecosystems. The global nitrogen cycle has been altered by human activity to such an extent that more nitrogen is fixed annually by humanity (primarily for nitrogen fertilizer, also by legume crops and as a byproduct of fossil fuel combustion) than by all natural pathways combined. This added nitrogen alters the chemistry of the atmosphere and of aquatic ecosystems, contributes to eutrophication of the biosphere, and has effects on biological diversity in the most affected areas. Finally, human land use/land cover change has transformed one-third to one-half of Earth's ice-free surface. This in and of itself probably represents the most important component of global change now and will for some decades to come; it has profound effects on biological diversity on land and on ecosystems downwind and downstream of affected areas. Overall, any clear dichotomy between pristine ecosystems and human-altered areas that may have existed in the past has vanished, and ecological research should account for this reality. These three and other equally certain components of global environmental change are the primary causes of anticipated changes in climate, and of ongoing losses of biological diversity. They are caused in turn by the extraordinary growth in size and resource use of the human population. On a broad scale, there is little uncertainty about any of these components of change or their causes. However, much of the public believes the causes-even the existence-of global change to be uncertain and contentious topics. By speaking out effectively, we can help to shift the focus of public discussion towards what can and should be done about global environmental change.

KEYWORDS: AMAZON DEFORESTATION, ATMOSPHERIC CO2, CARBON ISOTOPE DISCRIMINATION, CHALK GRASSLAND, CLIMATE CHANGE, CO2 CONCENTRATION, FRESH-WATER ECOSYSTEMS, NITROUS-OXIDE, PINNATUM L BEAUV, POPULATION GROWTH

2478

Vitousek, P.M., and C.B. Field. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry 46(1):179-202.*

The widespread occurrence of N limitation to net primary production (NPP) and other ecosystem processes, despite the ubiquitous occurrence of N-fixing symbioses, remains a significant puzzle in terrestrial ecology. We describe a simple simulation model for an ecosystem containing a generic nonfixer and a symbiotic N fixer, based on: (1) a higher cost for N acquisition by N fixers than nonfixers; (2) growth of fixers and fixation of N only when low N availability limits the growth of nonfixers, and other resources are available; and (3) losses of fixed N from the system only when the quantity of available N exceeds plant and microbial demands. Despite the disadvantages faced by the N fixer under these conditions, N fixation and loss adjust N availability close to the availability of other resources, and biomass and NPP in this simple model can be substantially but only transiently N limited. We then modify the model by adding: (1) losses of N in forms other than excess available N (e.g., dissolved organic N, trace gases produced by nitrification); and (2) constraints to the growth and activity of N fixers imposed by differential effects of shading, P limitation, and grazing. The combination of these processes is sufficient to describe an open system, with input from both precipitation and N fixation, that is nevertheless strongly N-limited at equilibrium. This model is useful for exploring causes and consequences of constraints to N fixation, and hence of N limitation, and we believe it will also be useful for evaluating how N fixation and limitation interact with elevated CO2 and other components

of global enviromental change.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, ELEVATED CO2, FIXATION, FOREST ECOSYSTEMS, GROWTH, LIMITATION, PHOSPHORUS, RESPONSES, TALLGRASS PRAIRIE

2479

Vivin, P., P. Gross, G. Aussenac, and J.M. Guehl. 1995. Whole-plant co2 exchange, carbon partitioning and growth in quercus-robur seedlings exposed to elevated co2. *Plant Physiology and Biochemistry 33(2):201-211.*

Pedunculate oak acorns (Quercus robur L.) were germinated and grown under nonlimiting nutritional and water conditions in controlled-environment greenhouses with ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) CO2 concentrations. A semiclosed gas exchange measurements, and (CO2)-C-13 labelling, system (1.5% (CO2)-C-13) was used to simultaneously assess (a) the CO2 exchange of both aerial and below-ground (roots plus soil) compartments of the soil-plant system and (b) the partitioning of the recently photo-assimilated carbon. Measurements were made during the fast aerial growth phase (July 30) and at the end of the growing season (October 15). On July 30, whole-plant dry mass had been increased by 44% since the beginning of the growing season in the elevated CO2 treatment, whereas at the end of the growing season the enhancing effect was only 17%. Elevated CO2 stimulated net CO2 assimilation rate per unit leaf area (A) in July (+40%), whereas in October this stimulation had disappeared. The respiratory CO2 evolution of the root-soil compartment (individual plant basis) was stimulated by 35% under the elevated CO2 conditions on July 30, but not on October 15. In July, relative specific allocation (RSA), a parameter expressing the sink strength, was higher in all compartments under 700 mu mol mol(-1) compared to 350 mu mol mol(-1). Moreover in root tips, the RSA values determined 4 h after the labelling were particularly high (7.8%)with elevated CO2, whereas under ambient CO2 RSA values were close to zero.

KEYWORDS: ALLOCATION, C-13, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, RESPIRATION, SOURCE-SINK RELATIONS, SOYA BEAN- PLANTS, STEADY-STATE CONDITIONS, ZEA MAYS L

2480

Vivin, P., and J.M. Guehl. 1997. Changes in carbon uptake and allocation patterns in Quercus robur seedlings in response to elevated CO2 and water stress: an evaluation with C-13 labelling. *Annales Des Sciences Forestieres 54(7):597-610.*

A semi-closed (CO2)-C-13 labelling system (1.5% C-13) was used to assess both carbon uptake and allocation within pedunculate oak seedlings (Quercus robur L) grown under ambient (350 vpm) and elevated (700 vpm) atmospheric CO2 concentration ([CO2]) and in either well-watered or droughted conditions. Pulse-chase C-13 labelling data highlighted the direct positive effect of elevated CO2 on photosynthetic carbon acquisition. Consequently, in well-watered conditions, CO2-enriched plants produced 1.52 times more biomass (dry mass at harvest) and 1.33 times more dry root matter (coarse plus fine roots) over the 22-week growing period than plants grown under ambient [CO2]. The root/shoot biomass ratio was decreased both by drought and [CO2], despite lower N concentrations in CO2-enriched plants. However, both long-term and short-term C allocation to fine roots were not altered by CO2, and relative specific allocation (RSA), a parameter expressing sink strength, was hip her in all plant organs under 700 vpm compared to 350 vpm. Results showed that C availability for growth and metabolic processes was greater in fine roots of oaks grown under an elevated CO2 atmosphere irrespective of soil water availability.

KEYWORDS: ATMOSPHERIC CO2, CASTANEA-SATIVA MILL, DRY-WEIGHT, ENRICHMENT, GAS-EXCHANGE, GROWTH-RESPONSE, LOBLOLLY-PINE, MINERAL NUTRITION, RADIATA D-DON, SOIL SYSTEM

2481

Vivin, P., J.M. Guehl, A.M. Clement, and G. Aussenac. 1996. The effects of elevated CO2 and water stress on whole plant CO2 exchange, carbon allocation and osmoregulation in oak seedlings. *Annales Des Sciences Forestieres 53(2-3):447-459.*

Seedlings of Quercus robur L grown under present (350 mu mol mol(-1)) or twice the present (700 mu mol mol(-1)) atmospheric CO2 concentrations, were either maintained well-watered or subjected to a drought constraint late in the growing season (25 August 1993). Despite an initial stimulation of biomass growth (+44%) by elevated CO2, there was no significant difference in plant dry weight at the end of the growing season (15 October 1993) between the two CO2 treatments, irrespective of watering regime. Under drought conditions, although there was no growth increase in response to elevated CO2 concentration, there was a stimulation in net photosynthesis. In addition, the respiration rate of the root + soil system (root dry matter basis) was slightly lower in the elevated than in the ambient CO2 concentration. These results, together with the results from short-term C-13 labelling, suggest enhanced plant carbon losses through processes not assessed here (aerial respiration, root exudation, etc) under elevated CO2 concentration. In the droughted conditions, new carbon relative specific allocation values (RSA) were greater under elevated CO2 than under ambient CO2 concentration in both leaf and root compartments. Osmotic potentials at full turgor (pi(o)) were lowered in response to water stress in leaves by 0.4 MPa for the elevated CO2 treatment only. In roots, osmotic adjustment (0.3 MPa) occurred in both the CO2 treatments.

KEYWORDS: ALBA L, AMBIENT, ATMOSPHERIC CO2, ENRICHMENT, GROWTH, LIMITED CONDITIONS, OSMOTIC ADJUSTMENT, PHOTOSYNTHESIS, RESOURCE USE, RESPONSES

2482

Vivin, P., F. Martin, and J.M. Guehl. 1996. Acquisition and within-plant allocation of C-13 and N-15 in CO2-enriched Quercus robur plants. *Physiologia Plantarum 98(1):89-96.*

We assessed the effects of doubling atmospheric CO2 concentration, [CO2], on C and N allocation within pedunculate oak plants (Quercus robur L.) grown in containers under optimal water supply. A short-term dual (CO2)-C-13 and (NO3-)-N-15 labelling experiment was carried out when the plants had formed their third growing flush. The 22-week exposure to 700 mu l l(- 1) [CO2] stimulated plant growth and biomass accumulation (+53% as compared with the 350 mu l l(-1) [CO2] treatment) but decreased the root/shoot biomass ratio (-23%) and specific leaf area (-18%). Moreover, there was an increase in net CO2 assimilation rate (+37% on a leaf dry weight basis; +71% on a leaf area basis), and a decrease in both above- and below- ground CO2 respiration rates (-32 and -26%, respectively, on a dry mass basis) under elevated [CO2]. C-13 acquisition, expressed on a plant mass basis or on a plant leaf area basis, was also markedly stimulated under elevated [CO2] both after the 12-h (CO2)-C-13 pulse phase and after the 60-h chase phase. Plant N content was increased under elevated CO2 (+36%), but not enough to compensate for the increase in plant C content (+53%). Thus, the plant C/N ratio was increased (+13%) and plant N concentration was decreased (-11%). There was no effect of elevated [CO2] on fine root-specific N-15 uptake (amount of recently assimilated N-15 per unit fine root dry mass), suggesting that modifications of plant N pools were merely linked to root size and not to root function. N concentration was decreased in the leaves of the first and second growing flushes and in the coarse roots, whereas it was unaffected by [CO2] in the stem and in the

actively growing organs (fine roots and leaves of the third growth flush). Furthermore, leaf N content per unit area was unaffected by [CO2]. These results are consistent with the short-term optimization of N distribution within the plants with respect to growth and photosynthesis. Such an optimization might be achieved at the expense of the N pools in storage compartments (coarse roots, leaves of the first and second growth flushes). After the 60-h C-13 chase phase, leaves of the first and second growth flushes were almost completely depleted in recent C-13 under ambient [CO2], whereas these leaves retained important amounts of recently assimilated C-13 (carbohydrate reserves?) under elevated [CO2].

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CASTANEA-SATIVA MILL, DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, GROWTH-RESPONSE, NITROGEN UPTAKE, SOIL SYSTEM, TREE SEEDLINGS, WOODY-PLANTS

2483

Vloedbeld, M., and R. Leemans. 1993. Quantifying feedback processes in the response of the terrestrial carbon-cycle to global change - the modeling approach of image-2. *Water, Air, and Soil Pollution 70(1-4):615-628.*

The terrestrial biosphere component of the Integrated Model to Assess the Greenhouse Effect (IMAGE 2) uses changes in land cover to compute dynamically the C fluxes between the terrestrial biosphere and the atmosphere. The model explores the potential impact of feedback processes incorporated in the model, which are the enhancement of plant growth (CO2 fertilization) and a more efficient use of water under increased CO2 concentrations in the atmosphere; the temperature response of photosynthesis and respiration of plants; the temperature and soil water response of decomposition processes; and the climate-induced changes in vegetation and agricultural patterns with the consequent changes in land cover. In this paper we discuss the implementation and operation of the different feedback processes in the IMAGE 2 model. Results are shown for each process separately as well as the combined processes. The aim of this paper is to quantify the importance of these feedback processes geographically. The main results are that vegetation shifts due to climatic change and increased water use efficiency, CO2 fertilization decreases net C emissions, while changed decomposition rates strongly increase C emissions to the atmosphere. Changes in the global balance between photosynthesis and respiration make little net difference. With the IPPC business-as-usual scenario the terrestrial biosphere continues to emit C into the atmosphere. This behavior is governed by changes in land-use, caused by a multitude of anthropogenic processes.

KEYWORDS: CLIMATE CHANGE, ELEVATED CO2, ENRICHMENT, MATTER, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY, SENSITIVITY, STORAGE, TEMPERATURE

2484

Voesenek, L.A.C.J., W.H. Vriezen, M.J.E. Smekens, F.H.M. Huitink, G.M. Bogemann, and C.W.P.M. Blom. 1997. Ethylene sensitivity and response sensor expression in petioles of Rumex species at low O-2 and high CO2 concentrations. *Plant Physiology 114(4):1501-1509.*

Rumex palustris, a flooding-tolerant plant, elongates its petioles in response to complete submergence. This response can be partly mimicked by enhanced ethylene levels and low O-2 concentrations. High levels of CO2 do not markedly affect petiole elongation in R. palustris. Experiments with ethylene synthesis and action inhibitors demonstrate that treatment with low O-2 concentrations enhances petiole extension by shifting sensitivity to ethylene without changing the rate of ethylene production. The expression level of the R. palustris gene coding for the putative ethylene receptor (RP-ERS1) is up- regulated by 3% O-2 and increases after 20 min of exposure to a low concentration of O-2, thus preceding the first significant increase in elongation observable after 40 to 50 min. In the flooding-sensitive species Rumex acetosa, submergence results in a different response pattern: petiole growth of the submerged plants is the same as for control plants. Exposure of R. acetosa to enhanced ethylene levels strongly inhibits petiole growth. This inhibitory effect of ethylene on R. acetosa can be reduced by both low levels of O-2 and/or high concentrations of CO2.

KEYWORDS: CARBON DIOXIDE, DEEP-WATER RICE, FLOODING RESISTANCE, GRASS ECHINOCHLOA-ORYZOIDES, GROWTH-RESPONSES, MARITIMUS L, ORYZA-SATIVA, OXYGEN, SHOOT ELONGATION, SUBMERGENCE

2485

Vogel, C.S., and P.S. Curtis. 1995. Leaf gas-exchange and nitrogen dynamics of n-2-fixing field- grown alnus-glutinosa under elevated atmospheric co2. *Global Change Biology 1(1):55-61.*

Few studies have investigated the effects of elevated CO2 on the physiology of symbiotic N-2-fixing trees. Tree species grown in low N soils at elevated CO2 generally show a decline in photosynthetic capacity over time relative to ambient CO2 controls. This negative adjustment may be due to a reallocation of leaf N away from the photosynthetic apparatus, allowing for more efficient use of limiting N. We investigated the effect of twice ambient CO2 on net CO2 assimilation (A), photosynthetic capacity, leaf dark respiration, and leaf N content of N-2- fixing Alnus glutinosa (black alder) grown in field open top chambers in a low N soil for 160 d. At growth CO2, A was always greater in elevated compared to ambient CO2 plants. Late season A vs. internal leaf p(CO2) response curves indicated no negative adjustment of photosynthesis in elevated CO2 plants. Rather, elevated CO2 plants had 16% greater maximum rate of CO2 fixation by Rubisco. Leaf dark respiration was greater at elevated CO2 on an area basis, but unaffected by CO2 on a mass or N basis. In elevated CO2 plants, leaf N content (mu g N cm(- 2)) increased 50% between Julian Date 208 and 264. Leaf N content showed little seasonal change in ambient CO2 plants. A single point acetylene reduction assay of detached, nodulated root segments indicated a 46% increase in specific nitrogenase activity in elevated compared to ambient CO2 plants. Our results suggest that N-2-fixing trees will be able to maintain high A with minimal negative adjustment of photosynthetic capacity following prolonged exposure to elevated CO2 on N-poor soils.

KEYWORDS: ACETYLENE-REDUCTION, CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, INHIBITION, NODULATION, PHOTOSYNTHESIS, PLANT RESPIRATION, TEMPERATURE, WHOLE PLANT

2486

Vogel, C.S., P.S. Curtis, and R.B. Thomas. 1997. Growth and nitrogen accretion of dinitrogen-fixing Alnus glutinosa (L) Gaertn under elevated carbon dioxide. *Plant Ecology 130(1):63-70.*

Short-term studies of tree growth at elevated CO2 suggest that forest productivity may increase as atmospheric CO2 concentrations rise, although low soil N availability may limit the magnitude of this response. There have been few studies of growth and N-2 fixation by symbiotic N-2-fixing woody species under elevated CO2 and the N inputs these plants could provide to forest ecosystems in the future. We investigated the effect of twice ambient CO2 on growth, tissue N accretion, and N-2 fixation of nodulated Alnus glutinosa (L.) Gaertn. grown under low soil N conditions for 160 d. Root, nodule, stem, and leaf dry weight (DW) and N accretion increased significantly in response to elevated CO2. Whole-plant biomass and N accretion increased 54% and 40%, respectively. Delta-N-15 analysis of leaf tissue indicated that

plants from both treatments derived similar proportions of their total N from symbiotic fixation suggesting that elevated CO2 grown plants fixed approximately 40% more N than did ambient CO2 grown plants. Leaves from both CO2 treatments showed similar relative declines in leaf N content prior to autumnal leaf abscission, but total N in leaf litter increased 24% in elevated compared to ambient CO2 grown plants, These results suggest that with rising atmospheric CO2 N-2-fixing woody species will accumulate greater amounts of biomass N through N-2 fixation and may enhance soil N levels by increased litter N inputs.

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, AUTUMN OLIVE, BLACK ALDER, CLIMATE CHANGE, FIXATION, LEAF GAS-EXCHANGE, MINERAL NUTRITION, SOIL-NITROGEN, TISSUE NITROGEN, WOODY-PLANTS

2487

Volin, J.C., and P.B. Reich. 1996. Interaction of elevated CO2 and O-3 on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. *Physiologia Plantarum 97(4):674-684.*

Seedlings of three species native to central North America, a C-3 tree, Populus tremuloides Michx., a C-3 grass, Agropyron smithii Rybd., and a C-4 grass, Bouteloua curtipendula Michx., were grown in all eight combinations of two levels each of CO2, O-3 and nitrogen (N) for 58 days in a controlled environment. Treatment levels consisted of 360 or 674 mu mol mol(-1) CO2, 3 or 92 nmol mol(-1) O-3, and 0.5 or 6.0 mM N. In situ photosynthesis and relative growth rate (RGR) and its determinants were obtained at each of three sequential harvests, and leaf dark respiration was measured at the second and third harvests. In all three species, plants grown in high N had significantly greater whole-plant mass, RGR and photosynthesis than plants grown in low N. Within a N treatment, elevated CO2 did not significantly enhance any of these parameters nor did it affect leaf respiration, However, plants of all three species grown in elevated CO2 had lower stomatal conductance compared to ambient CO2-exposed plants. Seedlings of P. tremuloides (in both N treatments) and B. curtipendula (in high N) had significant ozone-induced reductions in whole-plant mass and RGR in ambient but not under elevated CO2. This negative O-3 impact on RGR in ambient CO2 was related to increased leaf dark respiration, decreased photosynthesis and/or decreased leaf area ratio, none of which were noted in high O-3 treatments in the elevated CO2 environment. In contrast, A. smithii was marginally negatively affected by high O-3.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ENRICHMENT, GAS-EXCHANGE, LEAF, LIGHT ENVIRONMENT, NET PHOTOSYNTHESIS, OZONE, PINE SEEDLINGS, TUNDRA

2488

Volin, J.C., P.B. Reich, and T.J. Givnish. 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth: species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytologist 138(2):315-325.*

Due to their different physiological effects, elevated carbon dioxide and elevated ozone might have interactive impacts on plants, and differentially so on plants differing in photosynthetic pathway and growth rate. To test several hypotheses related to these issues, we examined the physiological, morphological and growth responses of six perennial species grown at various atmospheric concentrations of carbon dioxide and ozone. The species involved (two C-3 trees: Populus tremuloides Michx., Quercus rubra L.; two C-3 grasses: Agropyron smithii Rybd., Koeleria cristata L.; two C-4 grasses: Bouteloua curtipendula Michx., Schizachyrium scoparium Michx.) differed in growth form, stomatal conductance and photosynthetic pathway. In situ photosynthesis, relative growth rate (RGR) and its determinants (leaf area ratio, specific leaf area, leaf weight ratio and root weight ratio) were determined via sequential harvests of seedlings that were grown in all combinations of 366 or 672 mu mol mol(-1) CO2 and 3 or 95 nmol mol(-1) O-3 over a 101-d period. Elevated CO2 had minimal effect on either photosynthesis or RGR. By contrast, RGR for all six species was lower in high O-3 concentrations at ambient CO2, significantly so in A. smithii and P. tremuloides. Five of the six species also exhibited reductions in in situ photosynthesis at ambient CO2 in high-O-3-grown compared with low-O-3-grown plants. For all species, these O-3-induced reductions in RGR and photosynthesis were absent in the elevated CO2 environment. Root weight ratio was significantly reduced by elevated O-3 in A. smithii and P. tremuloides in ambient but not elevated CO2. Species with high stomatal conductance were the most susceptible to oxidant injury, while those with low stomatal conductance, such as the C-4 species and Q. rubra, were not as detrimentally affected by O-3. Elevated levels of CO2 will reduce stomatal conductance and O-3 uptake, and might therefore reduce the potential for oxidant damage. However, there was a stronger relationship of the percent reduction in whole-plant mass due to O-3, related to the ratio of photosynthesis to stomatal conductance. In general, results of this study of six functionally diverse plant species suggest that O-3 pollution effects on carbon balance and growth are likely to be ameliorated by elevated concentrations of atmospheric CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, DARK RESPIRATION, ENRICHMENT, NET PHOTOSYNTHESIS, NITROGEN-AVAILABILITY, O-3, PINE SEEDLINGS, SPRUCE PICEA-ABIES, WINTER HARDINESS

2489

Volin, J.C., M.G. Tjoelker, J. Oleksyn, and P.B. Reich. 1993. Light environment alters response to ozone stress in seedlings of acer-saccharum marsh and hybrid populus L .2. Diagnostic gas-exchange and leaf chemistry. *New Phytologist 124(4):637-646.*

Diagnostic gas exchange measurements and foliar chemical assays were conducted on hybrid poplar (Populus tristis Fisch. x P. balsamifera L. cv. Tristis) and sugar maple (Acer saccharum Marsh.) seedlings grown under contrasting light and ozone treatments. Seedlings were grown in low irradiance (c. 2.5 mol m-2 d-1) and six-fold greater irradiance (c. 16.6 mol m-2 d-1) in combination with low (< 10 nl l-1) and elevated (99-115 nl l-1) ozone. Analysis of light response curves showed ozone-induced reductions in photosynthetic capacity and quantum yield for unshaded poplar and shaded sugar maple, but not the contrasting light treatments. Photosynthesis at saturating CO2 concentrations was decreased in the elevated ozone treatment in both the unshaded and shaded poplar and in shaded sugar maple. Poplar had significant reductions in chlorophyll concentration due to ozone exposure in both unshaded and shaded treatments. Older leaves of unshaded poplar plants had significantly greater reductions in chlorophyll levels due to ozone than older leaves of shaded plants. In maple, only shade-grown leaves had significant decreases in chlorophyll concentration due to ozone exposure. The diagnostic gas exchange measurements in conjunction with chlorophyll measurements indicate that in hybrid poplar, unshaded leaves may be more sensitive to ozone than shade leaves, while in sugar maple, shade leaves are more sensitive to ozone. For hybrid poplar a decrease in photosynthetic capacity, quantum yield and chlorophyll concentration in the unshaded, moderately high light environment due to elevated ozone is consistent with prior studies. The results indicating that sugar maple seedlings may be more detrimentally affected by elevated ozone in the lower light environment may have serious implications for this and other shade-adapted species with respect to their performance in an understorey environment.

KEYWORDS: BIOSYNTHESIS, CARBOXYLASE, CHLOROPHYLL, CO2 EXCHANGE, CONDUCTANCE, GLUTATHIONE, LEAVES, NET PHOTOSYNTHESIS, PHOTON FLUX- DENSITY, POPLAR

2490

von Tiedemann, A., and K.H. Firsching. 1998. Combined whole-season effects of elevated ozone and carbon dioxide concentrations on a simulated wheat leaf rust (Puccinia recondita f. sp. tritici) epidemic. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection 105(6):555-566.*

A complete growth season with the physical climate and ozone pollution from 1 April to 31 July as recorded at a field site in Northern Germany, averaged over several years, was simulated in climate chambers and combined either with a current (370-400 mu l l(-1)) or enriched (620-650 mu l l(-1)) CO2 atmosphere. Wheat, grown from seedling emergence to maturity under the different physico-chemical climates, was inoculated with leaf rust (Puccinia recondita f. sp. tritici) at tillering stage and a rust epidemic was induced by repeated re-inoculations with the newly Formed inoculum. Ozone significantly reduced disease severity, uredospore production and increased the latent period of leaf rust on young planes, consequently inhibiting the epidemic spread on upper leaves of mature plants. Inhibiting effects of ozone on leaf rust development were not reflected by the early infection stages such as spore germination, germ tube growth, formation of infection hyphae, haustorial mother cells and haustoria, which remained largely unaffected by the ozone treatments. However, ozone induced a significantly higher extent of hypersensitive responses of the infected leaf tissue. Additionally, plants exposed to elevated ozone turned senescent much earlier than plants without this stress which prematurely degraded the growth conditions for the fungal pathogen. Enrichment with CO2 increased the rotal carbohydrate content in leaves but this had only minor effects on the disease. Thus, elevated CO2 only poorly compensated for the disease-inhibiting effects of ozone. The compensation of ozone effects on wheat leaf rust by elevated CO2 is much smaller than known compensatory effects of both gases on plans productivity.

KEYWORDS: CO2, GRAMINIS, GROWTH, INFECTION PROCESSES, O-3, OXIDATIVE BURST, RESISTANCE, RESPONSES

2491

Vose, J.M., K.J. Elliott, D.W. Johnson, D.T. Tingey, and M.G. Johnson. 1997. Soil respiration response to three years of elevated CO2 and N fertilization in ponderosa pine (Pinus ponderosa Dong Ex Laws). *Plant and Soil 190(1):19-28.*

We measured growing season soil CO2 evolution under elevated atmospheric [CO2] and soil nitrogen (N) additions. Our objectives were to determine treatment effects, quantify seasonal variation, and compare two measurement techniques. Elevated [CO2] treatments were applied in open-top chambers containing ponderosa pine (Pinus ponderosa L.) seedlings. N applications were made annually in early spring. The experimental design was a replicated factorial combination of CO2 (ambient, +175, and +350 mu L L-1 CO2) and N (0, 10, and 20 g m(-2) N as ammonium sulphate). Soils were irrigated to maintain soil moisture at > 25 percent. Soil CO2 evolution was measured over diurnal periods (20-22 hours) in October 1992, and April, June, and October 1993 and 1994 using a flow- through, infrared gas analyzer measurement system and corresponding pCO(2) measurements were made with gas wells. Significantly higher soil CO2 evolution was observed in the elevated CO2 treatments; N effects were not significant. Averaged across all measurement periods, fluxes, were 4.8, 8.0, and 6.5 for ambient + 175 CO2, and +350 CO2 respectively). Treatment variation was linearly related to fungal occurrence as observed in minirhizotron tubes. Seasonal variation in soil CO2 evolution was non-linearly related to soil temperature; i.e., fluxes increased up to approximately soil temperature (10cm soil depth) and decreased dramatically at temperatures > 18 degrees C. These patterns indicate exceeding optimal temperatures for biological activity. The dynamic, flow-through measurement system was weakly correlated (r = 0.57; p < 0.0001; n = 56) with the pCO(2) measurement method.

KEYWORDS: CARBON-DIOXIDE EVOLUTION, CHAMBERS, EFFLUX, FOREST FLOOR, INTERIOR ALASKA, MOISTURE, PATTERNS, TEMPERATURE, TRACE GAS FLUXES

2492

Vose, J.M., K.J. Elliott, D.W. Johnson, R.F. Walker, M.G. Johnson, and D.T. Tingey. 1995. Effects of elevated co2 and n fertilization on soil respiration from ponderosa pine (pinus-ponderosa) in open-top chambers. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(8):1243-1251.*

We measured growing season soil CO2 evolution under elevated atmospheric CO2 and soil nitrogen (N) additions. Our objectives were to determine treatment effects, quantify seasonal variation, and determine regulating mechanisms. Elevated CO2 treatments were applied in open-top chambers containing 3-year- old ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings. Nitrogen applications were made annually in early spring. The experimental design was a replicated factorial combination of CO2 (ambient, +175, and +350 mu L . L(-1) CO2) and N (0, 10, and 20 g . m(-2) N as ammonium sulfate). Soils were irrigated to maintain soil moisture at >25%. Soil CO2 evolution was measured over diurnal periods (20-22 h) in April, June, and October 1993 using a flow-through, infrared gas analyzer measurement system. To examine regulating mechanisms, we linked our results with other studies measuring root biomass with destructive sampling and root studies using minirhizotron techniques. Significantly higher soil CO2 evolution was observed in the elevated CO2 treatments in April and October; N effects were not significant. In October, integrated daily values for CO2 evolution ranged from 3.73 to 15.68 g CO2 . m(- 2)day(-1) for the ambient CO2 + 0 N and 525 mu L . L(-1) CO2 + 20 g . m(-2) N, respectively. Soil CO2 flux among treatments was correlated with coarse root biomass (r(2) = 0.40; p >F = 0.0380), indicating that at least some of the variation observed among treatments was related to variation in root respiration. Across ail sample periods and treatments, there was a significant correlation (r(2) = 0.63; p >F = 0.0001) between soil CO2 evolution acid percent fungal hyphae observed in minirhizotron tubes. Hence, some of the seasonal and treatment variation was also related to differences in heterotrophic activity.

KEYWORDS: CARBON-DIOXIDE EVOLUTION, DECIDUOUS FOREST FLOOR, ECOSYSTEMS, EFFLUX, HARDWOOD FOREST, INTERIOR ALASKA, MOISTURE, PATTERNS, ROOT RESPIRATION, TEMPERATURE

2493

Vourlitis, G.L., W.C. Oechel, S.J. Hastings, and M.A. Jenkins. 1993. A system for measuring insitu co2 and ch4 flux in unmanaged ecosystems - an arctic example. *Functional Ecology 7(3):369-379.*

1. A passive, rapid response, closed system was developed to measure in situ ecosystem CO2 and CH4 flux in 0.5-m2 plots over diurnal, seasonal, and annual time scales in arctic tundra ecosystems. The system consists of a chamber measuring 0.75 m on a side, 0.3 m in height, with acrylic sides, a mylar top, and 6-10 cm radial fans to ensure thorough mixing of the chamber environment. 2. CO2 concentration and flux rates were measured using a Li-Cor 6200 Portable Photosynthesis System, which is capable of measuring 0.1 p.p.m. s-1 changes in CO2 concentration. CH4 flux rates were measured by sequential sampling of the CH4 concentration in the chamber over the duration of a 15-20-min incubation period. 3. Performance analyses indicate that light attenuation was less-than-or- equal-to 10% of ambient light. The rate of temperature increase within the chamber over the duration of the measurement period was approximately 1-5-degrees-C and 0.2-degrees-

C for the majority of the sampling days at tussuck tundra and wet coastal tundra sites, respectively. The maximum increase in thaw depth due to the bases was approximately 10%, and was a function of the site water balance and the amount of time that the bases were in place. Generally, thaw depth in plots with bases was greater when the bases were in place for a longer period of time (greater-than-or-equal-to 1 year), while the bases that were installed during the current growing season had a small effect on plot thaw depths. 4. The system had a minimal effect on ecosystem CO2 flux, compared to plots that lacked bases in a wet coastal tundra and southern California turf ecosystem. 5. The system was successfully used to measure the effect of light intensity, soil temperature, and water balance on ecosystem CO2 flux. 6. Due to the rapid response of the system, high sensitivity to low flux rates, high portability, low cost, potential for use in field experiments, and non-invasive sampling design, the system allows for the reliable measurement of CO2, CH4, and other trace gas flux rates in a variety of ecosystem types.

2494

Vu, J.C.V., L.H. Allen, K.J. Boote, and G. Bowes. 1997. Effects of elevated CO2 and temperature on photosynthesis and Rubisco in rice and soybean. *Plant, Cell and Environment 20(1):68-76.*

Rice (Oryza sativa L. cv. IR-72) and soybean (Glycine max L. Merr. cv. Bragg), which have been reported to differ in acclimation to elevated CO2, were grown for a season in sunlight at ambient and twice-ambient [CO2], and under daytime temperature regimes ranging from 28 to 40 degrees C. The objectives of the study were to test whether CO2 enrichment could compensate for adverse effects of high growth temperatures on photosynthesis, and whether these two C-3 species differed in this regard. Leaf photosynthetic assimilation rates (A) of both species, when measured at the growth [CO2], were increased by CO2 enrichment, but decreased by supraoptimal temperatures. However, CO2 enrichment more than compensated for the temperature-induced decline in A. For soybean, this CO2 enhancement of A increased in a linear manner by 32-95% with increasing growth temperatures from 28 to 40 degrees C, whereas with rice the degree of enhancement was relatively constant at about 60%, from 32 to 38 degrees C. Both elevated CO2 and temperature exerted coarse control on the Rubisco protein content, but the two species differed in the degree of responsiveness. CO2 enrichment and high growth temperatures reduced the Rubisco content of rice by 22 and 23%, respectively, but only by 8 and 17% for soybean. The maximum degree of Rubisco down-regulation appeared to be limited, as in rice the substantial individual effects of these two variables, when combined, were less than additive. Fine control of Rubisco activation was also influenced by both elevated [CO2] and temperature. In rice, total activity and activation were reduced, but in soybean only activation was lowered. The apparent catalytic turnover rate (K-cat) of rice Rubisco was unaffected by these variables, but in soybean elevated [CO2] and temperature increased the apparent K-cat by 8 and 22%, respectively. Post-sunset declines in Rubisco activities were accelerated by elevated [CO2] in rice, but by high temperature in soybean, suggesting that [CO2] and growth temperature influenced the metabolism of 2-carboxyarabinitol-1-phosphate, and that the effects might be species-specific. The greater capacity of soybean for CO2 enhancement of A at supraoptimal temperatures was probably not due to changes in stomatal conductance, but may be partially attributed to less down- regulation of Rubisco by elevated [CO2] in soybean than in rice. However, unidentified species differences in the temperature optimum for photosynthesis also appeared to be important. The responses of photosynthesis and Rubisco in rice and soybean suggest that among C-3 plants species-specific differences will be encountered as a result of future increases in global [CO2] and air temperatures.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, GROWTH, LEAVES, LIGHT, METABOLISM, PLANTS, RESPIRATION, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SPECIFICITY

2495

Vu, J.C.V., L.H. Allen, G. Bowes, and K.J. Boote. 1997. Kinetic properties of rubisco in rice and soybean grown under elevated CO2, supraoptimal temperature, and drought. *Plant Physiology 114(3):1092.*

2496

Vu, J.C.V., J.T. Baker, A.H. Pennanen, L.H. Allen, G. Bowes, and K.J. Boote. 1998. Elevated CO2 and water deficit effects on photosynthesis, ribulose bisphosphate carboxylase-oxygenase, and carbohydrate metabolism in rice. *Physiologia Plantarum 103(3):327-339.*

Rice (Oryza sativa [L.] cv. IR-72) was grown for a season in sunlit, controlled-environment chambers at 350 or 700 mu mol CO2 mol(-1) under continuously flooded (unstressed) or drought- imposed periods at panicle initiation (stressed). The midday canopy photosynthetic rates (P-n), measured at the CO2 concentration ([CO2]) used for growth, were enhanced by high [CO2] but reduced by drought. High [CO2] increased P-n by 18 to 34% for the unstressed plants, and 6 to 12% for the stressed plants. In the unstressed plants, CO2 enrichment increased water-use efficiency (WUE) by 26%, and reduced evapotranspiration (ET) by 8 to 14%. Both high [CO2] and severe drought decreased the activity and content of ribulose bisphosphate carboxylase-oxygenase (Rubisco). High-CO2- unstressed plants had 6 to 22% smaller content and 5 to 25% lower activity of Rubisco than ambient-CO2-unstressed plants. Under severe drought, reductions of Rubisco were 53 and 27% in activity and 40 and 12% in content, respectively, for ambient- and high-CO2 treatments. The apparent catalytic turnover rate (K-cat) of midday fully activated Rubisco was not altered by high [CO2], but severe drought reduced K-cat by 17 to 23%. Chloroplasts of the high-CO2 leaves contained more, and larger starch grains than those of the ambient-CO2 leaves. High [CO2] did not affect the leaf sucrose content of unstressed plants. In contrast, severe drought reduced the leaf starch and increased the sucrose content in both CO2 treatments. The activity of leaf sucrose phosphate synthase of unstressed plants was not affected by high [CO2], whereas that of ambient- CO2-grown plants was reduced 45% by severe drought. Reduction in ET and enhancements in both P-n and WUE for rice grown under high [CO2] helped to delay the adverse effects of severe drought and allowed the stressed plants to assimilate CO2 for an extra day. Thus, rice grown in the next century may utilize less water, use water more efficiently, and be able to tolerate drought better under some situations.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CHAMBERS, CLIMATE, LEAVES, PHASEOLUS-VULGARIS, PLANTS, RESPONSES, STRESS, SUCROSE PHOSPHATE SYNTHASE

2497

Vu, J.C.V., R.W. Gesch, L.H. Allen, K.J. Boote, and G. Bowes. 1999. CO2 enrichment delays a rapid, drought-induced decrease in Rubisco small subunit transcript abundance. *Journal of Plant Physiology 155(1):139-142.*

Rice (Oryza sativa L. cv. IR-72) was grown in sunlit chambers at 350 and 700 mu mol CO2 mol(-1) under conditions of continuous flooding (control) or drought which was imposed at panicle initiation, to evaluate the effects of CO2 enrichment and soil water deficit on photosynthesis and Rubisco gene expression. Leaf and canopy photosynthetic rates were enhanced by high [CO2] but reduced by drought. High [CO2] and severe drought both reduced rbcS transcript abundance, along with the

activity, activation and protein content of Rubisco, but the K- m (CO2) was not affected. The transition from moderate to severe drought caused a rapid decline, within 24 h, in the rbcS transcript abundance. High [CO2], however, delayed the adverse effects of severe drought on rbcS transcript abundance and activities of Rubisco, and permitted photosynthesis to continue for an extra day during the drought-stress cycle.

KEYWORDS: ACCLIMATION, ARABIDOPSIS-THALIANA, ATMOSPHERIC CARBON-DIOXIDE, DOWN- REGULATION, ELEVATED CO2, EXPRESSION, PHOTOSYNTHESIS, RBCS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE, RICE RESPONSES

2498

Vugts, H.F. 1993. The need for micrometeorological research of the response of the energy-balance of vegetated surfaces to co2 enrichment. *Vegetatio 104:321-328.*

A Penman-Monteith equation has been used to evaluate a change in canopy resistance on the evapotranspiration of a savannah and agricultural area in Botswana. After a short introduction, some problems concerning the K-theory or 'first order closure' are indicated when one uses it for transport modelling within and above a canopy. The Penman-Monteith equation was used to calculate the canopy resistance for a savannah vegetation and sorghum under the same environmental conditions. After that, by changing the stomatal resistance due to an increase of the CO2 content, the change in the evapotranspiration was estimated. Finally some recommendations for future research are given and an outline of a proposed FACE experiment is presented.

KEYWORDS: WATER

2499

Vuorinen, A.H., and W.M. Kaiser. 1997. Dark CO2 fixation by roots of willow and barley in media with a high level of inorganic carbon. *Journal of Plant Physiology 151(4):405-408.*

Willow (Salix cv. Aquatica gigantea) and barley (Hordeum vulgare L.) plants were grown in a nutrient solution (pH 7) enriched with HCO3- or gaseous CO2. The initial and potential in vivo rates of dark CO2 fixation in the roots were measured using 0.015 mmol/L and 0.74 mmol/L (HCO3-)-C-14 as substrates of phosphoenolpyruvate carboxylase (PEPC). Enrichment of the nutrient solution with HCO3- or CO2 increased the initial rate of dark CO2 fixation in roots of both willow and barley compared with the corresponding control roots. In plants grown with NO3- the initial activity of PEPC was 38 and 89% higher than in control willow and barley, respectively, after the addition of HCO3-. When the nutrient solutions were enriched with CO2 the initial activity of PEPC increased 52% in willows and 58% in barley, compared with the controls. The supply of HCO3- into NH4+ media increased the initial activity of PEPC in the roots of willows and barley by 50% and 17%, respectively. The amount of soluble protein in the roots was also higher in plants grown with inorganic carbon than in the control plants.

KEYWORDS: AMMONIUM NUTRITION, DIOXIDE FIXATION, NITRATE, NODULE DEVELOPMENT, PHOSPHOENOLPYRUVATE CARBOXYLASE ACTIVITY, PLANTS

2500

Waibel, A.E., T. Peter, K.S. Carslaw, H. Oelhaf, G. Wetzel, P.J. Crutzen, U. Poschl, A. Tsias, E. Reimer, and H. Fischer. 1999. Arctic ozone loss due to denitrification. *Science 283(5410):2064-2069.*

Measurements from the winter of 1994-95 indicating removal of total reactive nitrogen from the Arctic stratosphere by particle sedimentation were used to constrain a microphysical model. The model suggests that denitrification is caused predominantly by nitric acid trihydrate particles in small number densities. The denitrification is shown to increase Arctic ozone Loss substantially. Sensitivity studies indicate that the Arctic stratosphere is currently at a threshold of denitrification. This implies that future stratospheric cooling, induced by an increase in the anthropogenic carbon dioxide burden, is likely to enhance denitrification and to delay until late in the next century the return of Arctic stratospheric ozone to preindustrial values.

KEYWORDS: CLIMATE, CO2, DEHYDRATION, DEPLETION, POLAR STRATOSPHERIC CLOUDS, VERTICAL PROFILES, VORTEX, WINTER

2501

Wait, D.A., C.G. Jones, J. Wynn, and F.I. Woodward. 1999. The fraction of expanding to expanded leaves determines the biomass response of Populus to elevated CO2. *Oecologia 121(2):193-200.*

We examined whether the effects of elevated CO2 on growth of 1- year old Populus deltoides saplings was a function of the assimilation responses of particular leaf developmental stages. Saplings were grown for; 100 days at ambient (approximately 350 ppm) and elevated (ambient + 200 ppm) CO2 in forced-air greenhouses. Biomass, biomass distribution, growth rates, and leaf initiation and expansion rates were unaffected by elevated CO2. Leaf nitrogen (N), the leaf C:N ratio, and leaf lignin concentrations were also unaffected. Carbon gain was significantly greater in expanding leaves of saplings grown at elevated compared to ambient CO2. The Rubisco content in expanding leaves was not affected by CO2 concentration. Carbon gain and Rubisco content were significantly lower in fully expanded leaves of saplings grown at elevated compared to ambient CO2, indicating CO2-induced down-regulation in fully expanded leaves. Elevated CO2 likely had no overall effect on bio mass accumulation due to the more rapid decline in carbon gain as leaves matured in saplings grown at elevated compared to ambient CO2. This decline in carbon gain has been documented in other species and shown to be related to a balance between sink/source balance and acclimation. Our data suggest that variation in growth responses to elevated CO2 can result from differences in leaf assimilation responses in expanding versus expanded leaves as they develop under elevated CO2.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, CARBOXYLASE, GROWTH, LEAF GAS-EXCHANGE, NITROGEN, PHOTOSYNTHESIS, SEEDLINGS, TOMATO PLANTS

2502

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1995. Enriched atmospheric co2 and soil p effects on growth and ectomycorrhizal colonization of juvenile ponderosa pine. *Forest Ecology and Management 78(1-3):207-215.*

Interactive effects of atmospheric CO2 enrichment and soil P fertility on above- and below-ground development of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Seedlings were reared from seed in atmospheres with 700 mu l l(-1), 525 mu l l(-1), or ambient CO2 concentrations, and in a potting mix with 68, 43, or 18 mu g g(-1) soil P, and all were inoculated with the mycobiont Pisolithus tinctorius (Pers.) Coker and Couch shortly after emergence. At 4-month intervals over the 1-year duration of the study, three whole seedlings of each combination of CO2 and P treatments were harvested to permit detailed assessment of shoot and root growth and ectomycorrhizal colonization. After 4 months, shoot volume, root dry weight, and total root length of seedlings grown in 700 mu l(-1) CO2 were greater than those of seedlings grown in the other atmospheres regardless of P

treatment, and shoot/root ratios decreased as the CO2 concentration increased within each P treatment as well. After 8 months, the smallest shoot volumes and root weights and lengths within each P treatment were those of seedlings grown in ambient CO2. Root weight and total length increased as the CO2 concentration increased in high soil P, but the greatest root weights and lengths within the medium and low P treatments were those of seedlings reared in the 525 mu l(-1) CO2 atmosphere. Nevertheless, shoot/root ratios decreased with increasing CO2 in both high and medium soil P at the second harvest, and the highest shoot/root ratio in low P was that of seedlings grown in ambient CO2. After 1 year, the largest shoot and root volumes within the high and medium P treatments were those of seedlings grown in intermediate CO2, while the reverse was true in low P. The effects of CO2 concentration on dry weights, total root length, and shoot/root ratio at the final harvest were nonsignificant. As proved true with seedling growth, CO2 effects on ectomycorrhizal colonization varied temporally, as mycorrhizal development was not affected by the atmospheric treatments after 4 months, while seedlings grown in ambient CO2 exhibited the highest percent infections within each P treatment at the second harvest but those grown in 700 mu l l(-1) CO2 had the highest percentages after 1 year. These results suggest that elevated CO2 exerts stimulatory effects on shoot and root development of juvenile ponderosa pine which may be dependent on P availability to some degree, but these effects are somewhat transient and vary in magnitude over time.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, INCREASES, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH, WATER

2503

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1995. Interactive effects of atmospheric co2 enrichment and soil n on growth and ectomycorrhizal colonization of ponderosa pine- seedlings. *Forest Science 41(3):491-500.*

Interactive effects of elevated atmospheric CO2 and soil N fertility on above- and belowground development of juvenile ponderosa pine (Pinus ponderosa Dougl, ex Laws.) were examined. Seedlings were grown from seed in atmospheres containing 700 mu l l(-1), 525 mu l l(-1), or ambient CO2. Medium and high soil N treatments were created by adding sufficient (NH4)(2)SO4 to the potting mix to increase total N by 100 mu g g(-1) and 200 mu g g(-1), respectively, while unamended mix, which had a total N concentration of approximately 300 mu g g(-1), served as the low N treatment. Three whole-seedling harvests at 4-month intervals permitted assessment of shoot and root growth and ectomycorrhizal formation resulting from inoculation with Pisolithus tinctorius (Pers.) Coker and Couch. After 4 months, CO2 enrichment increased shoot volume and dry weight of seedlings grown in high soil N, but this result was not evident in the other N treatments and did not persist to the second harvest. Root weight, however, increased, and shoot/root ratio decreased as the CO2 concentration increased within all three N treatments at the first harvest. At the second harvest, root weights within the high and intermediate N treatments were lowest in seedlings grown in ambient CO2 and shoot/root ratios decreased as CO2 increased in these two N treatments as well. Although the ectomycorrhizal infection percentage of seedlings grown in 700 mu l l(-1) CO2 was highest among the seedlings grown in high N after 4 months, mycorrhizal colonization was variable overall at the first and second harvests. After 1 yr, the 525 mu l l(-1) CO2 concentration stimulated above- and belowground growth more than the high CO2 atmosphere in both high and medium soil N. These seedlings also had relatively extensive ectomycorrhizal formation, but colonization was again variable. Results presented here suggest the response of juvenile ponderosa pine to CO2 enrichment is ephemeral, with the effects on roots more pronounced and persistent overall than those on shoots, and that the response is dependent on N availability.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, INCREASES, QUERCUS-ALBA, RESPONSES, WATER

2504

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1997. Elevated atmospheric CO2 and soil N fertility effects on growth, mycorrhizal colonization, and xylem water potential of juvenile ponderosa pine in a field soil. *Plant and Soil 195(1):25-36.*

Interactive effects of atmospheric CO2 enrichment and soil N fertility on above- and below-ground development and water relations of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Open-top field chambers permitted creation of atmospheres with 700 mu L L-1, 525 mu L L-1, or ambient CO2 concentrations. Seedlings were reared from seed in field soil with a total N concentration of approximately 900 mu g g(-1) or in soil amended with sufficient (NH4)(2)SO4 to increase total N by 100 mu g g(-1) or 200 mu g g(-1). The 525 mu L L-1 CO2 treatment within the intermediate N treatment was excluded from the study. Following each of three consecutive growing seasons, whole seedlings of each combination of CO2 and N treatment were harvested to permit assessment of shoot and root growth and ectomycorrhizal colonization. In the second and third growing seasons, drought cycles were imposed by withholding irrigation during which predawn and midday xylem water potential and soil water potential were measured. The first harvest revealed that shoot weight and coarse and fine root weights were increased by growth in elevated CO2. Shoot and root volume and weights were increased by CO2 enrichment at the second harvest, but growth stimulation by the 525 mu L L-1 CO2 concentration exceeded that in 700 mu L L-1 CO2 during the first two growing seasons. At the third harvest, above-and below-ground growth increases were largely confined to the 700 mu L L-1 CO2 treatment, an effect accentuated by high soil N but evident in all N treatments. Ectomycorrhizal formation was reduced by elevated CO2 after one growing season, but thereafter was not significantly affected by CO2 and was unaffected by soil N throughout the study. Results of the xylem water potential measurements were variable, as water potentials in seedlings grown in elevated CO2 were intermittently higher on some measurement days but lower on others than that of seedlings grown in the ambient atmosphere. These results suggest that elevated CO2 exerts stimulatory effects on shoot and root growth of juvenile ponderosa pine under held conditions which are somewhat dependent on N availability, but that temporal variation may periodically result in a greater response to a moderate rise in atmospheric CO2 than to a doubling of the current ambient concentration.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ECTOMYCORRHIZAL COLONIZATION, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, STRESS, TAEDA

2505

Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1998. Atmospheric CO2 enrichment and soil N fertility effects on juvenile ponderosa pine: Growth, ectomycorrhizal development, and xylem water potential. *Forest Ecology and Management 102(1):33-44.*

Interactive effects of elevated atmospheric CO2 and soil N fertility on above-and below-ground growth, mycorrhizal colonization, and water relations of juvenile ponderosa pine (Pious ponderosa Dougl. ex Laws.) were investigated. One-year- old seedlings were planted in undisturbed field soil within open-top chambers which permitted creation of atmospheres with 700 mu l l(-1), 525 mu l l(-1), or ambient CO2 concentrations. High and medium soil N treatments were imposed by incorporating sufficient (NH4)(2)SO4 to increase total N by 200 mu g g(-1) and 100 mu g g(-1), respectively, while unamended soil, which had

a total N concentration of approximately 900 mu g g(-1), constituted the low N treatment. Following each of two consecutive field growing seasons, whole seedlings of every combination of CO2 and N treatment were harvest-ed to permit assessment of shoot and root growth and quantification of ectomycorrhizal development. Late in the second growing season, a simulated drought episode was imposed by withholding irrigation during which predawn and midday xylem water potential and soil water potential were measured. The initial harvest revealed that coarse and fine root weights were increased by CO2 enrichment during the first growing season. This result was most apparent in the 525 mu l l(-1) CO2 treatment and high soil N, which produced the greatest root volume as well. Shoot/root ratio decreased with increasing CO2 at the first harvest. After two growing seasons, elevated CO2 increased seedling diameter, shoot and root volume, and shoot and coarse root weight, again most prominently in high N. Unlike the initial results, however, stimulation of seedling growth by the 700 mu l l(-1) CO2 atmosphere exceeded that in 525 mu l l(-1) CO2 after two growing seasons, and shoot/root ratio was unaffected by either CO2 or N. At both harvests, seedlings grown in the enriched atmospheres generally had higher mycorrhizal counts and greater percentages of colonized root length, but differences among treatments in ectomycorrhizal development were nonsignificant regardless of quantification method. During the imposed drought episode, xylem water potential of seedlings grown in elevated CO2 descended below that of seedlings grown in the ambient atmosphere as soil water potential decreased, most notably in the predawn measurements. These results suggest that CO2 enrichment stimulates shoot and root growth of juvenile ponderosa pine under field conditions, a response somewhat dependent on soil N availability. However, below-ground growth is not increased proportionally more than that above ground, which may predispose this species to greater stress when soil water is limited. (C) 1998 Elsevier Science B.V.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, MYCORRHIZAL COLONIZATION, NUTRIENT STATUS, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, TAEDA

2506

Walker, R.F., D.W. Johnson, D.R. Geisinger, and J.T. Ball. 1998. Growth and ectomycorrhizal colonization of ponderosa pine seedlings supplied different levels of atmospheric CO2 and soil N and P. *Forest Ecology and Management 109(1-3):9-20.*

Individual and interactive effects of atmospheric CO2 enrichment and soil N and P fertility on above- and below- ground growth and mycorrhizal colonization of juvenile ponderosa pine (Pinus ponderosa Dougl. ex Laws.) were examined. Seedlings were grown from seed in atmospheres with 700 mu 11(- 1), 525 mu 11(-1), or ambient CO2 concentrations. High and low soil N treatments were created by adding sufficient (NH4)(2)SO4 to an infertile soil mixture to establish total N concentrations of 500 mu g g(-1) and 400 mu g g(-1) respectively, while high and low P treatments consisted of 68 mu g g(-1) and 43 mu g g(-1) concentrations, respectively, of extractable P created by additions of CaHPO4. All seedlings were inoculated with the mycobiont Pisolithus tinctorius (Pers.) Coker and Couch shortly after emergence. Three whole- seedling harvests at four month intervals permitted assessment of treatment effects on shoot and root growth and ectomycorrhizal development. Initially, 525 mu 11(-1) CO2 and high N and P were all influential factors in aboveground growth, with each of these treatments increasing shoot weight while the latter increased height, diameter and volume. Stimulation of root growth was evident in dry weight and length measurements at the first harvest, with N and P main treatment effects again evident, but the response to elevated CO2 was most pronounced in the 700 mu 11(-1) atmosphere. After eight months, soil P was of little consequence above- or below- ground, but high N increased shoot dimensions, volume, and weight and root weight and length. Furthermore, the 525 mu 11(- 1) CO2 treatment emerged as the dominant stimulatory atmosphere both above- and belowground, as seedlings grown in intermediate CO2 exhibited the largest shoot diameters, greatest shoot and root weights, and the longest root systems at the second harvest. At the final harvest, interactive effects of 525 mu 11(-1) CO2 and high N were prominent, as this treatment combination produced the largest shoot dimensions, volume and weight, and the greatest root volume and coarse and fine root weights. Intermediate CO2 also produced the longest root systems after 12 months. Shoot/root ratios were lowered by growth in 700 mu 11(-1) CO2 after four months and by both enriched atmospheres after eight months, but this effect was no longer evident at the final harvest. Greater numbers of mycorrhizae were formed by seedlings grown in 700 mu 11(-1) CO2 after four months and by those grown in 525 mu 11(-1) CO2 after eight months. Both enriched atmospheres increased mycorrhizal counts after 12 months, and seedlings grown in high CO2 and low N exhibited the highest percentage of total root system length colonized at the final harvest as well. Overall, these results indicate that CO2 enrichment stimulates shoot and root growth of juvenile ponderosa pine, a response dependent on soil N rather than P availability, and that the magnitude of the growth increase is greater in 1.5 x ambient than in 2 x ambient CO2. (C) 1998 Elsevier Science B.V.

KEYWORDS: ANATOMY, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, MYCORRHIZAL COLONIZATION, NUTRIENT STATUS, PHOSPHORUS, QUERCUS-ALBA, RESPONSES, RHIZOSPHERE, WATER-USE

2507

Walklate, P.J., Z.G. Xu, and A.R. McLeod. 1996. A new gas injection method to enhance spatial utilization within a free-air CO2 enrichment (FACE) system. *Global Change Biology 2(1):75-78.*

Visual observations of smoke dispersion in a wind tunnel and a computational fluid dynamics (CFD) model were used to evaluate methods of improving the performance of Free-Air CO2 Enrichment (FACE) Systems for field studies of the effects of elevated CO2 on vegetation. A special baffle, named an Enhanced Local Mixing (ELM) system, was observed to increase the turbulence and consequent dilution of fumigant gas in the atmosphere. Modelling results suggest that the ELM design reduces the spatial variation of fumigant gas concentration in small experimental plots. The potential reduction in CO2 use and costs warrants further evaluation under field conditions.

2508

Wall, G.W., J.S. Amthor, and B.A. Kimball. 1994. Cotco2 - a cotton growth simulation-model for global change. *Agricultural and Forest Meteorology 70(1-4):289-342.*

In conjunction with the Free-Air-CO2-Enrichment (FACE) project, a new, physiologically based, mechanistic, modular simulation model of cotton (Gossypium hirsutum L.) physiology, growth, development, yield and water use has been constructed. It is named COTCO2 for cotton response to atmospheric CO2 concentration. The model is capable of predicting cotton crop responses to elevated atmospheric CO2 concentrations and potential concomitant changing climate variables. The major plant processes known to be influenced by CO2 are simulated explicitly, i.e. photosynthesis, photorespiration, and stomatal conductance, and its role in leaf energy balance. The model explicitly simulates the impact of atmospheric CO2 concentration on C3 photosynthesis and photorespiration at the level of carboxylation and oxygenation. Growth is simulated for individual organs, i.e. leaf blade, stem segment, taproot and lateral roots, and fruit which includes squares and bolls. Potential growth is calculated and the carbohydrate and nitrogen required to meet this potential are calculated. Actual growth is

based on substrate availability, the potential growth, and water stress. Our intent here is to describe the overall structure of the model, its present status, and future development plans. Further development, documentation, calibration, and validation of the model is in progress. The long range goal of the project is to provide quantitative estimates of global cotton production in a future higher-CO2 world.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, C-4 PLANTS, CLIMATE CHANGE, ELEVATED CO2, GOSSYPIUM HIRSUTUM L, INTACT LEAVES, LEAF GROWTH, QUANTUM YIELD, STOMATAL CONDUCTANCE, WATER-USE

2509

Wallick, K., and T.M. Zinnen. 1990. Basil chlorosis - a physiological disorder in CO2-enriched atmospheres. *Plant Disease 74(2):171-173.*

2510

Wand, S.J.E., G.F. Midgley, M.H. Jones, and P.S. Curtis. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO2 concentration: a meta-analytic test of current theories and perceptions. *Global Change Biology 5(6):723-741.*

C4 plants contribute approximate to 20% of global gross primary productivity, and uncertainties regarding their responses to rising atmospheric CO2 concentrations may limit predictions of future global change impacts on C4-dominated ecosystems. These uncertainties have not yet been considered rigorously due to expectations of C4 low responsiveness based on photosynthetic theory and early experiments. We carried out a literature review (1980-97) and meta-analysis in order to identify emerging patterns of C4 grass responses to elevated CO2, as compared with those of C3 grasses. The focus was on nondomesticated Poaceae alone, to the exclusion of C4 dicotyledonous and C4 crop species. This provides a clear test, controlled for genotypic variability at family level, of differences between the CO2-responsiveness of these functional types. Eleven responses were considered, ranging from physiological behaviour at the leaf level to carbon allocation patterns at the whole plant level. Results were also assessed in the context of environmental stress conditions (light, temperature, water and nutrient stress), and experimental growing conditions (pot size, experimental duration and fumigation method). Both C4 and C3 species increased total biomass significantly in elevated CO2, by 33% and 44%, respectively. Differing tendencies between types in shoot structural response were revealed: C3 species showed a greater increase in tillering, whereas C4 species showed a greater increase in leaf area in elevated CO2. At the leaf level, significant stomatal closure and increased leaf water use efficiency were confirmed in both types, and higher carbon assimilation rates were found in both C3 and C4 species (33% and 25%, respectively). Environmental stress did not alter the C4 CO2-response, except for the loss of a significant positive CO2-response for above-ground biomass and leaf area under water stress. In C3 species, stimulation of carbon assimilation rate was reduced by stress (overall), and nutrient stress tended to reduce the mean biomass response to elevated CO2. Leaf carbohydrate status increased and leaf nitrogen concentration decreased significantly in elevated CO2 only in C3 species. We conclude that the relative responses of the C4 and C3 photosynthetic types to elevated CO2 concur only to some extent with expectations based on photosynthetic theory. The significant positive responses of C4 grass species at both the leaf and the whole plant level demand a re-evaluation of the assumption of low responsiveness in C4 plants at both levels, and not only with regard to water relations. The combined shoot structural and water use efficiency responses of these functional types will have consequential implications for the water balance of important catchments and range lands throughout the world, especially in semiarid subtropical and temperate regions. It may be premature to predict that C4 grass species will lose their competitive advantage over C3 grass species in elevated CO2.

KEYWORDS: BOUTELOUA-GRACILIS C-4, BUNDLE SHEATH-CELLS, CARBON-DIOXIDE CONCENTRATIONS, LEAF GAS-EXCHANGE, OLD- FIELD PERENNIALS, OPEN-TOP CHAMBERS, PASCOPYRUM-SMITHII C-3, SOURCE-SINK RELATIONS, UV-B RADIATION, WATER-USE

2511

Wand, S.J.E., G.F. Midgley, and C.F. Musil. 1996. Growth, phenology and reproduction of an arid-environment winter ephemeral Dimorphotheca pluvialis in response to combined increases in CO2 and UV-B radiation. *Environmental Pollution 94(3):247-254.*

The winter ephemeral Dimorphotheca pluvialis was grown in open- top chambers in ambient or elevated CO2 (350 or 650 mu mol mol(-1)), combined with ambient (2.39 to 7.59 kJ m(-2) d(-1)) or increased (4.94 to 11.13 kJ m(-2) d(-1)) UV-B radiation. Net CO2 assimilation rate and leaf water use efficiency increased in elevated CO2, but increased UV-B did not affect gas exchange. Leaf biomass was greater under increased UV-B, but vegetative biomass was unaffected in elevated CO2. initiation of reproduction was delayed, and proportional investment in reproductive biomass at harvest was reduced in elevated CO2. increased UV-B stimulated reproduction, particularly in ambient CO2, but also in elevated CO2 at a later stage. Changes in reproductive phenology and prolonged development in elevated CO2 during the stressful late season could indirectly be detrimental to reproductive success of D. pluvialis, but stimulation of reproduction by enhanced UV-B may to some extent mitigate this. (C) 1997 Elsevier Science Ltd.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, DENSITY, ELEVATED CO2, ENRICHMENT, NAMAQUALAND, PHARBITIS, PHOTOSYNTHESIS, PLANTS, VEGETATION

2512

Wand, S.J.E., G.F. Midgley, and C.F. Musil. 1996. Physiological and growth responses of two African species, Acacia karroo and Themeda triandra, to combined increases in CO2 and UV-B radiation. *Physiologia Plantarum 98(4):882-890.*

The interactive effects of increased carbon dioxide (CO2) concentration and ultraviolet-B (UV-B, 280-320 nm) radiation on Acacia karroo Hayne, a C-3 tree, and Themeda triandra Forsk., a C-4 grass, were investigated. We tested the hypothesis that A. karroo would show greater CO2-induced growth stimulation than T. triandra, which would partially explain current encroachment of A. karroo into C-4 grasslands, but that increased UV-B could mitigate this advantage. Seedlings were grown in open-top chambers in a greenhouse in ambient (360 mu mol mol(-1)) and elevated (650 mu mol mol(-1)) CO2, combined with ambient (1.56 to 8.66 kJ m(-2) day(-1)) or increased (2.22 to 11.93 kJ m(-2) day(-1)) biologically effective (weighted) UV-B irradiances. After 30 weeks, elevated CO2 had no effect on biomass of A. karroo, despite increased net CO2 assimilation rates. Interaction between UV-B and CO2 on stomatal conductance was found, with conductances decreasing only where elevated CO2 and UV-B were supplied separately. Increases in water use efficiencies, foliar starch concentrations, root nodule numbers and total nodule mass were measured in elevated CO2. Elevated UV-B caused only an increase in foliar carbon concentrations. In T. triandra, net CO2 assimilation rates were unaffected in elevated CO2, but stomatal conductances and foliar nitrogen concentrations decreased, and water use efficiencies increased. Biomass of all vegetative fractions, particularly leaf sheaths, was increased in elevated CO2, and was accompanied by increased leaf blade lengths and individual leaf and leaf sheath masses. However, tiller numbers were reduced in elevated CO2. Significantly moderating effects of elevated UV-B were apparent only in individual masses of leaf blades and sheaths, and in total sheath and

shoot biomass. The direct CO2-induced growth responses of the species therefore do not support the hypothesis of CO2-driven woody encroachment of C-4 grasslands. Rather, differential changes in resource use efficiency between grass and woody species, or morphological responses of grass species, could alter the competitive balance. Increased UV-B radiation is unlikely to substantially alter the CO2 response of these species.

KEYWORDS: ATMOSPHERIC CO2, C-4, CARBON DIOXIDE, ELEVATED CO2, ENHANCEMENT, ENRICHMENT, GRASSLAND, NODULATION, PHOTOSYNTHETIC ACCLIMATION, PLANT-PLANT INTERACTIONS

2513

Wang, B., and K. Adachi. 1999. Methane production in a flooded soil in response to elevated atmospheric carbon dioxide concentrations. *Biology and Fertility of Soils 29(2):218-220.*

CH4 production in a flooded soil as affected by elevated atmospheric CO2 was quantified in a laboratory incubation study. CH4 production in the flooded soil increased by 19.6%, 28.2%, and 33.4% after a 2-week incubation and by 38.2%, 62.4%, and 43.0% after a 3-week incubation under atmospheres of 498, 820, and 1050 mu l l(-1) CO2, respectively, over that in soil under the ambient CO2 concentration. CH4 production in slurry under 690, 920, and 1150 mu l l(-1) CO2 increased by 2.7%, 5.5%, and 5.0%, respectively, after a 3-day incubation, and by 6.7%, 12.8%, and 5.4%, respectively, after a 6-day incubation over that in slurry under the ambient CO2 concentration. The increase in CH4 production in the soil slurry under elevated CO2 concentrations in a N-2 atmosphere was more pronounced than that under elevated CO2 concentrations in air. These data suggested that elevated atmospheric CO2 concentrations could promote methanogenic activity in flooded soil.

KEYWORDS: CO2, EMISSION, RICE

2514

Wang, D.L. 1999. Effect of elevated CO2 on CH4 emission. *Chinese Science Bulletin 44(13):1153-1157.*

Global CH4 emission may increase under CO2 enrichment condition, which is projected for the future. CO2 enrichment could affect CH4 emission in two ways: (i) Photosynthesis of plants that also include plants in rice paddies and natural wetlands will be stimulated under CO2 enrichment condition. CH4 emission rate may be increased due to the accumulation of more plant biomass, root exudes and soil organic matters. (ii) Combined with other global warming forces, CO2 enrichment may bring a change of atmospheric temperature and precipitation around the world. CH4 emission will also be changed with the variation of the area and distribution of rice paddies and natural wetlands.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, METHANE EMISSION, RESPONSES, RICE PADDIES

2515

Wang, K.Y. 1996. Apparent quantum yield in Scots pine after four years of exposure to elevated temperature and CO2. *Photosynthetica 32(3):339-353.*

The carbon-dioxide and temperature responses of the apparent quantum yield, alpha(A), were measured in a uniform, diffuse radiation field for two shoot age classes of Scots pine (Pinus sylvestris L.) that had been exposed to elevated CO2 and temperature for four years (1991-4) in open-top chambers. The treatments were (I) ambient temperature and CO2 concentration (ACT), (2) elevated temperature (ET), (3) elevated CO2 concentration (EC), and (4) elevated CO2 concentration and temperature (ECT). ET and ECT increased alpha(A) in the one- year-old shoots, but did not affect alpha(A) in the current- year shoots. When measured at the same partial pressure of CO2 and a leaf temperature of 20 degrees C, EC had no significant effect on alpha(A) in two shoot age classes. However, when the comparison was made between shoots grown in and measured in 35 Pa CO2 and those grown in and measured in 70 Pa CO2, EC and ECT led to a significant increase in alpha(A), by 22.4 and 24.5 %, respectively, for the current-year shoots and by 21.6 and 27.5 %, respectively, for one-year-old shoots. Furthermore, in the one-year-old shoots, ET and ECT led to relatively higher alpha(A) values at higher temperatures, but EC alone led to relatively lower values of alpha(A). In contrast, this effect was not significant in the current-year shoots. The differences in alpha(A) between different treatments and between the shoot age classes could be attributed separately to changes in the efficiency of radiant energy capture. The Kok effect was observed at all partial pressures of CO2 during measurements. However, with an increase in the partial pressure of CO2, a parallel decrease was observed in both the measured rate of dark respiration, R(D), and the regressed rate of dark respiration, R(r). This decrease occurred regardless of growth treatment and age class. Consequently, the ratio of R(r)/R(D) was nearly identical in all treatments and age classes having a mean of 0.69.

KEYWORDS: ABIES L KARST, CARBON DIOXIDE, DARK RESPIRATION, DIFFERENT AGES, LIGHT-RESPONSE, LONG-TERM EXPOSURE, NET PHOTOSYNTHESIS, NORWAY SPRUCE, OPEN-TOP CHAMBERS, PHOTOSYNTHETIC RESPONSE

2516

Wang, K.Y. 1996. Canopy CO2 exchange of Scots pine and its seasonal variation after four-year exposure to elevated CO2 and temperature. *Agricultural and Forest Meteorology 82(1-4):1-27.*

Single Scots pines (Pinus sylvestris L.), aged 20-25 years, have been grown in open-topped chambers with elevated temperature (during winter and summer, the mean temperature was 5-20 degrees C and 2 degrees C above the outside ambient temperature, respectively), elevated CO2 (550-600 mu mol mol(- 1) from 15 April to 15 September) and a combination of elevated temperature and CO2 for four years. The vertical and seasonal variations of key physiological parameters concerning photosynthesis and stomatal conductance were measured. The annual canopy photosynthesis and respiration were predicted by using a multilayer model in which the profile of the canopy properties and the microclimate data through a whole year (1994) were used as inputs to the model. The results indicate that during the main growing season (day number 121 to 243), the elevated CO2 increased the maximum apparent quantum yield by 24% and the mean light-saturated rate of assimilation by 41%, and decreased the mean light-saturated stomatal conductance by 13%. However, elevated temperature had no significant effect on these parameters. During early spring and late autumn, elevated temperature increased significantly the apparent quantum yield, the light-saturated rate of assimilation and stomatal conductance. The predicted annual net photosynthesis increased by 40% for elevated CO2 alone, by 58% for elevated CO2 and temperature, and by 10% for elevated temperature alone. The annual sum of respiration increased by 39% for elevated temperature alone and by 29% for elevated CO2 and temperature. Elevated CO2 alone caused a depression of 7% in the annual respiration. Seasonal variations of the CO2-exchange rate between treatments were evident, and they can be largely attributed to changes in the apparent quantum yield, the light-saturated rate of assimilation, leaf area index, and the ability to adapt to environmental stress conditions.

KEYWORDS: C-3, DECIDUOUS FOREST, LEAF NITROGEN, LEAVES, MIDDAY STOMATAL CLOSURE, MODEL, PHOTOSYNTHETIC ACCLIMATION, QUANTUM YIELDS, SCALING

CARBON-DIOXIDE, WATER-VAPOR EXCHANGE

2517

Wang, K.Y., and S. Kellomaki. 1997. Effects of elevated CO2 and soil-nitrogen supply on chlorophyll fluorescence and gas exchange in Scots pine, based on a branch- in-bag experiment. *New Phytologist 136(2):277-286.*

Applying the branch-in-bag method, naturally seeded Scots pine (Pinus sylvestris L.) trees, 25-30 yr old, were subjected to two CO2 concentrations (350 and 700 mu mol mol(-1)) and two soil-nitrogen-supply regimes for three growing seasons (1994- 96). Gas exchange and chlorophyll a fluorescence in detached shoots were measured simultaneously in a diffuse radiation field. Elevated CO2 did not lead to a significant 'downward regulation' in the light-saturated rate of net photosynthesis (P-n.max), the maximum apparent quantum yield (alpha(A.max)) or the maximum photochemical efficiency (F-v/F-m) of photosystem II (PS II). However, the elevated CO2 significantly decreased the light-saturated stomatal conductance and increased the sensitivity of stomatal conductance to change in low photon- flux densities. The high soil-nitrogen supply significantly increased photosynthetic capacity, as manifested by increases in P-n.max, alpha(A.max), F-v/F-m, and the effective photochemical efficiency (Delta F/F'(m)) at low photon-flux densities, did not, on the other hand, enhance the magnitude of photosynthetic response to elevated CO2 concentration. In addition, the treatment-induced modifications in fluorescence parameters are discussed in detail.

KEYWORDS: BETULA-PENDULA ROTH, CARBON DIOXIDE, ENHANCEMENT, ENRICHMENT, GROWTH, PHOTOSYNTHESIS, PLANTS, RESPONSES, SEEDLINGS, TEMPERATURE

2518

Wang, K.Y., and S. Kellomaki. 1997. Stomatal conductance and transpiration in shoots of Scots pine after 4-year exposure to elevated CO2 and temperature. *Canadian Journal of Botany-Revue Canadienne De Botanique 75(4):552-561.*

Single Scots pines (Pinus sylvestris L.) trees were subjected to elevated temperature (year-round elevation), elevated CO2 (elevation from April 15 to September 15), and a combination of elevated temperature and CO2 for 4 years in open-topped chambers. Measurements and modelling were performed to determine if long-term growth at elevated CO2 concentration and temperature altered water use efficiency (W-e) and the responses of stomatal conductance (g(s)) to photon flux density (Q(p)), the leaf-to-air vapour pressure difference (D-v), leaf temperature (T-l), and intercellular concentration of CO2 (C- i). Long-term elevation of CO2 led to a significant decline in the absolute value of g(s) at almost all levels of Q(p), D-v, C-i and T-l. Elevated temperature treatment increased the absolute value of g(s) only at higher D-v and T-l. The effect of the combination of elevated CO2 and temperature did not appear as a mean of the effects of the two single factors, while there was an interaction between the two factors. The modifications in the sensitivity of stomata, resulting from different treatments, did not have the same pattern as the change in g(s), but depended on levels of Q(p), D-v, and T-l. Compared with the control treatment, elevated concentration of CO2 or a combination of elevated CO2 and temperature led, on average, to 50 and 30% increases in W-E, respectively, which can be attributed mainly to an increase in the rate of net assimilation. In contrast, elevated temperature alone did not significantly change W-E, although transpiration rate was increased.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GAS-EXCHANGE, HUMIDITY, LIGHT, PHOTOSYNTHETIC RESPONSE, SITCHENSIS BONG CARR, SITKA SPRUCE, VAPOR-PRESSURE, WATER-USE EFFICIENCY

2519

Wang, K.Y., S. Kellomaki, and K. Laitinen. 1995. Effects of needle age, long-term temperature and co2 treatments on the photosynthesis of scots pine. *Tree Physiology 15(4):211-218.*

Naturally regenerated 20-25-year-old Scots pine (Pinus sylvestris L.) trees were grown in open-top chambers in the presence of an elevated temperature or CO2 concentration, or both. The elevated temperature treatment was administered year- round for 3 years. The CO2 treatment was applied between April 15 and September 15 for 2 years. The photosynthetic responses of 1- and 2-year-old needles to varying photon flux densities (0-1500 mu mol m(-2) s(-1)) and CO2 concentrations (350, 700 and 1400 mu mol mol(-1)) during measurement were determined. The CO2 treatment alone increased maximum photosynthetic rate and light-use efficiency, but decreased dark respiration rate, light compensation and light saturation regardless of needle age. In contrast, the temperature treatment decreased maximum photosynthetic rate and photosynthetic efficiency, but increased dark respiration rate, light compensation and light saturation. The aging of needles affected the photosynthetic performance of the shoots; values of all parameters except photosynthetic efficiency were less in 2- than in I-year-old needles. The CO2 treatment decreased and the temperature treatment enhanced the reduction in maximum photosynthesis due to needle aging.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE CONCENTRATION, DIRECT-RADIATION, ELEVATED CO2, GAS-EXCHANGE, GROWTH, LEAVES, RESPIRATION, RESPONSES, SHOOT

2520

Wang, K.Y., S. Kellomaki, and K. Laitinen. 1996. Acclimation of photosynthetic parameters in Scots pine after three years exposure to elevated temperature and CO2. *Agricultural and Forest Meteorology 82(1-4):195-217.*

Single Scots pine (Pinus sylvestris L.) was subjected to elevated temperature (year-round elevation), elevated CO2 (elevation from April 15 to September 15) and a combination of elevated temperature and CO2 for three years in open-topped chambers. Using the data obtained from field measurements of gas exchange, Farquhar and von Caemmerer's basic equations for photosynthesis of C-3 plants were parameterized. The values of the estimated parameters at five ranges of leaf-temperature for trees growing in four different environments are presented and discussed. The estimates of the parameters show that Scots pine grown at elevated CO2 or elevated temperature, compared to those grown in the ambient conditions, did not show significant decreases in the maximum RuP2 (ribulose-1,5-bisphosphate) saturated rate of carboxylation, V-cmax, the maximum rate of electron transport, J(max) and the 'day respiration rate', R(d), within a given range of measuring temperatures (5-25 degrees C). But at high measuring temperature (> 30 degrees C), the elevated CO2 treatment significantly decreased V(cmax) and J(max) whereas the elevated temperature or the combination of CO2 and temperature significantly increased V-cmax and J(max). Furthermore, elevated CO, led to a slight leftward drift of the whole temperature-response curves for V-cmax and J(max); while elevated temperature or the combination of CO2 and temperature led a slight rightward drift of the curves. The model computations show that given a constant intercellular CO2 concentration, C-i (230 or 540 mu mol mol(-1)), there are no significant differences in the maximum rates of assimilation among treatments; when C-i was doubled, the maximum rate of assimilation increased by 28%-34% with no significant differences among treatments.

KEYWORDS: CARBON DIOXIDE, EUCALYPTUS-PAUCIFLORA, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, NET

PHOTOSYNTHESIS, PLANT GROWTH, QUANTUM YIELD, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SCIRPUS- OLNEYI

2521

Wang, N., and P.S. Nobel. 1996. Doubling the CO2 concentration enhanced the activity of carbohydrate-metabolism enzymes, source carbohydrate production, photoassimilate transport, and sink strength for Opuntia ficus-indica. *Plant Physiology 110(3):893-902.*

After exposure to a doubled CO2 concentration of 750 mu mol mol(-1) air for about 3 months, glucose and starch in the chlorenchyma of basal cladodes of Opuntia ficus-indica increased 175 and 57%, respectively, compared with the current CO2 concentration of 370 mu mol mol(-1), but sucrose content was virtually unaffected. Doubling the CO2 concentration increased the nocturnal malate production in basal cladodes by 75%, inorganic phosphate (Pi) by 32%, soluble starch synthase activity by 30%, and sucrose-Pi synthase activity by 146%, but did not affect the activity of hexokinase. Doubling CO2 accelerated phloem transport of sucrose out of the basal cladodes, resulting in a 73% higher dry weight for the daughter cladodes. Doubling CO2 increased the glucose content in 14-d- old daughter cladodes by 167%, increased nocturnal malate production by 22%, decreased total amino acid content by 61%, and increased soluble starch synthase activity by 30% and sucrose synthase activity by 62%. No downward acclimation of photosynthesis during long-term exposure to elevated CO2 concentrations occurs for O. ficus-indica (M. Cui, P.M. Miller, P.S. Nobel [1993] Plant Physiol 103: 519-524; P.S. Nobel, A.A. Israel [1994] J Exp Bot 45: 295-303), consistent with its higher source capacity and sink strength than under current CO2. These changes apparently do not result in Pi limitation of photosynthesis or suppression of genes governing photosynthesis for this perennial Crassulacean acid metabolism species, as occur for some annual crops.

KEYWORDS: ACCLIMATION, ELEVATED CO2, HIGH ATMOSPHERIC CO2, LEAVES, PHOTOSYNTHESIS, PLANT, STARCH, SUCROSE PHOSPHATE SYNTHASE, SUGAR, WHEAT ENDOSPERM

2522

Wang, X.F., S.Y. Li, K.Z. Bai, and T.Y. Kuang. 1998. Influence of doubled CO2 on plant growth and soil microbial biomass C and N. *Acta Botanica Sinica 40(12):1169-1172.*

Salix babylonica L. Triticum aestivum L. Chenopodium album L. and Amaranthus cruentus L. were grown in the N-deficient soil in open-top chambers blown with ambient or doubled ambient CO2 air, and their growth was measured. Soil samples were collected to assess the influence of doubled CO2 on the soil microbial biomass C (C-mic) and N (N-mic). Results showed that the biomass of shoot and root was increased by doubled CO2 in the four species of plants. Doubled CO2 increased C-mic in S. babylonica and decreased C-mic in T. aestivum and C. album. On the other hand, N-mic in three species except T. aestivum was stimulated by doubled CO2. Doubled CO2 had no significant effect on C-mic in A. cruentus and N-mic in T. aestivum. However, the ratios of C-mic- to -N-mic of all four species were consistently declined under doubled CO2 treatment. It implies that CO2 enrichment may have positive influence on the quality of organic matter of N-low soil in global change.

KEYWORDS: CHLOROFORM FUMIGATION, EXTRACTION METHOD, NITROGEN, RELEASE, RESPONSES

2523

Wang, Y.P., A. Rey, and P.G. Jarvis. 1998. Carbon balance of young birch trees grown in ambient and elevated atmospheric CO2 concentrations. *Global Change Biology 4(8):797-807.*

We constructed a carbon budget for young birch trees grown in ambient and elevated CO2 concentrations over their fourth year of growth. The annual total of net leaf photosynthesis was 110% more in elevated CO2 than in ambient CO2. However, the trees in elevated COP grew only 59% more biomass than the trees in ambient COP over the year. Modelling studies showed that larger loss of carbon from fine-root production and growth of the root-associated mycorrhiza by the trees in elevated CO2 probably accounted for all the remaining difference in net photosynthesis between the two treatments. Our modelling also showed that the fraction of net photosynthate consumed by respiration of nonleaf tissue was similar in the two CO2 treatments, and was 26% and 24% for trees in ambient and elevated CO2, respectively. Trees in elevated CO2 had 43% more leaves, and produced 110% more net photosynthate than trees in ambient CO2, even though the maximum rate of carboxylation per unit leaf nitrogen decreased by 21%. Sensitivity studies showed that down-regulation reduced the annual net photosynthetic production of the trees in elevated CO2 by only 6%. Direct effects of higher CO2 on photosynthesis and greater leaf area of the trees in elevated CO2 increased the net photosynthesis of the trees by 68% and 60%, respectively; and together accounted for most of the difference in net photosynthesis between the two treatments.

KEYWORDS: CYCLE, DIOXIDE, ENRICHMENT, FORESTS, GAS-EXCHANGE, LEAVES, MAINTENANCE, MODEL, PHOTOSYNTHESIS, PLANTS

2524

Wang, Y.Q., H.J. Zhang, D. Yang, K.Z. Bai, and T.Y. Kuang. 1998. Fractal analysis for root growth of plant seedlings under doubled CO2 concentration. *Chinese Science Bulletin 43(22):1891-1893.*

Fractal geometry was applied and box dimension was used as an indicator to analyze the effects of doubled CO2 concentration on the root growth of plant seedlings. Results showed that doubled CO2 concentration displayed different effects on root branching characteristics of C-3 and C-4 plants. There was an obvious increase of root branches in spring wheat while there were no significant effects on roots of sweet sorghum, In different soil layers, root branching of spring wheat was stimulated and this promotion was most significant in the second layer (10-20 cm), which denoted that elevated CO2 altered the root branching pattern. That means higher CO2 concentration influences not only root growth but also its differentiation and development.

2525

Wang, Y.X., and G.M. Shpeyzer. 1997. Genesis of thermal groundwaters from Siping'an district, China. *Applied Geochemistry 12(4):437-445.*

Thermal groundwaters (40-52 degrees C, pH = 7.4-7.8, Eh = 210- 245 mV) from Siping' an district, Shanxi Province, northwestern China, are hydrogeochemically unique. Their occurrence is controlled by faulted structures in Precambrian host rocks. Their hydrochemical type (5 springs and 2 wells) is mainly Cl- SO4-Na, with TDS values around 1.0 g/l. Some minor elements such as Si, Pr, Sr, and Li, as well as neutral and acid bituminous substances are so enriched that the thermal waters can also be regarded as mineral waters. Their origin is meteoric, as indicated by 3 lines of geochemical evidence: (1) their delta D and delta(18)O compositions are very close to the Craig meteoric line; (2) their dissolved gas compositions are N-2-dominated, with less O-2 and CO2; and (3) the He-3/He-4 ratios are low (0.028). Geochemical processes responsible for the genesis of the hydrochemical features of the waters include dissolution, mixing, and oxidation. The most

important water- rock interaction is dissolution or hydrolysis of alumino-silicate minerals in the magmatic and metamorphic host rocks, since the waters are still undersaturated with respect to albite, anorthite, K-spar, and chlorite, as shown by saturation indices. The tritium contents of some thermal waters (46-53 TU), higher than the tritium concentration of local meteoric water, result from the mixing of thermal waters with cold, shallow-lying groundwaters that are from the 1960s. The predominant species of Fe in the thermal waters is Fe(OH)(3), as a result of oxidation processes under aerobic conditions of the aquifers. (C) 1997 Elsevier Science Ltd.

2526

Wang, Z.M., M.J. Lechowicz, and C. Potvin. 1994. Early selection of black spruce seedlings and global change - which genotypes should we favor. *Ecological Applications 4(3):604-616.*

We investigated the effects of both soil fertility and predicted changes in climate on the performance of different families of black spruce, Picea mariana (Mill.) B.S.P., during the first growing season. The results were used to examine whether reforestation programs should consider changing their preferred family lines in anticipation of altered performance given global climate change. We grew seedlings of 16 open- pollinated maternal families of black spruce under phytotron conditions simulating present and mid-21 st century climatic conditions during the growing season. The realistic, simulated future climate included both elevated CO2 levels and seasonally appropriate increases in mean daily temperature. To explore the dependence of climatic responses on site quality, seedlings were irrigated with solutions having either 5 or 100 mg/L of nitrogen. The lower nitrogen level represents a poor site for black spruce growth and survival, but the higher level provides ample nitrogen. We also recorded seed size for each seedling to evaluate the degree to which maternal investments might buffer responses to future climate and fertility during the first year on the seedbed. Seedling survival and growth increased both under the future climate regime and with nitrogen fertilization. The two factors interacted synergistically, with nitrogen enrichment significantly enhancing the positive effects of the future climate regime. Nitrogen-poor conditions, however, did not preclude a positive seedling response to the future climate. Our results indicate that seedling survival and height growth are highly dependent upon initial seed mass: larger seeds produced more vigorous 1 st-yr seedlings. The families differed in seed mass, seed germination, and seedling survival and growth, but their relative performances did not vary significantly among the treatments. These results suggest that black spruce families selected for rapid growth under present conditions will also do well in the future, at least in terms of early establishment and performance on sites regenerated by seeding.

KEYWORDS: ATMOSPHERIC CO2 CONCENTRATIONS, BOREAL FORESTS, CLIMATE CHANGE, COASTAL DOUGLAS-FIR, ELEVATED CO2, GROWTH, PRODUCTIVITY, SEED WEIGHT, TEMPERATURE, TUSSOCK TUNDRA

2527

Wang, Z.M., M.J. Lechowicz, and C. Potvin. 1995. Responses of black spruce seedlings to simulated present versus future seedbed environments. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 25(4):545-554.*

We investigated the effects of nitrogen availability and present versus future atmospheric environments (i.e., climate) on the seedling performance of 16 open-pollinated maternal families of Picea mariana (Mill.) B.S.P. over two simulated growing seasons. Diurnal and seasonal patterns of temperature, relative humidity, photoperiod, and light intensity were simulated. The simulated future climate included both elevated CO2 and seasonally appropriate increases in mean monthly temperatures. Compared with the present, the future climate increased seedling survival, total and root dry mass, rate of winter bud development, net photosynthetic rate, and water and nitrogen use efficiencies; decreased needle nitrogen content; and altered biomass allocation patterns. Greater nitrogen availability greatly improved seedling performance and changed biomass allocation patterns. Climate and nitrogen level interacted synergistically to promote seedling growth (branch number and root dry mass), survival, and bud development. The future climate increased seedling survival, rate of bud development, and nitrogen use efficiency much more in the low than in the high nitrogen regime. Seedling performance in the second season was dependent on initial seed mass, but less than in the 1st year. Some of the differences among the families and in their interactions with the climate and (or) nitrogen fertilization suggest that families selected for rapid growth under present conditions may not do well in the future, at least in terms of early establishment. Forest managers and tree breeders should take this possibility into consideration in their tree improvement and reforestation programs.

KEYWORDS: AMERICA, ATMOSPHERIC CARBON-DIOXIDE, ECOSYSTEMS, ELEVATED CO2, GLOBAL CLIMATE-CHANGE, GROWTH, NITROGEN, PHOTOSYNTHESIS, PRODUCTIVITY, STRATEGIES

2528

Wang, Z., Q. Pan, and B. Quebedeaux. 1999. Carbon partitioning into sorbitol, sucrose, and starch in source and sink apple leaves as affected by elevated CO2. *Environmental and Experimental Botany 41(1):39-46.*

Experiments were conducted in controlled growth chambers to evaluate how increases in CO2 concentration ([CO2]) affected carbon metabolism and partitioning into sorbitol, sucrose, and starch in;various ages of apple leaves. Apple plants (Mabs domestica), 1 year old, were exposed to [CO2] of 200, 360, 700, 1000, and 1600 mu l 1(-1) up to 8 days. Six groups of leaves (counted from the shoot apex): leaves 1-5 (sink), 6-7 (sink to source transition): 8-9 (sink to source transition), 10-11 (nearly-matured source), 21-22 (mid-age source), and 30-32 (aged source), were sampled at 1, 2, 4, and 8 days after [CO2] treatments for carbohydrate analysis. Increases in [CO2] from a sub-ambient (200 mu l 1(-1)) to an ambient level (360 mu l 1(- 1)) significantly increased the concentrations of sorbitol, sucrose, glucose, and fructose tested in all ages of leaves. Continuous increase in [CO2] from ambient to super-ambient levels up to 1600 mu l 1(-1) also increased sorbitol concentration by approximate to 50% in source leaves, but not in sink and sink to source transition leaves. Increases in [CO2] from 360 to 1600 mu l 1(-1), however, had little effect on sucrose content in all ages of leaves. Starch concentrations increased in all ages of leaves as [CO2] increased. Rapid starch increases (e.g. 5-, 6-, 20-, and 50-fold increases for leaf groups 1-5, 6-7, 10-11, and 21-22, respectively) occurred from 700 to 1600 mu l 1(-1) [CO2] during which increases in sorbitol concentration either ceased or slowed down. Our results indicate that changes in carbohydrates were much more responsive to CO2 enrichment in source leaves than in sink and sink to source transition leaves. Carbon partitioning was favored into starch and sorbitol over sucrose in all ages of leaves when [CO2] was increased from 200 to 700 mu l 1(-1), and was favored into starch over sorbitol from 700 to 1600 mu l 1(- 1) [CO2].

KEYWORDS: METABOLISM

2529

Wangwacharakul, V., and R. Bowonwiwat. 1995. Economic evaluation of CO2 response options in the forestry sector: The case of Thailand. *Biomass & Bioenergy 8(5):293-307.*

Using the benefit-cost analysis approach, this paper attempts to evaluate

the potential of the forestry sector in Thailand to reduce carbon emissions of the country. Protecting conserved forests can avoid a substantial amount of carbon emission from deforestation, although certain costs are attached. Reforestation also enhances carbon sequestration and, in most cases, incurs no cost to society. Under the present government's commitment to fully protect the conserved forests and reforest the deforested areas in the country, Thailand could reduce the growth of carbon emission by as much as 260 million tons over the next two decades. The costs to society, if any, would be small given other, non-quantifiable, benefits of the forests.

2530

Ward, J.K., and B.R. Strain. 1997. Effects of low and elevated CO2 partial pressure on growth and reproduction of Arabidopsis thaliana from different elevations. *Plant, Cell and Environment 20(2):254-260.*

Atmospheric CO2 partial pressure may have been as low as 18 Pa during the Pleistocene and is expected to increase from 35 to 70 Pa before the end of the next century. Low CO2 reduces the growth and reproduction of C-3 plants, whereas elevated CO2 often increases growth and reproduction. Plants at high elevation are exposed to reduced CO2 partial pressure and may be better adapted to the low CO2 of the Pleistocene, me examined genotypes of Arabidopsis thaliana from different elevations for variation in growth and reproduction at the CO2 levels of the Pleistocene, the present and the future. Genotypes exhibited limited genetic variation in the response of the production of biomass to changes in CO2, but showed significant variation in reproductive characters. We found evidence that plants from high elevations may be better adapted to low CO2 when considering seed number, which is an important component of fitness. Genotypes showed greater variation in the response of seed number between 35 and 20 Pa CO2 compared to 35 and 70 Pa CO2. We conclude that present-day C-3 annuals may have greater potential for evolution in response to the low CO2 of the Pleistocene relative to the elevated CO2 predicted for the future.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2, C-4 ANNUALS, CARBON DIOXIDE, ENRICHMENT, HIGH- ALTITUDES, INTRASPECIFIC VARIATION, PHOTOSYNTHESIS, PLANTS, RESPONSES

2531

Ward, J.K., and B.R. Strain. 1999. Elevated CO2 studies: past, present and future. *Tree Physiology 19(4-5):211-220.*

Increasing concentrations of atmospheric CO2 are predicted to impact both current and future ecosystems. Elevated CO2 is also predicted to affect biological processes at many levels of organization. In this overview, we summarize the responses of plants to elevated CO2 including primary physiological and molecular responses, growth and reproductive responses, effects on plant-plant competition and interactions with other organisms, evolutionary responses, and effects at the ecosystem level. The objectives of this paper are to: (a) overview studies in this issue that were presented at a 1997 meeting entitled "Critical Assessment of the Response of Forest Ecosystems to Elevated Atmospheric Carbon Dioxide," which was sponsored by the Global Change and Terrestrial Ecosystems (GCTE) group of the International Geosphere Biosphere Program (IGBP), (b) review areas of recent progress in CO2 research, (c) generalize patterns arising from past research, and (d) list critical areas of research for the future.

KEYWORDS: ARABIDOPSIS-THALIANA, ATMOSPHERIC CO2, C-4 ANNUALS, CARBON-DIOXIDE ENRICHMENT, GAS-EXCHANGE, LONG-TERM ELEVATION, PINUS-TAEDA, QUANTUM YIELD, REPRODUCTIVE EFFORT, STOMATAL CONDUCTANCE

2532

Wardle, D.A., K.I. Bonner, G.M. Barker, G.W. Yeates, K.S. Nicholson, R.D. Bardgett, R.N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: Vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs 69(4):535-568.*

The consequences of permanent loss of species or species groups from plant communities are poorly understood, although there is increasing evidence that individual species effects are important in modifying ecosystem properties. We conducted a field experiment in a New Zealand perennial grassland ecosystem, creating artificial vegetation gaps and imposing manipulation treatments on the reestablishing vegetation. Treatments consisted of continual removal of different subsets or "functional groups" of the flora. We monitored vegetation and soil biotic and chemical properties over a 3-yr period. Plant competitive effects were clear: removal of the C-3 grass Lolium perenne L. enhanced vegetative cover, biomass, and species richness of both the C-4 grass and dicotyledonous weed functional groups and had either positive or negative effects on the legume Trifolium repens L., depending on season. Treatments significantly affected total plant cover and biomass; in particular, C-4 grass removal reduced total plant biomass in summer, because no other species had appropriate phenology. Removal of C-4 grasses reduced total root biomass and drastically enhanced overall shoot-to-root biomass ratios. Aboveground net primary productivity (NPP) was not strongly affected by any treatment, indicating strong compensatory effects between different functional components of the flora. Removing all plants often negatively affected three further trophic levels of the decomposer functional food web: microflora, microbe-feeding nematodes, and predaceous nematodes. However, as long as plants were present, we did not find strong effects of removal treatments, NPP, or plant biomass on these trophic groupings, which instead were most closely related to spatial variation in soil chemical properties across all trophic levels, soil N in particular. Larger decomposer organisms, i.e., Collembola and earthworms, were unresponsive to any factor other than removal of all plants, which reduced their populations. We also considered five functional components of the soil biota at finer taxonomic levels: three decomposer components (microflora, microbe-feeding nematodes, predaceous nematodes) and two herbivore groups (nematodes and arthropods). Taxa within these five groups responded to removal treatments, indicating that plant community composition has multitrophic effects at higher levels of taxonomic resolution. The principal ordination axes summarizing community-level data for different trophic groups in the soil food web were related to each other in several instances, but the plant ordination axes were only significantly related to those of the soil microfloral community. There were time lag effects, with ordination axes of soil-associated herbivorous arthropods and microbial-feeding nematodes being related to ordination axes representing plant community structure at earlier measurement dates. Taxonomic diversity of some soil organism groups was linked to plant removals or to plant diversity. For herbivorous arthropods, removal of C-4 grasses enhanced diversity; there were negative correlations between plant and arthropod diversity, presumably because of negative influences of C-4 species in the most diverse treatments. There was evidence of lag relationships between diversity of plants and that of the three decomposer groups, indicating multitrophic effects of altering plant diversity. Relatively small effects of plant removal on the decomposer food web were also apparent in soil processes regulated by this food web. Decomposition rates of substrates added to soils showed no relationship with treatment, and rates of CO2 evolution from the soil were only adversely affected when all plants were removed. Few plant functional-group effects on soil nutrient dynamics were identified. Although some treatments affected temporal variability (and thus stability) of soil biotic properties (particularly CO2 release) throughout the experiment, there was no evidence of destabilizing effects of plant removals. Our data provide evidence that permanent exclusion of plant species from the species pool can have important consequences for overall vegetation composition in addition to the direct effects of

vegetation removal, and various potential effects on both the above- and belowground subsystems. The nature of many of these effects is driven by which plant species are lost from the system, which depends on the various attributes or traits of these species.

KEYWORDS: ASPARAGUS CROPPING SYSTEMS, EXPLOITATION ECOSYSTEMS, FOOD-WEB, INDUCED RESPIRATION METHOD, MICROBIAL BIOMASS, NEMATODE COMMUNITIES, OLD-FIELD COMMUNITY, SPECIES-DIVERSITY, TROPHIC RELATIONSHIPS, WEED-MANAGEMENT STRATEGIES

2533

Wardle, D.A., H.A. Verhoef, and M. Clarholm. 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. *Global Change Biology 4(7):713-727.*

In this article, we evaluate how global environmental change may affect microfood-webs and trophic interactions in the soil, and the implications of this at the ecosystem level. First we outline how bottom-up (resource control) and top-down (predation-control) forces regulate food-web components. Food- web components can respond either positively or negatively to shifts in NPP resulting from global change, thus creating difficulties in developing general principles about the response of soil biota to global change phenomena. We also demonstrate that top-down effects can be important in soil food-webs, creating negative feed-backs which may partially counter bottom-up effects. Secondly we determine how soil food- webs and the processes they regulate respond to various global change phenomena. Enhanced atmospheric CO2 levels can have two main effects on plants which are relevant for the sail food- web, i.e. enhanced NPP (often positive) and diminished organic matter quality (with negative effects, at least in the short term). Climate change effects resulting from elevated CO2 levels may be mainly secondary through alteration of vegetation, as shown by examples. Intensification of land management is usually associated with greater disturbance, which alters soil food-web composition and key processes; this is particularly apparent in comparisons of conventionally tilled and nontilled agroecosystems. Global change involves shifts in plant species composition and diversity, possibly affecting soil food-webs; we interpret this in terms of theories relating biodiversity to ecosystem function. We conclude that a more detailed understanding of interactions between NPP, soil organic matter and components of the soil food-web, as well as their regulation of biogeochemical processes and ultimately ecosystem-level properties, is essential in better understanding longterm aspects of global change phenomena.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, DECOMPOSITION PROCESSES, ECOSYSTEM FUNCTION, ELEVATED ATMOSPHERIC CO2, FOOD-WEBS, LEAF LITTER, MICROBIAL BIOMASS, PLANT GROWTH, TALLGRASS PRAIRIE

2534

Warwick, K.R., G. Taylor, and H. Blum. 1998. Biomass and compositional changes occur in chalk grassland turves exposed to elevated CO2 for two seasons in FACE. *Global Change Biology 4(4):375-385.*

Artificial turves composed of 7 chalk grassland species (Festuca ovina L; Briza media L.; Bromopsis erecta (Hudson) Fourr.; Plantago media L; Sanguisorba minor Scop.; Anthyllis vulneraria L. and Lotus corniculatus L.) were grown from seed and exposed to two seasons of elevated (600 mu mol mol(-1)) and ambient (340 mu mol mol(-1)) CO2 concentrations in free air CO2 enrichment (ETH-FACE, Zurich). The turves were clipped regularly to a height of 5 cm and assessed for above ground biomass production and relative abundance based on accumulated clipped dry biomass as well as by point quadrat recording. Below ground biomass production was assessed with root in- growth bags during the second season of growth. Increases in total biomass (> 30%) were noted in elevated CO2, but the differences did not become significant until the second season of growth. Individual species' biomass varied in response to elevated CO2, with significant increases in biomass in elevated CO2 turves for both legume species, and no significant CO2 effect on S. minor or P. media. An initial positive CO2 effect on biomass of combined grass species was reversed by the end of the experiment with less biomass and a significantly smaller proportion of total biomass present in elevated CO2, which was attributed primarily to changes in proportion of F. ovina. Species relative abundance was significantly affected by elevated CO2 in the final 4 of the 6 clip events, with the legume species increasing in proportion at the expense of the other species, particularly the grasses. Root length and dry weight were both significantly increased in elevated CO2 (77% and 89%, respectively), and these increases were greater than increases in shoot biomass (36%) from the same period. Species responses to elevated CO2, within the model community, were not consistent with predictions made from data on individual species, leading to the conclusion that responses to elevated CO2, at the community level, and species within the community level, are the result of direct physiological effects and indirect competitive effects. These conclusions are discussed with respect to the ecological responses of natural communities, and the chalk grassland community in particular, to elevated CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, COMMUNITY, ENRICHMENT, GAS-EXCHANGE, NATIVE HERBS, PLANT GROWTH, RESPONSES, ROOT-GROWTH, VEGETATION

2535

Watada, A.E., N.P. Ko, and D.A. Minott. 1996. Factors affecting quality of fresh-cut horticultural products. *Postharvest Biology and Technology 9(2):115-125.*

Fresh-cut products, also known as lightly or minimally processed products, are highly perishable because a large proportion of their surface area is without epidermis, the outer protective layer of tissue. Temperature, atmosphere, relative humidity and sanitation must be regulated to maintain quality of fresh-cuts. In the 0-10 degrees C range, Q(10) of respiration rates ranged from 2.0 to 8.6 among various fresh-cut fruits and vegetables. Low Oz and elevated CO2 atmosphere reduced the respiration rate; however, the respiratory quotient approached 3.0 with some fresh-cuts. Film bags or coatings are necessary to maintain high relative humidity. Microorganisms were present in chlorine-washed spinach, and populations increased during storage. Stress from the physical action of processing and low O-2 atmosphere affects physiology and biochemistry of the fresh-cuts, which can affect quality and shelf-life. Research in all of these areas is needed to ensure that wholesome, high-quality fresh-cut products are marketed to consumers.

KEYWORDS: ATMOSPHERE, CHLOROPHYLL, DEGRADATION, FILM, LIGHTLY PROCESSED FRUITS, PERMEABILITY, SHREDDED CARROTS, STORAGE, TEMPERATURE, VEGETABLES

2536

Watanabe, Y., N. Ohmura, and H. Saiki. 1992. Isolation and determination of cultural-characteristics of microalgae which functions under co2 enriched atmosphere. *Energy Conversion and Management 33(5-8):545-552.*

A fresh-water microalgae, which functions under CO2 enriched atmosphere conditions, was isolated and its cultural characteristics were investigated. The HA-1 strain, identified as genus Chlorella, was newly isolated from a paddy field by an enrichment culture using reproduced stack gases from a thermal power plant with a concentration of CO2 and O2 of 15 % and 2 % respectively. It showed maximum growth at 10 % CO2 enriched air flowing condition, and showed a good growth rate in

a broad range of physically controllable conditions, including CO2 enriched air flow rate, temperature and pH value. The results indicated the feasibility of the HA-1 strain for mass cultivation using stack gases.

2537

Watling, J.R., and M.C. Press. 1997. How does elevated CO2 affect the relationship between the C-3 root hemiparasite Striga hermonthica and the C-4 host Sorghum bicolor? *Plant Physiology 114(3):46.*

2538

Watling, J.R., and M.C. Press. 1997. How is the relationship between the C-4 cereal Sorghum bicolor and the C-3 root hemi-parasites Striga hermonthica and Striga asiatica affected by elevated CO2? *Plant, Cell and Environment 20(10):1292-1300.*

The C-4 cereal Sorghum bicolor was grown under either ambient (350 mu mol mol(-1)) or elevated (700 mu mol mol(-1)) [CO2] in either the presence or absence of the C-3 obligate root hemi- parasites Striga hermonthica or S. asiatica. Both uninfected and infected sorghum plants were taller and had greater biomass, photosynthetic rates, water-use efficiencies and leaf areas under elevated compared with ambient [CO2]. There was no evidence of any downregulation of photosynthesis in sorghum grown at elevated [CO2]. Biomass of infected sorghum was lower under both ambient and elevated [CO2], and although infected plants were larger under elevated [CO2] the relative impact of infection on host biomass was either the same (S. asiatica) or only slightly less (S. hermonthica) than under ambient [CO2]. In contrast, biomass of S. hermonthica and S. asiatica per host was lower under elevated than ambient [CO2], although rates of photosynthesis were higher at elevated [CO2] and parasite stomatal conductance was not responsive to [CO2]. Parasites emerged above-ground and flowered earlier under ambient compared with elevated [CO2]. It appears that the mechanism(s) by which the parasites affect host growth is (are) relatively insensitive to increased atmospheric [CO2] although the parasites themselves were adversely affected by growth at elevated [CO2].

KEYWORDS: ACQUISITION, ASSOCIATION, CARBON DIOXIDE, ENRICHMENT, FIELD, GAS-EXCHANGE, GROWTH, PHOTOSYNTHESIS, RESPONSES, WATER RELATIONS

2539

Watt, M., and J.R. Evans. 1999. Linking development and determinancy with organic acid efflux from proteoid roots of white lupin grown with low phosphorus and ambient or elevated atmospheric CO2 concentration (vol 120, pg 705, 1999). *Plant Physiology 121(3):1057.*

2540

Wayne, P.M., and F.A. Bazzaz. 1995. Seedling density modifies the growth-responses of yellow birch maternal families to elevated carbon-dioxide. *Global Change Biology 1(5):315-324.*

We studied seedling growth responses to ambient and elevated CO2 (350 and 700 mu L L(-1)) of three maternal families of yellow birch (Betula alleghaniensis), raised both individually and in high-density stands. Seedlings in competitive, dense stands exhibited markedly lower average CO2-induced growth enhancements than individually grown plants (16% vs. 49%). Maternal families differed in their growth responses to elevated CO2. However, differences among families were contingent upon density; families which exhibited the greatest CO2-induced growth at low density exhibited the least CO2- responsiveness at high density. These data are discussed in two separate contexts; the reliability of estimates of the CO2 fertilization potential of forest species based solely on individually grown plants, and the potential evolutionary consequences of rising CO2 on regenerating forest tree populations.

KEYWORDS: AMBIENT, ATMOSPHERIC CO2 ENRICHMENT, COMPETITION, ECOSYSTEMS, FOREST, GAS-EXCHANGE, INCREASE, NITROGEN, PLANTS, TREE

2541

Wayne, P.M., and F.A. Bazzaz. 1997. Light acquisition and growth by competing individuals in CO2- enriched atmospheres: Consequences for size structure in regenerating birch stands. *Journal of Ecology 85(1):29-42.*

1 To investigate how CO2-enriched atmospheres may influence plant competition and stand size structure in regenerating forests, experimental populations comprised of three maternal families of yellow birch (Betula alleghaniensis Britt.) were grown in both ambient (350 mu L L(-1)) and elevated (700 mu L L(-1)) CO2 concentrations in a controlled environment facility. Individual seedling growth, light acquisition, and stand size structure were monitored throughout the first year of growth. 2 Elevated CO2 increased average seedling biomass in stands by 14%, a value much lower than the average enhancement reported elsewhere for individually grown yellow birch seedlings. Maternal families within stands differed significantly in their growth responsiveness to elevated CO2, ranging from +51% to - 16%. As a result, CO2 altered the genetic identity of dominants in regenerating stands. 3 Seedling size inequalities were generally lower in CO2-enriched environments, a result that contrasts with other studies that have reported increased size inequality with increased productivity in resource-rich environments. Distribution modifying functions relating initial seedling size and subsequent growth suggest that there was a relatively smaller advantage to being larger in elevated vs. ambient CO2 environments. Together, these results suggest that competition in CO2-enriched environments was less size- asymmetric. 4 Differences in stand size structure between CO2 treatments were related to competition for light. Empirical measures of seedling light acquisition per unit biomass suggest competition for light was less size-asymmetric in CO2-enriched environments. Decreased size-asymmetric competition for light was attributable both to differences in the CO2-use efficiency of high-light canopy dominants vs. low-light canopy subordinates, and to CO2-induced differences in plant allometry. 5 This study highlights the importance of stand- level competition studies in global change research, and more generally, the value of studies that combine phenomenological descriptions of stand development with physiological mechanisms of competition.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, EMERGENCE TIME, ENRICHMENT, ENVIRONMENTS, EXPERIMENTAL POPULATIONS, PLANT-POPULATIONS, RADISH RAPHANUS-RAPHANISTRUM, SEED SIZE, SOURCE-SINK RELATIONS

2542

Wayne, P.M., A.L. Carnelli, J. Connolly, and F.A. Bazzaz. 1999. The density dependence of plant responses to elevated CO2. *Journal of Ecology 87(2):183-192.*

1 Stands of the annual Brassica kaber were grown at a range of six densities in both ambient and elevated CO2 environments, and measurements of shoot growth were made from seedling emergence through to reproduction. 2 Early in stand development (21 days following emergence), CO2 enhancement (beta) for above-ground biomass was highly density-dependent, ranging from 1.41 at the lowest density (20 plants m(-2)) to 0.59 at the highest density (652 plants m(-2)). 3 As stands matured and total biomass exceeded a relatively low threshold level (< 10.0 g m(-2); c. 20% of final yield), the density-

dependence of beta disappeared. Above this shoot biomass threshold, beta-values remained remarkably stable (beta = 0.34) across a broad range of stand biomass, independent of a stand's initial density or age. 4 Average stand-level reproductive beta-values at a final harvest were very similar to biomass values (beta = 0.38) and, as with biomass values at later stages, showed no apparent density-dependence. 5 These results highlight the importance of considering density and the time-course of stand development simultaneously when assessing the potential for CO2-induced growth enhancements in plants.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, ENVIRONMENTS, GROWTH-RESPONSE, POPULATIONS, REPRODUCTION

2543

Wayne, P.M., E.G. Reekie, and F.A. Bazzaz. 1998. Elevated CO2 ameliorates birch response to high temperature and frost stress: implications for modeling climate-induced geographic range shifts. *Oecologia 114(3):335-342.*

Despite predictions that both atmospheric CO2 concentrations and air temperature will rise together, very limited data are currently available to assess the possible interactive effects of these two global change factors on temperate forest tree species. Using yellow birch (Betula alleghaniensis) as a model species, we studied how elevated CO2 (800 vs. 400 mu l l(-1)) influences seedling growth and physiological responses to a 5 degrees C increase in summer air temperatures (31/26 vs. 26/21 degrees C day/night), and how both elevated CO2 and air temperature during the growing season influence seedling ability to survive freezing stress during the winter dormant season. Our results show that while increased temperature decreases seedling growth, temperature-induced growth reductions are significantly lower at elevated CO2 concentrations (43% vs. 73%). The amelioration of high-temperature stress was related to CO2-induced reductions in both whole-shoot dark respiration and transpiration. Our results also show that increased summer air temperature, and to a lesser degree CO2 concentration, make dormant winter buds less susceptible to freezing stress. We show the relevance of these results to models used to predict how climate change will influence future forest species distribution and productivity, without considering the direct or interactive effects of CO2.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, EFFICIENCY, FOREST, PICEA-SITCHENSIS, PLANT GROWTH, RESPIRATION, SCOTS PINE, SEEDLINGS

2544

Webb, A.A.R., M.R. McAinsh, T.A. Mansfield, and A.M. Hetherington. 1996. Carbon dioxide induces increases in guard cell cytosolic free calcium. *Plant Journal 9(3):297-304.*

The hypothesis that increases in cytosolic free calcium ([Ca2+](i)) are a component of the COP signal transduction pathway in stomatal guard cells of Commelina communis has been investigated. This hypothesis was tested using fura-2 fluorescence ratio photometry to measure changes in guard cell [Ca2+](i) in response to challenge with 700 mu l l(-1) CO2. Elevated CO2 induced increases in guard cell [Ca2+](i) which were similar to those previously reported in response to abscisic acid. [Ca2+](i) returned to resting values following removal of the CO2 and further application of CO2 resulted in a second increase in [Ca2+](i). This demonstrated that the CO2- induced increases in [Ca2+](i) were stimulus dependent. Removal of extracellular calcium both prevented the CO2-induced increase in [Ca2+](i) and inhibited the associated reduction in stomatal aperture. These data suggest that Ca2+ acts as a second messenger in the CO2 signal transduction pathway and that an increase in [Ca2+](i) may be a requirement for the stomatal response to CO2.

KEYWORDS: ABSCISIC- ACID, ANION CHANNELS, CA-2, CO2, ELEVATION, INDUCED STOMATAL CLOSURE, INOSITOL TRISPHOSPHATE, PLANT-CELLS, PLASMA-MEMBRANE, SIGNAL-TRANSDUCTION

2545

Webber, A.N., G.Y. Nie, and S.P. Long. 1994. Acclimation of photosynthetic proteins to rising atmospheric co2. *Photosynthesis Research 39(3):413-425.*

In this review we discuss how the photosynthetic apparatus, particularly Rubisco, acclimates to rising atmospheric CO2 concentrations (c(a)). Elevated c(a) alters the control exerted by different enzymes of the Calvin cycle on the overall rate of photosynthetic CO2 assimilation, so altering the requirement for different functional proteins. A decreased flux of carbon through the photorespiratory pathway will decrease requirements for these enzymes. From modeling of the response of CO2 uptake (A) to intracellular CO2 concentration (c(i)) it is shown that the requirement for Rubisco is decreased at elevated c(a), whilst that for proteins limiting ribulose 1,5 bisphosphate regeneration may be increased. This balance may be altered by other interactions, in particular plasticity of sinks for photoassimilate and nitrogen supply; hypotheses on these interactions are presented. It is speculated that increased accumulation of carbohydrate in leaves developed at elevated c(a) may signal the 'down regulation' of Rubisco. The molecular basis of this 'down regulation' is discussed in terms of the repression of photosynthetic gene expression by the elevated carbohydrate concentrations. This molecular model is then used to predict patterns of acclimation of perennials to long term growth in elevated c(a).

KEYWORDS: AIR- TEMPERATURE, CALVIN CYCLE ENZYMES, CARBONIC-ANHYDRASE, CARBOXYLASE-OXYGENASE, CHLAMYDOMONAS-REINHARDTII, ELEVATED CO2, GENE-EXPRESSION, SINK REGULATION, SPINACH LEAVES, TOBACCO PLANTS

2546

Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, R.L. Garcia, P.J. Pinter, and T. Kartschall. 1995. Biomass and growth rate of a spring wheat root system grown in free-air CO2 enrichment (FACE) and ample soil moisture. *Journal of Biogeography 22(4-5):623-634.*

The response of a wheat crop root system to full-season CO2-enrichment was investigated using a free-air CO2 enrichment (FACE) apparatus. A spring wheat (Triticum aestivum L. cv. Yecora Rojo) crop was growing at 0.25 m row spacing and 130 plants m(-2) on a Trix clay loam (hyperthermic Typic Torrifluvent) under two atmospheric CO2 concentrations (FACE: similar to 550 mu mol mol(-1); control: similar to 370 mu mol mol(-1)) and ample soil moisture (100% replacement of poten tial evapotranspiration). Irrigation was applied with a subsur face drip irrigation system. Root cores were collected at five growth stages (three-leaf, tillering, stem elongation, anthesis, dough development and final harvest, which corresponded with day of year (DOY) 16, 36, 63, 92, 113 and 159, respectively), using a soil core device (86 mm i). Two cores were taken in-row and one in the inter-row space position to examine the horizontal and vertical distribution of roots to a I-m depth. Root biomass was summed over the entire root profile across all positions to obtain a total. Total root mass was higher in FACE compared to control for all growth stages (i.e. 34% at three-leaf, 21% at tillering, 23% at stem elongation, 28% at dough development and 19% at harvest). Root growth rate was significantly higher in FACE compared to control for both in-row and inter-row positions. Root senescence rate were similar between FACE and control grown plants,

but the absolute difference in root mass during the senescence phase was greater in FACE compared to control grown plants. Roots from FACE grown plants explored a greater proportion of the soil profile earlier in the season than roots from control grown plants. However, there was no evidence that plants grown in FACE had a deeper root system than plants grown in control.

KEYWORDS: ELEVATED CARBON-DIOXIDE, FEEDBACK, NITROGEN, PARTIAL-PRESSURE

2547

Wechsung, G., F. Wechsung, G.W. Wall, F.J. Adamsen, B.A. Kimball, P.J. Pinter, R.L. Lamorte, R.L. Garcia, and T. Kartschall. 1999. The effects of free-air CO2 enrichment and soil water availability on spatial and seasonal patterns of wheat root growth. *Global Change Biology 5(5):519-529.*

Spring wheat [Triticum aestivum (L). cv. Yecora Rojo] was grown from December 1992 to May 1993 under two atmospheric CO2 concentrations, 550 mu mol mol(-1) for high-CO2 plots, and 370 mu mol mol(-1) for control plots, using a Free-Air CO2 Enrichment (FACE) apparatus. In addition to the two levels of atmospheric CO2, there were ample and limiting levels of water supply through a subsurface trip irrigation system in a strip, split-plot design. In order to examine the temporal and spatial root distribution, root cores were extracted at six growth stages during the season at in-row and inter-row positions using a soil core device (86 mm ID, 1.0 m length). Such information would help determine whether and to what extent root morphology is changed by alteration of two important factors, atmospheric CO2 and soil water, in this agricultural ecosystem. Wheat root growth increased under elevated CO2 conditions during all observed developmental stages. A maximum of 37% increase in total root dry mass in the FACE vs. Control plots was observed during the period of stem elongation. Greater root growth rates were calculated due to CO2 enhancement until anthesis. During the early vegetative growth, root dry mass of the inter-row space was significantly higher for FACE than for Control treatments suggesting that elevated CO2 promoted the production of first-order lateral roots per main axis. Then, during the reproductive period of growth, more branching of lateral roots in the FACE treatment occurred due to water stress. Significant higher root dry mass was measured in the inter-row space of the FACE plots where soil water supply was limiting. These sequential responses in root growth and morphology to elevated CO2 and reduced soil water supports the hypothesis that plants grown in a high-CO2 environment may better compensate soil-water-stress conditions.

KEYWORDS: BIOMASS, CARBON-DIOXIDE ENRICHMENT, COTTON, DECOMPOSITION, ELEVATED ATMOSPHERIC CO2, FACE, LOLIUM-PERENNE, NITROGEN, PRODUCTIVITY, RESPONSES

2548

Weerakoon, W.M., D.M. Olszyk, and D.N. Moss. 1999. Effects of nitrogen nutrition on responses of rice seedlings to carbon dioxide. *Agriculture Ecosystems & Environment 72(1):1-8.*

Global atmospheric CO2 concentration is increasing, likely increasing the productivity of crops as higher CO2 enhances plant photosynthesis. Responsiveness to nitrogen supply is an essential trait of modem rice cultivars, and may play a role in the response of rice cultivars to CO2. To determine the relationship between these two important production variables on young rice plants, seedlings of Oryza sativa L. 'IR72' and 'KDML 105' were exposed for 28 days after sowing to CO2 levels of 373, 545, 723 and 895 mu molmoI(-1), and 3 levels of nitrogen fertility. There were large increases in leaf CO2 assimilation and biomass production whereas leaf nitrogen concentration dropped sharply as CO2 increased from 373 to 545 mu mol mol(-l), with little additional effect from higher levels of CO2. Root and shoot biomass, and tiller number per plant increased with increasing nitrogen supply and with increasing atmospheric CO2 concentration. The biomass response to CO2 was slight at low N supply, but became dramatically greater as the N supply increased. Mean root/shoot ratio increased slightly as atmospheric CO2 concentration increased, but decreased sharply as nitrogen fertility rate increased. These results suggest that careful attention to nitrogen fertilization will be necessary for rice fanning to get the full benefit of any future increases in atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2, GROWTH, ORYZA-SATIVA, PHOTOSYNTHESIS, YIELD

2549

Weigel, H.J., and U. Dammgen. 1999. The Braunschweig carbon project - atmospheric flux monitoring and free air carbon dioxide enrichment. *Berichte Uber Landwirtschaft 77(1):49-58.*

With respect to the predicted climate change it has become evident that the role of terrestrial ecosystems in the global carbon turnover is not yet fully understood. This is also true for carbon fluxes in agricultural ecosystems. As increasing atmospheric CO2 concentrations will directly affect plant photosynthesis, plant biomass production and plant water relations, it is of particular importance to predict the dynamics of carbon fluxes between the atmosphere and agricultural canopies and the related consequences for agroecosystems under future atmospheric CO2 conditions. There are hardly any experimental approaches under real field conditions in crop rotation systems to simulate future CO2 scenarios. The Braunschweig carbon project is a combination of micrometeorological flux measurements of atmospheric trace gases and other air constituents and of a large scale free air carbon dioxide enrichment (FACE) experiment. The project is particularly designed to meet the data requirement of process and landscape models. The data will also contribute to the improvement and validation of models to predict the consequences of climate changes for agricultural ecosystems. The present contribution is a description of the structure of the experiments and the involvement of modelling approaches.

KEYWORDS: CYCLE, ELEVATED CO2, PLANTS, RESPONSES, SOIL

2550

Weigel, H.J., R. Manderscheid, H.J. Jager, and G.J. Mejer. 1994. Effects of season-long co2 enrichment on cereals .1. Growth-performance and yield. *Agriculture Ecosystems & Environment 48(3):231-240.*

Two cultivars each of spring wheat (Triticum aestivum L., cultivars 'Star' and 'Turbo') and spring barley (Hordeum vulgare L., cultivars 'Alexis' and 'Arena') were exposed throughout the growing season to ambient (384 p.p.m.) and above ambient CO2 concentrations (471, 551, 624,718 p.p.m.) in open- top chambers. Plant samples were taken four times during plant development and biomass partitioning into stem, leaves and ear was measured. Total above-ground biomass increased mainly in the C02 concentration range between 400-550 p.p.m. for wheat, and between 400-700 p.p.m. for barley. Stimulation of biomass was largely due to an increase in tillering rate. At the tiller level CO2 enrichment revealed a decrease in leaf dry weight at anthesis stage, which was due to a reduction in leaf size (barley) and in leaf number (wheat). Specific leaf weight of the mature flag leaf was unaffected by CO2. Stem biomass per tiller was temporarily ('Star', 'Alexis') or during the whole growth period ('Turbo', 'Arena') increased by CO2 exposure, while ear dry weight was increased (barley) or even decreased ('Star'). Except for the barley cultivar 'Arena', which showed a 84% increase in the number of grains per ear, the number of ears was almost entirely responsible for the

increased grain yield among the CO2 treatments. At the highest CO2 concentration yield increase amounted to 19% and 27% for the two wheat cultivars, and 5 2% and 8 9% for the two barley cultivars in comparison with the ambient CO2 level. Among all cultivars there was an inverse relationship between the total shoot biomass produced at ambient CO2 conditions and the plant's response to the CO2 enrichment. This indicates that the genetic potential of wheat unlike barley is highly adapted to present atmospheric CO2 conditions and thus responsible for the small CO2 effect on wheat.

KEYWORDS: ATMOSPHERIC CO2, DRY-MATTER, ELEVATED CARBON-DIOXIDE, ENVIRONMENTS, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGY, RESPONSES, SPRING WHEAT, WINTER-WHEAT

2551

Weishampel, J.F., R.G. Knox, and E.R. Levine. 1999. Soil saturation effects on forest dynamics: scaling across a southern boreal/northern hardwood landscape. *Landscape Ecology 14(2):121-135.*

Patch modeling can be used to scale-up processes to portray landscape-level dynamics. Via direct extrapolation, a heterogeneous landscape is divided into its constituent patches; dynamics are simulated on each representative patch and are weighted and aggregated to formulate the higher level response. Further extrapolation may be attained by coarsening the resolution of or lumping environmental data (e.g., climatic, edaphic, hydrologic, topographic) used to delimit a patch. Forest patterns at the southern boreal/northern hardwood transition zone are often defined by soil heterogeneity, determined primarily by the extent and duration of soil saturation. To determine how landscape-level dynamics predicted from direct extrapolation compare when coarsening soil parameters, we simulated forest dynamics for soil series representing a range of drainage classes from east-central Maine. Responses were aggregated according to the distribution of soil associations comprising a 600 ha area based on local- (1.12,000), county- (1:120,000) and state- (1:250,000) scale soil maps. At the patch level, simulated aboveground biomass accumulated more slowly in poorer draining soils. Different soil series yielded different communities comprised of species with various tolerances for soil saturation. When aggregated, removal of waterlogging caused a 20-60% increase in biomass accumulation during the first 50 years of simulation. However, this early successional increase and the maximum level of biomass accumulation over a 200 year period varied by as much as 40% depending on the geospatial data. This marked discrepancy suggests caution when extrapolating with forest patch models by coarsening parameters and demonstrates how rules used to rescale environmental data need to be evaluated for consistency.

KEYWORDS: BOREAL FORESTS, CO2-INDUCED CLIMATE CHANGE, ECOSYSTEMS, GAP MODELS, GLOBAL CHANGE, MOISTURE, MULTIFREQUENCY, NORTHERN FORESTS, SIMULATION, TEMPERATURE

2552

Welker, J.M., and D.D. Briske. 1992. Clonal biology of the temperate, caespitose, graminoid schizachyrium-scoparium - a synthesis with reference to climate change. *Oikos 63(3):357-365.*

Caespitose graminoids are characterized by the compact spatial arrangement of ramets within clones and the absence of rhizomes or stolons. Resource allocation is principally acropetal with established ramets supporting juvenile ramets during early development. However, after juvenile ramet maturation a responsive resource transfer system is maintained by a low level of continuous resource allocation between parental and juvenile ramets. Isotopic and severing experiments demonstrated that physiological integration in the caespitose graminoid Schizachyrium scoparium is restricted to individual ramet sequences consisting of three connected ramet generations as opposed to all ramets within the clone. This number of ramet generations comprising the physiological individual is determined by demographic variables influencing the recruitment and longevity of individual ramets. Restricted resource allocation among ramet sequences within clones is primarily caused by the disintegration of vascular connections among ramet sequences following death of the seminal ramet. The survival value conferred by a clonal architecture composed of an assemblage of autonomous physiological individuals growing within close proximity requires further evaluation but may center on intra-plant competitive interactions. The response of this large sub-group of clonal plants to climate change will significantly impact community structure and function because of their diversity and dominance in numerous biomes. The impact of climate change on the caespitose graminoid growth form is difficult to anticipate because: 1) caespitose graminoids consist of both C3 and C4 species which will complicate the response of the growth form, 2) our understanding about the clonal biology and population ecology of this growth form is still evolving and 3) the modular construction of this growth form may result in variable responses at the ramet, clone and population levels of organization.

KEYWORDS: DEFOLIATION, ELEVATED CO2, GLECHOMA-HEDERACEA, GROWTH, PHOTOSYNTHESIS, PLANT, POPULATIONS, RESPONSES, STRESS, WATER RELATIONS

2553

Wellburn, A.R. 1998. Atmospheric nitrogenous compounds and ozone - is NOx fixation by plants a possible solution? *New Phytologist 139(1):5-9.*

Air quality thresholds for O-3 for the protection of human health and vegetation set by the European Union (EU) have been exceeded in Europe regularly in the 1990s. Because target reductions for oxides of nitrogen (NOx) set for the year 2000 are unlikely to be achieved, these O-3 exceedances are likely to continue into the next millenium. Improvements of plant tolerance towards O-3 are being investigated but very little work has been done to explore NOx tolerance and plant acclimation to NO2 and NO. However, it is clear that within the populations of some plant species there is wide variation, and some individuals can fix NOx, and use the nitrogen directly from the atmosphere, rather than rely upon, for example, root uptake of nitrate. It is possible that individuals capable of fixing NOx could be selected for a range of species, and genotypes with high rates of uptake could be of value as crops or for forestation in polluted areas (e.g. landscaping in the vicinity of motorways) to reduce tropospheric concentrations of NOx significantly and also to decrease the potential for O-3 production.

KEYWORDS: CO2- ENRICHMENT, GROWTH, NITRATE, RESPONSES

2554

Welsh, D.T., S. Bourgues, R. deWit, and I. Auby. 1997. Effect of plant photosynthesis, carbon sources and ammonium availability on nitrogen fixation rates in the rhizosphere of Zostera noltii. *Aquatic Microbial Ecology 12(3):285-290.*

Rates of nitrogen fixation (measured as acetylene reduction) in the rhizosphere of the seagrass Zostera noltii were highly dependent upon plant photosynthetic activity being significantly stimulated at elevated CO2 concentrations and by light, both in the short-term and over diurnal cycles. Stimulation by light became insignificant when 5 mM sucrose was added to the sediment porewater, indicating that in the absence of added carbon sources, light stimulation was due to direct inputs of plant photosynthate to the rhizosphere. Addition of a range of carbon sources to the rhizosphere sediment stimulated rates of acetylene reduction, with this stimulation being significant for sucrose and lactate. Surprisingly,

whilst low additions of ammonium to the sediment porewater (10 to 50 mu M) inhibited 50% of acetylene reduction activity, approximately 30% of this activity persisted in the presence of 1 mM ammonium chloride; this indicating that in at least a proportion of the N-fixing community, nitrogenase activity was not regulated in the short term by the availability of alternative nitrogen sources.

KEYWORDS: AUSTRALIA, BACTERIAL PRODUCTIVITY, CARPENTARIA, GRASS SPARTINA-ALTERNIFLORA, GROWTH, GULF, ORGANIC-CARBON, SEDIMENTS

2555

Weltzin, J.F., S. Archer, and R.K. Heitschmidt. 1997. Small-mammal regulation of vegetation structure in a temperate Savanna. *Ecology 78(3):751-763.*

Explanations for documented increases in woody plant dominance in grasslands and savannas of North America include atmospheric CO2 enrichment and changes in climate, livestock grazing, and fire regimes. However, tree/shrub encroachment has also coincided with the eradication of a once widespread native herbivore, the black-tailed prairie dog (Cynomys ludovicianus). We used field experiments and repeat aerial photography to demonstrate that prairie dogs, and the herbivores and granivores associated with their colonies, probably maintained grassland and savanna by preventing woody species such as Prosopis glandulosa (honey mesquite) from establishing or attaining dominance. Prosopis seed and pod disappearance was 3- 99 times greater within prairie dog colonies. Ants were the primary agent of seed removal, whereas prairie dogs and associated vertebrates were the primary agents of pod removal. Survival of Prosopis seedlings protected from vertebrate herbivory was similar on and off prairie dog colonies (approximate to 60%), whereas survival of unprotected seedlings was 3 times greater off- than on-colony. On-colony, prairie dogs and associated herbivores girdled and destroyed all Prosopis saplings within 2 d of planting; survival of 1-yr-old seedlings was reduced by 50% after 3 mo of exposure to on- colony herbivores. Despite high levels of woody plant seed disappearance and seedling herbivory, on-colony "seedling" reserves were substantial (950 plants/ha). Thus, prairie dogs and the fauna that occur on their colonies suppressed rather than eliminated Prosopis from the colony site. Removal of prairie dogs led to rapid development of Prosopis stands. Repeat aerial photography showed that Prosopis canopy cover on a colony eradicated in 1950 (27%) increased to a level (61%) comparable to that of off-colony Prosopis stands (65%) within 23 yr. These data illustrate how transitions from grassland to woodland vegetation can be mediated by a rodent herbivore. They further demonstrate how purposeful or inadvertent removal of native herbivores can have unforeseen effects on plant species composition and landscape physiognomy. Investigations of environmental constraints on vegetation distribution and abundance should take into account the historical role of herbivores in shaping the present system. Inconsistencies among historic accounts of woody plant distribution and abundance in semiarid western North America may be resolved by considering population dynamics of prairie dogs. Widespread eradication of this formerly abundant rodent has eliminated a significant constraint to woody plant establishment on many semiarid grassland and savanna landscapes and has thereby facilitated transitions to shrubland and woodland states. Past land management designed to remove one perceived impediment to livestock production appears to have contributed significantly to development of another management problem that is now a major detriment to sustainable livestock production.

KEYWORDS: AMERICAN SOUTHWEST, C-4 GRASS, DYNAMICS, INCREASING CO2, MIXED-GRASS PRAIRIE, PLANT-HERBIVORE INTERACTIONS, PROSOPIS- GLANDULOSA, SERENGETI-NATIONAL-PARK, SOUTHERN NEW-MEXICO, WOODY PLANT

2556

West, D.C., T.W. Doyle, M.L. Tharp, J.J. Beauchamp, W.J. Platt, and D.J. Downing. 1993. Recent growth increases in old-growth longleaf pine. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 23(5):846-853.*

Longleaf pine (Pinus palustris Mill.) tree-ring data were obtained from an old-growth stand located in Thomas County, Georgia. The tree-ring chronology from the pine stand is composed of a collection of cores extracted from 26 trees ranging in age from approximately 100 to 400 years. These cores were prepared, dated, and measured, and the resulting data were examined with dendrochronological and statistical techniques. Beginning in approximately 1950 and continuing to the present, annual increments of all age classes examined in this study have increased. resulting in an average annual ring increment approximately 40% greater in 1987 than in 1950. When compared with expected annual increment, the increase for 100- to 150- year-old trees is approximately 45%, while the increase for 200- to 400-year-old trees is approximately 35%. In terms of stand-level aboveground biomass accumulation, the increased growth has resulted in approximately 5% more biomass than expected. The increased growth cannot be explained by disturbance; stand history; or trends in precipitation, temperature, or Palmer drought severity index over the last 57 years. Increased atmospheric CO2 is a possible explanation for initiation of the observed trend, while SO(x) and NO(x) may be augmenting continuation of this phenomenon.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO2-ENRICHMENT, COMPETITION, LIQUIDAMBAR- STYRACIFLUA, TAEDA SEEDLINGS, UNITED-STATES

2557

Wheeler, R.M., K.A. Corey, J.C. Sager, and W.M. Knott. 1993. Gas-exchange characteristics of wheat stands grown in a closed, controlled environment. *Crop Science 33(1):161-168.*

Information on gas exchange of crop stands grown in controlled environments is limited, but is vital for assessing the use of crops for human life-support in closed habitats envisioned for space. Two studies were conducted to measure gas exchange of wheat stands (Triticum aestivum L. cv. Yecora Rojo) grown from planting to maturity in a large (20 m2 canopy area), closed growth chamber. Daily rates of dark-period respiration and net photosynthesis of the stand were calculated from rates of CO2 build-up during dark cycles and subsequent CO2 drawdown in the light (i.e., a closed-system approach). Lighting was provided as a 20-h photoperiod by high-pressure sodium lamps, with canopy-level photosynthetic photon flux density (PPFD) ranging from 500 to 800 mumol m-2 s-1 as canopy height increased. Net photosynthesis rates peaked near 27 mumol CO2 m-2 s-1 at 25 d after planting, which corresponded closely with stand closure, and then declined slowly with age. Similarly, dark-period respiration rates peaked near 14 mumol CO2 m-2 s-1 at 25 d and then gradually declined with age. Responses to short-term changes in irradiance after canopy closure indicated the stand light compensation point for photosynthesis to be near 200 mumol m-2 s-1 PPFD. Tests in which CO2 concentration was raised to almost-equal-to 2000 mumol mol-1 and then allowed to draw down to a compensation point showed that net photosynthesis was nearly saturated at > 1000 mumol mol-1; below almost-equal-to 500 mumol mol-1, net photosynthesis rates dropped sharply with decreasing CO2. The CO2 compensation point for photosynthesis occurred near 50 mumol mol-1. Short-term (24 h) temperature tests showed net photosynthesis at 20-degrees-C greater-than- or-equal-to 16-degrees-C > 24-degrees-C, while dark-period respiration at 24-degrees-C > 20-degrees-C > 16-degrees-C. Rates of stand evapotranspiration peaked near Day 25 and remained relatively constant until about Day 75, after which rates declined slowly. Results from these tests will be used to model the use of plants for CO2 removal, O2 production, and water evaporation for controlled ecological life support systems proposed for

extraterrestrial environments.

KEYWORDS: CARBON-DIOXIDE EXCHANGE, CO2, CROP, ENRICHMENT, INHIBITION, LEAF-AREA INDEX, PHOTOSYNTHESIS, SHORT- TERM, SOYBEAN CANOPIES

2558

Wheeler, R.M., C.L. Mackowiak, J.C. Sager, and W.M. Knott. 1994. Growth of soybean and potato at high co2 partial pressures. *Life Sciences and Space Research XXV (3) 14(11):251-255.*

Soybean and potato plants were grown in controlled environments at carbon dioxide (CO2) partial pressures ranging from 0.05 to 1.00 kPa. The highest yields of edible biomass occurred at 0.10 kPa for both species, with higher CO2 levels being supraoptimal, but not injurious to the plants. Stomatal conductance rates of upper canopy leaves were lowest at 0.10 kPa CO2, while conductance rates at 0.50 and 1.00 kPa were significantly greater than 0.10 kPa. Total water use by the plants was greatest at the highest CO2 pressures (i.e. 0.50 and 1.00 kPa); consequently, water use efficiencies (biomass produced / water used) were low at the highest CO2 pressures. Based on previous CO2 studies in the literature, the increased conductance and water use at the highest CO2 pressures were surprising and pose interesting challenges for managing plants in a CELSS, where CO2 pressures may exceed optimal levels.

KEYWORDS: ENRICHMENT, GAS-EXCHANGE

2559

Wheeler, R.M., C.L. Mackowiak, L.M. Siegriest, and J.C. Sager. 1993. Supraoptimal carbon-dioxide effects on growth of soybean [glycine-max (L) merr]. *Journal of Plant Physiology 142(2):173-178.*

In tightly closed environments used for human life support in space, carbon dioxide (CO2) partial pressures can reach 500 to 1000 Pa, which may be supraoptimal or toxic to plants used for life support. To study this, soybeans [Glycine max (L.) Merr. cvs. McCall and Pixie] were grown for 90 days at 50, 100, 200, and 500 Pa partial pressure CO2 (500, 1000, 2000, and 5000 ppm). Plants were grown using recirculating nutrient film technique with a 12-h photoperiod, a 26-degrees-C/20-degrees-C thermoperiod, and approximately 300 mumol m-2 s-1 photosynthetic photon flux (PPF). Seed yield and total biomass were greatest at 100 Pa for cv. McCall, suggesting that higher CO2 levels were supraoptimal. Seed yield and total biomass for cv. Pixie showed little difference between CO2 treatments. Average stomatal conductance of upper canopy leaves at 50 Pa CO2 almost-equal-to 500 Pa > 200 Pa > 100 Pa. Total water use over 90 d for both cultivars (combined on one recirculating system) equalled 822 kg water for 100 Pa CO2, 845 kg for 50 Pa, 879 kg for 200 Pa, and 1194kg for 500 Pa. Water use efficiences for both cultivars combined equaled 3.03 (g biomass kg-1 water) for 100 Pa CO2, 2.54 g kg-1 for 200 Pa, 2.42 g kg-1 for 50 Pa, and 1.91 g kg-1 for 500 Pa. The increased stomatal conductance and stand water use at the highest CO2 level (500 Pa) were unexpected and pose interesting considerations,for managing plants in a tightly closed system where CO2 concentrations may reach high levels.

KEYWORDS: CO2, ENRICHMENT, EXPOSURE, PHOTOSYNTHESIS, PHYSIOLOGY, PLANTS, TEMPERATURE, YIELD

2560

Wheeler, R.M., C.L. Mackowiak, G.W. Stutte, N.C. Yorio, and W.L. Berry. UNKNOWN YEAR. Effect of elevated carbon dioxide on nutritional quality of tomato. *Life Sciences: Life Support Systems Studies-I :1975-1978.*

Tomato (Lycopersicon esculentum Mill.) cvs. Red Robin (RR) and Reimann Philipp (RP) were grown hydroponically for 105 d with a 12 h photoperiod, 26 degrees C /22 degrees C thermoperiod, and 500 mu mol.m(-2).s(-1) PPF at either 400, 1200, 5000, or 10,000 mu mol.mol(-1) (0.04, 0.12, 0.50, 1.00 kPa) CO2. Harvested fruits were analyzed for proximate composition, total dietary fiber, nitrate, and elemental composition. No trends were apparent with regard to CO2 effects on proximate composition, with fruit from all treatments and both cultivars averaging 18.9% protein, 3.6% fat, 10.2% ash, and 67.2% carbohydrate. In comparison, average values for field-grown fruit are 16.6% protein, 3.8% fat, 8.1% ash, and 71.5% carbohydrate (Duke and Atchely, 1986). Total dietary fiber was highest at 10,000 mu mol.mol(-1) (28.4% and 22.6% for RR and RP) and lowest at 1000 mu mol.mol(-1) (18.2% and 15.9% for RR and RP), but showed no overall trend in response to CO2. Nitrate values ranged from 0.19% to 0.35% and showed no trend with regard to CO2. K, Mg, and P concentrations showed no trend in response to CO2 but Ca levels increased from 198 and 956 ppm in RR and RP at 400 mu mol.mol(-1), to 2537 and 2825 ppm at 10,000 mu mol.mol(-1). This increase in Ca caused an increase in fruit Ca/P ratios from 0.07 and 0.37 for RR and RP at 400 mu mol.mol(-1). to 0.99 and 1.23 for RR and RP at 10,000 mu mol.mol(-1), suggesting that more dietary Ca should be available from high CO2-grown fruit. Published by Elsevier Science Ltd on behalf of COSPAR.

KEYWORDS: INCOMPLETE, CO2

2561

Wheeler, R.M., C.L. Mackowiak, N.C. Yorio, and J.C. Sager. 1999. Effects of CO2 on stomatal conductance: Do stomata open at very high CO2 concentrations? *Annals of Botany 83(3):243-251.*

Potato and wheat plants were grown for 50 d at 400, 1000 and 10 000 mu mol mol(-1) carbon dioxide (CO2), and sweetpotato and soybean were grown at 1000 mu mol mol(-1) CO2 in controlled environment chambers to study stomatal conductance and plant water use. Lighting was provided with fluorescent lamps as a 12 h photoperiod with 300 mu mol m(-2) s(-1) PAR. Mid-day stomatal conductances for potato were greatest at 400 and 10 000 mu mol mol(-1) and least at 1000 mu mol mol(-1) CO2. Mid-day conductances for wheat were greatest at 400 pmol mol(-1) and least at 1000 and 10 000 mu mol mol(-1) CO2. Mid-dark period conductances for potato were significantly greater at 10 000 mu mol mol(-1) than at 400 or 1000 mu mol mol(-1), whereas dark conductance for wheat was similar in all CO2 treatments. Temporarily changing the CO2 concentration from the native 1000 mu mol mol(-1) to 400 mu mol mol(-1) increased mid-day conductance for all species, while temporarily changing from 1000 to 10 000 mu mol mol(-1) also increased conductance for potato and sweetpotato. Temporarily changing the dark period CO2 from 1000 to 10 000 mu mol mol(-1) increased conductance for potato, soybean and sweetpotato. In all cases, the stomatal responses were reversible, i.e. conductances returned to original rates following temporary changes in CO2 concentration. Canopy water use for potato was greatest at 10 000, intermediate at 400, and least at 1000 mu mol mol(-1) CO2, whereas canopy water use for wheat was greatest at 400 and similar at 1000 and 10 000 mu mol mol(-1) CO2. Elevated CO2 treatments (i.e. 1000 and 10 000 mu mol mol(-1)) resulted in increased plant biomass for both wheat and potato relative to 400 mu mol mol(-1), and no injurious effects were apparent from the 10 000 mu mol mol(-1) treatment. Results indicate that super-elevated CO2 (i.e. 10 000 mu mol mol(-1)) can increase stomatal conductance in some species, particularly during the dark period, resulting in increased water use and decreased water use efficiency. (C) 1999 Annals of Botany Company.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, ENVIRONMENT, PLANT GROWTH, POTATO GROWTH, SOLANUM TUBEROSUM L, WHEAT, YIELD

2562

Wheeler, R.M., and T.W. Tibbitts. 1997. Influence of changes in daylength and carbon dioxide on the growth of potato. *Annals of Botany 79(5):529-533.*

Potatoes (Solanum tuberosum L.) are highly productive in mid- to high-latitude areas where photoperiods change significantly throughout the growing season. To study the effects of changes in photoperiod on growth and tuber development of potato cv. Denali, plants were grown for 112 d with 400 mu mol m(-2) s(-1) photosynthetic photon flux (PPF) under a 12-h photoperiod (short days, SD), a 24-h photoperiod (long days, LD), and combinations where plants were moved between the two photoperiods 28, 56, or 84 d after planting. Plants given LD throughout growth received the greatest total daily PPF and produced the greatest tuber yields. At similar levels of total PPF, plants given SD followed by LD yielded greater tuber dry mass (DM) than plants given IID followed by SD. Stem DM per plant, leaf DM, and total plant DM all increased with an increasing proportion of LD and increasing daily PPF, regardless of the daylength sequence. When studies were repeated, but at an enriched (1000 mu mol mol(-1)) CO2 concentration, overall growth trends were similar, with high CO2 resulting in greater stem length, stem DM, leaf DM, and total plant DM; but high CO2 did not increase tuber DM. (C) 1997 Annals of Botany Company.

KEYWORDS: CUTTINGS, LIGHT, PHOTOPERIODS, SOLANUM TUBEROSUM L, SYSTEMS, TEMPERATURE, TUBERIZATION, YIELDS

2563

Wheeler, R.M., T.W. Tibbitts, and A.H. Fitzpatrick. 1991. Carbon-dioxide effects on potato growth under different photoperiods and irradiance. *Crop Science 31(5):1209-1213.*

Carbon dioxide concentration can exert a strong influence on plant growth, but this influence can vary depending on irradiance. To study this, potato plants (Solanum tuberosum L.) cultivars 'Norland'. 'Russet Burbank', and 'Denali' were grown in controlled-environment rooms at different levels of CO2 and irradiance. Carbon dioxide levels were maintained either at 350 or 100-mu-mol mol-1 and applied in combination with 12- or 24-h photoperiods at 400 or 800-mu-mol m-2 s-1 photosynthetic photon flux. Air temperatures and relative humidity were held constant at 16-degrees-C and 70%, respectively, and plants were harvested 90 d after planting. When averaged across all cultivars, CO2 enrichment increased tuber yield and total plant dry weight by 39 and 34%, respectively, under a 12-h photoperiod at 400-mu-mol m-2 s-1; 27 and 19% under 12 h at 800-mu-mol m-2 s-1; 9 and 9% under 24 h at 400-mu-mol m-2 s-1. It decreased dry weights by 9 and 9% under 24 h at 800-mu-mol m-2 s-1. Tuber yield of Denali showed the greatest increase (21%) in response to increased CO2 across all irradiance treatments, while tuber yields of Russet Burbank and Norland were increased 18 and 9%, respectively. The results show a pattern of greater plant growth from CO2 enrichment under lower PPF and a short photoperiod.

KEYWORDS: ATMOSPHERIC CO2, CO2- ENRICHMENT, CONTROLLED ENVIRONMENTS, DRY-MATTER PRODUCTION, LIFE SUPPORT SYSTEMS, LIGHT, PHOTOSYNTHESIS, PLANT GROWTH, SPACE, TEMPERATURE

2564

Wheeler, T.R., G.R. Batts, R.H. Ellis, P. Hadley, and J.I.L. Morison. 1996. Growth and yield of winter wheat (Triticum aestivum) crops in response to CO2 and temperature. *Journal of Agricultural Science 127:37-48.*

Crops of winter wheat (Triticum aestivum L. cv. Hereward) were grown within temperature gradient tunnels at a range of temperatures at either c. 350 or 700 mu mol mol(-1) CO2 in 1991/92 and 1992/93 at Reading, UK. At terminal spikelet stage, leaf area was 45% greater at elevated CO2 in the first year due to more tillers, and was 30% greater in the second year due to larger leaf areas on the primary tillers. At harvest maturity, total crop biomass was negatively related to mean seasonal temperature within each year and CO2 treatment, due principally to shorter crop durations at the warmer temperatures. Biomass was 6-31% greater at elevated compared with normal CO2 and was also affected by a positive interaction between temperature and CO2 in the first year only. Seed yield per unit area was greater at cooler temperatures and at elevated CO2 concentrations. A 7-44% greater seed dry weight at elevated CO2 in the first year was due to more ears per unit area and heavier grains. In the following year, mean seed dry weight was increased by > 72% at elevated CO2, because grain numbers per ear did not decline with an increase in temperature at elevated CO2. Grain numbers were reduced by temperatures > 31 degrees C immediately before anthesis at normal atmospheric CO2 in 1992/93, and at both CO2 concentrations in 1991/92. To quantify the impact of future climates of elevated CO2 concentrations and warmer temperatures on wheat yields, consideration of both interactions between CO2 and mean seasonal temperature, and possible effects of instantaneous temperatures on yield components at different CO2 concentrations are required. Nevertheless, the results obtained suggest that the benefits to winter wheat grain yield from CO2 doubling are offset by an increase in mean seasonal temperature of only 1.0 degrees C to 1.8 degrees C in the UK.

KEYWORDS: CARBON DIOXIDE, DRY-MATTER, ELEVATED CO2, ENRICHMENT, FIELD, GRAIN DEVELOPMENT, NITROGEN, PLANT GROWTH, PRODUCTIVITY, REPRODUCTIVE GROWTH

2565

Wheeler, T.R., R.H. Ellis, P. Hadley, and J.I.L. Morison. 1995. Effects of co2, temperature and their interaction on the growth, development and yield of cauliflower (brassica-oleracea L botrytis). *Scientia Horticulturae 60(3-4):181-197.*

Stands of summer cauliflower were grown within polyethylene- covered tunnels along which a temperature gradient was imposed. Two tunnels were maintained at either normal or elevated CO2 concentrations. At the last harvest (88 days from transplanting) no interaction between CO2 and temperature on total biomass was detected. The total dry weight of plants grown at 531 mu mol mol-L CO2 was 34% greater than those grown at 328 mu mol mol(-1) CO2, whereas a 1 degrees C rise reduced dry weight by 6%. From serial harvests the radiation conversion coefficient was 2.01 g MJ(-1) and 1.42 g MJ(-1) at 531 mu mol mol(-1) CO2 and 328 mu mol mol(-1) CO2, respectively, but was not greatly affected by differences in temperature. No effect of either CO2 or temperature on the canopy light extinction coefficient was detected. The rate of progress towards curd initiation increased to a maximum at 15.5 degrees C, and declined thereafter. Provided the effect of temperature was accounted for, CO2 enrichment did not affect the time of curd initiation. From serial harvests after curd initiation, the logarithm of curd weight or diameter were negative linear functions of mean temperature from initiation. Increases in curd weight and diameter at 531 compared with 328 mu mol mol(- 1) CO2 were greater at warmer temperatures (27% at 13 degrees C compared with 47% at 15 degrees C, 57 days after initiation). Effects of CO2 on curd diameter were less than those on curd dry weight because the curd dry matter content was greater at 531 compared with 328 mu mol mol(-1) CO2. Thus, the effects of elevated CO2 concentrations on fresh weight based yield parameters of cauliflower were less than the increase in total dry matter production.

KEYWORDS: AIR- TEMPERATURE, CARBON DIOXIDE, CROP, CURD INITIATION, EFFICIENCY, ENRICHMENT, IRRADIANCE, MATURITY, PLANT GROWTH, PRODUCTIVITY

2566

Wheeler, T.R., T.D. Hong, R.H. Ellis, G.R. Batts, J.I.L. Morison, and P. Hadley. 1996. The duration and rate of grain growth, and harvest index, of wheat (Triticum aestivum L) in response to temperature and CO2. *Journal of Experimental Botany 47(298):623-630.*

Winter wheat (Triticum aestivum L. cv. Hereward) was grown in the field inside polyethylene-covered tunnels at a range of temperatures at either 380 or 684 mu mol mol(-1) CO2. Serial harvests were taken from anthesis until harvest maturity. Grain yield was reduced by warmer temperatures, but increased by CO2 enrichment at all temperatures, During grain-filling, individual grain dry weight was a linear function of time from anthesis until mass maturity (attainment of maximum grain dry weight) within each plot, The rate of progress to mass maturity (the reciprocal of time to mass maturity) was a positive linear function of mean temperature, but was not affected by CO2 concentration, The rate of increase in grain dry weight per ear was 2.0 mg d(-1) greater per 1 degrees C rise, and was 8.0 mg d(-1) greater at 684 compared with 380 mu mol mol(-1) CO2 at a given temperature, The rate of increase in harvest index was 1.0% d(-1) in most plots at 380 mu mol mol(-1) CO2 and in open field plots, compared with 1.18% d(-1) in all plots at 684 mu mol mol(-1) CO2. Thus, the increased rate of grain growth observed at an elevated CO2 concentration could be attributed partly to a change in the partitioning of assimilates to the grain, In contrast, the primary effect of warmer temperatures was to shorten the duration of grain-filling, The rate of grain growth at a given temperature and the rate of increase in harvest index were only independent of the number of grains per ear above a critical grain number of 23-24 grains per ear (similar to 20 000 grains m(-2)).

KEYWORDS: CROPS, DRY-MATTER ACCUMULATION, FIELD, PRODUCTIVITY, WINTER-WHEAT, YIELD

2567

Wheeler, T.R., J.I.L. Morison, R.H. Ellis, and P. Hadley. 1994. The effects of co2, temperature and their interaction on the growth and yield of carrot (daucus-carota L). *Plant, Cell and Environment 17(12):1275-1284.*

Stands of carrot (Daucus carota L.) were grown in the field within polyethylene-covered tunnels at a range of soil temperatures (from a mean of 7.5 degrees C to 10.9 degrees C) at either 348 (SE = 4.7) or 551 (SE = 7.7) mu mol mol(-1) CO2. The effect of increased atmospheric CO2 concentration on root yield was greater than that on total biomass, At the last harvest (137 d from sowing), total biomass was 16% (95% CI=6%, 27%) greater at 551 than at 348 mu mol mol(-1) CO2, and 37% (95% CI=30%, 44%) greater as a result of a 1 degrees C rise In soil temperature, Enrichment with CO2, or a 1 degrees C rise in soil temperature increased root yield by 31% (95% CI=19%, 45%) and 34% (95% CI=27%, 42%), respectively, at this harvest, No effect on total biomass or root yield of an interaction between temperature and atmospheric CO2 concentration at 137 DAS was detected, When compared at a given leaf number (seven leaves), CO2 enrichment increased total biomass by 25% and root yields by 80%, but no effect of differences in temperature on plant weights was found, Thus, increases in total biomass and root yield observed in the warmer crops were a result of the effects of temperature on the timing of crop growth and development, Partitioning to the storage roots during early root expansion was greater at 551 than at 348 mu mol mol(-1) CO2. The root to total weight ratio was unaffected by differences in temperature at 551 mu mol mol(-1) CO2, but was reduced by cooler temperatures at 348 mu mol mol(-1) CO2. At a given thermal time from sowing, CO2 enrichment increased the leaf area per plant, particularly during early root growth, primarily as a result of an increase in the rate of leaf area expansion, and not an increase in leaf number.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO2, CARBON DIOXIDE, CULTIVAR, DRY-MATTER, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, PRODUCTIVITY

2568

Whetton, P.H., A.M. Fowler, M.R. Haylock, and A.B. Pittock. 1993. Implications of climate-change due to the enhanced greenhouse- effect on floods and droughts in australia. *Climatic Change 25(3-4):289-317.*

Potential impacts of climate change on heavy rainfall events and flooding in the Australian region are explored using the results of a general circulation model (GCM) run in an equilibrium enhanced greenhouse experiment. In the doubled CO, simulation, the model simulates an increase in the frequency of high-rainfall events and a decrease in the frequency of low- rainfall events. This result applies over most of Australia, is statistically more significant than simulated changes in total rainfall, and is supported by theoretical considerations. We show that this result implies decreased return periods for heavy rainfall events. The further implication is that flooding could increase, although we discuss here the many difficulties associated with assessing in quantitative terms the significance of the modelling results for the real world. The second part of the paper assesses the implications of climate change for drought occurrence in Australia. This is undertaken using an off-line soil water balance model driven by observed time series of rainfall and potential evaporation to determine the sensitivity of the soil water regime to changes in rainfall and temperature, and hence potential evaporation. Potential impacts are assessed at nine sites, representing a range of climate regimes and possible climate futures, by linking this sensitivity analysis with scenarios of regional climate change, derived from analysis of enhanced greenhouse experiment results from five GCMs. Results indicate that significant drying may be limited to the south of Australia. However, because the direction of change in terms of the soil water regime is uncertain at all sites and for all seasons, there is no basis for statements about how drought potential may change.

KEYWORDS: CO2, GENERAL-CIRCULATION MODEL, RAINFALL, SOIL MOISTURE, VARIABILITY

2569

Whiley, A.W., C. Searle, B. Schaffer, and B.N. Wolstenholme. 1999. Cool orchard temperatures or growing trees in containers can inhibit leaf gas exchange of avocado and mango. *Journal of the American Society for Horticultural Science 124(1):46-51.*

Leaf gas exchange of avocado (Persea americana Mill.) and mango (Mangifera indica L.) trees in containers and in an orchard (field-grown trees) was measured over a range of photosynthetic photon fluxes (PPF) and ambient CO2 concentrations (C-a). Net CO2 assimilation (A) and intercellular partial pressure of CO2 (Ci) were determined for all trees in early autumn (noncold- stressed leaves) when minimum daily temperatures were greater than or equal to 14 degrees C, and for field-grown trees in winter (cold-stressed leaves) when minimum daily temperatures were less than or equal to 10 degrees C. Cold-stressed trees of both species had lower maximum CO2 assimilation rates (A(max)), light saturation points (Q(A)), CO2 saturation points (C-aSAT) and quantum yields than leaves of noncold-stressed, field-grown trees. The ratio of variable to maximum fluorescence (F-v/F-m) was approximate to 50% lower for leaves of cold-stressed, field-grown trees than for leaves of nonstressed, field-grown trees, indicating chill-induced photoinhibition of leaves had occurred in winter. The data indicate that chill-induced photoinhibition of A and/or sink limitations caused by root restriction in container-grown trees can limit carbon assimilation in avocado and mango trees.

KEYWORDS: ATMOSPHERIC CO2, CHLOROPHYLL, ELEVATED CARBON-DIOXIDE, ENRICHMENT, LEAVES, LIGHT, PHOTOINHIBITION, PHOTOSYNTHETIC ACCLIMATION, PLANTS,

ROOT RESTRICTION

2570

White, A., M.G.R. Cannell, and A.D. Friend. 1999. Climate change impacts on ecosystems and the terrestrial carbon sink: a new assessment. *Global Environmental Change-Human and Policy Dimensions 9:S21-S30.*

Climate output from the UK Hadley Centre's HadCM2 and HadCM3 experiments for the period 1860 to 2100, with IS92a greenhouse gas forcing, together with predicted patterns of N deposition and increasing CO2, were input (offline) to the dynamic vegetation model, Hybrid v4.1 (Friend et al., 1997; Friend and White, 1999). This model represents biogeochemical, biophysical and biogeographical processes, coupling the carbon, nitrogen and water cycles on a sub-daily timestep, simulating potential vegetation and transient changes in annual growth and competition between eight generalized plant types in response to climate. Global vegetation carbon was predicted to rise from about 600 to 800 PgC (or to 650 PgC for HadCM3) while the soil carbon pool of about 1100 PgC decreased by about 8%. By the 2080s, climate change caused a partial loss of Amazonian rainforest, C-4 grasslands and temperate forest in areas of southern Europe and eastern USA, but an expansion in the boreal forest area. These changes were accompanied by a decrease in net primary productivity (NPP) of vegetation in many tropical areas, southern Europe and eastern USA tin response to warming and a decrease in rainfall), but an increase in NPP of boreal forests. Global NPP increased from 45 to 50 PgC y(-1) in the 1990s to about 65 PgC y(-1) in the 2080s (about 58 PgC y(-1) for HadCM3). Global net ecosystem productivity (NEP) increased from about 1.3 PgC y(-1) in the 1990s to about 3.6 PgC y(-1) in the 2030s and then declined to zero by 2100 owing to a loss of carbon from declining forests in the tropics and at warm temperate latitudes - despite strengthening of the carbon sink at northern high latitudes. HadCM3 gave a mon erratic temporal evolution of NEP than HadCM2, with a dramatic collapse in NEP in the 2050s.

KEYWORDS: BALANCE, BIOSPHERE, CYCLE, DYNAMICS, FOREST, MODELS, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION

2571

White, N.D.G., D.S. Jayas, and W.E. Muir. 1995. Toxicity of carbon-dioxide at biologically producible levels to stored-product beetles. *Environmental Entomology 24(3):640-647.*

The effect of concentrations of carbon dioxide (CO2) that can be produced by biological respiration (7.5-19.2%) on oviposition of adult Tribolium castaneum (Herbst), Cryptolestes pusillus (Schonherr), or C. ferrugineus (Stephens) was determined. Relative to controls, T. castaneum, C. pusillus, and C. ferrugineus, exposed to 7.5% CO2 for 1 wk, had numbers of offspring reduced by 43, 94, and 50%, respectively, and the total population at 6 wk was reduced 53, 84, and 19%, respectively. With levels of greater than or equal to 17.1% CO2 for 1 wk, no offspring were produced and exposed adults had high mortality. Eggs and subsequent immatures of Tribolium confusum J. du Val, T. castaneum, or C. ferrugineus were exposed for 3 wk to elevated levels of CO2 at 22 degrees C. Insect development was similar at 7.5 and 8.6% CO2 with mean mortality 43, 62, and 30% greater than controls for T. confusum, T. castancum, and C. ferrugineus, respectively. Also, mean levels of 5.8-8.3% CO2 for 7 wk reduced, on all sampling dates, populations of T. confusum by 85%, T. castaneum by 99%, C. pusillus by 68%, and C. ferrugineus by 54%. Although T. castaneum had a greater oviposition rate than C. pusillus at 7.5% CO2, immature mortality was greater for T. castaneum. Based on long-term exposure to levels of CO2 which can be produced by biological activity that affects oviposition and immature development, species in increasing order of sensitivity to CO2 are C. ferrugineus, C. pusillus, T. confusum, and T. castaneum.

KEYWORDS: COLEOPTERA, CRYPTOLESTES-FERRUGINEUS, CUCUJIDAE, MODEL, RUSTY GRAIN BEETLE, WHEAT

2572

Whitehead, D., K.P. Hogan, G.N.D. Rogers, J.N. Byers, J.E. Hunt, T.M. McSeveny, D.Y. Hollinger, R.J. Dungan, W.B. Earl, and M.P. Bourke. 1995. Performance of large open-top chambers for long-term field investigations of tree response to elevated carbon dioxide concentration. *Journal of Biogeography 22(2-3):307-313.*

In preparation for an investigation of the effects of elevated carbon dioxide (CO2) concentration on the two tree species Pinus radiata D. Don and Nothofagus fusca (Hook. f.) Oerst, the environmental conditions inside sixteen open-top chambers, of the design described by Heagle et al. (1989), were measured and compared with those outside. During a period in late summer, both air temperature and air saturation deficit were greater inside the chambers, with mean increases of 0.3 degrees C and 0.1 kPa, respectively. The increases were closely related to solar irradiance, reaching maximum differences for temperature and air saturation deficit of 4.3 degrees C and 0.8 kPa, respectively, when solar irradiance was greater than 1600 mu mol m(-2)s(-1). The mean (+/- standard deviation) CO2 concentrations for the ambient and elevated treatments were 362+/-37 and 654+/-69 mu mol mol(-1), respectively. However, the CO2 concentration in the elevated treatment decreased as windspeed increased, owing to incursions of ambient air into the chambers. Transmittance of visible solar irradiance (400- 700 nm) through the plastic wall material decreased by 7% after 1 year of exposure at the site. In cloudy conditions the mean transmittance of solar irradiance into the chambers was 81% and on clear days this decreased from 80% to 74% with increasing solar zenith angle. The ratio of diffuse to total solar irradiance in the chambers was 13% and 21% greater than that outside for cloudy and clear conditions, respectively. The implications of these differences on water use efficiency for the trees growing inside and outside the chamber are discussed. A cost effective system, built to separate the CO2 required for the experiment from waste biogas, is described. This project is contributing to the Global Change and Terrestrial Ecosystems (GCTE) Core Research Programme by providing data on the long- term effects of elevated CO2 concentration on the above and below-ground carbon balance for the two tree species.

KEYWORDS: CO2, DESIGN, VENTILATED CHAMBER

2573

Whitehead, S.J., S.J.M. Caporn, and M.C. Press. 1997. Effects of elevated CO2, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: Calluna vulgaris and Pteridium aquilinum. *New Phytologist 135(2):201-211.*

Bracken (Pteridium aquilinum (L.) Kuhn) and heather (Calluna vulgaris (L.) Hull) are important upland species which often grow in close proximity in the UK. The effects of factorial treatments of elevated atmospheric CO2 (539 mu mol mol(-1) as opposed to ambient atmospheric CO2 concentrations of 355 mu mol mol(-1)), added N (50 kg N hs(-1) as NH4NO3) and added P (20 kg P ha(-1) as NaH2PO4) on the performance of these two species were studied under controlled environmental conditions using container-grown plants. Plants grown and measured at high CO2 had higher rates of net photosynthesis than those grown and measured in ambient CO2. This increase was greater in heather than in bracken and resulted in a large stimulation of growth in the former. In bracken there was no significant change in plant size or phenology. The increase in biomass of heather in high CO2 was greatest in the absence of added nutrients and lowest when both N and P were supplied. The growth and photosynthesis of both plants responded

positively to the supply of P alone or P with N (in both CO2 atmospheres), but there was little response to N alone. The implications of these findings for bracken and heather growing in the held under conditions of an elevated CO2 atmosphere and greater nutrient availability are discussed.

KEYWORDS: BRACKEN, CONSERVATION, ENGLAND, ENRICHMENT, L HULL, L KUHN, MANAGEMENT, NUTRIENTS, TEMPERATURE, VEGETATION

2574

Whiting, D.C., J. Vandenheuvel, and S.P. Foster. 1992. Potential of low oxygen moderate carbon-dioxide atmospheres for postharvest disinfestation of new-zealand apples. *New Zealand Journal of Crop and Horticultural Science 20(2):217-222.*

Work on the mortality responses of four lepidopteran pests of apples in New Zealand-Epiphyas postvittana (Walker), Cydia pomonella (L.), Planotortrix octo Dugdale, and Ctenopseustis obliquana (Walker)-to low O2/moderate CO2 atmospheres is reviewed and additional data are presented. For both E. postvittana and C pomonella, reducing the O2 concentration and elevating the treatment temperature enhanced controlled atmosphere (CA) efficacy more than did increasing the CO2 concentration. Thus at 20-degrees-C, a 0.4% O2/5.0% CO2 CA gave the most rapid kill of the mixtures tested. The order of lifestage tolerance to this CA was similar for E. postvittana, C. pomonella, P. octo, and C. obliquana i.e., fifth instar > third instar > 3-day eggs > first instar. The four species exhibited a trend of tolerance of C pomonella > E. postvittana = P. octo = C obliquana. An increase in the temperature to 30- degrees-C decreased the time for high mortality for all four species. However, this decrease was much greater for P. octo and C obliquana than for C pomonella and E. postvittana. The potential of these CA treatments for disinfestation of New Zealand apples for the Japanese and United States markets is discussed.

2575

Whiting, G.J., and J.P. Chanton. 1993. Primary production control of methane emission from wetlands. *Nature 364(6440):794-795.*

WETLANDS, both natural and agricultural, contribute an estimated 40 to 50% of the total methane emitted to the atmosphere each year. Recent efforts in atmospheric modelling1 and attempts to constrain CH4 source strengths2 have indicated the need to delineate the processes responsible for the large variations in emission rates found within and across wetland types. Numerous biogeochemical factors are known to affect the activity of methanogenic bacteria3,4 and although there has been some success in relating water level5-7 and temperature8,9 to CH4 emissions within particular systems, these variables are insufficient for predicting emissions across a variety of wetlands2,10. From simultaneous measurements of CO2 and CH4 exchange in wetlands extending from subarctic peatlands to subtropical marshes, we report here a positive correlation between CH4 emission and net ecosystem production and suggest that net ecosystem production is a master variable, integrating many factors which control CH4 emission in vegetated wetlands. We find that about 3 per cent of the daily net ecosystem production is emitted back to the atmosphere as CH4. With projected stimulation of primary production and soil microbial activity in wetlands associated with elevated atmospheric CO2 concentrations11, we envisage the potential for increasing CH4 emissions from inundated wetlands, further enhancing the greenhouse effect.

KEYWORDS: ARCTIC TUNDRA, ATMOSPHERE, BELOWGROUND BIOMASS, CO2 EXCHANGE, METHANOGENESIS, RICE PADDIES, SOIL, SPARTINA-ALTERNIFLORA, TRANSPORT, VEGETATION

2576

Whitney, S.M., S. von Caemmerer, G.S. Hudson, and T.J. Andrews. 1999. Directed mutation of the Rubisco large subunit of tobacco influences photorespiration and growth. *Plant Physiology 121(2):579-588.*

The gene for the large subunit of Rubisco was specifically mutated by transforming the chloroplast genome of tobacco (Nicotiana tabacum). Codon 335 was altered to encode valine instead of leucine. The resulting mutant plants could not grow without atmospheric CO2 enrichment. In 0.3% (v/v) CO2, the mutant and wildtype plants produced similar amounts of Rubisco but the extent of carbamylation was nearly twice as great in the mutants. The mutant enzyme's substrate-saturated CO2-fixing rate and its ability to distinguish between CO2 and O-2 as substrates were both reduced to 25% of the wild type's values. Estimates of these parameters obtained from kinetic assays with the purified mutant enzyme were the same as those inferred from measurements of photosynthetic gas exchange with leaves of mutant plants. The Michaelis constants for CO2, O-2, and ribulose-1,5-bisphosphate were reduced and the mutation enhanced oxygenase activity at limiting O-2 concentrations. Consistent with the reduced CO2 fixation rate at saturating CO2, the mutant plants grew slower than the wild type but they eventually flowered and reproduced apparently normally. The mutation and its associated phenotype were inherited maternally. The chloroplast-transformation strategy surmounts previous obstacles to mutagenesis of higher-plant Rubisco and allows the consequences for leaf photosynthesis to be assessed.

KEYWORDS: BISPHOSPHATE, CARBAMYLATION, CHLOROPLAST GENOME, GENE, NICOTIANA-TABACUM, PHOTOSYNTHESIS, PLASTID TRANSFORMATION, RIBULOSE 1;5-BISPHOSPHATE, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TRANSGENIC TOBACCO

2577

Whittaker, J.B. 1999. Impacts and responses at population level of herbivorous insects to elevated CO2. *European Journal of Entomology 96(2):149-156.*

Most studies of responses of insects to elevated carbon dioxide have been made using short-term exposures to treated food plants and have involved measurements of responses in growth, reproduction, food consumption and efficiencies of conversion at specific stages in the life cycle. These will be reviewed in the light of longer-term studies recently published where whole generations have been reared in chambers with simultaneous treatment of plants and where insects have been free to select their food and microenvironment. Factors such as seasonal change in plants, choice of food plant, mode of feeding, timing of exposure, temperature, the role of natural enemies are considered and the whole placed in the context of other aspects of climate change. It is concluded that in studies to date, the only feeding guild in which some species have shown increases in population density in elevated carbon dioxide are the phloem feeders. Chewing insects (both free-living,and mining) generally have shown no change or reduction in abundance, though relative abundance may be greatly affected. Compensatory feeding is common in these groups.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, AUCHENORRHYNCHA, CHAMBERS, CLIMATE CHANGE, COTTON, GROWTH, HOMOPTERA, LEPIDOPTERA, NOCTUIDAE, PERFORMANCE

2578

Wiemken, V., L. Kossatz, and K. Ineichen. 1996. Frost hardiness of Norway spruce grown under elevated atmospheric CO2 and increased nitrogen fertilizing. *Journal of Plant Physiology 149(3-4):433-438.*

Frost hardiness was tested on needles from 6-years-old Norway spruces that had been cultivated for 2 years in artificial ecosystems at an atmospheric CO2 concentration of 280, 420 or 560 ppm and a nitrogen fertilization corresponding to 0, 30, and 90 kg N ha(-1) yr(-1) (NH4NO3) as well as combinations of these treatments. Samples of previous year's needles were taken after completion of frost hardening in autumn, and at three dares during the dehardening process in spring when potentially harmful late frost events naturally occur. The needles were exposed to freezing temperatures down to -35 degrees C. Samples were taken at 5 degrees C intervals and frost injury was estimated by the electrolyte leakage technique. After autumnal hardening, needles were injured only below -25 degrees C (LT50 < -30 degrees C), while after dehardening in spring the critical frost temperature (LT50) was around -10 degrees C. Frost hardiness was not influenced by the different CO2 and nitrogen treatments of the trees neither in autumn nor during the dehardening phase in spring.

KEYWORDS: CARBOHYDRATE, CONTAINERIZED BLACK SPRUCE, METABOLISM, PHOTOPERIOD, RED SPRUCE, RESISTANCE, SEASONAL-CHANGES, SEEDLINGS, SITKA SPRUCE, TEMPERATURE

2579

Wiemken, V., L. Kossatz, K. Ineichen, and A. Wiemken. 1996. Frost hardiness of Norway spruce grown under elevated atmospheric CO2 and increased nitrogen fertilization. *Plant Physiology 111(2):612.*

2580

Wilkins, D., J.J. Vanoosten, and R.T. Besford. 1994. Effects of elevated co2 on growth and chloroplast proteins in prunus-avium. *Tree Physiology 14(7-9):769-779.*

To predict the future carbon sequestering capacity of trees, we need information about the possible acclimatory mechanisms of plant growth and photosynthesis in rising atmospheric CO2 under a variety of environmental conditions. We have, therefore, studied the growth response of a tree species (Prunus avium L. Stella (wild cherry)) to elevated CO2 and characterized the associated changes in photosynthetic machinery of the leaf tissue. Self-pollinated seedlings and mature cuttings (clones) from the same parent plant of P. avium were grown for two consecutive growing seasons (about 60 days each) in ambient CO2 (350 mumol mol-1 CO2) or elevated CO2 (700 mumol Mol-1 CO2) with a high or low nutrient supply. The degree of acclimation of leaf biochemistry and growth response to elevated CO2 was dependent on the plant material (seedling or mature cutting) and nutrient supply. There was little or no growth response to elevated CO2 in seedlings or cuttings in the low nutrient supply treatments, whereas, in both seasons, there was a strongly positive growth response to elevated CO2 in seedlings and cuttings in the high nutrient supply regimes, resulting in increases in the root/shoot ratio and in carbon allocation to the roots. In contrast, the protein content and activity of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco, EC 4.1.1.39) were down regulated in elevated CO2. The loss of Rubisco on an area basis in plants in the elevated CO2 treatments was compensated for at the canopy level by increased leaf area. The loss of Rubisco protein was accompanied by decreases in the contents of chlorophyll and the thylakoid membrane proteins D1, D2 and cytochrome f, which are involved in light harvesting and photo-electron transport. We conclude that, in the medium- to long-term, the initial stimulation of biomass production by elevated CO2 may be increasingly offset by a lower photosynthetic capacity per unit leaf area in perennial plants.

2581

Wilks, D.S., D.W. Wolfe, and S.J. Riha. 1995. Simple carbon assimilation response functions from atmospheric co2, and daily temperature and shortwave radiation. *Global Change Biology 1(5):337-346.*

A global 'CO2 fertilizer effect' multiplier is often used in crop or ecosystem models because of its simplicity. However, this approach does not take into account the interaction between CO2, temperature and light on assimilation. This omission can lead to significant under- or overestimation of the magnitude of beneficial effects from elevated CO2, depending on environmental conditions. We use a mechanistic model of the biochemistry of photosynthesis to represent the response of net assimilation to different levels of CO2, temperature and radiation, on the daily time scale. Instantaneous assimilation rates for an idealized canopy model are integrated through diurnal cycles of environmental variables derived from historical climate data at three locations in North America. The calculated CO2 fertilizer effect is greatest at high light and warm temperatures. The results are summarized by assimilation response surfaces specified by the CO2 concentration, the canopy leaf area index, and by daily values of temperature and radiation available from climatic records. These summary functions are suitable for incorporation into crop or ecosystem models for predicting carbon assimilation or biomass production on a daily time step. An example application of the function reveals that for a relatively cool, high latitude location, the beneficial effects from a CO2 doubling would be negligible during the early spring, even assuming a + 4 degrees C global warming scenario. In contrast, the beneficial effects from increasing CO2 at a relatively warm, lower latitude location are greatest in the spring, but decline in late summer because of excessively warm temperatures with a + 4 degrees C global warming.

KEYWORDS: C-3 PLANTS, CARBOXYLASE, DIOXIDE, ELECTRON-TRANSPORT, ELEVATED CO2, GROWTH, MODEL, PHOTOSYNTHESIS

2582

Will, R.E., and R. Ceulemans. 1997. Effects of elevated CO2 concentration on photosynthesis, respiration and carbohydrate status of coppice Populus hybrids. *Physiologia Plantarum 100(4):933-939.*

To determine how increased atmospheric CO2 will affect the physiology of coppiced plants, sprouts originating from two hybrid poplar clones (Populus trichocarpa x P. deltoides - Beaupre and P. deltoides x P. nigra - Robusta) were grown in open-top chambers containing ambient or elevated (ambient + 360 mu mol mol(-1)) CO2 concentration. The effects of elevated CO2 concentration on leaf photosynthesis, stomatal conductance, dark respiration, carbohydrate concentration and nitrogen concentration were measured. Furthermore, dark respiration of leaves was partitioned into growth and maintenance components by regressing specific respiration rate vs specific growth rate. Sprouts of both clones exposed to CO2 enrichment showed no indication of photosynthetic down-regulation. During reciprocal gas exchange measurements, CO2 enrichment significantly increased photosynthesis of all sprouts by approximately 60% ($P < 0.01$) on both an early and late season sampling date, decreased stomatal conductance of all sprouts by 10% ($P < 0.04$) on the early sampling date and nonsignificantly decreased dark respiration by an average of 11%. Growth under elevated CO2 had no consistent effect on foliar sugar concentration but significantly increased foliar starch by 80%. Respiration rate was highly correlated with both specific growth rate and percent nitrogen. Long-term CO2 enrichment did not significantly affect the maintenance respiration coefficient or the growth respiration coefficient. Carbon dioxide enrichment affected the physiology of the sprouts the same way it affected these plants before they were coppiced.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE ENRICHMENT, ECOPHYSIOLOGY, EURAMERICANA, GAS-

EXCHANGE, GROWTH, MAINTENANCE RESPIRATION, POPLAR, REINVIGORATION, SHOOT DECAPITATION

2583

Will, R.E., and R.O. Teskey. 1997. Effect of elevated carbon dioxide concentration and root restriction on net photosynthesis, water relations and foliar carbohydrate status of loblolly pine seedlings. *Tree Physiology 17(10):655-661.*

To determine the effects of CO2-enriched air and root restriction on photosynthetic capacity, we measured net photosynthetic rates of 1-year-old loblolly pine seedlings grown in 0.6-, 3.8- or 18.9-liter pots in ambient (360 mu mol mol(-1)) or 2x ambient CO2 (720 mu mol mol(-1)) concentration for 23 weeks. We also measured needle carbohydrate concentration and water relations to determine whether feedback inhibition or water stress was responsible for any decreases in net photosynthesis. Across all treatments, carbon dioxide enrichment increased net photosynthesis by approximately 60 to 70%. Net photosynthetic rates of seedlings in the smallest pots decreased over time with the reduction occurring first in the ambient CO2 treatment and then in the 2x ambient CO2 treatment. Needle starch concentrations of seedlings grown in the smallest pots were two to three times greater in the 2x ambient CO2 treatment than in the ambient CO2 treatment, but decreased net photosynthesis was not associated with increased starch or sugar concentrations. The reduction in net photosynthesis of seedlings in small pots was correlated with decreased needle water potentials, indicating that seedlings in the small pots had restricted root systems and were unable to supply sufficient water to the shoots. We conclude that the decrease in net photosynthesis of seedlings in small pots was not the result of CO2 enrichment or an accumulation of carbohydrates causing feedback inhibition, but was caused by water stress.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, COTTON, GAS-EXCHANGE, GROWTH, LEAF, PERSPECTIVE, RESPONSES, STRESS, TREES

2584

Will, R.E., and R.O. Teskey. 1997. Effect of irradiance and vapour pressure deficit on stomatal response to CO2 enrichment of four tree species. *Journal of Experimental Botany 48(317):2095-2102.*

The stomatal response of seedlings grown in 360 or 720 mu mol mol(-1) to irradiance and leaf-to-air vapour pressure deficit (VPD) at both 360 and 720 mu mol mol(-1) CO2, was measured to determine how environmental factors interact with CO2 enrichment to affect stomatal conductance, Seedlings of four species with different conductances and life histories, Cercis canadensis (L.), Quercus rubra (L.), Populus deltoides (Bartr. ex Marsh.) x P. nigra (L.), and Pinus taeda (L.), were measured in hopes of identifying general responses, Conductance of seedlings grown at 360 and 720 mu mol mol-l CO2 were similar and responded in the same manner to measurement CO2 concentration, irradiance and VPD, Conductance was lower for all species where measured at 720 than when measured at 360 mu mol mol(-1) CO2 at both VPDs (similar to 1.5 and similar to 2.5 kPa) and all measured irradiances greater than zero (100, 300, 600, > 1600 mu mol m(-2) s(-1)). The average decrease in conductance due to measurement in elevated CO2 concentration was 32% for Cercis, 29% for Quercus, 26% for Populus, and 11% for Pinus, For all species, the absolute decrease in conductance due to measurement in CO2 enrichment decreased as irradiance decreased or VPD increased, The proportional decrease due to measurement in CO2 enrichment decreased in three of eight cases: from 0.46 to 0.10 in Populus and from 0.18 to 0.07 in Pinus as irradiance decreased from > 1600 to 100 mu mol m(-2) s(-1) and from 0.35 to 0.24 in Cercis as VPD increased from 1.3 to 2.6 kPa.

KEYWORDS: ASSIMILATION, CONDUCTANCE, EFFICIENCY, ELEVATED CARBON-DIOXIDE, HUMIDITY, LEAF GAS-EXCHANGE, LIGHT, PINUS TAEDA L, SENSITIVITY, WATER-STRESS

2585

Willekens, H., S. Chamnongpol, M. Davey, M. Schraudner, C. Langebartels, M. VanMontagu, D. Inze, and W. VanCamp. 1997. Catalase is a sink for H2O2 and is indispensable for stress defence in C-3 plants. *Embo Journal 16(16):4806-4816.*

Hydrogen peroxide (H2O2) has been implicated in many stress conditions, Control of H2O2 levels is complex and dissection of mechanisms generating and relieving H2O2 stress is difficult, particularly in intact plants, We have used transgenic tobacco with similar to 10% wild-type catalase activity to study the role of catalase and effects of H2O2 stress in plants, Catalase-deficient plants showed no visible disorders at low Light, but in elevated light rapidly developed white necrotic lesions on the leaves, Lesion formation required photorespiratory activity since damage was prevented under elevated CO2, Accumulation of H2O2 was not detected during leaf necrosis, Alternative H2O2-scavenging mechanisms may have compensated for reduced catalase activity, as shown by increased ascorbate peroxidase and glutathione peroxidase levels, Leaf necrosis correlated with accumulation of oxidized glutathione and a 4-fold decrease in ascorbate, indicating that catalase is critical for maintaining the redox balance during oxidative stress, Such control may not be limited to peroxisomal H2O2 production, Catalase functions as a cellular sink for H2O2, as evidenced by complementation of catalase deficiency by exogenous catalase, and comparison of catalase- deficient and control leaf discs in removing external H2O2. Stress analysis revealed increased susceptibility-of catalase- deficient plants to paraquat, salt and ozone, but not to chilling.

KEYWORDS: ASCORBATE PEROXIDASE, DEFICIENT MUTANT, DISEASE RESISTANCE RESPONSE, GLUTATHIONE-REDUCTASE, HORDEUM VULGARE L, HYDROGEN- PEROXIDE, OXIDATIVE STRESS, SIGNAL-TRANSDUCTION, SUPEROXIDE-DISMUTASE, TRANSGENIC TOBACCO

2586

Williams, D.W., and A.M. Liebhold. 1995. Herbivorous insects and global change: Potential changes in the spatial distribution of forest defoliator outbreaks. *Journal of Biogeography 22(4-5):665-671.*

The geographical ranges and the spatial extent of outbreaks of herbivorous species are likely to shift with climatic change. We investigated potential changes in spatial distribution of outbreaks of the western spruce budworm, Choristoneura occidentalis Freeman, in Oregon, U.S.A. and the gypsy moth, Lymantria dispnr (L.), in Pennsylvania, U.S.A. using maps of historical defoliation, climate and forest composition in a geographic information system. Maps of defoliation frequency were assembled using historical aerial reconnaissance data. Maps of monthly means of daily temperature maxima and minima and of monthly precipitation averaged over 30 years were developed using an interpolation technique. All maps were at a spatial resolution of 2 x 2 km. Relationships between defoliation status and the environmental variables were modelled using a linear discriminant function. Five climatic change scenarios were investigated: an increase of 2 degrees C, a 2 degrees increase with an increase of 0.5 mm per day in precipitation, a 2 degrees C increase with an equivalent decrease in precipitation, and equilibrium projections of temperature and precipitation by two general circulation models (GCMs) at doubled CO2. With an increase in temperature alone, the projected defoliated area decreased relative to ambient conditions for the budworm and increased slightly for the gypsy moth. With an increase in temperature and precipitation the defoliated area increased for both species.

Conversely, the defoliated area decreased for both when temperature increased and precipitation decreased. Results for the GCM scenarios contrasted sharply. For the Geophysical Fluids Dynamics Laboratory model, defoliation by budworm was projected to cover Oregon completely, whereas no defoliation was projected by gypsy moth in Pennsylvania. For the Goddard Institute for Space Studies model, defoliation disappeared completely for the budworm and slightly exceeded that under ambient conditions for the gypsy moth. The results are discussed :in terms of potential changes in forest species composition.

KEYWORDS: CLIMATIC CHANGE, PESTS

2587

Williams, M., and J.L. Harwood. 1997. Effects of carbon dioxide concentration and temperature on lipid synthesis by young wheat leaves. *Phytochemistry 45(2):243-250.*

The effects of incubation temperature and CO2 concentration on lipid synthesis in leaves from 7-day-old wheat plants were studied. Plants were cultivated at 350 mu mol mol(-1) (approximately ambient CO2) and 20 degrees so that, irrespective of the subsequent incubation conditions, the samples were all derived from plants at the same phenological stage of development. Leaf tissue was incubated with [1-C-14]acetate at 350 mu mol mol(-1) or 700 mu mol mol(-1) CO2 concentration and at 20 degrees or 24 degrees. Doubling the CO2 concentration had little or no effect on lipid metabolism. In contrast, a 4 degrees rise in incubation temperature not only increased the rate of radiolabelling but also altered lipid synthesis qualitatively. Most noticeable of these changes was a marked increase in phosphatidylcholine labelling evidently at the expense of that of diacylglycerol. The increase in carbon flux to this extrachloroplastic lipid appeared to be restricted to the distal portions of the leaf tissue, thus indicating that the stage of tissue development was critical. Surprisingly, an increase of polyunsaturated fatty acid labelling was found at the higher incubation temperature. This increase was accompanied by a decrease in labelling of oleate in the main radiolabelled membrane lipids. In phosphatidylcholine the decrease in oleate labelling was compensated by a rise in that of linoleate while in monogalactosyldiacylglycerol, both linoleate and a-linolenate were better labelled at 24 degrees. A molecular basis for these alterations in lipid synthesis and acyl desaturation is suggested. (C) 1997 Elsevier Science Ltd.

KEYWORDS: CO2 CONCENTRATION, ELEVATED CO2, FATTY-ACID SYNTHESIS, GRAIN LIPIDS, GREEN LEAVES, METABOLISM, NITROGEN APPLICATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, WINTER-WHEAT

2588

Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, S.C. Wofsy, G.R. Shaver, J.M. Melillo, J.W. Munger, S.M. Fan, and K.J. Nadelhoffer. 1996. Modelling the soil-plant-atmosphere continuum in a Quercus-Acer stand at Harvard forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant, Cell and Environment 19(8):911-927.*

Our objective is to describe a multi-layer model of C-3-canopy processes that effectively simulates hourly CO2 and latent energy (LE) fluxes in a mixed deciduous Quercus-Acer (oak- maple) stand in central Massachusetts, USA, The key hypothesis governing the biological component of the model is that stomatal conductance (g(s)) is varied so that daily carbon uptake per unit of foliar nitrogen is maximized within the limitations of canopy water availability, The hydraulic system is modelled as an analogue to simple electrical circuits in parallel, including a separate soil hydraulic resistance, plant resistance and plant capacitance for each canopy layer, Stomatal opening is initially controlled to conserve plant water stores and delay the onset of water stress, Stomatal closure at a threshold minimum leaf water potential prevents xylem cavitation and controls the maximum rate of water flux through the hydraulic system, We show a strong correlation between predicted hourly CO2 exchange rate (r(2) = 0 . 86) and LE (r(2) = 0 . 87) with independent whole-forest measurements made by the eddy correlation method during the summer of 1992, Our theoretical derivation shows that observed relationships between CO2 assimilation and LE flux can be explained on the basis of stomatal behaviour optimizing carbon gain, and provides an explicit link between canopy structure, soil properties, atmospheric conditions and stomatal conductance.

KEYWORDS: BOUNDARY-LAYER, CANOPY STRUCTURE, CARBON GAIN, CO2 ASSIMILATION, ELEVATED CO2, GAS-EXCHANGE, TERRESTRIAL ECOSYSTEMS, WATER-STRESS, WOODY-PLANTS, XYLEM DYSFUNCTION

2589

Williams, M., E.J. Robertson, R.M. Leech, and J.L. Harwood. 1998. The effects of elevated atmospheric CO2 on lipid metabolism in leaves from mature wheat (Triticum aestivum cv Hereward) plants. *Plant, Cell and Environment 21(9):927-936.*

Winter wheat (Triticum aestivum L. cv, Hereward) plants were grown for 35 d either at 350 mu mol mol(-1) CO2 or at 650 mu mol mol(-1) CO2. Lipid synthesis was studied in these plants by incubating the 5th leaf on the main stem with [1-C-14]acetate. Increased CO2 concentrations did not significantly affect the total incorporation of radiolabel into lipids of whole leaf tissue, but altered the distribution for individual lipid classes. Most noticeable amongst acyl lipids was the reduction in labelling of diacylglycerol and a corresponding increase in the proportion of phosphatidylcholine labelling. In the basal regions, there were similar changes and, in addition, phosphatidylglycerol labelling was particularly increased following growth in an enriched CO2 atmosphere. The stimulation of labelling of the mitochondrial-specific lipid, diphosphatidylglycerol, prompted an examination of the mitochondrial population in wheat plants. Mitochondria were localized in intact wheat sections by immunolabelling for the mitochondrial-specific chaperonin probe. Growth in elevated CO2 doubled the number of mitochondria compared to growth in ambient CO2. Fatty acid labelling was also significantly influenced following growth at elevated CO2 concentrations. Most noticeable were the changes in 16C:18C ratios for the membrane lipids, phosphatidylcholine, phosphatidylglycerol and monogalactosyldiacylglycerol. These data imply a change in the apportioning of newly synthesized fatty acids between the 'eukaryotic' and 'prokaryotic' pathways of metabolism under elevated CO2.

KEYWORDS: ACID, BIOSYNTHESIS, CARBON DIOXIDE, GRAIN LIPIDS, GREEN LEAVES, GROWTH, NITROGEN APPLICATION, PHOTOSYNTHETIC ACCLIMATION, TEMPERATURE, YIELD

2590

Williams, M., E.J. Robertson, R.M. Leech, and J.L. Harwood. 1998. Lipid metabolism in leaves from young wheat (Triticum aestivum cv. Hereward) plants grown at two carbon dioxide levels. *Journal of Experimental Botany 49(320):511-520.*

Lipid synthesis was studied in primary leaves from 7-d-old wheat plants which had been grown at either ambient CO2 concentration (350 mu mol mol(-1)) or elevated CO2 (650 mu mol mol(-1)) by incubating tissue samples with [1-C-14]acetate, Growth at different CO2 concentrations did not affect the total incorporation of radiolabel into lipids but it did influence the relative labelling of individual lipid classes, such as

diacylglycerol. The leaf basal segment was also studied separately and growth in an enriched CO2 atmosphere was associated with a dramatic increase (over 6-fold) in diphosphatidylglycerol (cardiolipin) labelling, indicating an increased rate of mitochondrial membrane biogenesis, Immunocytological observations correlated with this metabolic result. Both leaf samples showed significant decreases in pigment and surface wax labelling caused by growth at elevated CO2. Growth at different CO2 concentrations also influenced fatty acid labelling patterns, particularly those of the major labelled membrane lipids of the primary leaf whereby there were changes in their ratios of radiolabelled 16 carbon to 18 carbon fatty acids. Phosphatidylglycerol was characterized, for instance, by increased palmitate labelling after wheat was grown in elevated CO2 concentrations, In contrast, phosphatidylcholine was marked by a dramatic decrease in palmitate labelling but a corresponding increase in labelling of its 18 carbon unsaturated fatty acids, The diacylglycerol fraction showed increased unsaturation of its C18 fatty acids. In addition, changes to the fatty acid moieties from the basal segment lipids were also associated with changes in the amount of labelling of the polyenoic fatty acids of monogalactosyldiacylglycerol. Possible reasons for these changes in lipid labelling are discussed. The data show that growth in elevated atmospheric CO2 concentrations causes significant changes in the metabolism of leaf lipids as well as increasing mitochondrial biogenesis.

KEYWORDS: ATMOSPHERIC CO2, CO2 CONCENTRATION, ELEVATED CO2, GRAIN LIPIDS, GREEN LEAVES, INCREASING CO2, NITROGEN APPLICATION, TEMPERATURE, WINTER-WHEAT, YIELD

2591

Williams, M., P.R. Shewry, and J.L. Harwood. 1994. The influence of the greenhouse-effect on wheat (triticum- aestivum L) grain lipids. *Journal of Experimental Botany 45(279):1379-1385.*

There have been few studies conducted with the objective of investigating comprehensively the 'greenhouse effect' on wheat growth using field-grown crops and even less on the effects on the lipid composition of harvested grains. Therefore, the aim of this study was to define any changes in wheat grain acyl lipids which could result from alterations in environmental growth conditions predicted to mimic the 'greenhouse effect'. Quantitative changes were recorded for both the non-starch and starch lipids. When supplied with low concentrations of nitrogen fertilizer, plants showed increased amounts of total grain lipids when grown under an elevated (700 mu l l(-1)) carbon dioxide atmosphere. Increasing the ambient temperature by 4 degrees C, however, reduced the total lipid content of grains. Wheat plants treated with high concentrations of nitrogen fertilizer accumulated less lipid compared to low nitrogen controls. Qualitative changes were also observed in the proportions of non-starch and starch lipid classes. However, changes in total acyl composition were limited to starch grain acyl lipids, as a result of changes in atmospheric carbon dioxide, growth temperature and nitrogen fertilizer application. The alterations in wheat lipids observed are likely to affect the properties of the flour produced from the grains.

KEYWORDS: CARBON DIOXIDE, CO2 CONCENTRATION, ELEVATED CO2, NITROGEN, PHOTOSYNTHESIS, PHYSIOLOGY, TEMPERATURE, YIELD

2592

Williams, M., P.R. Shewry, D.W. Lawlor, and J.L. Harwood. 1995. The effects of elevated-temperature and atmospheric carbon- dioxide concentration on the quality of grain lipids in wheat (triticum-aestivum L) grown at 2 levels of nitrogen application. *Plant, Cell and Environment 18(9):999-1009.*

Wheat plants were cultivated under growth regimes combining two temperatures (ambient and 4 degrees C above ambient temperature) with two concentrations of carbon dioxide (350 and 700 mu mol mol(-1)) and two nitrogen fertilizer applications (high and low), The aim of this study was to define any changes in the acyl lipid composition of wheat grains which could result from alterations in the growth conditions, Qualitative and quantitative changes were observed in both non-starch and starch lipid fractions, Temperature was by far the most influential growth factor, although interactions between all three growth conditions occurred, as confirmed by analysis of variance, Growth at elevated temperatures had the general effect of reducing the amounts of accumulated lipids, particularly non-polar lipids (1322mg fatty acids per 100g fresh weight at ambient temperatures as opposed to 777mg fatty acids per 100 g fresh weight at 4 degrees C above ambient temperatures), There were changes in the proportions of the major non-starch as well as the starch lipids, In the former category, non-polar lipids (principally triacylglycerols), the membrane glycosylglycerides and phosphatidylcholine were the main constituents, whereas in the starch lipids, lysophosphatidylcholine and lysophosphatidylethanolamine represented over 70% of the total, Depending on the growth conditions, the percentages of lipids such as monogalactosyldiacylglycerol, digalactosyldiacylglycerol and phosphatidylcholine (non-starch) or the starch lysophosphatidylethanolamine varied 2-fold or more, Significant changes in the acyl composition of individual lipids were also observed, most often in the proportions of palmitate, oleate and linoleate, The observed alterations in wheat lipids are likely to affect the properties of any flours derived from grain grown under climate change conditions.

KEYWORDS: ACCLIMATION, AGRICULTURE, CLIMATE CHANGE, CO2 CONCENTRATION, PHOTOSYNTHESIS, PLANT GROWTH, WINTER-WHEAT, YIELD

2593

Williams, M.W., P.D. Brooks, and T. Seastedt. 1998. Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic and Alpine Research 30(1):26-30.*

We have implemented a long-term snow-fence experiment at the Niwot Ridge Long-Term Ecological Research (NWT) site in the Colorado Front Range of the Rocky Mountains, U.S.A., to assess the effects of climate change on alpine ecology and biogeochemical cycles, The responses of carbon (C) and nitrogen (N) dynamics in high-elevation mountains to changes in climate ate investigated by manipulating the length and duration of snow cover with the 2.6 X 60 m snow fence, providing a proxy for climate change. Results from the first year of operation in 1994 showed that the period of continuous snow cover was increased by 90 d. The deeper and earlier snowpack behind the fence insulated soils from winter air temperatures, resulting in a 9 degrees C increase in annual minimum temperature at the soil surface. The extended period of snow cover resulted in subnivial microbial activity playing a major role in annual C and N cycling. The amount of C mineralized under the snow as measured by CO2 production was 22 g m(-2) in 1993 and 35 g m(-2) in 1994, accounting for 20% of annual net primary aboveground production before construction of the snow fence in 1993 and 31% after the snow fence was constructed in 1994. In a similar fashion, maximum subnivial N2O flux increased 3-fold behind the snow fence, from 75 mu g N m(-2) d(-1) in 1993 to 250 mu g N m(-2) d(-1) in 1994. The amount of N lost from denitrification was greater than the annual atmospheric input of N in snowfall. Surface litter decomposition studies show that there was a significant increase in the litter mass loss under deep and early snow, with no significant change under medium and little snow conditions. Changes in climate that result in differences in snow duration, depth, and extent may therefore produce large changes in the C and N soil dynamics of alpine ecosystems.

KEYWORDS: ALPINE TUNDRA, CATCHMENT, COLORADO, FOREST, LITTER, METHANE, NIWOT RIDGE, OXIDE FLUX

2594

Williams, R.S., D.E. Lincoln, and R.J. Norby. 1998. Leaf age effects of elevated CO2-grown white oak leaves on spring-feeding lepidopterans. *Global Change Biology 4(3):235-246.*

Folivorous insect responses to elevated CO2-grown tree species may be complicated by phytochemical changes as leaves age. For example, young expanding leaves in tree species may be less affected by enriched CO2-alterations in leaf phytochemistry than older mature leaves due to shorter exposure times to elevated CO2 atmospheres. This, in turn, could result in different effects on early vs. late instar larvae of herbivorous insects. To address this, seedlings of white oak (Quercus alba L.), grown in open-top chambers under ambient and elevated CO2, were fed to two important early spring feeding herbivores; gypsy moth (Lymantria dispar L.), and forest tent caterpillar (Malacosoma disstria Hubner). Young, expanding leaves were presented to early instar larvae, and older fully expanded or mature leaves to late instar larvae. Young leaves had significantly lower leaf nitrogen content and significantly higher total nonstructural carbohydrate:nitrogen ratio as plant CO2 concentration rose, while nonstructural carbohydrates and total carbon-based phenolics were unaffected by plant CO2 treatment. These phytochemical changes contributed to a significant reduction in the growth rate of early instar gypsy moth larvae, while growth rates of forest tent caterpillar were unaffected. The differences in insect responses were attributed to an increase in the nitrogen utilization efficiency (NUE) of early instar forest tent caterpillar larvae feeding on elevated CO2-grown leaves, while early instar gypsy moth larval NUE remained unchanged among the treatments. Later instar larvae of both insect species experienced larger reductions in foliage quality on elevated CO2-grown leaves than earlier instars, as the carbohydrate:nitrogen ratio of leaves substantially increased. Despite this, neither insect species exhibited changes in growth or consumption rates between CO2 treatments in the later instar. An increase in NUE was apparently responsible for offsetting reduced foliar nitrogen for the late instar larvae of both species.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO2 ENVIRONMENTS, FOREST TENT CATERPILLAR, GROWTH, GYPSY-MOTH, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LOBLOLLY-PINE, NUTRIENT BALANCE, NUTRITIONAL ECOLOGY

2595

Williams, R.S., D.E. Lincoln, and R.B. Thomas. 1994. Loblolly-pine grown under elevated co2 affects early instar pine sawfly performance. *Oecologia 98(1):64-71.*

Seedlings of loblolly pine Pinus taeda (L.), were grown in open-topped field chambers under three CO2 regimes: ambient, 150 mul l-1 CO2 above ambient, and 300 mul l-1 CO2 above ambient. A fourth, non-chambered ambient treatment was included to assess chamber effects. Needles were used in 96 h feeding trials to determine the performance of young, second instar larvae of loblolly pine's principal leaf herbivore, red-headed pine sawfly, Neodiprion lecontei (Fitch). The relative consumption rate of larvae significantly increased on plants grown under elevated CO2, and needles grown in the highest CO2 regime were consumed 21% more rapidly than needles grown in ambient CO2. Both the significant decline in leaf nitrogen content and the substantial increase in leaf starch content contributed to a significant increase in the starch:nitrogen ratio in plants grown in elevated CO2. Insect consumption rate was negatively related to leaf nitrogen content and positively related to the starch:nitrogen ratio. Of the four volatile leaf monoterpenes measured, only beta-pinene exhibited a significant CO2 effect and declined in plants grown in elevated CO2. Although consumption changed, the relative growth rates of larvae were not different among CO2 treatments. Despite lower nitrogen consumption rates by larvae feeding on the plants grown in elevated CO2, nitrogen accumulation rates were the same for all treatments due to a significant increase in nitrogen utilization efficiency. The ability of this insect to respond at an early, potentially susceptible larval stage to poorer food quality and declining levels of a leaf monoterpene suggest that changes in needle quality within pines in future elevated-CO2 atmospheres may not especially affect young insects and that tree-feeding sawflies may respond in a manner similar to herb-feeding lepidopterans.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, DILUTED DIETS, FOOD-CONSUMPTION, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, NUTRIENT BALANCE, PLANT-TISSUE, PSEUDOPLUSIA-INCLUDENS, SPRUCE BUDWORM, VELVETBEAN CATERPILLARS

2596

Williams, R.S., D.E. Lincoln, and R.B. Thomas. 1997. Effects of elevated CO2-grown loblolly pine needles on the growth, consumption, development, and pupal weight of red- headed pine sawfly larvae reared within open-topped chambers. *Global Change Biology 3(6):501-511.*

Seedlings of loblolly pine, Pinus taeda, were grown in open- topped chambers under four levels of CO2: two ambient and two elevated. Larvae of the red-headed pine sawfly, Neoniprion lecontei, were reared from early instar to pupation, primarily on branches within chambers. Larval growth and mortality were assessed and leaf phytochemistry samples of immature and mature leaves collected weekly. Mature leaves grown under elevated CO2 had significant reductions in leaf nitrogen and increases in non-structural carbohydrate contents, resulting in foliage being a poorer food source for larvae, i.e. higher carbohydrate:nitrogen ratio. Nutritional constituents of immature needles were unaffected by seedling CO2 treatment. Volatile mono-and sesquiterpenes were unrelated to plant CO2 treatments for either leaf age class. Larval consumption of immature needles significantly increased on seedlings grown under CO2 enrichment, while mature needle consumption was not different between the treatments. The average weight gain per larva significantly declined in late instar larvae consuming elevated CO2-grown needles. In spite of this reduced growth, neither the days to pupation nor pupal weights were different among the CO2 treatments. This study suggests that enriched CO2-induced alterations in pine needle phytochemistry can affect red-headed pine sawfly performance, However, compensatory measures by larvae, such as choosing to consume more nutritious immature needles, apparently helps offset enriched CO2-induced reductions in the leaf quality of mature needles.

KEYWORDS: CARBON-DIOXIDE ATMOSPHERES, ENRICHED CO2 ATMOSPHERES, INSECT HERBIVORE INTERACTIONS, JUNONIA-COENIA, LEPIDOPTERA, NUTRIENT BALANCE, NUTRITIONAL ECOLOGY, TAEDA L SEEDLINGS, WATER-STRESS, WESTERN SPRUCE BUDWORM

2597

Williams, R.S., R.B. Thomas, B.R. Strain, and D.E. Lincoln. 1997. Effects of elevated CO2, soil nutrient levels, and foliage age on the performance of two generations of Neodiprion lecontei (Hymenoptera : Diprionidae) feeding on loblolly pine. *Environmental Entomology 26(6):1312-1322.*

We investigated how changes in loblolly Dine needle phytochemistry caused by elevated CO2, leaf age, and soil nutrient levels affected the performance of 2 individual generations of the multivoltine folivorous insect pest Neodiprion lecontei (Fitch). In 2 feeding trials, mature needles produced in the previous (spring) and current (fall) year from seedlings grown in open-topped chambers under 4 CO2 and 2 soil

nutrient levels were fed to 2 separate generations of redheaded pine sawfly larvae. Strong seasonal differences (i.e., spring versus fall) in leaf nutritional and defensive constituents resulted in significant between-generation differences in the growth, consumption, and growth efficiency of sawfly larvae, Enriched CO2-grown needles had higher levels of starch and starch/nitrogen ratios in older, overwintering spring needles, which were lower in leaf nitrogen and monoterpenes than younger, current year needles (fall). Overall, larval growth was higher and consumption lower on the fall needles, presumably because of higher levels of leaf nitrogen compared with the spring needles. The plant CO2 concentration significantly contributed to the larval consumption responses between seasons (significant CO2 X season interaction), demonstrating that the 2 sawfly generations were affected differently by CO2-induced phytochemical alterations in spring versus fall needles. The data presented here suggests that when investigating multivoltine folivorous insect responses to elevated CO2-grown tree seedlings in which multiple leaf flushes within a growing season expose insects to an array of leaf phytochemical changes, >1 insect generation should be investigated.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, GROWTH, INSECT HERBIVORE INTERACTIONS, MINERAL NUTRITION, NITROGEN, PLANT-TISSUE, SAWFLY PERFORMANCE, SEASONAL-CHANGES, TAEDA L SEEDLINGS

2598

Williams, T.G., and B. Colman. 1993. Identification of distinct internal and external isozymes of carbonic-anhydrase in chlorella-saccharophila. *Plant Physiology 103(3):943-948.*

External carbonic anhydrase (CA) was detected in whole cells of alkaline-grown Chlorella saccharophila but was suppressed by growth at acid pH or growth on elevated levels of CO2. Internal CA activity was measured potentiometrically as an increase in activity in cell extracts over that of intact cells. Cells grown under all conditions had equal levels of internal CA activity. Two isozymes were identified after electrophoretic separation of soluble proteins on cellulose acetate plates. The fast isozyme was found in cells grown under all conditions, whereas the slow isozyme was found only in cells grown at alkaline pH. Western blot analysis following sodium dodecyl sulfate-polyacrylamide gel electrophoresis using antibodies produced against the periplasmic form of CA from Chlamydomonas reinhardtii revealed a single band at 39 kD, which did not change in intensity between growth conditions and was associated only with proteins eluted from the fast band. The slow isozyme was inactivated by incubation of cell extract at 30 degrees C and by incubation in 10 mM dithiothreitol, whereas the internal form was unaffected. These results indicate that external and internal forms of CA differ in structure and their activities respond differently to environmental conditions.

KEYWORDS: CHLAMYDOMONAS-REINHARDTII, CO2 CONCENTRATION, ENZYME, EXPRESSION, PLANTS, SEQUENCE, SYNECHOCOCCUS PCC7942

2599

Williams, T.G., and B. Colman. 1995. Quantification of the contribution of co2, hco3-, and external carbonic-anhydrase to photosynthesis at low dissolved inorganic carbon in chlorella-saccharophila. *Plant Physiology 107(1):245-251.*

An equation has been developed incorporating whole-cell rate constants for CO2 and HCO3- that describes accurately photosynthesis (Phs) in suspensions of unicellular algae at low dissolved inorganic carbon. At pH 8.0 the concentration of CO2 available to the algal cells depends on the rate of supply from, and the loss to, HCO3- and the rate of use by the cells. At elevated cell densities (>30 mg chlorophyll [Chl] L(-1)), at which CO2 use by the cells is high, the slope of a graph of absolute Phs versus Chl concentration approaches the rate of Phs on a milligram of Chl basis because of HCO3- use alone. The slope of a graph of Phs versus HCO3- will be the rate constant for HCO3- and for Chlorella saccharophila it was 0.16 L mg(-1) Chl h(-1). The difference between the constants for dissolved inorganic carbon (measured in cells with external carbonic anhydrase) and HCO3-1 is the constant for CO2, which was 26 L mg(-1) Chl h(-1). This difference causes the half-saturation constant for Phs to increase 5- to 6-fold at high cell densities. The increase in CO2 use as a result of external carbonic anhydrase is described mathematically as a function of cell density.

KEYWORDS: ALGAE, CHLAMYDOMONAS-REINHARDTII, CO2-DEPENDENT PHOTOSYNTHESIS, CYANOBACTERIA, DIOXIDE, ELLIPSOIDEA, INHIBITION, TRANSPORT

2600

Wilsey, B.J. 1996. Plant responses to elevated atmospheric CO2 among terrestrial biomes. *Oikos 76(1):201-206.*

Although many researchers have stressed the importance of among-species variation in plant response to elevated CO2, none have quantitatively tested whether variation exists among biomes. I compiled data from the literature and found that, although C-3 plants did respond more than C-4 plants (as predicted), biome origin was a better predictor (accounted for more of the variation) of plant response to elevated CO2 than mode of photosynthesis, Variation in plant response among biomes was found both between and within latitudinal zones, with plant species from tropical and temperate biomes responding more than plant species from a polar biome. Within the temperate zone, species from forested biomes responded more than species from a grassland biome, and this provides further evidence that forests are acting as major sinks for increasing levels of atmospheric CO2. A more than 4-fold difference was found among ecosystems in coefficients of variation (calculated across mean species response within each ecosystem). Based on this difference, I suggest that ecosystems may vary in the amount of change in species composition in response to elevated CO2.

KEYWORDS: C-4 GRASS, CARBON-DIOXIDE ENRICHMENT, COMPETITION, GROWTH-RESPONSE, LIQUIDAMBAR-STYRACIFLUA, MINERAL NUTRITION, OPUNTIA FICUS INDICA, PINUS-TAEDA SEEDLINGS, QUERCUS-ALBA, SHORT- TERM

2601

Wilsey, B.J. 1996. Urea additions and defoliation affect plant responses to elevated CO2 in a C-3 grass from Yellowstone National Park. *Oecologia 108(2):321-327.*

A common grass from Yellowstone National Park, Stipa occidentalis, was grown in a factorial experiment to determine if its response to the direct effects of elevated CO2 would be affected by defoliation, and urea additions simulating the N in a urine hit. Plants were grown in tall pots (to mimic rooting depth in the field) in growth chambers under elevated (700 ppm) and ambient (370 ppm) CO2, were defoliated or left undefoliated, and given N-supply rates based on field mineralization rates (untreated) or with an additional 40 g N/m(2). Growth increases in response to elevated CO2 were largest when plants remained unclipped and received urea additions, and were found primarily in crowns and roots (storage organs). Aboveground biomass, which is the part of the plant consumed by grazing mammals, was not affected by elevated CO2. The elevated CO2 treatment caused a reduction in leaf percent N. However, there was a significant interaction between the CO2 and urea treatments, resulting in a larger difference in leaf percent N between urea-treated and control plants under elevated than under ambient CO2. Hence, elevations in atmospheric CO2 may cause an increase in the amount of urine- hit-induced spatial variability in temperate grasslands.

Since food quantity remained largely unchanged in response to elevated CO2, and forage N content went down, grazing mammals may be negatively affected by increases in atmospheric CO2.

KEYWORDS: ATMOSPHERES, CARBON DIOXIDE, DYNAMICS, ECOSYSTEM, ENVIRONMENTS, ESTUARINE MARSH, INSECT HERBIVORE INTERACTIONS, MINERAL NUTRITION, NITROGEN, URINE DEPOSITION

2602

Wilsey, B.J., J.S. Coleman, and S.J. McNaughton. 1997. Effects of elevated CO2 and defoliation on grasses: A comparative ecosystem approach. *Ecological Applications 7(3):844-853.*

Three plant species from each of three grassland ecosystems were grown under elevated (700 mL/m(3)) and ambient (350 mL/m(3)) CO2 and were defoliated or left undefoliated to test whether species response to elevated CO2 and grazing is related to evolutionary grazing history or to mode of photosynthesis. The three ecosystems represented a tropical grassland dominated by C-4 species (the Serengeti of Africa), a temperate grassland dominated by a mixture of C-3 and C-4 species (Flooding Pampa of South America), and a northern temperate grassland dominated by C-3 species (Yellowstone National Park of North America). Plants were grown in growth chambers under common conditions to compare relative responses to grazing and elevated CO2. Elevated CO2 caused an increase in total biomass and total productivity (biomass + clippings) only in Yellowstone species, and increases in growth occurred primarily in crowns and roots (storage organs). There were no significant CO2 effects on biomass or productivity in Serengeti or Flooding Pampa species, and no CO2 effects on aboveground biomass or productivity (aboveground biomass + clippings) in species from any of the three ecosystems. Since aboveground plant parts are the portions that are available to grazing mammals, this suggests that increased atmospheric CO2 may not affect food quantity in these three grasslands. There was no interaction between CO2 and defoliation for any species; thus, it appears that herbivores will not affect how grasses respond to elevated CO2 (at least under average nutrient conditions). Elevated CO2 caused a reduction in leaf percentage of N in species from Yellowstone and Flooding Pampa (especially the C-3 species, Briza subaristata), but not in Serengeti species. Because the quantity of food was unaffected by the CO2 treatments and forage N was reduced, grazing mammals in Yellowstone (elk, Cervus elaphus, and bison, Bison bison) and the Flooding Pampa (cattle) may be negatively affected. Responses to defoliation were fairly consistent among ecosystems in aboveground productivity, which did not differ between defoliated and undefoliated plants, and in leaf water potentials and percentage of N, both of which increased in response to defoliation. However, differences among ecosystems were found for crown and root biomass in response to defoliation: Serengeti species, on average, had higher crown and similar root biomasses after defoliation, whereas defoliated species from the other two ecosystems had reduced crown and root biomass. We suggest that the lower intensity and increased temporal variance in grazing pressure in Yellowstone vs. the Serengeti, selected for plants that shift allocation away from roots and crowns in order to compensate for aboveground herbivory.

KEYWORDS: C-4 GRASSES, DYNAMICS, ESTUARINE MARSH, GROWTH, NITROGEN ACCUMULATION, PLANTS, SERENGETI, SIMULATED HERBIVORY, TEMPERATE GRASSLAND, YELLOWSTONE NATIONAL PARK

2603

Wilsey, B.J., S.J. McNaughton, and J.S. Coleman. 1994. Will increases in atmospheric co2 affect regrowth following grazing in C-4 grasses from tropical grasslands - a test with sporobolus-kentrophyllus. *Oecologia 99(1-2):141-144.*

We grew a C-4 grass from the Serengeti ecosystem under ambient (370 ppm) and elevated (700 ppm) CO2, and under clipped and unclipped conditions to test whether regrowth following grazing would be affected by elevated CO2. Above-ground productivity was slightly decreased under elevated CO2, and was similar between clipped and unclipped plants. Regrowth (clipping offtake) following clipping was similar in the two CO2 treatments, and there was no CO2 by clipping interaction on biomass, productivity, or leaf nutrient concentrations. Based on this evidence, we suggest that C-4 grasses from the Serengeti will show little direct response to future increases in atmospheric CO2.

KEYWORDS: DEFOLIATION, ECOSYSTEM, GROWTH, PLANTS, SERENGETI

2604

Wilson, J.W., D.W. Hand, and M.A. Hannah. 1992. Light interception and photosynthetic efficiency in some glasshouse crops. *Journal of Experimental Botany 43(248):363-373.*

Productivity of glasshouse crops is strongly limited by light receipt, and efficient interception and use of light in photosynthesis is correspondingly important. Mature row crop canopies of cucumber and tomato intercepted about 76% of the light incident on their upper surfaces; about 18% was lost through gaps between the rows. Light transmitted through the entire depth of the canopy was reflected back by white plastic on the ground, so that the lower surface of the canopy received approximately 13% of the light incident on the upper surface. The light flux incident on the sides of these canopies (c. 2 m tall and 6 m x 16 m in area) amounted to some 20-30% of that incident on the upper surface. About 32% of daylight falling on the glasshouse (c. 9 m x 18 m in area) was intercepted by the glasshouse structure and glazing; of the 68% entering the house, some fell on headlands occupying 35% of the glasshouse area. The loss of light to headlands, and the gain from canopy side-lighting, would be relatively smaller for larger glasshouses. At near-ambient CO2 concentrations, net photosynthetic rates of the cucumber canopy were comparable to those of closed canopies of other glasshouse and field crops which have maximum light conversion efficiencies of 5-8-mu-g CO2 J-1 at 50-200 W m-2 incident light flux density. Efficiency decreases only slightly with stronger light. Glasshouse crops with CO2 enrichment to 1200 vpm achieve conversion efficiencies of 7-10-mu-g CO2 J-1. Efficiencies of utilization of intercepted light, on an energy basis, reach 6-10% in various field and glasshouse crops with near-ambient CO2, and reached an exceptional 11% for the cucumber canopy. Glasshouse crops with CO2 enrichment achieve maximum efficiency of light energy utilization between 12% and 13%.

KEYWORDS: CARBON BUDGET, ENRICHMENT, ENVIRONMENT, GROWTH, PENETRATION, RESPONSES, SOLAR RADIATION, STAND

2605

Wilson, K.B., and J.A. Bunce. 1997. Effects of carbon dioxide concentration on the interactive effects of temperature and water vapour on stomatal conductance in soybean. *Plant, Cell and Environment 20(2):230-238.*

Soybeans were grown at three CO2 concentrations in outdoor growth chambers and at two concentrations in controlled- environment growth chambers to investigate the interactive effects of CO2, temperature and leaf-to-air vapour pressure difference (LAVPD) on stomatal conductance, The decline in stomatal conductance with CO2 was a function of both leaf temperature and LAVPD. In the field measurements, stomatal conductance was more sensitive to LAVPD at low CO2 at 30 degrees C but not at 35 degrees C, There was also a direct increase in conductance with temperature, which was greater at the two

elevated carbon dioxide concentrations, Environmental growth chamber results showed that the relative stomatal sensitivity to LAVPD decreased with both leaf temperature and CO2. Measurements in the environmental growth chamber mere also performed at the opposing CO2, and these experiments indicate that the stomatal sensitivity to LAVPD was determined more by growth CO2 than by measurement CO2. Two models that describe stomatal responses to LAVPD were compared with the outdoor data to evaluate whether these models described adequately the interactive effects of CO2, LAVPD and temperature.

KEYWORDS: ASSIMILATION, BOUNDARY-LAYER, CO2 CONCENTRATIONS, ELEVATED CO2, HUMIDITY, MODEL, PHOTOSYNTHESIS, RESPONSES, TRANSPIRATION RATE, USE EFFICIENCY

2606

Winder, T.L., J.C. Anderson, and M.H. Spalding. 1992. Translational regulation of the large and small subunits of ribulose bisphosphate carboxylase oxygenase during induction of the co2-concentrating mechanism in chlamydomonas-reinhardtii. *Plant Physiology 98(4):1409-1414.*

In conditions of limiting external inorganic carbon, the unicellular alga Chlamydomonas reinhardtii induces a mechanism to actively transport and accumulate inorganic carbon within the cell. A high internal inorganic carbon concentration enables the cell to photosynthesize efficiently with little oxygen inhibition, even in conditions of limiting external inorganic carbon. A correlation between limiting inorganic carbon-induced induction of the CO2-concentrating mechanism and decreased synthesis of the large and small subunits of ribulose 1,5-bisphosphate carboxylase/oxygenase has been observed. Cells that had been transferred from elevated CO2 to limiting CO2 exhibit transient declines of label incorporation into both subunit polypeptides. We have found that this decrease in synthesis of large and small subunits results from specific and coordinated down-regulation of translation of both subunits possibly resulting, at least in part, from modification of large and small subunit transcripts.

KEYWORDS: AMARANTH, CARBONIC-ANHYDRASE, CHLOROPLAST GENE, COORDINATE, GENE-EXPRESSION, MESSENGER-RNAS, MUTANT, TRANSPORT

2607

Winder, T.L., J.D. Sun, T.W. Okita, and G.E. Edwards. 1998. Evidence for the occurrence of feedback inhibition of photosynthesis in rice. *Plant and Cell Physiology 39(8):813-820.*

The response of photosynthesis in the flag leaf of rice (Oryza sativa) to elevated CO2 or reduced O-2 was investigated relative to other environmental factors using steady-state gas exchange techniques. We found under moderate conditions of temperature and photosynthetic flux density (PFD) (26 degrees C and 700 mu mol quanta m(-2)s(-1), similar to growth conditions) photosynthesis in the flag leaf of rice during heading and grain filling saturated at near ambient levels of CO2, with a concomitant loss of O-2 sensitivity, when a high stomatal conductance was maintained by high humidity (low vapor pressure deficit). Under 18 degrees C there was near complete loss of O- 2 sensitivity of photosynthesis at normal ambient levels of CO2, This is in contrast to the large enhancement of photosynthesis by supra-atmospheric levels of CO2 and sub- atmospheric levels of O-2 by suppression of photorespiration when there is no limitation on utilizing the initial product of CO2 assimilation (triose-beta) as predicted from Ribulose-1,5- bisphosphate carboxylase/oxygenase (Rubisco) kinetic properties. Thus, loss of sensitivity to CO2 and O-2 has been previously explained as a limitation on utilization of triose- beta to synthesize carbohydrates. Under high PFD at 25 degrees C, the rate of photosynthesis in rice declined over a period of hours around midday, while the intercellular levels of CO2 remained constant suggesting a limitation on utilization of photosynthate, Short-term fluctuations in climatic factors including temperature, light and humidity could result in a feedback limitation on photosynthesis in rice which may be exacerbated by rising CO2.

KEYWORDS: C-3 PLANTS, CARBON METABOLISM, CHILLING INJURY, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, ELEVATED CO2, MATURE LEAVES, ORYZA-SATIVA, STOMATAL CONDUCTANCE, VARIETAL DIFFERENCES

2608

Winjum, J.K., R.K. Dixon, and P.E. Schroeder. 1992. Estimating the global potential of forest and agroforest management-practices to sequester carbon. *Water, Air, and Soil Pollution 64(1-2):213-227.*

Forests play a prominent role in the global C cycle. Occupying one-third of the earth's land area, forest vegetation and soils contain about 60% of the total terrestrial C. Forest biomass productivity can be enhanced by management practices, which suggests that, by this means, forests could store more C globally and thereby slow the increase in atmospheric CO2. The question is how much C can be sequestered by forest and agroforest management practices. To address the question, a global database of information was compiled to assess quantitatively the potential of forestry practices to sequester C. The database presently has information for 94 forested nations that represent the boreal, temperate and tropical latitudes. Results indicate that the most promising management practices are reforestation in the temperate and tropical latitudes, afforestation in the temperate regions, and agroforestry and natural reforestation in the tropics. Across all practices, the median of the mean C storage values for the boreal latitudes is 16 tCha-1 (n=46) while in the temperate and tropical latitudes the median values are 71 tCha-1 (n=401) and 66 tCha-1 (n=170), respectively. Preliminary projections are that if these practices were implemented on 0.6 to 1.2 x 10(9) ha of available land over a 50-yr period, approximately 50 to 100 GtC could be sequestered.

2609

Winnett, S.M. 1998. Potential effects of climate change on US forests: a review. *Climate Research 11(1):39-49.*

Human-induced changes in climate are likely to affect U.S, domestic forests and the economic systems which rely on them. This paper reviews current knowledge of how changes in temperature and precipitation could affect tree species, forest ecosystems, and the forest products sector of the economy. The various types of models used to predict change and the results they calculate are examined. Models currently project both increases and decreases in the range of various species and ecosystems, and similar results for changes in the productivity, biomass and growth of forests in response to changes in climate. Results vary with the models used, the species or ecosystem studied, and the specific condition of the forest in question. The science of forests and global change is reviewed with regard to plant responses to enhanced CO2 environments and forests' response to other bioclimatic and indirect factors, such as insect predation, fire, climatic variation and ozone. Three studies of the economic effects of climate change on forests, which project a range of losses and benefits to the economy, are compared. Economic results vary directly with the results of the forest growth and productivity models which were employed as inputs. No one model can provide a complete answer, and current knowledge and models are limited in various ways which point to areas where further research could provide benefits.

KEYWORDS: AMBIENT OZONE, CARBON DIOXIDE, ELEVATED CO2, LOBLOLLY-PINE, NITROGEN LEVEL, NORTHEASTERN UNITED-STATES, NORTHERN HARDWOODS, OCEAN-

ATMOSPHERE MODEL, TRANSIENT-RESPONSE, WATER-STRESS

2610

Winter, K., and B. Engelbrecht. 1994. Short-term co2 responses of light and dark co2 fixation in the crassulacean acid metabolism plant kalanchoe-pinnata. *Journal of Plant Physiology 144(4-5):462-467.*

Short-term responses of net CO2 assimilation rate (A), in the light and dark, to ambient CO2 partial pressure (between about 30 and 1000 mu bar) were studied in leaves of the crassulacean acid metabolism (CAM) plant, Kalanchoe pinnata. The results show that it is possible to extrapolate from instantaneous measurements of net CO2 exchange to diurnal and nocturnal CO2 balances at different CO2 partial pressures. Instantaneous CO2 response curves were obtained by altering CO2 levels at 10-min intervals during the middle of the 12-h dark period (phase I of CAM) and during the last third of the 12-h light period (phase IV of CAM). CO2 partial pressures were also altered at longer, 12- to 24-h intervals and maximum rates of net CO2 uptake (A(max)) during light and dark periods were analysed in response to intercellular CO2 partial pressures (p(i)) occurring at the time of A(max). A(max)-p(i) relationships were identical to A-p(i)-curves from rapidly performed determinations during phases I and IV. Corresponding to previous findings with non-CAM species, A(max) and integrated net carbon gain during light and dark periods, respectively, showed a linear relationship. Nocturnal CO2 uptake in normal air was barely affected when light-period carbon gain was manipulated by alterations in CO2 partial pressure. Carbon gain during light periods, measured in normal air, was also independent of CO2-related changes in nocturnal carbon gain. Only after 12 h of darkness at the lowest CO2 concentration used (about 30 mu bar), was carbon gain increased under lighted conditions.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, EXCHANGE, PHOTOSYNTHESIS

2611

Winter, K., and C.E. Lovelock. 1999. Growth responses of seedlings of early and late successional tropical forest trees to elevated atmospheric CO2. *Flora 194(2):221-227.*

Seedlings of nine tropical forest tree species were grown outdoors in open-top chambers at ambient and elevated (two times ambient) CO2 concentrations at the Smithsonian Tropical Research Institute, Republic of Panama. Plants were kept individually in large pots and received non-limiting supplies of water and mineral nutrients. The enhancement of biomass accumulation at elevated CO2 increased with increasing relative growth rates (RGR) of species at ambient CO2. Early successional pioneer trees (Cecropia longipes, Ficus insipida, Castilla elastica, Antirrhoea trichantha, Luehea seemannii, Pseudobombax septenatum) grew rapidly, and, at the end of 25 to 39 day treatments, dry matter accumulation was 74 +/- 26% higher at elevated than at ambient CO2 (mean increase +/- SD, n = 6). By contrast, seedlings of three late successional tree species (Calophyllum longifolium, Tetragastris panamensis, Virola surinamensis) grew slowly and, over an 84 day period, elevated CO2 led to either no (C. longifolium, T. panamensis) or only small enhancement in dry matter accumulation (V. surinamensis). These different responses to CO2 enrichment are a result of differences in growth kinetics between early and late successional species at ambient CO2 rather than a result of intrinsic physiological differences in CO2 responsiveness between plants from these two functional groups.

KEYWORDS: CARBON, ECOSYSTEMS, PLANTS

2612

Winter, K., A. Richter, B. Engelbrecht, J. Posada, A. Virgo, and M. Popp. 1997. Effect of elevated CO2 on growth and crassulacean-acid-metabolism activity of Kalanchoe pinnata under tropical conditions. *Planta 201(4):389-396.*

Kalanchoe pinnata (Lam.) Pers. (Crassulaceae), a succulent- leaved crassulacean-acid-metabolism plant, was grown in open- top chambers at ambient and elevated (two times ambient) CO2 concentrations under natural conditions at the Smithsonian Tropical Research Institute, Republic of Panama. Nocturnal increase in titratable acidity and nocturnal carbon gain were linearly related, increased with leaf age, and were unaffected by CO2 treatments. However, under elevated CO2, dry matter accumulation increased by 42-51%. Thus, the increased growth at elevated CO2 was attributable entirely to increased net CO2 uptake during daytime in the light. Malic acid was the major organic acid accumulated overnight. Nocturnal malate accumulation exceeded nocturnal citrate accumulation by six- to eightfold at both CO2 concentrations. Basal (predawn) starch levels were higher in leaves of plants grown at elevated CO2 but diurnal fluctuations of starch were of similar magnitude under both ambient and elevated CO2. In both treatments, nocturnal starch degradation accounted for between 78 and 89% of the nocturnal accumulation of malate and citrate. Glucose, fructose, and sucrose were not found to exhibit marked day- night fluctuations.

KEYWORDS: CAM, CARBON DIOXIDE, CLADODE DEVELOPMENT, EXCHANGE, LIGHT, OPUNTIA FICUS INDICA, PARTIAL-PRESSURE, PLANT, RESPONSES, SHORT- TERM

2613

Winter, K., and A. Virgo. 1998. Elevated CO2 enhances growth in the rain forest understory plant, Piper cordulatum, at extremely low light intensities. *Flora 193(3):323-326.*

Seedlings of the rain forest understory shrub Piper cordulatum were grown for several months at ambient and elevated concentrations of atmospheric CO2. Photon flux density (PFD) during 12-h photoperiods was maintained at extremely low levels (< 10 mu mol m(-2) s(-1)). Despite these low PFDs, dry matter accumulation and leaf area production were increased in air containing elevated (approximately twice-ambient) CO2 concentrations compared to ambient air. In leaves that had developed in deep shade and at ambient CO2, rates of net CO2 uptake, measured at 6 mu mol photons m(-2)s(-1), were 30% higher at elevated than at ambient CO2. Rates of net CO2 loss in the dark were 10% lower at elevated than at ambient CO2.

KEYWORDS: ATMOSPHERIC CO2, C-4 PLANTS, CARBON DIOXIDE, DARK RESPIRATION, ENRICHMENT, FUTURE, QUANTUM YIELD, RESPONSES

2614

Wise, R.R., A. Ortizlopez, and D.R. Ort. 1992. Spatial-distribution of photosynthesis during drought in field- grown and acclimated and nonacclimated growth chamber-grown cotton. *Plant Physiology 100(1):26-32.*

Inhomogeneous photosynthetic activity has been reported to occur in drought-stressed leaves. In addition, it has been suggested that these water stress-induced nonuniformities in photosynthesis are caused by "patchy" stomatal closure and that the phenomenon may have created the illusion of a nonstomatal component to the inhibition of photosynthesis. Because these earlier studies were performed with nonacclimated growth chamber-grown plants, we sought to determine whether such "patches" existed in drought-treated, field-grown plants or in chamber-grown plants that had been acclimated to low leaf water potentials (psi(leaf)). Cotton (Gossypium hirsutum L.) was grown in the field and subjected to drought by withholding irrigation and rain from 24 d after planting. The distribution of photosynthesis, which may

reflect the stomatal aperture distribution in a heterobaric species such as cotton, was assayed by autoradiography after briefly exposing attached leaves of field-grown plants to (CO2)-C-14. A homogeneous distribution of radioactive photosynthate was evident even at the lowest psi(leaf) of -1.34 MPa. "Patchiness" could, however, be induced by uprooting the plant and allowing the shoot to air dry for 6 to 8 min. In parallel studies, growth chamber-grown plants were acclimated to drought by withholding irrigation for three 5-d drought cycles interspersed with irrigation. This drought acclimation lowered the psi(leaf) value at which control rates of photosynthesis could be sustained by approximately 0.7 MPa and was accompanied by a similar decline in the psi(leaf) at which patchiness first appeared. Photosynthetic inhomogeneities in chamber-grown plants that were visible during moderate water stress and ambient levels of CO2 could be largely removed with elevated CO2 levels (3000 muL L-1), suggesting that they were stomatal in nature. However, advanced dehydration (less than approximately 2.0 MPa) resulted in "patches" that could not be so removed and were probably caused by nonstomatal factors. The demonstration that patches do not exist in drought-treated, field-grown cotton and that the presence of patches in chamber-grown plants can be altered by treatments that cause an acclimation of photosynthesis leads us to conclude that spatial heterogeneities in photosynthesis probably do not occur frequently under natural drought conditions.

KEYWORDS: ABSCISIC-ACID, CO2 EXCHANGE, FLUORESCENCE, GAS-EXCHANGE, INHIBITION, LOW WATER POTENTIALS, STATISTICAL DISTRIBUTION, STOMATAL APERTURES, STRESS, SUNFLOWER LEAVES

2615

Witjaksono Schaffer, B.A., A.M. Colls, R.E. Litz, and P.A. Moon. 1999. Avocado shoot culture, plantlet development and net CO2 assimilation in an ambient and CO2 enhanced environment. *In Vitro Cellular & Developmental Biology-Plant 35(3):238-244.*

The proliferation and survival of avocado nodal cultures of juvenile origin were affected by the form anti concentration of nitrogen. Optimum growth was achieved on modified Murashige and Skoog medium containing 67% KNO3 and 33% NH4NO3 with total N of 40 mM supplemented with 100 mg 1 (1) myo-inositol, 1 mg 1 (-1) thiamine HCl, 30 g l (1) sucrose, and 4.44 mu M BA with a 16-h photoperiod (120-150 mu mol m(-2) s(-1)). Proliferating shoots and plantlets, were photosyntheticallS active. Better shoot growth and accumulation of higher biomass occurred in a CO2- enrichcd environment than under ambient CO2 conditions. CO2 assimilation efficiency, however, was higher under the latter conditions than in a CO2-enhanced ;environment, e.g., 31 +/- 7 and 17+/- 2 mu mol CO2 m(-2) s(-1), respectively. The net CO2 assimilation rates of in vitro grown plantlets were comparable to those of seedlings ex vitro.

KEYWORDS: ACCLIMATIZATION, CARBON DIOXIDE, ENRICHMENT, INVITRO, INVITRO-PROPAGATION, LIGHT-INTENSITY, MUSA, PHOTOSYNTHESIS, SUBSEQUENT GROWTH

2616

Wittwer, S.H. 1990. Implications of the greenhouse-effect on crop productivity. *Hortscience 25(12):1560-1567.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, CARBON DIOXIDE, CLIMATIC CHANGE, GROWTH, INCREASE, POTATO, SENSITIVITY, WATER, WHEAT, YIELD

2617

Wolf, J. 1996. Effects of nutrient (NPK) supply on faba bean response to elevated atmospheric CO2. *Netherlands Journal of Agricultural Science 44(3):163-178.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient for maximal growth. Increased atmospheric CO2 may also cause changes in maximum dilution of nutrients in plant tissue and hence, in the minimum nutrient concentration levels and the maximum yield-nutrient uptake ratios of crops. To study these effects for faba bean, pot experiments have been carried out in two glass houses at ambient and doubled CO2 concentration. Bean plants were grown at different supplies of N, P or K. Doubling of atmospheric CO2 resulted in a strong increase (+100%) in total yield. This CO2 effect disappeared rapidly with increasing nitrogen, phosphorus or potassium shortage. Doubling of atmospheric CO2 resulted in no change in minimum nitrogen concentration and a nil to slight decrease in minimum phosphorus concentration in crop residues. Nutrient requirements to attain a certain yield level might change with a future increase in atmospheric CO2. However, such conclusions cannot yet be drawn because nutrient concentrations in seeds were not available.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, NITROGEN, SEED YIELD, SOILS

2618

Wolf, J. 1996. Effects of nutrient supply (NPK) on spring wheat response to elevated atmospheric CO2. *Plant and Soil 185(1):113-123.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient for maximal growth. Increased atmospheric CO2 may also cause changes in minimum nutrient concentration in plant tissue and hence in the nutrient use efficiency or yield- nutrient uptake ratios of crops. To study these effects for spring wheat, pot experiments have been carried out in two glass houses at ambient and doubled CO2 concentration. Wheat plants were grown at different supplies of N, P or K. Doubling of ambient CO2 resulted in a large increase in total biomass (+70%) and grain yield when the nutrient supply was optimum. With strong N and K limitation this CO2 effect was about halved and with strong P limitation it became almost nil. Doubling of ambient CO2 resulted in a 10% lower minimum N concentration in plant tissue and in no change in the minimum P concentration.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PLANT GROWTH, SEED YIELD

2619

Wolf, J. 1998. Effects of nutrient (NPK) supply on sugar beet response to elevated atmospheric CO2. *Netherlands Journal of Agricultural Science 46(2):157-170.*

The effects of increased atmospheric CO2 on crop growth and dry matter allocation may change if nutrient supply becomes insufficient. Increased atmospheric CO2 may also cause changes in maximum dilution of nutrients in plant tissue and hence, in the minimum nutrient concentration levels and the maximum yield-nutrient uptake ratios of crops. To study these effects of increased CO2 for sugar beet (Beta vulgaris L.), pot experiments have been carried out at ambient and doubled CO2 concentration. Beet plants were grown for four monthes at different supplies of N, P or K. Doubling of ambient CO2 resulted in a moderate increase in total yield (+24%) and beet yield (+34%), however this CO2 effect disappeared with increasing nutrient shortage (in particular nitrogen). CO2 doubling did not result in significant changes in the minimum nutrient concentrations in leaves and beets.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PLANT GROWTH, SEED YIELD, SOILS, WHEAT

2620

Wolfe, D.W., R.M. Gifford, D. Hilbert, and Y.Q. Luo. 1998. Integration of photosynthetic acclimation to CO2 at the whole- plant level. *Global Change Biology 4(8):879-893.*

Primary events in photosynthetic (PS) acclimation to elevated CO2 concentration ([CO2]) occur at the molecular level in leaf mesophyll cells, but final growth response to [CO2] involves acclimation responses associated with photosynthate partitioning among plant organs in relation to resources limiting growth. Source-sink interactions, particularly with regard to carbon (C) and nitrogen (N), are key determinants of PS acclimation to elevated [CO2] at the whole-plant level. In the long term, PS and growth response to [CO2] are dependent on genotypic and environmental factors affecting the plant's ability to develop new sinks for C, and acquire adequate N and other resources to support an enhanced growth potential. Growth at elevated [CO2] usually increases N use efficiency because PS rates can be maintained at levels comparable to those observed at ambient [CO2] with less N investment in PS enzymes. A frequent acclimation response, particularly under N-limited conditions, is for the accumulation of leaf carbohydrates at elevated [CO2] to lead to repression of genes associated with the production of PS enzymes. The hypothesis that this is an adaptive response, leading to a diversion of N to plant organs where it is of greatest benefit in terms of competitive ability and reproductive fitness, needs to be more rigorously tested. The biological control mechanisms which plants have evolved to acclimate to shifts in source-sink balance caused by elevated [CO2] are complex, and will only be fully elucidated by probing at all scales along the hierarchy from molecular to ecosystem. Use of environmental manipulations and genotypic comparisons will facilitate the testing of specific hypotheses. Improving our ability to predict PS acclimation to [CO2] will require the integration of results from laboratory studies using simple model systems with results from whole-plant studies that include measurements of processes operating at several scales.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOMASS ALLOCATION, ELEVATED CO2, GAS-EXCHANGE, LEAF-AREA, PHASEOLUS-VULGARIS L, POPLAR CLONES, SOURCE-SINK RELATIONS, SUCROSE PHOSPHATE SYNTHASE, WATER-USE

2621

Wolfe, D.W., J.J. Melkonian, and S.R. Boese. 1997. Elevated CO2 ameliorates chilling-induced water stress, photosynthetic depression, and leaf damage. *Plant Physiology 114(3):483.*

2622

Wolfenden, J., and P.J. Diggle. 1995. Canopy gas-exchange and growth of upland pasture swards in elevated co2. *New Phytologist 130(3):369-380.*

Vegetation monoliths (450 x 450 mm) from two contrasting upland grassland communities were grown in Solardomes in either ambient air or ambient air enriched with 250 ppm CO2. During the first two growing seasons measurements of canopy gas exchange showed that rates of photosynthesis of limestone swards were enhanced by growth in elevated CO2, by approx. 50% during spring and early summer. Although canopy respiration was also greater in elevated CO2, the overall effect was an average increase of 33% in net CO2 assimilation. Enhanced respiration rates persisted into the autumn, whereas the effect on photosynthesis diminished through the growing season, so that in September swards growing in high CO2 had net photosynthesis rates similar to, or even lower than those in ambient air. This response varied between swards of differing species composition. In acidic grassland no significant effects of CO2 on respiration or net CO2 uptake rates were detected at any time. The above ground productivity of limestone grassland was measured in several harvests throughout both seasons, and was not affected by CO2 concentration at any time. Similarly, the acidic grassland, harvested at the end of the second season, showed no significant effect of CO2 on above-ground biomass. The results suggest that increasing atmospheric CO2 concentration is unlikely to cause large changes in net primary productivity in these grasslands.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, ENRICHMENT, NITROGEN, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, PLANT RESPIRATION, TEMPERATURE, TUSSOCK TUNDRA

2623

Wong, S.C. 1990. Elevated atmospheric partial-pressure of CO2 and plant-growth .2. Nonstructural carbohydrate content in cotton plants and its effect on growth-parameters. *Photosynthesis Research 23(2):171-180.*

2624

Wong, S.C. 1993. Interaction between elevated atmospheric concentration of co2 and humidity on plant-growth - comparison between cotton and radish. *Vegetatio 104:211-221.*

Cotton plants (Gossypium hirsutum L. var Deltapine 90) and radish plants (Raphanus sativus L var Round Red) were grown under full sunlight using a factorial combination of atmospheric CO2 concentrations (350 mumol mol-1 and 700 mumol mol-1) and humidities (35% and 90% RH at 32-degrees-C during the day). Cotton plants showed large responses to increased humidity and to doubled CO2. In cotton plants, the enhanced dry matter yield due to doubled CO2 concentration was 1.6-fold greater at low humidity than at high humidity. Apart from the direct effect of elevated CO2 level on photosynthesis, the greater effect of doubled CO2 concentration on dry matter yield at low humidity was probably due to: (1) increased leaf water potential caused by reduction of transpiration resulting from the negative CO2 response of stomata to increased CO2 concentration the consequence being greater leaf area expansion. (2) reduction of CO2 assimilation rate at low humidity and normal CO2 concentration as a result of humidity response of stomata causing reduction of intercellular CO2 concentration. In contrast, apart from the very early stage of development, radish plants do not respond to increased humidity but had a relatively large response to doubled CO2 concentration. Furthermore, due to the determinate growth pattern as well as having a prominent storage root, the extra photoassimilate derived at doubled CO2 level is allocated to the storage root.

KEYWORDS: PARTIAL-PRESSURE

2625

Wong, S.C., P.E. Kriedemann, and G.D. Farquhar. 1992. CO2 X nitrogen interaction on seedling growth of 4 species of eucalypt. *Australian Journal of Botany 40(4-5):457-472.*

Four eucalypt species were selected to represent two ecologically disparate groups which would be expected to contrast in seedling vigour and in the nature of growth responses to CO2 X nitrogen supply. Eucalyptus camaldulensis and E. cypellocarpa were taken as examples of fast-growing species with a wide distribution, that develop into large trees. By contrast, E. pauciflora and E. pulverulenta become smaller trees, and show a more limited distribution. Seedlings were established in pots (5 L) of a loamy soil and supplied with nutrient solution containing either 1.2 or 6.0 mM NO3- in both ambient (33 Pa) and CO2-enriched (66 Pa) greenhouses. Analysis of growth response to treatments

(2 X 2 factorial) was based on destructive harvest of plants sampled on four occasions over 84 days for E. camaldulensis and E. cypellocarpa, and 100 days for E. pulverulenta and E. pauciflora. A positive CO2 X N interaction on plant dry mass and leaf area was expressed in all species throughout the study period. In E. camaldulensis and E. cypellocarpa, plant mass was doubled by high N at 33 Pa CO2, compared with a three to four- fold increase at 66 Pa to reach 34 g by final harvest. In E. pulverulenta and E. pauciflora, slower growth resulted in about 50% less mass at a given age, but relative increases due to CO2 and N were of a similar order. A distinction can be made between N and CO2 effects on growth processes as follows. When trees were grown on low N, elevated CO2 increased nitrogen-use efficiency (NUE) at both leaf and whole plant levels. On high N, leaf NUE was increased in E. camaldulensis and E. cypellocarpa, but decreased in E. pulverulenta and E. pauciflora. Whole plant NUE showed no consistent response to elevated CO2 when plants were supplied high N. Net assimilation rate (NAR) was increased by elevated CO2 in all species on either N treatment. Moreover, high N increased NAR under either CO2 treatment in all species. There was a positive N X CO2 interaction on NAR in E. camaldulensis and E. cypellocarpa, but not in E. pulverulenta and E. pauciflora. Growth indices for E. camaldulensis and E. cypellocarpa species, and especially E. camaldulensis, generally exceeded those for E. pulverulenta and E. pauciflora in terms of NAR, leaf NUE, N-enhancement of CO2 effects on leaf area and biomass, and non-structural carbohydrate content of foliage.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GRANDIS SEEDLINGS, MODELS, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANTS

2626

Wong, S.C., and C.B. Osmond. 1991. Elevated atmospheric partial-pressure of CO2 and plant-growth .3. Interactions between Triticum aestivum (C3) and Echinochloa frumentacea (C4) during growth in mixed culture under different CO2, N-nutrition and irradiance treatments, with emphasis on belowground responses estimated using the delta-C-13 value of root biomass. *Australian Journal of Plant Physiology 18(2):137-152.*

Wheat (Triticum aestivum L.), a C3 species, and Japanese millet (Echinochloa frumentacea Link), a C4 species, were grown in pots in monoculture and mixed culture (2 C3:1 C4 and 1 C3:2 C4) at two ambient partial pressures of CO2 (320 and 640-mu-bar), two photosynthetic photon flux densities (PPFDs) (daily maximum 2000 and 500-mu-mol m-2 s-1) and two levels of nitrogen nutrition (12 mM and 2 mM NO3BAR). Growth of shoots of both components in mixed culture was measured by physical separation, and the proportions of root biomass due to each component were calculated from delta-C-13 value of total root biomass. In air (320-mu-bar CO2) at high PPFD and with high root zone-N, the shoot biomass of C3 and C4 components at the first harvest (28 days) was in proportion to the sowing ratio. However, by the second harvest (36 days) the C4 component predominated in both mixtures. Under the same conditions, but with low PPFD, C3 plants predominated at the first harvest but C4 plants had overtaken them by the time of the second harvest. Elevated atmospheric CO2 (640-mu-bar) stimulated shoot growth of Triticum in 15 of 16 treatment combinations and the stimulation was greatest in plants provided with low NO3BAR. Root growth of the C3 plants was generally stimulated by elevated CO2, but was only occasionally sensitive to the presence of C4 plants in mixed culture. However, growth of the C4 plants was often sensitive to the presence of C3 plants in mixed culture. In mixed cultures, elevated CO2 plants stimulated growth of C4 plants at high PPFD, high-N and in all low-N treatments but this was insufficient to offset a marked decline in shoot growth with increasing proportion of C3 plants in mixed cultures. The unexpected stimulation of growth of C4 plants by elevated CO2 was correlated with more negative delta- C-13 values of C4 root biomass, suggesting a partial failure of the CO2 concentrating mechanism of C4 photosynthesis in Echinochloa under low-N. These experiments show that for these species nitrogen was more important than light or elevated pCO2 in determining the extent of competitive interactions in mixed culture.

KEYWORDS: C-3, CARBON ISOTOPE DISCRIMINATION, COMPETITION, GRASSES, NITROGEN, PHOTOSYNTHESIS, SOIL ORGANIC MATTER, USE EFFICIENCY

2627

Wood, C.W., H.A. Torbert, H.H. Rogers, G.B. Runion, and S.A. Prior. 1994. Free-air co2 enrichment effects on soil carbon and nitrogen. *Agricultural and Forest Meteorology 70(1-4):103-116.*

Since the onset of the industrial revolution, atmospheric CO2 concentration has increased exponentially to the current 370 mumol mol-1 level, and continued increases are expected. Previous research has demonstrated that elevated atmospheric CO2 results in larger plants returning greater amounts of C to the soil. However, the effects of elevated CO2 on C and N cycling and long-term storage of C in soil have not been examined. Soil samples (in 0-50, 50-100, and 100-200 mm depth increments) were collected after 3 years of cotton (Gossypium hirsutum L.) production under free-air CO2 enrichment (FACE, at 550 mumol CO2 mol-1), in combination with 2 years of different soil moisture regimes (wet, 100% of evapotranspiration replaced, or dry, 75% and 67% of evapotranspiration replaced in 1990 and 1991, respectively) on a Trix clay loam (fine, loamy, mixed (calcareous), hyperthermic Typic Torrifluvent) at Maricopa, Arizona. Ambient plots (370 mumol CO2 mol-1 (control)), in combination with the wet and dry soil moisture regimes, were also included in the study. Soil organic C and N concentrations, potential C and N mineralization, and C turnover were measured. Increased input of cotton plant residues under FACE resulted in treatment differences and trends toward increased organic C in all three soil depths. During the first 30 days of laboratory incubation, available N apparently limited potential C mineralization and C turnover in all treatments. Between 30 and 60 days of incubation, soils from FACE plots had greater potential C mineralization with both water regimes, but C turnover increased in soils from the dry treatment and decreased in soils where cotton was not water stressed. These data indicate that in high-CO2 environments without water stress, increased C storage in soil is likely, but it is less likely where water stress is a factor. More research is needed before the ability of soil to store additional C in a high-CO2 world can be determined.

KEYWORDS: ATMOSPHERIC CO2, COTTON, DIOXIDE, GROWTH, MINERALIZATION, RESPONSES, RHIZOSPHERE, ROOT

2628

Woodbury, P.B., J.E. Smith, D.A. Weinstein, and J.A. Laurence. 1998. Assessing potential climate change effects on loblolly pine growth: A probabilistic regional modeling approach. *Forest Ecology and Management 107(1-3):99-116.*

Most models of the potential effects of climate change on forest growth have produced deterministic predictions. However, there are large uncertainties in data on regional forest condition, estimates of future climate, and quantitative relationships between environmental conditions and forest growth rate. We constructed a new model to analyze these uncertainties along with available experimental results to make probabilistic estimates of climate change effects on the growth of loblolly pine (Pinus taeda L.) throughout its range in the USA. Complete regional data sets were created by means of spatial interpolation, and uncertainties in these data were estimated. A geographic information system (GIS) was created to integrate current and predicted climate data with regional data including forest distribution, growth rate, and stand characteristics derived from USDA Forest Service data. A probabilistic

climate change scenario was derived from the results of four different general circulation models (GCM). Probabilistic estimates of forest growth were produced by linking the GIS to a Latin Hypercube carbon (C) budget model of forest growth. The model estimated a greater than 50% chance of a decrease in loblolly pine growth throughout most of its range. The model also estimated a 10% chance that the total regional basal area growth will decrease by more than 24 X 10(6) m(2) yr(-1) (a 92% decrease), and a 10% chance that basal area growth will increase by more than 62 X 10(6) m(2) yr(-1) (a 142% increase above current rates). The most influential factor at all locations was the relative change in C assimilation. Of climatic factors, CO2 concentration was found to be the most influential factor at all locations. Substantial regional variation in estimated growth was observed, and probably was due primarily to variation in historical growth rates and to the importance of historical growth in the model structure. (C) 1998 Elsevier Science B.V.

KEYWORDS: CARBON DIOXIDE, CO2, GLOBAL CHANGE, NAPAP, OZONE, SCALE, SENSITIVITY, TREES, UNCERTAINTY

2629

Woodin, S., B. Graham, A. Killick, U. Skiba, and M. Cresser. 1992. Nutrient limitation of the long-term response of heather [calluna-vulgaris (L) hull] to co2 enrichment. *New Phytologist 122(4):635-642.*

In a 27-month C2-enrichment experiment, Calluna vulgaris plants were grown on peat obtained from an upland heath in NE Scotland and given a nutrient supply which mimicked that in precipitation in the area. Three CO2 concentrations were used; ambient, + 100 ppm and + 200 ppm. Calluna showed a negative growth response to increased CO2 over the first year of treatment and a positive response by the end of the experiment. Final above-ground biomass was greatest in the enriched CO2 treatments, showing an increase of 30 % in + 100 ppm CO2. Determination of tissue nutrient concentration, and calculation of total nutrient uptake, demonstrated that nutrient uptake did not increase with increased growth, resulting in significant dilution of elements in leaf tissue. This suggests that, in its typical, nutrient poor habitats, the growth response of Calluna to CO2 will be limited by nutrient deficiency, and will reach a maximum with a relatively small increase in CO2 concentration. Flowering was advanced and extremely prolific in + 100 ppm CO2 grown plants, but the ecological significance of this is uncertain. The results highlight the need for long term studies of native species on their natural soils, using lower CO2 concentrations than the usual 'double CO2'.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, GROWTH, NITROGEN, NUTRITION, SEEDLINGS, TEMPERATURE, TUNDRA

2630

Woodrow, I.E. 1994. Control of steady-state photosynthesis in sunflowers growing in enhanced co2. *Plant, Cell and Environment 17(3):277-286.*

Control coefficients were used to describe the degree to which ribulose bisphosphate carboxylase/oxygenase (Rubisco) limits the steady-state rate of CO2 assimilation in sunflower leaves from plants grown at high (800 mu mol mol(-1)) and low (350 mu mol mol(-1)) CO2. The magnitude of a control coefficient is approximately the percentage change in the flux that would result from a 1% rise in enzyme active site concentration. In plants grown at low CO2, leaves of different ages varied considerably in their photosynthetic capacities. In a saturating light flux and an ambient CO2 concentration of 350 mu mol mol(-1), the Rubisco control coefficient was about 0.7 in all leaves, indicating that Rubisco activity largely limited the assimilation flux. The Rubisco control coefficient for leaves grown at 350 mu mol mol(-1) CO2 dropped to about zero when the ambient CO2 concentration was raised to 800 mu mol mol(-1). In relatively young, fully expanded leaves of plants grown at high CO2, the Rubisco control coefficient was also about 0.7 at a saturating light flux and at the CO2 concentration at which the plants were grown (800 mu mol mol(- 1)). This apparently resulted from a decrease in the concentration of Rubisco active sites. In older leaves, however, the control coefficient was about 0.2. Because, on the whole, Rubisco activity still largely limits the assimilation flux in plants grown at high CO2, the kinetics of this enzyme can still be used to model photosynthesis under these conditions. The relatively high Rubisco control coefficient under enhanced CO2 indicates that the young sunflower leaves have the capacity to acclimate their photosynthetic biochemistry in a way consistent with an optimal use of protein resources.

KEYWORDS: ANTISENSE RBCS, CARBON-DIOXIDE FIXATION, ELEVATED CO2, GROWTH, LEAVES, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO

2631

Woodrow, I.E. 1994. Optimal acclimation of the C-3 photosynthetic system under enhanced co2. *Photosynthesis Research 39(3):401-412.*

A range of studies of C-3 plants have shown that there is a change in both the carbon flux and the pattern of nitrogen allocation when plants are grown under enhanced CO2. This paper examines evidence that allocation of nitrogen both to and within the photosynthetic system is optimised with respect to the carbon flux. A model is developed which predicts the optimal relative allocation of nitrogen to key enzymes of the photosynthetic system as a function of CO2 concentration. It is shown that evidence from flux control analysis is broadly consistent with this model, although at high nitrogen and under certain conditions at low nitrogen experimental data are not consistent with the model. Acclimation to enhanced CO2 is also assessed in terms of resource allocation between photosynthate sources and sinks. A means of assessing the optimisation of this source-sink allocation is proposed, and several studies are examined within this framework. It is concluded that C-3 plants probably possess the genetic feedback mechanisms required to efficiently 'smooth out' any imbalance within the photosynthetic system caused by a rise in atmospheric CO2.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ELEVATED CO2, GROWTH, LEAVES, PHASEOLUS-VULGARIS L, PLANTS, RESPONSES, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS

2632

Woodrow, L., and B. Grodzinski. 1993. Ethylene exchange in lycopersicon-esculentum mill - leaves during short-term and long-term exposures to co2. *Journal of Experimental Botany 44(259):471-480.*

The effects of long-term and transient exposure to elevated CO2 concentrations on photosynthetic gas exchange and ethylene release by tomato leaves were investigated. The net CO2 assimilation rate was enhanced when leaf tissue grown at ambient (35 Pa CO2) levels was assayed at 100 Pa CO2. Leaf tissue grown at high (130 Pa) CO2 exhibited a lower net CO2 assimilation rate at high CO2 levels than leaf tissue grown at ambient (35 Pa) CO2. This decrease in CO2 exchange rate in response to growth at high CO2 is typical Of C3 species. Rates of endogenous and 1-aminocyclopropane-1-carboxylic acid (ACC)-Stimulated ethylene release from leaf tissue were enhanced by exposure to elevated CO2 levels whether the leaf tissue had been grown at ambient or enriched CO2 levels, The data demonstrate that CO2 enhanced C2H4 release from leaf tissue in response to both short-term perturbations in CO2 concentration and long-term growth and development under high CO2. Prolonged growth at elevated CO2 concentrations induced a higher endogenous rate of C2H4 release

relative to that of leaf tissue grown at lower CO2 levels. Leaf tissue from all leaf positions of plants grown at high CO2 consistently evolved more C2H4 than corresponding tissue from ambient-grown plants when assayed under standardized conditions. Endogenous (ACC) tissue contents and rates of ACC-stimulated ethylene release were also higher at all leaf positions in CO2-enriched tissue. Thus the higher rates appeared to be due to both higher endogenous precursor (ACC) levels in the tissue and greater ACC to C2H4 conversion capacity. Growth at elevated CO2 levels resulted in a persistent increase in the rate of endogenous C2H4 release in leaf tissue. The capacity for increased ethylene release in response to CO2 did not decline after prolonged growth at high CO2.

KEYWORDS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID, ACCLIMATION, CARBON DIOXIDE, GAS-EXCHANGE, HIGH ATMOSPHERIC CO2, PHOTOSYNTHESIS, RELEASE, WHOLE PLANT, XANTHIUM-STRUMARIUM L, ZEA-MAYS

2633

Woods, J., and W. Barkmann. 1993. The plankton multiplier - positive feedback in the greenhouse. *Journal of Plankton Research 15(9):1053-1074.*

The plankton multiplier is a positive feedback mechanism linking the greenhouse effect and biological pump (Woods,J.D., Royal Commission on Environmental Pollution, 1990). As pollution increases the atmospheric concentration of carbon dioxide, the enhanced greenhouse effect induces radiative forcing of the ocean, which diminishes the depth of winter convection, reducing the annual resupply of nutrients to the euphotic zone and therefore the annual primary production. That weakens the biological pump, which contributes to oceanic uptake of CO2. As the ocean takes up less CO2, more remains in the atmosphere, accelerating the rise in radiative forcing. We have used a mathematical model of the upper ocean ecosystem, based on the Lagrangian Ensemble method, to estimate the sensitivity of the biological pump to radiative forcing, which lies at the heart of the plankton multiplier. We conclude that increasing radiative forcing by 5 W m-2 (equivalent to doubling atmospheric CO2) reduces the deep flux of particulate carbon by 10%. That sensitivity is sufficient to produce significant positive feedback in the greenhouse. It means that the plankton multiplier will increase the rate of climate change in the 21st century. It also suggests that the plankton multiplier is the mechanism linking the Milankovich effect to the enhanced greenhouse effect that produces global warming at the end of ice ages.

KEYWORDS: BLOOM, CARBON DIOXIDE, DYNAMICS, MIXED LAYER, MODEL, NORTH-ATLANTIC, OCEAN, OXYGEN, SURFACE, WATERS

2634

Woodward, A. 1998. Relationships among environmental variables and distribution of tree species at high elevation in the Olympic mountains. *Northwest Science 72(1):10-22.*

Relationships among environmental variables and occurrence of tree species were investigated at Hurricane Ridge in Olympic National Park, Washington, USA. A transect consisting of three plots was established down one north-and one south-facing slope in stands representing the typical elevational sequence of tree species. Tree species included subalpine fir (Abies lasiocarpa), Douglas-fir (Pseudotsuga menziesii), mountain hemlock (Tsuga mertensiana), and Pacific silver fir (Abies amabilis). Air and soil temperature, precipitation, and soil moisture were measured during three growing seasons. Snowmelt patterns, soil carbon and moisture release curves were also determined. The plots represented a wide range in soil water potential, a major determinant of tree species distribution (range of minimum values = -1.1 to -8.0 MPa for Pacific silver fir and Douglas-fir plots, respectively). Precipitation intercepted at plots depended on topographic location, storm direction and storm type. Differences in soil moisture among plots was related to soil properties, while annual differences at each plot were most often related to early season precipitation. Changes in climate due to a doubling of atmospheric CO2 will likely shift tree species distributions within, but not among aspects. Change will be buffered by innate tolerance of adult trees and the inertia of soil properties.

KEYWORDS: CLIMATE, FIRE, PRECIPITATION, TOPOGRAPHY, WASHINGTON

2635

Woodward, F.I. 1992. Predicting plant-responses to global environmental-change. *New Phytologist 122(2):239-251.*

Predicting the future responses of plants and ecosystems to further changes in the CO2 concentration of the atmosphere and to the possibility of global warming are important current concerns. Predictions have been most frequently attempted using short-term, single-factor experiments in controlled environments. However, these experiments have failed to indicate the outcome of field experiments at larger spatial and temporal scales. Some of this failure is due to ignorance of environmental conditions and interactions while some is due to the use of inappropriate short-cuts, such as the addition of fertilizers for simulating enhanced mineralization, and some is due to ignorance of the processes involved in scaling-up from individual plants to populations. Long-term observations on plants in ecosystems nevertheless indicate that community-scale experiments may provide a useful but imperfect capacity to predict ecosystem responses. Although difficult to implement in practice, it is concluded that catchment-scale experiments offer the best opportunity to predict plant, community and ecosystem responses to environmental change.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CHENOPODIUM-ALBUM L, ELEVATED CO2, ESTUARINE MARSH, FAR-RED, GROWTH-RESPONSES, INSECT HERBIVORE INTERACTIONS, NITROGEN-FIXATION, PHOTOSYNTHESIS, SAXIFRAGA-CERNUA

2636

Woodward, F.I. 1993. The lowland-to-upland transition modeling plant-responses to environmental-change. *Ecological Applications 3(3):404-408.*

A published correlative model has predicted that the distributional limits of plants and vegetation zones on mountains will increase in altitude with global warming. I test this hypothesis using results from published experimental studies. Investigations and models of the responses of leaf growth to temperature are in accord with the prediction. However, the individualistic responses of species to CO2 enrichment indicate that the prediction is unlikely to be true for all species: growth is stimulated by CO2 enrichment for some species but not for others. Wind speed generally increases with altitude on mountains, and plants from high altitude tend to be more wind resistant than species from the lowland. Therefore it is expected that, particularly on wind-swept mountains, global warming will not necessarily be followed by the spread of lowland species into the uplands.

KEYWORDS: AREA, CLIMATE, DIVERSE ALTITUDINAL RANGES, DYNAMICS, ECOSYSTEMS, FIELD, GROWTH, LEAF EXTENSION, VEGETATION

2637

Woodward, F.I., and C.K. Kelly. 1995. The influence of co2 concentration on stomatal density. *New Phytologist 131(3):311-327.*

A survey of 100 species and 122 observations has shown an average reduction in stomatal density of 14.3% (SE+/-2.2%) with CO2 enrichment, with 74% of the cases exhibiting a reduction in stomatal density. A sign test demonstrated that stomatal density decreases, in response to CO2, significantly more often than expected by chance. Repeated observations on the same species indicated a significant repeatability in the direction of the stomatal response. Analyses which removed the potential effect of taxonomy on this data set showed no significant patterns in the dependency of the degree of stomatal change on growth form (woodiness vs. non-woodiness; trees vs. shrubs), habitat (cool vs. warm) or stomatal distribution on the leaf (amphi- vs. hypostomatous). Forty-three of the observations had been made in controlled environments and under a typical range in CO2 enrichment of 350-700 mu mol mol(-1). For these cases the average stomatal density declined by 9% (SE+/-3.3%) and 60% of the cases showed reductions in stomatal density. When analyses were restricted to these 43 observations, amphistomatous samples more frequently had greater changes in stomatal density than did hypostomatous samples. The degree of reduction in stomatal density with increasing CO2 increases with initial stomatal density, after the influence of taxonomy is removed using analyses of independent contrasts. When the data were examined for patterns that might be due explicitly to the effects of relatedness, the subclasses of the Hamamelidae and the Rosidae showed highly significant reductions in stomatal density with CO2 (87% of the species studied in the Hamamelidae and 80% of the species in the Rosidae showed reduction with CO2 enrichment) and correlations between initial stomatal density and degree of reduction in stomatal density. The species sampled in the Hamamelidae were dominantly trees, whereas herbs dominated the species in the Rosidae. There were insufficient species studied at lower taxonomic levels to warrant further statistical analyses. This problem results from experimental and observational data being most often restricted to one species per taxonomic level, typically up to the level of order, a feature which can severely limit the extraction of taxonomically-related and ecologically-related plant responses.

KEYWORDS: ATMOSPHERIC CO2, ELEVATED CO2, ENRICHMENT, GROWTH, INCREASE, LAST 3 CENTURIES, LEAF-AREA, LEAVES, RESPONSES, WATER-USE EFFICIENCY

2638

Woodward, F.I., T.M. Smith, and W.R. Emanuel. 1995. A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles 9(4):471-490.*

A global primary productivity and phytogeography model is described. The model represents the biochemical processes of photosynthesis and the dependence of gas exchange on stomatal conductance, which in turn depends on temperature and soil moisture. Canopy conductance controls soil water loss by evapotranspiration. The assignment of nitrogen uptake to leaf layers is proportional to irradiance, and respiration and maximum assimilation rates depend on nitrogen uptake and temperature. Total nitrogen uptake is derived from soil carbon and nitrogen and depends on temperature. The long-term average annual carbon and hydrological budgets dictate canopy leaf area. Although observations constrain soil carbon and nitrogen, the distribution of vegetation types is not specified by an underlying map. Variables simulated by the model are compared to experimental results. These comparisons extend from biochemical processes to the whole canopy, and the comparisons are favorable for both current and elevated CO2 atmospheres. The model is used to simulate the global distributions of leaf area index and annual net primary productivity. These distributions are sufficiently realistic to demonstrate that the model is useful for analyzing vegetation responses to global environmental change.

KEYWORDS: C-3 PLANTS, CARBON ALLOCATION, CLIMATE CHANGE, FOREST ECOSYSTEM PROCESSES, GENERAL-CIRCULATION MODEL, HIGH-RESOLUTION RADIOMETER, LEAF NITROGEN, NET PRIMARY PRODUCTION, REGIONAL APPLICATIONS, STOMATAL CONDUCTANCE

2639

Woodward, F.I., G.B. Thompson, and I.F. McKee. 1991. The effects of elevated concentrations of carbon-dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany 67:23-38.*

KEYWORDS: ATMOSPHERIC CO2 ENRICHMENT, BIOSPHERE EXCHANGE, CLOVER TRIFOLIUM-REPENS, CO2-ENRICHED ATMOSPHERE, DRY-MATTER, INSECT HERBIVORE, LONG-TERM EXPOSURE, PAST 2 CENTURIES, PHOTOSYNTHETIC INHIBITION, PISUM-SATIVUM

2640

Woolgrove, C.E., and S.J. Woodin. 1996. Ecophysiology of a snow-bed bryophyte Kiaeria starkei during snowmelt and uptake of nitrate from meltwater. *Canadian Journal of Botany-Revue Canadienne De Botanique 74(7):1095-1103.*

Snow is a very efficient scavenger of atmospheric pollutants and because of the dynamics of snowmelt, much of the pollutant load of a snowpack is released at very high concentrations in episodes known as the acid flush. The ecological effects of this are largely unknown, but any effects on the bryophyte- dominated vegetation of snow beds will depend in part on the physical environment and physiological state of plants under and just out of snow cover. These factors were investigated at a snow bed in the Cairngorm Mountains, Scotland. The subnivean environment is characterized by slightly elevated CO2 concentrations (up to 70 mu L/L above ambient), temperatures at and just above 0 degrees C, and very low light intensity, with no light penetrating through more than 50 cm depth of snow. Despite overwinter storage in these conditions, the bryophyte Kiaeria starkei is shown to be capable of photosynthetic activity immediately after removal of snow cover, and tissue chlorophyll and carbohydrate concentrations increase by 250 and 60%, respectively, during the 2 weeks thereafter. Comparison of photosynthetic light responses at 5 and 18 degrees C in plants collected from under and out of snow cover demonstrates acclimatization to seasonal environmental change that must enable maximization of growth during the short growing season available. Kiaeria starkei is also shown to be capable of nitrate reductase activity even at 2 degrees C and to assimilate more than 90% of the pollutant nitrate coming into contact with it in snowmelt. As nitrate is known to be damaging to bryophytes in excess, this demonstrates a real threat of pollutant deposition to rare snow-bed communities in Scotland today and is an important warning for other regions where snow- bed vegetation is important.

KEYWORDS: ATMOSPHERIC NITROGEN, CHEMICAL-COMPOSITION, CO2, COMMUNITY, DEPOSITION, ELEMENT, GROWTH, TEMPERATURE, TOLERANCE, WINTER

2641

Wright, R.F. 1998. Effect of increased carbon dioxide and temperature on runoff chemistry at a forested catchment in southern Norway (CLIMEX project). *Ecosystems 1(2):216-225.*

CLIMEX (Climate Change Experiment) is an integrated, whole-ecosystem research project that focuses on the response of forest ecosystems at the catchment scale to increased CO2 and temperature. I(IM catchment (860 m(2)) is completely enclosed by a transparent greenhouse, receives deacidifed "clean" rain, and has elevated CO2 (560 ppmv) and elevated air temperature (3 degrees-5 degrees C above ambient). The uppermost 20% of the catchment is partitioned off, is not subject to changed CO2 or temperature, and serves as an untreated control. Fluxes of nitrate and ammonium in runoff from I(IM catchment

increased from 2 mmol m(-2) y(-1) each in the 3 years before treatment to 6 and 3 mmol m(-2) y(-1), respectively, in the 3 years after treatment (May 1994-April 1997), despite a 15 mmol m(-2) y(-1) decrease in N dry deposition due to the sealing of the walls to the enclosure. N flux in runoff from three reference catchments and the control section did not change. The net loss of inorganic N was thus about 20 mmol m(-2) treated soil y(-1). There were no changes in organic N or total organic carbon in runoff. The ecosystem switched from a net sink to a net source of inorganic nitrogen (N). The increased loss of N may be due to accelerated decomposition of soil organic matter induced by higher temperature. Due to many decades of N deposition from long-range transported pollutants, the ecosystem prior to treatment was N saturated. If global change induces persistent losses of inorganic N on a regional scale, the result may be a significant increase in nitrate concentrations in fresh waters and N loading to coastal marine ecosystems. In regions with acid sensitive waters, such as southern Norway, the increased nitrate release caused by global change may offset improvements achieved by reduced sulfur and hi deposition.

KEYWORDS: NITROGEN

2642

Wu, W.H., J.Y. Lu, A.R. Jones, D.G. Mortley, P.A. Loretan, C.K. Bonsi, and W.A. Hill. 1997. Proximate composition, amino acid profile, fatty acid composition, and mineral content of peanut seeds hydroponically grown at elevated CO2 levels. *Journal of Agricultural and Food Chemistry 45(10):3863-3866.*

Peanut plants (Arachis hypogaea L. cv. Georgia Red) were grown hydroponically using a recirculating nutrient film technique. The effect of CO2 enrichment on nutritive composition of hydroponic peanut seeds was examined at two elevated CO2 levels (700 and 1400 ppm) that simulate potential conditions in National Aeronautics and Space Administration (NASA) Controlled Ecological Life-Support Systems (CELSS) and compared to ambient CO2 condition in hydroponics (the control). Plants were harvested at 97 days after planting, and the seeds were air- dried and analyzed for composition. Percentages of crude protein, crude fat, ash, and carbohydrate of hydroponic peanut seeds were around 30%, 30%, 3%, and 30%, respectively. The major amino acids were aspartic acid, glutamic acid, and arginine. The limiting amino acid of peanut, methionine, was 1.2%. Linoleic acid was the major fatty acid, followed by oleic and palmitic acids. The major mineral elements were K, P, Mg, and Ca. The results showed that certain peanut varieties can be grown hydroponically. The composition of the hydroponically grown peanuts is generally similar to reported peanut composition The nutrient composition was not affected at the elevated CO2 concentrations investigated.

KEYWORDS: STORAGE

2643

Wullschleger, S.D., J.P. Lynch, and G.M. Berntson. 1994. Modeling the belowground response of plants and soil biota to edaphic and climatic-change - what can we expect to gain. *Plant and Soil 165(1):149-160.*

As atmospheric CO2 concentrations continue to increase, so too will the emphasis placed on understanding the belowground response of plants to edaphic and climatic change. Controlled- exposure studies that address the significance of an increased supply of carbon to roots and soil biota, and the consequences of this to nutrient cycling will play a prominent role in this process. Models will also contribute to understanding the response of plants and ecosystems to changes in the earth's climate by incorporating experimental results into conceptual or quantitative frameworks from which potential feedbacks within the plant-soil system can be identified. Here we present five examples of how models can be used in this analysis and how they can contribute to the development of new hypotheses in the areas of root biology, soil biota, and ecosystem processes. Two examples illustrate the role of coarse and fine roots in nitrogen and phosphorus uptake from soils, the respiratory costs associated with this acquisition of nutrients, and the significance of root architecture in these relationships. Another example focuses on a conceptual model that has helped raise new ideas about the effects of elevated CO2 on root and microbial biomass, and on nutrient dynamics in the rhizosphere. Difficulties associated with modeling the contribution of mycorrhizal fungi to whole-plant growth are also discussed. Finally several broad-scale models are used to illustrate the importance of root turnover, litter decomposition, and nitrogen mineralization in determining an ecosystem's response to atmospheric CO2 enrichment. We conclude that models are appropriate tools for use both in guiding existing studies and in identifying new hypotheses for future research. Development of models that address the complexities of belowground processes and their role in determining plant and ecosystem function within the context of rising CO2 concentrations and associated climate change should be encouraged.

KEYWORDS: ALLOCATION, ATMOSPHERIC CO2 ENRICHMENT, CARBON, ELEVATED CO2, GLOBAL CHANGE, NITROGEN, QUERCUS-ALBA, ROOT, SEEDLING GROWTH, TERRESTRIAL ECOSYSTEMS

2644

Wullschleger, S.D., and R.J. Norby. 1992. Respiratory cost of leaf growth and maintenance in white oak saplings exposed to atmospheric co2 enrichment. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 22(11):1717-1721.*

Atmospheric CO2 enrichment reportedly reduces respiration of mature leaves in a number of woody and herbaceous perennials. It has vet to be determined, however, whether these reductions reflect changes in maintenance respiration alone or whether CO2 might affect growth respiration as well. This possibility was examined in white oak (Quercus alba L.) seedlings that had been planted directly into the ground within open-top chambers and exposed to ambient, ambient + 150 muL.L-1, and ambient + 300 muL.L-1 CO2 concentrations over a 3-year period. In the spring of 1992, respiration rates were measured repeatedly during leaf expansion, and the growth and maintenance coefficients were determined using a two-component model. Specific respiration rates (mg CO2.g-1.h-1) were consistently lower for leaves of CO2 enriched saplings than for leaves of ambient-grown saplings. Partitioning these reductions in leaf respiration to either the growth or maintenance coefficients indicated a strong effect of CO2 on both components. The growth coefficient for leaves exposed to the ambient CO2 treatment was 964 Mg CO2.g-1 compared with 849 and 664 mg CO2.g-1 for leaves from the two elevated CO2 concentrations, respectively. The maintenance coefficient was similarly reduced from a control rate of 114 mg CO2.g-1 d-1 to below 65 mg CO2.g-1.d-1 for leaves exposed to CO2 enrichment. Our results quantitatively describe the magnitude by which growth and maintenance respiration are affected by CO2 enrichment and as such should provide useful information for the future modeling of this phenomenon.

KEYWORDS: TREES

2645

Wullschleger, S.D., R.J. Norby, and C.A. Gunderson. 1992. Growth and maintenance respiration in leaves of liriodendron- tulipifera L exposed to long-term carbon-dioxide enrichment in the field. *New Phytologist 121(4):515-523.*

Specific respiration rate (SRR) was mathematically partitioned into its growth and maintenance components for leaves of yellow-poplar

(Liriodendron tulipifera L.) after 3 vr of CO2 enrichment in open-top field chambers. Despite the absence of a CO2 effect on individual leaf expansion or specific growth rate (SGR), increasing the CO2 concentration to ambient + 150 or + 300 cm3 m-3 decreased SRR by 28 to 45 % compared with ambient- grown controls. These lower leaf respiration rates were correlated with reduced leaf nitrogen concentrations. As described by the two-component model of growth and maintenance respiration, SRR was a linear function of SGR. Ambient-grown leaves had a growth respiration coefficient of 704 mg CO2 g-1 dry mass compared with 572 and 570 mg CO2 g-1 for leaves grown at the two higher CO2 concentrations. Leaves from the elevated CO2 treatments had an average maintenance respiration coefficient of 88 mg CO2 g-1 dry mass d-1 compared with 135 mg CO2 g-1 d-1 for leaves from the ambient treatment. Incorporating these growth and maintenance coefficients into a leaf growth simulation model indicated that total respiration would be reduced by 21 to 26 % for a leaf exposed to + 150 or + 300 cm3 m-3 CO2 throughout its 50-d lifespan compared with one grown at ambient CO2 conditions. Reductions in total respiration were dominated by a lower rate of maintenance respiration, while the contribution of a lower specific rate of growth respiration was largely offset by a greater dry mass for leaves grown at elevated CO2 concentrations. Although reductions in the respiratory loss of carbon could be beneficial, respiration is unlikely to decrease without a concomitant decrease in other metabolic processes. Whether these reductions are beneficial or detrimental to the long-term growth of plants exposed to elevated CO2 remains unresolved.

KEYWORDS: ATMOSPHERIC CO2, C-3, EFFLUX, ELEVATED CO2, INCREASE, MODEL, NITROGEN, PLANTS, RESPONSES

2646

Wullschleger, S.D., R.J. Norby, and P.J. Hanson. 1995. Growth and maintenance respiration in stems of quercus-alba after 4 years of co2 enrichment. *Physiologia Plantarum 93(1):47-54.*

Atmospheric CO2 enrichment is increasingly being reported to inhibit leaf and whole-plant respiration. It is not known, however, whether this response is unique to foliage or whether woody-tissue respiration might be affected as well. This was examined for mid-canopy stem segments of white oak (Quercus alba L.) trees that had been grown in open-top field chambers and exposed to either ambient or ambient + 300 mu mol mol(-1) CO2 over a 4-year period. Stem respiration measurements were made throughout 1992 by using an infrared nas analyzer and a specially designed in situ cuvette. Rates of woody-tissue respiration were similar between CO2 treatments prior to leaf initiation and after leaf senescence, but were several fold greater for saplings grown at elevated concentrations of CO2 during much of the growing season. These effects were most evident on 7 July when stem respiration rates for trees exposed to elevated CO2 concentrations were 7.25 compared to 3.44 mu mol CO2 m(-2) s(-1) for ambient-grown saplings. While other explanations must be explored, greater rates of stem respiration for saplings grown at elevated CO2 concentrations were consistent with greater rates of stem growth and more stem-wood volume present at the time of measurement. When rates of stem growth were at their maximum (7 July to 3 August), growth respiration accounted for about 80 to 85% of the total respiratory costs of stems at both CO2 treatments, while 15 to 20% supported the costs of stem-wood maintenance. Integrating growth and maintenance respiration throughout the season, taking into account treatment differences in stem growth and volume, indicated that there were no significant effects of elevated CO2 concentration on either respiratory process. Quantitative estimates that could be used in modeling the costs of woody-tissue growth and maintenance respiration are provided.

KEYWORDS: DARK RESPIRATION, EFFLUX, ELEVATED CARBON-DIOXIDE, FOREST, INHIBITION, LEAVES, PHOTOSYNTHESIS, PLANT RESPIRATION, TERM, TREE

2647

Wullschleger, S.D., R.J. Norby, and D.L. Hendrix. 1992. Carbon exchange-rates, chlorophyll content, and carbohydrate status of 2 forest tree species exposed to carbon-dioxide enrichment. *Tree Physiology 10(1):21-31.*

Seedlings of yellow-poplar (Liriodendron tulipifera L.) and white oak (Quercus alba L.) were exposed continuously to one of three CO2 concentrations in open-top chambers under field conditions and evaluated after 24 weeks with respect to carbon exchange rates (CER), chlorophyll (Chl) content, and diurnal carbohydrate status. Increasing the CO2 concentration from ambient to +150 or +300-mu-l l-1 stimulated CER of yellow- poplar and white oak seedlings by 60 and over 35%, respectively, compared to ambient-grown seedlings. The increases in CER were not associated with a significant change in stomatal conductance and occurred despite a reduction in the amounts of Chl and accessory pigments in the leaves of plants grown in CO2-enriched air. Total Chl contents of yellow-poplar and white oak seedlings grown at +300-mu-l l-1 were reduced by 27 and over 55%, respectively, compared with ambient-grown seedlings. Yellow-poplar and white oak seedlings grown at +300-mu-l l-1 contained 72 and 67% more morning starch, respectively, than did ambient-grown plants. In contrast, yellow-poplar and white oak seedlings grown at +300-mu-l l-1 contained 17 and 27% less evening sucrose, respectively, than did plants grown at ambient CO2 concentration. Diurnal starch accumulation and the subsequent depletion of sucrose contributed to a pronounced increase in the starch/sucrose ratio of plants grown in CO2-enriched air. All seedlings exhibited a substantial reduction in dark respiration as CO2 concentration increased, but the significance of this increase to the carbohydrate status and carbon economy of plants grown in CO2-enriched air remains unclear.

2648

Wullschleger, S.D., R.J. Norby, J.C. Love, and C. Runck. 1997. Energetic costs of tissue construction in yellow-poplar and white oak trees exposed to long-term CO2 enrichment. *Annals of Botany 80(3):289-297.*

Two methods were used to estimate construction costs for leaves, stems, branches and woody roots of yellow-poplar (Liriodendron tulipifera L.) trees grown at ambient (35 Pa) and elevated (65 Pa) CO2 for 2.7 years and trees of white oak (Quercus alba L.) grown at these same CO2 partial pressures for 4 years. Sample combustion in a bomb calorimeter combined with measurements of ash and nitrogen content provided the primary method of estimating tissue construction costs (W-G; g glucose g(-1) dry mass). These values were compared with a second, simpler method in which cost estimates were derived from tissue ash, carbon and nitrogen content (V-G). Estimates of W-G were lower for leaves, branches and roots of yellow-poplar and for leaves of white oak grown at elevated compared with ambient CO2 partial pressures. These CO2-induced differences in W-G ranged from 3.7% in yellow-poplar roots to 2.1% in white oak leaves. Only in the case of yellow-poplar leaves, however were differences in V-G observed between CO2 treatments. Leaf V-G was 1.46 g glucose g(-1) dry mass in ambient-grown trees compared with 1.41 g glucose g(-1) dry mass for CO2-enriched trees. Although paired-estimates of W-G and V-G clustered about a 1:1 line for leaves and branches, estimates of V-G were consistently lower than W-G for stems and roots. Construction costs per unit leaf area were 95 g glucose m(-2) for yellow- poplar trees grown at ambient CO2 and 106 g glucose m(-2) for trees grown at elevated CO2 partial pressures. No differences in area-based construction costs were observed for white oak. Whole-plant energy content was 1220 g glucose per tree in ambient-grown white oak compared with 2840 g glucose per tree for those grown at elevated CO2 partial pressures. These differences were driven largely by CO2-induced changes in total biomass. We conclude that while

construction costs were lower at elevated CO2 partial pressures, the magnitude of this response argues against an increased efficiency of carbon use in the growth processes of trees exposed to CO2 enrichment. (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED ATMOSPHERIC CO2, GROWTH EFFICIENCY, LEAF RESPIRATION, LEAVES, LIRIODENDRON-TULIPIFERA L, MAINTENANCE RESPIRATION, MAX L MERR, QUERCUS-ALBA, RESPONSES

2649

Wullschleger, S.D., L.H. Ziska, and J.A. Bunce. 1994. Respiratory responses of higher-plants to atmospheric co2 enrichment. *Physiologia Plantarum 90(1):221-229.*

Although the respiratory response of native and agricultural plants to atmospheric CO2 enrichment has been reported over the past 75 years, only recently have these effects emerged as prominent measures of plant and ecosystem response to the earth's changing climate. In this review we discuss this rapidly expanding field of study and propose that both increasing and decreasing rates of leaf and whole-plant respiration are likely to occur in response to rising CO2 concentrations. While the stimulatory effects of CO2 on respiration are consistent with our knowledge of leaf carbohydrate status and plant metabolism, we wish to emphasize the rather surprising short-term inhibition of leaf respiration by elevated CO2 and the reported effects of long-term CO2 exposure on growth and maintenance respiration. As is being found in many studies, it is easier to document the respiratory response of higher plants to elevated CO2 than it is to assign a mechanistic basis for the observed effects. Despite this gap in our understanding of how respiration is affected by CO2 enrichment, data are sufficient to suggest that changes in leaf and whole-plant respiration may be important considerations in the carbon dynamics of terrestrial ecosystems as global CO2 continues to rise. Suggestions for future research that would enable these and other effects of CO2 on respiration to be unravelled are presented.

KEYWORDS: CARBOHYDRATE STATUS, CARBON-DIOXIDE ENRICHMENT, CYANIDE- RESISTANT, DARK RESPIRATION, ELEVATED CO2, ENERGY OVERFLOW, EXCHANGE, GROWTH, PHOTOSYNTHESIS, SHORT- TERM

2650

Wurr, D.C.E., D.W. Hand, R.N. Edmondson, J.R. Fellows, M.A. Hannah, and D.M. Cribb. 1998. Climate change: a response surface study of the effects of CO2 and temperature on the growth of beetroot, carrots and onions. *Journal of Agricultural Science 131:125-133.*

Ten daylit, controlled-environment cabinets were used to investigate the possible impacts of global rises in atmospheric CO2 concentration and temperature on beetroot (Beta vulgaris L.), carrot (Daucus carota L.) and bulb onion (Allium cepa L.) plants. Their responses to CO2 concentrations of 350, 450, 550, 650 and 750 vpm and temperatures of 12, 13.5, 15, 16.5 and 18 degrees C were examined by using a fractional factorial design for the two treatment factors. Use of the daylit cabinets allowed the plants to be grown in natural light, common atmospheric humidities (vpd 0.7 kPa) and nonlimiting supplies of water and mineral nutrients. Polynomial models were used to summarize the whole plant dry weight and fresh weight yield responses and to indicate the potential impact of climate change. Additionally, the models were used to generate predictions of the percentage change in whole plant dry weight and plant fresh weight yield for the years 2025 and 2050 relative to 1992. Baseline values of 350 vpm for CO2 and a mean temperature of 13.5 degrees C for 1992 together with forecast CO2 values of 407 and 442 vpm and temperature increases of 0.7 and 1.1 C for 2025 and 2050 respectively were used. For 2025, fresh weight yield changes of + 19%, +9% and +13% were obtained for beetroot, carrot and onion crops respectively, while for 2050 the respective changes were + 32 %, + 13 % and +21 %. Measurements of the ratio of the maximum diameter of the bulb to the minimum diameter of the neck for onions showed that there was little or no influence of CO2, whereas the effect of temperature was substantial. Bulbing was accelerated by high temperature and was greatly delayed at low temperature. At temperatures < 15 degrees C, the delays to bulbing resulted in the development of undesirable, thick-necked onions which tended to remain green with erect leaves. These results suggest, therefore, that a warmer climate will be advantageous for the commercial production of bulb onions in Britain.

KEYWORDS: ATMOSPHERIC CO2, CROP, ENRICHMENT, YIELD

2651

Wurth, M.K.R., K. Winter, and C. Korner. 1998. In situ responses to elevated CO2 in tropical forest understorey plants. *Functional Ecology 12(6):886-895.*

1. Plants growing in deep shade and high temperature, such as in the understorey of humid tropical forests, have been predicted to be particularly sensitive to rising atmospheric CO2. We tested this hypothesis in five species whose microhabitat quantum flux density (QFD) was documented as a covariable. After 7 (tree seedlings of Tachigalia versicolor and Beilschmiedia pendula) and 18 months (shrubs Piper cordulatum and Psychotria limonensis, and grass Pharus latifolius) of elevated CO2 treatment (c. 700 mu l litre(-1)) under mean QFD of less than 11 mu mol m(-2) s(-1), ail species produced more biomass (25-76%) under elevated CO2. 2. Total plant biomass tended to increase with microhabitat QFD (daytime means varying from 5 to II mu mol m(-2) s(-1)) but the relative stimulation by elevated CO2 was higher at low QFD except in Pharus. 3. Non-structural carbohydrate concentrations in leaves increased significantly in Pharus (+ 27%) and Tachigalia (+ 40%). 4. The data support the hypothesis that tropical plants growing near the photosynthetic light compensation point are responsive to elevated CO2. An improved plant carbon balance in deep shade is likely to influence understorey plant recruitment and competition as atmospheric CO2 continues to rise.

KEYWORDS: CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ENVIRONMENTS, GROWTH-RESPONSES, MODEL, PHOTOSYNTHESIS, RAIN-FOREST, SEEDLINGS, TREE

2652

Wurth, M.K.R., K. Winter, and C. Korner. 1998. Leaf carbohydrate responses to CO2 enrichment at the top of a tropical forest. *Oecologia 116(1-2):18-25.*

The accumulation of non-structural leaf carbohydrates is one of the most consistent plant responses to elevated CO2. It has been found in both fast-and slow-growing plants and is largely independent of the duration of exposure. Changes in leaf quality are thus to be expected, irrespective of other plant responses to atmospheric CO2 enrichment. However, there is no experimental evidence from tropical forests, the biome with the largest biomass carbon pool. Here we report in situ mesophyll responses of mature tropical trees to a doubling of CO2, Individually CO2-enriched leaves on 25 to 35-m-tall forest trees living at 26-35 degrees C can be assumed to experience little sink limitation, and so, may be expected to exhibit no or very little carbohydrate accumulation. We tested this hypothesis using the leaf cup method on leaves accessible via the canopy crane of the Smithsonian Tropical Research Institute in a semi-deciduous tropical forest in Panama. We also investigated the influence of the leaf-specific light regime, another possible environmental determinant of leaf carbon gain and mobile leaf carbohydrates. Total non-structural carbohydrates (TNC) reached a new steady state concentration after less than 4 days of exposure to twice ambient CO2 concentration. Against expectation, all four tree species

investigated (Anacardium excelsum, Cecropia longipes, C. peltata, Ficus insipida) accumulated significant amounts of TNC (+41 to +61%) under elevated CO2. The effect was stronger at the end of the daylight period (except for Ficus), but was still significant in all four species at the end of the dark period. In contrast, neither artificial nor natural shading affected leaf TNC. Taken together, these observations suggest that TNC accumulation reflects a mesophyll-bound tissue response specific to elevated CO2, presumably unrelated to sink limitations. Thus, leaves of tropical forests seem not to be an exception, and will most likely contain more non-structural carbohydrates in a CO2-rich world.

KEYWORDS: CARBON, ELEVATED ATMOSPHERIC CO2, GROWTH, MODEL, PLANT-RESPONSES, TREES

2653

Xiao, X., D.S. Ojima, W.J. Parton, Z. Chen, and D. Chen. 1995. Sensitivity of Inner Mongolia grasslands to climate change. *Journal of Biogeography 22(4-5):643-648.*

We investigated the effects of global climate change and doubled atmospheric CO2 concentration to plant primary production and soil organic matter of typical steppe (Leymus chinense steppe and Stipa grandis steppe) and meadow steppe (Filifolium sibiricum steppe, S. baicalensis steppe and L. chinense steppe) at individual sites in Inner Mongolia, using the CENTURY ecosystem model. In the simulation of climate change, loss of soil organic C ranges from 783 gC.m(-2) in meadow steppe to 1485 gC.m(-2) in typical steppe, and annual above-ground net primary production (ANPP) decreases by 17.6 gC.m(-2) in meadow steppe to 29.5 gC.m(-2) in typical steppe under CCC (Canadian Climate Center). While under GFDL (Geophysical Fluid Dynamics Laboratory), loss of soil organic C varies from 584 gC.m(-2) in typical steppe to 1164 gC.m(-2) in meadow steppe, and ANPP decreases in the range of 18.3 gC.m(-2) in typical steppe to 32.1 gC.m(-2) in meadow steppe. In the simulations of climate change plus elevated CO2 (from 350 p.p.m. to 700 p.p.m.), ANPP decreases by 5.4 gC.m(-2) in meadow steppe to 11.3 gC.m(-2) in typical steppe under CCC + CO2, while ANPP varies from an increase of 1.8 gC.m(-2) in S. grrmdis steppe to a decrease of 20.6 gC.m(-2) in meadow steppe under GFDL + CO2. Losses of soil organic C are slightly lower (in the range of 42 gC.m(-2) to 248 gC.m(-2)) than losses of soil organic C under climate change only. These five steppe ecosystems are very sensitive to climate change, dependent upon projected change in temperature and precipitation by GCMs of CCC and GFDL.

KEYWORDS: BIOMASS, CO2, CONIFEROUS FORESTS, DYNAMICS

2654

Xu, D.Q., R.M. Gifford, and W.S. Chow. 1994. Photosynthetic acclimation in pea and soybean to high atmospheric co2 partial-pressure. *Plant Physiology 106(2):661-671.*

Nonnodulated pea (Pisum sativum L. cv Frosty) and soybean (Glycine max [L.] Merr. cv Wye) plants were grown under artificial lights from germination with ample nutrients, 600 mu mol photons m(-2) s(-1), and either 34 to 36 (control) or 64 to 68 Pa (enriched) CO2. For soybean, pod removal and whole-plant shading treatments were used to alter the source-sink balance and carbohydrate status of the plants. Growth of both species was substantially increased by CO2 enrichment despite some down-regulation of photosynthesis rate per unit leaf area ("acclimation"). Acclimation was observed in young pea leaves but not old and in old soybean leaves but not young. Acclimation was neither evident in quantum yield nor was it related to triose phosphate limitation of net photosynthesis. A correlation between levels of starch and sugars in the leaf and the amount of acclimation was apparent but was loose and only weakly related to the source-sink balance of the plant. A consistent feature of acclimation was reduced ribulose bisphosphate carboxylase (RuBPCase) content, although in vivo RuBPCase activity was not necessarily diminished by elevated growth CO2 owing to increased percentage of activation of the enzyme. A proposal is discussed that the complexity of photosynthetic acclimation responses to elevated CO2 is as an expression of re-optimization of deployment of within-plant resources at three levels of competition.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO2, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, PLANTS, RESPONSES, RUBISCO ACTIVITY, WATER HYACINTH

2655

Xue, X.P., D.A. Gauthier, D.H. Turpin, and H.G. Weger. 1996. Interactions between photosynthesis and respiration in the green alga Chlamydomonas reinhardtii - Characterization of light-enhanced dark respiration. *Plant Physiology 112(3):1005-1014.*

The rate of respiratory O-2 consumption by Chlamydomonas reinhardtii cell suspensions was greater after a period of photosynthesis than in the preceding dark period. This "light- enhanced dark respiration" (LEDR) was a function of both the duration of illumination and the photon fluence rate. Mass spectrometric measurements of gas exchange indicated that the rate of gross respiratory O-2 consumption increased during photosynthesis, whereas gross respiratory CO2 production decreased in a photon fluence rate-dependent manner. The rate of postillumination O-2 consumption provided a good measure of the O-2 consumption rate in the light. LEDR was substantially decreased by the presence of 3-(3,4-dichlorophenyl)-1,1- dimethylurea or glycolaldehyde, suggesting that LEDR was photosynthesis-dependent. The onset of photosynthesis resulted in an increase in the cellular levels of phosphoglycerate, malate, and phosphoenolpyruvate and a decrease in whole-cell ATP and citrate levels; all of these changes were rapidly reversed upon darkening. These results are consistent with a decrease in the rate of respiratory carbon flow during photosynthesis, whereas the increase in respiratory O-2 consumption during photosynthesis may be mediated by the export of photogenerated reductant from the chloroplast. We suggest that photosynthesis interacts with respiration at more than one level, simultaneously decreasing the rate of respiratory carbon flow while increasing the rate of respiratory O-2 consumption.

KEYWORDS: ALTERNATIVE PATHWAY, AMMONIUM ASSIMILATION, CO2- ENRICHED AIR, INORGANIC CARBON, MESOPHYLL PROTOPLASTS, MITOCHONDRIAL RESPIRATION, OXYGEN EVOLUTION, PLANT-CELLS, REGULATORY PROPERTIES, SELENASTRUM-MINUTUM

2656

Yakimchuk, R., and J. Hoddinott. 1994. The influence of ultraviolet-b light and carbon-dioxide enrichment on the growth and physiology of seedlings of 3 conifer species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 24(1):1-8.*

Anthropogenic production of CO2 and stratospheric ozone depleting chemicals is altering the plant growth environment. Numerous studies have examined the influence of increasing CO2 and UV-B levels on plant physiology, but few studies examine their interaction. Jack pine (Pinus banksiana Lamb.), black spruce (Picea mariana (Mill.) B.S.P.), and white spruce (Picea glauca (Moench) Voss) were raised in growth rooms from seed for 16 weeks in air with either 350 or 700 mumol.mol-1 of CO2 in the presence or absence of supplemental UV-B irradiation. Classical and functional growth analyses were performed to identify treatment effects. Biomass production in all three species was increased by high CO2 levels while UV-B light reduced it. Shade-intolerant jack pine showed a greater production of UV-B absorbing pigments in UV-B light than did shade-tolerant spruce species. Overall, white spruce was the most sensitive species to both treatment factors. The relative

magnitude of the effects in the three species caused by enhanced CO2 and UV-B levels indicate that future conifer seedling growth and competitive ability will be altered by the changing environment.

KEYWORDS: CHLOROPHYLL, CO2, FIELD, LOBLOLLY-PINE, PHOTOSYNTHETIC ACCLIMATION, RADIATION, RICE

2657

Yamashita, I., K. Dan, and M. Shimomura. 1999. Active modified atmosphere packaging storage of cabbage plug seedlings. *Journal of the Japanese Society for Horticultural Science 68(5):1015-1021.*

When cabbage plug seedlings were stored under a modified atmosphere packaging (MAP) at 15 degrees C in the dark for 2 weeks, a passive MAP did not create an environment to inhibit stem elongation of seedling in the 0.1mm thick polyethylene (PE) film pouch. An active MAP by adjusting N-2 rich air with 2% O-2 did not successfully retard elongation either. In the active MAP where the internal atmosphere was replaced with N-2 enriched air (2.5% O-2) with elevated CO2, the elongation was delayed as CO2 concentration increased. When 16% CO2 was introduced to the 0.08mm thick nylon/PE film pouch, the inhibit of stem elongation was most successful. Analysis of plant weight, total number of leaves, green color intensity, ascorbic acid content in the leaf blade and head weight of harvested cabbage revealed that the elevated CO2 active MAP is a favorable storage condition for cabbage plug seedlings. The elevated CO2 active MAP, however, caused CO2 injury when CO2 concentration exceeded 24%.

2658

Yamauchi, N., and A.E. Watada. 1998. Chlorophyll and xanthophyll changes in broccoli florets stored under elevated CO2 or ethylene-containing atmosphere. *Hortscience 33(1):114-117.*

Chlorophylls and xanthophylls were monitored in broccoli (Brassica oleracea L. var. italica Plen.) florets stored in air, air + 10 ppm ethylene, or 10% CO2 + 1% O-2 controlled atmosphere (CA) at 15 degrees C. Chlorophylls a and b, as measured with high-performance liquid chromatography, decreased in florets held in air. The decrease was accelerated by ethylene treatment and suppressed in CA. Chlorophyllide a and pheophorbide a were present in fresh broccoli florets, but the levels decreased significantly in all treatments during storage. The oxidized product of chlorophyll a, 13(2)- hydroxychlorophyll a, did not accumulate, Xanthophylls decreased, but new pigments, suggested to be esterified xanthophylls, formed with yellowing in stored florets. The chlorophyll degradative pathway in broccoli florets was not altered by ethylene or CA and differed from that reported for parsley (Petroselium crisum Nym.) and spinach (Spinacia oleracea L.) leaves.

KEYWORDS: BREAKDOWN, DEGRADATION, OXIDASE, PARSLEY LEAVES, STORAGE

2659

Yavitt, J.B., R.K. Wieder, and G.E. Lang. 1993. Co2 and ch4 dynamics of a sphagnum-dominated peatland in west- virginia. *Global Biogeochemical Cycles 7(2):259-274.*

Climatic change could bring about net release of carbon dioxide (CO2) and/or methane (CH4) from the deep peat deposits in northern peatlands into the atmosphere. To provide insight into this hypothesis, we studied net flux of CO2 and CH4 in Big Run Bog, West Virginia, which has a temperate climate, making it an analog to evaluate climatic change imposed on more northern counterparts. Net CO2 flux ranged from -564 to 300 mg C m-2 hr- 1. Measurements made during the nighttime showed that net CO2 flux increased exponentially with increasing air temperature, whereas CO2 sequestration increased with increasing air temperature for daytime measurements. Net CH4 flux ranged from -2.3 to 70 mg C m-2 hr-1, showing no consistent relationship to temperature or water table level. Net efflux for both CO2 and CH4 was tenfold higher from peat cores incubated in a greenhouse compared to field measurements. Even cores drained and allowed to dry for 8 days showed moderately high flux for both CO2 and CH4. The enhanced efflux seemed to be due to altered hydrology rather than increased rates of bacterial production (measured in anoxic, in vitro incubations) which could account for only 50% of the whole-core flux. Presumably the remainder was CO2 and CH4 stored in the peat cores at the time of collection. Overall, the results suggest that a temperate climate imposed on northern peatlands could mobilize stored carbon and increase CO2 and CH4 efflux into the troposphere. Studies involving peat cores must insure that CO2 and CH4 dynamics measured in vitro mimic those in situ.

KEYWORDS: BALANCE, CARBON DIOXIDE, ECOSYSTEM, METHANE, MOUNTAINS, RAISED BOG, REDUCTION, SOILS, TUSSOCK TUNDRA, WATER

2660

Yearsley, C.W., N.H. Banks, and S. Ganesh. 1997. Effect of carbon dioxide on the internal lower oxygen limits of apple fruit. *Postharvest Biology and Technology 12(1):1-13.*

The effect of elevated CO2 between 0 and 8 kPa on steady-state lower O-2 limits based on internal atmospheres (LOLi) was estimated for postclimacteric 'Cox's Orange Pippin' and 'Braeburn' apples at 0 and 20 degrees C. Two types of LOLi were estimated: the anaerobic compensation point (ACP(i)), and the internal fermentation threshold based either on the respiratory quotient (FTRQi) or ethanol (EtOH) accumulation (FTEtOHi). ACP(i), for both cultivars and temperatures, remained constant at 0.5 kPa O-2 for 'Cox's Orange Pippin' and 0.8-1.0 O-2 for 'Braeburn' apples for levels of CO2 external to the fruit between 0 and 8 kPa. However, for FTRQi and FTEtOHi no consistent trend with level of CO2 was evident at 20 degrees C for either cultivar. In contrast, at 0 degrees C FTRQi and FTEtOHi were 0.2-0.8 kPa O-2 higher at 8 kPa CO2 than at 0 kPa CO2 (with the exception of FTRQi for 'Cox's Orange Pippin'). A small decrease in O-2 uptake (estimated from the difference in external and internal O-2 atmospheres) was observed between 2 and 8 kPa CO2 at 20 degrees C. Elevated CO2 slightly lowered the respiratory quotient (RQ(i), estimated from the ratio of differences between external and internal atmosphere partial pressures of CO2 and O-2) of 'Cox's Orange Pippin' in 8 kPa CO2 and 'Braeburn' in 2 to 8 kPa CO2 at 20 degrees C, and more markedly in 8 kPa CO2 at 0 degrees C. The RQ(i) of 'Cox's Orange Pippin' and 'Braeburn' apples was slightly and markedly higher respectively at 0 degrees C compared to 20 degrees C, The lower RQ(i) of 'Braeburn' at 20 degrees C compared to 'Cox's Orange Pippin' apples indicated 'Braeburn had a higher permeance to CO2 relative to O-2 compared to 'Cox's Orange Pippin'. This study indicates the tolerance of 'Cox's Orange Pippin' and 'Braeburn' apples to low O-2 levels may be affected by levels of CO2. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERES, BLUEBERRY FRUIT, CO2, RESPIRATION, TEMPERATURE, VEGETABLES

2661

Yeates, G.W., P.C.D. Newton, and D.J. Ross. 1999. Response of soil nematode fauna to naturally elevated CO2 levels influenced by soil pattern. *Nematology 1:285-293.*

As experimental elevation of CO2 in short-term experiments may produce organic matter with decomposition characteristics different from those produced under long-term equilibrated conditions, we

sampled the soil nematode fauna near a natural CO2 vent in Northland, New Zealand. Various indices of the nematode fauna showed significant effects, with all being significantly correlated with soil pH, microbial carbon and atmospheric CO2 across the 33 sampling points. There was a general decrease in nematode abundance and diversity, but an increase in dominance and proportion of bacterial-feeding nematodes with increasing atmospheric CO2 concentration. However, when the nematode data from gley and organic soils present at the site were differentiated most of the significant correlations were with soil microbial carbon; they were positive in the organic soil but negative in the gley soil. That these responses can be related to soil carbon and to microbial carbon demonstrates that any general response to long-term CO2 enrichment represents an integration of specific responses by the soil biota in the various soils present.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, DECOMPOSITION, MICROBIAL BIOMASS

2662

Yeates, G.W., K.R. Tate, and P.C.D. Newton. 1997. Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. *Biology and Fertility of Soils 25(3):307-315.*

The effects of elevated CO2 on rhizosphere processes, including the response of soil faunal populations and community structure, have so far received little attention. We report on significant responses in the soil fauna of ryegrass/white clover swards to both increasing CO2 from 350 to 750 mu l . l(- 1) and, to a period of 60 days when some of the turves were subject to drought, in a controlled climate growth room experiment. The nematodes which increased were predominantly Enoplia, including dorylaimids, alaimids and trichodorids. This accords with both the doubling of Alaimus under elevated CO2 conditions reported in a similar experiment and with the common association of Enoplia with less disturbed habitats. The most marked decrease was in the bacterial-feeding Rhabditis (Secernentea). The increase in omnivorous and predacious nematodes may have been responsible for the decrease in populations of bacterial-feeding nematodes. However, in contrast to their standing crops, the turnover rate of bacterial-feeding nematodes and soil microbial biomass probably increased as a result of increased grazing by these omnivorous and predacious nematodes. Increases in earthworm and enchytraeid populations were related to increased below-ground productivity reported for the same trial.

KEYWORDS: ELEVATED CO2, ENRICHMENT, PASTURE, PLANT GROWTH, POPULATIONS, RHIZOSPHERE, TURVES

2663

Yelle, S., R.C. Beeson, M.J. Trudel, and A. Gosselin. 1990. Duration of CO2 enrichment influences growth, yield, and gas- exchange of 2 tomato species. *Journal of the American Society for Horticultural Science 115(1):52-57.*

2664

Yeo, A. 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae 78(1-4):159-174.*

The human population is expected to double so there will be at least a doubled demand for food production. This will increase the demand for irrigation because irrigation gives a higher potential yield per unit area than non-irrigated agriculture, together with more yield stability. The demand for irrigation will be especially focused in semi-arid regions supporting a large population, such as the Mediterranean basin and the Indo- Gangetic plain of northern India and Pakistan. The 'hot/warm semi-arid' agro-climatic zone is the one projected most to expand in relative proportion as a consequence of climate change brought about by the increase in atmospheric carbon dioxide concentration. Irrigation in semi-arid climates is a major cause of secondary salinisation (that due to human activity) which already affects 1 ha in five of the irrigated lands. Increased demand for irrigation in semi-arid climates, as a result of both population increase and climate change, will tend to increase the extent of secondary salinisation. Any increase in the extent of secondary salinisation could be offset by positive effects of elevated atmospheric CO2 on crop yield per unit area and per unit input of water. In protected environments, or where CO2 is the only experimental variable, elevated CO2 usually enhances plant growth and water-use- efficiency in the short-term and can also do so in the longer term. However, far crop production in the field world-wide, elevated CO2 per se is not a factor that can be viewed separately from the climate change that it will bring about. Neither the anticipated 'CO2-fertilisation' nor the 'water-use-efficiency' benefits to the plant of elevated CO2 is certain to outweigh the climatic effects of elevated CO2 on temperature, water availability and evaporative demand. Climate change is expected to cause a net increase in the proportion of land classed as semi-arid. Raised temperatures may benefit some crops in some places but disadvantage others through increased evapotranspiration and thermal damage. Increased water-use- efficiency may not reduce leaf salt concentration in a saline environment. Buffering and feedback effects in both agricultural and ecological systems conspire to moderate or even to confound the anticipated gains in net assimilation and water-use-efficiency found in experimental systems. Elevated CO2 may not, therefore, provide the anticipated decrease in water-use, decrease in leaf salt concentration, and increase in fixed carbon available for re-allocation: factors that might enhance crop performance under salinity stress. If these benefits are not realised then elevated atmospheric CO2 will exacerbate rather than moderate the problems of secondary salinity in agriculture.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CARBON-DIOXIDE, CO2, GAS-EXCHANGE, GROWTH, MODEL, RESPONSES, RICE, SODIUM UPTAKE, WHEAT

2665

Yokota, T., and A. Hagihara. 1998. Changes in the relationship between tree size and aboveground respiration in field-grown hinoki cypress (Chamaecyparis obtusa) trees over three years. *Tree Physiology 18(1):37-43.*

Respiration measurements of aerial parts of 18-year-old hinoki cypress (Chamaecyparis obtusa (Sieb. et Zucc.) Endl.) trees were made under field conditions over three years to study changing relationships with tree age between respiration and phytomass, phytomass increment, and leaf mass. The relationship between annual respiration (r(a)) and phytomass (w(T)) was approximated by a proportional function (r(a) = aw(T)), where the proportional constant (a) decreased year by year. The effect of time on the relationship between annual respiration and phytomass of each sample tree was fitted by a power function. Respiration of the tree suppressed by the canopy decreased year by year, but respiration of the other trees increased slightly with age. The relationship between annual respiration and leaf mass was also approximated by a generalized power function. Excluding the suppressed tree, the relationship between annual respiration (r(a)) and the annual increment of aboveground phytomass (Delta w(T)) was described by a proportional function (r(a) = 2.27 Delta w(T)), where the proportional constant, 2.27, was independent of sample tree and year, indicating that about 2.3 times of the annual aboveground phytomass increment equivalent was respired annually. For any tree. the time constant relationships between annual respiration and leaf mass and phytomass increment for different-sized trees were similar to the corresponding time continuum relationships. In contrast, the time continuum relationship between annual respiration and phytomass

differed from the time constant relationship, indicating that respiration of less active woody tissue contributed significantly to aboveground respiration. Based on the relationship between tree size and annual respiration, annual aboveground stand respiration was estimated to be 25.0, 26.9, and 25.8 Mg-dm ha(-1) year(-1) for the three consecutive years, respectively, and the corresponding above-ground stand biomass was 60.0, 69.0, and 76.8 Mg-dm ha(-1).

KEYWORDS: CO2- ENRICHMENT, FOREST TREE, MAINTENANCE RESPIRATION, PARTS, STAND DEVELOPMENT, STEMS

2666

Yoo, K.S., C.R. Andersen, and L.M. Pike. 1997. Internal CO2 concentrations in onion bulbs at different storage temperatures and in response to sealing of the neck and base. *Postharvest Biology and Technology 12(2):157-163.*

Internal CO2 concentrations were measured in onion (Allium cepa L. cv. TG 1015Y) bulbs stored at 1, 7, 13, 20, 27, or 34 degrees C for 12 weeks and their relationships with shoot growth and respiration rates were investigated. Maximum shoot growth was observed at 13 and 20 degrees C. Respiration rates were greatest at 13 and 20 degrees C for 8 weeks, then linearly increased with storage temperatures after 12 weeks. Internal CO2 concentrations ranging from 2 to 5% increased with increasing storage temperatures, while internal gas volume decreased. Bicarbonate concentrations in outer scales ranged from 130 to 190 mu M and increased with increasing storage temperatures. The centre scale tissues contained 11-17% CO2, which paralleled respiration rates. Searing the neck area of onion bulbs stored at 1 or 27 degrees C significantly increased internal CO2 concentrations, but had no effect on inhibiting shoot growth. Internal CO2 concentrations appeared to be regulated by gas exchange rates through the neck area and/or elevated HCO3- concentrations in outer scales. Elevated internal CO2 concentrations or high levels in centre scale tissues did not appear to be a primary reason for inhibited shoot growth at high storage temperatures. There seems to be thermo-dormancy controlling shoot growth and respiration in onion bulbs. (C) 1997 Elsevier Science B.V.

2667

Yoshioka, T., S. Satoh, and Y. Yamasue. 1998. Effect of increased concentration of soil CO2 on intermittent flushes of seed germination in Echinochloa crus-galli var. crus-galli. *Plant, Cell and Environment 21(12):1301-1306.*

Soil-buried seeds of barnyardgrass (Echinochloa crusgalli var. crus-galli) germinated from April to June in three intermittent flushes. The later two flushes of germination occurred after heavy rainfall. Carbon dioxide concentration in soil air transiently increased to 30 dm(3) m(-3) after the rainfall, probably due to the increase in soil temperature and water potential. Germination of exhumed seeds was stimulated by exposure to CO2 at 30 dm(3) m(-3). Fluctuating temperature, light, water, ethylene, and nitrate are known to promote seed germination in many species. However, of these environmental factors, within ranges found in the field, only CO2 was effective in enhancing the germination of barnyardgrass seeds. We conclude that soil CO2 is responsible for causing intermittent flushes of germination. Detection of vegetation gaps may be explained by the responsiveness of buried seeds to CO2.

KEYWORDS: TEMPERATURE

2668

Young, I.M., E. Blanchart, C. Chenu, M. Dangerfield, C. Fragoso, M. Grimaldi, J. Ingram, and L.J. Monrozier. 1998. The interaction of soil biota and soil structure under global change. *Global Change Biology 4(7):703-712.*

The structural framework of soil mediates all soil processes, at all relevant scales. The spatio-temporal heterogeneity prevalent in most soils underpins the majority of biological diversity in soil, providing refuge sites for prey against predator, flow paths for biota to move, or be moved, and localized pools of substrate for biota to multiply. Just as importantly, soil biota play a crucial role in mediating soil structure: bacteria and fungi aggregate and stabilize structure at small scales (mu m-cm) and earthworms and termites stabilize and create larger-scale structures (mm-m). The stability of this two-way interaction of structure and biota relations is crucial to the sustainability of the ecosystem. Soil is constantly reacting to changes in microclimates, and many of the soil-plant-microbe processes rely on the functioning of subtle chemical and physical gradients. The effect of global change on soil structure-biota interactions may be significant, through alterations in precipitation, temperature events, or land-use. Nonetheless, because of the complexity and the ubiquitous heterogeneity of these interactions, it is difficult to extrapolate from general qualitative predictions of the effects of perturbations to specific reactions. This paper reviews some of the main soil structure-biota interactions, particularly focusing on soil stability, and the role of biota mediating soil structures. The effect of alterations in climate and land-use on these interactions is investigated. Several case studies of the effect of land-use change are presented.

KEYWORDS: COTE- DIVOIRE, ECOSYSTEM, ELEVATED CO2, MACROTERMITINAE, MEGASCOLECIDAE, MICROBIAL PROCESSES, OLIGOCHAETA, ORGANIC-MATTER, POLYSACCHARIDE, TERMITES

2669

Yu, M., Q. Gao, and J.P. Guo. 1998. Sensitivity analysis of individual responses of plants to global change. *Acta Botanica Sinica 40(12):1143-1151.*

Today research on global change is becoming one of the three vital topics in ecology. Within this field, simulating an individual plant's physiological responses to global change, especially the combined effects of CO2 enrichment and the climatic change it caused, is a useful model in predicting the changes of either natural vegetation or agricultural crops, in that the physiological basis of the responses are mostly understood and the results of simulation can be checked with experiments at any level or step when needed. Since the scenarios of the global changes often differ with different GCM's, and will change as the GCM's are being improved, even though, the simulation programs can still be used to for new predictions. In this study, based on the physiological mechanisms, a systematic dynamic model of plant individual growth was established, which included a weather generator and a growth module. The combined effects of enriched CO2 and climatic change on the main physiological processes, such as photosynthesis, respiration, etc., and seasonal dynamics of biomass were considered in the model. The data sets of the long-term weather records of Beijing Meteorological Station and the observed values of many ecophysiological quantities, obtained in a CO2 enrichment experiment of soybean, were used to parameterize and to validate the model. The results showed that data obtained from the simulation were quite compatible with those from the observation. When the CO2 concentration was doubled, the peak values of the total biomass and green biomass were increased approximately by 70% and 56% respectively. Furthermore, the responses of the total net assimilation and the average specific dark respiration rate within the growth season explained the internal mechanism of the biomass responses. The result indicated that the total net assimilation increased, while the average specific dark respiration rate decreased. Thus, it can be deduced that the increase of biomass nas brought about not only by the increase of the net assimilation, but also by the decrease of the specific dark respiration rate. Sensitivity analysis was used to the soybean individual responses

to global change. The seasonal dynamics of the total biomass to the combined effects of different levels of CO2, temperature and precipitation were simulated. CO2 concentration and precipitation have positive, while temperature has negative effect on total biomass. The positive effect of precipitation became weaker with increasing temperatures, while the negative effect of temperature was strengthened by the increased precipitation. The positive effect of CO2 concentration became stronger with the increasing temperatures, but weaker under enhancing precipitations. The positive effect of precipitation and the negative effect of temperature were weakened by doubling the CO2 concentration. These are partly due to the enhanced water use efficiency caused by CO2 enrichment, which in turn renders the plant individual more resistant and adaptable to the environmental change.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ELEVATED CO2, RESPIRATION

2670

Zadrazil, F., and A.K. Puniya. 1994. Influence of carbon-dioxide on lignin degradation and digestibility of lignocellulosics treated with pleurotus-sajor- caju. *International Biodeterioration & Biodegradation 33(3):237-244.*

This study investigates the effect of different CO2 concentrations on lignin degradation and in vitro digestibility of wheat straw used as growth substrate for Pleurotus sajor- caju. The degradation of wheat straw lignin by P. sajor-caju increased under the influence of CO2 (0-20%) in the atmosphere and then started declining at higher levels. The maximum loss of lignin (39.7%) was found in cultures grown with passive air exchange through cotton plugs while digestibility was higher in cultures actively aerated with 0-30% CO2. Aside from gases, the period of incubation, i.e. 40 days rather than 20 days, seems to be the most important variable for improving the digestibility of the product. Generally, the process efficiency for change in digestibility per gram loss of organic matter enhanced from 0 to 30% CO2 at a fixed level of O2 (20%) in the gaseous phase.

KEYWORDS: INVITRO DIGESTIBILITY, OXYGEN, SOLID-STATE FERMENTATION, WHEAT STRAW, WHITE-ROT FUNGI, WOOD

2671

Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R. Fogel, and D.L. Randlett. 1993. Elevated atmospheric co2 and feedback between carbon and nitrogen cycles. *Plant and Soil 151(1):105-117.*

We tested a conceptual model describing the influence of elevated atmospheric CO2 on plant production, soil microorganisms, and the cycling of C and N in the plant-soil system. Our model is based on the observation that in nutrient- poor soils. plants (C3) grown in an elevated CO2 atmosphere often increase production and allocation to belowground structures. We predicted that greater belowground C inputs at elevated CO, should elicit an increase in soil microbial biomass and increased rates of organic matter turnover and nitrogen availability. We measured photosynthesis, biomass production, and C allocation of Populus grandidentata Michx. grown in nutrient-poor soil for one field season at ambient and twice-ambient (i.e., elevated) atmospheric CO2 concentrations. Plants were grown in a sandy subsurface soil i) at ambient CO2 with no open top chamber, ii) at ambient CO2 in an open top chamber, and iii) at twice-ambient CO2 in an open top chamber. Plants were fertilized with 4.5 g N m 2 over a 47 d period midway through the growing season. Following 152 d of growth, we quantified microbial biomass and the availabilities of C and N in rhizosphere and bulk soil. We tested for a significant CO2 effect on plant growth and soil C and N dynamics by comparing the means of the chambered ambient and chambered elevated CO2 treatments. Rates of photosynthesis in plants grown at elevated CO2 were significantly greater than those measured under ambient conditions. The number of roots, root length, and root length increment were also substantially greater at elevated CO2. Total and belowground biomass were significantly greater at elevated CO2. Under N-limited conditions, plants allocated 50-70% of their biomass to roots. Labile C in the rhizosphere of elevated-grown plants was significantly greater than that measured in the ambient treatments; there were no significant differences between labile C pools in the bulk soil of ambient and elevated-grown plants. Microbial biomass C was significantly greater in the rhizosphere and bulk soil of plants grown at elevated CO2 compared to that in the ambient treatment. Moreover, a short-term laboratory assay of N mineralization indicated that N availability was significantly greater in the bulk soil of the elevated-grown plants. Our results suggest that elevated atmospheric CO2 concentrations can have a positive feedback effect on soil C and N dynamics producing greater N availability. Experiments conducted for longer periods of time will be necessary to test the potential for negative feedback due to altered leaf litter chemistry.

KEYWORDS: BIOCIDAL TREATMENTS, DIOXIDE, MICROBIAL BIOMASS, MINERALIZATION, PLANTS, QUERCUS-ALBA, RESPONSES, SEEDLING GROWTH, SOIL ORGANIC-CARBON, TREES

2672

Zak, D.R., D.B. Ringelberg, K.S. Pregitzer, D.L. Randlett, D.C. White, and P.S. Curtis. 1996. Soil microbial communities beneath Populus grandidentata crown under elevated atmospheric CO2. *Ecological Applications 6(1):257-262.*

In most terrestrial ecosystems, the amount of substrate entering the soil from plant litter production is only sufficient to meet the maintenance requirements of soil microorganisms, allowing for no net annual growth. However, the rising atmospheric CO2 concentration has the potential to alter such a balance by increasing plant litter production, and hence the amount of substrate available for heterotrophic metabolism in soil. In a recent experiment, we observed that greater belowground plant litter production at elevated atmospheric CO2 significantly increased the biomass of soil microorganisms in both rhizosphere and non-rhizosphere soil. Because soil microorganisms differ in their ability to convert substrate into biomass, we hypothesized that greater plant litter production at elevated CO2 should shift community composition as fungal populations increase in response to greater substrate availability. We used a molecular technique, phospholipid fatty acid (PLFA) analysis, to gain insight into the composition of soil microbial communities beneath Populus grandidentata growing at ambient and twice-ambient atmospheric CO2. PLFAs extracted from rhizosphere and non-rhizosphere soil were derivatized and identified using gas chromatography and mass spectrometry. After one growing season the proportions of bacterial, actinomycetal, and fungal PLFAs were not significantly influenced by elevated atmospheric CO2 in either rhizosphere or non-rhizosphere soil. However, clear differences were present between microbial communities in rhizosphere and non-rhizosphere soil. Although enhanced belowground plant litter production under elevated atmospheric CO2 increased the biomass of soil microorganisms, we have no evidence to suggest that such an increase occurred through a shift in community composition, at least in the short term.

KEYWORDS: AMENDED SOIL, BIOMASS, CALIBRATION, CARBON DIOXIDE, CLIMATE CHANGE, FEEDBACK, FORESTS, GROWTH, NUTRIENT-UPTAKE, RHIZOSPHERE

2673

Zaller, J.G., and J.A. Arnone. 1997. Activity of surface-casting earthworms in a calcareous grassland under elevated atmospheric CO2. *Oecologia 111(2):249-254.*

Earthworms make up the dominant fraction of the biomass of soil animals in most temperate grasslands and have important effects on the structure and function of these ecosystems. We hypothesized that the effects of elevated atmospheric CO2 on soil moisture and plant biomass production would increase earthworm activity, expressed as surface cast production. Using a screen-aided CO2, control facility (open top and open bottom rings), eight 1.2-m(2) grassland plots in Switzerland have been maintained since March 1994 at ambient CO2 concentrations (350 mu l CO2 l(-1)) and eight at elevated CO2 (610 mu l CO2 l(-1)). Cumulative earthworm surface cast production measured 40 times over 1 year (April 1995-April 1996) in plots treated with elevated CO2 (2206 g dry mass m(-2) year(-1)) was 35% greater (P<0.05) than that measured in plant communities maintained at ambient CO2 (1633 g dry mass m(-2) year(-1)). At these rates of surface cast production, worms would require about 100 years to egest the equivalent of the amount of soil now found in the Ah horizon (top 15 cm) under current ambient CO2 concentrations, and 75 years under elevated CO2. Elevated atmospheric CO2 had no influence on the seasonality of earthworm activity. Cumulative surface cast production measured over the 7-week period immediately following the 6-week summer dry period in 1995 (no surface casting) was positively correlated (P<0.05) with the mean soil water content calculated over this dry and subsequent wetter period, when viewed across all treatments. However, no correlations were observed with soil temperature or with annual aboveground plant biomass productivity. No CO2- related differences were observed in total nitrogen (N-tot) and organic carbon (C-org) concentration of surface casts, although concentrations of both elements varied seasonally. The CO2- induced increase in earthworm surface casting activity corresponded to a 30% increase of the amount of N-tot (8.9 mg N m(-2) vs. 6.9 mg N m(-2)) and C-org (126 mg C m(-2) vs. 94 mg C m(-2)) egested by the worms in one year. m Thus, our results demonstrate an important indirect stimulatory effect of elevated atmospheric CO2 on earthworm activity which may have profound effects on ecosystem function and plant community structure in the long term.

KEYWORDS: BIOMASS PRODUCTION, CARBON DIOXIDE, COMMUNITY, ECOSYSTEM, LUMBRICIDAE, NITROGEN, PHOSPHORUS, RESPONSES, SOIL, TALLGRASS PRAIRIE

2674

Zaller, J.G., and J.A. Arnone. 1999. Earthworm responses to plant species' loss and elevated CO2 in calcareous grassland. *Plant and Soil 208(1):1-8.*

The objectives of this study were: (1) to quantify the effects of plant species' loss from designed calcareous grassland communities at a field site in northwestern Switzerland on the size and composition of earthworm communities, and (2) to evaluate how exposure of plant communities to elevated atmospheric CO2 might alter the effects of plant species' loss on earthworm communities. We non-destructively censused earthworm communities in each of 24 1.2 m(2) experimental plots in autumn 1996 when soils were wet and earthworms were active. Each plot contained an experimental plant community with 31, 12 or 5 native plant species (eight plots each). Half of the plots in each species treatment were exposed to ambient CO2 concentrations (350 mu L CO2 L-1) and half to elevated CO2 (600 mu L CO2 L-1) using screen-aided CO2 control. The study was conducted in the fourth year after community establishment and the third year of CO2 treatment as part of a long-term study on the interactive effects of plant species' loss and elevated CO2 on grassland communities. The size (density and biomass) of earthworm communities declined linearly when the number of plant species in the community was reduced from 31 to 5 species (e.g. 32 +/- 1 g m(-2) to 23 +/- 2 g m(-2)) due mainly to a decline in the endogeic worm species Allolobophora rosea which was the most abundant of nine earthworm species observed (nearly half of all worms in each plot). However, no changes in the relative contribution of individual species or the three main earthworm ecological groups (anecics, endogeics, epigeics) to the entire earthworm community were observed with declining number of plant species. The responses of earthworm communities to plant species' loss appear to reflect changes in community fine root biomass in the topsoil (e.g. declining worm biomass with declining fine root biomass) observed in parallel studies conducted at this site. Further the results of this study demonstrate that a loss of plant species' from these calcareous grassland communities may also alter the age structure of earthworm communities, but not significantly influence their diversity or composition. Our data also indicate that rising atmospheric CO2 may not greatly impact the size and composition of worm communities or alter the effects of plant species' loss on earthworm communities. Therefore, the disappearance of plant species from these native grasslands, as a result of ever increasing human activities, may be expected to lead to reductions in the size of earthworm communities and the ecosystem services they provide.

KEYWORDS: BIODIVERSITY, CARBON, DIVERSITY, ECOSYSTEMS, LUMBRICIDAE, SOIL, STABILITY

2675

Zaller, J.G., and J.A. Arnone. 1999. Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO2. *Ecology 80(3):873-881.*

We tested the hypothesis that the spatial proximity of a plant species to nutrient-rich earthworm casts (e.g., 100% more ammonium and 30% more phosphate than in adjacent soil) is an important determinant of a plant's responsiveness to elevated atmospheric CO2. In 1995 we mapped the location of both earthworm surface casts and plants in each of 16 1.2-m(2) plots in a species-rich calcareous grassland in northwestern Switzerland. Eight plots have been maintained under current ambient CO2 concentrations (350 mu L CO2/ L), and eight have been maintained at elevated CO2 (600 mu L CO2/L) since March 1994. in addition, total ramet production of each species, as a measure of performance, and cumulative cast production at each location (cell) were recorded at peak community biomass in 1995. Plant species within functional groups (graminoids, non- legume forbs, and legumes) differed markedly in their degree of association with casts; however, after two growing seasons elevated CO2 had no effect on plant species or functional group associations with casts. No statistically significant relationship could be demonstrated between plant-species response (i.e., ramet production) to elevated CO2 and the degree of association with casts within any of the functional groups. However, a positive relationship was observed between the mean response of graminoid species to elevated CO2 (measured as the percentage change in mean total ramet production of graminoid species, relative to mean total ramet production at ambient CO2) and their mean degree of association (%) with surface casts at ambient CO2. Thus, graminoid species more frequently associated with casts (e.g., Anthoxanthum odoratum and Carer caryophyllea) produced more ramets per square meter at elevated CO2 than those less frequently associated with casts (e.g., Agrostis tenuis and Danthonia decumbens). These results, along with the strong and significant positive correlations observed between ramet production and associated cumulative cast mass across CO2 treatments for most plant species in all functional groups demonstrate: (1) that plant species differ significantly in their degree of association with nutrient-rich earthworm surface casts, regardless of the relative abundance of plant species in the community; (2) that graminoid species that are more highly associated with casts may respond more strongly to rising CO2 than those less highly associated with casts; and (3) that nutrient-rich earthworm casts stimulate the growth (ramet production) of most plant species in these grassland communities, even at current levels of atmospheric CO2. The data further suggest that these species-specific relationships between plants and casts have helped define the current structure of these highly diverse grassland communities and will likely influence their future structure as global CO2 levels continue to rise.

KEYWORDS: CAPTURE, CARBON, ECOSYSTEMS, EXPLOITATION, LOCALIZED SOIL ENRICHMENT, MICROSITES, PERENNIALS, RESPONSES, ROOT-GROWTH

2676

Zamolodchikov, D.G., D.V. Karelin, and A.I. Ivaschenko. 1997. Carbon balance of tundra landscape in Central Siberia: Observations, simulation and GIS-modelling. *Zhurnal Obshchei Biologii 58(2):15-34.*

Comprehensive statistical analysis of field measurements of CO2 fluxes in ecosystems of typical subarctic tundra in Taymir Peninsula (Central Siberia, Russia) was performed. Simulation models allowing to compute integrate seasonal values of basic components of carbon balance in the most characteristic plant communities of typical tundra were built. To access the landscape pattern of tundra carbon balance we applied GIS-approach based on the original computer map of ecosystem borders. In 1994 the seasonal (from the beginning of snow melting till the end of total soil freezing) carbon balance of typical tundra landscape was estimated as -4 g C . m-(2) . year(-1) (carbon sink), the ecosystem total respiration as +145 g C . m(-2) . year(-1), and gross primary production as -149 g C . m(-2) year(-1). Such a poorly expressed carbon sink conceptually should be considered as landscape equilibrium. Nevertheless the subsequent computer simulation of climate changes confirmed the hypothesis of positive feedback between global warming and change of carbon balance pattern in tundra ecosystems from sink to source. From the other side we found that regional peculiarities of ecological and climatic conditions can strongly effect the climate global change appearance.

KEYWORDS: CLIMATE CHANGE, CO2, DIOXIDE, ECOSYSTEMS, SOILS

2677

Zamorano, J.P., R. Alique, and W. Canet. 1999. Mechanical parameters to assess quality changes in cherimoya fruit. *Zeitschrift Fur Lebensmittel-Untersuchung Und-Forschung A-Food Research and Technology 208(2):125-129.*

Several mechanical parameters obtained by means of compression and penetration tests, and changes in cherimoya (Annona cherimola Mill.) fruit quality during storage in air and two controlled atmospheres (CA), (3% O-2 + 0% CO2 and 3% O-2 + 3% CO?) were analysed. A gradient of softening was found among the equatorial and the apical areas of the flesh during CA storage, as assessed by localized penetration tests. The combination of low O-2/elevated CO2 (3% O-2 + 3% CO2) increased this gradient and had a greater inhibiting effect on skin softening than low O-2. It appeared that the prevention of softening by CA was stronger in the less mature tissues (equatorial and outer areas) than in the more mature tissues (apical and inner areas around the longitudinal axis). CA delayed or inhibited changes in fruit quality observed during air storage: increases in total soluble solids (TSS), titratable acidity (TA), and yellowness of the flesh (b), and diminution in flesh lightness of colour (L). A good relationship between an objective quality index (QI, where QI = TSS + TA + L/b) and the compression slope (CS) was found during storage under all the conditions tested. It is suggested that the relationship, QI = 29.25 + 0.04 x CS- 0.0023 x CS2 could be useful when assessing stages of cherimoya fruit quality during storage under different conditions by performing a nondestructive, compression test.

KEYWORDS: ANNONA-CHERIMOLA, MILL FRUIT, STORAGE, VEGETABLES

2678

Zanetti, S., and U.A. Hartwig. 1997. Symbiotic N-2 fixation increases under elevated atmospheric pCO(2) in the field. *Acta Oecologica-International Journal of Ecology 18(3):285-290.*

Plant growth is stimulated by elevated atmospheric pCO(2), and hence demand for nutrients increases. In this context, nitrogen is a very prominent element; it can either be supplied from the limited available soil N or through biological (e.g. symbiotic) nitrogen fixation. In this study, the effect of elevated pCO(2) (60 Pa) on symbiotic N-2 fixation (N-15-isotope dilution method) was investigated using Free-Air-CO2-Enrichment (FACE) technology over a period of two growing seasons. Trifolium repens L, was cultivated either alone or in mixed swards together with Lolium perenne L. (non-fixing reference crop). In T. repens, percentage of plant N derived from symbiotic N-2 fixation (%Nsym) increased from 59 to 66% under elevated pCO(2). The major part of the additionally assimilated N was derived from symbiotic N-2 fixation. In the mixed swards, increased N yield was entirely due to increased symbiotic N-2 fixation. It is suggested that increased N-2 fixation is an important factor in the satisfaction of increased N demand in both clover and the associated grass under elevated pCO(2).

KEYWORDS: CLOVER, CO2, GROWTH, NITROGEN-FIXATION, RATES, WHITE

2679

Zanetti, S., U.A. Hartwig, A. Luscher, T. Hebeisen, M. Frehner, B.U. Fischer, G.R. Hendrey, H. Blum, and J. Nosberger. 1996. Stimulation of symbiotic N-2 fixation in Trifolium repens L under elevated atmospheric pCO(2) in a grassland ecosystem. *Plant Physiology 112(2):575-583.*

Symbiotic N-2 fixation is one of the main processes that introduces N into terrestrial ecosystems. As such, it may be crucial for the sequestration of the extra C available in a world of continuously increasing atmospheric CO2 partial pressure (pCO(2)). The effect of elevated pCO(2) (60 Pa) on symbiotic N-2 fixation (N-15-isotope dilution method) was investigated using Free-Air-CO2-Enrichment technology over a period of 3 years. Trifolium repens was cultivated either alone or together with Lolium perenne (a nonfixing reference crop) in mixed swards. Two different N fertilization levels and defoliation frequencies were applied. The total N yield increased consistently and the percentage of plant N derived from symbiotic N-2 fixation increased significantly in T. repens under elevated pCO(2). All additionally assimilated N was derived from symbiotic N-2 fixation, not from the soil. In the mixtures exposed to elevated pCO(2), an increased amount of symbiotically fixed N (+7.8, 8.2, and 6.2 g m(-2) a(-1) in 1993, 1994, and 1995, respectively) was introduced into the system. Increased N-2 fixation is a competitive advantage for T. repens in mixed swards with pasture grasses and may be a crucial factor in maintaining the C:N ratio in the ecosystem as a whole.

KEYWORDS: ACETYLENE-REDUCTION, CARBON DIOXIDE, CO2-ENRICHMENT, CV FJORD, GROWTH, NITROGEN-FIXATION, PISUM-SATIVUM, PLANTS, ROOT NODULE ACTIVITY, WHITE CLOVER

2680

Zanetti, S., U.A. Hartwig, and J. Nosberger. 1998. Elevated atmospheric CO2 does not affect per se the preference for symbiotic nitrogen as opposed to mineral nitrogen of Trifolium repens L. *Plant, Cell and Environment 21(6):623-630.*

The objective of this investigation was to examine the effect of an elevated atmospheric CO2 partial pressure (pCO(2)) on the N-sink strength and performance of symbiotic N-2 fixation in Trifolium repens L. cv. Milkanova, After initial growth under ambient pCO(2) in a nitrogen-free nutrient solution, T. repens in the exponential growth stage was exposed to ambient and elevated pCO(2) (35 and 60 Pa) and two

levels of mineral N (N- free and 7.5 mol m(-3) N) for 36 d in single pots filled with silica sand in growth chambers. Elevated pCO(2) evoked a significant increase in biomass production from day 12 after the start of CO2 enrichment. For plants supplied with 7.5 mol m(-3) N, the relative contribution of symbiotically fixed N (%N-sym) as opposed to N assimilated from mineral sources (N- 15-isotope-dilution method), dropped to 40%, However, in the presence of this high level of mineral N, %N-sym was unaffected by atmospheric pCO(2) over the entire experimental period. In plants fully dependent on N-2 fixation, the increase in N yield reflects a stimulation of symbiotic N-2 fixation that was the result of the formation of more nodules rather than of higher specific N-2 fixation. These results are discussed with regard to physiological processes governing symbiotic N-2 fixation and to the response of symbiotic N-2 fixation to elevated pCO(2) in field-grown T. repens.

KEYWORDS: CARBOHYDRATE CONTENT, CARBON, DEFOLIATION, ENRICHMENT, GROWTH, N2 FIXATION, NODULATED WHITE CLOVER, NODULES, PERMEABILITY, PLANTS

2681

Zanetti, S., U.A. Hartwig, C. vanKessel, A. Luscher, T. Hebeisen, M. Frehner, B.U. Fischer, G.R. Hendrey, H. Blum, and J. Nosberger. 1997. Does nitrogen nutrition restrict the CO2 response of fertile grassland lacking legumes? *Oecologia 112(1):17-25.*

The extent of the response of plant growth to atmospheric CO2 enrichment depends on the availability of resources other than CO2. An important growth-limiting resource under field conditions is nitrogen (N). N may, therefore, influence the CO2 response of plants. The effect of elevated CO2 (60 Pa) partial pressure (pCO(2)) on the N nutrition of field-grown Lolium perenne swards, cultivated alone or in association with Trifolium repens, was investigated using free air carbon dioxide enrichment (FACE) technology over 3 years. The established grassland ecosystems were treated with two N fertilization levels and were defoliated at two frequencies. Under elevated pCO(2), the above-ground plant material of the L. perenne monoculture showed a consistent and significant decline in N concentration which, in general, led to a lower total annual N yield. Despite the decline in the critical N concentration (minimum N concentration required for non-N- limited biomass production) under elevated pCO(2), the index of N nutrition (ratio of actual N concentration and critical N concentration) was lower under elevated pCO(2) than under ambient pCO(2) in frequently defoliated L. perenne monocultures. Thus, we suggest that reduced N yield under elevated pCO(2) was evoked indirectly by a reduction of plant- available N. For L. perenne grown in association with T. repens and exposed to elevated pCO(2) there was an increase in the contribution of symbiotically fixed N to the total N yield of the grass. This can be explained by an increased apparent transfer of N from the associated N-2-fixing legume species to the non-fixing grass. The total annual N yield of the mixed grass/legume swards increased under elevated pCO(2). All the additional N yielded was due to symbiotically fixed N. Through the presence of an N-2-fixing plant species more symbiotically fixed N was introduced into the system and consequently helped to overcome N limitation under elevated pCO(2).

KEYWORDS: ATMOSPHERIC CO2, CARBON, DECOMPOSITION, ECOSYSTEMS, ELEVATED CO2, ENRICHMENT, GROWTH, SWARD, TEMPERATURE, WHITE CLOVER

2682

Zebian, K.J., and E.G. Reekie. 1998. The interactive effects of atmospheric carbon dioxide and light on stem elongation in seedlings of four species. *Annals of Botany 81(2):185-193.*

Four species, Sinapis alba L., Medicago saliva L., Gypsophila paniculata L, and Picea abies (L.) Karsten, were grown in three light regimes: darkness, low light (25 mu mol m(-2) s(-1) for 10 min d(-1)) and high light (120 mu mol m(-2) s(-1) for 12 h d(-1)) and four levels of carbon dioxide: 0, 350, 700 and 1400 +/- 50 mu l l(-1). Germination was not affected by any of the treatments. The effects of carbon dioxide on stem elongation were identical in low and high light: stem length increased at a decreasing rate with level of carbon dioxide in all species. Level of carbon dioxide also affected stem elongation in complete darkness, but the pattern was more complex and varied among species. Total weight did not vary with level of carbon dioxide to any significant extent in either darkness or low light, but increased with level of carbon dioxide at high light in all four species. Due to the absence of any effect of carbon dioxide on growth in darkness and low light, we suggest the effects of carbon dioxide on stem elongation are independent of effects on growth and may be due to a direct interaction with developmental processes. In contrast, level of carbon dioxide had little effect on allocation patterns in the dark and low light experiments, but had marked effects in high light. Therefore, the effect of carbon dioxide on allocation was probably due to the effects of carbon dioxide on growth rather than to any direct interaction between carbon dioxide and development. An understanding of the mechanisms by which carbon dioxide affects development may help us understand the often variable effects of carbon dioxide upon plants. (C) 1998 Annals of Botany Company.

KEYWORDS: AMBIENT, ELEVATED CO2, ENRICHMENT, FOREST, GROWTH, PHARBITIS, PLANTS, RESPIRATION, RESPONSES, TREES

2683

Zeng, W., and J.L. Heilman. 1997. Sensitivity of evapotranspiration of cotton and sorghum in west Texas to changes in climate and CO2. *Theoretical and Applied Climatology 57(3-4):245-254.*

In regions such as west Texas where water is scarce, changes in the water balance may have a significant impact on agricultural production and management of water resources. We used the mechanistic soil-plant-atmosphere simulation model ENWATBAL to evaluate changes in soil water evaporation (E) and transpiration (T) in cotton and grain sorghum that may occur due to climate change and elevated CO2 in west Texas. Climatic and plant factors were varied individually, and in combination, to determine their impact on E and T. Of the climatic factors, E was most sensitive to changes in vapor pressure, and T to changes in irradiance. Simulations suggest that if warming is accompanied by higher humidity, the impact of climate change may be minimal. However, if the climate becomes warmer and less humid, ET may increase substantially. Simulations also suggest that enhanced growth due to elevated CO2 may have a greater impact on ET than climatic change.

KEYWORDS: ATMOSPHERIC CO2, CARBON DIOXIDE, ENERGY, ENRICHMENT, ENVIRONMENT, EVAPORATION, FIELD, SIMULATION, SOIL, WHEAT

2684

Zhang, H.H., and P.S. Nobel. 1996. Photosynthesis and carbohydrate partitioning for the C-3 desert shrub Encelia farinosa under current and doubled CO2 concentrations. *Plant Physiology 110(4):1361-1366.*

Changes in photosynthesis (A) and carbohydrate partitioning were studied for Encelia farinosa, a common C-3 desert shrub in the southwestern United States, after a 3-month exposure to the current or a doubled CO2 concentration (750 mu L L(-1)). A remained unchanged under the current CO2 concentration but decreased during the day under the doubled CO2 concentration, resulting in a 46% enhancement in the

early morning, 26% at midday, and 15% in the late afternoon by the elevated CO2. The decrease during the day under the doubled CO2 concentration may represent end-product inhibition, because the sucrose and the starch contents increased during the day proportionally more than under the current CO2 concentration. The (CO2)-C-14 activity in sink leaves was maximal 3 h after labeling under the doubled and at 5 h under the current CO2 concentration, indicating faster movement of photosynthate out of source leaves and into sink tissues under the doubled CO2 concentration, which may have been responsible for the sustained enhancement in A under the doubled CO2 concentration.

KEYWORDS: ACCLIMATION, CARBOXYLASE, ELEVATED CO2, EXCHANGE, HIGH ATMOSPHERIC CO2, LEAVES, PHASEOLUS-VULGARIS, PLANT, STARCH, SUCROSE

2685

Zhang, J., and M.J. Lechowicz. 1995. Responses to co2 enrichment by 2 genotypes of arabidopsis- thaliana differing in their sensitivity to nutrient availability. *Annals of Botany 75(5):491-499.*

The responses of two genotypes of Arabidopsis thaliana, which differ in their sensitivities to nutrients to present and predicted future CO2 concentration were determined under rich vs. poor nutrient regimes on the basis of both single traits and the whole plant. Based on individual traits, the two genotypes responded similarly to CO2 enrichment for all the traits measured except for rate of increase in crown diameter, for which a decrease was observed in the less nutrient- sensitive genotype grown at increased CO2. Based on the overall response of the whole plant, by analysing groups of plant traits using multivariate analysis, the two genotypes differed substantially from one another and both responded more strongly to nutrient availability than to CO2 concentration, especially for traits measured at harvest that related to reproductive fitness. The less nutrient-sensitive genotype also showed a weaker overall response to CO2, and the pattern of the overall response was strikingly similar at different nutrient Supply. In contrast, the more nutrient-sensitive genotype responded more strongly to CO2 than the less nutrient-sensitive genotype, and responded differently to CO2 at low vs. high nutrient availability.

KEYWORDS: ACQUISITION, ALLOCATION, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO2, GROWTH, NITROGEN, PHENOTYPIC PLASTICITY, PLANTS, RADISH, STRESS

2686

Zhang, Y.Q., and J.M. Welker. 1996. Tibetan alpine tundra responses to simulated changes in climate: Aboveground biomass and community responses. *Arctic and Alpine Research 28(2):203-209.*

High-elevation ecosystems are predicted to be some of the terrestrial habitats most sensitive to changing climates. The ecological consequences of changes in alpine tundra environmental conditions are still unclear especially for habitats in Asia. In this study we report findings from a field experiment where an alpine tundra grassland on the Tibetan plateau (37 degrees N, 101 degrees E) was exposed to experimental warming, irradiance was lowered, and wind speed reduced to simulate a suite of potential changes in environmental conditions. Our warming treatment increased air temperatures by 5 degrees C on average and soil temperatures were elevated by 3 degrees C at 5 cm depth. Aboveground biomass of grasses responded rapidly to the warmer conditions whereby biomass was 25% greater than that of controls after only 5 wk of experimental warming. This increase was accompanied by a simultaneous decrease in forb biomass, resulting in almost no net change in community biomass after 5 wk. Lower irradiance reduced grass biomass during the same period. Under ambient conditions total aboveground community biomass increased seasonally from 161 g m(-2) in July to a maximum of 351 g m(-2) in September, declining to 285 g m(-2) in October. However, under warmed conditions, peak community biomass was extended into October due in part to continued growth of grasses and the postponement of senescence. Our findings indicate that while alpine grasses respond favorably to altered conditions, others may not. And, while peak community biomass may actually change very little under warmer summers, the duration of peak biomass may be extended having feedback effects on net ecosystem CO2 balances, nutrient cycling, and forage availability.

KEYWORDS: ANNUAL GRASSLAND, ARCTIC SOILS, BUNCHGRASS SCHIZACHYRIUM-SCOPARIUM, DWARF-SHRUB, ECOSYSTEMS, MANIPULATIONS, MINERALIZATION, PERTURBATIONS, TEMPERATURE, WATER

2687

Zhu, J., D.P. Bartholomew, and G. Goldstein. 1997. Effect of elevated carbon dioxide on the growth and physiological responses of pineapple, a species with Crassulacean acid metabolism. *Journal of the American Society for Horticultural Science 122(2):233-237.*

Despite the potential impact of rising global CO2 levels, only a limited number of studies have been conducted on the effects of ambient and elevated CO2 on plants having Crassulacean acid metabolism (CAM), To our knowledge, there are no studies for pineapple [Ananas comosus (L.) Merr.], the most commercially important CAM plant, Pineapple plants were grown at CO2 levels of approximate to 330 (ambient) and approximate to 730 (elevated) mu mol . mol(-1) in open-top chambers for 4 months, The mean air temperature in the chambers was approximate to 39 degrees C day/24 degrees C night, Average plant dry mass at harvest was 180 g per plant at elevated CO2 and 146 g per plant at ambient CO2. More biomass was partitioned to stem and root but less to leaf for plants grown at elevated CO2; leaf thickness was 11% greater at elevated than at ambient CO2. The diurnal difference in leaf titratable acidity (H+) at elevated CO2 reached 347 mmol . m(-2), which was up to 42% greater than levels in plants grown in ambient CO2. Carbon isotopic discrimination (Delta) of plants was 3.75% at ambient CO2 and 3.17% at elevated CO2, indicating that CO2 uptake via the CAM pathway was enhanced more by elevated CO2 than uptake via the C-3 pathway, The nonphotochemical quenching coefficient (q(N)) of leaves was approximate to 45% lower in the early morning for plants grown at elevated than at ambient CO2, while afternoon values were comparable, The q(N) data suggested that the fixation of external CO2 was enhanced by elevated CO2 in the morning but not in the afternoon when leaf temperature was greater than or equal to 40 degrees C. We found no effect of CO2 levels on leaf N or chlorophyll content, Pineapple dry matter gain was enhanced by elevated CO2, mainly due to increased CO2 dark fixation in environments with day temperatures high enough to suppress C-3 photosynthesis.

KEYWORDS: ACCUMULATION, CAM, CO2 UPTAKE, FLUORESCENCE, GAS-EXCHANGE, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, PLANTS, RUBISCO, SOLUBLE SUGARS

2688

Zhu, J., G. Goldstein, and D.P. Bartholomew. 1999. Gas exchange and carbon isotope composition of Ananas comosus in response to elevated CO2 and temperature. *Plant, Cell and Environment 22(8):999-1007.*

Ananas comosus L. (Merr.) (pineapple) was grown at three day/night temperatures and 350 (ambient) and 700 (elevated) mu mol mol(-1) CO2 to examine the interactive effects of these factors on leaf gas exchange and stable carbon isotope discrimination (Delta,parts per thousand). All data were collected on the youngest mature leaf for 24 h every 6 weeks. CO2 uptake (mmol m(-2) d(-1)) at ambient and elevated CO2, respectively, were 306 and 352 at 30/20 degrees C, 175 and 346 at 30/25

degrees C and 187 and 343 at 35/25 degrees C, CO2 enrichment enhanced CO2 uptake substantially in the day in all environments. Uptake at night at elevated CO2, relative to that at ambient CO2, was unchanged at 30/20 degrees C, but was 80% higher at 30/25 degrees C and 44% higher at 35/25 degrees C suggesting that phosphoenolpyruvate carboxylase was not CO2- saturated at ambient CO2 levels and a 25 degrees C night temperature. Photosynthetic water use efficiency (WUE) was higher at elevated than at ambient CO2. Leaf Delta-values were higher at elevated than at ambient CO2 due to relatively higher assimilation in the light, Leaf Delta was significantly and linearly related to the fraction of total CO2 assimilated at night. The data suggest that a simultaneous increase in CO2 level and temperature associated with global warming would enhance carbon assimilation, increase WUE, and reduce the temperature dependence of CO2 uptake by A. comosus.

KEYWORDS: CRASSULACEAN ACID METABOLISM, DIOXIDE, DISCRIMINATION, GROWTH, LIGHT, OPUNTIA FICUS INDICA, PHOTOSYNTHESIS, PRODUCTIVITY, RESPIRATION, SHORT- TERM

2689

Zimmerman, R.C., D.G. Kohrs, D.L. Steller, and R.S. Alberte. 1997. Impacts of CO2 enrichment on productivity and light requirements of eelgrass. *Plant Physiology 115(2):599-607.*

Seagrasses, although well adapted for submerged existence, are CO2-limited and photosynthetically inefficient in seawater. This leads to high light requirements for growth and survival and makes seagrasses vulnerable to light limitation. We explored the long-term impact of increased CO2 availability on light requirements, productivity, and C allocation in eelgrass (Zostera marina L.). Enrichment of seawater CO2 increased photosynthesis 3-fold, but had no longterm impact on respiration. By tripling the rate of light-saturated photosynthesis, CO2 enrichment reduced the daily period of irradiance-saturated photosynthesis (H-sat) that is required for the maintenance of positive whole-plant C balance from 7 to 2.7 h, allowing plants maintained under 4 h of H-sat to perform like plants growing in unenriched seawater with 12 h of H-sat. Eelgrass grown under 4 h of H-sat without added CO2 consumed internal C reserves as photosynthesis rates and chlorophyll levels dropped. Growth ceased after 30 d. Leaf photosynthesis, respiration, chlorophyll, and sucrose-phosphate synthase activity of CO2-enriched plants showed no acclimation to prolonged enrichment. Thus, the CO2-stimulated improvement in photosynthesis reduced light requirements in the long term, suggesting that globally increasing CO2 may enhance seagrass survival in eutrophic coastal waters, where populations have been devastated by algal proliferation and reduced water-column light transparency.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, ELEVATED CO2, GROWTH, HIGH ATMOSPHERIC CO2, HIGHER-PLANTS, MARINA L EELGRASS, PHOTOSYNTHESIS, SAN-FRANCISCO BAY, TOMATO

2690

Ziska, L.H. 1998. The influence of root zone temperature on photosynthetic acclimation to elevated carbon dioxide concentrations. *Annals of Botany 81(6):717-721.*

Soybean (Glycine max 'Clark') was grown from germination to 21 d after sowing (DAS) at ambient (similar to 360 mu mol mol(-1)) or elevated (similar to 720 mu mol mol(-1)) carbon dioxide (CO2) at either one of two soil temperatures, 25 or 30 degrees C to determine the influence of root zone temperature on root growth and photosynthetic stimulation at ambient and elevated concentrations of carbon dioxide. Although the photosynthetic rate became less stimulate over time, a significant stimulation of whole plant photosynthesis and plant dry weight was observed at the elevated CO2 concentration during the experimental period irrespective of soil temperature. At neither carbon dioxide concentration did the warmer soil temperature (30 degrees C) stimulate whole plant growth compared to a soil temperature of 25 degrees C, but it did increase root growth relative to shoot (top) growth with a subsequent increase in root/shoot ratio. Increasing soil temperature at either carbon dioxide concentration also significantly stimulated whole plant photosynthetic rate. However, the degree of stimulation was reduced with time irrespective of carbon dioxide concentration so that at 21 DAS no difference in photosynthesis between ambient and elevated soil temperatures was observed. Data from this experiment indicate that for soybean, a higher soil temperature stimulates root/shoot ratio and enhances photosynthetic response to elevated carbon dioxide in the short-term (i.e. days), but increasing root/shoot ratios does not provide a satisfactory explanation of long-term stimulation of photosynthesis at elevated levels of carbon dioxide. (C) 1988 Annals of Botany Company.

KEYWORDS: ATMOSPHERIC CO2, ENRICHMENT, GROWTH, LEAVES, PLANTS, RESPONSES

2691

Ziska, L.H., and J.A. Bunce. 1993. The influence of elevated co2 and temperature on seed- germination and emergence from soil. *Field Crops Research 34(2):147-157.*

Seed of six crop species, alfalfa, Medicago sativa L. cv. 'Arc', soybean, Glycine max L. (Merrill) cv. 'Williams', maize, Zea mays L. cv. SS 885, pea, Pisum sativum L. cv. 'Maestro', sunflower, Helianthus annuus L. cv. 'Mammoth', and pumpkin Cucurbita pepo L. cv. 'Big Max' and four weedy species, Amaranthus hypochondriacus L., Amaranthus hybridus L., Chenopodium album L. and Abutilon theophrasti, were grown at two different CO2 concentrations of 350 mul l-1 (ambient) and 700 mul l-1 (elevated) in controlled-environment chambers to determine the effect of elevated CO2 on germination and emergence. Doubling the CO2 concentration resulted in an increase in the rate and final percentage of germination, for M. sativa, A. hybridus and C album. In a separate field experiment (silt-loam soil), elevated CO2 resulted in a significant increase in the total number of weed seedlings present 3 weeks after tilling. In a second set of experiments using controlled-environment chambers, the interaction between increased temperature and CO2 was examined in seven of the species used previously. No significant interaction was observed between CO2 and temperature on the germination response. Overall, this investigation suggests that as CO2 increases, differential changes in germination and/or emergence between crops and weeds could occur.

KEYWORDS: CARBON DIOXIDE, ETHYLENE, GROWTH

2692

Ziska, L.H., and J.A. Bunce. 1993. Inhibition of whole-plant respiration by elevated co2 as modified by growth temperature. *Physiologia Plantarum 87(4):459-466.*

Plants of alfalfa (Medicago sativa) and orchard grass (Dactylus glomerata) were grown in controlled environment chambers at two CO2 concentrations (350 and 700 mumol mol-1) and 4 constant day/night growth temperatures of 15, 20, 25 and 30-degrees-C for 50-90 days to determine changes in growth and whole plant CO2 efflux (dark respiration). To facilitate comparisons with other studies, respiration data were expressed on the basis of leaf area, dry weight and protein. Growth at elevated CO2 increased total plant biomass at all temperatures relative to ambient CO2, but the relative enhancement declined (P less-than-or-equal-to 0.05) as temperature increased. Whole plant respiration (R(d)) at elevated CO2 declined at 15 and 20- degrees-C in D. glomerata on an area, weight or protein basis and in M. sativa on a weight or protein basis when compared to ambient CO2. Separation of R(d) into respiration required for growth (R(g)) and maintenance (R(m)) showed

a significant effect of elevated CO2 on both components. R(m) was reduced in both species but only at lower temperatures (15-degrees-C in M. sativa and 15 and 20-degrees-C in D. glomerata). The effect on R(m) could not be accounted for by protein content in either species. R(g) was also reduced with elevated CO2; however no particular effect of temperature was observed, i.e. R(g) was reduced at 20, 25 and 30-degrees-C in M. sativa and at 15 and 25-degrees-C in D. glomerata. For the two perennial species used in the present study, the data suggest that both R(g) and R(m) can be reduced by anticipated increases in atmospheric CO2; however, CO2 inhibition of total plant respiration may decline as a function of increasing temperature.

KEYWORDS: CARBON DIOXIDE, CROP, DARK RESPIRATION, ENRICHMENT, FIELD, MAINTENANCE, SORGHUM, TREES

2693

Ziska, L.H., and J.A. Bunce. 1994. Direct and indirect inhibition of single leaf respiration by elevated co2 concentrations - interaction with temperature. *Physiologia Plantarum 90(1):130-138.*

Two herbaceous perennials, alfalfa (Medicago sativa L. cv. Arc) and orchard grass (Dactylus glomerata L. cv. Potomac), were grown at ambient (367 mumol mol-1) and elevated (729 mumol mol- 1) CO2 concentrations at constant temperatures of 15, 20, 25 and 30-degrees-C in order to examine direct and indirect changes in nighttime CO2 efflux rate (respiration) of single leaves. Direct (biochemical) effects of CO2 on nighttime respiration were determined for each growth condition by brief (<30 min) exposure to each CO2 concentration. If no direct inhibition of respiration was observed, then long-term reductions in CO2 efflux between CO2 treatments were presumed to be due to indirect inhibition, probably related to long-term changes in leaf composition. By this criterion, indirect effects of CO2 on leaf respiration were observed at 15 and 20- degrees-C for M. sativa on a weight basis, but not on a leaf area or protein basis. Direct effects however, were observed at 15, 20 and 25-degrees-C in D. glomerata; therefore the observed reductions in respiration for leaves grown and measured at elevated relative to ambient CO2 concentrations could not be distinguished as indirect inhibition. No inhibition of respiration at elevated CO2 was observed at the highest growth temperature (30-degrees-C) in either species. CO2 efflux increased with measurement and growth temperature for M. sativa at both CO2 concentrations; however, CO2 efflux in D. glomerata showed complete acclimation to growth temperature. Stimulation of leaf area and weight by elevated CO2 levels declined with growth temperature in both species. Data from the present study suggest that both direct and indirect inhibition of respiration are possible with future increases in atmospheric CO2, and that the degree of each type of respiratory inhibition is a function of growth temperature.

KEYWORDS: ATMOSPHERIC CO2, CARBON-DIOXIDE EFFLUX, DARK RESPIRATION, ENRICHMENT, GROWTH, LEAVES, SATIVA, TREES

2694

Ziska, L.H., and J.A. Bunce. 1994. Increasing growth temperature reduces the stimulatory effect of elevated co2 on photosynthesis or biomass in 2 perennial species. *Physiologia Plantarum 91(2):183-190.*

We examined how anticipated changes in CO2 concentration and temperature interacted to alter plant growth, harvest characteristics and photosynthesis in two cold-adapted herbaceous perennials, alfalfa (Medicago sativa L. cv. Are) and orchard grass (Dactylis glomerata L. cv. Potomac). Plants were grown at two CO2 concentrations (362 [ambient] and 717 [elevated] mu mol mol(-1) CO2) and four constant day/night temperatures of 15, 20, 25 and 30 degrees C in controlled environmental chambers. Elevated CO2 significantly increased total plant biomass and protein over a wide range of temperatures in both species. Stimulation of photosynthetic rare, however, was eliminated at the highest growth temperature in M. sativa and relative stimulation of plant biomass and protein at high CO2 declined as temperature increased in both species. Lack of a synergistic effect between temperature and CO2 was unexpected since elevated CO2 reduces the amount of carbon lost via photorespiration and photorespiration increases with temperature. Differences between anticipated stimulatory effects of CO2 and temperature and whole plant single and leaf measurements are discussed. Data from this study suggest that stimulatory effects of atmospheric CO2 on growth and photosynthesis may decline with anticipated increases in global temperature, limiting the degree of carbon storage in these two perennial species.

KEYWORDS: ACCLIMATION, CARBON-DIOXIDE EFFLUX, CARBOXYLASE, ENRICHMENT, INHIBITION, LEAVES, LIGHT, RESPIRATION, SEEDLINGS, SOYBEAN CANOPY PHOTOSYNTHESIS

2695

Ziska, L.H., and J.A. Bunce. 1995. Growth and photosynthetic response of 3 soybean cultivars to simultaneous increases in growth temperature and co2. *Physiologia Plantarum 94(4):575-584.*

Three soybean (Glycine max L. Merr.) cultivars (Maple Glen, Clark and CNS) were exposed to three CO2 concentrations (370, 555 and 740 mu mol mol(-1)) and three growth temperatures (20/15 degrees, 25/20 degrees and 31/26 degrees C, day/night) to determine intraspecific differences in single leaf/whole plant photosynthesis, growth and partitioning, phenology and final biomass. Based on known carboxylation kinetics, a synergistic effect between temperature and CO2 on growth and photosynthesis was predicted since elevated CO2 increases photosynthesis by reducing photorespiration and photorespiration increases with temperature. Increasing CO2 concentrations resulted in a stimulation of single leaf photosynthesis for 40-60 days after emergence (DAE) at 20/15 degrees C in all cultivars and for Maple Glen and CNS at all temperatures. For Clark, however, the onset of flowering at warmer temperatures coincided with the loss of stimulation in single leaf photosynthesis at elevated CO2 concentrations. Despite the season-long stimulation of single leaf photosynthesis, elevated CO2 concentrations did not increase whole plant photosynthesis except at the highest growth temperature in Maple Glen and CNS, and there was no synergistic effect on final biomass. Instead, the stimulatory effect of CO2 on growth was delayed by higher temperatures. Data from this experiment suggest that: (1) intraspecific variation could be used to select for optimum soybean cultivars with future climate change; and (2) the relationship between temperature and CO2 concentration may be expressed differently at the leaf and whole plant levels and may not solely reflect known changes in carboxylation kinetics.

KEYWORDS: ATMOSPHERIC CO2, C-3, CANOPY PHOTOSYNTHESIS, CARBOXYLASE-OXYGENASE, ENRICHMENT, LEAVES

2696

Ziska, L.H., and J.A. Bunce. 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C-4 crops and weeds. *Photosynthesis Research 54(3):199-208.*

Plants of six weedy species (Amaranthus retroflexus, Echinochloa crus-galli, Panicum dichotomiflorum, Setaria faberi, Setaria viridis, Sorghum halapense) and 4 crop species (Amaranthus hypochondriacus, Saccharum officinarum, Sorghum bicolor and Zea mays) possessing the C-4 type of photosynthesis were,at-own at ambient (38 Pa) and elevated (69 Pa) carbon dioxide during early development (i.e. up to 60 days after sowing) to determine: (a) if plants possessing the C-4 photosynthetic pathway could respond photosynthetically or in biomass production to future increases in global carbon dioxide and (b) whether differences

exist between weeds and crops in the degree of response. Based on observations in the response of photosynthesis (measured as A, CO2 assimilation rate) to the growth CO2 condition as well as to a range of internal CO2 (C- i) concentrations, eight of ten C-4 species showed a significant increase in photosynthesis. The largest and smallest increases observed were for A. retroflexus (+30%) and Z. mays (+5%), respectively. Weed species (+19%) showed approximately twice the degree of photosynthetic stimulation as that of crop species (+10%) at the higher CO2 concentration. Elevated carbon dioxide also resulted in significant increases in whole plant biomass for four C-4 weeds (A. retroflexus, E. crus-galli, P. dichotomiflorum, S viridis) relative to the ambient CO2 condition. Leaf water potentials for three selected species (A. retroflexus, A. hypochondriacus, Z. mays) indicated that differences in photosynthetic stimulation were not due solely to improved leaf water status. Data from this study indicate that C-4 plants may respond directly to increasing CO2 concentration, and in the case of some C-4 weeds (e.g. A. retroflexus) may show photosynthetic increases similar to those published for C-3 species.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, ELEVATED CO2, GRASS, PLANTS, RESPONSES, TEMPERATURE, YIELD

2697

Ziska, L.H., and J.A. Bunce. 1997. The role of temperature in determining the stimulation of CO2 assimilation at elevated carbon dioxide concentration in soybean seedlings. *Physiologia Plantarum 100(1):126-132.*

Soybean (Glycine max cv. Clark) was gown at both ambient (ca 350 mu mol mol(-1)) and elevated (ca 700 mu mol mol(-1)) CO2 concentration at 5 growth temperatures (constant day/night temperatures of 20, 25, 30, 35 and 40 degrees C) for 17-22 days after sowing to determine the interaction between temperature and CO2 concentration on photosynthesis (measured as A, the rate of CO2 assimilation per unit leaf area) at both the single leaf and whole plant level. Single leaves of soybean demonstrated increasingly greater stimulation of A at elevated CO2 as temperature increased from 25 to 35 degrees C (i.e. optimal growth rates). At 40 degrees C, primary leaves failed to develop and plants eventually died. in contrast, for both whole plant A and total biomass production, increasing temperature resulted in less stimulation by elevated CO2 concentration. For whole plants, increased CO2 stimulated leaf area more as growth temperature increased. Differences between the response of A to elevated CO2 for single leaves and whole plants may be related to increased self-shading experienced by whole plants at elevated CO2 as temperature increased. Results from the present study suggest that self-shading could limit the response of CO2 assimilation rate and the growth response of soybean plants if temperature and CO2 increase concurrently, and illustrate that light may be an important consideration in predicting the relative stimulation of photosynthesis by elevated CO2 at the whole plant level.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CANOPY PHOTOSYNTHESIS, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHETIC RESPONSE, PLANTS

2698

Ziska, L.H., and J.A. Bunce. 1998. The influence of increasing growth temperature and CO2 concentration on the ratio of respiration to photosynthesis in soybean seedlings. *Global Change Biology 4(6):637-643.*

Using controlled environmental growth chambers, whole plants of soybean, cv. 'Clark', were examined during early development (7-20 days after sowing) at both ambient (approximate to 350 mu L L-1) and elevated (approximate to 700 mu L L-1) carbon dioxide and a range of air temperatures (20, 25, 30, and 35 degrees C) to determine if future climatic change (temperature or CO2 concentration) could alter the ratio of carbon lost by dark respiration to that gained via photosynthesis. Although whole-plant respiration increased with short-term increases in the measurement temperature, respiration acclimated to increasing growth temperature. Respiration, on a dry weight basis, was either unchanged or lower for the elevated CO2 grown plants, relative to ambient CO2 concentration, over the range of growth temperatures. Levels of both starch and sucrose increased with elevated CO2 concentration, but no interaction between CO2 and growth temperature was observed. Relative growth rate increased with elevated CO2 concentration up to a growth temperature of 35 degrees C. The ratio of respiration to photosynthesis rate over a 24-h period during early development was not altered over the growth temperatures (20-35 degrees C) and was consistently less at the elevated relative to the ambient CO2 concentration. The current experiment does not support the proposition that global increases in carbon dioxide and temperature will increase the ratio of respiration to photosynthesis; rather, the data suggest that some plant species may continue to act as a sink for carbon even if carbon dioxide and temperature increase simultaneously.

KEYWORDS: CANOPY PHOTOSYNTHESIS, CARBON-DIOXIDE CONCENTRATION, DARK RESPIRATION, ELEVATED CO2, ENRICHMENT, INHIBITION, LONG-TERM, RESPONSES, SHORT-TERM, WHOLE-PLANT RESPIRATION

2699

Ziska, L.H., and J.A. Bunce. 1999. Effect of elevated carbon dioxide concentration at night on the growth and gas exchange of selected C-4 species. *Australian Journal of Plant Physiology 26(1):71-77.*

Biomass of certain C-4 species is increased when plants are grown at elevated CO2 concentrations. Experiments using four C- 4 species (Amaranthus retroflexus L., Amaranthus hypochondriacus L., Sorghum bicolor (L.) Moench and Zea mays L.) exposed both day and night from sowing to carbon dioxide concentrations of 370 (ambient) or 700 mu mol mol(-1) (elevated) or to 370 mu mol mol(-1) during the day and 700 mu mol mol(-1) at night, determined whether any biomass increase at elevated CO2 concentrations was related to a reduction in the night-time rate of CO2 efflux at high night-time CO2 concentrations. Of the four species tested, only A. retroflexus significantly increased both CO2 assimilation (+13%) and plant biomass (+21%) at continuous elevated relative to continuous ambient concentrations of CO2. This increase was not associated with improvement in leaf water potential during dark or light periods. In contrast, high CO2 only during the night significantly reduced plant biomass compared to the 24 h ambient CO2 treatment for both A. retroflexus and Z. mays. This indicates that the observed increase in biomass at elevated CO2 for A. retroflexus was not caused by a reduction of carbon loss at night (i.e. increased carbon conservation), but rather a direct stimulation of daytime CO2 assimilation, independent of any improvement in leaf water potential.

KEYWORDS: ACCLIMATION, CO2- ENRICHMENT, DARK RESPIRATION, GRACILIS C-4, IRRADIANCE, LEAVES, PASCOPYRUM-SMITHII C-3, PLANTS, RESPONSES, TEMPERATURE

2700

Ziska, L.H., J.A. Bunce, and F. Caulfield. 1998. Intraspecific variation in seed yield of soybean (Glycine max) in response to increased atmospheric carbon dioxide. *Australian Journal of Plant Physiology 25(7):801-807.*

The growth characteristics of six and the reproductive development of five soybean [Glycine max (L.) Merr.] cultivars were examined at 39 Pa (ambient) and 70 Pa (elevated) CO2 partial pressures in temperature-controlled glasshouses. Significant intraspecific variation for both

growth and seed yield in response to elevated CO2 was observed among the cultivars. At elevated CO2, total biomass increased an average of 42% at the end of the vegetative stage, while average seed yield increased by only 28%. No changes in % protein or % oil were observed for any cultivar at elevated CO2, relative to ambient CO2. The relative enhancement of either vegetative or reproductive growth at elevated CO2 was not correlated with changes in the absolute or relative increase in single leaf photosynthetic rate among cultivars at elevated CO2. For soybean, the greatest response of seed yield to elevated CO2 was associated with increased production of lateral branches, increased pod production or increased seed weight, suggesting different strategies of carbon partitioning in a high CO2 environment. Data from this experiment indicates that differences in carbon partitioning among soybean cultivars may influence reproductive capacity and fecundity as atmospheric CO2 increases, with subsequent consequences for future agricultural breeding strategies.

KEYWORDS: CO2- ENRICHMENT, CULTIVARS, GROWTH, RICE ORYZA-SATIVA, TEMPERATURE

2701

Ziska, L.H., B.G. Drake, and S. Chamberlain. 1990. Long-term photosynthetic response in single leaves of a C3 and C4 salt-marsh species grown at elevated atmospheric CO2 in Situ. *Oecologia 83(4):469-472.*

2702

Ziska, L.H., K.P. Hogan, A.P. Smith, and B.G. Drake. 1991. Growth and photosynthetic response of 9 tropical species with long-term exposure to elevated carbon-dioxide. *Oecologia 86(3):383-389.*

Seedlings of nine tropical species varying in growth and carbon metabolism were exposed to twice the current atmospheric level of CO2 for a 3 month period on Barro Colorado Island, Panama. A doubling of the CO2 concentration resulted in increases in photosynthesis and greater water use efficiency (WUE) for all species possessing C3 metabolism, when compared to the ambient condition. No desensitization of photosynthesis to increased CO2 was observed during the 3 month period. Significant increases in total plant dry weight were also noted for 4 out of the 5 C3 species tested and in one CAM species, Aechmea magdalenae at high CO2. In contrast, no significant increases in either photosynthesis or total plant dry weight were noted for the C4 grass, Paspallum conjugatum. Increases in the apparent quantum efficiency (AQE) for all C3 species suggest that elevated CO2 may increase photosynthetic rate relative to ambient CO2 over a wide range of light conditions. The response of CO2 assimilation to internal C(i) suggested a reduction in either the RuBP and/or Pi regeneration limitation with long term exposure to elevated CO2. This experiment suggests that: (1) a global rise in CO2 may have significant effects on photosynthesis and productivity in a wide variety of tropical species, and (2) increases in productivity and photosynthesis may be related to physiological adaptation(s) to increased CO2.

KEYWORDS: C-3, CO2, LEAVES, PHYSIOLOGY, PLANTS

2703

Ziska, L.H., P.A. Manalo, and R.A. Ordonez. 1996. Intraspecific variation in the response of rice (Oryza sativa L) to increased CO2 and temperature: Growth and yield response of 17 cultivars. *Journal of Experimental Botany 47(302):1353-1359.*

Seventeen rice (Oryza sativa L.) cultivars of contrasting ecosystems and origins were exposed to two CO2 concentrations (373 [ambient] and 664 mu l l(-1) CO2 [elevated]) at two different day/night temperatures (29/21 degrees C and 37/29 degrees C) in glasshouses at the International Rice Research Institute phytotron during the dry seasons of 1994 and 1995, Growth at elevated CO2 (as determined by total plant biomass at maturity) increased by an average of 70% and 22%, respectively, for all cultivars for growth temperatures of 29/21 degrees C and 37/29 degrees C relative to the ambient CO2 treatment. At the 29/21 degrees C optimal growth temperature, grain yield increased on average c. 50% with enriched CO2. In contrast, at the higher growth temperature (37/29 degrees C), grain yield was almost zero, presumably due, in part, to temperature- induced infertility (i.e. the percentage of filled spikelets was < 1%), Among cultivars, IAC 165, a tropical japonica from Brazil, showed the largest relative increase in both biomass and grain yield, While the range of responses to increased CO2 and/or temperature were quite large (e.g. 10-250%) and may not be applicable to field conditions, data indicate that lines are available which could maximize productivity as CO2 concentration increases. Additional work, however, would be needed to identify cultivars which would maintain maximum yields in a high CO2, high temperature environment.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, ELEVATED CARBON-DIOXIDE, SEEDLINGS

2704

Ziska, L.H., T.B. Moya, R. Wassmann, O.S. Namuco, R.S. Lantin, J.B. Aduna, E. Abao, K.F. Bronson, H.U. Neue, and D. Olszyk. 1998. Long-term growth at elevated carbon dioxide stimulates methane emission in tropical paddy rice. *Global Change Biology 4(6):657-665.*

Recent anthropogenic emissions of key atmospheric trace gases (e.g. CO2 and CH4) which absorb infra-red radiation may lead to an increase in mean surface temperatures and potential changes in climate. Although sources of each gas have been evaluated independently, little attention has focused on potential interactions between gases which could influence emission rates. In the current experiment, the effect of enhanced CO2 (300 mu L L-1 above ambient) and/or air temperature (4 degrees C above ambient) on methane generation and emission were determined for the irrigated tropical paddy rice system over 3 consecutive field seasons (1995 wet and dry seasons 1996 dry season). For all three seasons, elevated CO2 concentration resulted in a significant increase in dissolved soil methane relative to the ambient control. Consistent with the observed increases in soil methane, measurements of methane flux per unit surface area during the 1995 wet and 1996 dry seasons also showed a significant increase at elevated carbon dioxide concentration relative to the ambient CO2 condition (+49 and 60% for each season, respectively). Growth of rice at both increasing CO2 concentration and air temperature did not result in additional stimulation of either dissolved or emitted methane compared to growth at elevated CO2 alone. The observed increase in methane emissions were associated with a large, consistent, CO2-induced stimulation of root growth. Results from this experiment suggest that as atmospheric CO2 concentration increases, methane emissions from tropical paddy rice could increase above current projections.

KEYWORDS: CO2- ENRICHMENT, PHOTOSYNTHETIC ACCLIMATION, RESPONSES, RHIZOSPHERE, VEGETATION, YIELD

2705

Ziska, L.H., O. Namuco, T. Moya, and J. Quilang. 1997. Growth and yield response of field-grown tropical rice to increasing carbon dioxide and air temperature. *Agronomy Journal 89(1):45-53.*

Although the response of rice (Oryza sativa L.) to increasing atmospheric CO2 concentration and air temperature has been examined at the greenhouse or growth chamber level, no field studies have been conducted under the tropical, irrigated conditions where the bulk of the world's rice is grown. At the International Rice Research Institute, rice

(cv. IR 72) was grown from germination until maturity for the 1994 wet and 1995 dry seasons at three different CO2 concentrations (ambient, ambient + 200, and ambient + 300 mu L L(-1) CO2) and two different air temperatures (ambient and ambient + 4 degrees C) using open-top field chambers. Averaged for both seasons, increases in CO2 concentration alone (+ 200, + 300 mu L L(-1)) resulted in a significant increase in total plant biomass (+ 31%, + 40%) and crop yield (+ 15%, + 27%) compared with the ambient control. The increase in crop yield was associated with an increase in the number of panicles per square meter and a greater percentage of filled spikelets. Simultaneous increases in CO2 and air temperature did not alter the biomass at maturity (relative to elevated CO2 alone), but plant development was accelerated at the higher growth temperature regardless of CO2 concentration. Grain yield, however, became insensitive to CO2 concentration at the higher growth temperature. Increasing both CO2 and air temperature also reduced grain quality (e.g., protein content). The combination of CO2 and temperature effects suggests that, in warmer regions (i.e., > 34 degrees C) where rice is grown, quantitative and qualitative changes in rice supply are possible if both CO2 and air temperature continue to increase.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, BIOMASS, ELEVATED CO2, ENRICHMENT, ORYZA-SATIVA, PHOTOSYNTHESIS

2706

Ziska, L.H., R.C. Sicher, and J.A. Bunce. 1999. The impact of elevated carbon dioxide on the growth and gas exchange of three C-4 species differing in CO2 leak rates. *Physiologia Plantarum 105(1):74-80.*

Recent work has suggested that the photosynthetic rate of certain C-4 species can be stimulated by increasing CO2 concentration, [CO2], even under optimal water and nutrients.To determine the basis for the observed photosynthetic stimulation, we tested the hypothesis that the CO2 leak rate from the bundle sheath would be directly related to any observed stimulation in single leaf photosynthesis at double the current [CO2]. Three C-4 species that differed in the reported degree of bundle sheath leakiness to CO2, Flaveria trinervia. Panicum miliaceum, and Panicum maximum, were grown for 31-38 days after sowing at a [CO2] of 350 mu l l(-1) (ambient) or 700 mu l l(-1) (elevated). Assimilation as a function of increasing [CO2] at high photosynthetic photon flux density (PPFD, 1 600 mu mol m(-2) s(-1)) indicated that leaf photosynthesis was not saturated under current ambient [CO2] for any of the three C-4 species. Assimilation as a function of increasing PPFD also indicated that the response of leaf photosynthesis to elevated [CO2] was light dependent for all three C-4 species, The stimulation of leaf photosynthesis at elevated [CO2] was not associated with previously published values of CO2 leak rates from the bundle sheath, changes in the ratio of activities of PEP-carboxylase to RuBP carboxylase/oxgenase, or any improvement in day time leaf water potential for the species tested in this experiment. In spite of the simulation of leaf photosynthesis, a significant increase in growth at elevated [CO2] was only observed for one species, F. trinervia. Results from this study indicate that leaf photosynthetic rates of certain C-4 species can respond directly to increased [CO2] under optimal growth conditions, but that the stimulation of whole plant growth at elevated carbon dioxide cannot be predicted solely on the response of individual leaves.

KEYWORDS: ATMOSPHERIC CO2, BUNDLE SHEATH-CELLS, CARBOXYLASE, ENRICHMENT, IRRADIANCE, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS, RESPONSES

2707

Ziska, L.H., R.C. Sicher, and D.F. Kremer. 1995. Reversibility of photosynthetic acclimation of Swiss chard and sugarbeet grown at elevated concentrations of CO2. *Physiologia Plantarum 95(3):355-364.*

Although leaf photosynthesis and plant growth are initially stimulated by elevated CO2 concentrations, increasing insensitivity to CO2 (acclimation) is a frequent occurrence. In order to examine the acclimation process, we studied photosynthesis and whole plant development in swiss chard (Beta vulgaris L. Koch ssp. ciela) and sugarbeet (Beta vulgaris L. ssp. vulgaris) grown at either ambient or twice ambient concentrations of CO2. In an initial controlled environment study, photosynthetic acclimation to elevated CO2 levels was observed in both subspecies 24 days after sowing (DAS) but was not observed at 42 and 49 DAS for sugarbeet or at 49 DAS for swiss chard. Although sugarbeet and swiss chard differed in root size and morphology, this was not a factor in the onset of photosynthetic acclimation. The reversal of photosynthetic acclimation that was observed in older plants grown at elevated CO2 concentrations was associated with a rapid increase in root development (i.e. increased root: shoot [R/S] ratio), increased sucrose levels in sinks (roots) and no differences in total soluble leaf protein of either subspecies relative to the ambient CO2 condition. In a second set of experiments, swiss chard and sugarbeet were grown in outdoor Plexiglass chambers at different times of the year (i.e. summer and early fall). Average 24-h temperature was 30.7 and 19.4 degrees C for the summer and fall plantings, respectively. In agreement with the controlled environment study, lack of photosynthetic acclimation, determined from the response of photosynthesic rate to internal CO2 concentration, was correlated with increased root biomass and sucrose concentration relative to the ambient condition. However, photosynthetic acclimation was observed depending on the season, i.e. summer (swiss chard) or fall (sugarbeet), suggesting that acclimation was affected by environmental factors, such as temperature. Data from both experiments suggest that continued long-term photosynthetic stimulation may be dependent upon the ability of increased CO2 to stimulate new sink development which would allow full utilization of the additional carbon made available in a high CO2 environment.

KEYWORDS: CARBON DIOXIDE, EXCHANGE, LEAVES, LIGHT, PLANTS, TEMPERATURE

2708

Ziska, L.H., J.R. Teasdale, and J.A. Bunce. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Science 47(5):608-615.*

We tested whether the efficacy of chemical weed control might change as atmospheric CO2 concentration [CO2] increases by determining if tolerance to a widely used, phloem mobile, postemergence herbicide, glyphosate, was altered by a doubling of [CO2]. Tolerance was determined by following the growth of Amaranthus retroflexus L. (redroot. pigweed), a C-4 species, and Chenopodium album L. (common lambsquarters), a C-3 species, grown at near ambient (360 mu mol mol(-1)) and twice ambient (720 mu mol mol(-1)) [CO2] for 14 d following glyphosate application at rates of 0.00 (control), 0.112 kg ai ha(-1) (0.1 x the commercial rate), and 1.12 kg ai ha(-1) (1.0 x the commercial rare) in four separate trials. Irrespective of [CO2], growth of the C-4 species, A. retroflexus, was significantly reduced and was eliminated altogether at glyphosate application rates of 0.112 and 1.12 kg ai ha(-1), respectively. However, in contrast to the ambient [CO2] treatment, an application rate of 0.112 kg ai ha(-1) had no effect on growth, and a 1.12 kg ai ha(-1) rate reduced but did not eliminate growth in elevated [CO2]-grown C. album. Although glyphosate tolerance does increase with plant size at the time of application, differences in glyphosate tolerance between CO2 treatments in C. album cannot be explained by size alone. These data indicate that rising atmospheric [CO2] could increase glyphosate tolerance in a C-3 weedy species. Changes in herbicide tolerance at elevated [CO2] could limit chemical weed control efficacy and increase weed-crop competition.

KEYWORDS: C-3, CO2- ENRICHMENT, CROP, GROWTH-

STIMULATION, PLANTS, WEEDS

2709

Ziska, L.H., and A.H. Teramura. 1992. Co2 enhancement of growth and photosynthesis in rice (oryza- sativa) - modification by increased ultraviolet-b radiation. *Plant Physiology 99(2):473-481.*

Two cultivars of rice (Oryza sativa L.) IR-36 and Fujiyama-5 were grown at ambient (360 microbars) and elevated CO2 (660 microbars) from germination through reproduction in unshaded greenhouses at the Duke University Phytotron. Growth at elevated CO2 resulted in significant decreases in nighttime respiration and increases in photosynthesis, total biomass, and yield for both curtivars. However, in plants exposed to simultaneous increases in CO2 and ultraviolet-B (UV-B) radiation, CO2 enhancement effects on respiration, photosynthesis, and biomass were eliminated in IR-36 and significantly reduced in Fujiyama-5. UV-B radiation simulated a 25% depletion in stratospheric ozone at Durham, North Carolina. Analysis of the response of CO2 uptake to internal CO2 concentration at light saturation suggested that, for IR-36, the predominant limitation to photosynthesis with increased UV- B radiation was the capacity for regeneration of ribulose bisphosphate (RuBP), whereas for Fujiyama-5 the primary photosynthetic decrease appeared to be related to a decline in apparent carboxylation efficiency. Changes in the RuBP regeneration limitation in IR-36 were consistent with damage to the photochemical efficiency of photosystem II as estimated from the ratio of variable to maximum chlorophyll fluorescence. Little change in RuBP regeneration and photochemistry was evident in cultivar Fujiyama-5, however. The degree of sensitivity of photochemical reactions with increased UV-B radiation appeared to be related to leaf production of UV-B- absorbing compounds. Fujiyama-5 had a higher concentration of these compounds than IR-36 in all environments, and the production of these compounds in Fujiyama-5 was stimulated by UV-B fluence. Results from this study suggest that in rice alterations in growth or photosynthesis as a result of enhanced CO2 may be eliminated or reduced if UV-B radiation continues to increase.

KEYWORDS: C-3, CARBON DIOXIDE, ELEVATED CO2, INHIBITION, LEAVES, LONG-TERM EXPOSURE, PLANTS, RESPIRATION

2710

Ziska, L.H., and A.H. Teramura. 1992. Intraspecific variation in the response of rice (oryza-sativa) to increased co2 - photosynthetic, biomass and reproductive characteristics. *Physiologia Plantarum 84(2):269-276.*

Two rice (Oryza sativa L.) cultivars of contrasting morphologies, IR-36 and Fujiyama-5, were exposed to ambient (360-mu-l l-1) and ambient plus 300-mu-l l-1 CO2 from time of emergence until ca 50% grain fill at the Duke University Phytotron, Durham, North Carolina. Exposure to increased CO2 resulted in about a 50% increase in the photosynthetic rate for both cultivars and photosynthetic enhancement was still evident after 3 months of exposure to a high CO2 environment. The photosynthetic response at 5% CO2 and the response of CO2 assimilation (A) to internal CO2 (C(i)) suggest a reallocation of biochemical resources from RuBP carboxylation to RuBP regeneration. Increases in total plant biomass at elevated CO2 were approximately the same in both cultivars, although differences in allocation patterns were noted in root/shoot ratio. Differences in reproductive characteristics were also observed between cultivars at an elevated CO2 environment with a significant increase in harvest index for IR-36 but not for Fujiyama-5. Changes in carbon allocation in reproduction between these two cultivars suggest that lines of rice could be identified that would maximize reproductive output in a future high CO2 environment.

KEYWORDS: ACCLIMATION, ASSIMILATION, C-3 PLANTS, CARBON DIOXIDE, CARBOXYLASE, ELEVATED CO2, HIGH ATMOSPHERIC CO2, INHIBITION, LEAVES, WHEAT

2711

Ziska, L.H., W. Weerakoon, and L.W. Hong. 1995. Photosynthetic acclimation of field-grown rice to elevated co2. *Plant Physiology 108(2):92.*

2712

Ziska, L.H., W. Weerakoon, O.S. Namuco, and R. Pamplona. 1996. Influence of nitrogen on the elevated CO2 response in field- grown rice. *Australian Journal of Plant Physiology 23(1):45-52.*

Rice (Oryza sativa L. cv. IR72) was grown in the tropics at ambient (345 mu L L(-1)) or twice ambient (elevated, 700 mu L L(-1)) CO2 concentration at three levels of supplemental nitrogen (N) (no additional N (N-0), 90 kg ha(-1) (N-1) and 200 kg ha(-1) (N-2)) in open-top chambers under irrigated field conditions from seeding until flowering. The primary objective of the study was to determine if N supply alters the sensitivity of growth and photosynthesis of field-grown rice to enriched CO2. A second objective was to determine the influence of elevated CO2 on N uptake and tissue concentrations. Although photosynthesis was initially stimulated at the leaf and canopy level with elevated CO2 regardless of supplemental N supply, with time the photosynthetic response became highly dependent on the level of supplemental N, increasing proportionally as N availability increased. Similarly, a synergistic effect was noted between CO2 and N with respect to above-ground biomass with no effect of elevated CO2 observed for the N-0 treatment. Most of the increase in above-ground biomass with increasing CO2 and N was associated with increased tiller and, to a lesser extent, root production. The concentration of above-ground N decreased at elevated CO2 regardless of N treatment; however, total aboveground N did not change for the N-1 and N-2 treatments because of the greater amount of biomass associated with elevated CO2. For rice, the photosynthetic and growth response to elevated CO2 may be highly dependent on the supply of N. If additional CO2 is given and N is not available, lack of sinks for excess carbon (e.g. tillers) may limit the photosynthetic and growth response.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO2, CARBON DIOXIDE, ENRICHMENT, NUTRITION, PLANTS, SEEDLINGS, STRESS, WHEAT, YIELD

2713

Zobayed, S.M.A., F. Afreen-Zobayed, C. Kubota, and T. Kozai. 1999. Stomatal characteristics and leaf anatomy of potato plantlets cultured in vitro under photoautotrophic and photomixotrophic conditions. *In Vitro Cellular & Developmental Biology-Plant 35(3):183-188.*

Potato plantlets (Solanum tuberosum L. cv. Benimaru) were cultured under photoautotrophic (without an) sucrose in the nutrient medium and with enriched CO2 and high photosynthetic photon flux and photomixotrophic conditions (20 g l(-1) sucrose in the medium). Leaf anatomy and stomatal characteristics of the leaves were studied in relation to stomatal size and density. Leaf diffusive resistance, transpiration rater and was content of the leaves were also investigated. In the photoautotrophic treatment, stomata behaved normally LI closing in the dark and opening in the light. The stomatal density increased twofold compared to that of the photomixotrophic treatment. Relatively thick leaves and an organized palisade layer were observed and the epicuticular wax content was remarkably higher in this treatment. i.e., seven times greater than that of photomixotrophic treatment. In general,

higher diffusive resistance of the leaves was observed than under photomixotrophic conditions; also the resistance increased in darkness and decreased in the light. All these characteristics led the plantlets to have a normal and controlled transpiration rater which was exceptionally; high in the photomixotrophic treatment throughout the light and the dark period.

Keyword index to citations in "Bibliography on CO2 Effects on Vegetation and Ecosystems: 1990-1999 Literature" (Michael H. Jones and Peter S. Curtis, editors), ORNL/CDIAC-129, July 2000 (http://cdiac.esd.ornl.gov/epubs/cdiac/cdiac129/cdiac129.html)

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1,5-BISPHOSPHATE CARBOXYLASE 98, 878
1,5-BISPHOSPHATE CARBOXYLASE OXYGENASE 370
1,5-DIPHOSPHATE CARBOXYLASE 253
16S RDNA 1452
18TH-CENTURY ENGLAND 45
1989 FACE EXPERIMENT 1155
1-AMINOCYCLOPROPANE-1-CARBOXYLATE OXIDASE 667
1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID 524, 762-764, 1241, 1471, 1472, 1622, 1696, 2632
2,4-DICHLOROPHENOL 1368
24-H 317
280-320 NM 2475
2-CARBOXYARABINITOL 1-PHOSPHATE 55
32-KILODALTON PROTEIN 891
3-DIMENSIONAL SYNTHESIS 856
4-YEAR EXPOSURE 165, 1133, 1135, 1136
AAA 2136
ABANDONED PASTURES 1526
ABANDONMENT 2280
ABIES-ALBA MILL 159
ABIES AMABILIS 2002
ABIES KARST L 2162
ABIES L KARST 120, 305, 590, 802, 1044, 1130, 1133, 1374, 1445, 1510, 1545, 1870, 2011, 2515
ABILITY 2270
A-BINDING SITES 1213
ABITIBI GREENSTONE-BELT 1199
ABOVEGROUND PARTS 324
ABSCISIC- ACID 34, 206, 237, 262, 480, 563, 585, 643, 806, 885, 1268, 1330, 1445, 1466, 1635, 1655, 1867, 2011, 2103, 2116,
2132, 2269, 2312, 2544, 2614
ABSCISSION 18, 2447
ABSORBANCE CHANGES 1379, 1826
ABSORPTION 135, 924
ABUNDANCE 1300, 1648, 1812, 2097
ABUTILON-THEOPHRASTI 152
ACCLIMATION 4, 11, 18, 77, 88, 92, 93, 106, 125, 126, 148, 160, 187, 205, 249, 255, 257, 283,

324, 334, 342, 343, 345, 346, 415, 420, 430, 450, 476, 482, 502, 508, 511, 512, 522, 545, 561, 575, 589, 618, 636, 639, 640, 649, 652, 680, 681, 704, 713, 715, 729, 730, 733, 735, 743, 784, 796, 804, 806, 808, 826, 834, 875, 907, 912, 918, 922, 937, 938, 942, 959, 981, 986, 987, 1035, 1038, 1058, 1065, 1066, 1070, 1091, 1106, 1131, 1137, 1153, 1173, 1197, 1222, 1243, 1255, 1284, 1301, 1349, 1351, 1365, 1379, 1389, 1406, 1428, 1448, 1449, 1511, 1519, 1532, 1536, 1538, 1553, 1564, 1584, 1588, 1606, 1619, 1627, 1637, 1645, 1663, 1676, 1677, 1689, 1751, 1754, 1793, 1796-1799, 1819, 1824, 1854, 1899, 1900, 1938, 1939, 1962, 1988, 2004, 2006, 2016, 2034, 2035, 2101, 2155, 2195, 2203-2205, 2221, 2234, 2242, 2253, 2315, 2317, 2326, 2365, 2368, 2414, 2415, 2435, 2436, 2439, 2455, 2457, 2476, 2487, 2488, 2494, 2497, 2501, 2519, 2521, 2583, 2592, 2632, 2664, 2684, 2689, 2694, 2696, 2697, 2699, 2703, 2705, 2710, 2712
ACCLIMATIZATION 500, 514, 574, 1109, 1171, 2357, 2615
ACC OXIDASE 524, 667
ACC SYNTHASE 1622
ACCUMULATION 52, 59, 94, 123, 207, 280, 366, 386, 729, 740, 907, 980, 1033, 1071, 1138, 1166, 1297, 1437, 1622, 1915, 1938, 1990, 2019, 2070, 2143, 2192, 2199, 2203, 2254, 2255, 2315, 2687
ACER- SACCHARUM MARSH 1374
ACETABULARIA- MEDITERRANEA 248
ACETALDEHYDE 1181, 1623
ACETALDEHYDE VAPOR 1930
ACETYLENE 2473
ACETYLENE-REDUCTION 266, 2485, 2679
ACETYLENE-REDUCTION ACTIVITY 2250
ACETYLENE-REDUCTION ASSAY 89, 465, 1990
ACID 544, 2447, 2589
ACIDIC DEPOSITION 1510
ACIDIC RAIN 235
ACIDIFICATION 260, 1694, 1773, 2152, 2302
ACID METABOLISM 1727
ACID METABOLISM PLANT 1404
ACID MIST 120, 121, 1831
ACID PEAT 1734
ACID-RAIN 1103, 2196
ACIDS 2187
ACID SYNTHASE 989, 1473
ACQUISITION 88, 150, 1818, 2538, 2685
ACTINIDIA-DELICIOSA VINES 783
ACTION SPECTRA 230
ACTION SPECTRUM 2247
ACTIVATED CARBON 1804
ACTIVATED-CHARCOAL 557
ACTIVATION 212, 667, 938, 1050, 1448, 1472, 1880, 1939, 1965, 1989, 2060
ACTIVE OXYGEN 95
ACTIVE-SITE 98

ACTIVE-TRANSPORT 1339
ACTIVE ULTRAVIOLET-RADIATION 1280
ACTIVITY C2H2 REDUCTION 2473
ACTIVITY INVIVO 55
ADAPTATION 1446, 2295
ADDITIONS 1639
ADJUSTMENTS 644, 1194
ADP-GLUCOSE PYROPHOSPHORYLASE 724, 803, 1223, 1395, 2275, 2459
ADULT DIET 2076
AEDES-TRISERIATUS DIPTERA 2285
AERATION 1628, 1650, 2109
AERENCHYMA 955
AEROSOL 429
AEROSOL FORMATION 426
AEROSOLS 1118, 1262
AFFINITY 1421
AFRICAN SAVANNA ECOSYSTEMS 1475
AGARICUS-BISPORUS 265
AGASP 429
AGAVE-DESERTI 986, 1700
AGAVE-VILMORINIANA 469, 470, 1035, 1291, 1701, 1704, 1707, 1933 AGE 915, 1068, 1111, 1547
AGE-AGE CORRELATIONS 314
AGGREGATE STABILITY 2322
AGRICULTURAL CROPS 881, 884
AGRICULTURAL PRODUCTIVITY 45, 2024
AGRICULTURAL YIELD 765
AGRICULTURE 592, 1710, 1795, 1891, 2026, 2592
AGROBACTERIUM 2357
AGROBACTERIUM-TUMEFACIENS 355
AGROFOREST MANAGEMENT-PRACTICES 551
AGROPYRON-SMITHII 1582
AIR 36, 384, 627, 1009, 1813, 1894, 1950, 2448
AIR CO-2 ENRICHMENT 700, 772, 898, 1052, 1914, 2058, 2383, 2384
AIR HUMIDITY 1655
AIR- POLLUTANTS 107, 119-121, 497, 1076, 1133, 1218, 1252, 1305, 1545, 1616, 1745, 1927, 1959, 2068, 2174, 2324, 2325
AIR-POLLUTION 78, 429, 535, 555, 860, 863, 1144, 1294, 1366, 1715, 1920, 1958
AIR- POLLUTION GRADIENT 1418
AIR- TEMPERATURE 18, 103, 493, 586, 686, 1291, 1507, 1600, 1685, 1687, 1935, 1947, 2024, 2048, 2061, 2062, 2094-2096, 2400,
2543, 2545, 2565, 2567
AJUGA- REPTANS L 280
ALASKA 429, 740, 1094, 1735, 1736, 2303
ALASKAN TUNDRA 904, 1086, 1198, 1734, 2284

ALASKAN TUSSOCK TUNDRA 136, 430, 660, 1140, 1141, 1297, 1502, 2192
ALASKA PAPER BIRCH 1289
ALBA L 1836, 2481
ALCOHOL-DEHYDROGENASE 1119, 1470, 1623
ALGA 1619
ALGA BOTRYOCOCCUS-BRAUNII 956
ALGAE 1679, 2599
ALKANES 1649
ALLELOCHEMICALS 615, 911, 1114, 1290, 1360, 1813, 1814, 1901, 1970
ALLIUM 655
ALLOCATION 15, 73, 85, 129, 146, 324, 409, 410, 450, 623, 641, 796, 798, 801, 825, 916, 918, 919, 924, 971, 985, 1032, 1055, 1100, 1102, 1113, 1268, 1289, 1306, 1353, 1354, 1420, 1427, 1483, 1527, 1630, 1654, 1662, 1663, 1686, 1815, 1816, 1820, 1910, 1984, 2054, 2195, 2273, 2332, 2344, 2352, 2380, 2386, 2388, 2435, 2479, 2643, 2685
ALLOCATION PATTERNS 440, 529, 974, 1361, 1970, 2087
ALLOMETRY 2346
ALNUS-GLUTINOSA 2159
ALNUS-RUBRA 916
ALOCASIA-MACRORRHIZA 1861, 2016, 2222
ALPHA- PINENE 426
ALPINE 80
ALPINE GRASSLAND 689, 861, 1654, 1722, 2102
ALPINE LIFE ZONE 660, 840, 1280, 2246, 2438, 2439
ALPINE TUNDRA 274, 2593
ALTER 2277
ALTERED FEEDING PREFERENCE 880
ALTERNATIONS 1217
ALTERNATIVE OXIDASE ACTIVITY 1020
ALTERNATIVE PATHWAY 2655
ALTITUDES 1170, 2355
ALTITUDINAL VARIATION 840
ALUMINUM 2196, 2321
AMARANTH 2606
AMAZON 536, 1884, 2244
AMAZON BASIN 645, 1501
AMAZON DEFORESTATION 936, 2477
AMAZONIA 1347, 1349
AMAZONIAN FOREST 2177
AMAZONIAN FORESTS 65
AMAZONIAN RAINFOREST 1461, 2212
AMAZONIAN RAIN FORESTS 204
AMBIENT 70, 72, 90, 154, 188, 343, 371, 485, 641, 659, 662, 690, 714, 843, 965, 1018, 1022, 1045, 1201, 1226, 1296, 1298, 1490, 1653, 1673, 1767, 1768, 1850, 1856, 1954, 2057, 2094-2096, 2114, 2117, 2142, 2346, 2481, 2511, 2530, 2540, 2622, 2682
AMBIENT AIR 634

AMBIENT AIR-POLLUTION 880
AMBIENT ATMOSPHERE 815, 1983
AMBIENT CO2 1324
AMBIENT OZONE 2609
AMBIENT PARTIAL-PRESSURE 1372
AMELONADO 665
AMENDED SOIL 2672
AMERICA 1051, 2305, 2527
AMERICAN SOUTHWEST 61, 2555
AMINO-ACID 2186
AMINO-ACIDS 487, 1261, 1790, 1971, 2076
AMMONIA 2232
AMMONIUM 132, 133, 135, 455, 456, 466, 1036
AMMONIUM ASSIMILATION 467, 2655
AMMONIUM-ENRICHED RAINWATER 2462
AMMONIUM INHIBITION 1991
AMMONIUM NUTRITION 454, 457, 458, 2499
AMMONIUM-SULFATE 1819, 1995
AMMOPHILA-BREVILIGULATA 1822
ANABAENA 1619
ANACYSTIS-NIDULANS 499, 1562, 1625, 1728, 2032
ANAEROBIC CONDITIONS 750, 1930
ANAEROBIC NITROGEN 1119
ANAEROBIOSIS 207
ANATOMY 354, 515, 588, 625, 840, 984, 1072, 1258, 1590, 1721, 1910, 2109, 2221, 2502-2504, 2506
ANDOSOLS 2321
ANDROPOGON-GERARDII 264, 1188-1190, 1859
ANESTHESIA 2267
ANESTHETIZED DOGS 2267
ANHYDRASE 707, 2208
ANHYDRASE ACTIVITY 454
ANION CHANNELS 1331, 2544
ANNONA-CHERIMOLA 2677
ANNUAL GRASSLAND 703, 961, 963, 1046, 2686
ANNUALS 6, 70, 923, 1047, 1652, 1667, 1672, 1969, 2141, 2188, 2400
ANODA ANODA-CRISTATA 1791, 1792
ANOXIA 207, 258
ANTARCTIC ICE 503, 582
ANTARCTIC LAKES 1992
ANTENNA SIZE 1307
ANTHER-CULTURE RESPONSE 557
ANTHRACNOSE 1904
ANTHROPOGENIC CO2 498
ANTIFUNGAL DIENE 1903

ANTIOXIDATIVE ENZYMES 639, 988
ANTIOXIDATIVE SYSTEMS 1252
ANTISENSE GENE 55, 178
ANTISENSE RBCS 146, 1508, 2001, 2204, 2208, 2460, 2630
ANTISENSE REPRESSION 893
ANTISENSE RNA 1428
APHID INFESTATION 880
APICAL DEVELOPMENT 1334
APPARATUS 1379, 1755
APPLE 939
APPLE FRUIT 989
APPLES 524
APRIL 429
AQUATIC CAM PLANTS 88
AQUATIC MACROPHYTES 369, 1422, 1740, 2371, 2372, 2472
AQUATIC SYSTEMS 329
AQUIFER 902
ARABIDOPSIS 238
ARABIDOPSIS-THALIANA 87, 244, 1287, 1473, 1536, 1626, 1709, 1956, 2056, 2057, 2233, 2497, 2531
ARABIDOPSIS-THALIANA L 2275
ARBUSCULAR MYCORRHIZAE 1385
ARBUSCULAR MYCORRHIZAL FUNGI 1182, 1183, 1995, 1997, 1998
ARBUSCULAR MYCORRHIZAL FUNGUS 487
ARBUSCULAR MYCORRHIZAL INFECTION 1411
ARBUTUS-UNEDO 288
ARBUTUS-UNEDO L 2383, 2384
ARCHITECTURAL ANALYSIS 1460
ARCHITECTURE 201, 460
ARCTIC HAZE 429
ARCTIC SOILS 2686
ARCTIC TUNDRA 155, 394, 740, 793, 926, 1086, 1198, 1282, 1396, 1502, 1736, 1807, 2303, 2575
AREA 537, 608, 924, 1321, 1757, 1918, 2636
ARGININE DECARBOXYLASE 1622
ARID TROPICAL ENVIRONMENT 1611
ARMILLARIA-OSTOYAE 2072
ASCORBATE 2165, 2166
ASCORBATE PEROXIDASE 63, 87, 1680, 1927, 2585
ASCORBIC-ACID 1218, 1252
ASEASONAL TROPICS 432
ASIA 490
ASPARAGUS 611, 1171, 2042
ASPARAGUS CROPPING SYSTEMS 2532
ASPEN CLONES 96, 535, 1113

ASPEN FOREST 39
ASPERGILLUS-NIGER A60 1500
ASSAY 1241, 1471, 2174
ASSEMBLAGE 765, 1969
ASSESSING IMPACTS 881, 884
ASSIMILATION 53, 110, 129, 135, 180, 296, 297, 342, 368, 454, 457, 486, 499, 511, 512, 517, 621, 679, 705, 733, 792, 868, 918, 937, 988, 1056, 1209, 1318, 1349, 1352, 1407, 1449, 1682, 1685, 1826, 2104, 2231, 2272, 2331, 2437, 2472, 2584, 2605, 2710
ASSIMILATION RATE 2057
ASSOCIATION 465, 2538
ASSOCIATIONS 1388
ASTER-TRIPOLIUM L 2011
ATMOSPHERE 39, 158, 191, 273, 279, 334, 404, 569, 594, 832, 902, 939, 941, 1046, 1177, 1181, 1343, 1534, 1575, 1659, 1736, 1904, 2264, 2535, 2575
ATMOSPHERE-BIOSPHERE EXCHANGE 1057
ATMOSPHERE INTERACTIONS 838
ATMOSPHERES 51, 524, 938, 1116, 1120, 1241, 1242, 1273, 1304, 2238, 2299, 2351, 2422, 2561, 2601, 2660
ATMOSPHERIC AMMONIA 683, 1971
ATMOSPHERIC BOUNDARY-LAYER 496
ATMOSPHERIC CARBON 79, 550, 1152, 1403, 1526, 2151
ATMOSPHERIC CARBON-DIOXIDE 48, 49, 119, 124, 127, 146, 155, 157, 195, 197-200, 202, 245, 249, 276, 283, 306, 321, 335, 344, 362, 377, 388, 389, 394, 430, 436, 440, 453, 460, 468, 469, 478, 482, 508, 526-530, 551, 566, 575, 585, 624, 652, 654, 658, 672, 680, 696, 717, 729, 766, 780, 784, 792, 793, 825, 839, 846, 898, 916, 922, 931, 970, 990, 996, 999, 1001, 1029, 1048, 1072, 1108, 1117, 1151, 1165, 1198, 1209, 1224, 1282, 1311, 1386, 1391, 1405, 1417, 1431, 1438, 1454, 1455, 1492, 1494, 1515, 1571, 1607, 1646, 1667, 1692, 1704, 1713, 1717, 1729, 1732, 1737, 1746-1748, 1751, 1760, 1798, 1819, 1830, 1832, 1854, 1855, 1875, 1891, 1893, 1915, 1918, 1922, 1968, 1975, 1995, 2074, 2076, 2084, 2107, 2142, 2153, 2158, 2187, 2213, 2284, 2327, 2337, 2358, 2362, 2367-2369, 2376, 2377, 2382, 2396, 2409, 2414, 2415, 2421, 2450, 2475, 2482, 2494, 2497, 2508, 2511, 2527, 2556, 2577, 2620, 2622, 2635, 2664
ATMOSPHERIC CHEMISTRY 427
ATMOSPHERIC CO2 6, 50, 61, 66, 70-72, 74, 75, 81, 82, 85, 91, 96, 100, 102, 106, 113, 121, 123, 138, 147, 149, 150, 160, 162, 164, 166, 169, 171, 174, 176, 180, 186, 188, 196, 204, 206, 215, 218, 221, 235, 241, 244, 264, 269, 277, 278, 281, 292, 293, 299, 303, 311, 314, 315, 333, 337, 340, 342, 343, 345, 346, 352-354, 373-375, 381, 397-399, 402, 409, 433, 437-439, 473, 475, 485, 488, 493, 512, 513, 516, 517, 522, 523, 532, 533, 535, 541, 542, 547, 554, 558, 562, 577, 580, 586-588, 595, 600, 636, 642, 646, 648, 649, 651, 659, 661, 670, 678, 685, 687, 719, 720, 751, 752, 758, 761, 770, 776, 779, 782, 790, 794, 797, 804, 806, 808, 811, 823, 833, 834, 843, 856-858, 860, 863, 865, 866, 871, 882, 885, 886, 889, 901, 906, 909, 911, 918, 932, 936, 937, 950, 952, 956, 961-963, 981, 983, 986, 995, 1012, 1024, 1026, 1030, 1035, 1038, 1045, 1051, 1052, 1056, 1058, 1063, 1065, 1066, 1070, 1080, 1081, 1086, 1091, 1098-1100, 1112, 1113, 1124, 1125, 1132, 1135, 1138, 1139, 1146, 1148, 1155, 1160,
1168, 1172-1175, 1187, 1190, 1197, 1201, 1207, 1225, 1233, 1235-1237, 1245, 1250, 1255, 1257, 1270, 1280, 1289, 1291, 1294, 1296, 1301, 1320, 1324, 1327, 1329, 1331, 1337, 1348,

1352, 1365-1367, 1370, 1374, 1376-1378, 1388, 1390, 1397, 1402, 1414, 1427, 1428, 1437, 1439, 1444, 1448, 1449, 1458, 1477, 1483, 1484, 1488, 1504, 1505, 1508, 1519, 1521, 1546, 1549, 1550, 1577, 1585-1587, 1593, 1600, 1634, 1637, 1642, 1651, 1653, 1654, 1663, 1666, 1668, 1670, 1672, 1691, 1693, 1701, 1706, 1710, 1726, 1730, 1749, 1754, 1755, 1765, 1768, 1785, 1787, 1795-1797, 1806, 1807, 1810, 1813, 1817, 1821, 1831, 1833, 1835, 1836, 1838, 1841, 1842, 1847, 1848, 1850-1853, 1856, 1857, 1862, 1863, 1866, 1884, 1892, 1899, 1902, 1909, 1924, 1931, 1932, 1934, 1935, 1939, 1943, 1945, 1961, 1966, 1985, 1986, 1988, 1993, 2004, 2006, 2010, 2013, 2017, 2040, 2049, 2051, 2055, 2056, 2068, 2071, 2093, 2095, 2101, 2114, 2116, 2120, 2126, 2130, 2139, 2143, 2150, 2155, 2168, 2177, 2191, 2202, 2205, 2210, 2211, 2218, 2219, 2229, 2231, 2250, 22
5, 2437, 2453, 2469, 2470, 2476, 2477, 2480, 2481, 2488, 2496, 2501, 2512, 2518, 2530, 2531, 2534, 2542, 2543, 2548, 2550, 2563, 2567, 2569, 2582, 2583, 2590, 2597, 2613, 2627, 2631, 2637, 2645, 2650, 2661, 2681, 2683, 2690, 2693, 2695, 2697, 2703, 2705, 2706, 2712
ATMOSPHERIC CO2 CONCENTRATION 163, 179, 582, 697, 725, 800, 892, 1023, 1204, 1459, 1664, 1786, 1927, 1964, 2313
ATMOSPHERIC CO2 CONCENTRATIONS 167, 1371, 1436, 1538, 1580, 1633, 1781, 1846, 1937, 1938, 1983, 2353, 2526
ATMOSPHERIC CO2 ENRICHMENT 16, 31, 32, 229, 476, 724, 731, 744, 796, 879, 881, 884, 929, 930, 964, 972, 992, 1042, 1082, 1192, 1211, 1268, 1269, 1400, 1435, 1457, 1632, 1712, 1752, 1792, 1894, 1897, 1936, 1947, 2048, 2087, 2149, 2157, 2160, 2201, 2248, 2275, 2316, 2478, 2486, 2540, 2616, 2639, 2643
ATMOSPHERIC DEPOSITION 859
ATMOSPHERIC METHANE 252, 503, 1991, 2161
ATMOSPHERIC METHANE CONSUMPTION 38
ATMOSPHERIC NITROGEN 1060, 2640
ATMOSPHERIC OZONE 304
ATMOSPHERIC PARTIAL-PRESSURE 1829, 2028, 2183
ATMOSPHERIC SULFUR 1118
ATMOSPHERIC WATER-VAPOR 1648
ATTACHMENT 1213
ATTRIBUTES 531
AUCHENORRHYNCHA 2577
AUREA MUTANT 874
AUSTRALIA 116, 2262, 2554
AUSTRALIAN MANGROVE FOREST 117
AUTOTROPHY 1427
AUTUMN 695
AUTUMN OLIVE 2486
AVAILABILITY 132, 150, 256, 399, 438, 516, 538, 688, 689, 927, 986, 1143, 1165, 1225, 1226, 1413, 1642, 1662, 1752, 1853, 1860, 1863, 1879, 1896, 2054
AVHRR DATA 1438
AVICENNIA-MARINA 116, 117, 642, 663
AVOCADO FRUIT 524
AVOIDANCE 2355
AZOSPIRILLUM- BRASILENSE 600

BACILLUS-CEREUS 850
BACTERIA 962, 1991, 2161
BACTERIAL-POPULATIONS 1577, 1578
BACTERIAL PRODUCTIVITY 2554
BACTERIOPLANKTON 799
BALANCE 494, 498, 542, 586, 838, 896, 911, 926, 1039, 1040, 1060, 1094, 1102, 1322, 1377, 1525, 1575, 1734, 1737, 1766, 1812, 1850, 1860, 2075, 2142, 2184, 2226, 2570, 2659
BARLEY 117, 132, 135, 149, 454, 457, 802, 1670, 2231, 2349, 2350
BARLEY HORDEUM-VULGARE 980
BARLEY LEAVES 1728
BARLEY PRIMARY LEAVES 2293
BARLEY YELLOW DWARF 1437
BARORECEPTOR 2267
BARROW 429
BARTLETT PEARS 1470
BASE-LINE ANALYSIS 993
BASE TEMPERATURE 2228
BASIC DEVELOPMENT RATE 2229
BEAN-LEAVES 1504, 1989
BEAN-PLANTS 36, 1591, 2345
BEAVER-DAM DEPOSIT 1199
BEECH 771
BEECH FAGUS- SYLVATICA 2134
BEECH STANDS 811
BEETLE EPILACHNA- VARIVESTIS 880
BEHAVIOR 206, 920, 2312
BELOWGROUND BIOMASS 2575
BELOWGROUND RESPONSES 2348
BENTHIC PLANTS 1992
BETA-AMYLASE 2233
BETAINE 1566
BETA-PINENE 426
BETULA 656
BETULA- PAPYRIFERA 2348
BETULA-PENDULA 770
BETULA-PENDULA ROTH 15, 174, 343, 350, 440, 445, 478, 519, 565, 621, 895, 1196, 1200, 1496, 1630, 1829, 2134, 2285, 2326, 2379, 2380, 2442, 2517
BETULA-PUBESCENS EHRH 535
BICARBONATE 1421, 1422, 2295, 2430
BICOLOR 606
BINDING 2464
BINDING PROTEIN 1473
BIOCHEMICAL-MODEL 774, 775
BIOCHEMISTRY 82, 228, 278, 450, 1149
BIOCIDAL TREATMENTS 528, 2039, 2040, 2671

BIOCULATA 742
BIODEGRADATION 902
BIODIVERSITY 201, 532, 1640, 2277, 2674
BIOGENIC EMISSIONS 426
BIOGEOCHEMISTRY 1783
BIOLOGICAL-CONTROL 2262
BIOLOGICAL INVASION 904
BIOMASS 15, 65, 79, 126, 277, 490, 506, 528, 550, 551, 623, 673, 708, 740, 798, 799, 836, 848, 925, 933, 1029, 1113, 1122, 1163, 1297, 1370, 1414, 1455, 1652, 1686, 1690, 1691, 1704, 1723, 1730, 1745, 1855, 1928, 1937, 1946, 1960, 1985, 2000, 2057, 2065, 2151, 2244, 2281, 2347, 2354, 2547, 2653, 2672, 2705
BIOMASS ALLOCATION 343, 648, 697, 950, 1044, 1747, 1974, 2055, 2089, 2370, 2375, 2384, 2620
BIOMASS-C 1908, 2160
BIOMASS CARBON 437, 1651
BIOMASS DISTRIBUTION 753
BIOMASS DYNAMICS 972
BIOMASS PRODUCTION 401, 403, 670, 843, 965, 1715, 1732, 1831, 1859, 1994, 2673
BIOMES 1195
BIOPHYSICS 717
BIOSPHERE 736, 738, 749, 837, 1162, 1349, 1639, 1885, 1922, 2139, 2150, 2244, 2328, 2433, 2449, 2570
BIOSPHERE EXCHANGE 2639
BIOSPHERE-MODEL 697, 1151, 1805
BIOSYNTHESIS 158, 258, 524, 704, 939, 940, 989, 1622, 1990, 2251, 2489, 2589
BIRCH 1814, 1816, 1860, 2045, 2215
BIRCH BETULA 1362, 1491
BIRCH LEAVES 2132
BIRCH SEEDLINGS 15, 621, 1025
BIRDSFOOT-TREFOIL 2250
BISPHOSPHATE 1823, 2576
BISPHOSPHATE CARBOXYLASE ACTIVITY 741
BISPHOSPHATE CARBOXYLASE OXYGENASE 109, 1245, 1545, 1616, 1959
BLACK ALDER 2486
BLACK LOCUST 2427
BLACK SPRUCE 773
BLACK SPRUCE SEEDLINGS 314, 350, 759, 929, 930
BLOOD-FLOW 232
BLOOM 2633
BLUE 2092
BLUEBERRY 1089
BLUEBERRY FRUIT 158, 2660
BLUE-GRAMA 972
BLUE GREEN ALGA 805, 2410
BLUE-GREEN PHYCOBIONTS 2246

BLUE-LIGHT 2312
BLUESTEM 1766
BOMB-PRODUCED C-14 852
BONG CARR 345
BOREAL FOREST 1175, 1322, 1659
BOREAL FOREST ECOSYSTEMS 1553, 1921
BOREAL FORESTS 832, 2192, 2197, 2526, 2551
BOREAL VEGETATION 165, 186
BORYA-NITIDA LABILL 2411
BOUNDARY-CONDITIONS 463
BOUNDARY-LAYER 2310, 2588, 2605
BOUTELOUA-GRACILIS 16, 530, 843, 931, 972, 1029, 1185, 1743, 1938, 1994, 1997, 2053, 2091, 2256-2258, 2260, 2261
BOUTELOUA-GRACILIS C-4 952, 1301, 2510
BP 1483
BRACKEN 2573
B RADIATION 304, 672, 1234, 1745, 1752, 1927, 2048, 2062
BRANCH BAG 349, 595, 793, 1011, 1209, 1367, 1634
BRASSICA 1878
BRASSICA-CAMPESTRIS L 1166
BRASSICA-NAPUS L 487, 1616-1618
BRAZIL 1475
BREAKDOWN 447, 2658
BRECKLAND 668
BREVICORYNE-BRASSICAE 219
BREVIFOLIA 986
BRITAIN 302
BRITISH BUTTERFLY FAUNA 313
BRITISH-ISLES 979
BROADLEAF WEEDS 1791
BROCCOLI 158
BROOKS-RANGE 1735, 1736
BROWN RUST 912
BUDBURST 59, 180, 301, 821, 847, 1302, 1972, 2305
BUDGET 498, 551, 736, 857, 964, 1195, 2152, 2328
BUNCHGRASS SCHIZACHYRIUM-SCOPARIUM 2686
BUNDLE-SHEATH 598
BUNDLE SHEATH-CELLS 370, 1393, 2510, 2706
BURN AGRICULTURE 1526
BURST 1746
BUSH PLANT- RESPONSE 1007
BUTTERFLIES 1261
C-13 272, 1924, 2479
C 13/C 12 204, 582
C-13/C-12 RATIO 163, 1924, 2469

C-13/C-12 RATIOS 164
C-13 NATURAL ABUNDANCE 1265, 1698, 2157
C-14-LABELED RYEGRASS 1062
C2H4 PRODUCTION 1472
C-3 7, 70, 72, 75, 77, 93, 278, 295, 411, 418, 545, 741, 923, 960, 984, 1050, 1065, 1085, 1315, 1515, 1565, 1569, 1653, 1672, 1765, 1770, 1954, 1984, 2055, 2102, 2263, 2269, 2330, 2368, 2425, 2426, 2464, 2516, 2626, 2645, 2695, 2702, 2708, 2709
C-3 BROMELIADS 52
C3-C4 2331
C-3 PHOTOSYNTHESIS 480
C-3 PHOTOSYNTHETIC SYSTEM 1146
C-3 PLANTS 42, 43, 164, 165, 185, 425, 489, 638, 743, 783, 792, 815, 851, 924, 937, 1043, 1132, 1178, 1236, 1329, 1369, 1400, 1406, 1429, 1431, 1433, 1516, 1538, 1637, 1646, 1681, 1682, 1796, 1803, 1824, 1835, 1868, 2001, 2022, 2099, 2124, 2205, 2219, 2222, 2276, 2412, 2414, 2581, 2607, 2638, 2710
C-4 370, 572, 1458, 2512
C-4 ANNUALS 449, 450, 922, 2530, 2531
C-4 GRASS 401, 843, 1190, 1284, 1767, 1768, 1849, 1859, 2400, 2555, 2600
C-4 GRASSES 956, 2602
C-4 PHOTOSYNTHESIS 598, 1381, 2217, 2331
C-4 PLANTS 166, 281, 283, 312, 409, 971, 1380, 1393, 1498, 1514, 2063, 2508, 2613
CA 570
CA-2 2544
CACAO SEEDLINGS 2388
CACTACEAE 1701, 1702
CACTOBLASTIS-CACTORUM 448
CACTUS 1702, 1705
CADDISFLY POPULATION 329
CALAMOVILFA-LONGIFOLIA 1822
CALCAREOUS GRASSLAND 67, 533
CALCIFICATION 1679
CALCIUM 206, 701, 1330, 1657
CALCIUM-OXALATE 505
CALCIUM-OXALATE CRYSTALS 1901
CALIBRATION 1438, 2672
CALIFORNIA 780, 1694
CALLUS LINES 2216
CALVIN-CYCLE 907, 2209
CALVIN CYCLE ENZYMES 148, 212, 1222, 1223, 1508, 1796, 2274, 2275, 2456, 2458-2460, 2545 CAM 480, 2612, 2687
CAMPANULA-ISOPHYLLA MORETTI 1217
CAM PLANT 572, 573
CANADA 191, 268, 488, 1198
CANADIAN CORDILLERA 1199
CANOPIES 204, 1093

CANOPY 7, 43, 110, 210, 216, 228, 241, 632, 1048, 1369, 1399, 1543, 1553, 2177, 2249, 2337
CANOPY DIEBACK 1613
CANOPY LEAF-AREA 2189
CANOPY PHOTOSYNTHESIS 100, 442, 562, 774, 775, 842, 892, 1131, 1517, 1666, 1682, 1859, 1861, 1868, 1949, 2058, 2310, 2695, 2697, 2698
CANOPY REFLECTANCE 1840
CANOPY RESISTANCE 496
CANOPY STRUCTURE 382, 1974, 2588
CANTALOUPE 989
CAPABILITY 1471
CAPACITY 4, 468, 489, 715, 783, 1389, 1991, 2106
CAPTURE 2675
CARBAMYLATION 878, 2021, 2576
CARBOHYDRATE 356, 420, 635, 636, 704, 1243, 1278, 1439, 1458, 1509, 1968, 2022, 2023, 2176, 2199, 2206, 2578
CARBOHYDRATE ACCUMULATION 1331, 1778
CARBOHYDRATE-COMPOSITION 1437
CARBOHYDRATE CONTENT 74, 148, 643, 679, 1207, 1865, 2028, 2290, 2343, 2680
CARBOHYDRATE-METABOLISM 1536
CARBOHYDRATE STATUS 86, 752, 1020, 1558, 2649
CARBON 15, 109, 118, 192, 196, 227, 264, 301, 324, 343, 371, 427, 447, 465, 491, 553, 600, 638, 645, 799, 836, 837, 859, 862, 888, 913, 971, 1015, 1057, 1068, 1125, 1188, 1194, 1296, 1332, 1388, 1397, 1401, 1402, 1462, 1513, 1537, 1627, 1693, 1723, 1730, 1785, 1789, 1864, 1908, 1987, 1996, 2022, 2079, 2104, 2178, 2179, 2221, 2225, 2277, 2416, 2611, 2643, 2652, 2674, 2675, 2680, 2681
CARBON ALLOCATION 1290, 2638
CARBON ASSIMILATION 88, 675, 731, 1259, 1579, 2220
CARBON BALANCE 186, 341, 539, 868, 1399, 1464, 2140, 2222, 2279, 2304
CARBON BUDGET 1928, 2604
CARBON CATABOLITE REPRESSION 1573
CARBON CONTENT 718
CARBON-CYCLE 26, 57, 2354
CARBON DIOXIDE 11, 16, 21, 29, 36, 41, 42, 45, 46, 61, 64, 65, 70, 75, 77, 80, 82, 89, 93, 97, 107, 110, 116, 117, 120, 121, 123, 126, 128, 132, 134, 136, 142, 143, 145, 159, 160, 162, 169, 173, 180, 183, 194, 201, 213, 215, 219, 234, 235, 246, 250, 251, 257, 259, 269, 270, 282, 295, 297, 312, 327, 330, 333, 337, 340, 346, 349, 352, 353, 357, 360, 366, 369, 373, 374, 378, 381, 382, 385, 391, 397, 403, 418, 420, 421, 426, 429, 433, 437-439, 441-443, 445, 450, 456, 470, 475, 479, 483, 490, 493, 494, 496-498, 505, 509, 511, 512, 522, 523, 533, 535, 542, 545, 547, 555, 558, 561, 572, 579, 581, 588, 589, 593, 595, 602, 603, 610, 618, 635-637, 639, 641, 642, 655-657, 667, 679, 687-689, 698, 702, 714, 720, 722, 730, 733, 745-747, 754, 761, 763, 767, 770-772, 779, 781, 790, 794, 803, 810, 816, 833, 838, 842, 845, 850, 851, 856, 860, 861, 863, 865-867, 886, 887, 896, 902, 909, 912, 915, 921, 925, 933, 937, 941, 942, 944, 946, 950, 959-961, 966, 968, 972, 974, 977, 987, 994, 1004, 1006, 100
8, 1009, 1011, 1013, 1014, 1017, 1018, 1026, 1035, 1038, 1045, 1046, 1052, 1056, 1058, 1060, 1067, 1069, 1077, 1079, 1081, 1083, 1092, 1096, 1100, 1104, 1106, 1107, 1111, 1112, 1116,

1124, 1129, 1130, 1132, 1133, 1137, 1139, 1144, 1148, 1153, 1154, 1156-1160, 1167, 1173, 1176, 1177, 1180, 1182-1185, 1189, 1190, 1192, 1193, 1197, 1201, 1206, 1207, 1211, 1225, 1230, 1235, 1236, 1238, 1245, 1250, 1251, 1260, 1263, 1264, 1270, 1271, 1277, 1280, 1284, 1285, 1287, 1294, 1297, 1301, 1305, 1329-1331, 1336, 1342-1345, 1348, 1350, 1352, 1365-1367, 1370, 1375, 1389, 1390, 1392, 1395, 1396, 1406, 1410, 1411, 1416, 1422, 1435, 1440-1442, 1445, 1449, 1450, 1452, 1466, 1467, 1477, 1503, 1504, 1507, 1508, 1511, 1517, 1519, 1521, 1531, 1535, 1539-1542, 1548, 1557, 1558, 1572, 1576, 1577, 1582, 1604-1606, 1612, 1614, 1616-1618, 1628, 1630, 1635, 1642, 1650, 1651, 1660-1662, 1666, 1668, 1670, 1672, 1676, 1680, 1681, 1683, 1686, 1688, 1690, 1691, 1706, 1712, 1719, 1734-1736, 1740, 1749, 1754, 1764, 1
766-1768, 1778, 1779, 1781, 1797, 1800, 1811, 1815, 1831, 1833, 1839, 1868, 1871, 1876, 1883, 1895, 1896, 1904, 1906, 1912, 1931, 1933, 1944, 1945, 1951, 1953, 1961, 1962, 1969, 1974, 1976, 1980, 1984, 1985, 1989, 1994, 1998, 2001, 2002, 2006, 2007, 2009, 2011, 2013, 2014, 2017, 2019-2021, 2026, 2030, 2034, 2042, 2046, 2053, 2055, 2056, 2063, 2068, 2071, 2080, 2081, 2088, 2089, 2093-2096, 2112, 2114, 2116, 2121-2124, 2127, 2133, 2135, 2141, 2145, 2146, 2150, 2155, 2159, 2161, 2162, 2166, 2175-2177, 2180, 2181, 2183, 2184, 2191, 2196, 2208, 2214, 2219, 2224, 2226, 2230, 2234, 2242, 2246, 2248, 2253, 2254, 2263, 2267, 2271-2273, 2303, 2307, 2308, 2310, 2312, 2324-2326, 2328, 2329, 2332, 2339, 2350, 2351, 2355, 2359, 2365, 2366, 2374, 2375, 2386, 2388, 2391, 2397, 2403, 2405, 2408, 2412, 2417, 2419, 2427, 2435, 2436, 2440, 2451-
2453, 2463, 2476, 2478, 2484, 2485, 2487, 2512, 2514, 2515, 2517, 2518, 2520, 2530, 2533, 2534, 2538, 2541-2543, 2561, 2564, 2565, 2567, 2589, 2591, 2597, 2601, 2609, 2610, 2612, 2613, 2615-2619, 2625, 2628, 2629, 2631-2633, 2651, 2654, 2659, 2661, 2672, 2673, 2679, 2683, 2689, 2691, 2692, 2707, 2709, 2710, 2712
CARBON-DIOXIDE ATMOSPHERES 73, 217, 313, 410, 413, 584, 629, 958, 1114, 1119, 1266, 1283, 1354, 2398, 2404, 2595, 2596
CARBON-DIOXIDE CO2 2438, 2439
CARBON-DIOXIDE CONCENTRATION 85, 91, 100, 104, 113, 114, 133, 254, 255, 399, 402, 425, 502, 564, 586, 650, 651, 795, 834, 889, 897, 923, 928, 943, 981, 984, 1050, 1085, 1243, 1324, 1326, 1362, 1587, 1588, 1600, 1602, 1677, 1685, 1687, 1718, 1745, 1829, 1850-1852, 2054, 2061, 2082, 2117, 2204, 2218, 2249, 2297, 2338, 2348, 2400, 2401, 2413, 2420, 2454, 2459, 2519, 2669, 2698
CARBON-DIOXIDE CONCENTRATIONS 32, 253, 300, 401, 752, 1484, 1591, 2164, 2458, 2510
CARBON-DIOXIDE EFFLUX 751, 1191, 1761, 2693, 2694
CARBON-DIOXIDE ENRICHMENT 2, 7, 30, 51, 53, 67, 71, 74, 86, 144, 205, 209, 222, 256, 347, 350, 393, 492, 516, 562, 563, 565, 580, 587, 608, 626, 715, 776, 786, 815, 823, 963, 991, 1012, 1043, 1044, 1055, 1078, 1146, 1155, 1200, 1278, 1314, 1327, 1372, 1376, 1425, 1429, 1439, 1468, 1476, 1543, 1585, 1590, 1620, 1636, 1654, 1755, 1763, 1810, 1836, 1862, 1863, 1866, 1870, 1872, 1899, 1900, 1902, 1910, 1935, 1943, 1983, 2010, 2028, 2029, 2057, 2064, 2070, 2130, 2137, 2200, 2223, 2228, 2229, 2231, 2290, 2346, 2379, 2496, 2501-2506, 2531, 2547, 2582, 2594, 2600, 2648, 2649, 2685
CARBON-DIOXIDE EVOLUTION 1921, 2491, 2492
CARBON-DIOXIDE EXCHANGE 1275, 1276, 1309, 2557
CARBON-DIOXIDE FIXATION 2630

CARBON-DIOXIDE FLUX 605
CARBON DYNAMICS 832
CARBON FIXATION 2047, 2399
CARBON FLOW 1574, 1932
CARBON FLUXES 487
CARBON GAIN 871, 924, 1131, 1237, 1553, 2106, 2588
CARBONIC-ANHYDRASE 247, 248, 676, 806, 1381, 1823, 2545, 2606
CARBONIC-ANHYDRASE ACTIVITY 2295
CARBON INCORPORATION 1358
CARBON ISOTOPE DISCRIMINATION 108, 163, 164, 168, 178, 179, 185, 204, 273, 449, 451, 582, 597, 1459, 1835, 2132, 2316,
2477, 2626
CARBON-ISOTOPE FRACTIONATION 956
CARBON ISOTOPES 170
CARBON ISOTOPIC COMPOSITION 191
CARBON METABOLISM 387, 599, 935, 1584, 1793, 2209, 2298, 2607
CARBON-MONOXIDE 1475
CARBON NUTRIENT BALANCE 223, 495, 660, 743, 1090, 1103, 1168, 1361, 1363, 1444, 1491, 1813, 1901, 2043-2045, 2285, 2381
CARBON RELATIONS 2189
CARBON-SOURCE UTILIZATION 782
CARBON STORAGE 904, 1195
CARBOXYLASE 34, 106, 205, 255, 368, 415, 589, 681, 730, 806, 830, 1058, 1065, 1178, 1460, 1579, 1600, 1797, 2195, 2203, 2205, 2234, 2263, 2295, 2345, 2489, 2501, 2581, 2684, 2694, 2706, 2710
CARBOXYLASE ACTIVITY 244, 430, 2191, 2278, 2420
CARBOXYLASE-OXYGENASE 119, 246, 312, 502, 545, 598, 774, 1365, 1515, 1538, 2032, 2545, 2695
CARBOXYLASE OXYGENASE ACTIVITY 1963
CARBOXYLASE OXYGENASE CONTENT 1823
CARBOXYLASE SMALL-SUBUNIT 1573
CARBOXYSOME 2032
CARIBBEAN REGION 642
CAROTENOID COMPOSITION 1276
CAROTENOIDS 935
CARPENTARIA 2554
CARROT 396, 788, 1800
CASE-STUDY BFTCS 1806
CASSIA-FASCICULATA 641
CASTANEA-SATIVA 2388
CASTANEA-SATIVA MILL 350, 352, 438, 447, 478, 824, 931, 1496, 1558, 1607, 1630, 2396, 2480, 2482
CATALASE 2339
CATALYSIS 55
CATCHMENT 2593

CATERPILLARS 1363
CAULERPALES 706
CAVENDISH SUBGROUP 2136
CAVITATION 81, 2385
CDNA CLONE 2459
CELERY LEAVES 1574
CELL 280, 1070, 1923
CELL-CULTURES 2216
CELL-GROWTH 650
CELLS 161, 364, 373, 466, 655, 1020, 1255, 1256, 1274, 1310, 2001, 2171
CELL-SURFACE 40
CELL-SUSPENSION CULTURES 11, 231
CELLULAR MECHANISMS 461, 467
CELLULASE 2251
CELLULASE ACTIVITY 1577
CELLULOSE 646
CELL-WALL 1222
CELL-WALL POLYSACCHARIDES 2251
CELL-WALLS 22, 249
CELSS 1453
CENTERS 128
CENTRAL CANADA 1806
CENTRAL EUROPEAN HEDGEROW 2189
CENTRAL GREENLAND ICE 503
CENTRAL OREGON 2248
CENTURIES 102, 170, 171, 176, 582
CERATONIA-SILIQUA 467
CEREALS 465, 1615
CERES 2038
CHALKBROOD 748
CHALK GRASSLAND 1296, 2279, 2281, 2477
CHALK GRASSLANDS 670
CHAMBER 1380, 1768
CHAMBERS 31, 78, 879, 882, 883, 958, 1157, 1549, 1920, 2065, 2491, 2496, 2577
CHANGE IMPACTS 2297
CHANGING CLIMATE 1127
CHELEX-100 RESIN 1244
CHEMICAL-COMPOSITION 433, 533, 564, 624, 974, 1090, 2157, 2640
CHEMICAL DEFENSE 224, 631, 1266, 1353, 1362, 2043
CHEMISTRY 1168, 1360
CHENOPODIUM-ALBUM L 150, 409, 1496, 1498, 1829, 2099, 2101, 2330, 2635
CHENOPODIUM-RUBRUM 947, 2233
CHESAPEAKE BAY 892
CHIHUAHUAN DESERT 1138
CHILLING INJURY 1472, 2298, 2607

CHILLING REQUIREMENT 59
CHLAMYDOMONAS-REINHARDTII 248, 364, 365, 750, 1339, 1428, 2295, 2545, 2598, 2599
CHLAMYDOMONAS-SEGNIS 2154
CHLORELLA 109, 1823
CHLORELLA-SACCHAROPHILA 1071
CHLOROFORM 2040
CHLOROFORM FUMIGATION 2522
CHLOROPHYCEAE 706
CHLOROPHYLL 182, 618, 1178, 2201, 2368, 2489, 2535, 2569, 2656
CHLOROPHYLL-A FLUORESCENCE 1339, 1697, 2090
CHLOROPHYLL CONTENT 71, 73, 332, 796, 881, 1223, 1289, 1636, 2199, 2414
CHLOROPHYLL FLUORESCENCE 63, 92, 109, 128, 285, 312, 374, 486, 617, 639, 640, 675, 677, 731, 750, 766, 770, 829, 830, 869, 891, 930, 935, 1041, 1106, 1133, 1166, 1275, 1379-1381, 1385, 1449, 1562, 1728, 1826, 1872, 1959, 2013-2015, 2135, 2200, 2246, 2253, 2298, 2607
CHLOROPHYLL FLUORESCENCE- KINETICS 1545
CHLOROPHYLL METER 12, 1955
CHLOROPHYLLS 2411
CHLOROPHYLL SYNTHESIS 1255, 1256
CHLOROPHYTA 108
CHLOROPLAST 247, 599, 891, 1612
CHLOROPLAST GENE 2606
CHLOROPLAST GENOME 2576
CHLOROPLAST PROTEIN 486, 2103
CHLOROPLASTS 285, 499, 1020, 1314, 1562, 1584, 1826, 1843, 2296, 2464, 2468
CHLORORESPIRATION 364, 365
CHLOROSIS 1847, 2201
CHOLINE 1566
CHONDRUS-CRISPUS 705
CHROMATOGRAPHY 2076
CHRONIC OZONE 1617, 1745, 2067
CHRONOLOGIES 865, 867
CHRONOLOGY 488
CHRYSANTHEMUM-MORIFOLIUM RAMAT 2318, 2448
CHRYSOGENUM 1500
CHRYSOMELIDAE 1290
CHRYSOMELID BEETLE 1798
CICADELLIDAE 271
CI CELLS 2295, 2296
CIRCULATION 488, 1212, 2267
CITRIC-ACID 487
CITRUS RED MITE 1200
CITY 2310
CLADODE DEVELOPMENT 2612
CLASSIFICATION 531, 1039

CL CONCENTRATIONS 1670
CLEAR-CUT 536, 1397
CLIMATE 15, 45, 138, 167, 173, 178, 234, 245, 407, 416, 417, 453, 494, 498, 506, 541, 581, 606, 627, 629, 633, 668, 696, 700, 708, 736, 740, 840, 865, 949, 952, 1192, 1193, 1251, 1309, 1346, 1462, 1492, 1513, 1884, 1928, 1931, 1946, 1948, 1984, 2015, 2075, 2130, 2140, 2158, 2192, 2196, 2332, 2389, 2419, 2451, 2496, 2500, 2556, 2634, 2636
CLIMATE CHANGE 107, 111, 162, 166, 179, 186, 217-219, 312, 314, 388, 389, 442, 448, 449, 491, 527, 550, 634, 642, 644, 702, 793, 794, 868, 871, 926, 936, 950, 971, 1085, 1092, 1094, 1122, 1135, 1152, 1174, 1175, 1183, 1194, 1203, 1212, 1280, 1293, 1403, 1407, 1416, 1418, 1499, 1501, 1512, 1515, 1528, 1534, 1540, 1558, 1571, 1576, 1578, 1672, 1711, 1732, 1735, 1736, 1743, 1747, 1779, 1783, 1787, 1821, 1827, 1849, 1874, 1878, 1885, 1958, 1964, 2009, 2036, 2038, 2072, 2074, 2100, 2145, 2148, 2165, 2168, 2239, 2256, 2258, 2260, 2261, 2303, 2322, 2353, 2356, 2417, 2418, 2445, 2477, 2483, 2485, 2486, 2508, 2526, 2533, 2577, 2592, 2622, 2638, 2672, 2676
CLIMATE-CHANGE SCENARIOS 905, 1151
CLIMATE MODEL 684
CLIMATE SENSITIVITY 100, 103, 104, 1945, 2061
CLIMATE VARIABILITY 757, 1877
CLIMATIC CHANGE 870, 1086, 1139, 1161, 1311, 1450, 1833, 1921, 2024, 2088, 2107, 2449, 2586, 2616
CLIMATIC CONTROL 1859
CLIMATIC IMPACTS 983
CLIMATIC VARIABILITY 657, 658
CLONAL VARIATION 895, 1444
CLONES 249, 349, 352, 1112
CLONING 1395
CLOUD CONDENSATION NUCLEI 1841
CLOVER 1076, 1601, 2678
CLOVER TRIFOLIUM-REPENS 71, 440, 670, 1664, 1692, 1760, 2250, 2639
CLUTCH-SIZE 473
CO2 18, 26, 29, 40, 54, 79, 131, 184, 190, 194, 210, 223, 224, 226, 231, 245, 263, 274, 276, 284, 286, 295, 301, 324, 366, 454, 457, 591, 633, 664, 684, 756, 757, 828, 831, 832, 838, 841, 849, 850, 854, 883, 890, 901, 926, 939, 949, 978, 994, 1027, 1034, 1037, 1067, 1071, 1089, 1094, 1096, 1120, 1140, 1191, 1227, 1232, 1239, 1241, 1254, 1263, 1264, 1274, 1277, 1292, 1302, 1304, 1311, 1313, 1357, 1382, 1394, 1396, 1421, 1424, 1434, 1450, 1453, 1462, 1497, 1500, 1502, 1534, 1565, 1598, 1639, 1640, 1658, 1659, 1684, 1688, 1702, 1705, 1708, 1744, 1756, 1758, 1769, 1770, 1774, 1777, 1800, 1812, 1816, 1825, 1840, 1875, 1878, 1885, 1887, 1925, 1948, 1999, 2005, 2026, 2030, 2043, 2052, 2059, 2065, 2074, 2077, 2078, 2110, 2132, 2133, 2148, 2152, 2156, 2158, 2174, 2192, 2194, 2215, 2226, 2240, 2247, 2255, 2264, 2269, 2282, 2283, 2286, 2287, 2321, 2360, 2392, 2402, 2416, 2465, 2474, 2490, 2500, 2513, 2544, 2557, 2559, 2560, 2568, 2572, 2628, 2640, 2653, 2656, 2660, 2664, 2676, 2678, 2702
CO2 ASSIMILATION 281, 590, 677, 1545, 1697, 1728, 2124, 2588
(CO2) C 14 500
CO2 CONCENTRATING MECHANISM 2031
CO2 CONCENTRATION 96, 287, 357, 473, 485, 550, 738, 853, 1022, 1093, 1437, 1498, 1543,

1562, 1713, 1720, 1823, 1828, 2199, 2357, 2477, 2587, 2590-2592, 2598
CO2 CONCENTRATIONS 111, 178, 526, 749, 809, 844, 871, 1460, 1516, 1665, 2118, 2442, 2605
CO2-DEPENDENT PHOTOSYNTHESIS 2599
CO2 DIFFUSION 676
CO2 ELEVATION 924
CO2 EMISSIONS 855
CO2- ENRICHED AIR 2655
CO2-ENRICHED ATMOSPHERE 253, 1291, 1862, 2639
CO2-ENRICHED ATMOSPHERES 823, 1150, 1470, 2379
CO2- ENRICHMENT 19, 41, 74, 103, 105, 129, 145, 147, 150, 154, 185, 193, 222, 238, 254, 266, 282, 290, 294, 316, 317, 320, 359, 385, 386, 400, 406, 437, 467, 470, 472, 531, 534, 559, 566, 574, 606, 643, 665, 668, 673, 674, 686, 765, 773, 787, 789, 801, 812, 877, 905, 919, 920, 927, 938, 943, 966, 969, 973, 974, 996, 1006, 1054, 1066, 1078, 1099, 1100, 1134, 1135, 1180, 1215, 1248, 1267, 1288, 1289, 1338, 1383, 1398, 1416, 1481, 1493-1496, 1527, 1531, 1532, 1564, 1596, 1597, 1608, 1615, 1628, 1657, 1663, 1682, 1711, 1719, 1743, 1748, 1750, 1782, 1820, 1848, 1857, 1871, 1873, 1889, 1909, 1911, 1912, 1929, 1955, 1966, 1967, 1989, 2062, 2073, 2138, 2140, 2144, 2170, 2176, 2188, 2193, 2217, 2223, 2224, 2228, 2243, 2252, 2257, 2259, 2304, 2315, 2318, 2343, 2344, 2349, 2390, 2406, 2428, 2443, 2446, 2449, 2473, 2553, 2556, 2563, 2665, 2679, 2696, 2699, 2700, 2704, 2708
CO2 ENVIRONMENTS 1970, 2594
CO2 EVOLUTION 1081
CO2 EXCHANGE 1275, 1317, 1729, 1818, 1958, 2190, 2489, 2575, 2614
CO2 EXPOSURE 2185
CO2 FIXATION 2209, 2298
CO2 FLUXES 1575
CO2-INDUCED CLIMATE CHANGE 6, 16, 241, 361, 551, 1357, 1875, 2197, 2264, 2313, 2551
CO2-INDUCED CLIMATIC-CHANGE 329, 1710
CO2-INDUCED GROWTH ENHANCEMENTS 2134
CO2 LEVELS 903, 1261, 1490
CO2/O2 SPECIFICITY 98, 246, 296, 917, 1868
CO2 REDUCTION 191
CO2 UPTAKE 2687
COASTAL DOUGLAS-FIR 2526
COAT 742
COCCINEUS-L 2447
CO-CULTURE 1566
COEFFICIENTS 1307
COLD-ACCLIMATED SEEDLINGS 1381
COLD HARDINESS 2467
COLD-INDUCED PHOTOINHIBITION 2015
COLD-STORAGE 2169
COLD TOLERANCE 1139, 1141
COLEOPTERA 1290, 2571
COLLEMBOLA 1097, 1182, 2071

COLLETOTRICHUM-GLOEOSPORIOIDES 1903
COLONIZATION 1097, 1117, 1182, 1183, 1185, 1993-1996, 2053, 2054, 2123, 2149, 2257, 2307
COLOR 739
COLORADO 274, 2593
COMBINATION 1967
COMBUSTION 718
COMMELINA-BENGHALENSIS 1393
COMMON ICE PLANT 480
COMMUNITIES 64, 70, 76, 147, 157, 272, 402, 417, 481, 528, 531, 532, 542, 594, 652, 825, 860, 867, 933, 978, 1015, 1029, 1097, 1108, 1204, 1294, 1315, 1356, 1488, 1490, 1565, 1572, 1581, 1665, 1667, 1730, 1740, 1763-1766, 1995, 1998, 1999, 2114, 2412, 2415, 2430, 2651
COMMUNITY 581, 1358, 1652, 2053, 2330, 2534, 2640, 2673
COMMUNITY STRUCTURE 1822, 2304
COMPARATIVE ECOPHYSIOLOGY 52
COMPARTMENTAL ANALYSIS 913
COMPARTMENTATION 280
COMPATIBILITY 993
COMPENSATORY INCREASES 2079
COMPENSATORY RESPONSES 428, 505, 863, 1055, 1326, 2370, 2375
COMPETITION 6, 72, 76, 134, 152, 154, 202, 396, 547, 572, 801, 1069, 1201, 1293, 1477, 1589, 1651, 1666, 1672, 1722, 1879, 1929, 2111, 2160, 2294, 2330, 2346, 2400, 2466, 2540, 2556, 2600, 2626
COMPETITIVE ABILITY 1287
COMPETITIVE INTERACTIONS 1767
COMPLEX 1625, 1697
COMPONENTS 1442, 1611, 1626, 2226
COMPUTATIONS 2313
COMPUTER-AIDED RECONSTRUCTION 1435
COMPUTER-MODEL 1313, 2197
COMPUTER-TOMOGRAPHY 2383, 2384
CONCENTRATING MECHANISM 1446, 1463, 2296
CONDENSED TANNINS 2285
CONDUCTANCE 53, 58, 83, 215, 222, 249, 496, 608, 632, 661, 672, 792, 840, 984, 1056, 1173, 1220, 1284, 1407, 1586, 1717, 1771, 1799, 1855, 2139, 2241, 2255, 2310, 2312, 2489, 2584
CONDUCTIVITY 299
CONIFEROUS FORESTS 836, 1414, 2168, 2653
CONSEQUENCES 272, 432, 581, 722, 1311, 1874
CONSERVATION 855, 2393, 2573
CONSTITUTIVE EXPRESSION 649
CONSTRAINTS 1088
CONSTRUCTION 2376
CONSTRUCTION COST 1558
CONSTRUCTION COSTS 564

CONSUMPTION 252, 1990, 1991
CONTAINERIZED BLACK SPRUCE 2578
CONTAINER SEEDLINGS 1269
CONTINENTAL ANTARCTICA 1139
CONTINENTAL ANTARCTIC CRYPTOGAMS 1276
CONTINENTAL-SCALE 1039
CONTINENTAL WESTERN CANADA 1575
CONTINUOUS CULTIVATION 1265
CONTINUOUS CULTURES 1500
CONTORTA 911
CONTRASTED ECOLOGY 361
CONTRASTING SHADE TOLERANCE 337
CONTROLLED ATMOSPHERES 1470, 1471
CONTROLLED-ATMOSPHERE STORAGE 434
CONTROLLED-ENVIRONMENT CHAMBER 319
CONTROLLED ENVIRONMENTS 2563
CONTROLLED INVITRO ENVIRONMENT 282
CONVERSION 989, 1241
COOCCURRING BIRCH 151, 157, 196, 337, 1236, 1400, 2335, 2396
COOL 2096
COOL-SEASON GRASSES 844
COOL TEMPERATURES 1938
COORDINATE 2606
COPEPODS 1358
CORE 1884
CORN 591, 1335, 1960
CORN CANOPIES 1840
CORN-ROOTWORM COLEOPTERA 448
CORNUS-SERICEA L 847
CORN ZEA-MAYS 1791
COST 325, 540
COSTA-RICA 432, 936, 1957
COTE- DIVOIRE 2668
COTTON 4, 18, 29, 77, 116, 229, 286, 339, 489, 580, 662, 680, 969, 1001, 1029, 1111, 1128, 1155, 1160, 1204, 1208, 1248, 1354, 1377, 1539, 1540, 1683, 1726, 1810, 1851, 1996, 2112, 2184, 2255, 2393, 2547, 2577, 2583, 2627
COTTON GOSSYPIUM- HIRSUTUM 1791, 1792
COTTON LEAVES 2090
COTTON PLANTS 74, 148, 299, 615, 2014
COTTON ROOT 2348
COTYLEDONS 211
COVARIANCE 2045
COVER 605
COWPEA LEAVES 1843
COWPEA VIGNA-UNGUICULATA 1178

CPMAS 945
CRASSULACEAN ACID METABOLISM 52, 470, 767, 1035, 1345, 1382, 1703, 1707, 1721, 1933, 2688
CRATER 1785
CRESTED WHEATGRASS 972
CRISPHEAD LETTUCE 2465
CROP 12, 56, 97, 209, 359, 610, 718, 842, 892, 1595, 2226, 2419, 2446, 2557, 2565, 2650, 2692, 2708
CROPLAND 1335
CROP MANAGEMENT 1940
CROP PHOTOSYNTHESIS 845
CROPPING SYSTEMS 605
CROP PLANTS 91, 102, 1454, 2475
CROP PRODUCTIVITY 2417
CROP RESIDUES 2433
CROP RESPONSE 1485, 2038
CROP RESPONSES 193, 213, 769, 825, 909, 938, 1009, 1010, 1305, 1620, 1661, 1751, 1795, 1810, 1832, 1969, 1989, 2006, 2091, 2412, 2476
CROP ROTATIONS 1894
CROPS 29, 37, 509, 626, 1239, 1241, 1242, 1312, 1555, 1556, 1655, 1656, 1800, 2193, 2287, 2566
CROP TRANSPIRATION 580
CROP YIELD 335, 579, 802, 1012, 1156, 1160, 1172, 1948, 1949, 2067
CROP YIELDS 657, 658
CRUCIFERAE 1114
CRUSGALLI L BEAUV 2217
CRYPTOLESTES-FERRUGINEUS 2571
CRYPTOPYGUS- ANTARCTICUS 1139
C SOURCE UTILIZATION 782
C STORAGE 139, 1174, 1805, 2471
CUCUJIDAE 2571
CUCUMBER 19
CUCUMBER LEAF EXPANSION 2188
CUCUMBERS 1782, 1811
CUCUMBER SEEDLINGS 2333
CUCUMIS-MELO L 280
CUCUMIS-SATIVUS L 487
CUCURBITA-MAXIMA 1469
CUCURBITA-PEPO CUCURBITACEAE 1287
CULTIVAR 105, 1936, 2567
CULTIVAR ENREI 89
CULTIVARS 675, 939, 940, 2700
CULTIVATED INVITRO 666
CULTIVATION 20, 1605, 2234
CULTURE 386, 443, 514, 515, 574, 682, 766, 1037, 1171, 1385, 1478, 1560, 2041, 2042, 2109,

2175
CULTURED APPLE SHOOTS 1873
CULTURED INVITRO 583, 726, 2092
CULTURES 1214, 1650
CULTURE VESSEL 1215
CURD INITIATION 2565
CURVE 1321
CUTICLES 1781
CUTINASE 1213
CUTTINGS 777, 2562
CUZN- SUPEROXIDE 2164
CV BRAGG 89
CV FJORD 2679
CYANIDE 1019
CYANIDE-INSENSITIVE RESPIRATION 1776
CYANIDE- RESISTANT 2077, 2649
CYANIDE-RESISTANT RESPIRATION 1272
CYANOBACTERIA 1071, 1463, 1619, 2032, 2296, 2599
CYANOBACTERIAL PHOTOSYNTHETIC SYSTEM 1625
CYANOBACTERIUM 1339
CYANOBACTERIUM SYNECHOCOCCUS PCC7942 40
CYCLE 139, 177, 277, 453, 503, 761, 861, 1161, 1162, 1170, 1370, 1494, 1501, 1639, 1660, 1690, 1807, 1885, 2139, 2152, 2168, 2226, 2244, 2523, 2549, 2570
CYCLES 152, 1077
CYSTEINE 1064
CYSTOSEIRA-ELEGANS SAUVAGEAU 2399
CYTOCHROME-OXIDASE 1625
CYTOSOLIC CA-2 1331
CYTOSOLIC-FREE CALCIUM 262, 1445, 2011
D1 PROTEIN 750
DACP 1471
DAILY CANOPY PHOTOSYNTHESIS 871, 2352
DAILY PRECIPITATION 1986, 2402
DAMAGE 1946, 1972, 2247, 2468
DANJOU PEAR 568, 569
DARK RESPIRATION 41, 42, 86, 100, 251, 290, 473, 561, 564, 643, 718, 751, 752, 795, 943, 1129, 1132, 1134, 1176, 1267, 1288, 1381, 1454, 1508, 1558, 1568, 1606, 1607, 1629, 1761, 1911, 1958, 1979, 2037, 2077, 2128, 2343, 2482, 2488, 2515, 2613, 2646, 2649, 2692, 2693, 2698, 2699
DARK RESPIRATION RATE 1978
DATA SET 1438
DEATH 402
DECAY 1059, 1120, 1279, 2237, 2422
DECAY-RATES 536, 1576
DECIDUOUS FOREST 43, 54, 155, 632, 859, 860, 906, 1078, 1326, 1418, 1436, 1957, 2516

DECIDUOUS FOREST FLOOR 593, 2492
DECIDUOUS TREES 219, 303, 313, 699, 866, 1143, 1196, 1230, 1361, 2072, 2271
DECIDUOUS WOODLAND 1293
DECIDUOUS WOODLAND SOILS 447
DECISION-SUPPORT SYSTEMS 140
DECISION-TREE 1039
DECLINE 336, 1270, 1613, 2132
DECOMPOSING LEAF LITTER 1577
DECOMPOSITION 14, 139, 197, 218, 315, 321, 416, 437, 533, 702, 721, 758, 836, 867, 961, 967, 1029, 1032, 1062, 1097, 1107, 1348, 1377, 1412, 1468, 1513, 1714, 1763, 1767, 1784, 1814, 1885, 1898, 1925, 1999, 2040, 2152, 2158, 2160, 2392, 2445, 2547, 2661, 2681
DECOMPOSITION DYNAMICS 199, 696
DECOMPOSITION PROCESSES 2533
DECOMPOSITION RATES 954, 1391, 1922, 2072, 2285
DEEP-WATER RICE 258, 2484
DEER CERVUS-ELAPHUS 1200
DEFENSE 721, 1363, 2044
DEFICIENCY 126, 421, 927, 1079, 1949
DEFICIENT 1446
DEFICIENT MUTANT 1709, 2585
DEFICITS 1550, 1887
DEFOLIATION 1271, 2367, 2552, 2603, 2680
DEFORESTATION 490, 949, 1833, 2158, 2264
DEGRADATION 750, 2251, 2535, 2658
DEHYDRATION 2500
DEHYDROGENASE 1019
DELAWARE RIVER BASIN 2297
DELAYED INDUCIBLE RESISTANCE 1090, 1200
DELTA 2090
DELTA C 13 176, 181, 1934, 1959
DELTA O 18 1548
DEMAND 1388
DENITRIFICATION 14, 38, 67, 1024, 1468, 1605
DENOVO SHOOT REGENERATION 282
DENSITY 154, 165, 177, 333, 405, 488, 648, 655, 1284, 1589, 1654, 1771, 1839, 2271, 2511
DENSITY RECORD 1251
DEPENDENCE 93, 127, 312, 851, 2357
DEPENDENCY 2307
DEPENDENT GLUTAMATE SYNTHASE 2275
DEPLETION 1232, 2500
DEPOSITION 5, 802, 1077, 1161, 1694, 2640
DEPRESSION 783
DESERT 987, 1192, 1705, 1852
DESERT CONDITIONS 2234
DESERT ECOSYSTEMS 308

DESERT EVERGREEN SHRUB 1858
DESERTIFICATION 61
DESERT SHRUB 917
DESERT STREAM 329
DESERT SUCCULENTS 573
DESIGN 372, 1096, 1141, 2005, 2572
DESORPTION 1804
DETACHED LEAVES 907
DETOXIFICATION 95
DETOXIFICATION ENZYME-ACTIVITY 1360
DETRITUS 1138
DEUTERIUM 676
DEVELOPING MAIZE LEAVES 731
DEVELOPMENTAL-CHANGES 92
DEVELOPMENTAL STAGES 31, 100
D-H RATIO 646
D/H RATIOS 646
DIAGNOSIS 1184
DIAMETER 81
DIAMONDBACK MOTH 1114
DIATOM 705
DIATOMS 1679
DIET 2044
DIETARY FIBER 1290
DIETARY NITROGEN 270, 1361
DIFFERENCE VEGETATION INDEX 1438
DIFFERENT AGES 2515
DIFFERENT CLIMATES 1370
DIFFERENT CO2 ENVIRONMENTS 33, 34, 101, 106
DIFFERENTIAL ABILITY 1421
DIFFERENTIAL EXPRESSION 480
DIFFERENTIAL RESPONSE 87, 1245
DIFFERENTIATION 238, 2216
DIFFERENT IRRADIANCE LEVELS 797, 906, 1326, 1634, 1975, 2284, 2408
DIFFERENT IRRADIANCES 1507, 1517, 1620, 1861, 2062, 2093
DIFFUSION-MODEL 453
DIGESTIBILITY 331, 2176
DILUTED DIETS 2595
DIMETHYL SULFIDE 996
DINITROGEN 805
DINITROGEN FIXATION 118
DIOXIDE 56, 62, 72, 149, 151, 163, 166, 170, 181, 187, 225, 273, 277, 310, 311, 319, 395, 396, 518, 582, 615, 620, 683, 685, 703, 735, 736, 759, 760, 782, 797, 798, 852, 914, 926, 949, 957, 1023, 1080, 1086, 1101, 1103, 1121, 1147, 1174, 1195, 1299, 1347, 1349, 1351, 1369, 1377, 1403, 1413, 1414, 1427, 1497, 1501, 1528, 1584, 1648, 1653, 1679, 1707, 1726, 1774, 1788,

1812-1814, 1823, 1837, 1846, 1901, 1924, 2040, 2050, 2051, 2143, 2151, 2154, 2192, 2256, 2278, 2296, 2316, 2322, 2380, 2430, 2437, 2444, 2455, 2470, 2523, 2581, 2599, 2627, 2671, 2676, 2688
DIOXIDE ATMOSPHERES 631, 1087
DIOXIDE CONCENTRATION 44, 334, 477, 911, 1400, 1448, 1459, 1568, 1645, 2147
DIOXIDE EFFLUX 148, 1865
DIOXIDE ENRICHMENT 50, 517, 649, 1152, 1378, 1698, 2190, 2283, 2335, 2381
DIOXIDE EVOLUTION 1122
DIOXIDE FIXATION 2499
DIOXIDE METABOLISMS 956
DIOXIDE STARVATION 451
DIRECT COMPONENT 246
DIRECT EQUILIBRATION 1548
DIRECT EXTRACTION 199, 200
DIRECT EXTRACTION METHOD 2040
DIRECT-RADIATION 2519
DISCONTINUOUS PERMAFROST 1575
DISCRIMINATION 181, 272, 281, 856, 1369, 1757, 1837, 1924, 2688
DISEASE RESISTANCE RESPONSE 2585
DISPERSAL 1313
DISSOLVED INORGANIC CARBON 1071, 2372
DISSOLVED ORGANIC-CARBON 1418, 1575
DISSOLVED ORGANIC-MATTER 693
DISTRIBUTIONS 84, 852
DISTURBANCE 581, 1357, 1879, 2471
DIURNAL CHANGES 2191
DIURNAL PATTERN 280
DIVERSE ALTITUDINAL RANGES 650, 2636
DIVERSITY 1185, 1452, 1999, 2016, 2053, 2674
DIVISION 1170, 1310
DNA 1310
DNA HYBRIDIZATION 799, 800
DNA TRANSFORMED ROOTS 355, 1880
DOGS 232
DORMANCY 59, 821
DORMANCY RELEASE 847
DOUBLED ATMOSPHERIC CO2 1322
DOUBLED CO2 CLIMATE 846
DOUGLAS-FIR 49, 140, 582, 760, 847, 1136, 1459, 1464, 1819
DOUGLAS-FIR ECOSYSTEM 1750
DOUGLAS-FIR FOREST 536
DOUGLAS-FIR STANDS 2079
DOWN- REGULATION 639, 2497
DOWNWIND EVOLUTION 1155
DRIVEN 1335

DROUGHT 50, 117, 230, 249, 336, 428, 486, 593, 607, 656, 887, 983, 1128, 1187, 1398, 1717, 1757, 1838, 2013, 2378, 2386
DROUGHT STRESS 95, 213, 362, 829, 1847, 2073, 2090, 2166
DRY DEPOSITION 683
DRY FOREST 145, 432, 1957
DRYING SOIL 1267, 1466
DRY-MATTER 25, 36, 77, 102, 133, 134, 225, 420, 477, 516, 519, 558, 635, 730, 779, 833, 927, 959, 1099, 1100, 1439, 1483, 1495, 1507, 1521, 1557, 1618, 1629, 1657, 1662, 1788, 1829, 1839, 1862, 2028, 2067, 2069, 2131, 2224, 2249, 2462, 2550, 2564, 2567, 2639
DRY-MATTER ACCUMULATION 140, 2566
DRY-MATTER PRODUCTION 91, 101, 106, 943, 991, 1383, 1429, 1870, 2037, 2070, 2128, 2213, 2274, 2421, 2563
DRY SEASON 1475
DRY SOIL 967
DRY-WEIGHT 344, 362, 610, 1615, 1670, 2176, 2480
DUPLEX SOIL 787
DURATION 51, 142, 143, 2181
DURUM-WHEAT 675
DUST 503
DWARF-SHRUB 327, 2686
DWARF SHRUBS 828
DWARF WILLOW 1095
DYNAMIC CHAMBER EXPERIMENTS 1971
DYNAMICS 91, 114, 191, 218, 252, 315, 327, 417, 446, 538, 735, 836, 837, 852, 903, 925, 961, 965, 1098, 1177, 1299, 1311, 1356, 1357, 1513, 1644, 1654, 1698, 1750, 1764, 1795, 1985, 2052, 2159, 2178, 2340, 2433, 2445, 2555, 2570, 2601, 2602, 2633, 2636, 2653
EAR DEVELOPMENT 1333
EARLY SELECTION 314, 1074
EARLY TERTIARY 167
EARTH 684
EARTHS RADIATION BUDGET 846
EARTHWORM POPULATIONS 1188
EASTERN AMAZONIA 1526
EASTERN NORTH-AMERICA 1435, 2356
EASTERN SIBERIA 1450
EASTERN UNITED STATES 1078
ECHINOCHLOA CRUS GALLI 253
ECOLOGICAL DISTRIBUTION 598
ECOLOGICAL MODEL 372
ECOLOGICAL STRATEGIES 801
ECOLOGY 205, 531, 1088, 1185, 1858, 2277
ECONOMIC-GROWTH 543
ECONOMICS 1827
ECONOMY 464
ECOPHYSIOLOGY 501, 2582

ECOSYS 2418
ECOSYSTEM 66, 694, 1409, 1450, 1519, 1653, 1667, 1690, 1879, 2601, 2603, 2659, 2668, 2673
ECOSYSTEM COLLAPSE 642
ECOSYSTEM EXPERIMENTS 168
ECOSYSTEM FUNCTION 2533
ECOSYSTEM PROCESSES 1177, 1805, 2356
ECOSYSTEM RESPONSES 1045, 1280
ECOSYSTEMS 5, 15, 22, 23, 39, 61, 67, 69, 70, 73, 84, 91, 113, 136, 138, 154, 156, 196, 198, 201, 218, 252, 279, 310, 321, 341, 373, 377, 379, 406, 416, 433, 435, 451, 494, 513, 529, 534, 542, 553, 652, 681, 696, 703, 736, 745, 759, 790, 791, 797, 862, 865, 898, 905, 911, 923, 925, 961, 962, 970, 987, 1046, 1069, 1077, 1080-1084, 1094, 1122, 1138, 1141, 1161, 1164, 1167, 1183, 1201, 1237, 1296, 1356, 1357, 1370, 1371, 1388, 1391, 1394, 1396, 1399, 1487, 1488, 1490, 1497, 1569, 1572, 1580, 1613, 1644, 1672, 1734, 1737, 1751, 1768, 1774, 1783, 1812, 1821, 1833, 1846, 1853, 1874, 1920, 1929, 1975, 1984, 1985, 1998, 2053, 2152, 2159, 2168, 2193, 2239, 2264, 2281, 2316, 2358-2360, 2362, 2367, 2433, 2449, 2451, 2466, 2470, 2492, 2527, 2540, 2551, 2611, 2636, 2651, 2674-2676, 2681, 2686
ECOTRON 220
ECOTYPES 2217
ECTOMYCORRHIZAL COLONIZATION 1257, 2052, 2504
ECTOMYCORRHIZAL FUNGI 530, 931
ECTOMYCORRHIZAL PLANTS 747
ECTOMYCORRHIZAS 1213
EDDY-CORRELATION 1309, 2074
EDDY-COVARIANCE 1152, 1735
EFFECTIVE PARTICLE RADIUS 1118
EFFICIENCIES 675
EFFICIENCY 12, 80, 126, 288, 330, 335, 460, 464, 681, 718, 816, 1318, 1864, 1925, 1929, 2106, 2140, 2171, 2326, 2378, 2417,
2543, 2565, 2584
EFFLUX 86, 290, 298, 1094, 1397, 1911, 1977, 2343, 2491, 2492, 2645, 2646
ELECTRICAL CHARACTERISTICS 262
ELECTRICITY 855
ELECTROMAGNETIC DETERMINATION 690
ELECTRON FLOW 1339
ELECTRON-TRANSPORT 127, 192, 213, 511, 677, 731, 829, 900, 917, 935, 1130, 1132, 1259, 1275, 1429, 1431, 1626, 1646, 1681, 1826, 2013-2016, 2099, 2135, 2209, 2210, 2298, 2338, 2366, 2368, 2468, 2581, 2607
ELECTRON-TRANSPORT CAPACITY 562
ELECTRON-TRANSPORT COMPOSITION 1625
ELEMENT 2640
ELEMENTAL ORGANIC-ANALYSIS 1970
ELEMENT CONCENTRATIONS 1061
ELEMENTS 1244
ELEVATED ATMOSPHERIC CO2 115, 132, 151, 305, 347, 369, 371, 413, 417, 441, 505, 563,

584, 615, 699, 700, 703, 733, 743, 754, 795, 799, 895, 896, 933, 1079, 1085, 1090, 1122, 1143, 1200, 1206, 1284, 1286, 1342, 1363, 1392, 1412, 1491, 1536, 1576, 1578, 1629, 1630, 1645, 1718, 1788, 1898, 1980, 2003, 2053, 2089, 2147, 2206, 2225, 2533, 2547, 2648, 2652
ELEVATED CARBON-DIOXIDE 38, 154, 174, 221, 325, 435, 472, 577, 607, 648, 661, 693, 769, 773, 774, 811, 824, 885, 905, 906, 952, 954, 1010, 1036, 1061, 1084, 1203, 1208, 1226, 1291, 1306, 1409, 1488, 1490, 1581, 1586, 1640, 1701, 1759, 1792, 1824, 1859, 1860, 1888, 1977, 1978, 1981, 2024, 2048, 2067, 2069, 2077, 2086, 2091, 2099-2101, 2118, 2128, 2134, 2136, 2157, 2193, 2261, 2293, 2370, 2546, 2550, 2569, 2584, 2646, 2703
ELEVATED CO2 2, 4-7, 15, 43, 44, 56, 61, 95, 100, 106, 108, 111, 133, 134, 136, 139, 140, 143-145, 152, 156, 157, 160, 162, 164, 166-168, 170, 176, 180, 186, 192, 197, 205, 213, 214, 225, 246, 251, 254, 264, 283, 290, 297, 298, 313, 327, 332, 334-336, 340, 341, 362, 375, 379, 391, 396, 397, 409, 411, 415, 425, 426, 428, 432, 445, 446, 449, 451, 467, 477, 481, 490, 494, 501, 502, 506, 511, 512, 536, 550, 553, 554, 565, 572, 573, 575, 579, 581, 585, 586, 588, 589, 606, 617, 621, 624, 626, 632, 637, 643, 644, 650, 659, 662, 663, 668, 669, 688, 689, 696, 698, 704, 714, 715, 718, 719, 722, 725, 729, 730, 735-738, 749, 779, 781, 786, 791-794, 833, 837, 844, 871, 875, 881, 882, 884, 889, 892, 893, 898, 907, 913, 914, 916, 917, 921, 925, 934, 945, 960, 965, 972, 985, 988, 990, 991, 1000, 1006, 1007, 1011, 1015, 1047, 1052, 1056, 1058, 1059, 1065, 1075, 1078, 1082, 1087, 1095, 1097, 1125, 1126, 1136, 1141, 1151, 1165, 1167, 1168, 1173, 1174, 1176, 1177, 1183, 1188, 1196, 1198, 1222-1224, 1
228, 1230, 1231, 1238, 1250, 1251, 1255, 1256, 1266, 1280, 1282, 1293, 1310, 1315, 1321, 1324, 1337, 1341, 1345, 1347, 1349, 1353, 1356, 1361, 1369, 1371, 1376, 1385, 1401, 1403, 1406, 1407, 1410, 1413, 1414, 1417, 1428-1430, 1433, 1435, 1439-1442, 1445, 1455, 1459, 1467, 1468, 1489, 1507, 1513, 1515, 1516, 1527, 1532, 1538, 1540, 1568, 1570, 1572, 1574, 1579, 1580, 1582, 1585, 1587, 1599, 1627, 1632-1634, 1636, 1637, 1664, 1677, 1682, 1683, 1689, 1691, 1707, 1712-1715, 1719, 1721, 1722, 1732, 1734, 1751, 1757, 1771, 1778, 1781, 1793, 1803, 1805-1807, 1813, 1815, 1821, 1848, 1851-1853, 1856-1858, 1864, 1868, 1879, 1889, 1894, 1896, 1922, 1927, 1928, 1933, 1936, 1938, 1941, 1942, 1945, 1954, 1964, 1965, 1971, 1975, 1979, 1983, 1998, 2000, 2002, 2018, 2020, 2028, 2029, 2035, 2046, 2050, 2062, 2070, 2079, 2087, 2098, 2102, 2105, 2106, 2123, 2131, 2137, 2149, 2151, 2153, 2160, 2182, 2188, 2189, 2204, 2211, 2213, 2214, 2220, 2222, 2224, 2229, 2233, 2249, 2260, 2262, 2268, 2284, 2285, 2
297, 2299, 2304, 2313, 2316, 2323, 2330, 2332, 2337, 2341, 2351-2354, 2376-2378, 2383-2385, 2397, 2400, 2427-2429, 2436, 2445, 2450, 2451, 2455, 2457, 2460, 2466, 2467, 2471, 2475, 2476, 2478, 2482, 2483, 2497, 2502, 2503, 2505, 2506, 2508, 2511, 2512, 2519, 2521, 2526, 2527, 2541, 2545, 2549, 2552, 2561, 2564, 2581, 2587, 2588, 2590, 2591, 2605, 2607, 2609, 2610, 2620, 2629-2631, 2635, 2637, 2643, 2645, 2649, 2654, 2662, 2668, 2669, 2681, 2682, 2684, 2685, 2689, 2696, 2698, 2705, 2709, 2710
ELEVATED CO2 CONCENTRATION 1601
ELEVATED CO2 CONCENTRATIONS 442, 524, 660, 870, 1045, 1381, 1470, 1776, 1849, 2239
ELEVATED LEVELS 63, 482, 1001, 1157, 2459
ELEVATION 2037, 2544
ELEVATIONAL GRADIENT 1636, 2333, 2438
ELICITOR 1472
ELLIPSOIDEA 2599

EL-NINO 1512, 1613
ELODEA 1869
ELONGATION 48, 573, 1070, 1215, 1923
ELYMUS-ATHERICUS 1315
EMBOLISM 81, 336
EMBRYOS 788, 1166
EMERGENCE 1860
EMERGENCE TIME 2541
EMERGENT MACROPHYTES 974
EMISSION 227, 395, 2513
EMISSIONS 453, 490, 551, 941, 967, 1027, 1312, 1475, 1734, 2321, 2328, 2445
EMPIRICAL-MODEL 163, 1056, 1803
ENCHYTRAEIDAE OLIGOCHAETA 2304
ENCODING 1-AMINOCYCLOPROPANE-1-CARBOXYLATE SYNTHASE 1469
ENERGY 798, 2090, 2177, 2683
ENERGY-BALANCE 684, 776, 1914
ENERGY-CHARGE 158
ENERGY- DISSIPATION 1382
ENERGY-DISTRIBUTION 750
ENERGY EFFICIENCY 855
ENERGY OVERFLOW 41, 2649
ENERGY-PRODUCTION 1931
ENERGY- TRANSPORT 1136
ENGLAND 318, 2573
ENHANCED CO2 2191
ENHANCED OZONE 1228, 1680, 2166
ENHANCED RADIATION 28
ENHANCEMENT 488, 548, 879, 937, 1051, 1079, 1306, 1318, 1976, 2064, 2476, 2512, 2517
ENRICHED CO2 ATMOSPHERES 313, 339, 448, 1353, 2596
ENRICHED RHIZOSPHERE CO2 2104
ENRICHMENT 6, 21, 25, 36, 38, 45, 46, 48, 65, 66, 70, 72, 73, 76, 77, 85, 102, 104, 116, 120, 126, 138, 142, 156, 157, 165, 167, 169, 171-173, 176, 189, 197, 201, 202, 212, 225, 241, 249, 251, 257, 269, 279, 286, 289, 298-300, 306, 307, 311, 319, 321, 325, 330, 333, 344-346, 348, 349, 352, 356, 361, 378-381, 389, 391, 399, 403, 405, 409-411, 415, 418, 420, 421, 430, 435, 438, 439, 460, 461, 469, 475, 477, 479, 482, 493, 508, 511, 518, 519, 522, 527-529, 541, 545, 547, 548, 566, 567, 581, 585, 595, 602, 603, 610, 618, 625, 638, 641, 646, 648, 651, 652, 655, 656, 658, 662, 672, 676, 680, 681, 685, 713, 717, 720, 725, 747, 759, 766, 767, 769, 778, 782, 791, 797, 800, 810, 811, 816, 825, 833, 834, 839, 845, 851, 864, 888, 896, 901, 932, 942, 950, 959, 977, 984, 985, 994, 1003, 1005, 1014, 1022, 1023, 1029, 1037, 1046, 1047, 1050, 1057, 1063, 1069, 1072, 1079, 1080, 1085, 1091, 1092, 1107, 1108, 1117, 1121, 1124, 1131, 1137, 1148, 1157-1159, 1165, 1172, 1177, 1182, 1185, 1196, 1204, 12
07-1209, 1214, 1224-1226, 1231, 1238, 1250, 1251, 1295, 1296, 1298, 1301, 1305, 1306, 1318, 1336, 1343, 1344, 1350, 1352, 1354, 1364, 1377, 1386, 1390, 1391, 1399, 1401-1403, 1406, 1411, 1414, 1427, 1441, 1448, 1449, 1452, 1454, 1458, 1460, 1479, 1483, 1484, 1487, 1503, 1511, 1516, 1521, 1535, 1536, 1542, 1557, 1565, 1580, 1584, 1589, 1593, 1595, 1600, 1601,

1604, 1606, 1607, 1617, 1618, 1633, 1634, 1648, 1650, 1652, 1655, 1661, 1662, 1666, 1667, 1670, 1686, 1692, 1699, 1706, 1717, 1721, 1723, 1724, 1740, 1751, 1758, 1760, 1761, 1764, 1765, 1786, 1788, 1789, 1795, 1800, 1811, 1814, 1818, 1828, 1830, 1832, 1833, 1854, 1856, 1865, 1887, 1896, 1905, 1907, 1915, 1923, 1925, 1927, 1933, 1937, 1939, 1941, 1949, 1950, 1952, 1953, 1968-1970, 1975-1980, 1984, 1985, 1988, 1993, 1995-1997, 2000, 2004, 2006, 2007, 2012, 2021, 2023, 2041, 2042, 2049-2051, 2054-2056, 2059, 2060, 2063, 2076, 2080-2084, 2088, 2091, 2093-2096, 2108, 2109, 2114, 2117, 2121, 2122, 2126, 2145, 2155, 2159, 2162, 2173,
2175, 2181, 2199, 2202, 2203, 2213, 2214, 2221, 2222, 2234, 2258, 2260, 2261, 2272, 2273, 2281, 2294, 2307, 2322, 2327, 2336, 2345, 2358, 2362, 2364-2367, 2369, 2371, 2374, 2376, 2377, 2380, 2382, 2386, 2388, 2391, 2393, 2398, 2401, 2403, 2405, 2408, 2409, 2414, 2417, 2419, 2435, 2444, 2454, 2463, 2470, 2479-2483, 2485, 2487, 2488, 2511, 2512, 2514, 2517, 2523, 2530, 2534, 2538, 2541, 2542, 2557-2559, 2561, 2564, 2565, 2567, 2569, 2573, 2604, 2613, 2615, 2617-2619, 2622, 2625, 2637, 2650, 2654, 2662, 2680-2683, 2690, 2692-2695, 2697, 2698, 2705, 2706, 2712
ENVIRONMENT 144, 214, 229, 369, 400, 681, 845, 984, 1015, 1059, 1096, 1295, 1315, 1453, 1665, 1688, 1703, 1897, 1966, 2232, 2318, 2441, 2448, 2454, 2561, 2604, 2683
ENVIRONMENTAL-CHANGE 164, 176, 177, 327, 541, 1492, 2097
ENVIRONMENTAL-FACTORS 1421, 2197
ENVIRONMENTAL PHYSIOLOGY 769
ENVIRONMENTAL-QUALITY 543
ENVIRONMENT ALTERS RESPONSE 1374
ENVIRONMENTS 103, 220, 415, 431, 784, 844, 1173, 1409, 1620, 1723, 2080, 2147, 2266, 2541, 2542, 2550, 2601, 2651
ENZYME 112, 813, 2205, 2598
ENZYME-ACTIVITIES 2210
ENZYME LEVEL 2217
ENZYMES 95, 640, 1034, 1910, 2166, 2174
EOCENE 1492
EPIC MODEL 276, 526, 527, 591
EPICUTICULAR WAX 1721, 1781, 1888
EPICUTICULAR WAX LOAD 769
EPIDERMAL STRUCTURE 185
EQUATORIAL PACIFIC-OCEAN 996
EQUILIBRIUM RESPONSES 1729
ERIOGONUM-INFLATUM 1695
ERIOPHORUM VAGINATUM 327, 430, 1140, 1141, 1297, 1502, 1577, 2192
EROSION 276, 591
ERYTHRONIUM-GRANDIFLORUM 1287
ESCHERICHIA-COLI 1473
ESTABLISHMENT 1255, 1313, 1857, 2216, 2364
ESTABLISHMENT-YEAR 535
ESTUARINE MARSH 32, 72, 75, 155, 417, 481, 562, 566, 567, 642, 837, 1015, 1085, 1266, 1294, 1315, 1468, 1571, 1653, 1665, 1763-1766, 2062, 2063, 2143, 2239, 2284, 2329, 2601, 2602, 2635

ETHANOL 1181
ETHYLENE 158, 242, 443, 614, 806, 817, 1242, 1272, 1273, 1373, 1628, 1696, 2315, 2317, 2691
ETHYLENE BIOSYNTHESIS 816, 1473
ETHYLENE-FORMING ENZYME 989
ETHYLENE INHIBITORS 282
ETHYLENE PRODUCTION 762, 1623, 1976
ETHYLENE RELEASE 283, 808
ETIOLATED BARLEY LEAVES 649
ETIOLATING TOMATO SEEDLINGS 1636
EUCALYPTUS-GRANDIS 1131, 1868
EUCALYPTUS- GRANDIS SEEDLINGS 192
EUCALYPTUS-PAUCIFLORA 312, 1514, 2520
EURAMERICANA 2582
EURASIAN SNOW COVER 463
EUROPE 216, 1212
EUROPEAN FORESTS 1371
EUTROPHICATION 1773, 2302
EVALUATING PERFORMANCE 2197
EVAPORATION 496, 579, 690, 948, 1156, 1375, 1611, 2683
EVAPOTRANSPIRATION 662, 905, 1057
EVEN- AGED STANDS 16
EVOLUTION 184, 333, 593, 605, 1397, 1494, 1644, 2331
EVOLUTIONARY CONSEQUENCES 501
EVOLUTIONARY-THEORY 2270
EVOLUTION RATE 1500
EXCESS LIGHT 2090
EXCESS SULFUR 94, 95, 1709
EXCHANGE 51, 64, 108, 160, 245, 264, 286, 296, 407, 443, 494, 573, 620, 683, 690, 806, 832, 841, 842, 1048, 1137, 1394, 1398, 1420, 1446, 1450, 1483, 1503, 1511, 1525, 1548, 1591, 1648, 1660, 1778, 1826, 1865, 1877, 1933, 1966, 1988, 2074, 2106, 2161, 2177, 2191, 2201, 2232, 2254, 2345, 2415, 2610, 2612, 2649, 2654, 2684, 2707
EXCHANGE-RATE 881
EXCHANGE-RATES 1955
EXCHANGES 39, 53
EXCISED LEAVES 149, 1324
EXCLUSION LIMIT 1393
EXCRETION 742, 1446
EXPANSION 461, 650, 653, 1923, 2069
EXPERIMENTAL ECOLOGICAL GENETICS 631
EXPERIMENTAL MICROCOSMS 533
EXPERIMENTAL POPULATIONS 2541
EXPERIMENTAL- VERIFICATION 775, 776
EXPLOITATION 2675
EXPLOITATION ECOSYSTEMS 2532

EXPORT 30, 901
EXPOSURE 147, 215, 257, 384, 468, 567, 627, 849, 898, 1001, 1011, 1045, 1058, 1096, 1228, 1233, 1284, 1447, 1503, 1505, 1539, 1745, 1848, 1920, 1959, 1967, 2206, 2272, 2355, 2380, 2414, 2415, 2429, 2559
EXPOSURES 1113, 1181, 1232
EXPRESSION 92, 160, 242, 255, 355, 500, 640, 679, 762, 764, 893, 907, 957, 1255, 1277, 1337, 1395, 1627, 1676, 1754, 1930, 2102, 2456, 2457, 2464, 2497, 2598
EXTENSION 393, 2131
EXTERNAL HYPHAE 530, 1743
EXTRACTABLE CHLOROPHYLL 1016, 1839
EXTRACTION METHOD 14, 1908, 2039, 2522
EXTRUSION 1281
EXVITRO 514, 1258
FACE 882, 897, 1652, 2547
FACE EXPERIMENT 772
FACE SYSTEM 1539
FACILITY 220, 969, 1539
FAGUS-SYLVATICA 174, 595, 885, 2162, 2385
FAGUS-SYLVATICA L 886, 1146, 1228, 1445, 1870
FALLOPIA-JAPONICA 2097
FAMILIES 950, 1075
FAMILY POACEAE 1124
FARMER SCENARIO 644, 1194
FAR-RED 2635
FASCICULATA 668
FATE 54, 1951
FATTY-ACIDS 799, 2000
FATTY-ACID SYNTHESIS 2587
FAUNA 447
FECUNDITY 641
FEEDBACK 64, 477, 791, 800, 962, 1077, 1079, 1182, 1206, 1412, 1668, 1690, 1691, 1995, 1999, 2088, 2403, 2444, 2546, 2672
FEEDBACK PROCESSES 749, 1118
FEEDBACKS 1659, 2107
FEEDING RESPONSE 303
FERRICYANIDE 1281
FERTILIZATION 139, 435, 911, 1027, 1032, 1163, 1516, 1605, 1795, 1879, 1931, 2316, 2349, 2352
FERTILIZER APPLICATION 1267, 2304
FERTILIZERS 1990
FERULIC ACID 2188
FESTUCA-PRATENSIS 719
FICUS-BENJAMINA 1758
FIELD 33, 34, 75, 76, 84, 96, 143, 144, 194, 195, 221, 251, 325, 363, 393, 406, 481, 493, 509, 510, 522, 567, 698, 714, 754, 783, 793, 810, 830, 833, 839, 879, 883, 892, 896, 898, 969, 1000,

1011, 1062, 1093, 1101, 1113, 1117, 1157, 1233, 1292, 1293, 1295, 1333, 1406, 1499, 1505, 1543, 1544, 1611, 1715, 1755, 1759, 1824, 1825, 1840, 1848, 1889, 1895, 1911, 1920, 1955, 1967, 2058, 2065, 2066, 2068, 2073, 2111, 2112, 2116, 2148, 2187, 2282, 2283, 2320, 2336, 2341, 2355, 2360, 2393, 2454, 2463, 2538, 2564, 2566, 2636, 2656, 2683, 2692
FIELD CHAMBERS 841, 1294, 1618, 1720
FIELD CONDITIONS 101, 230, 787, 902, 1835, 2333
FIELD CROPS 897, 899, 1641, 1645
FIELD EXPERIMENT 983
FIELD EXPERIMENT FIFE 1450, 2177
FIELD-GROWN SOYBEANS 2029
FIELD-GROWN TOMATO 2263
FIELD PLANT COMMUNITY 1879
FIELD PLOTS 1932
FIFE 2178
FILM 2535
FINE ROOTS 196-199, 758, 1122, 1238, 1711, 2079, 2358, 2442
FINE-STRUCTURE 2216
FINLAND 2313
FINNISH LAPLAND 537
FIR 336
FIRE 2634
FIRES 1475
FIRMNESS 739
FIR PSEUDOTSUGA-MENZIESII 1816, 1819
FISH 948
FITNESS 1389, 1589
FIXATION 368, 454, 500, 514, 910, 1166, 1562, 1823, 2108, 2276, 2283, 2344, 2410, 2478, 2486
FLAGELLATE CHLOROGONIUM-ELONGATUM 813
FLAG LEAF 228
FLAVERIA 2331
FLAVOR 1033
FLOATING FENS 2087
FLOODING RESISTANCE 2484
FLOODS 1212
FLOODWATER 1227
FLOOR 2075
FLORA 623, 840
FLORAL INITIATION 606
FLORAL NECTARY 1756
FLOW 94, 127, 263, 839, 842, 932, 1691, 1768, 2078, 2225
FLOWER CONSTANCY 1261
FLUENCE RATE 2092
FLUID 271
FLUORESCENCE 599, 1307, 1382, 2614, 2687

FLUOROMETER 1041
FLUSHING TEMPERATURE 847
FLUX 274, 394, 949, 1402
FLUX-CONTROL COEFFICIENTS 2274
FLUX-DENSITY 1864
FLUXES 54, 57, 135, 245, 264, 913, 983, 1300, 1309, 1347, 1519, 1693, 1844
FLUX MEASUREMENT 892
FLUX MEASUREMENTS 110
FOLIAGE 866, 1271, 2045
FOLIAGE TEMPERATURE 138
FOLIAR CHEMISTRY 895, 1444
FOLIAR DEFORMATION 1811, 2199-2201
FOLIAR GAS-EXCHANGE 754, 1011, 1445, 1634, 1981, 2365, 2370, 2381
FOLIAR GLUTATHIONE 1709
FOLIAR INJURY 1211
FOLIAR NITROGEN 1369
FOLIAR NUTRIENT STATUS 1510
FONTINALIS-ANTIPYRETICA 1992
FOOD-CONSUMPTION 1363, 2595
FOOD PLANTS 866
FOOD-WEB 2532
FOOD-WEBS 2533
FORAGE 1076
FORECAST WIND-SPEED 2446
FOREST 73, 80, 84, 159, 186, 205, 216, 245, 272, 274, 340, 361, 399, 407, 426, 435, 446, 496, 520, 781, 838, 867, 886, 902, 925, 961, 967, 1059, 1079, 1080, 1082, 1084, 1163, 1226, 1388-1390, 1392, 1402, 1525, 1605, 1712, 1786, 2009, 2012, 2030, 2035, 2074, 2079, 2106, 2152, 2320, 2332, 2427, 2451, 2540, 2543, 2570, 2593, 2646, 2682
FOREST-BGC 1779
FOREST DECLINE 590, 1523
FOREST ECOSYSTEM PROCESSES 708, 868, 1151, 1435, 2638
FOREST ECOSYSTEMS 79, 168, 202, 300, 311, 315, 449, 535, 1231, 1713, 1931, 2150, 2151, 2153, 2478
FORESTED ECOSYSTEMS 1711
FOREST FLOOR 2491
FOREST LITTER 858
FORESTS 114, 135, 169, 179, 287, 382, 416, 453, 603, 674, 709, 717, 780, 797, 812, 929, 930, 1039, 1040, 1072, 1127, 1167, 1311, 1394, 1498, 1527, 1606, 1613, 1719, 1747, 1820, 1828, 1874, 1875, 1883, 1918, 2118, 2196, 2239, 2244, 2264, 2305, 2348, 2359, 2369, 2378, 2409, 2441, 2523, 2672
FOREST SOIL 2304
FOREST SOILS 1397, 2089
FOREST SUCCESSION MODELS 2197
FOREST TENT CATERPILLAR 2594
FOREST TENT CATERPILLARS 895, 1361, 1444, 1491

FOREST TREE 325, 2665
FOREST TREES 269, 2383-2385
FORMER SOVIET-UNION 1195
FORMING ENZYME 258, 667, 1469
FORMS 1909
FOSSIL-FUELS 453
FOSSIL LEAVES 1250, 1251
FOSSIL PLANTS 167
FOSSILS 840
FRACTIONATION 1121, 1812
FRACTIONS 2321
FRAGMENTATION 722
FRANCE 2030
FRANKFURT BIOSPHERE MODEL 1729
FREEZE-THAW CYCLES 1577
FREEZING-INJURY 2324
FREEZING RESISTANCE 301
FREEZING TEMPERATURES 1381
FREQUENCY 2402
FRESH PRODUCE 1089
FRESH-WATER 341
FRESH-WATER ECOSYSTEMS 2477
FRESH-WATER MACROPHYTES 1421, 1422, 1424, 2372, 2430
FRESH- WATER PLANTS 956
FRONT RANGE 274
FROST DAMAGE 59, 821, 847, 1044, 1302, 2305
FROST HARDINESS 167, 345, 930, 1269, 2324
FRUCTAN ACCUMULATION 820, 913, 2211
FRUCTAN BIOSYNTHESIS 1324
FRUCTOSE 2,6-BISPHOSPHATE 1470, 2209
FRUIT 17, 373, 459, 762, 1120, 1279, 1930, 2341
FRUIT CROP 1701
FRUIT-DEVELOPMENT 1702
FRUIT- GROWTH 19, 492
FRUIT PRODUCTION 2199, 2200
FRUIT-QUALITY 1481
FRUITS 739, 1033, 1434, 1903, 2405
FRUIT TOLERANCE 1119
FULL-SIB FAMILIES 1074
FUMIGATION 29, 83, 497, 899, 1144, 1305, 1908, 2040
FUNCTIONAL EQUILIBRIUM 2087
FUNGI 611, 746, 747, 1097, 1426, 1464, 1993, 2053
FUNGUS-GROWING TERMITES 1286
FUNGUS PISOLITHUS-TINCTORIUS 1327
FUSICOCCIN ACTION 262

FUTURE 855, 2613
GAILLARDIA-PULCHELLA 201
GAIN 2124
GAMETOPHYTIC SELECTION 1287
GAMMA-GLUTAMYLCYSTEINE SYNTHETASE 1709
GAP MODELS 2551
GASEOUS CO2 TRANSPORT 614
GAS-EXCHANGE 41, 43, 44, 50, 56, 66, 107, 109, 116, 117, 119, 121, 124, 169, 174, 176, 192, 210, 215, 228, 244, 257, 269, 270, 278, 310, 311, 333, 337, 340, 342, 344, 346, 349, 352, 353, 401, 415, 428, 450, 475, 477, 489, 541, 563, 564, 567, 577, 582, 585, 597, 608, 617, 618, 651, 658, 661, 699, 724, 743, 776, 786, 794, 802, 808, 809, 812, 816, 824, 829, 830, 834, 844, 851, 869, 878, 881, 906, 912, 917, 922, 923, 931, 952, 987, 991, 1000, 1074, 1091, 1092, 1095, 1124-1126, 1128, 1129, 1131, 1132, 1134, 1148, 1149, 1189, 1190, 1225, 1230, 1231, 1235, 1237, 1238, 1245, 1257, 1259, 1284, 1314, 1318, 1326, 1329, 1336, 1337, 1344, 1365, 1374, 1390, 1397, 1417, 1428, 1429, 1431, 1433, 1434, 1448, 1454, 1455, 1458, 1460, 1508, 1515, 1517, 1532, 1545, 1546, 1573, 1574, 1582, 1585, 1586, 1633, 1637, 1642, 1645, 1646, 1664, 1720, 1749, 1755, 1759, 1760, 1766, 1779, 1793, 1803, 1824, 1825, 1836, 1852-1854, 1860, 1872, 1873, 1961, 1964, 1968, 1980, 2004, 2019, 2035, 2046, 2068, 2073, 2084, 2098, 2101, 2103, 2126, 2132,
540, 2558, 2582, 2583, 2588, 2614, 2620, 2632, 2664, 2687
GAS-EXCHANGE RESPONSES 165, 168, 186, 2134
GAS FLUXES 38, 1468, 1605
GAS-PRODUCTION 331
GAS-TRANSPORT 2194
GCM 1264
GENE 1463, 2576
GENE-EXPRESSION 342, 649, 731, 878, 981, 1124, 1458, 1573, 2137, 2218, 2220, 2339, 2545, 2606
GENERAL-CIRCULATION 1419
GENERAL-CIRCULATION MODEL 449, 684, 753, 757, 846, 983, 1198, 1534, 1986, 1987, 2177, 2226, 2239, 2297, 2568, 2638
GENERAL-CIRCULATION MODELS 452, 463, 678
GENERAL-MODEL 708, 868, 1525, 1779, 1805
GENERIC PLANT SIMULATOR 1151
GENES 160, 640, 803, 957, 1277, 1337, 1395, 1469, 1556, 1627, 2456, 2457
GENETIC-MARKERS 557
GEN-NOV 1368
GENOTYPES 234, 2020, 2351
GEOGRAPHICAL-DISTRIBUTION 598
GEOMETRIDAE 302
GERMANY 1027
GERMINATION 207, 985
GERMINATION CHARACTERISTICS 801
GERMLING DEVELOPMENT 915
GIBBERELLIC-ACID 1702

GIGASPORA-MARGARITA 1880
GLACIAL PERIOD 503
GLANDULOSA 1852
GLASSHOUSE TOMATOES 1782
GLECHOMA-HEDERACEA 2552
GLOBAL CARBON-CYCLE 311, 685, 936, 1005, 1080, 1121, 2212, 2258, 2260, 2356
GLOBAL CHANGE 79, 313, 389, 532, 749, 860, 863, 904, 926, 1312, 1357, 1378, 1502, 1783, 1874, 1879, 2152, 2323, 2551, 2628, 2643
GLOBAL CLIMATE 301, 463, 513, 846, 1161, 1322
GLOBAL CLIMATE-CHANGE 573, 855, 1653, 1894, 2151, 2469, 2527
GLOBAL CLIMATE MODEL 1375, 1718
GLOBAL CLOUD ALBEDO 1118
GLOBAL ENVIRONMENTAL-CHANGE 174
GLOBAL ENVIRONMENT CHANGE 1587, 2048
GLOBAL-MODEL 315, 1806
GLOBAL RADIATION 246
GLOBAL-SCALE 1877
GLOBAL VEGETATION 832
GLOMUS-MOSSEAE 931, 2259
GLOMUS-RHIZOBIUM SYMBIOSIS 1743
GLUCOSE 37, 799, 2233
GLUCOSE REPRESSION 2458
GLUTAMINE-SYNTHETASE 87, 649, 907, 2339
GLUTAMINE-SYNTHETASE ISOFORMS 1971
GLUTATHIONE 95, 2165, 2489
GLUTATHIONE-REDUCTASE 87, 1680, 2164, 2585
GLYCINE 95
GLYCINE DECARBOXYLASE 2339
GLYCINE-MAX 89, 123, 1305, 2086, 2401
GLYCOLATE DEHYDROGENASE 1446
GOLDEN DELICIOUS APPLES 1283
GOSSYPIUM HIRSUTUM L 1944, 2508
GRACILIS C-4 699, 700, 2699
GRADIENT 173, 1855, 2017, 2439
GRADIENT ANALYSIS 2097
GRADIENT HEADWATER STREAMS 329
GRADIENTS 84, 538, 978, 979, 1703, 1958
GRADUAL CHANGES 853
GRAIN DEVELOPMENT 2564
GRAIN-GROWTH 2203
GRAIN LEGUMES 1263
GRAIN LIPIDS 2587, 2589, 2590
GRAIN QUALITY 626, 1503, 1615, 1618, 2020, 2067
GRAIN-SORGHUM 718, 787, 2077
GRAIN-YIELD 1180, 2211, 2228, 2349

GRAMINIS 2490
GRANDIS SEEDLINGS 2625
GRASS 76, 436, 889, 952, 974, 1413, 1580, 1582, 2009, 2039, 2084, 2696
GRASS ANDROPOGON-GERARDII 843
GRASS-CLOVER LEYS 2389
GRASS ECHINOCHLOA-ORYZOIDES 2484
GRASSES 465, 516, 674, 2273, 2323, 2626
GRASSLAND 38, 79, 80, 215, 299, 310, 465, 532, 888, 925, 965, 985, 1108, 1185, 1644, 1652, 1857, 1860, 1879, 1922, 2010, 2139, 2352, 2512
GRASSLAND BIOGEOCHEMISTRY 1495, 1497
GRASSLAND ECOSYSTEMS 1435, 1763
GRASSLANDS 416, 417, 941, 1394, 2144, 2158
GRASSLAND SOILS 1985
GRASS SPARTINA-ALTERNIFLORA 2554
GREAT-BASIN 306, 1852
GREAT-LAKES 2297
GREAT- LAKES BASIN 329
GREAT-PLAINS 1435, 1495, 1497, 1783, 1784, 1795
GREEN-ALGA 742
GREEN-ALGAL 2413
GREEN-ALGAL LICHENS 1276
GREENHOUSE 513, 855, 870, 1086, 1109, 1179, 1224, 1800, 2438
GREENHOUSE GASES 1262, 1263, 1841
GREENHOUSE PLANTS 2318, 2448
GREENHOUSE ROSES 1529
GREENHOUSES 19, 1034, 1243, 2405
GREENHOUSE TOMATO 718
GREEN LEAVES 2587, 2589, 2590
GREY MANGROVE 663
GROSS NITROGEN TRANSFORMATIONS 1908
GROSS PRIMARY PRODUCTIVITY 1438
GROWING LEAVES 650
GROWN IN-VITRO 1872, 1873
GROWN SEEDLINGS 2294
GROWN SOYBEANS 29
GROWN WHEAT LEAVES 1310
GROWTH 2, 7, 20, 25, 34, 36, 41, 43, 47, 53, 55, 61, 65, 71-73, 76, 84, 88, 93, 96, 104, 108, 109, 117, 118, 124, 125, 127, 132, 144, 148, 149, 152, 159, 169, 170, 173, 174, 176, 178, 187, 188, 192, 194, 202, 210, 213, 217, 220, 222, 224, 225, 230, 234, 241, 251, 255, 258, 259, 270, 271, 286, 290, 297-299, 303, 316-321, 331, 333-336, 339, 340, 346, 354, 356, 357, 361, 366, 371, 372, 375, 379, 381, 382, 386, 389, 391, 393, 406, 410, 411, 415, 417, 418, 420, 426, 427, 435-437, 461, 465, 467, 472, 481-483, 489-491, 501, 502, 509, 514, 515, 526, 534, 536, 541, 554, 555, 564, 566, 575, 577, 586-590, 593, 600, 603, 606-608, 610, 611, 614, 615, 618, 620, 625, 626, 630, 637, 638, 648, 651, 655, 656, 661, 663, 665, 667, 669, 670, 672-674, 679, 685, 686, 695, 700, 702, 704, 706, 715, 718, 719, 721, 722, 725, 735, 737, 743, 746, 751, 752, 759,

766, 769, 771, 778, 779, 782-784, 789-791, 796, 800, 804, 809, 810, 812, 820, 826, 828, 853, 854, 864, 866, 867, 872, 879-884, 886, 888, 896, 897, 905
, 910, 916, 919, 922, 923, 927, 932, 952, 958, 959, 961, 964, 966, 984-987, 995, 997, 1000, 1008, 1009, 1012, 1016-1018, 1022, 1025-1027, 1031, 1036, 1037, 1042, 1043, 1047, 1048, 1051-1055, 1059-1061, 1067, 1085, 1087, 1092, 1095, 1098, 1099, 1103, 1106, 1112-1114, 1117, 1131, 1132, 1135, 1140, 1141, 1143, 1148, 1149, 1160, 1163, 1165, 1168, 1170, 1173, 1178, 1191, 1192, 1196, 1201, 1204, 1207-1209, 1220, 1227, 1235, 1243, 1250, 1254, 1256, 1266-1268, 1270, 1271, 1278, 1289, 1294, 1296-1298, 1306, 1311, 1313, 1315, 1321, 1328, 1332, 1333, 1336, 1337, 1342-1344, 1347, 1353, 1354, 1357, 1365-1368, 1376, 1383, 1392, 1399, 1401, 1403, 1409, 1411, 1416, 1422, 1425, 1426, 1437, 1439, 1441, 1448, 1449, 1452, 1459, 1464, 1466, 1476, 1477, 1483, 1489, 1495, 1503, 1509, 1516, 1527, 1528, 1532, 1541, 1542, 1544, 1546, 1549, 1551, 1553, 1555, 1556, 1558, 1560, 1565, 1569, 1572, 1573, 1581, 1586, 1589-1591, 1593, 1597, 1598, 1602, 1610, 1629, 1633, 1635, 1645, 1652, 1653, 1662, 1665, 1672, 16
77, 1679, 1683, 1687-1689, 1693, 1699, 1701, 1702, 1706, 1708, 1710-1712, 1721-1723, 1727, 1737, 1740, 1744, 1745, 1747, 1754, 1755, 1758, 1760, 1761, 1763-1766, 1778, 1786, 1788, 1789, 1798, 1799, 1813-1815, 1818, 1819, 1825, 1830-1833, 1839, 1840, 1843, 1846, 1848, 1850, 1852, 1854, 1874, 1880, 1888, 1891, 1892, 1895, 1896, 1900, 1905, 1906, 1909, 1911-1913, 1915, 1925, 1929, 1933, 1938, 1940, 1941, 1947, 1948, 1953, 1955, 1964, 1968, 1969, 1974, 1976, 1977, 1979, 1981, 1984, 1986, 1988, 1997, 1998, 2000-2003, 2017-2019, 2023, 2025, 2026, 2037, 2041, 2042, 2046, 2049, 2051, 2052, 2054, 2058-2062, 2064, 2068, 2071, 2073, 2076, 2077, 2080, 2083, 2086, 2092, 2096, 2097, 2102, 2104, 2109, 2111, 2112, 2118, 2123, 2126, 2131, 2132, 2137, 2138, 2140, 2143, 2147, 2148, 2155, 2160, 2162, 2171, 2173, 2176, 2179, 2180, 2184, 2186-2189, 2191, 2192, 2195, 2200, 2204, 2206, 2208, 2211, 2214-2216, 2218, 2219, 2222, 2224, 2228, 2229, 2234, 2243, 2246-2249, 2252, 2253, 2256-2260, 2268, 2269, 227
2, 2278, 2280, 2281, 2283, 2291, 2299, 2330, 2336, 2341, 2346, 2350-2352, 2354, 2364, 2366, 2367, 2381, 2385, 2386, 2389, 2397, 2398, 2400, 2401, 2412, 2413, 2415, 2417, 2418, 2424, 2426, 2427, 2434, 2436, 2438, 2439, 2444, 2451, 2453, 2455, 2463, 2466-2468, 2470, 2472, 2475, 2478, 2481, 2490, 2494, 2501, 2517, 2519, 2526, 2527, 2538, 2548, 2552-2554, 2577, 2581-2583, 2589, 2594, 2597, 2602-2604, 2616, 2617, 2627, 2629-2631, 2636, 2637, 2640, 2649, 2652, 2654, 2664, 2672, 2678-2682, 2685, 2688-2691, 2693, 2697, 2700
GROWTH-ANALYSIS 977, 1791
GROWTH-CONDITIONS 1626, 2465
GROWTH-DIFFERENTIATION BALANCE 1200
GROWTH DYNAMICS 2379
GROWTH EFFICIENCY 2648
GROWTH ENHANCEMENT 199, 1391
GROWTH FORM 1189
GROWTH FORMS 64
GROWTH IRRADIANCE 1307
GROWTH-MODEL 2446
GROWTH-MODELS 140
GROWTH RATE 341, 531, 2161
GROWTH-RATES 1934

GROWTH REDUCTION 1481
GROWTH-RESPONSE 50, 151, 154, 196, 636, 963, 970, 1015, 1211, 1231, 1236, 1287, 1405, 1410, 1496, 1498, 1682, 1863, 1866, 1932, 2056, 2100, 2144-2146, 2151, 2279, 2353, 2374, 2396, 2480, 2482, 2542, 2600
GROWTH-RESPONSES 156, 311, 476, 668, 689, 1079, 1080, 1146, 1203, 1228, 1326, 1362, 1413, 1531, 1571, 1632, 1651, 1717, 1931, 2122, 2448, 2484, 2635, 2651
GROWTH-STIMULATION 2708
GROWTH TEMPERATURE 917, 2377
GROWTH TRENDS 506, 781
GUARD-CELL 885
GUARD-CELL PROTOPLASTS 1281
GUARD-CELLS 1330, 1331, 1629, 1635, 1803, 2011, 2312
GULF 2554
GYPSY-MOTH 448, 1491, 2594
GYPSY MOTHS 1444
HABITAT 1059, 1126, 1127
HABITATS 1141
HABITAT TEMPLET 1376
HALIMEDA 706
HALOPHYTES 1315
HALOTHANE ANESTHESIA 232
HARDINESS 590, 1746
HARDWOOD FOREST 2492
HARDWOOD LEAF LITTER 113, 199, 660, 858
HARDWOOD SEEDLINGS 895
HARTIG NET 1213
HARVEST 434
HCO3 2296, 2472
HEALTHY 1252
HEALTHY CELLS 742
HEAT 1735
HEAT-BALANCE 579, 580
HEATHER MOORLAND 1143
HEATHLAND ECOSYSTEMS 77
HEAT-ISLAND 990
HEAT-SHOCK 1983
HEAT-SHOCK PROTEINS 59, 138, 411
HEAT-STORAGE 2172
HEAT-STRESS 18
HEAT TOLERANCE 2037
HEAVY-METALS 37, 1244
HEIGHT 228
HEMODIALYSIS 1186
HERB 538, 859
HERBACEOUS VEGETATION 1293

HERBAGE INTAKE 2389
HERBIVORE 1363
HERBIVORE INTERACTIONS 219, 303, 313, 448, 694, 743, 880, 1143, 2046, 2236, 2293
HERBIVORE RESPONSES 2045
HERBIVORY 218, 341, 721, 1114, 1303, 1798, 1957
HETEROGENEITY 491
HETEROTHECA-SUBAXILLARIS 631
HETEROTROPHIC BACTERIA 2160
HIGH- ALTITUDES 541, 2143, 2530
HIGH AMBIENT CO2 795
HIGH ATMOSPHERIC CO2 101, 148, 212, 253, 257, 415, 502, 1050, 1517, 1606, 1676, 1677, 2195, 2204, 2208, 2234, 2263, 2274, 2345, 2456, 2457, 2459, 2460, 2520, 2521, 2632, 2684, 2689, 2710
HIGHBUSH BLUEBERRY 1037
HIGH CO2 1243, 1717, 2060
HIGH CO2 CONCENTRATIONS 1458
HIGH-ELEVATION SITES 2030
HIGHER-PLANT MITOCHONDRIA 1272
HIGHER-PLANTS 28, 300, 729, 807, 1071, 1454, 1573, 1635, 1793, 1956, 2104, 2217, 2294, 2689
HIGH-LATITUDES 162, 838
HIGH LIGHT 2164
HIGH LIGHT LEVELS 1381
HIGH-PRESSURE SODIUM 356, 2199
HIGH-RESOLUTION RADIOMETER 1438, 2150, 2638
HIGH-TEMPERATURE 1878, 2037
HILARIA-RIGIDA 572
HINOKI FOREST TREE 324
HISTORY 1547
HOLCUS- LANATUS 1099
HOLE ECOSYSTEMS 2285
HOLOCENE 1659
HOLOCENE ANALOGS 642
HOMALODISCA-COAGULATA 271
HOMOPTERA 218, 1663, 2111, 2577
HONEY BEES 1756
HONEY MESQUITE 1854
HORDEUM-JUBATUM 501
HORDEUM VULGARE L 87, 557, 1971, 2585
HOST 355, 1880
HOST-PARASITOID ASSOCIATIONS 1293
HOST PLANTS 303, 880
HUMAN SKELETAL-MUSCLE 1790
HUMIC SUBSTANCES 1032
HUMIDITY 206, 259, 993, 1173, 1602, 1782, 1803, 1855, 1887, 2124, 2182, 2518, 2584, 2605

HYBRIDIZATION TECHNIQUE 800
HYBRID POPLAR 353, 460
HYBRID POPULUS L 1374
HYDRAULIC ARCHITECTURE 2421
HYDRAULIC CONDUCTANCE 885
HYDRAULIC CONDUCTIVITY 2385
HYDROCARBONS 1991, 2286
HYDROGEN 191, 676
HYDROGEN EVOLUTION 2250
HYDROGEN- PEROXIDE 13, 63, 503, 1504, 1680, 2174, 2585
HYDROLOGIC SENSITIVITIES 1524
HYDROXYPYRUVATE REDUCTASE 2339
HYPERSALINE MONO-LAKE 1524
HYPERSENSITIVE REACTION 1610
HYPHAE 1993, 2078, 2215
HYPOCOTYL ELONGATION 1636
HYPOCOTYLS 2131
HYPOXIC HYPERCAPNIA 2267
ICE 172, 1121
ICE-AGE 1884, 2292
ICE CORE 102, 449, 513, 598, 1738, 1924, 1934, 2286, 2469
ICE-CORE RECORD 163, 166, 1282, 1849
ICE CORES 1139
ICE-FORMING NUCLEI 996
IDENTIFICATION 355, 1114, 1241, 2296
II LIGHT 1625
IMAGE- ANALYSIS 1500
IMMOBILIZATION 14, 945
IMPACT 144, 178, 216, 964, 1264, 1419, 1467, 1617, 1744, 2139, 2264, 2302
IMPACT ASSESSMENT 1416
IMPACTS 193, 909, 1615
IMPATIENS-CAPENSIS 1878
IMPORT 492
IMPROVEMENT 1442
IN-BAG EXPERIMENT 2220
INBREEDING DEPRESSION 501, 1878
INCOMPATIBILITY 145
INCOMPLETE 357, 431, 647, 808, 817, 1509, 2412, 2560
INCREASE 67, 105, 169, 215, 345, 354, 405, 410, 513, 548, 761, 876, 999, 1027, 1091, 1187, 1198, 1224, 1251, 1263, 1302, 1492, 1768, 1812, 1817, 1830, 2120, 2213, 2239, 2240, 2540, 2616, 2637, 2645
INCREASED ATMOSPHERIC CO2 2067
INCREASED CO2 452
INCREASED CO2 CONCENTRATION 2018
INCREASES 40, 381, 587, 655, 662, 1328, 1375, 1541, 1542, 1771, 1945, 2455, 2502, 2503

INCREASING ATMOSPHERIC CO2 310, 607, 736, 1032, 1156, 1203, 2024, 2203
INCREASING CARBON-DIOXIDE 853, 1744
INCREASING CO2 61, 330, 403, 550, 1435, 1483, 1874, 2196, 2332, 2353, 2364, 2555, 2590
INCREASING CO2 CONCENTRATION 1954
INDEX 1212, 1492, 1543
INDIVIDUAL TUBERS 1420
INDOLEACETIC-ACID 1473
INDUCED NITROGEN MINERALIZATION 1750
INDUCED RESPIRATION METHOD 2532
INDUCED STOMATAL CLOSURE 2544
INDUCED XYLEM EMBOLISM 2421
INDUCTION 248, 285, 480, 557, 1064, 1119, 1360, 1470, 1562, 1823, 1867, 2045, 2295
INDUCTION STATE 1861
INFECTED TALL FESCUE 1457
INFECTION 611, 746, 1328, 1385, 1386, 1388, 1663, 1880, 1995, 1997, 2026, 2257
INFECTION PROCESSES 2490
INFECTION UNITS 2256
INFESTATION 555
INFLORESCENCE DEVELOPMENT 1333
INFLORESCENCES TELOPEA-SPECIOSISSIMA 2169
INHERITANCE 557
INHIBITION 86, 290, 298, 319, 444, 482, 500, 704, 741, 878, 893, 935, 1001, 1218, 1222, 1395, 1448, 1449, 1591, 1761, 1915, 1979, 1990, 2094, 2188, 2263, 2345, 2414, 2415, 2438-2440, 2485, 2557, 2599, 2614, 2646, 2694, 2698, 2709, 2710
INHIBITOR 2060
INHIBITORS 1867
INITIAL GROWTH 1217
INITIATION 144, 1944
INJURY 332, 802, 882
INORGANIC CARBON 254, 370, 455, 458, 707, 744, 996, 1339, 1424, 1562, 1610, 1801, 1823, 1869, 1934, 2031, 2295, 2296, 2472, 2655
INORGANIC CARBON FLUXES 1463
INORGANIC CARBON-SOURCES 2154
INORGANIC-CARBON UPTAKE 705, 2032
INORGANIC NITROGEN 274
INORGANIC- PHOSPHATE 213, 2210
INOSITOL TRISPHOSPHATE 2544
INSECT HERBIVORE 410, 411, 529, 533, 694, 880, 936, 1087, 1098, 1100, 1266, 1444, 1663, 1765, 1846, 2349, 2372, 2404, 2639
INSECT HERBIVORE INTERACTIONS 85, 151, 339, 350, 413, 554, 631, 866, 958, 1304, 1457, 1815, 2268, 2271, 2398, 2594-2597,
2601, 2635
INSECT HERBIVORES 2111
INSECT HERBIVORY 2017
INSECT PERFORMANCE 218, 219, 303, 440, 555, 699, 1230, 1361, 1363, 2072

INSECTS 24, 2110
INSITU 75, 114, 115, 250, 1351
INSOLUBLE SILICON 915
INTACT CHLOROPLASTS 40
INTACT LEAVES 917, 987, 1433, 1843, 2098, 2099, 2103, 2508
INTACT SUNFLOWER PLANTS 816, 1976
INTEGRATED ANALYSIS 319, 973
INTEGRATED PEST-MANAGEMENT 1970
INTEGUMENT 1649
INTERANNUAL CLIMATE VARIABILITY 1436
INTERANNUAL FLUCTUATIONS 1524
INTERFERENCE 810, 2189
INTERFERENCE INTERACTIONS 811
INTERIOR 59
INTERIOR ALASKA 1417, 2197, 2491, 2492
INTERMITTENT 1031
INTERNAL BREAKDOWN 1973
INTERNAL NITROGEN CONCENTRATION 697, 1176, 1489
INTERSPECIFIC VARIATION 642
INTRA-ABDOMINAL PRESSURE 232
INTRACELLULAR GLYCEROL 742
INTRACELLULAR PH 300, 524
INTRASPECIFIC VARIATION 475, 501, 641, 1723, 2056, 2530
INVENTORY 1605
INVERTASE 1033, 1034, 1038, 2233
INVITRO 386, 500, 611, 766, 767, 872, 910, 1037, 1109, 1171, 1215, 1217, 1345, 1479, 1559, 1560, 1628, 1650, 1669, 1699, 1739, 1872, 1873, 1880, 1882, 2041, 2042, 2108, 2109, 2175, 2243, 2315, 2357, 2615
INVITRO DIGESTIBILITY 2670
INVITRO-PROPAGATION 2615
INVIVO 1166, 2098, 2209
INVOLVEMENT 1903, 1904
ION CONCENTRATION 1481
ION CONTENT 1843
ION-TRANSPORT 1801
IPRODIONE 17
IRRADIANCE 256, 281, 357, 476, 587, 731, 1126, 1128, 1314, 1318, 1344, 1540, 1855, 1915, 1954, 1992, 2201, 2294, 2312, 2476, 2565, 2699, 2706
IRRADIATION 849, 2247
IRRIGATION 229
ISLANDS 1613
ISOLATED- CHLOROPLASTS 750
ISOLATED SPINACH- CHLOROPLASTS 92
ISOPRENE 426, 427
ISOPRENE EMISSION 1841, 2242, 2382

ISOSYNTHETIC STRAINS 331
ISOTOPE 227, 398
ISOTOPE DISCRIMINATION 844, 1853
ISOTOPE EVIDENCE 2292
ISOTOPE FRACTIONATION 2010, 2286
ISOTOPIC COMPOSITION 1548, 1836, 1850
JACK PINE 773
JACK PINE-SEEDLINGS 1269
JIMSONWEED DATURA-STRAMONIUM 1791
JUICE 739
JUNONIA-COENIA 73, 217, 270, 313, 339, 631, 1353, 1354, 2398, 2594-2596
JUVENILE PONDEROSA PINE 1257, 2052
KALANCHOE- DAIGREMONTIANA 1727
KAPPAPHYCUS-ALVAREZII 1610
KENYA 2292
KINETIC-PROPERTIES 253, 2210
KIWIFRUIT ACTINIDIA-DELICIOSA 2348
KRAKOW REGION 170
KUDZU PUERARIA-LOBATA 1935, 2029, 2130, 2346
LADINO CLOVER 884
LAKE ACIDIFICATION 2371
LAKE PAAJARVI 1740
LAMPS 356
LANCEOLATA L 631
LAND 216, 1946, 2127
LAND-ATMOSPHERE 838
LAND BIOSPHERE 1660
LANDFILL SITE RESTORATION 305
LANDSCAPES 1357, 1547
LAND-SURFACE 2177
LAND-USE 79, 749, 1175, 1605, 1805, 1821, 1921, 2153
LAND-USE CHANGE 277, 490, 949, 1151, 1152, 1436, 1526, 2356
LAPAROSCOPIC CHOLECYSTECTOMY 232
LARGE SUBUNIT 98
LARIX-DECIDUA MILL 1228
LARREA- DIVARICATA 917
LARREA-TRIDENTATA 1858
LARVAE 270
LARVAL EMERGENCE 313, 584, 1143
LAST 3 CENTURIES 165, 597, 1810, 1811, 1813, 1815, 2637
LAST GLACIAL MAXIMUM 451, 463, 598, 1175, 1282, 1436
LATENCY 1903, 1904
LATENT-HEAT 1156
LATE QUATERNARY 166, 463, 1884
LATIN-AMERICA 490

LATITUDINAL DISTRIBUTION 857, 1846
LATITUDINAL GRADIENT 840, 1280
LAW 2194
LAYER 2172
L BRASSICACEAE 475
LEADS 1395
LEAF 30, 41, 52, 182, 185, 297, 402, 492, 510, 538, 559, 585, 602, 612, 632, 669, 678, 699, 715, 719, 754, 807, 815, 921, 922, 974, 1048, 1065, 1068, 1070, 1196, 1218, 1231, 1238, 1253, 1296, 1390, 1494, 1582, 1607, 1634, 1637, 1683, 1685, 1686, 1695, 1703, 1776, 1888, 1956, 1981, 2006, 2112, 2116, 2147, 2190, 2193, 2200, 2203, 2218, 2249, 2336, 2365, 2374, 2429, 2487, 2583
LEAF ABSCISSION 1111
LEAF AGE 1066, 1237, 1751
LEAF ANATOMY 71, 173, 514, 598, 652, 655, 786, 1225, 1871, 1899, 1909, 1918, 1980, 2003, 2222, 2241, 2331
LEAF APPEARANCE 144
LEAF-AREA 80, 102, 176, 306, 335, 344, 349, 493, 517, 519, 558, 661, 863, 1291, 1352, 1367, 1430, 1550, 1632, 1670, 1713, 1810, 1902, 1974, 1975, 2048, 2118, 2419, 2620, 2637
LEAF-AREA INDEX 110, 449, 709, 2557
LEAF BLADES 107, 913
LEAF CO2 EXCHANGE 753
LEAF CONDUCTANCE 97, 281, 579, 580, 868, 1843, 2058, 2124
LEAF DARK RESPIRATION 2376
LEAF DEVELOPMENT 82, 238, 353, 387, 731, 1573, 1793, 2458
LEAF-DISKS 1307, 1469
LEAF EXPANSION 1935, 2293
LEAF EXTENSION 2636
LEAF GAS- EXCHANGE 237, 347, 440, 442, 478, 565, 607, 700, 770, 885, 1056, 1146, 1236, 1681, 1786, 1870, 2137, 2486, 2501,
2510, 2584
LEAF GREENNESS 1016, 1839
LEAF GROWTH 249, 654, 1757, 2221, 2327, 2508
LEAFHOPPER 271
LEAF LIFE-SPAN 1176, 1553, 1957
LEAF LITTER 114, 196, 200, 410, 445, 685, 702, 758, 761, 961, 1032, 1082, 1266, 1391, 1412, 1468, 1513, 1576, 1767, 1999, 2009, 2072, 2089, 2148, 2432, 2443, 2471, 2533
LEAF-LITTER DECOMPOSITION 49
LEAF LITTERS 1107
LEAF-MINER 554
LEAF NITROGEN 150, 246, 409, 924, 1131, 1369, 1400, 1498, 1514, 1517, 1536, 1861, 1868, 2516, 2638
LEAF NITROGEN DISTRIBUTION 871
LEAF PEROXISOMES 1709
LEAF PHOTOSYNTHESIS 319, 1406, 2310
LEAF PRODUCTION 413

LEAF PROTEINS 1961
LEAF RESPIRATION 86, 450, 456, 564, 672, 751, 752, 1405, 1558, 1866, 2437, 2648
LEAF TISSUE 1481
LEAF WATER 646, 856, 1121, 1548, 1648
LEAF WATER POTENTIALS 658
LEAVES 2, 4, 7, 18, 30, 33, 34, 46, 50, 58, 74, 75, 86, 92, 95, 97, 114, 123, 124, 127, 128, 163, 177, 181, 185, 187, 189, 204, 206, 209, 210, 212, 214, 215, 228, 230, 255, 257, 259, 278, 281, 286, 288, 298, 325, 326, 332, 333, 339, 346, 363, 368, 370, 371, 393, 443, 444, 450, 466, 476, 489, 497, 514, 515, 561, 574, 583, 597, 599, 618, 624, 640, 648, 651, 653, 676, 700, 719, 741, 771, 783, 786, 790, 807, 808, 813, 815, 816, 823, 829, 830, 851, 858, 859, 875, 878, 900, 912, 915, 918, 919, 924, 938, 943, 950, 981, 988, 1020, 1026, 1043, 1050, 1065, 1066, 1070, 1091, 1115, 1121, 1128, 1137, 1144, 1149, 1189, 1191, 1208, 1218, 1222, 1253, 1259, 1277, 1284, 1314, 1318, 1336, 1341, 1369, 1373, 1379, 1380, 1382, 1393, 1406, 1407, 1442, 1449, 1458, 1459, 1464, 1466, 1467, 1494, 1508, 1516, 1532, 1538, 1540, 1543, 1568, 1584, 1586, 1591, 1592, 1600, 1620, 1626, 1637, 1655, 1658, 1676, 1677, 1682, 1685, 1697, 1703, 1712, 1721, 1752, 1758, 1771, 1772, 1776, 1781, 1796, 1803, 1818, 1820, 1824
-1826, 1828, 1835, 1837, 1838, 1851, 1861, 1864, 1867, 1887, 1888, 1900, 1901, 1910, 1911, 1915, 1918, 1933, 1944, 1945, 1948, 1959, 1962, 1963, 1976, 1977, 1979, 2003, 2004, 2013, 2015, 2017, 2019, 2022, 2057, 2058, 2061, 2069, 2084, 2094, 2102, 2105, 2108, 2131, 2135-2137, 2155, 2165, 2173, 2179, 2190, 2191, 2204, 2205, 2219, 2220, 2230, 2231, 2242, 2253-2255, 2269, 2276, 2325, 2339, 2343, 2345, 2352, 2355, 2366, 2368, 2376, 2377, 2411, 2412, 2414, 2415, 2425, 2447, 2453, 2456, 2457, 2464, 2468, 2474, 2489, 2494, 2496, 2516, 2519, 2521, 2523, 2569, 2630, 2631, 2637, 2646, 2648, 2654, 2684, 2690, 2693-2695, 2697, 2699, 2702, 2706, 2707, 2709, 2710
LEGUME 464
LEGUME NODULES 2250, 2473
LEGUMES 118, 2160
LEMNA-GIBBA 2234
LENGTH 198
LEOPOLIENSIS 1339
LEPIDOPTERA 73, 85, 217, 270, 302, 584, 629, 958, 959, 1087, 1353, 1354, 1360, 1457, 2046, 2076, 2262, 2271, 2398, 2404, 2577, 2596
LESSER SNOW GEESE 1280
LETTUCE 2314, 2446
LETTUCE TISSUE 939
LEVEL 2173
LEVEL RESPONSES 1296, 2279, 2281
L HULL 1143, 2573
LICHENS 2320, 2413
LIFE 538, 1279, 1474
LIFE-CYCLE 56
LIFE-HISTORY 475
LIFE-HISTORY STRATEGIES 801, 1376
LIFE-SPAN 1825
LIFE-SUPPORT 1453

LIFE SUPPORT SYSTEMS 316, 317, 1420, 2291, 2563
LIGHT 7, 11, 30, 127, 160, 210, 231, 237, 241, 296, 312, 322, 340, 356, 400, 443, 444, 486, 515, 587, 613, 649, 675, 677, 714, 805, 816, 859, 869, 873, 874, 919, 1037, 1041, 1171, 1178, 1179, 1215, 1225, 1307, 1379, 1382, 1421, 1422, 1467, 1487, 1490, 1551, 1562, 1564, 1593, 1599, 1652, 1679, 1682, 1688, 1752, 1770, 1861, 1864, 1974, 1976, 1988, 2001, 2006, 2013, 2014, 2016, 2060, 2082, 2108, 2124, 2136, 2206, 2208, 2218, 2247, 2252, 2291, 2318, 2330, 2337-2339, 2430, 2494, 2518, 2562, 2563, 2569, 2584, 2612, 2688, 2694, 2707
LIGHT ACTIVATION 1223
LIGHT CONDITIONS 1236
LIGHT-DARK MODULATION 957
LIGHT-DEPENDENT REGULATION 1965, 2102
LIGHT ENVIRONMENT 1626, 2487
LIGHT FRACTION 605
LIGHT INHIBITION 1469
LIGHT-INTENSITY 20, 42, 51, 891, 1243, 1344, 1489, 1619, 1872, 2101, 2366, 2615
LIGHT INTERCEPTION 319, 973, 1800
LIGHTLY PROCESSED FRUITS 2535
LIGHT-MODULATION 2210
LIGHT-QUALITY 71, 1217
LIGHT REGIME 1625
LIGHT-RESPONSE 1449, 2515
LIGHT-RESPONSE CURVES 1130
LIGNIFICATION 2216
LIGNIN CONTENT 113, 199, 858, 1138
LIGNIN CONTROL 397, 438, 439, 441, 445-447, 536, 1576, 1578
LIGNIN DEGRADATION 112
LIGNINS 23
LIGNOCELLULOSE 112
LIMITATION 133, 687, 1353, 1527, 1584, 1662, 1685, 2209, 2478
LIMITATIONS 117, 124, 125, 548, 851, 918, 937, 1080, 1197, 1407, 2276
LIMITED CONDITIONS 335, 656, 1174, 1343, 2481
LIMITING CO2 907, 2300
LIMITING CONDITIONS 631, 1087
LIPID-PEROXIDATION 1610
LIPIDS 1649, 2187
LIPOXYGENASE 1903
LIQUIDAMBAR- STYRACIFLUA 6, 74, 76, 156, 241, 337, 349, 476, 759, 797, 810-812, 1069, 1072, 1148, 1196, 1236, 1326, 1327, 1329, 1336, 1342, 1344, 1531, 1585, 1590, 1632, 1634, 1786, 1836, 1862, 1896, 1964, 1975, 2012, 2076, 2130, 2284, 2290, 2293, 2294, 2369, 2382, 2388, 2396, 2408, 2421, 2556, 2600
LIQUIDAMBAR-STYRACIFLUA HAMAMELIDACEAE 1871
LIRIODENDRON-TULIPIFERA L 205, 350, 440, 473, 565, 786, 823, 1200, 1374, 1496, 1718, 2335, 2648
LISCOMB COMPLEX 1199
LITTER 14, 54, 245, 1122, 1644, 2329, 2593

LITTER DECOMPOSITION 397, 440, 738, 1484, 1578, 1866, 1875, 1994, 2212, 2268, 2442, 2443, 2471
LITTER PRODUCTION 1821
LITTER QUALITY 634, 954, 967, 1032, 1082, 1107, 1378, 1698, 2056, 2285, 2391, 2392
LIVE OAK 2382
L KARST 1103, 1129, 1134, 1366, 1831, 1971, 2429
L KARST STANDS 660
L KUHN 2573
L LEAVES 244, 589
L MERRILL MUTANTS 118
L MERR PLANTS 30
LOA ENVIRONMENTAL MATRIX 2212
LOBLOLLY-PINE 201, 337, 448, 506, 607, 720, 724, 747, 906, 937, 1055, 1072, 1075, 1078, 1117, 1165, 1245, 1326, 1401, 1642, 1713, 2073, 2196, 2333, 2362, 2370, 2380, 2381, 2480, 2594, 2609, 2656
LOBLOLLY-PINE SEEDLINGS 305, 350, 478, 1069, 1148, 1496, 1510, 2382
LOBLOLLY-PINE TREES 342, 2002
LOCAL ADVECTION 1155
LOCAL FLORA 801, 973
LOCALIZATION 2007
LOCALIZED SOIL ENRICHMENT 2675
LOHMANN KAMPTNER 1679
LOLIUM 700, 2082
LOLIUM-MULTIFLORUM 2077
LOLIUM-PERENNE 334, 335, 401, 545, 564, 834, 839, 1093, 1099, 1201, 1288, 1409, 1440, 1468, 1664, 1666, 1683, 1722, 1787, 1911, 1978, 2018, 2039, 2089, 2091, 2128, 2145, 2146, 2193, 2337, 2354, 2442, 2466, 2547
LOLIUM-PERENNE L 16, 884, 1692, 1760, 1986, 2279
LOLIUM-TEMULENTUM 650
LOLIUM-TEMULENTUM L 2230
LONG 1261
LONG-DISTANCE TRANSPORT 2171
LONGEVITY 540, 1957
LONGLEAF PINE 2072
LONG-TERM 79, 187, 388, 657, 963, 1174, 1587, 2191, 2211, 2308, 2365, 2698
LONG-TERM ACTION 1989
LONG-TERM CO2 347
LONG-TERM DECOMPOSITION 49, 397, 446
LONG-TERM ELEVATION 353, 697, 906, 1344, 1718, 2531
LONG-TERM EXPOSURE 18, 74, 121, 123, 253, 283, 286, 362, 413, 476, 562, 563, 565, 792, 794, 796, 823, 988, 1129, 1130, 1137, 1203, 1204, 1314, 1327, 1405, 1429, 1431, 1545, 1571, 1645, 1646, 1676, 1792, 1829, 1849, 1862, 1968, 2029, 2099, 2128, 2134, 2143, 2200, 2274, 2335, 2345, 2383, 2406, 2437, 2515, 2639, 2709
LONG-TERM EXPOSURES 957
LONG-TERM MEASUREMENTS 1436

LONG-TERM RESPONSE 197, 1177, 1578, 2322
LONG-TERM TRENDS 1265
LONG VALLEY CALDERA 227
LOSSES 2392
LOWBUSH BLUEBERRY 1037
LOWLAND COASTAL FYNBOS 623
LOWLANDS 1957
LOW-LIGHT 1146
LOW OXYGEN 1283
LOW-OXYGEN ATMOSPHERES 242, 1119
LOW OZONE CONCENTRATIONS 770, 1365
LOW-TEMPERATURE 237, 980, 2015, 2143, 2298
LOW WATER POTENTIALS 2614
L SEEDLINGS 132, 2148
LUCERNE CANOPY 1861
LUMBRICIDAE 2673, 2674
LUPINUS-ALBUS 125
LUPINUS-ANGUSTIFOLIUS L 657
LUQUILLO EXPERIMENTAL FOREST 2212
L VAR AMELONADO 666
LYCOPERSICON-ESCULENTUM MILL 19, 492, 808, 1007
LYMANTRIA-DISPAR 303
MACROCLIMATE 684
MACROPHYTE COMMUNITIES 1773, 1992, 2302
MACROPHYTES 88, 1801
MACROTERMITINAE 2668
MAESTRO 1057
MAGNESIUM 1624
MAGNESIUM-DEFICIENCY 36, 1847
MAGNETIC-RESONANCE MICROSCOPY 250
MAINE 1639
MAINTENANCE 46, 290, 1789, 1866, 2523, 2692
MAINTENANCE REQUIREMENTS 298
MAINTENANCE RESPIRATION 107, 300, 324, 564, 796, 1134, 1288, 1372, 1553, 1911, 1921, 1958, 1978, 2077, 2341, 2376, 2377,
2582, 2648, 2665
MAIZE 2, 33, 37, 366, 679, 774, 932, 1789, 1955, 2462
MAIZE LEAVES 192
MAIZE PLANTS 1268
MAIZE ROOTS 458, 654
MAIZE ROOT-TIPS 158
MALATE 1332
MANAGED FORESTS 749
MANAGED MODEL-ECOSYSTEMS 884, 1521, 1692, 1760
MANAGEMENT 139, 318, 1108, 1946, 2573

MANDUCA-SEXTA CATERPILLARS 270
MANGLE L 116
MANIPULATION 1551, 2107
MANIPULATIONS 2686
MANNITOL 1574
MANURE 37
MARANTHES-CORYMBOSA 589, 754
MARINA L EELGRASS 2689
MARINE 1424
MARINE BOUNDARY-LAYER 1841
MARINE DIATOMS 2246, 2247
MARINE MACROALGAE 705, 707, 2047
MARINE-PHYTOPLANKTON 742, 1358
MARINE PLANTS 706
MARINE WATERS 341
MARITIME CLIMATE 2096
MARITIMUS L 2484
MARKET QUALITY 850
MARSH 1380, 2114, 2214
MARSH PLANTS 1853
MASS-FLOW 579
MASS-LOSS 113, 446, 1576
MASS-SPECTROMETRIC DETERMINATION 444
MASS- SPECTROMETRY 799
MASS-TRANSFER 1804
MASTIGOCLADUS-LAMINOSUS 1619
MAT 2047
MATHEMATICAL-MODEL 599, 1259, 1772
MATTER 284, 825, 1125, 2483
MATTER CONTENTS 1411
MATTER DYNAMICS 1032, 1175
MATURATION 1111
MATURE LEAVES 1288, 1978, 2298, 2607
MATURITY 2565
MAXIMUM 526
MAX L MERR 795, 1866, 2648
MBALMAYO FOREST RESERVE 1286
MECHANICAL IMPEDANCE 2028
MECHANICAL PERTURBATION 2332
MECHANISM 247, 370, 500, 640, 729, 750, 1277, 1337, 1428, 1573, 2014, 2032
MECHANISMS 2268, 2439
MEDIA 557
MEDICAGO-SATIVA 2250
MEGAGAMETOPHYTE 2216
MEGASCOLECIDAE 2668

MEHLER-PEROXIDASE REACTION 677
MELILOTI NODULATION GENES 355
MERISTEM CULTURE 1109, 1871
MESEMBRYANTHEMUM-CRYSTALLINUM L 480
MESOPHYLL 280, 1281
MESOPHYLL CONDUCTANCE 617, 900, 2338
MESOPHYLL PROTOPLASTS 1020, 2655
MESSENGER-RNA 387, 1469, 1676
MESSENGER-RNA LEVELS 2459
MESSENGER-RNAS 2606
METAANALYSIS 890
METABOLIC-RATE 207
METABOLIC REPRESSION 387
METABOLISM 1, 149, 224, 225, 231, 266, 278, 331, 421, 455, 457, 483, 600, 679, 721, 742, 744, 947, 980, 981, 1038, 1272, 1273, 1281, 1437, 1566, 1579, 1610, 1627, 1702, 1776, 1867, 1910, 1991, 2023, 2104, 2190, 2230, 2276, 2340, 2341, 2399, 2436, 2437, 2494, 2528, 2578, 2587
METABOLITE CONCENTRATIONS 1709
METABOLITE LEVELS 794, 1574
METABOLITES 1814
METER 1016
METHANE 67, 429, 1086, 1475, 1499, 1734, 2075, 2593, 2659
METHANE EMISSION 2089, 2450, 2514
METHANE EMISSIONS 513, 1282, 1519, 1575, 2303
METHANE FLUX 2088
METHANE FLUXES 1736
METHANE-OXIDIZING BACTERIA 191
METHANOGENESIS 2161, 2575
METHANOSARCINA-BARKERI 1566
METHODOLOGY 276
METHYLATED AMINES 1566
METHYLESTERASE 2422
METHYL-FLUORIDE 2161
MEXICO 361
MICROALGAE 40, 1071, 2032
MICROBIAL ACTIVITY 902, 1577
MICROBIAL BIOMASS 39, 225, 388, 703, 758, 839, 945, 967, 1030, 1108, 1377, 1411, 2039, 2050, 2321, 2322, 2442, 2444, 2445, 2462, 2532, 2533, 2661, 2671
MICROBIAL BIOMASS-C 2040
MICROBIAL BIOMASS CARBON 14
MICROBIAL BIOMASS DYNAMICS 37
MICROBIAL BIOMASS NITROGEN 199, 200
MICROBIAL COMMUNITIES 1484
MICROBIAL PROCESSES 2668
MICROBIAL RESPIRATION 1418

MICROCLIMATE 2320
MICROCYSTIS- AERUGINOSA 1619
MICROORGANISMS 605, 1500, 1990, 2127
MICROPROPAGATED PLANTS 1873
MICROPROPAGATION 1109
MICROSITES 65, 491, 2675
MICROSOMAL OXIDASES 1360
MICROSPECTROPHOTOMETRY 22
MIDDAY DEPRESSION 288
MIDDAY STOMATAL CLOSURE 1133, 2516
MIGRATION 978, 979, 1040
MILD WATER-STRESS 101
MILL 1623
MILL FRUIT 2677
MILLSONIA-ANOMALA 1286
MIMULUS-GUTTATUS 1287
MINERALIZATION 447, 945, 962, 1396, 2009, 2040, 2321, 2433, 2443, 2451, 2627, 2671, 2686
MINERAL NUTRITION 134, 225, 256, 420, 440, 519, 634, 636, 724, 725, 863, 889, 895, 928, 1044, 1090, 1131, 1168, 1362, 1376, 1386, 1400, 1516, 1564, 1632, 1711, 1732, 1810, 1829, 1831, 1862, 1863, 1918, 1955, 1980, 2024, 2087, 2100, 2146, 2170, 2284, 2290, 2379, 2380, 2396, 2480, 2486, 2597, 2600, 2601
MINERAL-SOIL 703
MINIMALLY PROCESSED FRUITS 850
MINIMUM TEMPERATURE 526
MINIRHIZOTRON 2434
MINOR-VEIN ANATOMY 280
MINOR VEINS 1393
MIRE WATER 1061
MISSING CO2 SINK 1806, 1807, 2356
MITES 1111
MITOCHONDRIA 1956, 1979, 2455
MITOCHONDRIAL RESPIRATION 2655
MIXED-GRASS PRAIRIE 2555
MIXED LAYER 2633
MIXED-LAYER MODEL 442
MOBILIZATION 2144
MODEL 5, 19, 143, 216, 272, 277, 284, 295, 370, 396, 404, 433, 551, 560, 620, 632, 647, 696, 709, 749, 772, 815, 836, 838, 848, 857, 918, 924, 926, 941, 948, 971, 978, 1039, 1077, 1115, 1162, 1186, 1194, 1212, 1220, 1231, 1308, 1312, 1322, 1342, 1356, 1370, 1462, 1485, 1489, 1501, 1512, 1528, 1544, 1555, 1659, 1686, 1769, 1774, 1784, 1802, 1824, 1825, 1827, 1832, 1885, 1905, 1937, 1985, 2034, 2038, 2047, 2061, 2097, 2118, 2150, 2158, 2172, 2178, 2194, 2310, 2337, 2389, 2402, 2432, 2445, 2516, 2523, 2571, 2581, 2605, 2633, 2645, 2651, 2652, 2664
MODEL ECOSYSTEM 954

MODEL-ECOSYSTEMS 1203, 2146
MODELING SYNTHESIS 1577, 1578
MODELS 43, 1088, 1173, 1193, 1321, 1450, 1694, 1710, 1914, 2570, 2625
MODEL SYSTEMS 151
MODERATELY ENHANCED LEVELS 326
MODERN GREEK CULTIVARS 119
MODIFIED ATMOSPHERES 739
MODIFIED STOMATA 1756
MODULATION 2159
MOIST FOREST 432
MOISTURE 1276, 2491, 2492, 2551
MOLD 17
MOLECULAR-HYDROGEN 464
MONOCULTURES 1589
MONOECIOUS CUCUMBERS 253, 942, 2060
MONOTERPENES 1816
MOORLAND 683
MORIFOLIUM RAMAT 400, 1243
MORPHOGENESIS 682
MORPHOLOGY 129, 238, 581, 588, 1185, 1217, 1500, 1590, 1695, 1721, 1822, 2346
MORTALITY 1613
MOSSES 1060
MOSS HYLOCOMIUM-SPLENDENS 1058
MOTH 584, 1271, 2045
MOUND-BUILDING TERMITES 1286
MOUNTAIN FYNBOS 1535
MOUNTAIN HEMLOCK 1875
MOUNTAINS 159, 1027, 1833, 2659
MOUNTAIN SITES 1252
MOUNT KENYA 956
MOVEMENT 2447
MOWN GRASSLAND 1267, 2304
MULTIFREQUENCY 2551
MULTIPLE ALLELOCHEMICALS 413
MULU NATIONAL PARK 2212
MUNG BEAN HYPOCOTYLS 1473
MUSA 2615
MUSHROOMS 1105
MUSKMELON 1481
MUSKMELON FRUIT 1034
MUSTARD 1114
MUTANT 1446, 1533, 2606
MUTANTS 231, 461, 849, 1330, 1697
MUTATIONS 1330
MYCELIUM 746, 2052

MYCORRHIZAL 1750, 2358, 2359
MYCORRHIZAL COLONIZATION 347, 388, 528, 1257, 1371, 1455, 1484, 2000, 2079, 2091, 2362, 2450, 2505, 2506
MYCORRHIZAL FUNGAL INOCULUM 1385
MYCORRHIZAL FUNGI 772, 1765
MYRICA-FAYA 904
MYRIOPHYLLUM- SPICATUM 2372
MYZUS-PERSICAE 219
N-15 1, 1812, 1908, 2010
N2 FIXATION 266, 330, 483, 508, 1400, 1409, 1410, 1743, 2427, 2680
N2O 1605
NACL 1481
NACL-TREATED PLANTS 1670
NADH-FE(III)EDTA OXIDOREDUCTASE 1990
NADP+-MALATE DEHYDROGENASE 1259, 2217
NADP-MALIC ENZYME 480
N-ALKANES 956
NAMAQUALAND 2511
NAPAP 2628
NAPUS 695, 1166
NATIVE HERBS 2534
NATIVE SHORTGRASS ECOSYSTEM 972
NATURAL ABUNDANCE 1854, 1934, 2010
NATURAL C-13 ABUNDANCE 1299, 1378
NATURAL ECOSYSTEMS 1182, 2259
NATURAL- ENVIRONMENT 929
NATURAL-POPULATIONS 1587, 1902
NATURAL SEDIMENTS 2371, 2372
NATURAL-SELECTION 1112, 1113
NATURAL VEGETATION 61
N-AVAILABILITY 624, 954, 2348
NDVI DATA SET 1877
NECTARINES 242, 571
NECTRIA-HAEMATOCOCCA 1213
NEEDLE LITTER 858
NEEDLES 1781, 1847, 1901, 2003, 2164-2166, 2429
NEIGHBORHOOD MODELS 152
NEMATODE COMMUNITIES 2532
NERIIFOLIA R 459
NERIUM-OLEANDER 917, 2101
NET 277
NET ASSIMILATION RATE 1864
NET CO2 ASSIMILATION 829
NET CO-2 EXCHANGE 1066
NET CO2 UPTAKE 288

NET NITROGEN 1418
NET NITROGEN MINERALIZATION 2223
NET PHOTOSYNTHESIS 97, 101, 121, 246, 334, 428, 607, 754, 809, 988, 990, 991, 1129, 1130, 1133, 1218, 1245, 1374, 1454, 1505, 1545, 1616, 1637, 1959, 1961, 1962, 1965, 2002, 2132, 2133, 2137, 2352, 2487-2489, 2515, 2520
NET PHOTOSYNTHETIC RATE 1989
NET PRIMARY 1174
NET PRIMARY PRODUCTION 478, 697, 753, 1122, 1152, 1371, 1372, 1394, 1405, 1436, 1718, 1729, 1779, 1825, 1924, 2074, 2356, 2445, 2451, 2469, 2638
NET PRIMARY PRODUCTIVITY 708
NEW-ZEALAND 1163, 1199, 1613, 2321
N-FERTILIZATION 1991
NH3 1820
NH4 458
NICHE SEPARATION 1582
NICOTIANA-PLUMBAGINIFOLIA 231
NICOTIANA-PLUMBAGINIFOLIA L 87
NICOTIANA-TABACUM 875, 2216, 2576
NIGHT TEMPERATURE 138, 1217
NINHYDRIN-REACTIVE NITROGEN 1108
NITRATE 396, 420, 457, 467, 517, 797, 928, 962, 1036, 1043, 1509, 1639, 1908, 1990, 1995, 2392, 2499, 2553
NITRATE ABSORPTION 132
NITRATE APPLICATION 118
NITRATE ASSIMILATION 455, 456, 458, 1372
NITRATE CONCENTRATIONS 503
NITRATE INHIBITION 2250
NITRATE REDUCTASE 454, 1061, 1324, 1971
NITRATE REDUCTASE-ACTIVITY 1773, 2231, 2275
NITRATE UPTAKE 1345
NITRIC-OXIDE 967
NITRIFICATION 703, 962, 1991, 2010
NITRITE 1509
NITRITE-REDUCTASE 679, 725, 957
NITROGEN 2, 25, 33, 46, 69, 72, 114, 115, 118, 123, 133, 134, 136, 139, 142, 146, 154, 198, 205, 212, 229, 252, 303, 304, 310, 316, 318, 321, 332, 334, 341, 379, 397, 399, 425, 427, 433, 435-439, 441, 445-447, 455, 472, 477, 479, 483, 492, 493, 516, 518, 529, 536, 573, 581, 593, 624, 683, 685, 688, 689, 694, 696, 699, 721, 725, 735, 738, 743, 758, 761, 782, 789, 815, 825, 833, 834, 837, 839, 843, 866, 872, 903, 904, 925, 933, 959, 964, 965, 967, 971, 977, 1027, 1029, 1030, 1046, 1048, 1054, 1055, 1061, 1087, 1098, 1100, 1126, 1127, 1163, 1167, 1168, 1181, 1183, 1184, 1237, 1261, 1266-1268, 1270, 1290, 1298, 1315, 1334, 1354, 1358, 1359, 1371, 1377, 1392, 1401, 1402, 1409-1411, 1464, 1485, 1487, 1495, 1511, 1513, 1527, 1555, 1564, 1581, 1599, 1615, 1627, 1630, 1642, 1661, 1667, 1668, 1685, 1689-1691, 1698, 1704, 1754, 1755, 1757, 1763, 1767, 1783, 1784, 1788, 1789, 1794, 1812, 1820, 1821, 1839, 1863, 1865, 1866, 1888, 1894, 1901, 1924, 1932, 1937, 1960, 1967, 1984, 1985, 2004, 2009

, 2010, 2012, 2017, 2020, 2043-2045, 2050, 2052, 2054, 2057, 2059, 2063, 2071, 2073, 2081, 2082, 2084, 2093, 2095, 2096, 2106, 2126, 2137, 2138, 2142, 2145, 2150, 2153, 2158, 2179, 2181, 2183, 2192, 2213, 2224, 2254, 2268, 2276, 2307, 2316, 2322, 2329, 2340, 2347, 2348, 2362, 2369, 2371, 2376, 2390-2393, 2400, 2410, 2414, 2432, 2433, 2442, 2443, 2449, 2453, 2462, 2463, 2465, 2466, 2470, 2479, 2501, 2522, 2527, 2540, 2546, 2547, 2550, 2564, 2567, 2570, 2591, 2597, 2601, 2617-2619, 2622, 2626, 2629, 2641, 2643, 2645, 2673, 2685, 2706
NITROGEN ACCUMULATION 2602
NITROGEN ALLOCATION 1431
NITROGEN APPLICATION 234, 2587, 2589, 2590
NITROGENASE ACTIVITY 66, 89, 388, 389, 2186
NITROGEN ASSIMILATION 1956
NITROGEN-AVAILABILITY 49, 64, 1146, 1864, 1929, 2488
NITROGEN CONCENTRATION 132, 150, 519, 720, 722, 922, 970, 1376, 1405, 1686, 2055, 2056, 2396
NITROGEN CONCENTRATIONS 418, 1439
NITROGEN-CONTENT 1107, 1353, 2354, 2398, 2404
NITROGEN CYCLES 954, 961, 1452
NITROGEN DEFICIENCY 920, 921
NITROGEN DEPOSITION 553, 863, 1152, 1510, 2151
NITROGEN-DIOXIDE 83, 1211, 1971, 2133
NITROGEN DISTRIBUTION 923
NITROGEN DYNAMICS 113, 858
NITROGEN ECONOMY 80
NITROGEN- FERTILIZATION 664, 1289, 2089, 2350
NITROGEN-FERTILIZER 889
NITROGEN-FIXATION 464, 1692, 2100, 2279, 2473, 2635, 2678, 2679
NITROGEN LEVEL 906, 2609
NITROGEN LIMITATIONS 1194, 1611
NITROGEN- METABOLISM 957
NITROGEN MINERALIZATION 14, 274, 1078, 1175, 1418, 1875, 1921, 2157, 2471
NITROGEN NUTRITION 530, 881, 1372, 1433, 1646, 2460
NITROGEN PRODUCTIVITY 16
NITROGEN REDISTRIBUTION 2203
NITROGEN RESPONSE 2409
NITROGEN SATURATION 197
NITROGEN STATUS 1955
NITROGEN STRESS 621, 1025, 1238, 1403, 2069
NITROGEN UPTAKE 2482
NITROGEN-USE 1197, 1430, 2374
NITROGEN-USE EFFICIENCY 409, 660, 733, 1381, 2368
NITROUS-OXIDE 38, 773, 1499, 2450, 2477
NITROUS-OXIDE EMISSIONS 1605
NITROUS-OXIDE EVOLUTION 1335
NITROUS-OXIDE PRODUCTION 67
NIWOT RIDGE 274, 2593

NMR-SPECTROSCOPY 1, 945
N,N-DIMETHYLFORMAMIDE 400, 849, 1918
NO2 83, 320
NO3 458
NO3 AVAILABILITY 895, 1230, 1361, 1491
NOCTUIDAE 85, 217, 629, 958, 1087, 1353, 1354, 1360, 2262, 2404, 2577
NODAL REGION 1237
NODULATED WHITE CLOVER 2680
NODULATION 66, 266, 916, 2071, 2344, 2367, 2427, 2485, 2512
NODULATION GENES 1880
NODULATION MUTANTS 89
NODULE DEVELOPMENT 266, 2499
NODULES 360, 2680
NON-EXCHANGEABLE HYDROGEN 646
NONHEME IRON PROTEIN 1649
NONSTOMATAL LIMITATION 121, 1545
NONSTRUCTURAL CARBOHYDRATE CONTENT 1134
NORTH-AMERICA 84, 185, 361, 646, 786, 867, 978, 979, 1188, 1875, 2402
NORTH-ATLANTIC 2633
NORTH-ATLANTIC OCEAN 846
NORTHEASTERN FRANCE 1931
NORTHEASTERN UNITED-STATES 156, 1196, 2609
NORTHERN 39, 838
NORTHERN CONIFERS 1269
NORTHERN FINLAND 2353
NORTHERN FORESTS 1356, 2551
NORTHERN HARDWOOD FOREST 198
NORTHERN HARDWOOD FORESTS 1418
NORTHERN HARDWOODS 49, 2609
NORTHERN PEATLANDS 1058, 2450
NORTHWESTERN MINNESOTA 1885
NORWAY SPRUCE 305, 634, 770, 771, 863, 1103, 1129, 1130, 1134, 1252, 1257, 1445, 1680, 1781, 1848, 2164, 2174, 2429, 2515 NOTHOFAGUS-FUSCA 2420
NO-TILLAGE 1265, 2153
NO-TILLAGE AGROECOSYSTEMS 1286
NTS1007 118
NUCLEAR 1676
NUCLEAR-FUEL WASTE 2194
NUCLEAR MAGNETIC-RESONANCE 1
NUMBER 1544, 1555, 1556
NUMBERS 354, 655, 876, 1187, 1541, 1542, 1771
NUMERICAL- ANALYSIS 2097
N-UPTAKE 1743
NUTRIENT 224, 505, 740, 747, 1163, 1328, 1399, 1513, 1737, 1875, 2056, 2149, 2192, 2323
NUTRIENT ACQUISITION 136

NUTRIENT AVAILABILITY 64, 344, 519, 2212
NUTRIENT BALANCE 217, 584, 624, 721, 1114, 1266, 1289, 1362, 1814, 1970, 2072, 2594-2596
NUTRIENT BALANCE HYPOTHESIS 1143
NUTRIENT CONCENTRATION 928, 2290
NUTRIENT CONCENTRATIONS 959, 1681
NUTRIENT CULTURE 2188
NUTRIENT DYNAMICS 536, 1501
NUTRIENT LIMITATION 79, 341, 1203, 1358
NUTRIENT RELEASE 2157
NUTRIENTS 687, 798, 1167, 1226, 1298, 1306, 1630, 2252, 2573
NUTRIENT STATUS 440, 489, 1082, 1980, 2420, 2505, 2506
NUTRIENT-UPTAKE 439, 931, 1107, 1413, 1571, 1576, 1607, 1760, 1815, 2122, 2353, 2672
NUTRIENT USE EFFICIENCY 1853
NUTRITION 4, 15, 77, 105, 129, 133, 136, 183, 234, 257, 281, 342, 345, 410, 455, 456, 489, 516, 534, 635, 730, 927, 937, 1043, 1270, 1278, 1306, 1527, 1535, 1633, 1661, 1662, 1812, 1818, 1830, 1864, 2002, 2020, 2021, 2055, 2086, 2104, 2121, 2148, 2214, 2249, 2254, 2261, 2437, 2629, 2712
NUTRITIONAL ECOLOGY 270, 2594, 2596
NUTRITIONAL-VALUE 2389
O-18 676, 1548
O-18 CONTENT 856
O-18 EXCHANGE 40
O2 13, 443, 444, 955, 1434, 1474, 1770, 2108, 2263
O-2 EVOLUTION 2135
O-2 PHOTOREDUCTION 1339
O-3 96, 193, 771, 883, 1032, 1052, 1598, 1599, 1615, 1962, 1963, 2065, 2325, 2429, 2488, 2490
OAK 2106
OAK LEAVES 354, 1251, 1492
OAK SEEDLINGS 1835
OCCIDENTALIS 2248
OCEAN 560, 757, 2061, 2172, 2633
OCEAN-ATMOSPHERE MODEL 853, 905, 1264, 2609
OCEANIC UPTAKE 857, 2152
OF-THE- ART 1151
OILSEED RAPE 695, 1166
OLD-FIELD ANNUALS 409
OLD-FIELD COMMUNITY 2532
OLD-FIELD MICROCOSMS 2279
OLD- FIELD PERENNIALS 6, 155, 1085, 1664, 1836, 1857, 1969, 2421, 2510
OLD-GROWTH FOREST 703
OLIGOCHAETA 2668
OLIGOTROPHIC PINE FEN 2089
OMEGA- HYDROXYLASE 1649
ONISCUS-ASELLUS 436

ONTARIO 191
OPEN-AIR FUMIGATION 32, 637, 1426
OPEN-PATH 1735
OPEN-TOP CHAMBER 898
OPEN-TOP CHAMBERS 32, 56, 107, 121, 229, 347, 558, 567, 627, 793, 897, 1129, 1130, 1134, 1440, 1545, 1587, 1749, 1824, 1825, 1870, 1961, 2029, 2066, 2262, 2510, 2515
OPTICAL- THICKNESS 1118
OPTIMIZATION 359, 1686
OPUNTIA FICUS INDICA 52, 767, 1701, 1727, 1933, 2600, 2612, 2687, 2688
OPUNTIA-STRICTA 2262
ORANGE 587, 1828
ORANGES 1930
ORANGE TREE LEAVES 2095
ORDERED DEVELOPMENT 1664
ORGANIC-ACIDS 125, 738
ORGANIC-CARBON 329, 1335, 1526, 1787, 2153, 2469, 2554
ORGANIC-COMPOUND EMISSIONS 426
ORGANIC-MATTER 54, 139, 196, 277, 310, 341, 435, 439, 445, 598, 605, 758, 852, 903, 945, 954, 956, 1029, 1030, 1176, 1286, 1370, 1391, 1492, 1502, 1578, 1698, 1711, 1794, 1795, 1894, 1985, 2212, 2286, 2321, 2393, 2433, 2450, 2462, 2668
ORGANIC-MATTER DYNAMICS 1151, 1525, 1784, 2354
ORGANIC-MATTER TURNOVER 1265, 1821
ORGANIC PHOSPHORUS 126
ORGANIZATION 875, 1619
ORIENTED GROWTH 140
ORYZA-SATIVA 28, 366, 1153, 1154, 1744, 2484, 2548, 2607, 2705
ORYZA SATIVA L 103-105, 207, 1054
OSMOREGULATION 1838
OSMOTIC ADJUSTMENT 33, 117, 775, 1757, 1835, 1838, 1843, 2481
OUTBREAKS 302
OUTCROSSED PROGENY 1878
OVULE ABORTION 641
OXIDASE 763, 764, 1272, 1472, 1979, 2658
OXIDATION 252, 2161
OXIDATIVE BURST 2490
OXIDATIVE- PHOSPHORYLATION 980
OXIDATIVE STRESS 87, 2585
OXIDATIVE STRESS TOLERANCE 63
OXIDE FLUX 2593
OXIDES 957, 2133
OXYGEN 368, 499, 1273, 1470, 1548, 1610, 2410, 2473, 2484, 2633, 2670
OXYGENASE 178, 247, 741, 878, 1505, 2001, 2098, 2103, 2208
OXYGEN CONCENTRATION 1989
OXYGEN EVOLUTION 285, 2655
OXYGEN- EXCHANGE 231, 444, 677

OXYGENIC PHOTOSYNTHESIS 2047
OXYGEN PARTIAL PRESSURES 158
OXYGEN PERMEABILITY 2186
OZONE 107, 109, 194, 235, 672, 760, 849, 879, 909, 1052, 1103, 1144, 1218, 1234, 1366, 1426, 1503, 1618, 1720, 1749, 1819, 1831, 1920, 2066, 2068, 2196, 2325, 2468, 2487, 2628
OZONE ALTERS 120
OZONE DEPLETION 1139, 1841, 2293, 2333
OZONE EXPOSURE 428
OZONE POLLUTION 1133
OZONE STRESS 1505
OZONE TOLERANCE 1112
OZONE UPTAKE 269
PACIFIC NORTHWEST 753, 1752
PACIFIC-OCEAN 1648
PACKAGE 1434
PADDY FIELDS 982
PADDY RICE 1744
PALISADE TISSUE 1703
PALUSTRIS 1899
PANICUM PANICUM-TEXANUM 1792
PANICUM-VIRGATUM 264, 1188
PAPER BIRCH 217, 413, 721, 958, 1168, 1303, 1363, 2398
PAR ABSORPTION 1514, 1515
PARAMETERIZATION 1419
PARAMETERIZATIONS 1118
PARAMETERS 874, 2389
PARAMETRIZATION 452
PARASITIC PLANT 1477
PAR INTERCEPTION 1700, 1705
PARMELIA-SULCATA 109
PAROPSIS-ATOMARIA OLIVIER 1290
PARSLEY LEAVES 2658
PARTIAL-PRESSURE 44, 281, 425, 733, 790, 868, 1056, 1407, 1430, 1459, 1467, 1711, 1866, 2219, 2272, 2278, 2546, 2612, 2624, 2625
PARTICLE-SIZE 945
PARTICLE-SIZE FRACTIONS 1265
PARTICULATE 1358
PARTITIONING EFFICIENCY 2351
PARTITIONING MODEL 697
PARTS 2665
PASCOPYRUM-SMITHII 843
PASCOPYRUM-SMITHII C-3 699, 700, 952, 1301, 2510, 2699
PAST 2 CENTURIES 44, 61, 453, 513, 781, 1009, 1251, 1817, 2458, 2639
PASTURE 1038, 1076, 1599, 1998, 2662
PASTURE TURVES 669, 1099, 1440, 2039, 2145, 2146

PAST VITALITY 159
PATCHY ENVIRONMENTS 1293
PATHWAY 223, 1020, 1776, 2399
PATHWAYS 751, 2331
PATTERN 779
PATTERNS 111, 149, 189, 314, 432, 674, 690, 1069, 1185, 1187, 1276, 1313, 1358, 1389, 1999, 2075, 2097, 2121, 2323, 2340, 2491, 2492
PCC-6714 1625
PCC6803 2031
PCC7942 1463, 2032
PEA 828, 1020
PEACHES 1973
PEA-CHLOROPLASTS 1626
PEAR 1623
PEAR FRUIT 751, 1273, 1776
PEARL-MILLET 1611
PEA-SEEDLINGS 1622
PEAT 2303
PEAT BOGS 1061
PEATLANDS 1885, 2088, 2303
PEAT MOSSES 1058, 1059
PEDUNCLE PERFUSION 2
PEDUNCULATUS 331
PENDULA ROTH 1600-1602
PENETRATION 2604
PENICILLIN FERMENTATIONS 1500
PEPPER 557, 2314
PERENNE CV S23 1288
PERENNIAL RYEGRASS 335, 658, 719, 784, 834, 1093, 1440, 1457, 1599, 1629, 1651, 1667, 1683, 1698, 1787, 1902, 1911, 2193, 2249, 2622
PERENNIALS 76, 547, 2675
PERFORMANCE 217, 270, 271, 333, 413, 533, 584, 670, 721, 722, 866, 911, 958, 1102, 1303, 1444, 1453, 1457, 1477, 1970, 2015, 2111, 2271, 2277, 2577
PERIODS 339
PERMAFROST 1737
PERMEABILITY 1144, 2535, 2680
PERMIAN TRIASSIC BOUNDARY 166
PERSISTENCE 1293
PERSPECTIVE 567, 638, 1519, 1755, 2195, 2583
PERSPECTIVES 855
PERTURBATIONS 2686
PESTS 2586
PETROSELINUM- HORTENSE 11
PH 207, 763, 1041, 1421, 1776, 2430
PHAEOPHYTA 705

PHALARIS-PARADOXA 891
PHANEROZOIC TIME 162
PHARBITIS 942, 1951, 1953, 1954, 2511, 2682
PHASEOLUS-VULGARIS 451, 643, 981, 1245, 1324, 1441, 1532, 2128, 2221, 2365, 2420, 2468, 2496, 2684
PHASEOLUS-VULGARIS L 53, 96, 213, 237, 238, 244, 254, 362, 511, 565, 589, 704, 792, 794, 1235, 1329, 1429, 1431, 1433, 1466, 1504, 1586, 1646, 1681, 1829, 1963, 1965, 1968, 2098, 2099, 2101, 2165, 2274, 2275, 2338, 2366, 2368, 2460, 2620, 2631 PHENOLIC-COMPOUNDS 355, 721
PHENOLIC CONSTITUENTS 22, 23, 1102
PHENOLIC GLYCOSIDES 1362, 1491
PHENOLICS 939, 1213, 1266
PHENOLOGY 145, 183, 853, 1074, 1261
PHENOTYPIC PLASTICITY 314, 2466, 2685
PHENYLALANINE AMMONIA-LYASE 940, 1090
PHENYLPROPANOID METABOLISM 1090
PHLEUM-PRATENSE 1722
PHLOEM SAP 555
PHLOEM TRANSPORT 2220
PHLOX 201
PH MICRO-ELECTRODES 2105
PHOSPHATASE-ACTIVITIES 1577
PHOSPHATASE-ACTIVITY 505
PHOSPHATE 125, 134, 1098, 1826, 2276
PHOSPHATE ABSORPTION 136
PHOSPHATE CONCENTRATION 1681
PHOSPHATE NUTRITION 1743
PHOSPHATE STATUS 146, 2254
PHOSPHATE SYNTHASE 1532
PHOSPHATE SYNTHASE ACTIVITY 1624
PHOSPHOENOLPYRUVATE 2341
PHOSPHOENOLPYRUVATE CARBOXYLASE 253, 266, 454, 457, 458, 480, 795, 1259, 2174, 2217, 2455, 2464
PHOSPHOENOLPYRUVATE CARBOXYLASE ACTIVITY 1257, 2499
PHOSPHOGLUCOMUTASE 2205
PHOSPHOGLYCOLATE 444
PHOSPHORUS 36, 146, 222, 379, 575, 772, 928, 1079, 1100, 1315, 1328, 1371, 1386, 1410, 1464, 1535, 1581, 1836, 1863, 1889, 1896, 1900, 1915, 2095, 2149, 2478, 2504-2506, 2673
PHOSPHORUS DEFICIENCY 473, 824, 1327, 1342, 1367, 1571, 1717, 2408
PHOSPHORUS DYNAMICS 1138
PHOSPHORUS-NUTRITION 123, 192, 1372
PHOSPHORUS UPTAKE 773
PHOSPHORYLATION 2209
PHOTOAUTOTROPHIC GROWTH 1215
PHOTOBIONTS 108

PHOTOCHEMICAL EFFICIENCY 486, 1382
PHOTOCURRENTS 1697
PHOTOINHIBITION 63, 128, 237, 285, 559, 675, 677, 935, 1276, 1307, 1379, 1728, 2014, 2016, 2253, 2355, 2473, 2569
PHOTON FLUX DENSITIES 2222
PHOTON FLUX- DENSITY 11, 101, 519, 621, 1517, 1536, 1636, 1829, 1830, 2293, 2333, 2489
PHOTON YIELD 2135
PHOTOOXIDATIVE STRESS 2164
PHOTOPERIOD 847, 1317, 1333, 1383, 1544, 1624, 1702, 1936, 2228, 2229, 2448, 2578
PHOTOPERIODS 316, 317, 1420, 2562
PHOTOREDUCTION 1826
PHOTORESPIRATION 211, 444, 486, 829, 1847, 1989, 2234, 2242, 2339, 2473
PHOTORESPIRATORY MUTANT 2300
PHOTOSYNTHATE 1420
PHOTOSYNTHESIS 2, 7, 31, 34, 40, 41, 45, 46, 55, 56, 86, 93, 103, 104, 108-111, 117, 120, 125, 126, 128, 133, 136, 142, 146, 147, 156, 162, 163, 167, 173, 174, 183, 185, 204, 205, 209, 210, 214, 221, 222, 230, 235, 238, 247, 249, 255, 256, 259, 263, 272, 281, 289, 292, 295, 298, 310, 315, 317, 318, 330, 335, 336, 339, 343, 345, 356, 373, 387, 391, 399, 402, 403, 418, 420, 425, 444, 451, 452, 467, 469, 470, 472, 477, 479, 482, 485, 492, 493, 497, 508, 512, 517, 518, 520, 529, 547, 548, 559, 586, 587, 597, 599, 608, 612, 621, 627, 632, 636, 637, 648, 649, 652, 653, 657, 661, 672, 678-680, 687-689, 694, 698, 702, 705, 706, 708, 709, 719, 720, 726, 729, 730, 735, 752, 767, 769, 779, 788, 790, 795, 802, 804-806, 808, 815, 833-835, 839, 844, 868, 874, 878, 886, 891, 896-898, 907, 914, 922, 928, 930, 935, 938, 947, 950, 964, 970, 981, 986, 1016, 1026, 1035, 1038, 1041, 1043, 1044, 1048, 1054, 1059-1061, 1067, 1068, 1085, 1091-1093, 1098, 1111, 1112, 1117, 1125-1127, 1187, 1207, 1219, 122
0, 1228, 1253, 1255, 1256, 1260, 1276, 1277, 1294, 1297, 1301, 1305, 1311, 1324, 1339, 1342, 1343, 1345, 1349, 1358, 1369, 1392, 1395, 1403, 1428, 1430, 1446, 1459, 1460, 1463, 1464, 1468, 1479, 1483, 1495, 1498, 1503, 1504, 1511, 1514, 1525, 1543, 1556, 1557, 1574, 1581, 1584, 1586, 1596, 1598, 1600-1602, 1610, 1615, 1618, 1620, 1627, 1635, 1642, 1661, 1662, 1670, 1683, 1686, 1688, 1707, 1713, 1723, 1749, 1752, 1757, 1766, 1771, 1772, 1776, 1789, 1797, 1799, 1803, 1818, 1822, 1826, 1837, 1854, 1855, 1858, 1863, 1865, 1869, 1872, 1873, 1887, 1888, 1895, 1900, 1906, 1912, 1913, 1918, 1928, 1929, 1936, 1938, 1947, 1952, 1954, 1958, 1963, 1964, 1967, 1974, 1977, 1978, 1984, 1996, 2001, 2006, 2007, 2018, 2021, 2022, 2031, 2046, 2054, 2055, 2057, 2059, 2060, 2062, 2064, 2080, 2081, 2088, 2098, 2103, 2105, 2109, 2112, 2114, 2122, 2124, 2126, 2139, 2147, 2150, 2165, 2179, 2185, 2190, 2201, 2204, 2205, 2211, 2214, 2215, 2221, 2230, 2243, 2249, 2253-2255, 2259, 2273, 2278, 2294-2296, 2299,
2302, 2308, 2313, 2314, 2316, 2320, 2323, 2326, 2327, 2332, 2335-2337, 2343, 2350, 2355, 2357,
2360, 2377, 2382, 2401, 2411, 2413, 2419, 2424, 2426, 2430, 2435, 2436, 2438, 2453, 2456, 2460, 2463, 2476, 2479, 2481, 2483, 2485, 2497, 2501, 2511, 2517, 2521, 2523, 2527, 2530, 2538, 2548, 2552, 2557, 2559, 2563, 2567, 2570, 2576, 2581, 2591, 2592, 2605, 2610, 2615, 2622, 2625, 2626, 2632, 2635, 2646, 2649, 2651, 2687-2689, 2705, 2706
PHOTOSYNTHESIS- NITROGEN RELATIONS 753, 1553
PHOTOSYNTHETIC ACCLIMATION 29, 44, 82, 116, 129, 150, 157, 181, 188, 195, 347, 483,

519, 562, 577, 595, 759, 781, 792, 816, 879, 893, 931, 1007-1012, 1015, 1124, 1147, 1148, 1176, 1190, 1201, 1204, 1230, 1306, 1327, 1337, 1341, 1362, 1366, 1367, 1405, 1413, 1467, 1488, 1490, 1533, 1535, 1546, 1568, 1580, 1616, 1704, 1706, 1732, 1763, 1839, 1851, 1889, 1891-1893, 1897, 1909, 1966, 2028, 2069, 2100, 2102, 2136, 2138, 2338, 2359, 2375, 2379, 2386, 2397, 2512, 2516, 2550, 2569, 2587, 2589, 2656, 2704
PHOTOSYNTHETICALLY ACTIVE RADIATION 1840
PHOTOSYNTHETIC APPARATUS 875, 1307, 1962
PHOTOSYNTHETIC CAPACITY 288, 428, 733, 809, 1284, 1401, 1466, 1516, 1798, 1843, 2017, 2412, 2415
PHOTOSYNTHETIC CHARACTERISTICS 282, 540, 919, 1215, 1454, 2041, 2246, 2247
PHOTOSYNTHETIC CO2 ASSIMILATION 1796
PHOTOSYNTHETIC CO2 FIXATION 42
PHOTOSYNTHETIC ELECTRON FLOW 486
PHOTOSYNTHETIC ELECTRON-TRANSPORT 28, 92, 617, 988
PHOTOSYNTHETIC INDUCTION STATE 1189
PHOTOSYNTHETIC INHIBITION 18, 283, 362, 385, 476, 563, 796, 1314, 1571, 1645, 1862, 2143, 2406, 2455, 2639
PHOTOSYNTHETIC METABOLISM 1020
PHOTOSYNTHETIC OXYGEN EVOLUTION 148
PHOTOSYNTHETIC PERFORMANCE 88
PHOTOSYNTHETIC PERIOD DURATION 1624
PHOTOSYNTHETIC PROPERTIES 1703
PHOTOSYNTHETIC RATE 943, 1248, 2116, 2213
PHOTOSYNTHETIC REACTIONS 2090
PHOTOSYNTHETIC REINVIGORATION 187
PHOTOSYNTHETIC RESPONSE 30, 168, 178, 369, 409, 754, 1139, 1664, 1859, 1927, 2515, 2518, 2697
PHOTOSYNTHETIC RESPONSES 96, 936, 1133, 1135
PHOTOSYSTEM 28, 50, 128, 486, 639, 675, 731, 750, 770, 869, 891, 1106, 1385, 1454, 1626, 1697, 2013, 2135, 2298
PHOTOSYSTEM- 2 1562
PHOTOSYSTEM-I 285
PHOTOSYSTEM-II ACTIVITY 988, 1130
PHYCOBILISOME STRUCTURE 1619
PHYSICAL-PROPERTIES 1265
PHYSIOLOGICAL DISORDERS 571
PHYSIOLOGICAL INDICATORS 2409
PHYSIOLOGICAL INVESTIGATIONS 1276
PHYSIOLOGICAL-RESPONSES 1706, 2136
PHYSIOLOGY 3, 229, 266, 345, 470, 668, 680, 686, 707, 830, 986, 1026, 1072, 1095, 1112, 1162, 1178, 1180, 1238, 1243, 1349, 1439, 1568, 1976, 2122, 2169, 2185, 2344, 2414, 2550, 2559, 2591, 2702
PHYTOCHEMISTRY 85, 218, 223, 584, 1361, 1363, 2045, 2271
PHYTOCHROME 11, 929, 930, 2092, 2330
PHYTOPLANKTON 1071, 1679, 2286, 2472

PICEA 2004
PICEA-ABIES 95, 1445, 1510, 1680
PICEA-ABIES L 107, 119, 478, 639, 1129, 1134, 1257, 1366, 1504, 1847, 2134, 2164-2166, 2324, 2429
PICEA MARIANA 314
PICEA-RUBENS 2149
PICEA-SITCHENSIS 554, 753, 821, 2002, 2305, 2543
PIGMENTATION 939
PIGMENTS 2092
PIGWEED AMARANTHUS-RETROFLEXUS 1791
PIMA COTTON 1943, 1945
PINE 129, 159, 304, 435, 746, 780, 1039, 1252, 1413, 1746, 1748, 1952, 2004, 2121, 2174, 2344
PINE CANOPY 1375
PINE FOREST 39
PINE NEEDLE LITTER 446, 1138
PINE NEEDLES 2324
PINE PINUS-PONDEROSA 347
PINE PINUS-SYLVESTRIS 1381
PINE PINUS- TAEDA 897
PINE PLANTATIONS 300, 1122, 1921
PINE SEEDLINGS 388, 389, 1484, 2054, 2487, 2488
PINNATUM L BEAUV 2477
PINUS-CONTORTA 2384
PINUS-PINASTER AIT 1136
PINUS-RADIATA 140, 473, 824, 930, 1007, 1516, 1571, 1717
PINUS-RADIATA FOLIAGE 1176
PINUS-RADIATA SEEDLINGS 1078
PINUS SYLVESTRIS 590
PINUS-TAEDA 324, 595, 724, 2380, 2531
PINUS TAEDA L 1200, 1981, 2584
PINUS-TAEDA SEEDLINGS 6, 74, 76, 156, 241, 337, 349, 476, 759, 906, 991, 1072, 1196, 1236, 1326, 1336, 1342, 1344, 1531, 1585, 1590, 1836, 1862, 1902, 1964, 1975, 2012, 2029, 2076, 2284, 2290, 2293, 2388, 2396, 2408, 2421, 2600
PINUS-TAEDA TREES 1390
PISOLITHUS-TINCTORIUS 1213
PISUM-SATIVUM 28, 266, 326, 388, 389, 966, 1750, 2290, 2333, 2344, 2367, 2639, 2679
PISUM SATIVUM L 237, 1166
PIT ORGAN 2262
PLAINS 1832
PLANT 48, 145, 197, 200, 211, 219, 264, 315, 413, 460, 509, 567, 690, 699, 722, 738, 740, 765, 769, 791, 962, 1045, 1046, 1048, 1092, 1100, 1183, 1185, 1209, 1238, 1261, 1317, 1360, 1389, 1414, 1457, 1494, 1553, 1690, 1693, 1705, 1898, 1933, 2012, 2141, 2147, 2176, 2278, 2364, 2443-2445, 2464, 2521, 2552, 2612, 2684
PLANT-AGE 2465
PLANTAGO 1298

PLANTAGO-LANCEOLATA 2261, 2307
PLANTAGO-MAJOR 343, 1055, 1267, 1388, 2056, 2159, 2273, 2435, 2436, 2450
PLANTAGO-MAJOR L 2011
PLANTATIONS 1081, 2189, 2347
PLANT CANOPIES 111
PLANT-CELL GROWTH 653, 717
PLANT-CELLS 2105, 2544, 2655
PLANT- COMMUNITIES 65, 870, 1176, 1203, 1859, 2197
PLANT COMMUNITY 530
PLANT COMPETITION 2293
PLANT CUTICLES 1144
PLANT DRY- WEIGHT 1851
PLANTED WHITE-PINE 1269
PLANT FUNCTIONAL TYPES 678, 1391
PLANT GROWTH 16, 31, 33, 74, 91, 101-103, 106, 119, 150, 278, 396, 403, 425, 470, 493, 535, 558, 585, 643, 650, 724, 736, 775, 833, 845, 860, 901, 928, 942, 943, 971, 973, 977, 981, 1107, 1157, 1231, 1291, 1371, 1453, 1458, 1498, 1502, 1507, 1535, 1538, 1557, 1620, 1654, 1666, 1667, 1682, 1752, 1792, 1820, 1829, 1849, 1899, 1936, 1954, 1975, 1983, 2024, 2028, 2055, 2063, 2081, 2084, 2114, 2116, 2117, 2142, 2183, 2193, 2231, 2290, 2343, 2349, 2419, 2428, 2449, 2483, 2520, 2533, 2534, 2543, 2561, 2563-2565, 2567, 2592, 2618, 2619, 2662
PLANT-GROWTH ANALYSIS 1324
PLANT- GROWTH RATE 1090
PLANT-HERBIVORE INTERACTIONS 2555
PLANTLETS 583, 665, 872, 1479, 1628, 2243
PLANTLETS INVITRO 515
PLANT- MATERIAL 113, 945, 1062
PLANT MATERIALS 2442
PLANT-MEDIATED INTERACTIONS 2111
PLANT-MITOCHONDRIA 1020, 1776
PLANT NUTRITION 132, 213, 621, 1025
PLANT-PLANT INTERACTIONS 1235, 2512
PLANT POLYPHENOLS 224
PLANT-POPULATIONS 1589, 1651, 2541
PLANT RESIDUES 14
PLANT RESPIRATION 290, 298, 325, 1134, 1558, 1979, 2377, 2485, 2622, 2646
PLANT-RESPONSE 1521
PLANT-RESPONSES 116, 142, 174, 180, 193, 194, 214, 229, 244, 255, 303, 311, 334, 433, 615, 663, 697, 782, 787, 793, 824, 826, 879, 881, 882, 933, 950, 990, 1044, 1097, 1190, 1251, 1252, 1282, 1440, 1536, 1549, 1599, 1600, 1604, 1615, 1616, 1630, 1715, 1723, 1888, 1894, 1896, 1900, 2000, 2070, 2073, 2091, 2107, 2144-2146, 2188, 2322, 2370, 2380, 2381, 2393, 2452, 2454, 2463, 2652
PLANT-ROOTS 126, 2088
PLANT-ROOT SYSTEMS 202, 1460
PLANTS 4, 11, 13, 19, 25, 29, 41, 46, 47, 53, 58, 70, 71, 75, 80, 83, 86, 94, 96, 108, 115, 118, 120, 123, 124, 133-136, 138, 147, 151, 156, 162, 169, 170, 195, 196, 201, 220, 231, 238, 251,

256-258, 269, 273, 286, 289, 296, 317, 319, 320, 327, 333, 340, 342, 352, 360, 368, 370, 371, 373, 374, 377, 381, 382, 386, 393, 397, 399, 400, 421, 430, 436, 438, 450, 456, 457, 466-468, 472, 477, 481, 485, 490, 492, 500-502, 505, 523, 537, 538, 541, 547, 555, 557, 561, 575, 577, 579, 584, 594, 603, 613, 617, 627, 639, 641, 654, 658, 667, 669, 676, 677, 681, 686, 687, 689, 694, 703, 705, 713, 733, 741, 744, 745, 754, 772, 789, 790, 795, 798, 803, 804, 810, 820, 828, 835, 837, 844, 847, 849, 865, 867, 871, 886, 887, 909, 913, 920, 921, 930, 935, 957-959, 963, 965, 966, 984-986, 997, 1001, 1010, 1015, 1018, 1019, 1022, 1035, 1036, 1038, 1047, 1050, 1064-1066, 1068-1070, 1076, 1091, 1096, 1098, 1106, 1121, 1124, 1137, 1138, 1140, 1147, 1148, 1161, 1165, 1167-1170, 1179, 1191, 1197, 1206, 1218, 1
230, 1237, 1253, 1270, 1278, 1289, 1290, 1297, 1301, 1305, 1306, 1328, 1332, 1335, 1343, 1349, 1361, 1363, 1365, 1386, 1398, 1403, 1410, 1412, 1413, 1421, 1422, 1424, 1441, 1442, 1447, 1455, 1481, 1487, 1490, 1505, 1540, 1543, 1554, 1564, 1570, 1579-1581, 1590, 1593, 1595, 1601, 1607, 1623, 1624, 1642, 1645, 1653, 1661-1663, 1672, 1680, 1685, 1687, 1689, 1698, 1702, 1703, 1707, 1722, 1727, 1740, 1744, 1755, 1756, 1759, 1761, 1763-1765, 1770, 1798, 1810, 1811, 1814, 1816, 1823, 1837, 1839, 1843, 1847, 1852, 1856, 1857, 1866, 1869, 1874, 1878, 1880, 1883, 1889, 1901, 1918, 1929, 1932, 1934, 1938, 1939, 1941, 1945, 1952, 1958, 1959, 1963, 1968, 1969, 1978, 1981, 1988, 1996, 2003, 2004, 2006, 2019, 2021, 2039, 2043-2045, 2051, 2057, 2059, 2068, 2082, 2086, 2100, 2102, 2132, 2136-2138, 2148, 2155, 2162, 2163, 2171, 2174, 2179, 2189, 2191, 2195, 2199, 2201, 2202, 2208, 2215, 2218, 2221, 2230, 2232, 2242, 2246, 2247, 2252, 2256, 2266, 2269-2272, 2279, 2281, 2286, 2291, 2299, 2302, 2308,
2312, 2323, 2326, 2330, 2338, 2340, 2341, 2344, 2346, 2351, 2352, 2365, 2368, 2375, 2404, 2415, 2426, 2437-2440, 2456, 2459, 2466, 2494, 2496, 2499, 2511, 2517, 2523, 2530, 2540, 2549, 2559, 2569, 2587, 2598, 2602, 2603, 2611, 2625, 2630, 2631, 2645, 2654, 2671, 2679, 2680, 2682, 2685, 2687, 2690, 2696, 2697, 2699, 2702, 2706-2709, 2712
PLANTS CULTURED INVITRO 1871
PLANT SILENE LATIFOLIA 1095
PLANT-TISSUE 1087, 2374, 2595, 2597
PLANT WATER RELATIONS 1187
PLASMA-MASS SPECTROMETRY 1199
PLASMA-MEMBRANE 262, 1281, 2011, 2544
PLASMODESMATAL FREQUENCY 1393
PLASTICITY 361, 1489
PLASTID PHOSPHOGLUCOMUTASE 599
PLASTID TRANSFORMATION 2576
PLATINIZED CHLOROPLASTS 1697
PLUTELLA-XYLOSTELLA 1114
PNEUMOPERITONEUM 232
POA-PRATENSIS 1936
POD WALL 1166
POLAR 1141
POLAR ICE CORES 582
POLAR LIPIDS 326
POLAR STRATOSPHERIC CLOUDS 2500
POLLEN 451, 978, 979, 2292

POLLUTANTS 672, 1920, 2454
POLLUTION 683, 899, 1118, 2133
POLLUTION GRADIENT 1455
POLYACANTHA CACTACEAE 1721
POLYAMINES 207
POLY BETA HYDROXYBUTYRATE 600, 2000
POLYGALACTURONASE 2251
POLYGONUM-CUSPIDATUM 2323
POLYMERIC LIGNIN 112
POLYMORPHIC DIASPORES 1636
POLYPHENOL OXIDASE 223
POLYSACCHARIDE 2668
POLYSACCHARIDES 1290
PONDEROSA PINE 54, 343, 427, 593, 950, 1055, 1348, 1402, 1747, 2348, 2370, 2375, 2381
PONDEROSA PINE- SEEDLINGS 1718, 2134
PONTOSCOLEX-CORETHRURUS GLOSSOSCOLECIDAE 1286
POOL DILUTION 199, 200
POOL SIZES 1963, 1965, 2103
POOR FEN 1575
POPLAR 2489, 2582
POPLAR CLONES 169, 348, 651, 655, 824, 1250, 1899, 1902, 1915, 1918, 1919, 1980, 2386, 2620
POPLAR POPULUS 1237
POPULATION 220, 2271
POPULATION-DYNAMICS 219, 313, 1271, 1651, 1992
POPULATION GROWTH 2477
POPULATIONS 59, 85, 534, 555, 800, 898, 1157, 1411, 1860, 1878, 2403, 2464, 2542, 2552, 2662
POPULUS 382, 1106
POPULUS- EURAMERICANA 353
POPULUS-TREMULOIDES 1112
POPULUS-TREMULOIDES MICHX 895, 1245
POPULUS X EURAMERICANA 535
POROMETRY 993
PORTABLE CHAMBER 32
POSTHARVEST APPLICATION 1930
POSTHARVEST DECAY 158
POSTHARVEST PHYSIOLOGY 1469
POST- HARVEST QUALITY 1119
POSTTRANSLATIONAL REGULATION 725
POTASSIUM 1624, 1847
POTATO 357, 443, 803, 1384, 2616
POTATO GROWTH 2561
POTATO PLANTS 854, 893, 2283
POTATO-TUBERS 643, 1573

POTENTIAL CHANGES 329, 948
POTENTIALS 741
POWDERY MILDEW 915, 2350
PRAIRIE 1397, 1580
PRAIRIE ECOSYSTEM 1582
PRAIRIE GRASS 2018
PRAIRIE WETLANDS 1280
PRECIPITATION 646, 647, 999, 1212, 1729, 2172, 2634
PRECIPITATION FLUCTUATIONS 2469
PRECIPITATION VARIABILITY 1524
PRECLIMACTERIC TOMATO 1471
PRE-CONCENTRATION EFFICIENCY 1244
PREDICT 1220
PREDICTING RESPONSES 1401
PREDICTION 1706
PREDICTIONS 1700, 1951
PREFERENCE 271
PREFERENCES 1097
PRENUCLEAR MINITUBERS 1385
PRESENT TECHNOLOGY 644, 1194
PRESSURE 206, 1590, 1801, 2378
PRESSURE PROBE 654
PRESSURE-VOLUME 2386
PRICKLY PEAR CACTUS 1706
PRIMARY PENETRATION 915
PRIMARY PRODUCTIVITY 277, 1921
PRIMORDIUM INITIATION 1333
PRINCIPLES 1434
PROANTHOCYANIDINS 331
PROBABILITY 821
PROCESS MODEL 1547
PRODUCTION ECOLOGY 1992
PRODUCTIVITY 82, 97, 142, 143, 180, 292, 417, 431, 469, 470, 481, 485, 493, 508, 509, 517, 527, 559, 591, 615, 627, 638, 653, 657, 709, 714, 715, 745, 784, 826, 832, 836, 865, 925, 1010, 1015, 1027, 1035, 1043, 1046, 1113, 1163, 1292, 1453, 1460, 1488, 1497, 1501, 1513, 1514, 1525, 1554, 1557, 1580, 1685, 1701, 1704, 1713, 1830, 1833, 1846, 1925, 1934, 1936, 2168, 2189, 2195, 2277, 2359, 2374, 2419, 2483, 2526, 2527, 2547, 2564-2567, 2688
PROFILES 799
PROGRAM 396
PROJECT 452
PROLIFERATION 65, 666
PROLINE ACCUMULATION 1871
PROPAGATION 386, 611, 666
PROPYLENE 764
PROSOPIS 2364

PROSOPIS- GLANDULOSA 2555
PROTEACEAE 1535, 2169
PROTECT 193
PROTECTION 326
PROTECT VEGETATION 1233
PROTEIN 248, 331, 502, 741, 762, 764, 912, 1797, 1939, 2006, 2021, 2043, 2044, 2187, 2208, 2251, 2456
PROTEIN ACCUMULATION 1983
PROTEIN-KINASE 2458
PROTEIN PHOSPHATASE 262, 1330
PROTEIN- PHOSPHORYLATION 1473, 1910
PROTEINS 640, 681, 715, 719, 1070, 1546, 1554, 1754, 1927, 2201-2203
PROTEIN-SYNTHESIS 207
PROTEOID ROOTS 125
PROTOPLASTS 280, 980
PRUNUS-AVIUM 82
PSEUDOCYPHELLARIA 2320
PSEUDOMONAS 1452
PSEUDOMONAS- FLUORESCENS 487, 850, 1787
PSEUDOMONAS-OLEOVORANS 1649
PSEUDOPLUSIA-INCLUDENS 2595
PUERTO-RICO 2212
PURIFICATION 762-764, 2217
PUTRESCINE 1472
PYRUVATE 1259
PYRUVATE DECARBOXYLASE 1119, 1623
QUAKING ASPEN 1362, 1491
QUALITY 48, 235, 438, 441, 685, 739, 849, 1076, 1089, 1120, 1179, 1181, 1273, 1279, 1283, 1303, 1434, 1470, 1474, 1617, 1696, 1730, 1782, 2009, 2111, 2237, 2238, 2314, 2422, 2443, 2465, 2471
QUANTIFICATION 1069
QUANTITATIVE GENETICS 2331
QUANTUM YIELD 63, 92, 128, 283, 363, 598, 675, 677, 731, 830, 988, 1017, 1018, 1132, 1379, 1385, 1514, 1685, 1754, 1868, 2014, 2015, 2090, 2298, 2508, 2520, 2531, 2613
QUANTUM YIELDS 312, 869, 2135, 2516
QUARANTINE PROCEDURE 2169
QUATERNARY 2286
QUATERNARY LANDSCAPE DYNAMICS 1435
QUEBEC APPALACHIANS 1510
QUERCUS 2385
QUERCUS-ALBA 155, 202, 388, 478, 479, 530, 603, 1328, 1354, 1457, 1496, 1581, 1712, 1750, 1759, 2000, 2051, 2079, 2149, 2257, 2258, 2260, 2261, 2344, 2358, 2359, 2362, 2502-2506, 2600, 2643, 2648, 2671
QUERCUS-ROBUR 2388
QUERCUS-ROBUR L 584, 2165

QUERCUS-ROBUR SEEDLINGS 1427
QUERCUS-RUBRA L 50
RABBITS 2267
RADIATA 1909, 2118
RADIATA D-DON 418, 421, 824, 991, 1007, 1327, 1862, 1863, 2421, 2480
RADIATION 11, 193, 226, 783, 840, 924, 1194, 1450, 1528, 1557, 1656, 2068, 2246, 2417, 2656
RADIATION BUDGET 1224
RADIATION BUDGET EXPERIMENT 996
RADIATIVE SURFACE-TEMPERATURE 1155, 1156
RADIOCARBON 852
RADISH 1966, 2685
RADISH RAPHANUS-RAPHANISTRUM 2541
RAFFINOSE FAMILY OLIGOSACCHARIDES 280
RAIN 590
RAINFALL 1512, 2568
RAINFALL EVENTS 1335
RAIN-FOREST 65, 71, 432, 856, 936, 1152, 1309, 1313, 1349, 1391, 1436, 1526, 2017, 2651
RAIN FORESTS 536
RAIN-FOREST TREES 1146, 1386
RAISED BOG 1060, 2659
RANGE 1040
RAPHANISTRUM 1043
RAPHANUS-RAPHANISTRUM 1287, 1444
RAPID MODULATION 679
RASPBERRY 1171, 1650, 2243
RATE-CONSTANT 1307
RATES 384, 441, 445, 686, 858, 873, 1170, 1908, 1939, 2190, 2364, 2678
RATE VARIABILITY 427
RATIO 977
RATIOS 227, 273
RAW HUMUS 447
RAY-FLUORESCENCE SPECTROSCOPY 1940
RBCS 178, 1467, 1556, 2497
RBCS GENES 387
REACTION CENTER PROTEIN 2333
REACTION CENTERS 750, 1619
RECEPTORS 2262
RECONSTITUTION 2411
RECORD 170-172, 177, 179, 184, 999, 1483, 1492, 1738, 1884, 2292
RECOVERY 1728
RED 12, 2092, 2312
RED EDGE 332
REDISTRIBUTION 1755
RED MANGROVE 116

REDOX 1519
REDOX STATE 1625
REDOX SYSTEM 1281
RED RASPBERRY 1818
RED SEAWEEDS 1610
RED SPRUCE 1078, 1228, 1366, 1848, 2324, 2578
RED SPRUCE SAPLINGS 1510
RED SPRUCE SEEDLINGS 305
REDUCED-ACTIVITY 599
REDUCED HUMIDITY 1628
REDUCED TILLAGE 1265
REDUCTASE-ACTIVITY 2254
REDUCTION 66, 127, 455, 456, 464, 499, 829, 855, 1281, 1339, 2659
REDUCTION ACTIVITY 2186
REDUCTION STATE 1382
RED WINTER-WHEAT 1617, 2066, 2067
REFLECTANCE 1450, 1703
REFLEX CONTROL 2267
REGENERANTS 574, 1215, 2357
REGENERATION 1126
REGIMES 1745
REGINA 1317, 2448
REGION 1463, 1648, 2031
REGIONAL-ANALYSIS 5
REGIONAL APPLICATIONS 868, 1525, 1779, 1805, 2638
REGIONAL CLIMATE 1659
REGRESSION 979
REGULATORY PROPERTIES 2655
REHYDRATION 2411
REINVIGORATION 2582
RELATIVE GROWTH-RATE 478, 517, 518, 533, 680, 801, 1230, 1864
RELEASE 441, 1976, 2447, 2522, 2632
REPRODUCTION 1261, 2141, 2542
REPRODUCTIVE ACTIVITY 555
REPRODUCTIVE DEVELOPMENT 1616-1618, 2097
REPRODUCTIVE EFFORT 631, 2531
REPRODUCTIVE GROWTH 30, 402, 2564
REPRODUCTIVE PHENOLOGY 432
REPRODUCTIVE RESPONSES 18
REQUIREMENTS 1288
RESIDUE 37
RESIDUE DECOMPOSITION 2393
RESIDUES 2040
RESISTANCE 129, 299, 915, 1332, 1628, 1892, 1893, 1904, 1970, 2111, 2350, 2490, 2578
RESISTANCES 802, 1275, 1656, 1658

RESOLUTION 285
RESOURCE AVAILABILITY 2043
RESOURCE AVAILABILITY HYPOTHESIS 1090
RESOURCES 1694
RESOURCE USE 6, 151, 2188, 2481
RESPECT 918
RESPIRATION 14, 46, 94, 114, 135, 147, 148, 157, 225, 231, 252, 266, 289, 291, 296, 306, 330, 343, 368, 375, 393, 443, 460, 468, 469, 497, 511, 512, 523, 528, 605, 617, 667, 669, 680, 702, 706, 713, 728, 730, 744, 745, 784, 816, 825, 874, 923, 955, 980, 1018, 1026, 1108, 1121, 1122, 1126, 1174, 1188, 1207, 1241, 1242, 1274, 1348, 1385, 1388, 1399, 1407, 1416, 1417, 1427, 1434, 1460, 1474, 1515, 1557, 1602, 1623, 1647, 1667, 1751, 1789, 1796, 1798, 1818, 1856, 1948, 1964, 2007, 2050, 2051, 2058, 2075, 2081, 2108, 2127, 2139, 2147, 2173, 2230, 2273, 2335, 2347, 2375, 2411, 2435, 2457, 2470, 2479, 2494, 2519, 2543, 2660, 2669, 2682, 2688, 2694, 2709
RESPIRATORY RESPONSES 615
RESPIRED CO2 856
RESPONSES 5, 7, 38, 45, 46, 64, 66, 69-71, 73, 82, 85, 91, 93, 104, 113, 123, 127, 133, 143, 145, 146, 157, 170, 173, 185, 198, 200, 201, 215, 217, 218, 222-224, 232, 235, 238, 242, 251, 252, 259, 263, 276, 286, 287, 289, 292, 295, 297, 310, 314, 316, 317, 321, 322, 327, 332, 339, 340, 344, 349, 352, 373-375, 377, 379, 389, 396, 397, 399, 400, 403, 405, 406, 411, 430, 435-437, 439, 456, 461, 467, 469, 481, 485, 491, 492, 494, 502, 506, 508, 512, 527-529, 531, 533, 541, 542, 547, 554, 559, 572, 573, 575, 577, 585, 595, 600, 607, 613, 618, 635, 638, 644, 650-652, 657, 658, 662, 674, 681, 685-688, 690, 694, 696, 700, 702, 733, 736, 744-747, 752, 759, 766, 771, 780, 789, 791, 796, 800, 810, 811, 828, 832-834, 839, 842, 845, 854, 859-861, 866, 880, 885, 886, 896, 903-905, 911, 921, 923, 925, 926, 932, 934, 935, 943, 946, 952, 958, 960, 962, 964, 965, 971, 981, 984, 985, 987, 1011, 1018, 1023, 1027, 1034-1036, 1039, 1040, 1046-1048, 1050, 1052, 1056, 1061, 1063, 1074, 1081-1083, 1086, 1
092, 1093, 1100, 1107, 1117, 1138, 1140, 1141, 1165, 1168, 1172, 1173, 1187, 1192, 1197, 1202, 1207, 1208, 1224-1226, 1232, 1233, 1248, 1261, 1288, 1290, 1294, 1301, 1303, 1314, 1342, 1343, 1347, 1348, 1352, 1360, 1375, 1382, 1386, 1389, 1390, 1396, 1398, 1399, 1409, 1439, 1441, 1457, 1476, 1484, 1487-1490, 1494, 1499, 1501, 1503, 1504, 1527, 1535, 1565, 1568, 1572, 1580, 1582, 1588, 1591, 1593, 1595, 1601, 1607, 1633, 1634, 1654, 1655, 1663, 1666, 1677, 1686, 1690, 1692, 1693, 1700, 1704, 1705, 1712, 1713, 1719, 1721, 1722, 1745, 1746, 1763, 1764, 1766-1769, 1781, 1786, 1788, 1797, 1803, 1805, 1811, 1816, 1818, 1819, 1838, 1851, 1853, 1855-1857, 1874, 1879, 1883, 1887, 1891-1893, 1895, 1897-1899, 1901, 1912, 1913, 1922, 1925, 1937, 1941-1943, 1945, 1948, 1954, 1955, 1966, 1967, 1970, 1981, 1983, 1986, 1990, 1993, 1996, 1999, 2002, 2003, 2014, 2016, 2017, 2030, 2046, 2048, 2061, 2065, 2066, 2068, 2076, 2082, 2097, 2114, 2117, 2118, 2124, 2126, 2138, 2160, 2166, 2184, 2193, 2196, 2
211, 2214, 2252, 2256, 2257, 2259-2261, 2268, 2272, 2273, 2305, 2308, 2316, 2318, 2323, 2326, 2330, 2335-2337, 2343, 2347, 2358, 2369, 2371, 2376-2378, 2398, 2405, 2406, 2408, 2413, 2416-2418, 2424, 2435, 2437, 2439, 2443, 2453, 2457, 2470, 2478, 2481, 2490, 2496, 2502-2506, 2514, 2517, 2519, 2522, 2530, 2534, 2538, 2547, 2549, 2550, 2552, 2553, 2583, 2604, 2605, 2612, 2613, 2627, 2630, 2631, 2637, 2645, 2648, 2654, 2664, 2671, 2673, 2675, 2682, 2690, 2696, 2698, 2699, 2704, 2706

RESTRICTION 195, 1488, 1490
RETENTION 1942
RHIZOBIA 464
RHIZOBIUM 355
RHIZOSPHERE 54, 134, 321, 505, 528, 760, 782, 791, 799, 932, 1097, 1182, 1183, 1332, 1348, 1411, 1484, 1750, 1897, 1993, 1995, 1996, 1998, 2000, 2051, 2053, 2091, 2126, 2393, 2403, 2443, 2444, 2470, 2504-2506, 2627, 2662, 2672, 2704
RHIZOSPHERE PH 2039
RHODOSPIRILLUM-RUBRUM 98
RHYNCHAENUS-FAGI 554
RHYTHM 805
RHYTHMS 1624
RIBOSOMAL-RNA GENES 891, 1452
RIBULOSE 1,5-BISPHOSPHATE 296, 562, 1329, 1433, 1579, 1963, 2520, 2576
RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE 28, 42, 43, 98, 187, 228, 254, 353, 676, 741, 769, 813, 851, 917, 987, 1050, 1132, 1223, 1405, 1407, 1429, 1431, 1448, 1573, 1646, 1681, 1868, 1965, 2021, 2218, 2220, 2366, 2497
RIBULOSE-1,5- BISPHOSPHATE CARBOXYLASE ACTIVITY 2099
RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE 4, 44, 55, 146, 192, 212, 257, 296, 500, 565, 617, 704, 724, 725, 795, 829, 869, 893, 907, 912, 1106, 1222, 1223, 1259, 1329, 1406, 1430, 1463, 1508, 1517, 1676, 1677, 1793, 1961, 1962, 2031, 2060, 2101, 2128, 2202, 2204, 2219, 2242, 2275, 2455-2460, 2494, 2520, 2576, 2630, 2631
RIBULOSE BISPHOSPHATE CARBOXYLASE 55, 98, 187, 253, 254, 362, 794, 878, 912, 1137, 1429, 1467, 1505, 1508, 1517, 1645, 1915, 1965, 1968, 2098, 2103, 2204, 2206, 2208, 2274, 2368, 2460, 2474
RICE 212, 255, 425, 849, 1778, 1939, 1940, 1943, 2064, 2117, 2185, 2232, 2472, 2513, 2656, 2664
RICE LEAVES 1431
RICE ORYZA-SATIVA 2475, 2700
RICE PADDIES 481, 2514, 2575
RICE PADDY 982
RICE RESPONSES 2497
RING DATA 488
RINGS 227
RING-WIDTH 865
RISING ATMOSPHERIC CO2 108, 168, 489, 506, 634, 638, 639, 867, 988, 1554, 2019, 2164, 2166, 2338, 2365, 2420, 2458
RISING CO2 43, 50, 127, 371, 442, 595, 608, 694, 743, 769, 970, 1379, 1706, 1828, 1835, 1837, 2004, 2100, 2122, 2278, 2381, 2436
RISING SEA-LEVEL 846
RISK 821
RIVER BASIN 1694
RNA 2251
ROBUR PLANTS 2379
ROBUST 543

ROOT 410, 437, 517, 586, 603, 825, 914, 964, 970, 974, 977, 1029, 1072, 1296, 1300, 1376, 1393, 1412, 1489, 1750, 1839, 1986, 2050, 2055, 2087, 2160, 2257, 2258, 2261, 2307, 2326, 2627, 2643
ROOT-DERIVED MATERIAL 225, 758-760, 2462
ROOT DISTRIBUTIONS 2451
ROOTED SOYBEAN LEAVES 2274
ROOT ENVIRONMENT 614
ROOT EXUDATION 125, 932, 1787, 1788
ROOT FRACTION 694, 699, 2426
ROOT-GROWTH 142, 311, 744, 773-776, 889, 1238, 1378, 1413, 1417, 1488, 1585, 1897, 2157, 2327, 2534, 2675
ROOT-GROWTH CAPACITY 1269
ROOT LENGTH 720
ROOT NODULE ACTIVITY 89, 963, 2186, 2223, 2250, 2679
ROOT-NODULES 2473
ROOT RESPIRATION 264, 593, 751, 752, 791, 1335, 1372, 1397, 1921, 2077, 2376, 2492
ROOT RESTRICTION 809, 1007, 2117, 2569
ROOTS 118, 321, 377, 378, 454, 455, 457, 465, 528, 615, 746, 747, 766, 800, 839, 933, 1023, 1182, 1183, 1254, 1411, 1414, 1424, 1452, 1455, 1932, 1993, 1994, 1999, 2052, 2053, 2078, 2123, 2144, 2149, 2171, 2256, 2260
ROOT-SYSTEM 361
ROOT TEMPERATURE 1268
ROOT ZONE 854, 2282, 2283
ROSE 51
ROSE PLANTS 1873
ROSETTE SIZE 1951
ROTATIONS 1795
ROTATION SYCAMORE PLANTATION 2409
ROTH 2054
RUBENS SARG 2324
RUBISCO 430, 502, 640, 729, 812, 829, 875, 1106, 1754, 1981, 2219, 2242, 2453, 2630, 2687
RUBISCO ACTIVASE 878, 2103, 2457, 2474
RUBISCO ACTIVITY 1508, 2420, 2654
RUBP CARBOXYLASE 1965
RUMEN 331
RUMEX 271
RUMEX-OBTUSIFOLIUS L 1797
RURAL TRANSECT 990
RUST 914
RUSTY GRAIN BEETLE 2571
RYEGRASS 669, 888, 889, 1760, 2018, 2139, 2389
RYEGRASS LOLIUM-PERENNE 670, 1521
SACCHAROMYCES- CEREVISIAE 2233
SACRED-LAKE 2286
SAGEBRUSH 1663

SALINA 40
SALINITY 457, 663
SALIX-MYRSINIFOLIA 1289
SALIX-VIMINALIS 653, 717
SALT-MARSH 566
SALT STRESS 480, 1843
SALT TOLERANCE 1481
SALVIA-SPLENDENS 807
SANDY LOAM 1932
SAN-FRANCISCO BAY 2689
SAO-MIGUEL 1785
SAP 271, 1801
SAP FLOW 580, 1136, 1155, 1786, 2383
SATELLITE 708, 709, 1877
SATELLITE DATA 1438, 1526
SATIVA 2693
SATIVUS L 475, 1472
SATURATING LIGHT 92
SATURATION 274
SAWFLY PERFORMANCE 2597
SAXIFRAGA-CERNUA 2635
SCALAR FLUXES 1155
SCALE 186, 301, 452, 496, 690, 1088, 1729, 1799, 2156, 2628
SCALING CARBON-DIOXIDE 632, 2516
SCALING CHARACTERISTICS 983
SCALING SUN 2222
SCENARIO 610
SCENARIOS 1312, 2389, 2451
SCHEMES 452
SCIENCE 376
SCIRPUS- OLNEYI 567, 648, 661, 714, 823, 1011, 1329, 1468, 2293, 2335, 2520
SCOTLAND 302
SCOTS PINE 165, 168, 305, 324, 347, 590, 905, 1125, 1126, 1136, 1321, 1518, 1752, 2003, 2015, 2220, 2313, 2353, 2543
SCOTS PINE FOREST 49, 397, 441
SEA 498, 1121
SEA-LEVEL 663
SEA-LEVEL RISE 642
SEASON 2355
SEASONAL ALLOCATION 2087
SEASONAL-CHANGES 540, 1044, 1099, 1848, 1972, 2578, 2597
SEASONAL CYCLE 684, 1924
SEASONAL DROUGHT 1957
SEASONALITY 1746
SEASONAL PATTERN 1921

SEASONAL-VARIATION 2074, 2161, 2324
SEASON GAS- EXCHANGE 1849
SEASONS 1632, 1652
SEA-SURFACE TEMPERATURE 463
SEAWATER 1244
SECONDARY METABOLISM 1090
SECONDARY METABOLITES 448, 1362, 1491, 1813, 2285
SECULAR VARIATIONS 1648
SEDIMENT INTERACTIONS 2372
SEDIMENTS 1368, 2286, 2554
SEED 538, 974
SEED-GERMINATION 48, 501
SEEDLING ESTABLISHMENT 2268
SEEDLING GROWTH 155, 205, 479, 529, 530, 931, 1455, 1457, 1750, 1759, 2091, 2149, 2349, 2502, 2504, 2505, 2643, 2671 SEEDLINGS 53, 54, 59, 134, 154, 157, 181, 187, 195, 200, 202, 207, 222, 235, 238, 251, 256, 273, 306, 325, 336, 342, 345, 348, 352, 361, 407, 421, 427, 430, 433, 438, 439, 454, 455, 473, 482, 489, 547, 548, 586-590, 593, 603, 607, 608, 614, 618, 656, 680, 698, 717, 720, 744, 746, 747, 786, 789, 798, 809, 823, 847, 860, 864, 886, 887, 919, 933, 977, 1008-1010, 1047, 1074, 1103, 1147, 1167, 1177, 1201, 1204, 1217, 1225, 1226, 1228, 1230, 1235, 1252, 1258, 1278, 1306, 1314, 1318, 1321, 1341, 1365, 1367, 1392, 1401, 1403, 1417, 1460, 1464, 1487, 1550, 1564, 1600-1602, 1606, 1607, 1630, 1633, 1642, 1661, 1666, 1715, 1719, 1745, 1751, 1757, 1786, 1819, 1820, 1828, 1830, 1837, 1838, 1863, 1888, 1889, 1893, 1897, 1899, 1900, 1909-1911, 1925, 1972, 1980, 2013, 2014, 2016, 2046, 2051, 2069, 2073, 2078, 2104, 2159, 2162, 2170, 2171, 2206, 2213, 2257, 2269, 2335, 2336, 2358, 2359, 2367, 2369, 2386, 2397,
SEEDLINGS CASTANEA-SATIVA 1902
SEED PRODUCTION 641
SEED SIZE 531, 2541
SEED WEIGHT 2526
SEED-WEIGHT VARIATION 475
SEED YIELD 472, 1036, 1557, 1935, 1967, 2086, 2223, 2617-2619
SEGREGATION 557
SELECTION 154, 1288, 1978, 2262
SELENASTRUM-MINUTUM 2655
SELF- RESTORATION 1272
SEMI-ARID REGIONS 983
SEMINAL ROOT-SYSTEM 2079
SENECIO-VULGARIS 48
SENESCENCE 147, 402, 450, 937, 1613, 1622, 1677, 2140, 2213
SENSIBLE HEAT 111
SENSITIVE METHOD 1272
SENSITIVE PLANTS 237
SENSITIVITY 11, 26, 128, 144, 216, 269, 276, 301, 496, 513, 526, 551, 678, 684, 708, 1112, 1113, 1118, 1140, 1162, 1198, 1224, 1263, 1264, 1309, 1311, 1525, 1527, 1547, 1659, 1777, 1783, 1802, 1855, 1885, 1905, 2172, 2226, 2239, 2263, 2336, 2402, 2438, 2483, 2584, 2616,

2628
SENSITIVITY ANALYSIS 1986
SEQUENCE 211, 1368, 2598
SEQUENCE DATA 1124
SEQUESTRATION 892, 949, 1312
SERENGETI 2602, 2603
SERENGETI- NATIONAL-PARK 2555
SERINE 869, 1709
SERPENTINE GRASSLAND 685
SHADE 52
SHADE PLANTS 618, 875, 919, 1626
SHEEP 331
SHELF-LIFE 850
SHOOT 59, 386, 455, 456, 458, 720, 977, 1072, 1267, 1268, 1393, 2087, 2397, 2519
SHOOT APEX 1170, 1334
SHOOT COMPETITION 2337
SHOOT DECAPITATION 187, 2582
SHOOT DEVELOPMENT 772
SHOOT ELONGATION 2484
SHOOT GROWTH 787, 1237, 2396
SHOOT PROLIFERATION 665
SHOOT RATIO 410, 517, 519, 1400
SHOOT RATIOS 697, 1176, 1376, 1489
SHOOTS 2435
SHORTGRASS PRAIRIE 970, 971
SHORTGRASS STEPPE 67
SHORT-LIVED FORBS 670
SHORT- TERM 100, 254, 300, 470, 477, 482, 751, 752, 795, 897, 1035, 1119, 1331, 1345, 1382, 1607, 1740, 1798, 2084, 2343, 2353, 2460, 2557, 2600, 2612, 2649, 2688, 2698
SHORT-TERM EXPOSURE 1120
SHREDDED CARROTS 2535
SHRUB 540
SIEB EX SPRENG 1372
SIERRA NEVADA 780, 1524
SIGNAL COMPOUNDS 355
SIGNAL-TRANSDUCTION 262, 885, 1330, 2233, 2544, 2585
SIMPLE BIOSPHERE MODEL 1461
SIMULATED ACIDIC RAIN 1211
SIMULATED ACID-RAIN 305, 1078, 2148
SIMULATED CONVECTIVE STORMS 1512
SIMULATED HERBIVORY 1389, 2602
SIMULATED SEASONAL-CHANGES 401, 403, 669, 1440, 2039, 2145, 2146
SIMULATED SWARDS 1288
SIMULATING CARBON DYNAMICS 1806
SIMULATION 84, 276, 315, 398, 513, 668, 696, 708, 905, 948, 1125-1127, 1162, 1262, 1263,

1356, 1485, 1495, 1795, 1948, 1986, 2433, 2551, 2683
SIMULATION-MODEL 16, 91, 371, 773-776, 853, 1940, 2264, 2313
SIMULATIONS 644, 662, 852, 1884, 2418
SINAPIS 1170
SINGLE-SPECIES POPULATIONS 152, 668
SINK 315, 394, 553, 620, 1396, 1639, 2260, 2273
SINK ACTIVITY 2258
SINK METABOLISM 1034
SINK REGULATION 500, 725, 1627, 1981, 2001, 2210, 2220, 2545
SINKS 277, 453, 857, 1057
SINK STRENGTH 1535, 2428
SITCHENSIS BONG CARR 269, 344, 350, 548, 753, 802, 1870, 2134, 2518
SITE-DIRECTED MUTAGENESIS 98
SITE INDEX 140
SITKA SPRUCE 192, 302, 554, 1057, 1514, 1515, 2518, 2578
SITKA SPRUCE PLANTATION 2358
SIZE 327, 501, 695, 722, 840, 1974, 2214
SIZE-FRACTIONS 1526, 2157
SIZE HIERARCHIES 155, 202, 1651
SIZE VARIATION 475
SLASH PINE 332, 2118
SLOW ANION CHANNELS 1330
SLOW INACTIVATION 55
SMALL-SUBUNIT 387, 1433, 2219
SO2 83, 320
SODA-LIME 506
SODIUM UPTAKE 2664
SOFT WATERS 1773, 2302
SOIL 113, 114, 126, 200, 202, 306, 315, 348, 446, 460, 508, 514, 515, 534, 574, 614, 615, 702, 735, 738, 744, 751, 761, 782, 800, 836, 927, 971, 1046, 1080, 1097, 1117, 1157, 1162, 1182, 1258, 1328, 1386, 1390, 1398, 1484, 1565, 1581, 1611, 1650, 1719, 1730, 1737, 1783, 1820, 1822, 1837, 1846, 1891, 1908, 1932, 1987, 1993, 2010, 2026, 2050, 2078, 2126, 2144, 2185, 2257-2259, 2264, 2354, 2359, 2442, 2549, 2575, 2673, 2674, 2683
SOIL BIOTA 436, 932, 933, 1165, 1994
SOIL CARBON 334, 441, 445, 1377, 1414, 1779, 2072, 2168
SOIL CARBONATE 597
SOIL CARBON-DIOXIDE 407, 955
SOIL COMPACTION 775
SOIL DENITRIFICATION 2232
SOIL-EROSION 644
SOIL EXTRACTS 2372
SOIL FERTILITY 2370
SOIL MICROBIAL BIOMASS 1789, 2157
SOIL MICROCLIMATE 2107
SOIL MOISTURE 843, 882, 1125, 1127, 1135, 1191, 2313, 2568

SOIL-MOISTURE STRESS 1445, 1757
SOIL N 1082, 1743, 2052, 2149, 2358
SOIL N-AVAILABILITY 1718
SOIL-NITROGEN 64, 67, 1925, 2486
SOIL-NITROGEN MINERALIZATION 1416, 1417
SOIL NUTRIENT 1143, 1391, 2381
SOIL O2 300, 667
SOIL ORGANIC-CARBON 2671
SOIL ORGANIC MATTER 49, 199, 347, 388, 773, 1299, 1378, 1805, 1806, 2100, 2158, 2443, 2445, 2626
SOIL PROPERTIES 740, 2153
SOIL RESOURCE AVAILABILITY 1902
SOIL RESPIRATION 39, 110, 155, 593, 902, 1309, 1402, 1807, 1960, 2079, 2362, 2413
SOIL-ROOT INTERFACE 487
SOILS 79, 452, 505, 633, 962, 1094, 1453, 1501, 1736, 1844, 2009, 2223, 2239, 2245, 2433, 2617, 2619, 2659, 2676
SOIL SYSTEM 197, 437, 758, 1788, 2480, 2482
SOIL TEMPERATURE 776, 982, 1269, 1732
SOIL TEMPERATURES 2397
SOIL-WATER 686, 972, 2070
SOIL-WATER DEFICIT 1967
SOLANUM- DULCAMARA 1728
SOLANUM-MELONGENA 206
SOLANUM-TUBEROSUM 317
SOLANUM TUBEROSUM L 2037, 2291, 2561, 2562
SOLAR IRRADIANCE 996
SOLAR RADIATION 43, 684, 871, 1133, 1555, 1556, 1840, 2604
SOLAR-RADIATION MEASUREMENTS 1118
SOLAR ULTRAVIOLET-RADIATION 230, 1232
SOLID-STATE FERMENTATION 2670
SOLLING SPRUCE SITE 1151
SOLUBILIZATION 125
SOLUBLE SUGARS 2687
SOMATIC EMBRYOGENESIS 788
SONORAN DESERT 1857
SORBITOL-RELATED ENZYMES 1038
SORGHUM 483, 920, 1611, 2391, 2454, 2692
SOURCE SINK BALANCE 2274
SOURCE-SINK RELATIONS 36, 42, 107, 119, 124, 150, 157, 249, 254-256, 283, 350, 509, 565, 575, 624, 636, 652, 660, 668, 729, 730, 784, 1129, 1130, 1270, 1292, 1405, 1455, 1538, 1568, 1704, 1798, 1828, 1830, 1902, 2019, 2070, 2101, 2155, 2195, 2259, 2327, 2374, 2375, 2380, 2396, 2479, 2510, 2541, 2620, 2631
SOURCE-SINK RELATIONSHIPS 189, 209
SOUR ORANGE 2307
SOUR ORANGE TREES 100, 251, 350, 448, 526, 714, 724, 781, 991, 994, 1006-1008, 1038,

1207, 1596, 1633, 1711, 1718, 1815, 1980, 2029, 2037, 2137, 2353, 2369, 2370, 2420
SOUTH-AFRICA 1536
SOUTH-DOWNS 644
SOUTHEAST-ASIA 1946
SOUTHEASTERN ALASKA 1199
SOUTHEASTERN UNITED-STATES 1510, 1841
SOUTHERN AFRICA 1475
SOUTHERN APPALACHIANS 2427
SOUTHERN FINLAND 1059, 1060, 1740
SOUTHERN GUINEA SAVANNA 1286
SOUTHERN NEW-MEXICO 2555
SOUTHERN OSCILLATION 1524
SOUTHERN QUEENSLAND 1265
SOUTH MOUNTAIN BATHOLITH 1199
SOWING DATE 787, 2229
SOYA BEAN- PLANTS 2479
SOYBEAN CANOPIES 32, 246, 562, 1947, 2557
SOYBEAN CANOPY 2024
SOYBEAN CANOPY PHOTOSYNTHESIS 101, 991, 1856, 2128, 2694
SOYBEAN GLYCINE-MAX 1792, 2029
SOYBEAN GRAIN PRODUCTION 1611
SOYBEAN LEAVES 106, 254, 563, 765, 774, 1624, 1646, 1912, 2060, 2218, 2341
SOYBEAN PHYSIOLOGY 566, 643, 1137, 1291
SOYBEAN PLANTS 2069, 2290
SOYBEAN RESPONSE 882
SOYBEANS 221, 574, 1895, 2345
SOYBEANS GLYCINE-MAX 1791
SOYBEAN YIELD 1194
SPACE 317, 722, 1420, 2291, 2563
SPANS 540
SPARSE CROPS 1136
SPARTINA-ALTERNIFLORA 2575
SPATIAL DISTRIBUTIONS 1131
SPATIAL-RESOLUTION 2074
SPATIAL VARIABILITY 1212, 1264, 1497
SPATIAL VARIATION 273
SPATIAL VARIATIONS 856
SPEARS 434
SPECIES-DIVERSITY 2532
SPECIES RESPONSE 84, 979
SPECIFICITY 443, 465, 851, 869, 2494
SPECIFICITY FACTOR 617
SPECTRA 1697
SPECTRAL REFLECTANCE 332
SPECTROMETRY 1244

SPECTROPHOTOMETRIC ASSAY 2455
SPECULATIONS 45
SPERMIDINE 1472, 1622
SPHAGNUM 2152
SPIKELET NUMBER 1333, 2228
SPINACH-CHLOROPLASTS 63, 869
SPINACH LEAF-DISKS 2209
SPINACH LEAVES 148, 285, 575, 704, 1574, 1579, 1709, 1793, 2210, 2545
SPITTLEBUG 271
SP-NOV 1566
SPODOPTERA-ERIDANIA 1360
SPODOPTERA-EXIGUA 448
SPORE GERMINATION 355, 1880
SPORES 1213
SPRING BARLEY 915
SPRING BLOOM 1358
SPRING WHEAT 119, 228, 234, 244, 558, 771, 820, 844, 927, 1180, 1503, 1507, 1511, 1528, 1544, 1555, 1556, 1620, 1905, 1935, 1961, 1963, 2050, 2067, 2224, 2228, 2229, 2550
SPRUCE 140, 1177, 1416, 2216, 2397
SPRUCE BUDWORM 2595
SPRUCE-FIR FOREST 1175
SPRUCE-LICHEN WOODLAND 49
SPRUCE MODEL-ECOSYSTEMS 858, 1718, 2030
SPRUCE NEEDLES 1252, 1257, 1900
SPRUCE PICEA-ABIES 634, 770, 1103, 1971, 2148, 2488
SPRUCE PICEA-SITCHENSIS 1044, 1231
SPRUCE SEEDLINGS 1079, 1080, 1082, 1632
SPRUCE TREES 1305
SP STRAIN PCC-7942 1463, 2031
STABILITY 2674
STABLE ISOTOPE 1199
STABLE ISOTOPES 2161
STABLE OXYGEN 676, 856
STAGE 2185
STAGE-II MICROPROPAGATION 282
STAND 2604
STAND DEVELOPMENT 1163, 2197, 2665
STAND-LEVEL DIEBACK 1613
STANDS 336, 1057, 1321, 1589, 2121, 2122
STARCH 188, 213, 339, 366, 508, 704, 804, 807, 913, 959, 1033, 1137, 1222, 1624, 1676, 1811, 1938, 1968, 1988, 2059, 2081, 2155, 2180, 2206, 2254, 2374, 2436, 2521, 2684
STARCH CONCENTRATION 30
STARCH CONTENT 2475
STARCH FORMATION 472
STATE GAS-EXCHANGE 1963

STATISTICAL DISTRIBUTION 2614
STEADY-STATE 599, 1625, 2205
STEADY-STATE CONDITIONS 2479
STEADY-STATE PHOTOSYNTHESIS 807, 1065, 1149
STEM-FLOW 579
STEM-FLOW GAUGE 580
STEMS 635, 2665
STEPPE 2308
STIMULATION 194, 258, 285, 1024
STOMATA 1855, 1867
STOMATAL APERTURES 2614
STOMATAL BEHAVIOR 237
STOMATAL CLOSURE 230, 262, 2263, 2269
STOMATAL CONDUCTANCE 34, 42, 110, 111, 121, 129, 163, 164, 168, 181, 273, 297, 428, 442, 449, 452, 473, 478, 485, 497, 563, 589, 607, 617, 662, 678, 698, 753, 775, 776, 809, 815, 824, 871, 897, 912, 919, 921, 1007, 1128, 1135, 1136, 1209, 1245, 1291, 1367, 1374, 1379, 1466, 1481, 1507, 1585, 1637, 1681, 1693, 1695, 1751, 1803, 1868, 1873, 1959, 1961, 1981, 2002, 2003, 2099, 2106, 2112, 2116, 2150, 2308, 2365, 2366, 2379, 2385, 2408, 2420, 2508, 2531, 2570, 2607, 2638
STOMATAL CONTROL 346, 496, 690, 1092
STOMATAL DENSITY 44, 166, 183, 185, 214, 278, 362, 548, 582, 597, 651, 719, 806, 1091, 1250, 1492, 1494, 1541, 1542, 1629, 1712, 1768, 1781, 1849, 1851, 1899, 1945, 1975
STOMATAL GUARD-CELLS 585
STOMATAL-RESISTANCE 463, 1282, 1375
STOMATAL RESPONSE 269
STOMATAL RESPONSES 67, 401, 663, 1635, 1854, 1859, 2277, 2279
STORAGE 241, 242, 453, 550, 551, 633, 635, 673, 738, 749, 939, 1005, 1057, 1077, 1089, 1094, 1119, 1120, 1161, 1181, 1239, 1279, 1373, 1394, 1470, 1472, 1474, 1497, 1639, 1644, 1731, 1784, 1807, 1821, 1904, 1930, 1946, 2107, 2144, 2151, 2153, 2168, 2239, 2244, 2354, 2405, 2449, 2483, 2535, 2642, 2658, 2677
STORAGE LIFE 850
STORAGE PROCEDURES 1283
STORAGE PROTEINS 788
STORED BROCCOLI 850
STRATEGIES 531, 974, 1869, 1992, 2527
STRATEGY 359
STRATIFICATION 204
STRATOSPHERIC OZONE 1232, 1233, 1841, 2246, 2475
STRAW 112, 1062
STRAWBERRIES 768, 1474
STRAWBERRY 375, 515, 665, 1650, 2243
STRAWBERRY FRUIT 939
STRAWBERRY PLANTLETS 282, 514, 766, 767, 1871, 2357, 2461
STREAMFLOW VARIABILITY 1524
STREAMS 1421

STRESS 15, 33, 53, 76, 77, 147, 222, 299, 336, 344, 375, 379, 384, 418, 421, 585, 588, 635, 636, 656, 811, 830, 921, 986, 1124, 1128, 1144, 1157, 1191, 1218, 1337, 1389, 1521, 1557, 1581, 1590, 1717, 1819, 1835-1837, 1857, 1860, 1878, 1889, 1893, 1895, 1896, 1920, 1936, 1959, 1988, 2013, 2020, 2021, 2023, 2046, 2062, 2104, 2111, 2117, 2136, 2186, 2251, 2255, 2409, 2468, 2496, 2504, 2552, 2583, 2614, 2685, 2712
STRESSES 428
STRESS RESPONSES 1680
STRIGA-HERMONTHICA 483
STRUCTURAL CHARACTERIZATION 1473
STUBBLE 2144
SUBALPINE PLANTS 1189
SUBAMBIENT 547, 1853
SUBCELLULAR VOLUMES 1709
SUBMERGENCE 258, 2472, 2484
SUBMERSED MACROPHYTE GROWTH 996
SUBSEQUENT GROWTH 1872, 2615
SUBSPECIES PUBESCENS 623
SUB-STOMATAL CAVITIES 2421
SUBSTRATE QUALITY 439, 446
SUBSTRATE-SPECIFICITY 98
SUBTERRANEUM L 36, 1098, 2258
SUBTROPICS 2136
SUBUNIT 2031
SUBUNITS 813
SUCCESSION 801
SUCCESSIONAL STATUS 895, 1146, 1235
SUCCESSION MODEL 1313
SUCCULENTS 572
SUCROSE 231, 767, 804, 807, 913, 1109, 1395, 1584, 1793, 2230, 2456, 2684
SUCROSE ACCUMULATION 1574
SUCROSE CONCENTRATION 2175
SUCROSE EXPORT 2233
SUCROSE METABOLISM 228
SUCROSE PHOSPHATE SYNTHASE 362, 938, 980, 1034, 1223, 1579, 1909, 1910, 2209, 2242, 2274, 2275, 2496, 2521, 2620
SUCROSE SUPPRESSION 1255, 1256
SUCROSE SYNTHASE 366
SUCROSE SYNTHESIS 599, 1222, 2206
SUCROSE SYNTHESIS ENZYMES 1433, 1646
SUGAR 1033, 2312, 2521
SUGAR ACCUMULATION 1034
SUGAR-BEET 643
SUGAR-BEET LEAVES 1437
SUGAR-FREE MEDIUM 1872
SUGAR MAPLE DIEBACK 1510

SULFATE AEROSOLS 1263, 1841
SULFATE-REDUCING BACTERIUM 1368
SULFATE REDUCTION 1566
SULFATE TRANSPORT 2171
SULFUR 304, 1543, 2171
SULFUR-DIOXIDE 29, 83, 96, 235, 320, 497, 990, 1305, 1426, 1927, 2011
SULFUR- DIOXIDE MIXTURES 1211
SULFURIC-ACID 1841
SULFUR NUTRITION 2162
SULFUR-OXIDES 2469
SUMMER CO2 ENRICHMENT 358, 1592
SUMMER TEMPERATURES 867
SUMMIT 503
SUN 875
SUNFLECKS 204
SUNFLOWER 7, 288, 920, 1050
SUNFLOWER LEAVES 42, 160, 2614
SUNSHINE 1534
SUPERNODULATING MUTANT 89
SUPEROXIDE-DISMUTASE 87, 244, 639, 1504, 1927, 2164, 2174, 2585
SUPEROXIDE-DISMUTASE ACTIVITY 1848, 2163
SUPPLEMENTARY 1529
SUPPRESSION 17
SURFACE 230, 1213, 1232, 1233, 1548, 1884, 2633
SURFACE AIR-TEMPERATURE 846, 996
SURFACE ALBEDO 1322
SURFACE OCEAN 1934
SURFACE PARAMETERIZATION SIB2 697
SURFACES 978
SURFACE-TEMPERATURE 684, 1136
SUSCEPTIBILITY 1813
SUSPENSION 788
SUSPENSION-CULTURE 1255
SWARD 1377, 2140, 2681
SWARDS 402, 1409
SWEDISH LAPLAND 1992
SWEDISH RAISED BOG 1059
SWEET CHERRIES 17
SWEET CORN 2131
SWEET-PEPPER 97
SWEET-POTATO 229, 2128
SYCAMORE APHID 555
SYLVESTRIS 1820
SYLVESTRIS L 1103, 1958
SYMBIOSIS 611

SYMBIOTIC N-2 FIXATION 963, 1452, 1994
SYMPATHETIC-NERVE ACTIVITY 2267
SYMPLASTIC CONNECTIONS 1393
SYNECHOCOCCUS 2031
SYNECHOCOCCUS PCC7942 2598
SYNTHASE 763, 764, 1471
SYNTHETASE 1956
SYSTEM 29, 56, 57, 83, 142, 382, 389, 894, 899, 918, 1023, 1144, 1347, 1562, 1641, 1690, 1891, 1940, 1997, 2346
SYSTEM ARCHITECTURE 196
SYSTEMS 145, 358, 372, 903, 1108, 1453, 1847, 1998, 2562
TAEDA 798, 1642, 2504, 2505
TAEDA L 1392
TAEDA L CALLUS 1871
TAEDA L SEEDLINGS 305, 505, 724, 791, 1257, 2596, 2597
TAEDA SEEDLINGS 797, 810-812, 1069, 1148, 1632, 1634, 1896, 2294, 2382, 2556
TAEDA TREES 809
TAIGA TREES 1929
TALL FESCUE 2249
TALL FESCUE PASTURE 884
TALLGRASS PRAIRIE 38, 308, 321, 370, 441, 442, 703, 889, 954, 965, 970, 1107, 1108, 1187, 1189-1191, 1378, 1414, 1692, 1698, 1779, 1783, 1806, 1849, 1854, 1859, 1894, 1998, 2091, 2150, 2322, 2478, 2533, 2673
TANNIN 911, 1901
TAXONOMIC RELATEDNESS 176
TELECONNECTION PATTERN 1524
TEMPERATE 683, 1499, 2168, 2378
TEMPERATE ECOSYSTEMS 49
TEMPERATE FOREST ECOSYSTEMS 197, 660
TEMPERATE FOREST SOILS 38
TEMPERATE GRASSLAND 264, 1188, 2602
TEMPERATE GRASS SWARD 2304, 2450
TEMPERATE TREES 897, 1302
TEMPERATURE 19, 20, 30, 41, 48, 63, 91, 93, 94, 102, 106, 111, 147, 149, 151, 156, 162, 167, 173, 186, 226, 234, 256, 272, 273, 285, 289, 291, 300, 302, 324, 325, 342, 348, 353, 354, 357, 386, 393, 403, 407, 415, 417, 460, 469, 482, 483, 488, 497, 508, 511, 512, 522, 523, 527, 545, 566, 575, 606, 610, 626, 635, 647, 652, 653, 658, 669, 670, 680, 694, 714, 718, 729, 730, 733, 736, 742, 745, 757, 767, 774, 790, 792, 807, 814, 820, 825, 851, 853, 896, 901, 914, 918, 922, 923, 930, 935, 965, 973, 987, 993, 995, 1000, 1016, 1039, 1052, 1054, 1055, 1060, 1066, 1125, 1140, 1158-1160, 1162, 1170, 1177, 1178, 1180, 1194, 1198, 1204, 1208, 1231, 1253, 1262-1264, 1267, 1277, 1297, 1298, 1301, 1310, 1333, 1334, 1368, 1375, 1394, 1402, 1406, 1407, 1409, 1415, 1417, 1418, 1420, 1430, 1438, 1442, 1448, 1494, 1497, 1505, 1512, 1514, 1519, 1525, 1528, 1532, 1536, 1538, 1540, 1543, 1553-1555, 1564, 1568, 1579, 1586, 1588, 1601, 1602, 1604, 1617, 1637, 1644, 1654, 1682, 1689, 1700, 1704, 1706, 1728, 1734, 1737, 1744, 1756, 1761, 1765, 1770, 1793, 1800, 1810, 1815, 1824, 1830, 1832, 1856,

1865, 1872, 1887, 1928, 1929, 1934, 1952, 1954, 1958, 1966, 1967, 1978, 1979, 1983, 1991, 2018, 2020, 2030, 2039, 2057, 2063, 2075, 2093, 2098, 2107, 2139, 2141, 2142, 2147, 2176, 2181, 2185, 2206, 2214, 2217, 2221, 2224, 2229, 2231, 2268, 2310, 2337, 2345, 2346, 2362, 2382, 2417, 2418, 2428, 2430, 2433, 2444, 2449, 2453, 2454, 2467, 2468, 2471, 2483, 2485, 2491, 2492, 2517, 2526, 2535, 2551, 2559, 2562, 2563, 2573, 2578, 2589-2591, 2622, 2629, 2640, 2660, 2667, 2681, 2686, 2696, 2699, 2700, 2707 TEMPERATURE-DEPENDENCE 368, 370, 371, 738, 1175
TEMPERATURE DEPRESSION 414
TEMPERATURE-GRADIENT CHAMBERS 2048
TEMPERATURE INCREASE 2140
TEMPERATURE-RANGE 1416
TEMPERATURES 179, 590, 902, 1193, 1313, 1321, 1592, 1677, 1782, 1973, 2230, 2448
TEMPORAL ANALYSIS 990
TEMPORAL VARIABILITY 1575
TENSION 232
TERM 290, 586, 1006, 1132, 1189, 1191, 1427, 1704, 1707, 1865, 2117, 2263, 2341, 2425, 2646
TERM DECOMPOSITION 445, 1378, 1576
TERM ELEVATED CO2 1870
TERMITES 2668
TERM PHOTOINHIBITION 980
TERRESTRIAL 1741, 1821, 2471
TERRESTRIAL BIOSPHERE 678, 708, 1370, 1806, 1807, 1894, 1924
TERRESTRIAL CARBON STORAGE 463, 1062, 2264
TERRESTRIAL ECOSYSTEMS 200, 219, 241, 311, 337, 417, 702, 832, 863, 904, 926, 954, 964, 983, 1086, 1174, 1392, 1405, 1436, 1491, 1495, 1501, 1502, 1513, 1514, 1576, 1578, 1636, 1639, 1713, 1729, 1767, 1787, 1805, 1815, 1875, 1925, 2212, 2285, 2469, 2588, 2643
TERRESTRIAL ISOPODS 858
TERRESTRIAL PLANTS 230, 2475, 2476
TERTIARY BOUNDARY 162
TERTIOLECTA 742
TEXAS 1860
THALLUS WATER-CONTENT 2320
THEORETICAL- ANALYSIS 16
THERMAL HABITAT 329, 948
THERMAL TIME 847
THERMOHALINE CIRCULATION 1827
THERMOTOLERANCE 138, 411
THIOBACILLUS-NEAPOLITANUS 1463
THORNTHWAITE MOISTURE INDEX 2297
THYLAKOID MEMBRANES 875, 1626
TILIA-CORDATA 979
TILLAGE 1335
TILLAGE SYSTEM 1960
TILLER 402

TIME 1702
TISSUE 17, 524, 665, 1551, 1689
TISSUE CHEMISTRY 2371, 2372
TISSUE-CULTURE 282, 767
TISSUE NITROGEN 2486
TISSUES 666, 1956
TISSUE-SPECIFIC EXPRESSION 2233
TOBACCO 146, 160, 893, 1106, 1178, 1272, 1680, 2021, 2041
TOBACCO-LEAVES 869
TOBACCO MUTANTS 873
TOBACCO NICOTIANA-TABACUM 55
TOBACCO PLANTS 2545
TOLERANCE 1178, 1227, 1701, 2472, 2640
TOLERANT 2016
TOMATO 56, 97, 320, 353, 396, 649, 764, 808, 938, 957, 1066, 1179, 1564, 1799, 1811, 2104, 2200, 2201, 2231, 2282, 2283,
2436, 2459, 2689
TOMATOES 1248
TOMATO FRUIT 1622
TOMATO FRUITS 1469
TOMATO GENOTYPES 2199
TOMATO LYCOPERSICON-ESCULENTUM 1473
TOMATO PLANTS 82, 387, 743, 912, 955, 1149, 1395, 1428, 1546, 1962, 2173, 2253, 2458, 2501
TOMATO PRODUCTS 17
TOMGRO 2173
TOP FIELD CHAMBERS 626, 634, 637, 880, 2067
TOPOGRAPHIC POSITION 843
TOPOGRAPHY 2634
TOTAL NITROGEN 2086
TOXIC ACTION 1116
TOXICITY 1988, 1989
TRACE GASES 793, 846, 1539
TRACE GAS FLUXES 1175, 1282, 1348, 1418, 2075, 2107, 2491
TRANSCRIPTION FACTOR 92
TRANSCRIPT LEVELS 1627, 2019, 2210
TRANSFER SCHEME LSX 463, 678
TRANSFORMED TOBACCO 1546
TRANSGENIC PLANTS 63, 1277, 2210
TRANSGENIC TOBACCO 87, 1433, 1504, 1517, 1574, 2576, 2585
TRANSGENIC TOBACCO PLANTS 387, 1222, 1223, 1428, 1437, 1732, 2275
TRANSIENT 1697
TRANSIENT HIGH-TEMPERATURES 657
TRANSIENT-RESPONSE 550, 551, 949, 1357, 2356, 2449, 2609
TRANSIENT RESPONSES 853, 2313

TRANSITION 1170, 1946
TRANSLOCATION 189, 472, 492, 621, 760, 1065, 1066, 1386, 1900, 2171, 2190
TRANSLOCATOR 499
TRANSMITTANCE 1703
TRANSPIRATION 56, 81, 93, 97, 103, 104, 106, 111, 174, 179, 188, 259, 272, 288, 292, 295, 297, 346, 452, 496, 520, 559, 661, 662, 678, 690, 698, 802, 868, 894, 943, 969, 1017, 1018, 1048, 1144, 1219, 1263, 1294, 1350, 1375, 1430, 1479, 1592, 1602, 1683, 1772, 1797, 1856, 1887, 1949, 2058, 2112, 2116, 2184, 2185, 2255, 2277, 2308, 2310, 2412, 2570
TRANSPIRATION EFFICIENCY 597
TRANSPIRATION RATE 34, 2605
TRANSPIRATION RESPONSES 31, 32, 562, 563, 566, 1135, 1947
TRANSPLANTS 1215
TRANSPORT 40, 250, 262, 364, 559, 611, 705, 902, 955, 1036, 1068, 1281, 1584, 1660, 1771, 2031, 2032, 2295, 2296, 2437, 2575, 2599, 2606
TREE 224, 235, 433, 1111, 1250, 1887, 1997, 2540, 2646, 2651
TREE GROWTH 167, 506, 786, 1372, 2151, 2332
TREE LEAF LITTER 1293
TREE-RING CHRONOLOGY 1931
TREE-RINGS 1524
TREES 80-82, 129, 130, 145, 159, 180, 215, 259, 292, 301, 302, 346, 352, 379, 399, 432, 479, 485, 577, 587, 594, 595, 608, 638, 640, 728, 754, 778, 790, 821, 826, 860, 977, 1022, 1047, 1055, 1074, 1091, 1127, 1201, 1203, 1219, 1224-1226, 1271, 1392, 1417, 1593, 1606, 1630, 1722, 1746, 1824, 1831, 1833, 1909, 1910, 1920, 1957, 1972, 2003, 2012, 2016, 2044, 2122, 2166, 2213, 2307, 2583, 2628, 2644, 2652, 2671, 2682, 2692, 2693
TREE SEEDLINGS 151, 811, 1558, 1712, 2196, 2379, 2381, 2482
TREMBLING ASPEN 773
TRENDS 45, 159, 488, 1051, 1931, 2030, 2248, 2332, 2402
TRIAZINE RESISTANCE 891
TRIFOLIUM- REPENS 401, 465, 669, 963, 1099, 1477, 2145, 2147, 2259, 2261, 2466
TRIFOLIUM-REPENS L 66, 1440, 1521, 1722, 1986, 1994, 2019, 2146, 2159, 2279, 2427
TRIFOLIUM-SUBTERRANEUM L 1327, 1743, 2001, 2256, 2339
TRIMETHYLAMINE 1566
TRIN EX STEUD 2225
TRIOSE-PHOSPHATE TRANSLOCATOR 893
TRITICUM-AESTIVUM 326, 627
TRITICUM-AESTIVUM CROPS 142, 143
TRITICUM-AESTIVUM L 48, 194, 545, 558, 626, 634, 637, 1505, 1587, 1749, 1831, 1961, 1962, 2067, 2126, 2203, 2211, 2351, 2454 TROPHIC RELATIONSHIPS 2532
TROPICAL CONDITIONS 2157
TROPICAL DEFORESTATION 696, 1152, 1161, 1282, 1659, 2297, 2356, 2469
TROPICAL FORESTS 550, 904, 949, 1370, 1846
TROPICAL GEOPHAGOUS EARTHWORM 1286
TROPICAL RAIN-FOREST 1347, 1371
TROPICAL RICE 1744
TROPICAL TREES 1235

TROPOSPHERIC OZONE 535, 558, 634, 683, 770, 771, 1117, 1232, 1233, 1374, 2429
TUBERIZATION 614, 2562
TUBERS 803
TUNDRA 64, 66, 534, 567, 982, 1690, 1737, 1928, 2009, 2088, 2268, 2487, 2629
TUNDRA ECOSYSTEMS 57, 1735
TUNDRA PLANTS 1992
TURGOR 654
TURNOVER 139, 198, 310, 398, 674, 758, 760, 852, 1162, 1348, 2043, 2050, 2051, 2158, 2347, 2362, 2393, 2442, 2444, 2462, 2470
TURVES 2662
TUSSOCK GRASSES 632
TUSSOCK TUNDRA 72, 149, 155, 327, 541, 542, 563, 566, 659, 735, 793, 794, 823, 870, 896, 901, 922, 970, 1011, 1015, 1060, 1085, 1094, 1139, 1197, 1198, 1204, 1329, 1402, 1488, 1515, 1578, 1653, 1732, 1734, 1736, 2089, 2141-2143, 2153, 2278, 2284, 2526, 2622, 2659
ULMUS-AMERICANA SEEDLINGS 1200
ULTRASTRUCTURE 109, 766, 1109, 1888, 2155, 2331
ULTRAVIOLET-B 244, 2294, 2333, 2476
ULTRAVIOLET-B RADIATION 101, 366, 936, 2099, 2269
ULTRAVIOLET-RADIATION 28, 828, 1140, 2438, 2475
ULVA-FASCIATA 1610
ULVA-ROTUNDATA 891
ULVA SP 161
UNBURNED TALLGRASS PRAIRIE 1188
UNCERTAINTY 2628
UNDERSTORY COMMUNITY 413, 1957
UNFERTILIZED MOWN MEADOWS 2280
UNITED-STATES 308, 506, 527, 550, 610, 647, 855, 1195, 1233, 1327, 1534, 1700, 1701, 1783, 2248, 2369, 2402, 2556
UNITED-STATES CLIMATE 1524
UNMANAGED ECOSYSTEMS 1732
UNREST 227
UNSATURATED ZONE 2194
UPLAND OAK FOREST 1416
UPPER RIO NEGRO 1526
UPPER TROPOSPHERE 1475
UPTAKE KINETICS 65
URINE DEPOSITION 2601
USA 1094, 1639
USE EFFICIENCY 33, 50, 120, 246, 273, 428, 648, 656, 689, 776, 892, 919, 928, 972, 1092, 1309, 1369, 1440, 1496, 1498, 1582, 1585, 1825, 1858, 1861, 1870, 1949, 2018, 2070, 2072, 2259, 2287, 2323, 2418, 2605, 2626
USNEA-SPHACELATA 1276
UV-B 624, 1636, 1752
UV-B RADIATION 1232, 2247, 2510
VACUOLAR PH 1274

VADOSE ZONE 2194
VALENCIA ORANGE 259
VALIDATION 2389
VALLISNERIA-AMERICANA 2371, 2372
VALUES 204
VA-MYCORRHIZAL 611
VAPOR 110, 1735
VAPOR-PRESSURE 2518
VAPOR-PRESSURE DEFICIT 288, 1870
VARIABILIS 2410
VARIABILITY 138, 143, 276, 429, 526, 646, 1438, 1589, 1729, 1802, 2402, 2568
VARIABLES 1193
VARIABLE SUNLIGHT 1190
VARIETAL DIFFERENCES 2298, 2607
VARIETIES 1442
VAR RADICULA-PERS 1211
VARYING NITROGEN 1858
VASCULAR CAPACITANCE 2267
VASCULAR EPIPHYTES 52
VASCULAR PLANTS 184, 312, 1754, 2087, 2135
VASE LIFE 2169
VASOPRESSIN RELEASE 232
VEGETABLE PLANTS 1211
VEGETABLES 524, 1241, 1242, 1373, 1434, 2535, 2660, 2677
VEGETABLE TRANSPLANT PRODUCTION 664
VEGETATED SURFACES 683
VEGETATION 84, 159, 179, 193, 245, 304, 306, 451, 476, 531, 532, 581, 636, 637, 709, 801, 859, 865, 898, 909, 941, 949, 979, 983, 1039, 1040, 1088, 1140, 1162, 1207, 1224, 1232, 1309, 1311, 1348, 1357, 1375, 1394, 1495, 1547, 1548, 1615, 1648, 1659, 1660, 1708, 1729, 1736, 1759, 1789, 1807, 1850, 1874, 1877, 1885, 1891-1893, 1966, 2065, 2066, 2088, 2107, 2305, 2321, 2413, 2439, 2511, 2534, 2573, 2575, 2636, 2704
VEGETATION CHANGE 956, 1192, 2248
VEGETATION DYNAMICS 2197
VEGETATION INDEXES 12, 1840
VEGETATION TYPES 740, 904, 1297, 1502
VEGETATIVE DEVELOPMENT 1511
VEGETATIVE MYCELIUM 747
VELVETBEAN CATERPILLARS 2595
VELVETLEAF ABUTILON-THEOPHRASTI 1791, 1792
VENTILATED CHAMBER 32, 520, 2572
VENTILATION 19, 359
VERNALIZATION 1544
VERTICAL- DISTRIBUTION 1502
VERTICAL PROFILES 2500
VESICULAR-ARBUSCULAR MYCORRHIZAE 305, 611

VESICULAR-ARBUSCULAR MYCORRHIZAS 530
VICIA-FABA 943, 1281, 1331
VICIA-FABA L 779, 1616, 1635, 2011
VIGNA-SINENSIS L 28
VIGNA UNGUICULATA L 606
VIOLAXANTHIN CYCLE 1635, 2090
VIOLAXANTHIN DEEPOXIDATION 128
VISIBLE-LIGHT 2294, 2333
VITIS 583
VITIS-VINIFERA L 677, 682
VOLATILE COMPOUNDS 158
VOLATILE EMISSIONS 282
VOLATILE LEAF TERPENES 631, 1087
VOLATILES 1120, 1930
VOLTAGE 262
VORTEX 2500
VOSTOK 503
VOSTOK ICE-CORE 44, 171, 179, 597, 846
VULCANO-ISLAND 1785
VULGARE L CULTIVARS 787
VULGARIS L 1400, 1861
WALL EXTENSIBILITY 653, 654, 717, 1923, 2327
WALLS 2131
WALNUT SEEDLINGS 1427
WASHINGTON 2634
WATER 191, 252, 485, 573, 651, 667, 675, 705, 735, 744, 796, 809, 838, 853, 892, 928, 964, 1032, 1127, 1163, 1165, 1347, 1368, 1498, 1544, 1633, 1700, 1735, 1737, 1802, 1858, 1936, 2118, 2140, 2282, 2344, 2352, 2371, 2434, 2498, 2502, 2503, 2616, 2659, 2686
WATER-BALANCE 2297
WATER CHEMISTRY 1061
WATER-CONTENT 108, 1058, 2411, 2413
WATER DEFICIT 384, 672, 1228, 1268, 2037, 2186
WATER HYACINTH 1740, 2654
WATER-LIMITED CONDITIONS 717
WATER-LIMITED GRASSLAND 689
WATER-LOSS 1109
WATER-LOSS REGULATION 885, 2134
WATER POTENTIALS 2327
WATER RELATIONS 195, 263, 293, 340, 425, 530, 572, 650, 654, 920, 936, 955, 1095, 1188, 1190, 1236, 1269, 1404, 1683, 1728, 1767, 1791, 1873, 1893, 1949, 1974, 1994, 2062, 2100, 2189, 2221, 2383, 2386, 2409, 2538, 2552
WATER-RESOURCES 329, 1320
WATERS 2633
WATER-STABLE AGGREGATION 1265
WATER-STRESS 81, 206, 229, 283, 288, 330, 337, 349, 472, 486, 529, 548, 558, 608, 657, 661,

792, 797, 824, 906, 993, 1044, 1074, 1235, 1314, 1318, 1326, 1330, 1336, 1344, 1365-1367, 1466, 1496, 1531, 1571, 1632, 1655, 1670, 1707, 1749, 1778, 1786, 1814, 1838, 1871, 1964, 2015, 2028, 2058, 2162, 2165, 2185, 2187, 2228, 2284, 2290, 2350, 2370, 2385, 2397, 2408, 2584, 2588, 2596, 2609
WATER-TABLE 1086, 1519
WATER TRANSPORT 299, 1801
WATER-USE 31, 183, 371, 374, 401, 418, 442, 460, 469, 473, 527, 579, 624, 786, 787, 815, 823, 884, 887, 952, 968, 990, 1007, 1012, 1155-1157, 1203, 1378, 1390, 1458, 1507, 1565, 1587, 1593, 1620, 1664, 1666, 1673, 1779, 1891, 1892, 1906, 1914, 1935, 1984, 2010, 2048, 2106, 2184, 2316, 2506, 2508, 2510, 2620
WATER-USE EFFICIENCY 42, 44, 97, 100, 163-166, 168, 169, 173, 179, 272, 306, 449, 451, 470, 510, 545, 565, 580, 597, 660, 687, 715, 749, 753, 775, 844, 886, 921, 991, 1135, 1189, 1192, 1291, 1331, 1459, 1564, 1586, 1616, 1629, 1681, 1693, 1717, 1766, 1772, 1792, 1797, 1828, 1835, 1837, 1846, 1849, 1851, 1852, 1983, 2024, 2029, 2073, 2124, 2128, 2379, 2412, 2518, 2637 WATER-VAPOR 39, 757, 1056, 1152, 1397, 2074, 2177, 2402
WATER-VAPOR EXCHANGE 32, 632, 1309, 1436, 2132, 2516
WEATHER 1057
WEED-MANAGEMENT STRATEGIES 2532
WEEDS 2708
WEIGHT 31, 973, 1412
WEIGHT-LOSS 447
WESTERN AFRICA 1475
WESTERN-AUSTRALIA 14, 1199
WESTERN NORWAY 164
WESTERN SPRUCE BUDWORM 2596
WET HEATHLAND ECOSYSTEMS 2471
WETLAND PLANTS 2450
WETLANDS 191, 481, 982, 1575, 2303
WHEAT 2, 4, 25, 34, 45, 48, 102-105, 120, 212, 256, 289, 316, 344, 357, 366, 391, 418, 420, 421, 431, 444, 516, 610, 638, 681, 760, 779, 915, 973, 980, 984, 1016, 1026, 1253, 1268, 1292, 1338, 1342, 1343, 1425, 1437, 1441, 1453, 1454, 1539, 1540, 1550, 1568, 1579, 1590, 1599, 1611, 1889, 1893, 1895, 1932, 1955, 1962, 2018, 2022, 2026, 2093, 2095, 2096, 2112, 2138, 2181, 2185, 2200, 2226, 2232, 2350, 2401, 2425, 2428, 2444, 2467, 2561, 2571, 2616, 2619, 2664, 2683, 2710, 2712
WHEAT CANOPY 1156
WHEAT ENDOSPERM 2521
WHEAT GENOTYPES 741
WHEAT LEAVES 83, 564, 1431
WHEAT PLANTS 425
WHEAT RHIZOSPHERE 487
WHEAT ROOTS 2462
WHEAT SEEDLINGS 1053, 1466, 1467, 2098, 2103
WHEAT STRAW 2670
WHEAT TRITICUM- AESTIVUM 621
WHEAT YIELD 644

WHITE 2678
WHITE CLOVER 298, 330, 401, 403, 464, 483, 670, 784, 888, 889, 954, 963, 1098, 1099, 1400, 1521, 1599, 1629, 1651, 1664, 1667, 1692, 1698, 1760, 1787, 1865, 2141, 2142, 2144, 2146, 2186, 2250, 2367, 2679, 2681
WHITE-ROT FUNGI 2670
WHITE-TAILED DEER 1088
WHOLE-CATCHMENT 165, 186, 1396
WHOLE PLANT 806, 2485, 2632
WHOLE-PLANT LEVEL 1788
WHOLE-PLANT PERFORMANCE 2222
WHOLE-PLANT RESPIRATION 2698
WHOLE PLANTS 2077
WHOLE SOILS 945
WIDE-RANGE 433
WIDTH 488
WILDFIRE 39
WILD RADISH 1043, 1287, 1444, 1489
WILD-TYPE 89
WILLOW ECTOMYCORRHIZAS 1464
WILLOW LEAVES 1728
WILLOWS 1102
WIND 1974
WIND-TUNNEL 841
WINTER 2500, 2640
WINTER ANNUALS 1101
WINTER CONDITIONS 1211
WINTER HARDINESS 2488
WINTER LETTUCE 319
WINTER MOTH 554
WINTER SQUASH FRUIT 989
WINTER-WHEAT 12, 110, 119, 228, 393, 497, 509, 626, 627, 635, 637, 686, 715, 772, 774, 787, 1285, 1333, 1430, 1439, 1442, 1507, 1511, 1538, 1585, 1587, 1618, 1749, 1840, 1906, 1935, 2020, 2024, 2048, 2211, 2224, 2228, 2229, 2231, 2338, 2349, 2351, 2417, 2418, 2453, 2463, 2550, 2566, 2587, 2590, 2592
WOOD 2670
WOODY PLANT 2555
WOODY-PLANTS 81, 306, 720, 931, 1196, 1250, 1313, 1427, 1692, 1746, 2367, 2384, 2421, 2427, 2482, 2486, 2588
WORLD 86, 139, 407, 1497, 1540
WORLD OCEAN MODEL 852
WORLDWIDE 398, 2168
WOUND ETHYLENE 1469
XANTHIUM-STRUMARIUM L 808, 2632
X ENVIRONMENT INTERACTIONS 314
XEROPHYTA-SCABRIDA 2411

XYLEM 81
XYLEM DYSFUNCTION 2588
XYLOGLUCAN ENDOTRANSGLYCOSYLASE 653, 654, 2327
XYLOGLUCAN ENDOTRANSGLYCOSYLASE ACTIVITY 1923
YEAST- DERIVED INVERTASE 387, 893, 1223
YEAST GROWTH 1500
YELLOWSTONE NATIONAL PARK 2602
YIELD 2, 12, 31, 33, 46, 51, 53, 77, 103, 104, 140, 141, 144, 188, 195, 210, 221, 222, 234, 276, 289, 299, 330, 358, 369, 381, 391, 393, 415, 469, 512, 522, 526, 527, 545, 559, 580, 606, 610, 627, 637, 656, 686, 714, 717, 771, 784, 789, 820, 849, 901, 921, 927, 928, 938, 960, 968, 969, 973, 990, 1004, 1026, 1052, 1070, 1076, 1158, 1159, 1192, 1233, 1248, 1292, 1307, 1308, 1333, 1343, 1351, 1426, 1430, 1442, 1476, 1511, 1532, 1550, 1556, 1565, 1592, 1608, 1617, 1620, 1654, 1687, 1744, 1749, 1782, 1800, 1810, 1811, 1828, 1840, 1844, 1865, 1889, 1891-1893, 1895, 1897, 1905-1907, 1912, 1944, 1947, 1966, 2020, 2026, 2059, 2066, 2069, 2080, 2093, 2095, 2096, 2110, 2112, 2114, 2116, 2117, 2173, 2176, 2200, 2202, 2224, 2226, 2350, 2400, 2401, 2418, 2419, 2428, 2454, 2464, 2467, 2548, 2559, 2561, 2566, 2589-2592, 2616, 2650, 2696, 2704, 2712
YIELD COMPONENTS 626, 1180, 1935
YIELD PERFORMANCE 2037
YIELD RESPONSE 879, 882
YIELD RESPONSES 2028
YIELDS 2562
YIELD THRESHOLD 654, 2327
YIELD TURGOR 653
YIELD VARIABILITY 779
YOUNG CONIFEROUS TREES 2462
YOUNGER DRYAS 164
YR BP 1807
ZEALAND 852
ZEA-MAYS 237, 772, 808, 900, 2464, 2632
ZEA MAYS L 487, 932, 933, 1259, 1787, 2479
ZEAXANTHIN 1635
ZEAXANTHIN EPOXIDATION 2090
ZONE 538
ZOSTERA-CAPRICORNI 1629
ZUCCHINI SQUASH 850, 1218, 1622