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Soil Carbon Dynamics Along an Elevation Gradient in the Southern Appalachian Mountains

March 2004

C.T. Garten, Jr.

Environmental Sciences Division

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SOIL CARBON DYNAMICS ALONG AN ELEVATION GRADIENT IN THE SOUTHERN APPALACHIAN MOUNTAINS

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ABSTRACT

The role of soil C dynamics in the exchange of CO_2 between the terrestrial biosphere and the atmosphere is at the center of many science questions related to global climate change. The purpose of this report is to summarize measured trends in environmental factors and ecosystem processes that affect soil C balance along elevation gradients in the southern Appalachian Mountains of eastern Tennessee and western North Carolina, USA. Three environmental factors that have potentially significant effects on soil C dynamics (temperature, precipitation, and soil N availability) vary in a predictable manner with altitude. Forest soil C stocks and calculated turnover times of labile soil C increase with elevation, and there is an apparent inverse relationship between soil C storage and mean annual temperature. Relationships between climate variables and soil C dynamics along elevation gradients must be interpreted with caution because litter chemistry, soil moisture, N availability, and temperature are confounded; all potentially interact in complex ways to regulate soil C storage through effects on decomposition. Some recommendations are presented for untangling these complexities. It is concluded that past studies along elevation gradients have contributed to a better but not complete understanding of environmental factors and processes that potentially affect soil C balance. Furthermore, there are advantages linked to the use of elevation gradients as an approach to climate change research when hypotheses are placed in a strong theoretical or mechanistic framework. Climate change research along elevation gradients can be both convenient and economical. More importantly, ecosystem processes and attributes affecting soil C dynamics along elevation gradients are usually the product of the long-term interactions between climate, vegetation, and soil type. Investigations along elevation gradients are a useful approach to the study of environmental change, and its effect on soil processes, which can complement data obtained from controlled, large-scale, field experiments as well as other empirical and theoretical approaches to climate change research.

Keywords: soil organic matter, soil N, particulate organic matter, mineral-associated organic matter, soil C turnover, forest soil C, leaf litter chemistry, climate change

1. INTRODUCTION

Increasing atmospheric concentrations of CO_2 and projected global climate change have dominated the Earth sciences research agenda for the last part of the 20th century. Scientists have used a variety of tools ranging from field experiments to mathematical modeling to better understand the exchange of C between the atmosphere and the biosphere. Recently, numerous field experiments, at a variety of scales, have been utilized to investigate the effects of several anticipated effects of climate change (increasing CO_2, altered precipitation regimes, regional warming, and changes in atmospheric N deposition) on plant and soil processes. Large-scale field experiments that involve the manipulation of one or more environmental factors have become a popular approach to answering questions about how a changing climate will impact ecosystem structure and function.

For example, free-air carbon dioxide enrichment (FACE) experiments have been used to determine the effect of elevated atmospheric CO_2 concentrations on plant communities that range from agricultural crops (Leavitt et al., 1996) to grass pastures (Luscher et al., 1998) to forest stands (Norby et al., 2002). Controlled, large-scale field experiments to measure the effect of altered precipitation regimes on tree physiology and ecosystem processes have also been put into place in temperate hardwood forests (Hanson and Wullschleger, 2003). Other large-scale field experiments have been conducted to determine the effect of soil warming (Lukewille and Wright, 1997) and atmospheric N deposition (Emmett et al., 1998) on ecosystem processes, such as biogeochemical cycling, and determinants of ecosystem structure, such as species composition.

Controlled, large-scale field experiments have been successful in determining how ecosystems respond to changes in interacting environmental variables. Such experiments are especially important when ecosystem response to a changing environment is more complicated than a simple combination of effects by single factors (Shaw et al., 2002). However, these experiments have some shortcomings that can limit their usefulness in climate change research. First, controlled, large-scale field experiments often utilize a factorial type design that involves a step change or, at least, a limited range of possible combinations for the environmental treatments. Second, due to their short duration, these experiments are best suited for the study of processes that develop a treatment response over a period of months to several years. Finally, although not prohibitive, the high costs associated with such experiments puts this approach to the study of climate change effects on ecosystems beyond the financial resources of many research sponsors, especially in developing countries.

Recently, Rustad et al. (2001) identified studies along natural climatic and environmental gradients as an approach to climate change research that circumvents potential shortcomings associated with controlled, large-scale field experiments. It is widely recognized that many environmental properties vary in a more or less continuous manner with elevation, and the effects of climate change on species' ranges have been examined along altitudinal gradients (Parmesan, 1996). One of the primary advantages is that elevation gradients reflect multiple dimensions of climate change (involving numerous interacting abiotic and biotic factors) and, importantly, the long-term influence of climate on processes that affect ecosystem structure and function. However, the use of elevation gradients as a potential resource for the study of climate change effects on processes affecting soil C balance has not received much attention.

Soil C balance has been at the center of many science questions related to the exchange of CO_2 between the terrestrial biosphere and the atmosphere because most of the global C inventory resides in soil (Post, 1990; Schimel, 1995). For this reason, environmental factors that produce even a small change in global soil C stocks (through changes in soil C inputs or decomposition rates) have the potential to produce a disproportionately large change in levels of atmospheric CO_2. Forests in the Blue Ridge and Ridge and Valley Ecoregions (McMahon et al., 2001) of eastern Tennessee and western North Carolina range from low-elevation deciduous and mixed mesic forests to mid-elevation cove-hardwood forests to high-elevation evergreen needle forests. Climate changes with elevation include varying regimes of temperature, precipitation, N availability, and litter quality (all of which potentially affect soil C and N dynamics). For example, potential net soil N mineralization (Garten and Van Miegroet, 1994), forest soil respiration (Chambers, 1998), and turnover times of labile soil C (Garten et al., 1999) reportedly vary along climate gradients associated with changes in elevation.

The objectives of this report are: (1) to summarize measured trends in environmental variables (i.e., temperature, precipitation, N availability, litter chemistry) and ecosystem processes (e.g., aboveground net primary production and soil respiration) that potentially influence soil C balance along elevation gradients in the southern Appalachian Mountains of eastern Tennessee and western North Carolina, USA, and (2) to summarize recent research along elevation gradients in the southern Appalachian Mountains, particularly the Great Smoky Mountains National Park, that indicates a dependence of soil C dynamics on climate regime, N availability, and litter chemistry.

2. CONCEPTUAL FRAMEWORK

Two current hypotheses, with very different outcomes, can be used to predict the potential dynamics of forest soil C stocks in a changing environment. The first hypothesis involves the interaction among increasing atmospheric CO_2 concentrations, global warming, and increased rates of soil organic matter decomposition (Fig. 1). The main premise associated with the first hypothesis is that decomposition of soil organic matter is more sensitive to temperature change than net primary production (NPP) and increased surface soil temperatures will result in a net transfer of soil C to the atmosphere by increasing soil organic matter decomposition more than NPP (Kirschbaum, 1995; Kirschbaum, 2000). The subsequent release of soil C will feed increasing atmospheric CO_2 concentrations, leading to further increases in surface temperatures and further soil C loss through accelerated decomposition of organic matter. There is a potential brake on this positive feedback. Decomposition rates accelerated by soil warming may also stimulate greater soil N availability (Melillo et al., 2002) leading to higher NPP and increased soil

C inputs that would tend to offset soil C loss through accelerated decomposition rates. In the first hypothesis, soil C dynamics in a changing environment are highly dependent on the balance of processes determining soil C inputs and outputs.

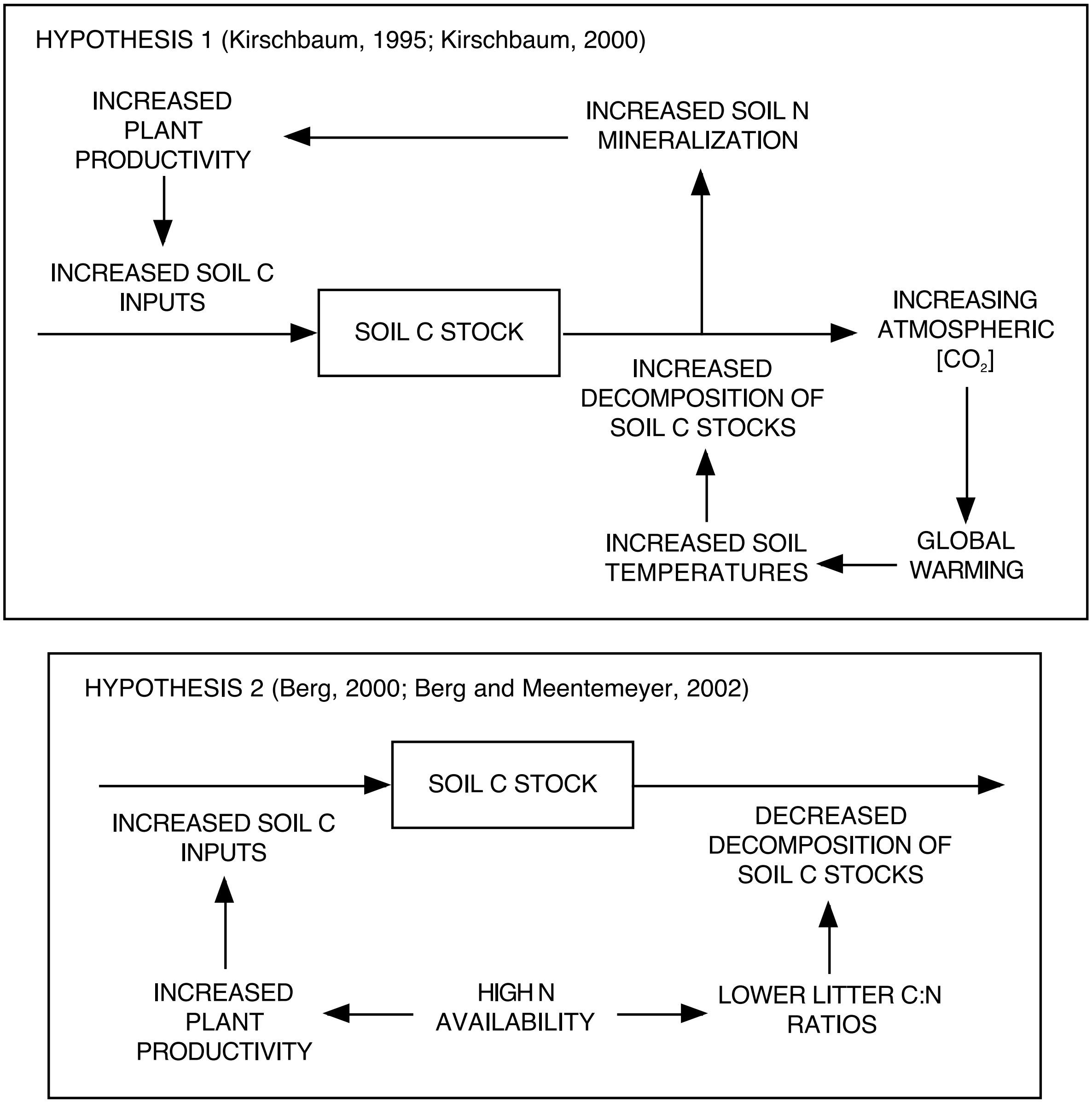

Fig. 1. Hypothetical effects of a changing environment on soil C dynamics. In hypothesis 1 (upper panel), the change in soil C stocks depends on the net balance between processes affecting soil C inputs and outputs. In hypothesis 2 (lower panel), soil C stocks increase.

The second hypothesis involves interactions among elevated atmospheric N deposition, NPP, litter chemistry, and the decomposition of soil organic matter (Fig. 1). The main premise associated with the second hypothesis is that soil C stocks will increase in a N-rich environment because more humus formation occurs when litter has a high N content or a low C:N ratio (Berg, 2000; Berg and Meentemeyer, 2002). Litter with elevated N concentrations potentially contributes to increased soil C stocks in two ways. N-rich litter releases more N during initial stages of decomposition (i.e., increased soil N mineralization) and inhibits soil organic matter decomposition in the later stages. Greater soil N availability can stimulate higher NPP and increased soil C inputs. In the second hypothesis, soil C stocks increase because greater N availability promotes an increase in soil C inputs while simultaneously inhibiting losses of soil organic matter.

3. METHODS

Forested sites on federal lands, like the Great Smoky Mountains National Park and the U.S. Department of Energy's Oak Ridge Reservation near Oak Ridge, TN, have been largely protected from direct human disturbance and land cover change for more than 55 years. Measurements at mature forest sites on these government lands are assumed to represent near steady state soil C stocks. Detailed descriptions of field and laboratory methods have been published in other papers (Garten et al., 1999; Garten et al., 2000; Garten and Ashwood, 2002) and are briefly summarized below for the reader's convenience.

Leaf litterfall was collected at various forest sites on different occasions from 1995 to 1997 (Garten et al., 1999) and in the autumn of 2002 using litter baskets. Following removal of the O-horizon from a known area, mineral soil samples were collected using a 2.45 cm diameter soil probe (AMS Soil Sampling Equipment, American Falls, ID). The mineral soil sampling depth varied among studies, but the data presented in this report are based on a 0-20 cm depth increment. Litterfall and O-horizon material was dried (70 °C) in an oven and ground to a fine powder using a sample mill prior to analysis for C and N concentrations. Mineral soil samples were air-dried to a constant weight in a laboratory equipped with a dehumidifier, crushed and sieved (2 mm), and ground to a fine powder in a ball-mill prior to elemental analysis.

Analysis of C and N was performed with elemental analyzers that converted C and N to CO_2 and N_2, respectively, by sample combustion. Carbon stocks in the O-horizon were calculated as the product of dry mass (g m^{-2}) and concentration (g C g^{-1} dry mass). Mineral soil C and N stocks (g m^{-2}) were calculated as the product of soil density (g dry soil cm^{-3}), concentration (g C or N g^{-1} dry soil), and sampling depth (20 cm). Carbon in the surface mineral soil was separated into two pools (particulate organic matter and organo-mineral soil C) using wet sieving methods (Garten et al., 1999; Garten, 2002; Garten and Ashwood, 2002).

Data from forests at different elevations across the southeastern U.S. (Table 1) were summarized using a simple, two compartment model of soil C dynamics (Garten et al., 1999; Garten and Wullschleger, 2000). Calculated C stocks in the O-horizon and particulate organic matter from the surface (0-20 cm) mineral soil were combined and designated "labile" soil C in the model. Organo-mineral soil C was primarily C associated with the soil silt and clay fraction. The model was used to calculate the turnover time of labile soil C and to examine associations between forest soil C dynamics and elevation in the southern Appalachian Mountains.

Table 1. Elevation, mean annual temperature (MAT), number of measurements (n), O-horizon and mineral soil (0-20 cm) C stocks, fraction of mineral soil C in particulate organic matter (fPOM-C), and calculated labile soil C stocks in undisturbed forest ecosystems at various locations in the southeastern USA. A site identification code is shown in parenthesis. GRSM = Great Smoky Mountains National Park, ORR = Oak Ridge Reservation.

Location (Site code)	Elevation (m)	MAT (°C)	n	O-horizon (g C m^{-2})	Soil (g C m^{-2})	fPOM-C	Labile (g C m^{-2})	Note
Ft. Benning, GA	–	18.3	52	440	2490	0.35	1312	1
ORR, TN (LP)	235	12.6	18	780	2750	0.22	1385	2
ORR, TN	295[a]	13.8	48	840	2440	0.31	1584	3
ORR, TN (WB)	335	13.1	18	660	2740	0.29	1455	2
GRSM (MB)	530	12.0	9	1950	4190	0.25	2998	1
GRSM (MC)	560	11.8	5	1850	3660	0.22	2655	1
GRSM (RB)	620	11.5	6	1320	4730	0.23	2408	1
GRSM (SB)	940	10.3	18	960	7280	0.21	2489	2
GRSM (MH)	1000	10.5	18	2480	5270	0.26	3850	2
GRSM (TD)	1430	7.7	9	2250	6150	0.19	3418	1
GRSM (NFG)	1570	7.0	6	2130	5790	0.12	2825	1
GRSM (BB)	1650	6.2	18	1680	5650	0.17	2640	2
GRSM (SP)	1670	6.3	18	5380	5900	0.17	6383	2

[a] An average for 48 sites that ranged in elevation from 235 to 355 m
[1] Garten (unpublished research)
[2] Garten et al. (1999)
[3] Garten and Ashwood (2002)

4. RESULTS

4.1 ENVIRONMENTAL TRENDS ALONG ELEVATION GRADIENTS

Multiple environmental and ecological attributes vary along elevation gradients (Harmon et al., 1983). Some attributes have relatively little influence on soil C because the change with altitude is too narrow (e.g., concentrations of atmospheric CO_2) or variation contributed to the attribute by altitude is overwhelmed by other sources of variation (such as temporal variability). However, three environmental factors that have potentially significant effects on soil C dynamics (temperature, precipitation, and soil N availability) vary in a systematic and predictable manner with altitude in the southern Appalachian Mountains.

Smallshaw (1953) and Shanks (1954) first published summaries of changes in precipitation and temperature with elevation in the Great Smoky Mountains National Park based on meteorological data collected from 1946-1950. At this location, Shanks (1954) found that temperature decreased by ≈0.41 °C for every 100 m rise in altitude. It was reported that annual precipitation increased by about 50% over a 1000 m rise in elevation and that potential evapotranspiration also increased with altitude (Shanks, 1954; Stephens, 1969). At elevations above ≈610-760 m in the Park, the climate regime is best described as "rain forest" (Shanks, 1954).

Figure 2 illustrates changes in precipitation (Stephens, 1969) and temperature with elevation at various sites in the Great Smoky Mountains National Park. The temperature data are summarized from Stephens (1969) and from other more recent studies (Garten et al., 1999), including ongoing unpublished research, on forest soil C. Temperatures increase by ≈0.46 °C and precipitation increases by ≈5.7 cm for every 100 m rise in elevation. High elevation forests are cooler and wetter than low elevation forests. The linear relationships between temperature or

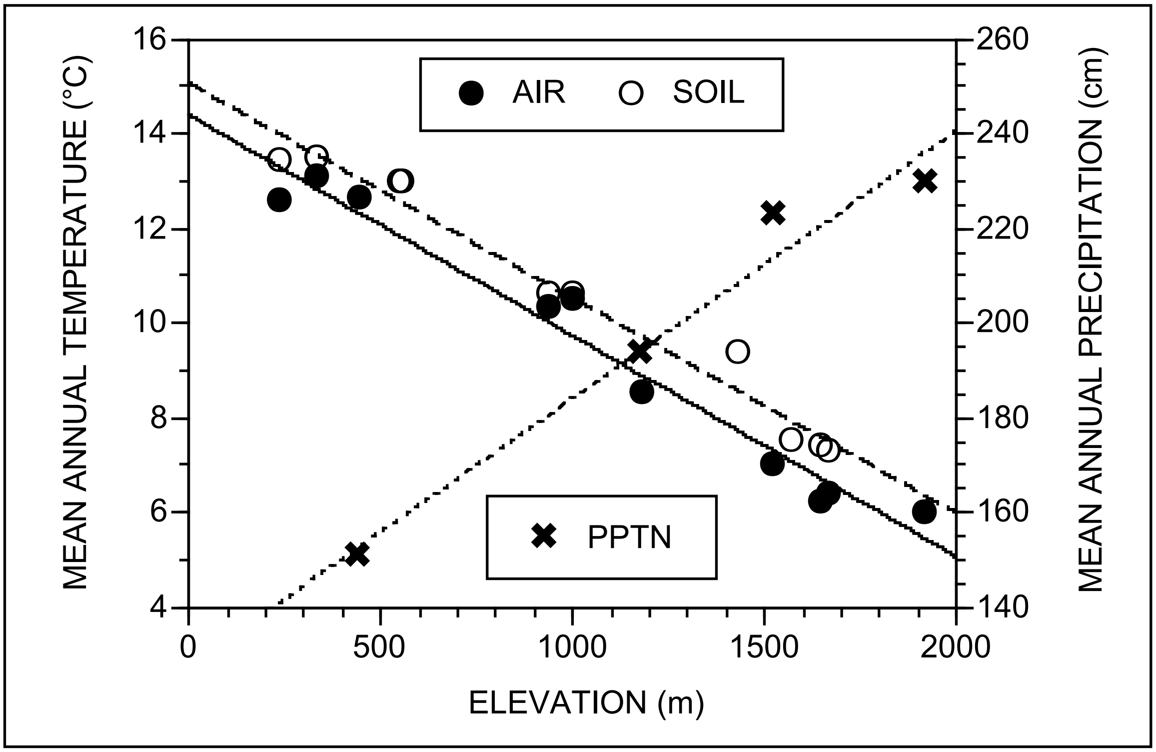

Fig. 2. Relationship between mean annual air temperatures, mean annual soil temperatures, mean annual precipitation, and elevation in the southern Appalachian Mountains. The data are from various sources including Stephens (1969) and Garten et al. (1999). Soil temperatures were measured at a depth of ≈10 cm using temperature probes connected to Li-Cor LI-1000 data logger (LI-COR, Lincoln, Nebraska) or StowAway® Tidbit® temperature loggers (Onset Computer Corp., Bourne, Maine).

precipitation and elevation indicate that there are continuous climate gradients in the southern Appalachian Mountains that can be used as a surrogate for changes in climate over time. Moreover, these differences in climate have persisted for centuries allowing biotic controls on soil C and N dynamics to adapt to long-standing climate regimes.

There are two processes contributing to the change in N availability along elevation gradients: atmospheric N deposition and net soil N mineralization (Fig. 3). Typically, high elevation forest ecosystems in the southern Appalachian Mountains receive more atmospheric N deposition than low elevation forests (Lindberg et al., 1988; Lovett and Kinsman, 1990). The annual total flux of N to high elevation (1740 m) sites is ≈28 kg N ha^{-1} and that to low elevation sites is on the order of 6 to 14 kg N ha^{-1} (Lovett and Lindberg, 1993). Cloud immersion and orographic precipitation at high elevations are the primary causes of differences in N deposition between high- and low-elevation forests in the Great Smoky Mountains National Park. For this reason, the relationship between atmospheric N deposition and elevation could more closely resemble an exponential function, with a sharp increase above 1700 to 1800 m, rather than a continuous linear association. Other studies, like those in the Adirondack Mountains of New

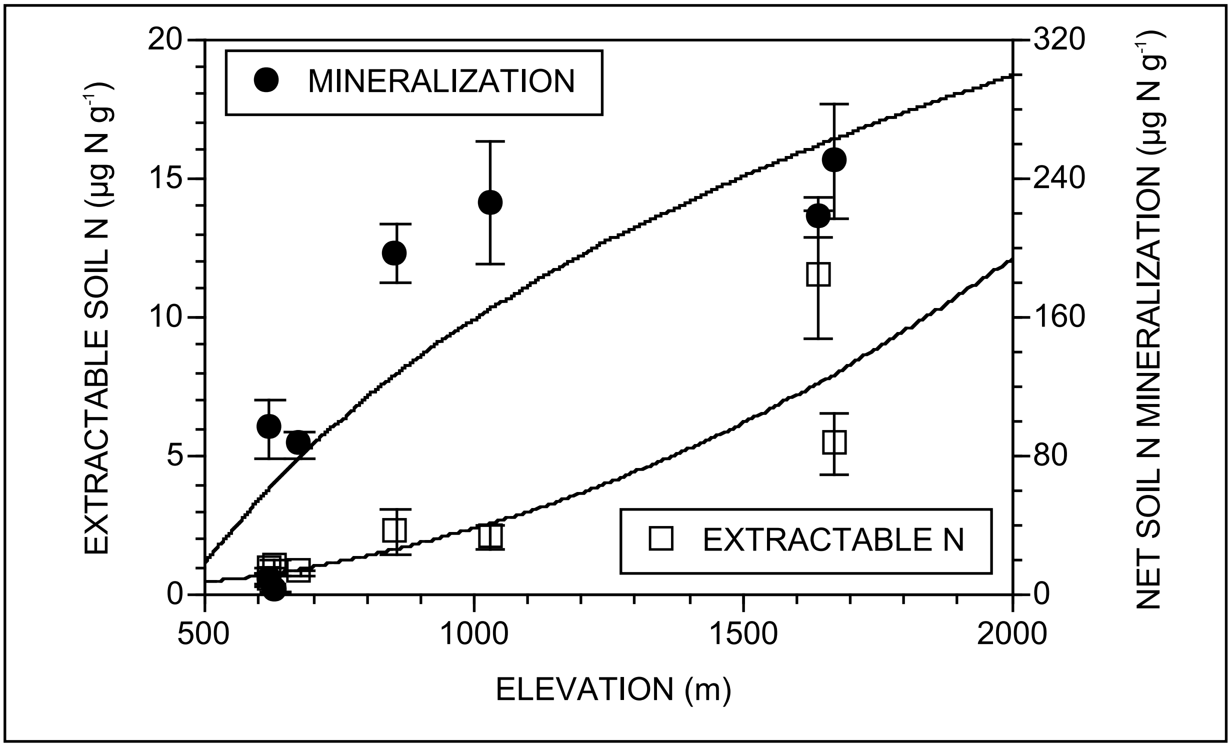

Fig. 3. Relationships between elevation and extractable inorganic soil N or potential net soil N mineralization in a 6-week aerobic laboratory incubation of forest soils from an elevation gradient in the Great Smoky Mountains National Park. Error bars show one standard error about the mean. Data are from Table 1 in Garten and Van Miegroet (1994). A power function ($Y = 2.46E\text{-}07 \bullet X^{2.33}$; $r^2 = 0.91$) was used to describe the relationship between extractable soil N and elevation. A logarithmic function ($Y = -1237 + 202 \bullet \ln(X)$; $r^2 = 0.73$) was used to describe the relationship between potential net soil N mineralization and elevation.

York state, demonstrate an exponential increase in annual atmospheric N deposition from low-elevation (7 kg N ha^{-1} at 600 m) to high-elevation (29.5 kg N ha^{-1} at 1275 m) forests and the important contribution of cloud water to N deposition at high elevations (Miller et al., 1993).

The contribution of net soil N mineralization to site N availability commonly exceeds that of atmospheric deposition in most forest ecosystems. Various studies indicate that net soil N mineralization tends to increase with elevation in mountainous terrain (Powers, 1990; Garten and Van Miegroet, 1994; Knoepp and Swank, 1998). Figure 3 illustrates the change in extractable inorganic soil N and potential net soil N mineralization potential, as measured in laboratory incubations, along a 1000 m elevation gradient in the southern Appalachian Mountains. There were statistically significant differences between potential net soil N mineralization along the elevation gradient with a marked increase in net nitrification potential at four sites above 700 m (Garten and Van Miegroet, 1994). Other studies have reported increasing net soil N mineralization, and thus greater soil N availability, over more narrow elevation gradients in the northeastern (Bohlen et al., 2001) and southeastern (Knoepp and Swank, 1998) US. Similar studies of soil N availability in New Mexico failed to reveal clear trends between N mineralization and elevation, with the possible exception of mineralization in the forest floor (Gosz and White, 1986). Increases in soil N concentrations with declines in mean annual temperature are well known from studies along latitudinal gradients (Schreiner and Brown, 1938). Increasing soil N stocks with elevation (Fig. 4) can also contribute to greater overall levels of N availability because higher soil N stocks produce a greater N mineralization flux (g N m^{-2} yr^{-1})

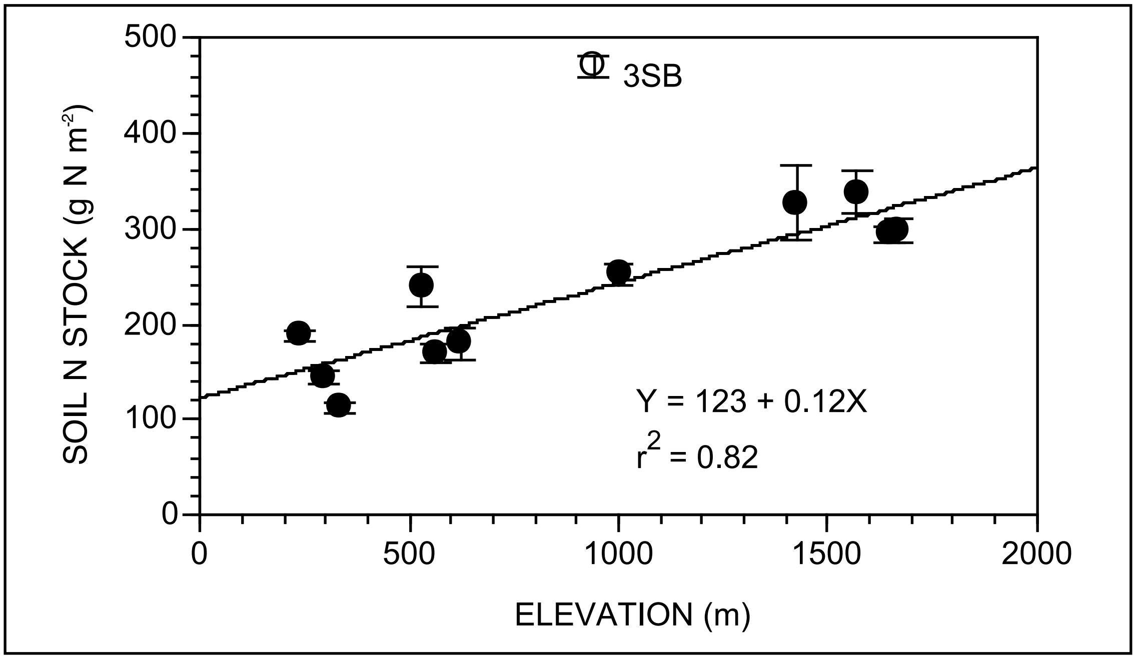

Fig. 4. Relationship between mean (±SE) surface mineral soil (0-20 cm) N stock and elevation at forest sites along an elevation gradient in the southern Appalachian Mountains. The twelve study sites are among those listed in Table 1. Site 3SB is located on an alluvium and is not included in the linear regression.

even if the annual rate (i.e., fraction of mineral soil N mineralized per year) remains relatively constant with changes in altitude.

Both atmospheric deposition and soil N mineralization contribute to greater soil N availability with increasing elevation in the southern Appalachian Mountains. The trends can also be influenced by topography in both low elevation (Garten et al., 1994) and high elevation forests (Garten, 2000). Differences in site N availability along elevation gradients appear to have direct effects on litter quality which, in combination with temperature, govern the process of soil organic matter decomposition (Garten et al., 2000). Figure 5 illustrates the increase in leaf litter N concentrations and the corresponding decline in leaf litter C:N ratios with increasing elevation in the Great Smoky Mountains National Park from two different data sets. Leaf litterfall C:N

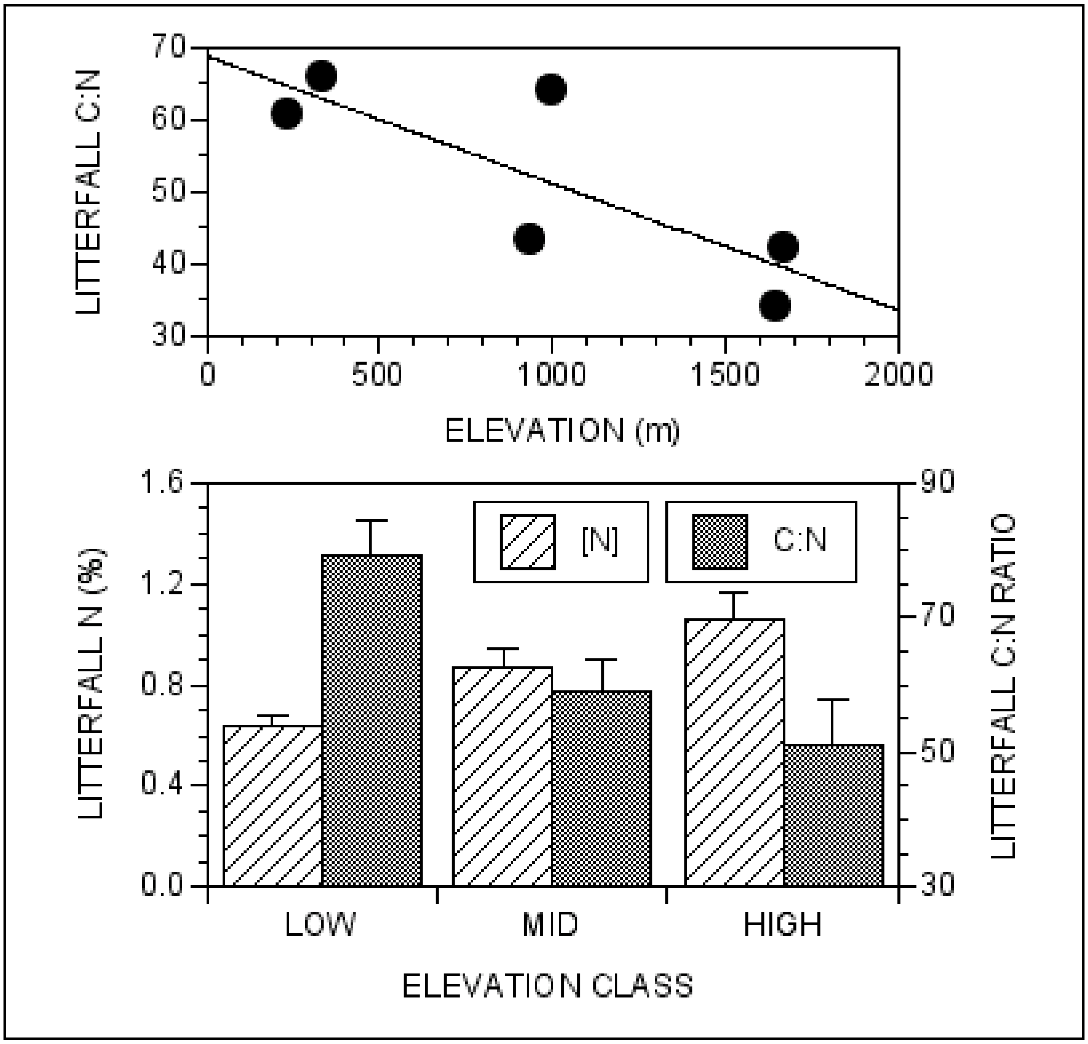

Fig. 5. Relationship of leaf litterfall C:N ratios to elevation at forest sites in the southern Appalachian mountains. Upper panel: data from six sites over a three year period, 1995-1997 (Garten et al. 1999). The linear regression is: $Y = 68.8 - 0.0176 \bullet X$; $r^2 = 0.66$. Lower panel: mean (±SE) deciduous leaf litterfall N concentrations and C:N ratios at low (335-560 m), mid (940-1000 m), and high (1425-1670 m) elevation forest sites in 2002.

ratios decline with elevation because increasing litterfall N concentrations can be traced to greater site N availability at higher elevations. Similar associations between soil N availability and forest litter N or C:N ratios have been reported in other field studies (Bohlen et al., 2001; Ollinger et al., 2002). The differences in litter chemistry have potential ramifications for processes that control relationships between elevation and forest soil C storage.

4.2 TRENDS IN SOIL CARBON DYNAMICS

Numerous studies indicate that soil C concentrations or stocks increase with altitude in mountainous terrain (Townsend et al., 1995; Turmbore et al., 1996; Conant et al., 1998; Garten et al., 1999; Bolstad and Vose, 2001). Field measurements that were the basis for trends reported in this report on changes in soil C stocks with elevation are summarized in Table 1. When data from multiple studies that employed similar sampling methods (Garten et al., 1999; Garten and Wullschleger, 2000; Garten and Ashwood, 2002) were combined, it was evident that surface mineral soil C stocks from forest ecosystems increase with elevation in the southern Appalachian Mountains (Fig. 6). There is also an apparent inverse relationship between soil C stocks and mean annual temperature. The differences between study sites reflect a changing balance of soil C inputs and soil C losses that are potentially related to changes in both abiotic (e.g., temperature) and biotic (e.g., litter quality) factors.

Changes in forest soil C inputs could be one factor underlying the association between forest soil C stocks and elevation. Greater soil C stocks at higher elevations could be the product of increased C inputs in combination with a relatively constant rate of soil C loss through decomposition of organic matter. Aboveground litterfall and root mortality are the two primary processes that contribute to soil C inputs along elevation gradients, and relatively little is known about how belowground C inputs might vary with elevation. Although regional data on aboveground litter fall is available from various sources, this process also presents an opportunity for further study along elevation gradients.

In a regional context, Sharpe et al. (1980) examined foliage litterfall in the southeastern USA and derived an annual estimate of 408 g m^{-2} yr^{-1}, based on 252 USDA Forest Service study plots, with no significant difference among forest types. This estimate corresponds reasonably well with measurements of annual leaf litterfall inputs across the region. Reported annual leaf litterfall at Walker Branch Watershed, TN (378 g m^{-2}; Edwards et al., 1989), Coweeta, NC (399 g m^{-2}; Johnson and Lindberg, 1992), and Duke, NC (377 g m^{-2}; Johnson and Lindberg, 1992) are all within 10% of the estimate derived by Sharpe et al. (1980). The estimate of Sharpe et al. (1980) is also within 25% of litterfall inputs for temperate coniferous and deciduous forests studied during the IBP (Cole and Rapp, 1981). Using a litterfall C concentration of 0.50 g C g^{-1}, annual aboveground C inputs beneath forests in this region are $\approx$204 g C m^{-2}. Based on data provided by Garten et al. (1999), for five forests along an elevation gradient in the southern Appalachian Mountains, annual C return to forest soils (measured over 3 years) in aboveground litterfall was 250 g C m^{-2} (about 25% greater than a general estimate of 204 g C m^{-2} yr^{-1}).

Bolstad et al. (2001) recently reported significant declines in leaf area index and aboveground NPP (from 12 to 5 Mg ha^{-1} yr^{-1}) by deciduous forest stands along an elevation gradient in North Carolina. The changes in aboveground NPP with elevation were not related to changes in precipitation or site N status even though other studies indicate that aboveground NPP is directly related to annual net soil N mineralization in temperate forests of the north-central USA (Reich et al., 1997). Other studies in forests of the northeastern US also indicate declining aboveground NPP (from 4 to 1.7 Mg ha^{-1} yr^{-1}) with increasing elevation (Joshi et al., 2003). Decreasing aboveground NPP and leaf area index with increasing altitude in North Carolina forests suggest that aboveground leaf litter inputs do not increase with elevation in the southern Appalachian mountains, possibly due to an indirect constraint on forest productivity by declining mean annual temperature or fewer growing season degree-days (Joshi et al., 2003). Instead, reported trends indicate less NPP and lower leaf litterfall inputs; both would contribute to declining soil C inputs with increasing elevation. Consequently, one must look to processes other than soil C inputs to explain increasing soil C stocks with elevation in the southern Appalachian mountains.

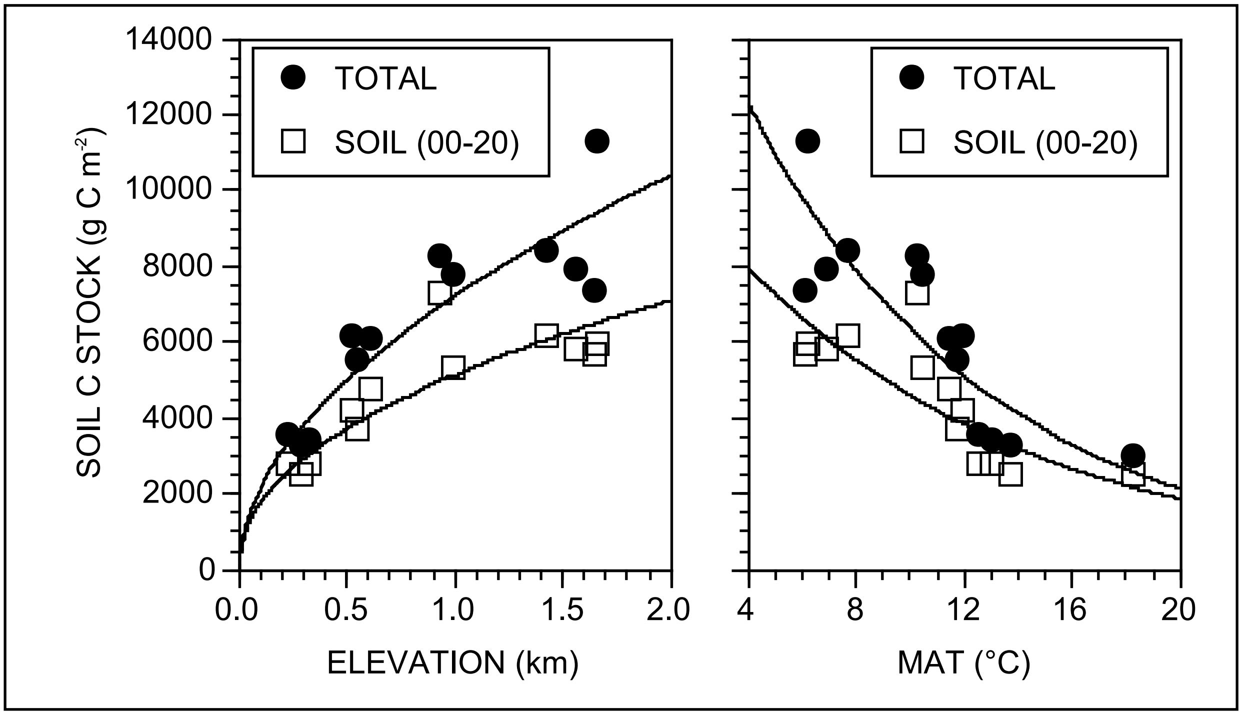

Fig. 6. Relationships between total soil C stocks (O-horizon plus top 20 cm of mineral soil) or mineral soil (0-20 cm) C stocks and elevation (left panel) or mean annual temperature (right panel) at different forest sites in the southern Appalachian Mountains. Left panel: data for both total and mineral soil C stocks are from Table 1; power functions were fitted to the data for both total ($Y = 187 \cdot X^{0.529}$; $r^2 = 0.86$) and surface mineral soil ($Y = 204 \cdot X^{0.468}$; $r^2 = 0.82$) C stocks along the elevation gradient. Right panel: exponential functions were fitted to the data for both total ($Y = 18973 \cdot \exp(-0.1093X)$; $r^2 = 0.75$) and surface mineral soil ($Y = 11464 \cdot \exp(-0.0913X$; $r^2 = 0.67$) C stocks along the elevation gradient. Mean annual temperatures were based on field data or predicted from elevation (Fig. 2).

4.3 SOIL CARBON LOSSES THROUGH DECOMPOSITION

Carbon losses from decomposition of soil organic matter are difficult to quantify directly and are sometimes inferred from studies of soil CO_2 efflux or soil respiration. There are several potential complications linked to this approach. First, both microorganisms and plant roots contribute to the CO_2 flux from soils (for review see Hanson et al., 2000). Second, the timing of these measurements can be critical because there are seasonal variations in the relative contribution of root respiration and heterotrophic microbial respiration to the CO_2 efflux (Dorr and Munnich, 1986; Dorr and Munnich, 1987; Wang et al., 2000). Finally, measurements of soil respiration may disproportionately reflect the decomposition of labile soil organic matter (Janzen et al., 1992; Janssens et al., 2001) and thereby under represent decomposition losses from more refractory soil C pools. Mindful of these potential limitations, measurements of soil CO_2 efflux are frequently used to infer differences in soil organic matter decomposition.

In the Great Smoky Mountains National Park, *in situ* spring and summer measurements of soil respiration decline with increasing altitude (Chambers 1998) consistent with other field studies that indicate correlations between rates of soil respiration and elevation or mean annual temperature (Simmons et al., 1996; Conant et al., 1998; Wang et al., 2000; Kane et al., 2003). The role of temperature in regulating soil organic matter decomposition under field conditions is not always straightforward and may be influenced by both soil moisture (Conant et al., 1998; Wang et al., 2000; Borken et al., 2002; Rey et al. 2002) and N availability (Berg and Matzner, 1997; Kuperman, 1999; Neff et al., 2002). Root respiration in forest soils is also a function of root N concentrations as well as soil temperature (Burton et al., 2002).

In the mountains of northern Arizona, measured annual rates of soil respiration decreased from warm-xeric to cool-mesic sites, but soil moisture was judged to be a more important control on soil C stocks and fluxes than temperature under semi-arid conditions that prevailed at warmer sites along the elevation gradient (Conant et al., 1998). Field studies in the mountains of the Sierra Nevada also indicate that a positive correlation between temperature and the decomposition rate of soil organic matter is dependent on soil moisture not limiting the decomposition process (Wang et al., 2000). Although seasonal and annual moisture differences contribute to pronounced short-term variations in soil respiration (Hanson et al., 1993; Hanson et al., 2003), long-term site differences in soil moisture are not considered a limiting factor to organic matter decomposition along elevation gradients in the southern Appalachian Mountains. All of the sites listed in Table 1 have historically humid climates with more than 100 cm of annual precipitation.

Soil C stocks under forests that have been protected from human disturbance for many decades, such as those on the Oak Ridge Reservation and in the Great Smoky Mountains National Park (Table 1), can be used to estimate the turnover time of labile soil C and its relationship to elevation or climate. A simple two compartment model (Fig. 7) that partitions soil C stocks into labile and organo-mineral pools has been previously described for this purpose

(Garten et al., 1999). Labile soil C is the sum of C stocks in the forest floor O-horizon and C stocks in particulate organic matter from the surface mineral soil (in this case, 0-20 cm). When field estimates of the aboveground litterfall were not available, data from Sharpe et al. (1980) were used in model calculations. For the purpose of estimating soil C inputs, it was assumed that aboveground and belowground inputs are equivalent. Figure 8 illustrates the correlation between the predicted turnover time of labile soil C and elevation (or temperature) in the southern Appalachian Mountains.

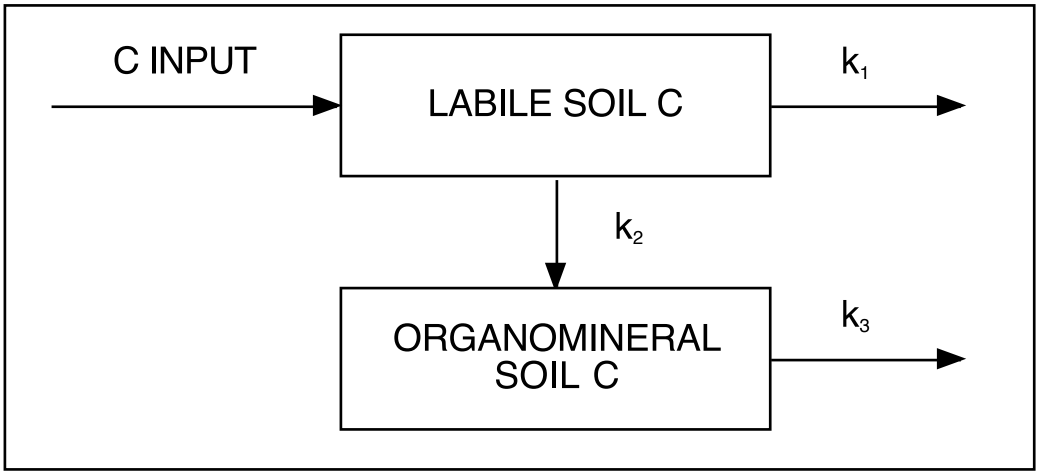

Fig. 7. A simple two-compartment model of soil C dynamics (adopted from Garten et al. 1999). Soil C inputs include both litter inputs above and belowground. Labile soil C includes C contained in the O-horizon and in particulate organic matter from the surface (0-20 cm) mineral soil. Organo-mineral soil C is chiefly associated with the soil silt and clay fraction. At steady state, the decomposition rate of labile soil C (k_1) is derived from: k_1 = (C input/labile soil C stock) - k_2. The humification rate (k_2) is derived by dividing the organo-mineral soil C stock by the product of the labile soil C stock and the turnover time ($1/k_3$) of organo-mineral soil C.

Similar to studies from other locations (Townsend et al., 1995; Trumbore et al., 1996), the turnover times of labile soil C in the southern Appalachian Mountains appear to increase with elevation or decreasing mean annual temperature (Fig. 8). In studies along an elevation gradient in the Sierra Nevada (California), Trumbore et al. (1996) also found that the turnover time of soil C increased with elevation or declining mean annual temperatures, and concluded that temperature was the dominant controlling factor in soil C dynamics. It is tempting to infer relationships between soil C turnover and mean annual temperature on the basis of elevation gradients because so many studies demonstrate that soil respiration increases with temperature (Raich and Schlesinger, 1992; Kirschbaum, 1995; Raich and Potter, 1995). Nonetheless, inferences about relationships between decomposition rates and temperature derived from field studies along elevation gradients must be interpreted with caution.

One reason for caution is research challenging the premise that temperature is the primary environmental driver governing soil C dynamics through effects on soil organic matter decomposition (Liski et al., 1999; Giardina and Ryan, 2000; Janssens et al., 2001). For example, Liski et al. (1999) argue that the decomposition of older, more refractory soil organic matter is relatively insensitive to temperature. In the calculations performed with the model (Fig. 7), I have held the turnover time of organo-mineral soil C constant at 56 years (Garten and Ashwood, 2002) on the premise that the decomposition rate of organo-mineral soil C is independent of temperature. The latter assumption is not in complete agreement with empirical studies indicating that the turnover time of organo-mineral soil C (Garten and Wullschleger, 2000; Garten and Ashwood, 2002) or more recalcitrant soil organic matter (Townsend et al., 1995) declines with increasing temperature. However, the incorporation of a temperature dependent decomposition rate for organo-mineral soil C in the model had little effect on the predicted turnover times of labile soil C (data not shown).

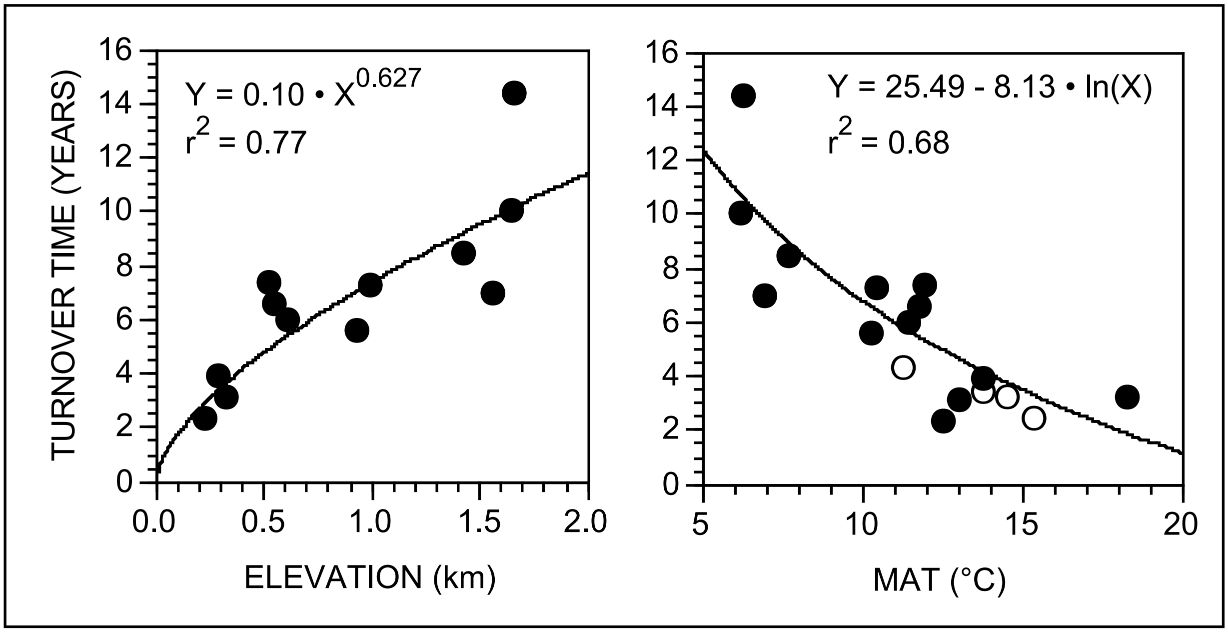

Fig. 8. Predicted turnover times of labile forest soil C in relation to study site elevation (left panel) or mean annual temperature (right panel) in the southern Appalachian Mountains. The turnover times were calculated based on measured soil C stocks (Table 1) using the model described in Figure 7. For the purpose of comparison, independent estimates of labile soil C turnover beneath four switchgrass field trials (open symbols) are shown in the right panel (data from Garten and Wullschleger, 2000).

A second reason for caution is the oversimplification of interpreting predicted turnover times of labile soil C within the framework of a single variable (temperature) when multiple environmental factors vary along elevation gradients. As indicated previously, available data suggest that both aboveground forest productivity and soil respiration decline with elevation in the southern Appalachian Mountains. Other studies suggest that forest productivity (and not temperature) is a primary factor controlling soil respiration and, possibly, soil organic matter decomposition (Janssens et al., 2001). Litter chemistry, soil moisture, N availability, and temperature all potentially interact to regulate soil C losses through decomposition along elevation gradients. Although the environmental factors determining the relationships illustrated in Figures 6 and 8 are not completely understood, additional research along elevation gradients within a strong theoretical framework could help to unravel the various environmental factors regulating forest soil C dynamics at regional and global scales.

5. DISCUSSION

Past studies along elevation gradients have contributed to a better but not complete understanding of environmental factors and processes that potentially affect soil C balance (Table 2). Such studies can not replace or substitute for large-scale field experiments because they lack some aspects of dimensionally and methodological rigor that are more easily incorporated into a controlled experiment. For example, although there are minor changes in the concentration of atmospheric CO_2 with elevation, the differences are not of sufficient magnitude to test questions about the effect of potential future CO_2 concentrations on ecosystem processes. Those questions are best answered through the use of FACE-like experiments or laboratory studies. Similarly, some environmental factors exhibit too much within site variation to be treated as independent variables in studies of ecosystem processes along elevation gradients. Such limitations can restrict the applicability of elevation gradients for some aspects of climate change research, but not others (like effects of temperature, moisture, and litter chemistry). Thus, studies along elevation gradients can be viewed as climate change research that seeks to complement or otherwise benefit the findings and interpretations that arise from short-term, large-scale, field experiments.

There are some important advantages to research along elevation gradients when hypotheses about the effect of climate on ecosystem processes are placed in a strong theoretical or mechanistic framework. First, convenience – climate gradients associated with changes in elevation can be found in many parts of the world wherever there is mountainous terrain. Second, economy – studies along elevation gradients (as well as other naturally occurring environmental gradients) are relatively inexpensive to establish and maintain and do not involve the expense associated with building and maintaining engineering infrastructures for the control of environmental factors. This particular advantage can be of considerable importance to studies of climate change in developing countries that may lack the financial resources to support a network of controlled, large-scale, field experiments. Last, adaptation – ecosystem processes and attributes along elevation gradients are the product of long-term interactions between climate, vegetation, and soil type. Thus, in the absence of recent disturbance, biotic components that are important in regulating soil C inputs and outputs, like soil microbial communities, are adapted to the prevailing environment.

There remain unresolved questions about whether soil C dynamics in a changing climate will have a positive or negative feedback on atmospheric CO_2 concentrations. Contemporary research along elevation gradients (Table 2) indicates that both temperature and litter quality are important controls on soil C storage (see e.g., Garten et al., 2000), but these controls can have counteracting or synergistic effects on soil C balance depending on the prevailing climate. On one hand, hypotheses about the acceleration of soil organic matter decomposition under elevated ambient CO_2 concentrations suggest a positive feedback on global warming as a consequence of greater soil organic matter decomposition in a warming climate (Jenkinson et al., 1991; Kirschbaum, 1995; Kirschbaum, 2000). This feedback operates under circumstances where the temperature sensitivity of organic matter decomposition (i.e., soil C losses) exceeds that of NPP (i.e., soil C inputs). Relationships between temperature and soil C stocks, or turnover times, derived from research along elevation gradients are directly pertinent to the development of hypotheses about the response of soil C to regional warming. Predictions from prior research indicate a potential loss of forest soil C stocks in the southern Appalachians with regional warming due to accelerated decomposition of soil organic matter (Garten et al., 1999). Furthermore, warming could negatively impact high elevation forests more than those at low elevations by contributing to disruption of the N cycle (Joslin and Wolfe, 1993; Joslin and Johnson, 1998; Melillo et al., 2002).

Table 2. Trends in aboveground net primary production, soil moisture, vegetation type, N availability, and temperature with elevation, their potential effects on soil C or N, and some supporting studies along elevation gradients.

Environmental factor	Association with elevation	Potential effect on soil C or N with increasing elevation	Supporting studies along elevation gradients
Aboveground productivity	negative correlation	reduced inputs lower soil C stocks	Bolstad et al. (2001); Joshi et al. (2003)
Soil moisture	positive correlation	decomposition rates increase from xeric to mesic sites (up to a limit where saturation inhibits decomposition)	Conant et al. (1998); Conant et al. (2000); Wang et al. (2000)
Vegetation type	–	poor substrate quality limits N mineralization	Knoepp and Swank (1998)
Nitrogen availability	positive correlation	greater soil N availability contributes to higher soil C stocks through effects on decomposition*	Lindberg et al. (1988); Lovett and Kinsman (1990); Miller et al. (1993); Garten and Van Miegroet (1994); Lawrence et al. (2000); Bohlen et al. (2001)
Temperature	negative correlation	reduced decomposition rates and longer turnover times increase soil C stocks	Townsend et al. (1995); Trumbore et al. (1996); Chambers (1998); Conant et al. (1998); Garten et al. (1999); Wang et al. (2000); Kane et al. (2003)

*Details about the hypothesized effect of N availability on litter decomposition are explained by Berg and Matzner (1997) and Berg et al. (2001)

On the other hand, hypotheses about changing litter C:N ratios and higher limit values to litter decomposition (Berg et al., 1996; Berg, 2000) suggest a negative feedback on global warming as a consequence of greater humus formation (Berg and Matzner, 1997; Berg et al., 2001) and reduced decomposition losses of forest soil C in a N-rich environment. Emissions of nitrogen oxides from fossil fuel combustion and the use of inorganic N fertilizers in the USA more than tripled during the last four decades of the 20th century (Howarth et al., 2002). Anthropogenic alterations of the N cycle on a regional and global scale are an important component climate change. Elevated N availability may lead to an accelerated short-term loss of labile soil C and a long-term stabilization of organo-mineral soil C (Neff et al., 2002). Greater site N availability and declining litter C:N ratios, as a consequence of increasing atmospheric N deposition or fertilizer inputs, may lead to longer turnover times for soil C and greater soil C sequestration by increasing the fraction of soil organic matter inputs that are resistant to decomposition (Berg, 2000).

Studies along elevation gradients in the southern Appalachian Mountains are relevant to the two preceding hypotheses about the effect of temperature and litter quality on soil C dynamics, but the potential effects are confounded. Declining temperatures, greater site N availability, and declining litter C:N ratios potentially act independently or together (i.e., synergistically) to produce increasing soil C stocks and longer turnover times of labile soil C with increasing elevation. At low elevations, both higher mean annual temperatures and lower site N availability (as reflected in higher litter C:N ratios) potentially contribute to lower soil C stocks and shorter turnover times for labile soil C.

The confounding effects of independent variables is a common problem in many areas of science and has been recognized as a potential methodological issue in correlational studies of climate change by the IPCC (McCarthy et al., 2001). In the Great Smoky Mountains National Park, gradients of past disturbance (such as fire and exotic species invasion) can covary with gradients of elevation, temperature, and moisture (White, 1979; Harmon et al., 1983). At other locations in the southern Appalachian Mountains, changes in vegetation type with elevation sometimes play a larger role than climate as a control on forest soil N dynamics (e.g., Knoepp and Swank, 1998). The potential for confounding factors is of considerable importance in studies along elevation gradients. This problem can also occur, although not to the same extent, in controlled field experiments that test the effects of climate change on ecosystem processes. In either case, confounding factors can lead to problems with the determination of causation and the validity of data interpretations.

In medicine, epidemiology, and psychology the problem of confounding factors in correlational studies is frequently addressed through experimental designs that involve subject matching. In other words, experimental units along known gradients are selected such that they are as similar as possible except for the variable of interest. Experimental designs can be imposed along elevation gradients to minimize the influence of some confounding factors. For example, elevation gradients are well suited to studies of temperature effects when other potentially covarying factors can be held constant or their effects are accounted for through appropriate statistical methods. Some forest ecosystems at different elevations in the Great Smoky Mountains National Park have similar litter chemistries (i.e., similar C:N ratios) due to similarities in soil N availability. Depending on how closely such sites are matched, they are useful for studies on the long-term effect of temperature on soil C and N in the absence of litter chemistry differences. Other forest ecosystems in the National Park have different litter C:N ratios at the same elevation (for example, two mid-elevation sites in Fig. 5). The latter sites are useful for studies of the long-term effect of litter chemistry on soil C and N in the absence of temperature effects.

Strict matching criteria can lead to difficulties in site selection, one of the biggest disadvantages to matched designs along environmental gradients. Although no two ecosystems are identical, particularly at different elevations, broad criteria such as forest type (e.g., deciduous or coniferous), basal area, topographic position (e.g., ridge or valley), aspect, and generalized soil orders or soil type (e.g., mor or mull) can be used to adjust for confounding factors that may or may not be recognized prior to the start of the study. Vegetation maps, digital elevation models, and maps of soil type can be used together in a GIS framework to identify potentially similar sites along elevation gradients in mountainous terrain. More stringent matching criteria will better control confounding factors but can lead to difficulties in site selection. Less stringent matching criteria will simplify site selection but can result in less control of confounding. It is impossible to control everything in studies along elevation gradients, but at a minimum efforts can be undertaken to control readily recognized confounding factors through experimental designs that allow a clearer interpretation of effects caused by the variable of interest. Special attention should be given to potential confounding factors that are mechanistically linked to the process under study.

In those cases where ecosystem matching is unduly difficult or impractical, elevation gradients are still useful for both experimental studies and correlational studies involving sets of variables. Studies of soil transplants in the Oregon Cascade Mountains (Hart and Perry, 1999) illustrate the importance of combining field and laboratory experiments to achieve a more complete understanding of the effects of climate on soil C and N dynamics when there are potential confounding effects of temperature and organic matter quality. High elevation forests (1310 m) in the Oregon Cascades have greater soil C and N stocks than those at low elevations (490 m) because cooler temperatures at high elevations limit decomposition of organic matter and soil N mineralization (Hart and Perry, 1999). Experimental transplants along elevation gradients may also be useful to study the temperature acclimatization of decomposer communities which potentially limit the positive feedback between soil warming and increasing atmospheric CO_2 concentrations through accelerated decomposition (Luo et al., 2001). When a sufficient number of covarying environmental factors are measured across a range of sites, approaches utilizing multiple linear regression or multivariate statistics seem well suited to studies along elevation gradients. The latter techniques may not completely separate the influence of confounded factors on ecosystem processes but allow a ranking of factors within particular sets of interrelated variables based on the relative importance of each factor's association with the dependent variable.

6. CONCLUSION

This report has summarized studies indicating that elevation gradients in the southern Appalachian Mountains are useful for the study of abiotic controls (such as temperature) and biotic controls (such as litter chemistry) that regulate long-term forest soil C and N storage. Studies of ecosystem processes along elevation gradients represent an approach to the study of environmental change and its effect on ecosystems which can complement data obtained from controlled, large-scale field experiments as well as other empirical and theoretical approaches to climate change research. More research on methodological approaches that will strengthen the validity of interpretations from studies of climate change along elevation gradients by minimizing or quantifying the role of confounding factors is needed to further advance the usefulness of this approach for studies of soil C and N dynamics.

Research on the effects of climate on ecosystem processes along elevation gradients has lagged behind research directed at controlled, large-scale field experiments due, in part, to the difficulties that are often associated with working in remote, natural areas. Nonetheless, more research on forest soil C and N in mountainous terrain is needed to better understand the complexities of regional and global C budgets. This recently recognized need can be addressed through proposed large-scale monitoring efforts directed at a better understanding of the terrestrial C cycle. Field research along elevation gradients can be a convenient and economical approach to testing hypotheses about the long-term effects of climate on ecosystem processes. Process based studies along elevation gradients can make a significant contribution to a better understanding of how climate change impacts soil C and N dynamics and feedbacks between climate and soil C storage.

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