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Role of Osmotic Adjustment in Plant Productivity

A Summary Report and Review of Current Literature

G. M. Gebre and T. J. Tschaplinski

Environmental Sciences Division
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ENVIRONMENTAL SCIENCES

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A SUMMARY REPORT AND REVIEW OF CURRENT LITERATURE

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ABSTRACT

Successful implementation of short rotation woody crops requires that the selected species and clones be productive, drought tolerant, and pest resistant. Since water is one of the major limiting factors in poplar (*Populus* sp.) growth, there is little debate for the need of drought tolerant clones, except on the wettest of sites (e.g., lower Columbia River delta). Whether drought tolerance is compatible with productivity remains a debatable issue. Among the many mechanisms of drought tolerance, dehydration postponement involves the maintenance of high leaf water potential due to, for example, an adequate root system. This trait is compatible with productivity, but requires available soil moisture. When the plant leaf water potential and soil water content decline, the plant must be able to survive drought through dehydration tolerance mechanisms, such as low osmotic potential or osmotic adjustment. Osmotic adjustment and low osmotic potential are considered compatible with growth and yield because they aid in the maintenance of leaf turgor. However, it has been shown that turgor alone does not regulate cell expansion or stomatal conductance and, therefore, the role of osmotic adjustment is debated. Despite this finding, osmotic adjustment has been correlated with grain yield in agronomic crop species, and gene markers responsible for osmotic adjustment are being investigated to improve drought tolerance in productive progenies.

Although osmotic adjustment and low osmotic potentials have been investigated in several forest tree species, few studies have investigated the relationship between osmotic adjustment and growth. Most of these studies have been limited to greenhouse or container-grown plants. Osmotic adjustment and rapid growth have been specifically associated in *Populus* and black spruce (*Picea mariana* (Mill.) B.S.P.) progenies. We tested whether these relationships held under field conditions using several poplar clones. In a study of two hybrid poplar clones (*P. trichocarpa* Torr. & Gray x *P. deltoides* Bartr., TD and *P. deltoides* x *P. nigra* L., DN), we determined the TD clone, which was more productive during the first three years, had slightly lower osmotic potential than the DN clone, and also indicated a small osmotic adjustment compared with the DN hybrid. However, the productivity differences were negligible by the fifth growing season. In a separate study with several *P. deltoides* clones, we did not observe a consistent relationship between growth and osmotic adjustment. Some clones that had low osmotic potential and osmotic adjustment were as productive as another clone that had high osmotic potential. The least productive clone also had low osmotic potential and osmotic adjustment. The absence of a correlation may have been partly due to the fact that all clones were capable of osmotic adjustment and had low osmotic potential. In a study involving an inbred three-generation TD F_2 pedigree (family 331), we did not observe a correlation between relative growth rate and osmotic potential or osmotic adjustment. However, when clones that exhibited osmotic adjustment were analyzed, there was a negative correlation between growth and osmotic potential, indicating clones with lower osmotic potential were more productive. This was observed only in clones that were exposed to drought. Although the absolute osmotic potential varied by growing environment, the relative ranking among progenies remains generally the same, suggesting that osmotic potential is genetically controlled. We have identified a quantitative trait locus for osmotic potential in another three-generation TD F_2 pedigree (family 822). Unlike the many studies in agricultural crops, most of the forest tree studies were not based on plants exposed to severe stress to determine the role of osmotic adjustment. Future studies should consider using clones that are known to be productive but have contrasting osmotic adjustment capability as well as clones with contrasting growth and osmotic adjustment.

1. INTRODUCTION

Plants differ in their ability to survive and grow under water stress. Some of the drought resistance mechanisms are useful for survival during mild to severe droughts, whereas other mechanisms enable the plant to continue its growth, albeit, at a reduced rate. One such mechanism is dehydration postponement (sensu Kramer 1983), which involves maintenance of high leaf water potential (ψ_w) either through stomatal regulation or extraction of water through an extensive root system. Maintenance of high ψ_w, due to increased water availability, allows the plant to continue carbon assimilation. Such a mechanism is useful in areas where the dry period is short and/or the site has available soil moisture. Lilley and Fukai (1994a) reported that rice (*Oryza sativa* L.) cultivars, with inherently greater root length density and root depth, were able to prolong their growth during a short water deficit period. Maintenance of high ψ_w by better stomatal control is also useful for moderate stress but growth is reduced because of a reduction in CO_2 assimilation. Such a mechanism is useful only for a short period since the stomatal closure will result in increased leaf temperature and then leaf senescence.

Plants that are exposed to severe drought use dehydration tolerance mechanisms. Such plants are able to survive low water potentials by several characteristics, including low baseline osmotic potential (ψ_π), lowering their ψ_π (i.e., active solute accumulation), or by protoplasmic resistance (Jones et al. 1981). Generally, growth of all plants exposed to low ψ_w is reduced, but dehydration tolerant plants are more productive compared to non-tolerant plants. Such plants can continue to grow at a reduced rate under low ψ_w, because of low ψ_π or osmotic adjustment (OA), which maintain turgor. The lowering of ψ_π by solute accumulation, known as OA, has been shown to benefit plants in survival of and recovery from short dry periods (Meyer and Boyer 1981, Bennett and Sullivan 1981). Tree species growing in xeric sites generally have low leaf ψ_π even under well-watered conditions (Abrams 1988). Although it has been suggested that OA competes with productivity (Munns 1988), several studies with agricultural crops have shown a relationship between OA and grain yield (Morgan et al. 1991, Fukai and Cooper 1995, Tangpremsri et al. 1995).

The ideal drought tolerant and productive plant would be one that can conserve its water loss through some stomatal regulation but continue its assimilation even at low ψ_w. With the progress that has been achieved in genetic mapping and marker-aided selection, plant breeders have the tools to select for better traits, but only if they know what the goals are (Tauer et al. 1992). A plant with low ψ_π and/or is capable of OA would maintain growth because of turgor maintenance, or increased water potential gradient from soil to leaf resulting in water uptake. However, maintenance of turgor alone may not be sufficient for continued growth (Munns 1988). Even with turgid leaves, soil moisture will be depleted and the plant will close its stomata or reduce its leaf area during a prolonged dry period, causing the plant to stop growing, thus reducing productivity. Although high root-to-shoot ratio is reported in drought-adapted plants, rooting depth has not been associated with OA. In fact, Lilley et al. (1996) reported that OA and rooting were negatively correlated and suggested that the linkage between high OA and poor root traits needs to be broken if both were considered desirable. Blum (1996) also questioned the role of an increased rooting depth and root density when there is no available moisture to extract.

In this report, we examine the role of OA in plant survival, recovery from stress and its relationship with productivity. Productivity in agricultural crops is generally measured in terms of grain yield, although total dry matter or biomass is also used. The productive crop would have to produce grain within the growing season and water stress during grain filling would reduce yield. Thus, time is a factor even when the plant survives a drought. For a successful short rotation woody crops (SRWC) program, the species selected, such as *Populus* and *Eucalyptus*, need to remain productive. Unlike annual crops, however, SRWC productivity is cumulative over the rotation period and therefore survival during drought periods and recovery capabilities are important. Thus, dehydration tolerance mechanisms, such as OA, would be expected to benefit tree species more than annual crop species.

1.1 OSMOTIC ADJUSTMENT AND LOW BASELINE OSMOTIC POTENTIAL

Both OA and low baseline ψ_π serve the same purpose, i.e., maintaining turgor at low ψ_w. However, there are studies that suggest the benefit of one over the other (Ranney et al. 1991, Tuomela 1997, Li 1998). In a survey of several North American tree species, Abrams (1988) observed ψ_π ranging from –1.0 to –2.6 MPa, with tree species growing in xeric sites generally exhibiting lower ψ_π. We also observed ψ_π ranging from –1.0 to –2.0 MPa among six hardwood species (Tschaplinski et al. 1998b). Dogwood (*Cornus florida* L.) and American beech (*Fagus grandifolia* Ehrh.) had the highest ψ_π compared to white oak (*Q. alba* L.), and chestnut oak (*Quercus prinus* L.). Although both dogwood and chestnut oak displayed some capability for OA, dogwood saplings had the highest mortality rates among the species studied during a severe and prolonged drought. Tuomela (1997) reported two groups of *Eucalyptus microtheca* F. Muell. provenances with different baseline ψ_π and OA. Three provenances from northwestern Australia (drier region) with a high baseline ψ_π (–1.63 to –1.78 MPa) had OA ranging from 0.29 to 0.46 MPa under water stress. Three southeastern provenances that had low baseline ψ_π (–1.90 to –2.02 MPa) did not exhibit significant OA under water stress. The two groups of provenances were also different in their ψ_w, although the differences were less pronounced under dry conditions. The northwestern provenances had higher minimum ψ_w (–0.87 to –0.97 MPa) than the southeastern provenances (–1.35 to –1.39 MPa) in the control treatment. In general the northwestern provenances had higher ψ_w at a given relative water content (RWC) than the southeastern provenances. Li (1998) also observed that two other northern and central Australian provenances that exhibited OA, whereas southeastern provenances did not. Based on these data, the two studies suggested that drought tolerance was associated with OA and not with baseline ψ_π. However, the southeastern provenances (with low ψ_π) maintained vigorous growth under favorable water conditions and mild water-stress compared to the slow growth of the northern and northwestern provenances (Tuomela 1997, Li 1998).

Ranney et al. (1991) compared the OA of two cherry (*Prunus avium* L. x *P. pseudocerasus* Lindel. ‘Colt’ and *P. cerasus* L. ‘Meteor’) cultivars with different baseline ψ_π. The cultivar ‘Colt’ had higher ψ_π than the cultivar ‘Meteor’ in the well-watered treatment. The degree of OA was however similar in both cultivars. In a study of reciprocal graft combinations between the two cultivars, plants with ‘Meteor’ scions maintained higher stomatal conductance (g_s) and had higher mean net assimilation rates under water-stressed conditions than plants with ‘Colt’ scions regardless of the rootstock. They suggested that the greater conductance and mean net assimilation rate of ‘Meteor’ scions may have been the result of lower ψ_π and greater capacity for turgor maintenance.

In a field study at Boardman, Oregon, that involved 59 poplar clones (two grandparents, two F_1 parents, and 55 F_2 progenies) of a *Populus trichocarpa* x *P. deltoides* family 331, we observed a wide range of ψ_π, varying between –1.38 and –2.35 MPa (unpublished data). Most of the clones that demonstrated OA were those that had high baseline ψ_π. Out of the 25 clones that exhibited an OA of at least 0.1 MPa, there were 21 clones with $\psi_\pi > -1.70$ MPa and only four with $\psi_\pi < -1.70$ MPa. The two parents (most productive) of the F_2 clones had ψ_π that were in the middle to low range (–1.71 and –1.84 MPa) and did not exhibit OA in this study, despite displaying OA in an earlier study using container-grown plants (Tschaplinski et al. 1994). Considering that the grandparents, *P. deltoides* (–1.90 MPa) and *P. trichocarpa* (–1.55 MPa), also did not exhibit OA in this study and *P. deltoides* is more drought tolerant than *P. trichocarpa*, low ψ_π is as important as OA in determining overall dehydration tolerance.

The range of OA reported for different species or clones varies from 0.1 to 1.7 MPa (Gebre et al. 1994, Tschaplinski and Tuskan 1994, Fukai and Cooper 1995, Gebre et al. 1998b, Tschaplinski et al. 1998b, Zhang et al. 1999). It is not known if there is a threshold level at which OA benefits the survival and growth of a plant. Blum (1989) suggested that an OA of up to 0.2 MPa did not benefit plants by minimizing growth reduction under stress, but there was a positive linear relationship between growth and OA when OA $\geq$ 0.2 MPa. Bolanos and Edmeades (1991) reported OA of 0.40 MPa or greater only in 7% of 204 maize (*Zea mays* L.) genotypes they tested. Genotypes with lower ψ_π did not result in higher yield under stress and suggested that the observed average OA of 0.17 MPa may have been below the threshold for any benefit. The authors also reported that 36% of their genotypes had minor negative adjustments, i.e., towards more positive ψ_π. Blum (1989) also reported that some genotypes had negative adjustments of up to –0.15 MPa. We have also observed negative adjustment with clones that had low ψ_π in the TD F_2 family 331 pedigree.

In summary, the lowering of ψ_π during a stress period, i.e., OA, should serve the same purpose as having low baseline ψ_π; i.e., the maintenance of leaf turgor at low ψ_w. However, having accumulated solutes during the stress period, and thus lowering ψ_π, may benefit the plant during recovery, particularly during grain filling in crops and therefore OA may be preferred over low ψ_π. This may also be evident during the recovery of tree species from water stress, where some species recover sooner than other species. However, this hypothesis needs further testing under controlled conditions.

1.2 IMPORTANT FACTORS FOR GROWTH

It is well known that water stress reduces plant growth. To address the role of OA or low ψ_π in growth, it is essential to look at the factors that are important for plant productivity. One of these factors is photosynthesis, which is reduced by water stress through stomatal and non-stomatal effects. However, the relationship between net photosynthesis (P_n) and growth has not been consistent (e.g., Rhodenbaugh and Pallardy 1993). The authors reported that a clone that exhibited low P_n was the most productive in terms of leaf area, leaf dry weight, total dry weight and root dry weight. Under optimal conditions in greenhouse and field studies, the hybrid poplar 'Eugenei' had lower P_n and g_s than 'Tristis' (Nelson and Ehlers 1984), but 'Eugenei' produced more leaf area, particularly late in the growing season (Michael et al. 1990). Liu and Dickmann (1996) concluded that 'Tristis' would be more adaptable to cyclic drought than 'Eugenei', because 'Tristis' had lower g_s and maintained equivalent P_n as 'Eugenei' across a range of soil moisture. Stressed plants commonly produce greater root/shoot ratio indicating an effect on carbon allocation. For example, the hybrid poplar clone 'Tristis' invests more biomass in roots than on leaves. Many plants also reduce their leaf size and total leaf area when exposed to drought. Although this reduces water loss, the reduction of leaf area also reduces total carbon assimilation and then growth. There are several studies that indicate a strong correlation between stem volume (or aboveground biomass) and total leaf area in hybrid poplars and their parents (Roden et al. 1990, Ridge et al. 1986, Harrington et al. 1997). Harrington et al. (1997) suggested that leaf size characteristics were correlated with biomass/growth. The effect of water stress on leaf growth and hence productivity varies by clone. For example, Roden et al. (1990) observed that the rate of individual leaf growth was reduced more in the parents than the hybrid clone under water stress. Rapid early leaf and root growth were reported as key attributes associated with productivity in three *Populus* clones regardless of soil water availability (Rhodenbaugh and Pallardy 1993).

Osório et al. (1998) reported that the reduction in biomass accumulation in water-stressed *Eucalyptus* was a result of decreased leaf area and intercepted solar radiation. However, they had also observed that drought-induced reductions in g_s paralleled the drought-induced reductions in total biomass. However, Osonubi and Davies (1978) found that growth of oak seedlings was not affected after 10 days of stress, although g_s was reduced. Osório and Pereira (1994) reported that fast-growing clones of *Eucalyptus globulus* Labill. had larger leaf area than slow-growing clones. Although the predawn ψ_w remained high, the fast-growing clone had lower ψ_w (–0.62 MPa) than the slow-growing clone (–0.22 MPa). Despite this high predawn ψ_w, there was a large reduction in g_s in the fast-growing clone in response to water stress. Total plant biomass of the fast-growing clone was also reduced more than the slow-growing clone. The midday ψ_w was only slightly lower in the fast-growing clone (–1.56 MPa) than the slow growing clone (–1.39 MPa). Ibrahim et al. (1997) reported that drought reduced the number of leaves and the specific leaf area without an effect on the average leaf size. However, Gebre (1993) observed that water stress significantly reduced average leaf size of greenhouse-grown *Populus deltoides* clones. 'Ohio Red' which had lower baseline ψ_π and larger leaves than 'Platte', also had greater leaf size reduction (about 50%) during the stress period.

Longer leaf retention has been reported as an important component for growth in hybrid poplars (Nelson and Isebrands 1983). The authors reported that most of the fixed CO_2 during late season P_n was allocated to the stem and roots resulting in radial stem and root growth. Plants with OA or low ψ_π have the advantage of maintaining leaves for a longer period under stress compared to plants without adjustment because of their ability to tolerate low ψ_w. Tangpremsri et al. (1991b) observed that OA was associated with green leaf area retention during grain filling and with increased root length density in sorghum (*Sorghum bicholor* (L.) Moench.). Stettler et al. (1988) reported that larger leaf number, higher g_s, larger leaf area index and better drought tolerance were among the characteristics of the F_1 hybrids that favor growth. The F_1 hybrids lost the least number of leaves during a dry period compared to one of the parents (*P. trichocarpa*) and the backcross clones. However, some plants maintain their leaves longer by maintaining high ψ_w either by stomatal regulation or deep rooting.

Lilley and Fukai (1994b) have also shown that rice (*Oryza sativa* L.) cultivars capable of maintaining more green leaf area under water-limited conditions had better grain yield. Fukai and Cooper (1995) had suggested the maintenance of high ψ_w or the retention of green leaves, even at low ψ_w, were good characteristics to select. Leaf retention was also associated with the ability of rice to recover rapidly from water deficit. The authors concluded that the differences among cultivars in the rate of recovery were related to dehydration tolerance during water deficit (i.e., retention of green leaves), although other factors such as potential crop growth rate also may have been involved. Jearakongman et al. (1995) had also shown maintenance of green leaves during a late drought period was a useful indicator for some productive rice cultivars. The number of green leaves in sorghum exposed to a series of drought periods remained similar to control plants although the green leaf area was reduced (Bennett and Sullivan 1981).

In summary, leaf area and leaf retention are correlated with productivity both in fast-growing trees and agricultural crops. The advantage of OA or low ψ_π in maintaining leaf turgor suggests OA plays a role in growth.

1.3 SOLUTE ACCUMULATION AND ITS LIMITS

Osmotic adjustment by definition is a measure of active solute accumulation. Most plants accumulate organic solutes and inorganic ions (Morgan 1984). Several poplar clones have been shown to adjust osmotically, mainly as a result of accumulation of carbohydrates (Tschaplinski and Blake 1989, Gebre et al. 1994) as well as inorganic ions (Tschaplinski and Tuskan 1994). Different species are able to accumulate different solutes. Morgan (1992) determimed that potassium was the major solute that accumulated in wheat. In poplars, the major solutes are carbohydrates, such as fructose, glucose, and sucrose (Tschaplinski and Blake 1989, Gebre et al. 1994, Tschaplinski et al. 1994). Sucrose and potassium were the major solutes contributing to ψ_π of hybrid poplars (Gebre et al. 1998b). Sorbitol was the major solute that contributed to OA in cherry (*Prunus* sp.) trees, although potassium was the dominant solute contributing to ψ_π (Ranney et al. 1991). The source of the solutes accumulated is photosynthesis, but glucose production from starch degradation is also assumed. Stoneman et al. (1994) observed that P_n in water-stressed *Eucalyptus marginata* Donn ex Sm. was reduced to 17% of that of well-watered plants at ψ_w of –1.5 MPa and reached zero at about –2.2 MPa, but it recovered rapidly after rewatering. The authors concluded that the accumulation of solutes that contribute to OA was the result of the continued P_n after the cessation of leaf growth. A decline in the degree of OA has been reported in some species under severe stress. For example, a decrease in the accumulation of solutes was reported when ψ_w decreased to –1.7 to –2.0 MPa in pea (*Pisum sativum* L.) cultivars (Sanchez et al. 1998), suggesting that severe stress reduced the source of solutes. An increase in ψ_π in severely stressed plants has also been measured in eastern cottonwood clones which was attributed to stomatal closure and zero or negative P_n (Gebre and Kuhns 1993).

2. OSMOTIC ADJUSTMENT AND GROWTH

For a successful and economically competitive production of biomass for fuel and fiber, the ideal sites for short rotation woody crops are high quality, idle or excess agricultural lands that have high water tables or high water holding capacity and adequate precipitation or supplemental irrigation (Tuskan 1998). Whether there is supplemental irrigation or adequate precipitation, however, there are bound to be dry periods within a growing season. Therefore, there is an advantage for selecting varieties that are drought tolerant and productive. Before selecting species and clones for drought tolerance, it is important to determine if drought tolerance is compatible with productivity. The preferred clone or cultivar will be productive under well-watered conditions without a reduction in its productivity under dry conditions. For example, the *Populus* clone 'Beaupre,' a TD hybrid, which had greater leaf area and dry matter production under well-watered conditions, also had greater productivity under dry conditions than other clones tested (Souch and Stephens 1998).

A few studies with tree species had shown that clones with faster growth performance have more organic solute accumulation and lower ψ_π than slow growing clones (Tschaplinski and Blake 1989, Tan et al. 1992b). Tan et al. (1992b) reported that two fast-growing black spruce progenies had lower ψ_π than other slow-growing progenies under a moderate osmotic stress, although there were no differences among the progeny in the control treatment. The fast-growing progenies also had higher P_n and g_s during osmotic stress and higher total soluble carbohydrate concentration than the slow-growing progenies, suggesting an active accumulation of solutes (i.e., OA). Tan et al. (1992b) concluded that the OA capability and turgor maintenance could be useful criteria for the early selection of faster-growing and drought tolerant genotypes of black spruce.

Several studies on agronomic crops have shown that plants that display OA were more productive than plants that lack adjustment when exposed to drought, although there were no differences under well-watered conditions (Fukai and Cooper 1995). For example, high OA lines of sorghum produced higher maximum leaf area at anthesis and maintained higher leaf area during grain filling under dry conditions (Tangpremsri et al. 1995). Sorghum cultivars with high OA capability had slightly higher turgor than the low OA lines. Drought reduced total dry matter by 12% in high and 24% in low OA plants and high OA plants had 11% higher grain yield compared to low OA cultivars. The authors reported a yield advantage of about 0.5-t ha^{-1} in the high OA group over low OA group although these groups had similar yield under well-watered conditions. Meyer and Boyer (1981) have demonstrated the contribution of OA to a continuation of slow growth of soybean seedlings under water stress.

Morgan et al. (1991) reported a positive relationship between OA and grain yield of chickpea (*Cicer arietinum* L.) in water-limited field experiments. Ludlow et al. (1990) also observed the mean grain yield of a high OA-line of sorghum was 24% higher than that of a low OA-line under water stress. There was no difference in leaf area index (LAI) and leaf retention between the high and low OA lines, and that both traits declined with water stress. The authors concluded that higher yield in dryland crops could be obtained by selecting for higher OA. Prasertsak and Fukai (1997) also reported a clone with OA that had higher LAI and a faster decline in ψ_w under water stress. Morgan and Condon (1986) reported that grain yield of wheat (*Triticum aestivum* L.) was strongly correlated with ψ_π at turgor loss at high and low water deficits.

Since OA inolves solute accumulation and can correspond with growth reduction, its benefits for the productivity have been questioned (Munns 1988). Stoneman et al. (1994) reported that an OA of 0.4 MPa in greenhouse-grown *Eucalyptus marginata* did not enhance seedling growth, because OA was not observed until the stress level reached a predawn leaf ψ_w of –1.5 MPa (midday –2.5 to –3.0 MPa), after which leaf growth also ceased. Blum et al. (1997) compared the drought tolerance of several spring wheat (*Triticum aestivum* L.) genotypes with different height growth. There was no difference in RWC among genotypes and stress treatments. However, the tallest genotypes exhibited the largest OA and obtained higher absolute growth and biomass than the smaller plants, although the growth rate of the smaller plants was better than the large plants. They concluded that growth was sustained 1) by potential growth rate and plant size of the genotype when the stress is mild and 2) by tolerance (even at the expense of potential growth and size) when the stress is more severe. Sanchez et al. (1998) reported that pea cultivars that best maintained turgor were more drought tolerant and had better grain yield, but total biomass was reduced. Although the cultivars with higher OA maintained turgor, there was no relationship between OA and grain yield or biomass production. Other studies have shown no association between yield and OA (e.g., Bolanos and Edmeades 1991). The authors did not advocate selecting for OA or low ψ_π as drought adaptive traits, because of the weak or inconsistent correlation between OA or ψ_π and yield. Flower et al. (1990) also reported that despite an advantage of maintaining a positive leaf turgor at low ψ_w, sorghum lines with OA did not have a productivity advantage over the non-adjusting lines in a very dry environment.

The contribution of OA or low ψ_π to drought tolerance and growth of trees has been demonstrated mostly in greenhouse-grown plants with limited work on field-grown trees. In one of the few field studies conducted on black spruce trees, Major et al. (1998) reported a high correlation between mean family predawn turgor and mean family growth (r = 0.82). Among the four families chosen for examination, the two stable families sharing one maternal parent, had high growth rate regardless of site, but the two unstable families sharing another maternal parent, displayed fast growth only on the wetter sites. The stable families had lower ψ_π at full turgor across all years and maintained higher turgor than the unstable families.

We tested the role of OA in growth of two productive hybrid poplar clones in a large-scale plantation at Wallula, Washington (Tschaplinski et al. 1998a, Gebre et al. 1998b). Although there was no data on the water relations of these clones, anecdotal evidence suggested that the TD clone was considered drought sensitive with good growth, whereas the DN clone was considered drought resistant with slower growth. The TD hybrid had lower ψ_w at midday than the DN hybrid across all three treatments, although there was no clonal difference at predawn. During the first three growing seasons, the TD clone was more productive (higher D^2H) than the DN clone. By the end of the fifth growing season, however, there were no significant differences between clones in any of the treatments. The TD clone had lower ψ_π and an OA of about 0.2 MPa, which may have been too small to contribute to any advantage for the TD hybrid. Although the level of OA and the difference in ψ_π between the two poplar clones in our study were small, the fact that the TD clone had lower midday ψ_w is consistent with other species that have the capacity for OA. Tangpremsri et al. (1995) had reported that midday ψ_w of sorghum decreased more in the high OA plants than the low OA plants, consistent with an earlier finding that genotypes with high OA or with low ψ_π used more water than other genotypes (Tangpremsri et al. 1991b). Morgan and Condon (1986) had also reported that water use of wheat genotypes with higher turgor maintenance was approximately 50% higher than genotypes with low turgor maintenance. The genotype with high OA extracted water from deeper soil zone (up to 1.5 m), whereas there was little root growth in the low OA genotype below 77 cm. The highest water loss in the 25-150 cm zone occurred in the high OA genotypes. As a result, they suggested that the higher dry matter and grain yield by the high OA genotype was the result of better extraction of water from the soil by these plants.

The soil water content of the two poplar clones during the third growing season was not different between the two clones in the lowest (46 cm) and highest (137 cm) irrigation treatments. There was a difference in the intermediate stress level (76 cm) towards the end of

August with the DN clone having lower soil water content than the TD hybrid. The lower soil water content was also observed in ψ_w during the same period when the DN hybrid had lower predawn ψ_w than the TD hybrid, although the midday ψ_w was higher for the DN clone. Thus, despite the lower soil water content and predawn ψ_w of the DN clone in late August, its maintenance of high midday ψ_w suggests that it had better stomatal control than the TD clone. It is possible that the lower soil water content of the DN hybrid in the 76-cm treatment during the third growing season indicates greater access to soil water that was also reflected in higher relative growth rate. A sampling of root weight density a year later indicated that the DN clone had higher root weight density than the TD hybrid in the 76-cm supplemental irrigation as well as the highest root weight density:stem volume ratio of all treatment/clone combinations. The characteristics of the TD clone resemble that of hybrid poplar clone 'Eugenei' that also had high leaf abscission, but was more productive than 'Tristis' under drought conditions (Dickmann et al. 1992, Tschaplinski et al. 1998a). The growth of the TD clone was not better than the DN clone after the third growing season. The results of this study confirm previous reports of the importance of long-term studies to better understand the growth and drought tolerance responses. For example, Nelson and Ehlers (1984) had reported that early growth patterns may not always correlate well with subsequent biomass yields many years later. Heilman and Stettler (1985) also reported shifts in clonal ranking and suggested the limitation of clonal evaluations for SRWC based on 1-2 years of growth. Brown et al. (1996) observed that height of clones at the end of the first year did not correlate with rankings at the end of the fifth year, although correlations improved in the second and third year. Thus, assessments of OA or ψ_π early in the development of a clonal stand may not reflect the ultimate performance under drought stress at older ages. We have observed that ψ_π of a clone declines from the first growing season through the third growing season and stabilizes thereafter.

In a separate study at Sumter, South Carolina, we observed significant clonal differences in ψ_π and OA of several *P. deltoides* clones, although the differences varied by treatment and season (unpublished data). The ψ_π varied from –1.87 to –2.02 MPa in the dry treatment during the first growing season in 1995 when plants were sampled after a dry period. The ψ_w at midday remained high, ranging from –0.76 to –1.13 MPa. During the study period from1995 to 1997, clone YB had one of the highest ψ_π compared to the least productive clone Y in the dry treatment. Clone YB is also one of the most productive clones together with clones R and RB at this site. The latter two clones had low ψ_π throughout the study period. However, during a sampling period in July 1998, when plants were exposed to a severe drought and leaves were collected from the top crown using a lift, clone YB had low ψ_π in both dry and well-watered treatments. Despite the significant treatment differences in diameter growth, there was no clonal difference in ψ_π in the unirrigated as well as the low irrigation treatments. Combining data collected from several studies, we conclude that *P. deltoides* has consistently low ψ_π across all clones and sites, and therefore, has to be considered one of the most drought tolerant *Populus* sp.

In general, despite the reduced growth in all clones in the unirrigated plot, the degree of OA was small and at times only a few of the clones exhibited OA. The OA observed in these clones was small because the plants in the wet treatment were also stressed to some degree and had osmotically adjusted, thus lowering their ψ_π, or they typically had low ψ_π and did not exhibit OA. Although all clones exhibited low ψ_π in the unirrigated treatment, there were also occasions when all clones had somewhat higher ψ_π, ranging from –1.53 to –1.84 MPa (in May and July 1997). Therefore, the lack of OA may be related to adjustment by all clones, including trees in the irrigated treatments, again reflecting the general drought tolerance of *P. deltoides*. During late season samplings or during a severe drought period as in July 1998, ψ_π of all clones had lowered to –2.1 MPa. The decline in ψ_π of all clones over the season also confirms the suggestion that all the clones investigated were capable of OA. During the July 1998 sampling, there was no difference in ψ_π among treatments except for the least productive clone Y, which had the highest ψ_π under high irrigation. Clone Y also had the largest OA (0.29 MPa) among the four clones measured because it lowered its ψ_π in the unirrigated plot to similar level as other clones. The greater OA of the Y clone did not result in a productivity advantage for this clone.

In a separate study of TD F_2 family 331, some of the least productive clones had the lowest ψ_π and some of the most productive clones had the highest ψ_π (unpublished data). Although relative growth rate was not related to ψ_π, there was a correlation ($r^2 = 0.38$) between growth (D^2H) and ψ_π at full turgor in the dry plot for the F_2 clones that had an OA of ≥ 0.08 MPa. The clones that had no OA showed no correlation. The same clones under wet treatment indicated only a weak correlation. Height was also slightly correlated ($r^2 = 0.29$) with ψ_π among the clones that exhibited OA in the dry treatment. These correlations were observed only in plants grown at Boardman, in eastern Oregon, a drier and sunnier site than Clatskanie, Oregon, in the lower Columbia River delta. Other studies have indicated a correlation exists between yield and OA in dry years but not in wet years (Rodriguez-Maribona et al. 1992). Together, these studies suggest that selection studies have to be conducted at different locations, taking into consideration dry and wet conditions. The ψ_π of the same clones grown at a much cooler and cloudier site of Clatskanie, Oregon, were slightly higher than those at the dry and sunny site of Boardman, Oregon. The correlation coefficient (r^2) for ψ_π between the two different sites was 0.38, suggesting the ranking remained similar for most clones. The ψ_π values observed in the South Carolina study were similar to other eastern cottonwood clones measured in the field or greenhouse (Gebre and Kuhns 1991, Gebre et al. 1998a). Santamria et al. (1990) compared the OA ranking of several sorghum lines in different studies and observed that although the absolute values differ, the OA ranking remained the same in two different studies.

In summary, there is a strong correlation between OA or low ψ_π and productivity in annual crops and an indication of a correlation in some tree species. However, the fact that growth responses change with age suggest more long-term studies are needed before making conclusions. It is also important that gas exchange data be known to fully understand contribution of OA. Regardless of the shortcomings, however, there is evidence that suggest drought tolerance is compatible with productivity.

2.1 ROLE OF OSMOTIC POTENTIAL IN PLANT SURVIVAL AND RECOVERY FROM STRESS

Dehydration tolerance in its general meaning indicates survival under severe drought conditions. Although this has no meaning for annual crops during grain filling, where the yield of the crop is the measure of the success of the plant, its importance for trees and other perennials is unquestionable. Even for annual crops, however, the survival of the plant is essential when the stress period occurs during the vegetative stage. In fact, Munns (1988) theorized that genotypes with smaller leaf area or more roots could have higher yield if water is available at a later stage of development such as anthesis or seed development. Unlike agronomic crops, vigorous growth of trees during favorable conditions is beneficial because it adds to the total biomass, even if the growth rate is reduced during the stress period. However, there is a limit for the contribution of OA in plant survival as was observed for dogwood saplings (Tschaplinski et al. 1998b).

Braatne et al. (1992) reported differences in survival of hybrid poplars and their parents under drought stress. Although there were no significant clonal differences in ψ_π at turgor loss, the two F_1 hybrid poplars survived longer than their parental species *P. trichocarpa* and *P.*

deltoides. Survival time was based on the number of days from zero transpirable soil water to complete abscission of mature leaves. The longest survival times were 14.5 and 16 days for the hybrids, whereas the lowest survival time was three days for *P. trichocarpa*, followed by eight days for *P. deltoides*. The authors suggested that survival might have been enhanced among the F_1 hybrids by low cuticular conductance and selective leaf abscission. There was also a correlation between survival and hydraulic conductivity of xylem tissues.

Besides survival during a stress period, an equally important factor in drought tolerance and growth would be the ability of the plant to recover after the relief of water stress. The capability for rapid recovery is an important advantage in the overall productivity of a tree when some level of stress can not be avoided even under irrigation (e.g., disruption of irrigation or suboptimal irrigation). Although the contribution of OA in recovery from stress has not been well documented in forest trees, variation in recovery among species and clones has been reported (Gebre and Kuhns 1993, Liu and Dickmann 1993). Osonubi and Davies (1978) reported a faster recovery in the g_s of seedlings of English oak (*Quercus robur* L.) than silver birch (*Betula verrucosa* Ehrl.) when plants were rewatered after 10 days of stress. There was no recovery in the g_s of silver birch seedlings until 2-3 days later. The oak seedlings had lower ψ_π and developed higher root: shoot ratio than silver birch. Such a response may provide an advantage for trees growing in short-rotation plantations. Osório et al. (1998) reported resumption of leaf expansion was more evident in a *Eucalyptus globulus* clone known to exhibit OA than in other clones. The final leaf area, maximum relative expansion rate, and duration of leaf growth were altered by soil water deficits in three *Eucalyptus globulus* clones. However, severe stress had smaller effect on the final leaf size and relative growth rate of the clone with OA than other clones.

Wullschleger and Oosterhuis (1991) compared several crops and reported a 25% increase in leaf length of sorghum after six days of rewatering. Sorghum also had the greatest OA of all the crops studied, but there was no direct association between OA and post-stress leaf extension in the other crops. Bennett and Sullivan (1981) had reported that preconditioned sorghum exhibited P_n level that was similar to or slightly greater than control plants after relief of water stress. Liu and Dickmann (1993) reported quick recovery of P_n of *Populus* clones upon relief of stress. A rapid recovery in P_n upon rewatering was also reported in a *P. deltoides* clone that also exhibited lower basal ψ_π than another clone (Gebre and Kuhns 1993). A similar observation of fast recovery has been reported in many species capable of OA (Barlow et al. 1977, Tan et al. 1992a). Survival and recovery of stressed tall fescue (*Festuca arundincaea* Schreb.) was associated with low basal ψ_π before stress (White et al. 1992). During stress however, recovery was associated with delayed leaf rolling, OA, and prolonged turgor maintenance. Prasertsak and Fukai (1997) also noted that a clone capable of OA recovered completely from water stress, resulting in similar grain yield to that of the irrigated trial. The mechanism for the better performance during recovery is not understood. However, an accumulation of soluble carbohydrates is expected to benefit a plant's recovery. Fukai and Cooper (1995) suggest that accumulation of solutes can benefit rice which relies on translocation of previously produced assimilates for grain filling. It has also been suggested that there may be an increased root activity in drought-stressed rubber trees (*Hevea brasiliensis* Willd. ex A. Juss.) after rehydration (Ceulemans et al. 1983). Similarly, BassiriRad and Caldwell (1992) reported that previously droughted roots of *Artemisia tridentata* Nutt. exhibited nearly three times greater relative growth rate than control plant roots, but this did not result in more nitrate uptake.

In summary, OA and low ψ_π are useful in extending the number of days a plant can tolerate low leaf ψ_w. Plants with OA also exhibit faster recovery from a drought period compared to non-adjusting plants. Thus, the productivity of a clone with fast recovery from drought stress would be affected less than a clone with slow recovery.

2.2 OSMOTIC ADJUSTMENT AND STOMATAL REGULATION

One advantage of OA is the maintenance of leaf turgor, which is expected to improve g_s for continued photosynthesis and growth. Gunasekera and Berkowitz (1992) reported that two wheat genotypes that had exhibited OA continued to photosynthesize at lower ψ_w than the genotype without OA. There was no effect of drought conditioning on the latter, but one of the genotypes with OA of 0.4 MPa maintained P_n at ψ_w. When the OA was lower (0.2 MPa), its P_n declined at ψ_w of –1.5 MPa. McCree et al. (1984) reported that P_n of sorghum continued at a high rate beyond the point where leaf area expansion was inhibited. According to Blum (1996), leaf area was significantly reduced under water stress before the reduction in g_s. Although P_n declined with stress, photosynthate accumulation and OA continued to the lowest ψ_w and zero leaf pressure potential. Thus, OA enhanced the ability of sorghum to continue carbon assimilation at low ψ_w. However, maintenance of turgor is not always associated with g_s or growth. Turgor alone could not explain lower leaf growth rate in stressed poplars, because both irrigated and unirrigated plants maintained turgor by lowering ψ_π (Roden et al. 1990). Girma and Krieg (1992) also did not find an association between OA and g_s and P_n in sorghum under water stress.

A weak relationship between g_s and turgor pressure was also reported in white oak (*Quercus alba*) and sugar maple (*Acer saccharum* Marsh.), whereas no relationship was observed in black oak (*Q. velutina* Lam.) and northern red oak (*Q. rubra* L.) (Hinckley et al.1978). Stomata of black oak were more sensitive to vapor pressure deficit (VPD) than to turgor pressure, whereas the opposite was evident in white oak, sugar maple, and northern red oak. Hinckley et al. (1979) also reported sugar maple had the most sensitive stomata, closing for the longest period (52% of the season) during a severe drought, compared to 18-28% for the oaks. Maintenance of leaf turgor could also result in less regulation of water loss that may result in severe water stress. Seemann et al. (1986) also reported that OA contributes to the desiccation tolerance of photosystem II. However, Ludlow and Muchow (1990) did not observe a difference in g_s or a consistent relationship between OA and g_s.

Pallardy and Kozlowski (1981) and Tschaplinski and Blake (1989) reported that slow-growing *Populus* clones exhibited extended periods of lower ψ_w than that of fast-growing clones, despite high evaporative demand and the much greater transpiring surfaces of the fast-growing clones, which may have been related to stomatal regulation. When evaporative demand was high, g_s was greater in the slow than fast-growing clones. Lags in recovery of ψ_w were also pronounced more in the slow and intermediate-growing clones, despite their smaller crowns. They reported that the rapid recovery of ψ_w of the productive clones under high evaporative demand was linked with greater stomatal closure in response to high vapor pressure deficit (VPD) than in the slow clones. Pallardy and Kozlowski (1979) had earlier reported that the stomata of one of these productive clones were sensitive to VPD, reflecting the drought resistance characteristics of its parentage. Thus a clone with large leaf surface area and sensitive adaxial stomata at high VPD was more productive.

However, McCree and Richardson (1987) reported that there was little or no carbon gain advantage of OA in sugarbeet (*Beta vulgaris* L.) compared to cowpea (*Vigna unguiculata* L.). These two species had different patterns of stomatal closure and degrees of OA. Cowpea adjusted by 0.4 MPa and maintained higher daytime ψ_w of –1.2 MPa, whereas sugarbeet adjusted by 0.8 MPa and had lower ψ_w of –2.6 MPa. The authors concluded that although OA has the potential to increase the net carbon gain per unit of water lost during an irrigation cycle, the full potential will not be realized unless the length of the irrigation cycle can also be increased through some degree of stomatal control. Sugarbeet required rewatering earlier than cowpea, and displayed some leaf expansion at ψ_w as low as –2.0 MPa and there was no leaf senescence in this species. However, a carbon gain advantage from OA was reported in sorghum (McCree et al. 1984). Compared to cowpea and sugarbeet, sorghum did not show a higher carbon exchange rate than sugarbeet, but sorghum had 44% less water loss, which allowed the plants to continue to maintain a high rate of carbon gain for a longer time. Sorghum reached zero turgor four days later than sugarbeet at a lower ψ_w (–3.0 MPa). The same plants were able to gain twice as much carbon per cycle compared to sugarbeet, because sorghum had reduced water loss and a longer irrigation cycle.

In summary, although maintenance of turgor is not always associated with stomatal regulation, plants with OA exhibit continued carbon assimilation at low ψ_w compared to plants without OA. However, the level of OA and water stress may be important factors that determine the balance between the benefits of the maintenance of turgor and continued carbon assimilation and stomatal control.

2.3 OSMOTIC ADJUSTMENT AND PEST RESISTANCE

Among the solutes that accumulate during OA are metabolites that are either nutritive or toxic for tree pests. Higher concentration of sugars and amino acids would be expected to attract some herbivores (Roth et al. 1997), although leaf palatability is thought to increase with a decrease in concentrations of carbon-based chemical defenses and an increase in nitrogen (Crone and Jones 1999). Roth et al. (1997), however, reported that droughted aspen (*Populus tremuloides* Michx.)-fed forest tent caterpillar (*Malacosoma disstria* Hbn.) larvae grew more slowly and processed food less efficiently compared to the control. They attributed the decrease in growth rates of larvae to the decreased leaf water content in the stressed plants. Some of the accumulated phenolics are also known to be toxic to leaf-feeding insects. Young poplar leaves (less than LPI 4) have higher concentrations of phenolic compounds than older leaves, and the cottonwood leaf beetles (*Chrysomela scripta* F.) prefer leaf tissue approaching full expansion to the expanding leaves or the fully expanded leaves (Coleman 1986, Bingaman and Hart 1993). Field-grown leaves have different leaf toughness than those grown in a controlled environment. Leaf beetles may eventually adapt to eat even younger leaves with high concentrations of phenolic compounds. Despite a clear separation in survival rate and growth among several poplar clones, Robison and Raffa (1998) did not observe a correlation between growth and pest resistance even during a drought period.

Lin et al. (1998a) identified leaf surface chemicals that were stimulants to cottonwood leaf beetle (*Chrysomela scripta* F.) feeding in a susceptible poplar clone, 'Eugenei'. The content and amount of wax and other chemicals deposited on leaf surface under dry conditions is known to reduce cuticular transpiration (Kramer 1983). Besides its role in gas exchange, the chemicals that constitute the wax may also be important in determining susceptibility/resistance to pests. The relationship among drought tolerance, growth, and pest resistance/susceptibility has not been a focus for investigation. Floate et al. (1993) reported that leaf beetles affected hybrid poplars more than native trees, possibly a result of early leaf flushes. Augustin et al. (1995) stated that pathogen resistance was higher in *P. deltoides* parents than *P. trichocarpa* and DxD hybrids than TxD hybrids. There were species-specific qualitative and quantitative variation of phenolic glycosides, such as salicortin and tremulacin. However, Roth et al. (1997) reported a decline in these two phenolic glycosides under drought conditions. Lin et al. (1998b) found clonal differences in feeding preferences of cottonwood leaf beetle among parent clones, F_1 and F_2 clones. Contents of alcohols, tremulacin, and salicortin did not explain adult beetle feeding preference, although there were clonal differences in the content of some of these chemicals. The *P. deltoides* (ILL-129) parent had the highest leaf surface long-chain fatty alcohol, αtocopherylquinone (α-TQ), and the least salicortin content. The *P. trichocarpa* (93-968) parent had the lowest leaf surface alcohol and α-TQ, a phytochemical common on leaf surface wax. However, the beetles preferred to feed on clones with α-TQ rather than without, and the preference increased with increase in α-TQ to a moderate level. This increase was not linear since a further increase reduced feeding.

According to Bingaman and Hart (1993) feeding and oviposition preferences of adult cottonwood leaf beetles vary among leaf age classes and *Populus* clones. The non-preferred leaf age class (LPI 12) had lower concentrations of phenolic glycosides than the most preferred class (LPI 3). They concluded that salicin and salicortin content did not negatively influence host selection but tremulacin may negatively influence such behavior. However, salicin is suggested as an inhibitor of another beetle species (*Plagiodera versicolora* Laicharting) (Crone and Jones 1999). A *P. deltoides* clone that had high salicin concentration (Gebre et al. 1994) was the least susceptible to spider mite (personal observation), although the same clone also had greater concentration of leaf surface wax than other clones (313 to 390 vs. 163 to 284 mg m^{-2}, unpublished data). Crone and Jones (1999) raised seedlings of *P. deltoides* saplings either under continuous high light (HH) or continuous low light (LL) to simulate long-term shade, and switched saplings from high to low (HL) or low to high (LH) light to simulate short term shading. Although shading (LL, HL, LH) increased total nitrogen and decreased total phenolic glycoside concentrations relative to HH saplings, and the beetles tended to prefer the LL to HH plants as expected. They also preferred HH plants to HL and LH after the switch. The authors suggested the presence of high concentration of salicin in the switched saplings may have inhibited beetle feeding. Hwang and Lindroth (1997) also reported that phenolic glycosides were the dominant factors responsible for aspen (*P. tremuloides*) clonal variation in leaf-feeding insect performance with moderate to high levels of phenolic glycosides being toxic. They reported a negative genetic correlation between growth and defense among aspen clones.

In summary, the accumulation of certain organic solutes during water stress period has the potential of attracting certain pests, although some of the solutes may also be toxic and useful for pest resistance. Investigations on some of phenolic glycosides suggest an association between the concentration of the metabolites and pest resistance but there are inconsistencies. More studies are also needed to determine the relationship between drought tolerance and pest resistance/susceptibility.

2.4 IDENTIFICATION OF MOLECULAR MARKERS FOR OSMOTIC ADJUSTMENT

With the advance in molecular genetics, it is now becoming a reality to indirectly select for important characteristics, such as high productivity, drought tolerance, and pest resistance based on DNA marker occurrence. However, as discussed above, some of the physiological mechanisms responsible for these characteristics are still not well known. Despite the genetic variations in dehydration tolerance characteristics of several agricultural crops (e.g., Blum 1989, Morgan 1991) and some tree species (e.g., Gebre and Kuhns 1991, Tschaplinski et al. 1994, Tschaplinski et al. 1998b), the correlation between OA (or low ψ_π) and growth or yield is not always evident. However, there are studies investigating the genetic basis for OA and/or low ψ_π (Zhang et al. 1999). Based on a quantitative trait loci (QTL) analysis, Lilley et al. (1996) reported that a single locus was associated with OA of several varieties of rice. In the population of rice they studied, OA and dehydration tolerance were negatively correlated with root morphological characteristics that are associated with drought avoidance (root thickness, root/shoot ratio, root dry weight per tiller). Of two parents with contrasting OA, the cultivar with a dehydration postponement mechanism (an extensive root system), had smaller OA and desiccated at higher lethal ψ_π than another cultivar considered drought susceptible. The cultivar that was considered drought susceptible exhibited lower ψ_π and had greater OA. They suggested that desirable combinations (not single traits) of responses to water deficits should be considered when developing plant improvement programs for water-limited environments. The authors suggested that selection for drought tolerance characteristics, without consideration of the extent of the root system, may be most appropriate in areas exposed to brief water deficits, because the rice lines with desirable root systems had poor dehydration tolerance and OA. However, if high OA capacity and good root morphology were combined, a yield advance in the reasonably well-watered crops could occur. They suggested that coupling an extensive root system with a high capacity for OA might increase the risk of crop failure because of more rapid water extraction during unfavorable conditions. They concluded that the absence of lines containing both high OA and well-developed root systems is probably caused by strong linkage between the traits and if breeding for both characteristics is considered desirable, then the linkage between high OA and poor root traits needs to be broken.

According to Lilley et al. (1996), the putative locus for OA they identified in rice may be homologous with a single recessive gene previously identified for the same trait in wheat by Morgan (1991). In a review paper, Quarrie (1996) suggested that applying marker-assisted selection to a QTL of major effect on OA would allow rapid progress in introducing the trait into a breeding program. QTL of several characteristics of *Populus* have been identified (Bradshaw 1996), including markers for drought tolerance, such as ψ_π (unpublished data). Our ψ_π data of 55 F_2 progenies *P. trichocarpa* x *P. deltoides* family 331 and parents and grandparents indicate several putative QTL for drought tolerance. Two QTL on linkage groups M and P explained 25 and 31% of the variation of ψ_π under dry conditions, respectively. Additionally, one QTL was identified on linkage group F in another inbred TxD F_2 family 822 that explained 35% of the variation in ψ_π.

3. WEAKNESSES IN METHODS OF OSMOTIC POTENTIAL DETERMINATION

Given that OA is based on differences in ψ_π of stressed and non-stressed plants, factors such as cell shrinkage that contribute to solute concentration need to be removed before measurement. To address this problem, plants are either rehydrated before measurement of ψ_π (full turgor) or it is determined at a given RWC. Even when ψ_π is determined at a known RWC, however, measurements of the stressed and well-watered plants are sometimes not made at the same time. For example, some studies compare ψ_π of plants before the stress began with ψ_π at the end of the stress period and do not consider the difference in leaf or plant age and size (McCree and Richardson 1987). Such an approach may not be appropriate if there is a long interval, considering the seasonal declines observed in ψ_π of some species (Tyree et al. 1978, Gebre and Kuhns 1991, Tschaplinski et al. 1998b). Others compare ψ_π taken during dry and wet seasons (see Abrams 1988). For the most part, when comparisons are among clones or species, the relative ranking within a study is maintained and, therefore, may be appropriate. However, one can not obtain the degree of adjustment of a clone/species or compare results from studies of different seasons.

Another difficulty in OA measurements and comparing ψ_π of different plants has been the lack of uniformity in the stress level applied (Blum 1989, Ludlow and Muchow 1990, Tangpremsri et al. 1991a). For example, a clone/species may maintain higher ψ_w than other clones/species by stomatal regulation. Therefore, the level of water stress imposed on all plants when all are compared at the same ψ_w becomes very difficult. Tangpremsri et al. (1991a) reported that ψ_w accounted for 40% of the variation in OA of sorghum. Ludlow and Muchow (1990) stressed the importance of imposing a reproducible stress level if OA is to be useful as a selection criterion. Blum (1989) also recommended OA be evaluated when all genotypes are subjected to the same leaf water status.

Osmotic adjustment and ψ_π have been determined mostly based on greenhouse or container-grown plants. Although the rankings usually remain the same, there have been some contradictory results in ψ_π and OA between field and greenhouse grown plants. For example, Gebre and Kuhns (1991) reported that one of their *P. deltoides* clones, 'Ohio Red', had higher ψ_π than the clone 'Platte' under field conditions except late in the season, when the ψ_w and ψ_π of both clones had declined and there were no differences. However, 'Ohio Red' had mostly lower ψ_π than 'Platte' both in well-watered and stressed plants when the same clones were grown in the greenhouse (Gebre and Kuhns 1993, Gebre et al. 1994, 1998a). Similarly, Tuomela (1997) reported *Eucalyptus microtheca* provenances from northwestern Australia were more drought tolerant than southeastern provenances based on greenhouse study, although a field study had shown the northwestern provenances were more drought sensitive. Generally, OA requires a dry-wet period and a slow drying process. Thus, field conditions favor greater OA than greenhouse conditions, although greenhouse conditions can achieve more severe droughts than in the field. However, the limited light level in greenhouses may also limit metabolite production. It is possible that root growth, which may be limited in container-grown plants, influences these responses. Most of the studies on agricultural crops that are attempting to locate genes responsible for OA and/or ψ_π have exposed the plants to severe stress to a point when only the last mature leaf remains (Lilley et al. 1996). Similar stress treatments had rarely been imposed in tree species either in controlled or field conditions. Our studies at the Wallula, Washington, and Sumter, South Carolina, sites, although stressed to a certain level, all poplar clones did not experience severe stress. Even when trees are similarly stressed, a sampling period can occasionally confounded by a coincident rain event.

Osmotic potential and OA are determined either on a whole leaf using the pressure bomb to obtain pressure-volume (PV) curves (Cheung et al. 1975), or expressed sap from a frozen leaf using vapor pressure osmometer or thermocouple psychrometer (Jones and Turner 1980, Gebre et al. 1998b). The PV curve procedure is based on relative water content determination from either periodic collection and weighing of exuded sap or periodic weighing of leaves that are allowed to dry on the bench (Abrams 1988). Measurement of expressed sap from frozen leaves underestimates the ψ_π because of a possible dilution by the apoplastic water fraction and generally gives higher ψ_π than the PV curve method (Markhart and Lin 1985). As a result, one can not compare studies based on the two different methods although the ranking of species or clonal differences based on a given method remains similar. Osmotic adjustment also generally remains the same within a method. If absolute values are important, however, relative water content can be used to correct for the dilution factor.

Another factor contributing to differences in baseline ψ_π and OA among studies is the different genotypes used in the different studies. Although the baseline ψ_π were similar for American sycamore (*Platanus occidentalis* L.) at Oak Ridge, Tennessee, and Sumter, South Carolina, OA was not observed in the South Carolina study (unpublished data), unlike the earlier OA of 0.30 MPa (Tschaplinski et al. 1995). Similarly, there was no OA in field-grown sweetgum (Liquidambar styraciflua L.) clones, although Tschaplinski et al. (1995) had reported OA of 0.61 MPa in container-grown seedlings.

4. CONCLUSION

While there is evidence that suggest low ψ_π or OA and yield are related in agricultural crops grown under drought conditions, there is only very limited evidence that is the case in forest trees grown in the field. One of the problems has been that the experiments were not designed to compare plants with known differences in ψ_π. Our study of TD F_2 poplar family 331 in the dry region of eastern Oregon had shown large differences in growth and ψ_π. However, the ψ_π data was limited to second year growth. Similar to some studies on *Eucalyptus* sp., our results suggest that OA was more common in clones with high ψ_π. It is not clear which group of plants would have indicated a better correlation between OA and growth. Among clones that are considered productive under well-watered conditions, it can be expected that clones with low ψ_π would outperform clones with high ψ_π during recovery, because plants with high ψ_π, typically require more time for g_s to recover. The net effect may be similar final productivity or differences in productivity, depending on severity (intensity and length) of the water stress period.

The findings of McCree and Richardson (1987) that sorghum had 44% less water loss and benefited from OA, supports the suggestion that plants that incorporate some degree of stomatal control and have OA are at a competitive advantage. Before any decision is made based on OA, however, it is important that all the drought tolerance characteristics, such as carbon allocation (e.g., rooting patterns) and gas exchange, be known over the full rotation of the trees. Unlike annual crops where the results could be based on one growing season, several studies indicate that early juvenile responses may not be reliable for mature forest trees.

Given that our studies were based on industry-selected clones, selected for their productivity without regard to their drought tolerance characteristics, the comparisons among clones are to some degree limited. It may have been more useful to compare productive clones with known differences in baseline ψ_π or OA under well-watered and stressed conditions. By including low productivity clones that differ in OA or baseline ψ_π, it is possible to get a better understanding of the contribution of OA or baseline ψ_π to growth and dehydration tolerance. This has been the approach taken in many agricultural crop studies. Although the degree of OA and clonal difference in ψ_π between the two poplar clones we studied at Wallula was small, there were seasonal differences suggesting that both clones were capable of OA. Questions that were not addressed in that study included the following. What would have happened under a severe or prolonged drought? How do the clones differ in recovery? Which clone would have maintained its leaves longer under sever stress? The DN clone generally maintained higher midday ψ_w than the TD clone, although there was no clonal difference at predawn, suggesting stomatal regulation was occurring, rather than extraction of water from deep soil layers. However, later in the growing season, the DN clone had lower soil water content and lower predawn ψ_w than the TD clone. Maintenance of higher ψ_w by stomatal closure and increased retention of leaves may be useful for withstanding stresses of moderate or short duration. Our study with several *P. deltoides* clones at a Union Camp Corp. site in South Carolina indicated that all clones had similar ψ_π and all were capable of OA based on the low ψ_π observed in the dry treatment. As a result, there was no clear relationship between productivity and ψ_π or OA.

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