Tree Physiology 19, 367–374
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Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate. I. Family and site effects over three growing seasons

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Received December 1, 1997

Summary Pressure–volume curves were determined for black spruce (*Picea mariana* (Mill.) BSP) trees from four full-sib families. During the first two years, trees were measured from a plantation on a dry site. In the third year, trees were sampled from the dry site and a wet site. Diurnal measurements of shoot water potential allowed *in situ* shoot turgor to be estimated in addition to standard water relations traits. Over all years, Female 59 progeny displayed lower osmotic potentials at saturation (Ψ_{sat}) than Female 63 progeny. Genetic differences in Ψ_{sat} were similar on both the dry and wet sites. Modulus of elasticity (ε) was greater for Female 59 progeny than for Female 63 progeny, producing a compensatory effect resulting in no genetic or site differences in osmotic potential at turgor loss point (Ψ_{tlp}) or relative water content at turgor loss point (RWC_{tlp}). Mean and predawn shoot turgor pressures (P_x and P_{pd}) were higher for Female 59 progeny than for Female 63 progeny and higher at the wet site than the dry site. Genotype × environment trends were observed; compared to Female 63 progeny, Female 59 progeny displayed 9.8 and 5.1% higher P_{pd} on the dry and wet sites, respectively, and 3.4 and 9.8% greater P_{pd} values in wet and dry years, respectively. Tree volume growth showed no relationship to Ψ_{tlp} or RWC_{tlp}, but was correlated with Ψ_{sat} and P_x; however, the strongest correlation was with P_{pd} ($r = 0.90$).

Keywords: genetic variation, growth, Picea mariana, turgor.

Introduction

Shoot water relations can provide a link between plant water status and many growth-related processes that are sensitive to water availability (Kramer 1983, White et al. 1996). Physiological responses to water availability vary among and within tree species and are often difficult to interpret on the basis of component physiological processes considered in isolation. Although there have been many greenhouse and growth chamber studies on water relations of trees, few studies have examined genetic variation in shoot water relations of field-grown trees *in situ*.

A standard quantitative genetic analysis of a 7 × 7 black spruce (*Picea mariana* (Mill.) B.S.P.) diallel on three sites at the Petawawa Research Forest indicated a genotype × environment interaction (G × E) on growth characteristics (Boyle 1987). Four families that exhibited this growth variation among the three sites were selected for further examination. One female parent produced families that displayed relatively high productivities on the three sites, whereas the other female parent produced families that had high growth rates on the wet and moderately dry sites but not on the dry site. The sites are in close proximity and can be assumed to receive the same rainfall. Differences in drainage account for the differences in water availability among the sites (S. Brown and R. Ponce Hernandez, Trent University, Peterborough, ON, Canada, unpublished data).

Shoot water relations parameters were measured in mature black spruce trees from the same four full-sib families studied above. Our objectives were to: (1) test for genetic and site variations in water relations traits; (2) assess G × E interaction on water relations traits; and (3) determine if any water relations traits were related to growth. The companion paper (Major and Johnsen 1999) examines the temporal variation in water relations traits and their relationship to soil water availability.

Materials and methods

Site location and plant material

The four full-sib families of black spruce measured in this study are a subset of a complete 7 × 7 diallel experiment established in 1973, with two-year-old stock, at three sites within a 5-km radius located at the Petawawa Research Forest (46° N, 77°30′ W) (Morgenstern 1974, Boyle 1987). The four families comprise a 2 female parent × 2 male parent breeding structure (Table 1). The parent trees originated from the Lakes Simcoe-Rideau Region of Ontario (Hills 1960). In 1992, the three sites displayed a range of productivities. Mean heights for all four families were 8.09, 7.57 and 8.63 m for Sites 1, 2

Table 1. Parentage of the four full-sib families (7122, 7125, 7143 and 7146) of black spruce.

Male	Female 59	Female 63
52	7122	7125
62	7143	7146

(dry) and 3 (wet), respectively. Full-sib families 7122 and 7143 maintained relatively high productivities across all three sites, whereas families 7125 and 7146 had high and moderate growth rates on sites 1 and 3, but significantly lower growth rates on site 2 (Figure 1). Air temperature (1.3 m) and rainfall data for the period 1973–1993 were collected from a weather station located within 8 km of the study sites.

In 1991 and 1992, the dry site (Site 2) was selected for pressure–volume assessment because it showed the lowest productivity and the greatest difference in growth among progeny of females. In 1993, the dry and wet sites (Sites 2 and 3), representing growth extremes, were studied. All sites have plantations with randomized complete block designs: the dry site has four blocks of 16-tree plots (4 × 4) and the wet site has three blocks of 9-tree plots (3 × 3). Trees were planted at a 1.8 m × 1.8 m spacing. Trees within family/block plots were randomly assigned to each date; individual trees were only measured on one date. The first three of four blocks from the dry site and the three blocks from the wet site were used for sampling. Each time, one tree per family per block was measured. In addition, xylem water potentials were measured on each tree at predawn (0400–0500 h) and at 0830–0930, 1030–1130, 1230–1330, and 1430–1530 h on different branches within minutes of excision.

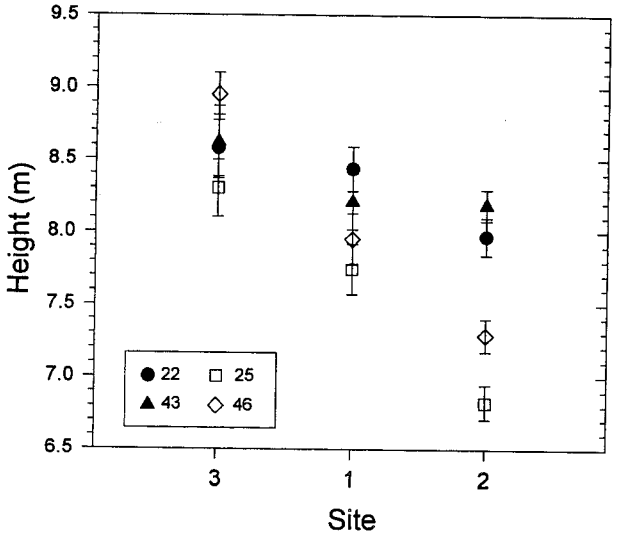

Figure 1. Family height (mean ± SD) for four full-sib families from three sites located at the Petawawa Research Forest, Ontario, Canada. Families 7122 and 7143 are progeny from Female 59 (filled symbols) and families 7125 and 7146 are progeny from Female 63 (open symbols). Measurements were taken in 1992.

Methodology

On days of pressure–volume measurements, lateral shoots (15–20 cm) from the upper third of the crown were collected at dawn and allowed to rehydrate briefly by placing the shoots in 4 cm of water in a beaker located inside a large opaque plastic bag and sealing the bag. After about 2 h, shoots were removed and the saturated weight of each shoot was measured. For each shoot, a pressure–volume curve was constructed from measurements of shoot mass and xylem water potential (Ψ_x), the latter determined with a pressure chamber (Model 3005, Soil Moisture Corp., Santa Barbara, CA) (Hinckley et al. 1980, Grossnickle 1989). Between measurements, the shoot transpired outside the pressure chamber on the laboratory bench (22 ± 2 °C air temperature, 50 ± 10% relative humidity, and 60 ± 20 μmol m^{-2} s^{-1} irradiance). Pressure–volume curves were completed within one day of the diurnal Ψ_x measurements. Shoot dry weights were measured after oven drying at 65 °C for 48 h and dry weight fraction (DWF) was determined by dividing dry weight by saturated weight. Tree volume of the sample trees was calculated from the heights and diameters measured in the fall of 1992 using the formula $1/3\pi r^2 h$ (r = radius and h = height).

The pressure–volume curve was used to determine osmotic potential at saturation (Ψ_{sat}) and turgor loss point (Ψ_{tlp}), relative water content at turgor loss point (RWC_{tlp}), and modulus of elasticity (ε) (Schulte and Hinckley 1985, Grossnickle 1989). *In situ* shoot turgor pressure was estimated as the difference between Ψ_x and the corresponding osmotic potential. Predawn shoot turgor pressure (P_{pd}) was determined by using only predawn xylem water potential (Ψ_{pd}). Mean shoot turgor pressure (P_x) was determined from the five diurnal xylem water potential measurements including the predawn measurement.

Measurements on dry site, 1991

Water relations measurements were taken on five dates between July 4 and August 13, 1991. Current-year foliage was used for determining pressure–volume curves. Xylem water potentials were not measured on the same trees and hence turgor pressure could not be accurately estimated. For each sampling time, an average of three replicates was used from the four families on the dry site, resulting in a total of 60 samples.

Measurements on dry site, 1992

Water relations measurements of one-year-old foliage were made on six dates between July 5 and August 9, 1992. Pressure–volume curves and Ψ_x were determined for the same trees, except for the first sampling time (July 5). For each sampling time, an average of six replicates was used from the four families on the dry site, resulting in a total of 140 samples.

Measurements on dry and wet sites, 1993

Water relations measurements were taken on seven dates between July 5 and August 9, 1993. One-year-old foliage was used, and pressure–volume curves and Ψ_x were determined for the same trees. For each sampling time, three replicates were

used from the four families on both sites, resulting in a total of 168 samples.

Statistical analysis

Analysis of variance (ANOVA) was used to assess the influence of female parent, male parent, date, and site (1993 only), as well as their interactions, using a randomized complete block design. Female parent, male parent, site, date and block were all considered to be fixed effects. Because water relations measurements took place over an approximately 6-week period and changes occurred in response to seasonal and environmental variations (Major and Johnsen 1999), results were summarized for the season and compared with growth. Correlation analysis was used to examine the relationship between water relations traits and tree volume.

Results

Total rainfall, and mean maximum and minimum temperatures are summarized for 45 days between July 1 and August 14, (the period for which physiological data were collected) for 1991, 1992 and 1993 (Figure 2). Plantation means for the 1973–1993 period were 116.4 mm of rainfall and maximum and minimum temperatures of 25.4 and 12.7 °C, respectively. Rainfall for the 1992 summer season was the second wettest (204 mm) and 1993 was among the driest (70.1 mm) seasons in plantation history. Mean maximum temperature was low in 1992 (22.7 °C) and above average for 1991 (26.7 °C) and 1993 (26.2 °C). Mean minimum temperature in 1992 was the lowest thus far recorded (10.4 °C), and the third highest in 1993 (13.8 °C).

Male or female parent was not a significant source of variation for any water relations trait in 1991. Date was a significant source of variation for Ψ_{sat}, Ψ_{tlp}, and ε. Although not statistically significant, Female 59 progeny had lower Ψ_{sat} (−1.37 versus −1.29 MPa) and Ψ_{tlp} (−2.09 versus −1.90 MPa) than Female 63 progeny. Relative water content at turgor loss point and ε were similar between progeny of females.

In 1992 (the wettest year), Female 59 progeny had significantly lower Ψ_{sat} (−1.73 versus −1.68 MPa, $P = 0.050$) than Female 63 progeny, but equal Ψ_{tlp} (−2.35 versus −2.33 MPa, $P = 0.333$) and RWC_{tlp} (79.9 versus 79.7%, $P = 0.729$) (Table 2). Female 59 progeny had higher P_x (0.77 versus 0.71 MPa, $P = 0.043$) and P_{pd} (1.50 versus 1.45 MPa, $P = 0.085$) than Female 63 progeny (Figure 3A). Modulus of elasticity did not differ significantly between progeny of Females 59 and 63 (8.23 versus 7.62 MPa, respectively, $P = 0.182$) (Table 2). Date was a significant ($P < 0.0001$) source of variation for Ψ_{sat}, Ψ_{tlp}, RWC_{tlp}, and P_x. Other sources of variation including male, interactions between female and male, female and date, male and date, and female × male × date had no significant effects on any of the water relations traits tested in 1992.

In 1993 (the driest year), the predominant genetic differences in water relations trends measured were also between progeny of the two female parents (Table 3). Female 59 progeny had significantly lower Ψ_{sat} (−1.83 versus −1.72 MPa, $P = 0.0013$) but similar Ψ_{tlp} (−2.55 versus −2.51 MPa, $P = 0.2017$) and RWC_{tlp} (78.0 versus 78.1, $P = 0.9336$) than Female 63 progeny (Table 2). Female 59 progeny had significantly higher P_{pd} (1.55 versus 1.44 MPa, $P = 0.0004$) (Figure 3A), P_x (0.91 versus 0.83 MPa, $P = 0.0005$), and ε (7.00 versus 6.14 MPa, $P = 0.003$) (Table 2) than progeny of Female 63. Comparing 1992 and 1993 data, all water relations traits displayed the same rank trends.

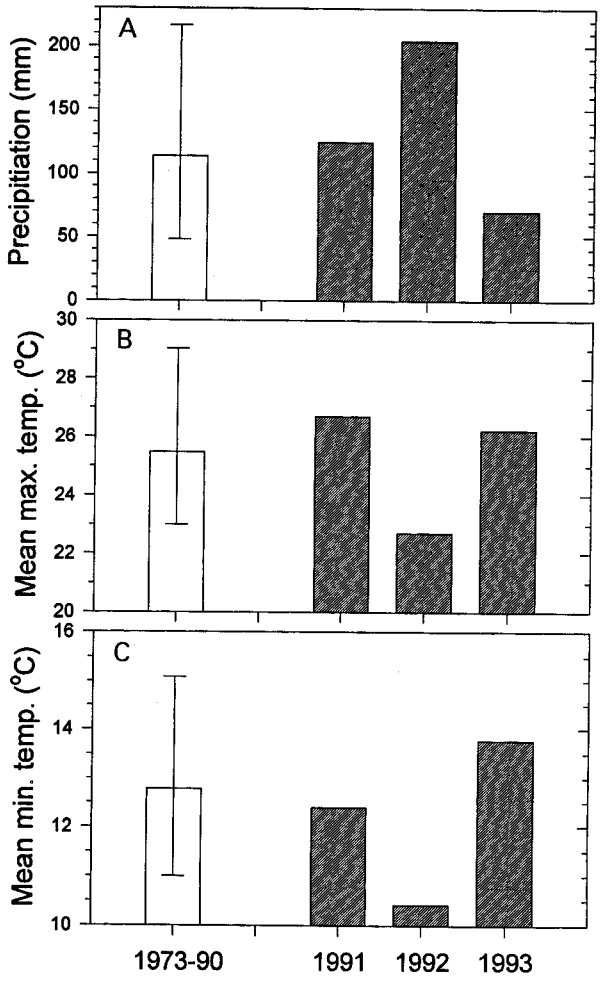

Figure 2. Mean and range of (A) precipitation, (B) maximum and (C) minimum temperatures (1.3 m) between July 1 and August 14 at Petawawa Research Forest for the years 1973–90 and 1991, 1992, and 1993.

In 1993, midsummer mean soil water potentials were −0.46 and −0.33 MPa for Sites 2 and 3, respectively. Trees on the dry site (Site 2) had higher Ψ_{sat} (−1.71 versus −1.84 MPa, $P = 0.0004$) but similar Ψ_{tlp} (−2.52 versus −2.54 MPa, $P = 0.529$) and RWC_{tlp} (77.4 versus 78.7%, $P = 0.1779$) compared with trees on the wet site (Site 3) (Table 2). Trees on the dry site had a lower P_{pd} (1.40 versus 1.60 MPa, $P < 0.001$), and P_x (0.80 versus 0.94 MPa, $P < 0.001$) than trees on the wet site. Modulus of elasticity of the trees was similar ($P = 0.188$) for the dry (6.40 MPa) and wet sites (6.76 MPa).

No water relations trait showed a significant female × site interaction (Table 3). However, Female 59 progeny showed

Table 2. Overall means and standard errors of water relations traits by female progeny for one-year-old foliage in 1992 from Site 2 and for one-year-old foliage in 1993 from Sites 2 and 3. Abbreviations: Ψ_{sat} = osmotic potential at saturation; Ψ_{tlp} = osmotic potential at turgor loss point; RWC_{tlp} = relative water content at turgor loss point; ε = modulus of elasticity; and P_x = mean shoot turgor ($n = 7$).

Female progeny	Ψ_{sat} (MPa)	Ψ_{tlp} (MPa)	RWC_{tlp} (%)	ε (MPa)	P_x (MPa)
Site 2 1992 (n = 70)					
59	−1.73 ± 0.03	−2.35 ± 0.03	79.9 ± 0.7	8.23 ± 0.26	0.77 ± 0.03
63	−1.68 ± 0.03	−2.33 ± 0.04	79.7 ± 0.7	7.62 ± 0.30	0.71 ± 0.03
Site 2 1993 (n = 42)					
59	−1.77 ± 0.04	−2.57 ± 0.05	77.1 ± 1.0	6.62 ± 0.34	0.86 ± 0.04
63	−1.65 ± 0.04	−2.47 ± 0.05	77.7 ± 1.0	6.17 ± 025	0.75 ± 0.03
Site 3 1993 (n = 42)					
59	−1.89 ± 0.03	−2.53 ± 0.04	78.9 ± 0.8	7.38 ± 0.33	0.97 ± 0.04
63	−1.79 ± 0.03	−2.55 ± 0.04	78.5 ± 0.8	6.12 ± 0.29	0.91 ± 0.03

14.7 and 6.6% higher P_x than Female 63 progeny on the dry and wet sites, respectively. Predawn shoot pressure potential also displayed twofold differences with 9.8 and 5.1% higher values for Female 59 progeny compared to Female 63 progeny on the dry and wet sites, respectively (Figure 3B).

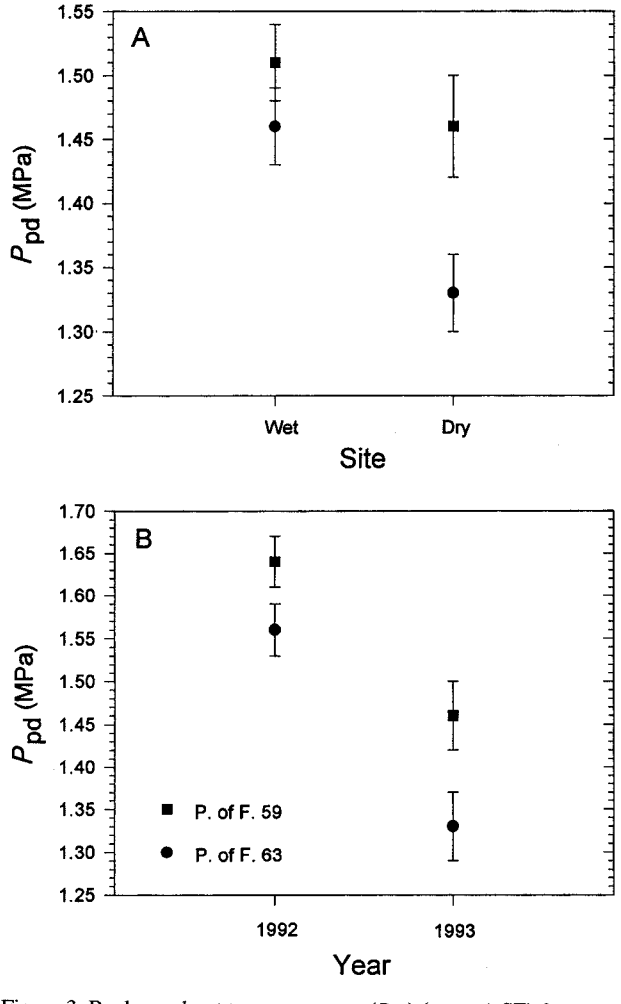

Figure 3. Predawn shoot turgor pressure (P_{pd}) (mean ± SE) for progeny of Females 59 and 63, (A) by site measured in 1993, and (B) by year on the dry site.

No significant correlations were found between mean family tree volumes from both sites and the corresponding mean Ψ_{tlp} ($P = 0.535$, $r = 0.26$, Figure 4A), RWC_{tlp} ($P = 0.187$, $r = 0.52$, Figure 4B), ε ($P = 0.237$, $r = 0.47$, Figure 5A), and Ψ_x ($P = 0.072$, $r = 0.67$, data not shown). Significant relationships were found between tree volume and mean Ψ_{sat} ($P = 0.011$, $r = 0.83$) (Figure 5B) and P_x ($P = 0.017$, $r = 0.80$) (Figure 6A). Predawn pressure potential had the highest correlation to tree volume ($P = 0.002$, $r = 0.90$) (Figure 6B).

Discussion

Site variation

The sites are in close proximity and can be assumed to receive the same rainfall. Differences in drainage account for the differences in water availability between the two sites (S. Brown and R. Ponce Hernandez, unpublished data). Predawn shoot turgor and P_x were 14.3 and 17.5% higher on Site 3 (wet site) than on Site 2 (dry site). There was no difference in Ψ_{tlp} between sites, as a result of compensatory ε effects. Differences in overall mean Ψ_x were small because the overriding influence of vapor pressure deficit on daily measures minimized the soil water availability effects (Hinckley et al. 1978). Interestingly, mean Ψ_{sat} was lower on the wet site than the dry site, which is intuitively contrary to what might be expected. This aspect is discussed further in Major and Johnsen (1999).

Genetic variation

Genetic effects on water relations were consistent between years, especially between progeny of Females 59 and 63. This finding is consistent with results of gas exchange (Johnsen and Major 1995, Major and Johnsen 1996) and stable isotope (Flanagan and Johnsen 1995) studies. In 1991, 1992 and 1993, Female 59 progeny had Ψ_{sat} values that were 6.2, 3.0, and 6.4% lower, respectively, than the corresponding values for Female 63 progeny. During 1992 and 1993, Female 59 progeny displayed consistently greater P_x and P_{pd} than Female 63 progeny. Within a species, consistent differences in turgor or Ψ_{sat} be-

Table 3. Sources of variation, degrees of freedom (DF) and *P*-values from ANOVA of 1993 water relations traits. Abbreviations: Ψ_{sat} = osmotic potential at saturation; Ψ_{tlp} = osmotic potential at turgor loss point; RWC_{tlp} = relative water content at turgor loss point; ε = modulus of elasticity; P_x = mean shoot turgor pressure; and P_{pd} = predawn shoot turgor pressure.

Source	DF	Ψ_{sat}	Ψ_{tlp}	RWC_{tlp}	ε	P_x	P_{pd}
Female (F)	1	0.0013	0.2017	0.9336	0.0025	0.0005	0.0004
Male (M)	1	0.4048	0.6769	0.0037	0.0530	0.6242	0.4690
Site (S)	1	0.0004	0.5290	0.1779	0.1883	< 0.0001	< 0.0001
Date (D)	6	0.0118	0.0005	0.0014	< 0.0001	< 0.0001	< 0.0001
F × M	1	0.2315	0.0958	0.8795	0.7649	0.1517	0.2746
F × S	1	0.8579	0.0950	0.3809	0.1526	0.6224	0.5192
F × D	6	0.6798	0.7877	0.8301	0.5228	0.4543	0.7059
M × S	1	0.3866	0.0246	0.3159	0.4464	0.0559	0.1712
M × D	6	0.6827	0.8124	0.3757	0.9094	0.7165	0.8540
S × D	6	0.798	0.0707	0.0949	0.8783	0.0008	0.0095
F × M × S	1	0.6661	0.7214	0.6751	0.7376	0.9155	0.4465
F × M × D	6	0.5545	0.3499	0.1335	0.2849	0.1867	0.6057
F × S × D	6	0.2654	0.3484	0.8658	0.7755	0.2249	0.2040
M × S × D	6	0.8235	0.2339	0.7903	0.9129	0.1749	0.8119
Block (site)	4	0.4431	0.1671	0.4192	0.7071	0.0483	0.2994
Error	108						
Total	161						

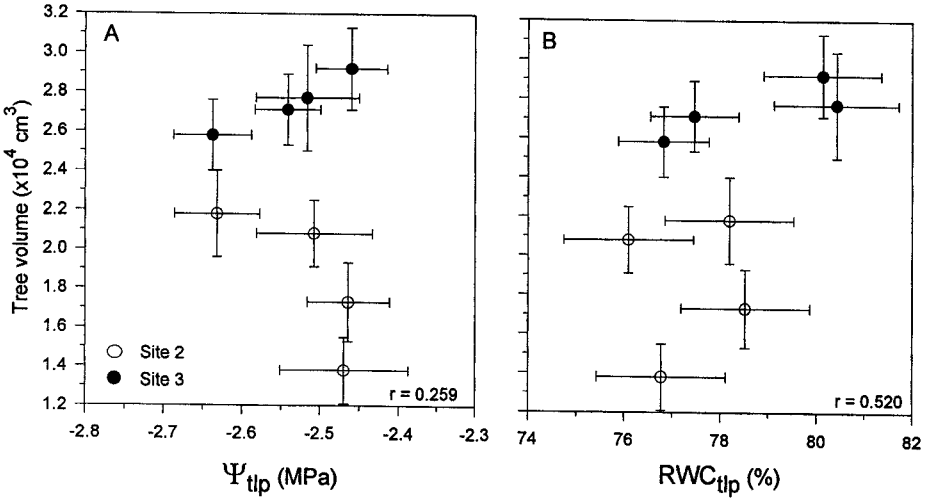

Figure 4. Relationship between tree volume (mean ± SE) and (A) osmotic potential at turgor loss point (Ψ_{tlp}) (mean ± SE), and (B) relative water content at turgor loss point (RWC_{tlp}) (mean ± SE) of four full-sib families from the dry and wet sites.

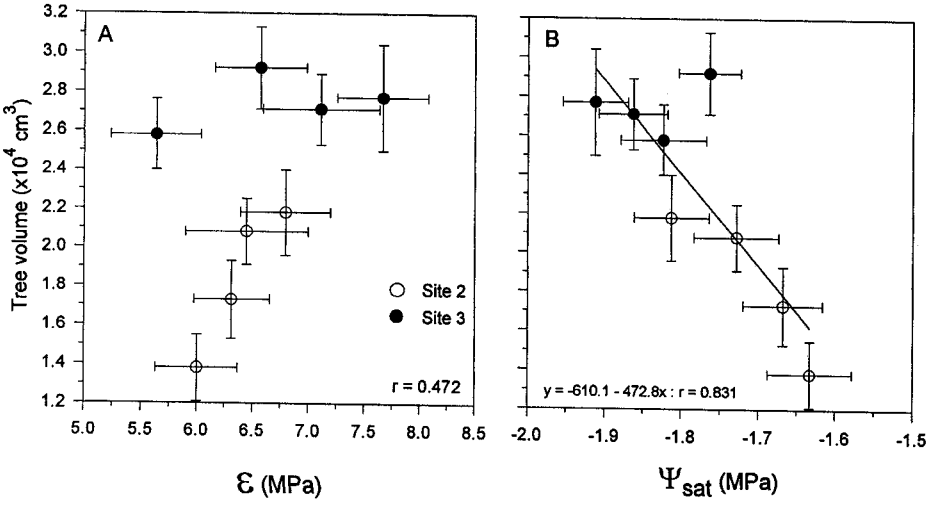

Figure 5. Relationship between tree volume (mean ± SE) and (A) modulus of elasticity (ε) (mean ± SE), and (B) osmotic potential at saturation (Ψ_{sat}) (mean ± SE) of four full-sib families from the wet and dry sites.

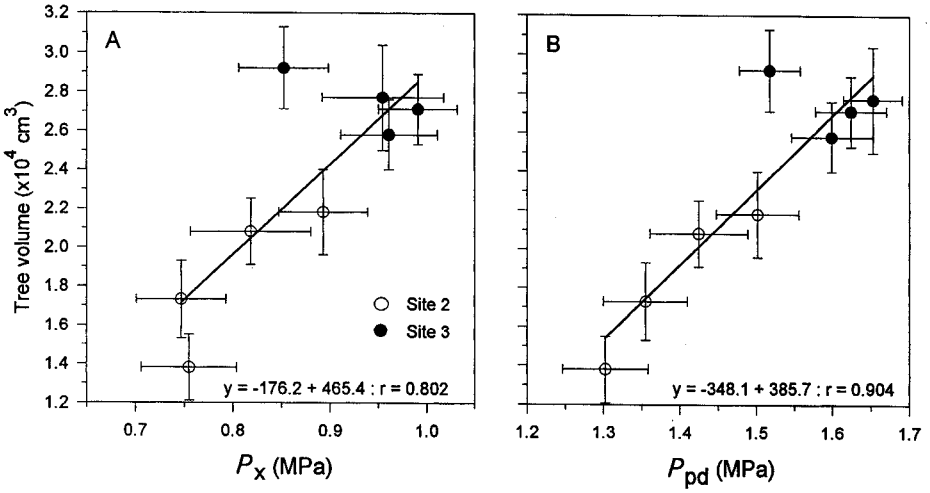

Figure 6. Relationship between tree volume (mean ± SE) and (A) mean shoot turgor P_x (mean ± SE), and (B) predawn shoot turgor (P_{pd}) (mean ± SE) of four full-sib families from the wet and dry sites.

tween families have been reported only for agricultural species (e.g., Morgan 1995, Premachandras et al. 1995).

In both 1992 and 1993, modulus of elasticity was greater for Female 59 progeny than for Female 63 progeny, creating a compensatory effect resulting in little or no difference in Ψ_{tlp} or RWC_{tlp} between the progeny of the females over a range of conditions. In addition, even during the exceptionally dry growing season of 1993, turgor was estimated to be negative for only three Ψ_x measurements out of more than 670. Moreover, Ψ_{tlp} had the lowest correlation with growth. These data contrast with the conclusions drawn by Tan et al. 1992*a*, 1992*b*. They suggest that growth differences are a result of stomatal limitation or closure or both. These authors based their conclusions about turgor loss on inference rather than measurements. Our results are in agreement with the finding that net photosynthesis in these trees is more affected by non-stomatal limitations than by stomatal limitations (Major and Johnsen 1996). We conclude that, at least in older trees, Ψ_{tlp} did not greatly influence growth.

Genotype × site interaction

Several trends indicated that variation in water relations traits contributed to the observed G × E on growth; however the G × E interaction of water relations traits were never statistically significant.

Genetic differences in Ψ_{sat} were proportional in magnitude to annual rainfall. That is, the degree of difference in Ψ_{sat} between female progeny was highest in 1993 (0.11 MPa) the driest year, followed by 1991 (0.08 MPa) with intermediate rainfall and 1992 (0.05 MPa), the wettest year during our study. Although Ψ_{sat} appeared to be the water relations trait underlying the observed G × E on growth, when families were compared directly on the two sites in 1993, progeny of both females exhibited similar differences in Ψ_{sat} on both sites (0.12 MPa, dry site and 0.10 MPa, wet site).

Mean shoot turgor pressure also displayed inconsistent G × E trends. Females 59 and 63 progeny showed similar differences in mean shoot turgor pressure between 1992 (wet) and 1993 (dry), (0.06 MPa, 8.4% and 0.08 MPa, 9.6%, respectively). Nevertheless, in 1993, Female 59 progeny showed 0.11 (14.7%) and 0.06 MPa (6.6%) greater mean turgor pressures than Female 63 progeny on the dry and wet sites, respectively. This inconsistency between years and sites is reconciled by the fact that, although 1992 was wetter than 1993, VPD was higher on measurement days in 1992 (2.01 kPa) than in 1993 (1.57 kPa).

Among the water relations traits measured, P_{pd} displayed the most consistent G × E trends. For instance, Female 59 progeny showed 0.05 MPa (3.4%) and 0.11 MPa (7.6%) greater predawn shoot turgor pressures in 1992 and 1993, respectively, than Female 63 progeny, which is consistent with 1992 having three times the rainfall of 1993. Furthermore, P_{pd} of Female 59 progeny showed 0.13 (9.8%) and 0.08 MPa (5.1%) greater values than Female 63 progeny on the dry and wet sites, respectively. In addition, family mean P_{pd} was highly correlated with growth across the two sites.

Relationship to growth

Based on a review of the older literature, Zahner (1968) reported that up to 80 and 90% of the variation in diameter growth of trees were attributable to variations in rainfall and plant water stress in humid and arid areas, respectively. However, the physiology of cell enlargement is complex and dependent on many factors such as cell wall extensibility, water relations, energy and carbohydrate supply, time of day and season. As developed by Lockhart, a generally accepted conceptual growth equation is that the rate of cell volume growth equals the product of effective turgor pressure (turgor pressure minus cell wall yield threshold) times irreversible cell wall extensibility (plasticity) (Lockhart 1965, Cleland 1987, Okamoto 1996).

We found that shoot turgor pressure was correlated with growth. Mean daytime shoot turgor showed the weakest correlation with growth ($r = 0.75$), followed by mean diurnal turgor ($r = 0.80$), and predawn shoot turgor pressure displayed the strongest relationship to growth ($r = 0.90$). Lockhart (1965) describes the minimum turgor necessary for cell expansion, also known as cell wall yield threshold, as the pressure at

which the cell wall begins irreversible expansion. These conditions prevail in the predawn and early dawn hours when turgor is highest and likely to exceed cell wall threshold (Boyer 1987, Randell and Sinclair 1987). Often, daytime turgor is below the minimum for growth but enough to maintain stomatal opening and processes other than growth. Thus, our finding that P_{pd} exhibited the highest correlations with growth (r = 0.90) is in agreement with the concept of Lockhart's equation.

The very strong relationship between P_{pd} and growth indicates the families may have similar cell wall extensibility and yield threshhold traits. The exception was family 7146 on the wet site, which displayed a much higher growth rate than expected based on the observed general relationship between P_{pd} and growth. One possible explaination, based on the Lockhart model, is that family 7146 has a higher cell wall plasticity or a lower cell wall yield threshold than the other families when grown on a wetter site.

Relationships between turgor and growth vary widely. Short-term studies with maize, pea plants or fungal hyphae have resulted in varying results (Amir et al. 1995, Harold et al. 1995, Neumann 1995, Okamoto et al. 1995). With woody trees, both poor relationships (e.g., *Pinus* roots, Tomos and Pritchard 1994, *Salix* leaves, Stadenberg et al. 1994) and close relationships (e.g., *Pinus* roots Triboulot et al. 1995, *Poplus* roots, Bosac et al. 1995) between turgor and growth have been reported. In our study, the mature full-sib families, with no inbreeding, had widely different volume growth ($1.2–3.2 \times 10^4$ cm^3), but the overall range in mean family P_{pd} was small (0.5 to 0.11 MPa). However, it appears that small physiological differences can contribute to large productivity differences as a result of the compounding effect (Major and Johnsen 1996).

Acknowledgments

Thanks are extended to Trina Price for assisting with and supervising the data collection.

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