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Stable carbon isotope discrimination: an indicator of cumulative salinity and boron stress in *Eucalyptus camaldulensis*

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Summary Saplings of *Eucalyptus camaldulensis* Dehn. Clone 4544, irrigated with water of differing salinities (2 to 28 dS m^{-1}) and boron concentrations (1 to 30 mg l^{-1}), integrated the history of these stresses through the discrimination of stable isotopes of carbon in leaf and woody tissues. Carbon isotope discrimination (Δ) was reduced primarily by salinity. Decreases in discrimination in response to boron stress were detected in the absence of salinity stress, but the decreases were significant only in leaf tissues with visible boron injury. Sapwood core samples indicated that salinity- and boron-induced reductions in Δ increased with increasing tree age. Absolute values of Δ varied with location of leaf or wood tissue, but relative effects of salinity on the relationship between Δ and transpiration efficiency (W) were similar. In response to increasing salinity stress, relative decreases in Δ paralleled relative decreases in biomass and both indices yielded similar salt tolerance model parameters. The strong correlations between Δ, tree fresh weight, leaf area and W suggest that Δ is a useful parameter for evaluating salt tolerance of eucalypts.

Keywords: boron, ^{13}C discrimination, salt tolerance, transpiration efficiency.

Introduction

Determination of stable carbon isotopic composition ($\delta^{13}C$) of plants has resulted in significant progress toward understanding the influence of environmental stresses (water, light, salinity and air pollution) on CO_2 fixation and transpiration (O'Leary 1981, Farquhar et al. 1989, Ehleringer et al. 1993). Components of carbon isotope fractionations are associated, principally, with photosynthesis, and are separated into physical and chemical processes that contribute to the overall fractionation in plant tissues (O'Leary et al. 1992). Carbon isotope discrimination (Δ) is usually expressed as the difference in $\delta^{13}C$ between source and product. A theory relating Δ to the ratio of internal to external CO_2 (C_i/C_a) in C_3 plants has been developed by Farquhar et al. (1989) and is supported by a host of experimental studies. According to the theory, Δ is determined primarily by fractionations of carbon during diffusion of CO_2 through stomata, and enzymatic fractionations related to the C_i/C_a ratio. A major advantage of characterizing plant stress based on Δ over instantaneous measurements of gas exchange or water potential is that it provides an integrated index of stress history rather than a snapshot in time.

Stable carbon isotopic investigations involving *Eucalyptus* have focused primarily on water-use or transpiration efficiency, but have also reported a positive relationship between biomass and Δ (Bond and Stock 1990, Olbrich et al. 1993, Osório and Pereira 1994, Anderson et al. 1996, Osório et al. 1998). Transpiration efficiency—a whole-plant measure of biomass or yield as a function of water loss over extended periods—and Δ are indirectly negatively related through effects of water stress on C_i/C_a. High C_i/C_a ratios lead to high Δ values and are associated with low transpiration efficiency. Relationships between Δ and biomass are less clear. We postulated that if growth conditions were optimal except for the presence of salinity, variation in Δ would reflect biomass production through the effects of salinity on stomatal conductance and C_i/C_a ratios (Farquhar et al. 1989).

Boron toxicity and salinity are common in many parts of the world; however, little is known about their interactive effects (Ferreyra et al. 1997). In a previous study, we found that salinity reduced the effects of boron toxicity in *Eucalyptus camaldulensis* Dehn. (Poss et al. 1999). Boron toxicity in eucalypts was associated with leaf injury and ultimately with leaf necrosis when B concentrations exceeded a threshold value (Poss et al. 1999). In theory, variations in Δ may be triggered by any factor causing an increase in heterogeneity in leaf photosynthetic characteristics (Farquhar and Lloyd 1993). If it is assumed that B-related necrosis and reductions in active leaf area result in increased photosynthetic variation across the leaf surface, reductions in Δ should be associated with boron stress. Furthermore, boron-induced reductions in Δ may be decreased by salinity stress.

The present study was undertaken to examine effects of salinity and high boron concentrations on Δ and transpiration efficiency (W). Specifically, we tested the hypothesis that Δ is a cumulative indicator of salinity and boron stress and W in *E. camaldulensis* growing in an outdoor sand-tank lysimeter facility.

Materials and methods

An experiment was conducted at the U.S. Salinity Laboratory in Riverside, CA, where *Eucalyptus camaldulensis*, Clone 4544 trees were grown in sand irrigated with water of differing salinities and boron concentrations. Two trees were planted on June 15, 1995, in each of 23 lysimeters (1.5 × 3 × 2 m deep) containing sand with a mean bulk density of 1.4 Mg m^{-3} and a volumetric water content at saturation of 0.34 m^3 m^{-3}. Evaporation was estimated from one lysimeter without trees. Trees were irrigated once daily with a nutrient solution containing (mol m^{-3}) 5.0 Ca^{2+}, 1.25 Mg^{2+}, 15 Na^+, 3.2 K^+, 6.9 SO_4^{2-}, 7.0 Cl^-, 5.0 NO_3^-, 0.2 $H_2PO_4^-$, 0.05 Fe as sodium ferric diethylenetriamine pentaacetate (NaFeDTPA), 0.023 H_3BO_3, 0.005 $MnSO_4$, 0.0004 $ZnSO_4$, 0.0002 $CuSO_4$, and 0.0001 H_2MoO_4, made up with Riverside municipal water. This base nutrient solution served as the control treatment. The 23 treatments were chosen from 36 possible combinations of six irrigation water salinities (2, 6, 10, 15, 22 and 28 dS m^{-1}) and six boron concentrations (1, 4, 8, 15, 25 and 30 mg l^{-1}). The two-way factorial experimental design was partially replicated with five treatments replicated twice. The final 23 treatments selected were: 2 dS m^{-1} with 1, 8 and 25 mg B l^{-1}; 6 dS m^{-1} with 4, 15 and 30 mg B l^{-1}; 10 dS m^{-1} with 1, 8 and 25 mg B l^{-1}; 15 dS m^{-1} with 4, 15 and 30 mg B l^{-1}; 22 dS m^{-1} with 1, 8 and 25 mg B l^{-1}; and 28 dS m^{-1} with 4, 15 and 30 mg B l^{-1}. The irrigation waters contained predominately salts of Na^+, Mg^{2+}, SO_4^{2-} and Cl^-, with B added as H_3BO_3 (Grattan et al. 1997). Treatments were imposed beginning on September 21, 1995. The pH was uncontrolled but was essentially constant (~7.5) as a result of chemical equilibrium. Treatment irrigation waters were pumped from 4000-dm^3 reservoirs into the lysimeters and returned by gravity through a subsurface drainage system to maintain a homogeneous profile of salt and boron with depth. Water lost to evapotranspiration was replenished daily by an automated refill system and volumes were recorded with an automated data collection system. Tree canopy heights and diameters at breast height (DBH) were measured periodically.

On May 1, 1996, one tree in each tank was harvested (hereafter referred to as Harvest 1). Four leaf sample locations (1–4) were identified as the lowest and highest fourth of the branches of each tree at proximal and distal locations (Figure 1). The relative age of the leaves was $2 < 1 \le 4 < 3$. Several leaves were sampled at each location, oven-dried at 60 °C, and ground to pass a 60-mesh screen. Wood cross sections were also sampled from trunks at a height of approximately 1.4 m from the soil surface. Air-dried wood samples were drilled out at three locations (center (a), middle (b) and outer (c)) proportional to the diameter of each trunk and ground to pass a 60-mesh screen. The relative age of the sapwood samples was: a > b > c.

On November 11, 1996, the second tree in each tank was harvested (hereafter referred to as Harvest 2). Total tree leaf area was determined with a Li-Cor 3100 (Li-Cor Inc., Lincoln, NE) leaf area meter. For each tree, all leaves were weighed, oven-dried, and ground in a large mill to pass a 10-mesh screen. The total ground leaf sample was mixed thoroughly and spread over a 1-m^2 area and subsampled at 16 locations in a grid pattern. The subsample was reground to pass a 60-mesh screen. Wood cross sections were also sampled as described for Harvest 1. At Harvest 2, a few individual leaves from trees exhibiting boron injury were divided into injured and non-injured areas for $\delta^{13}C$ analysis.

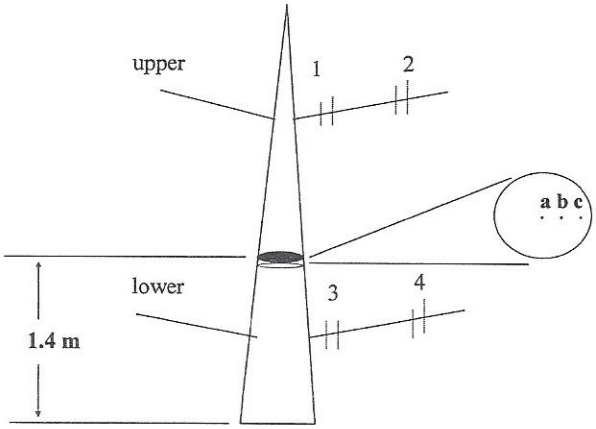

Figure 1. Leaf and wood sampling locations for stable carbon isotope analysis of *E. camaldulensis* (after Lamb 1976).

The stable carbon isotope compositions of leaf and woody tissues were measured by mass spectrometry (ANCA-SL Stable Isotope Analysis System, Europa Scientific, Crewe, U.K.) with a sample precision of ± 0.03 × 10^{-3}. The $^{13}C/^{12}C$ isotope ratios (δ^{13} C) were calculated relative to the Pee Dee Belemnite international standard. Each treatment tissue sample was processed in duplicate. Carbon isotope discrimination was calculated as: $\Delta = (\delta_a - \delta_p)/(1 + \delta_p)$, where δ_a and δ_p are the isotopic compositions of air and plant material, respectively (Farquhar et al. 1989). The isotopic composition of air was assumed to be -8.0×10^{-3}.

Transpiration estimates for trees in Harvest 1 were calculated as total water use per tank minus the evaporation tank value divided by 2 (two trees per tank). For Harvest 2, the calculated transpiration for trees in Harvest 1 was subtracted from the total water use for both trees and the evaporation of the total experiment subtracted to estimate transpiration for trees in Harvest 2. To compare our water consumption volume data to literature values, the ground area of each sand tank (4.5 m^2) was used to convert liters to millimeters. Quadratic surface regressions were performed with the RSREG procedure, biomass–salinity response functions were fitted with the NLIN procedure, and linear regressions were calculated with the GLM procedures (1985, SAS Institute, Cary, NC).

Results

Leaf tissue Δ

Relative differences in carbon isotope discrimination (Δ) of leaf tissue in response to salinity and boron stress were similar at all four sampling positions for trees in Harvest 1. However, the range of Δ values was greater by nearly 1.5‰ for leaf Positions 1 and 4 than for leaf Positions 2 and 3 (Figure 2).

Discrimination was primarily reduced by salinity ($P < 0.05$) at all four leaf sampling positions and quadratic surface regression correlation was highest ($r^2 = 0.72$) for leaf Position 2. Trends in boron effects on Δ were greater for leaf Positions 2 and 3 ($P < 0.28$ and 0.37, respectively) than for leaf Positions 1 and 4 ($P < 0.59$ and 0.60, respectively). Mean standard errors between replicate leaf samples ranged from 0.07 ± 0.01 to 0.10 ± 0.02‰.

In the absence of salinity stress (≤ 2 dS m^{-1}), a significant influence of boron on Δ was evident in leaf Position 3 only, where isotopic composition increased as boron concentration increased (Table 1). As salinity increased (> 6 dS m^{-1}), boron effects on Δ were no longer significant. Isotopic discrimination of leaves (± SE) from Position 3 was 23.65 ± 0.14‰ for trees irrigated with water containing 2 dS m^{-1} + 1 mg B l^{-1}. For trees grown with water containing 28 dS m^{-1}, Δ values of leaves from the same position (± SE) were 22.28 ± 0.01‰ at 4 mg B l^{-1} and 21.98 ± 0.21‰ at 30 mg B l^{-1}.

When averaged across boron concentrations, linear regressions indicated positive relationships between Δ and fresh weight at all four leaf sampling positions for trees in Harvest 1 (Figure 3). Similar linear relationships were found when expressing Δ as a function of total leaf area for trees in Harvest 1 ($r^2 = 0.59-0.91$). When averaged across salinity and boron treatments, Δ values of leaves near the trunk (Positions 1 and 3) were 1.74 ± 0.13 and 1.16 ± 0.14‰ lower, respectively, than Δ values of leaves near branch tips (Positions 2 and 4).

Surface regression analysis of composite leaf samples from trees at Harvest 2 yielded similar Δ–salinity relationships to those found at all four leaf sampling positions for trees in Harvest 1; however, a significant positive relationship with increasing boron concentration was also found ($P < 0.015$). The Δ values of B-induced necrotic leaf tissue of six individual leaves from trees at Harvest 2 averaged 0.56‰ lower than that of green leaf tissue with a range of −0.32 to 1.28‰. When averaged across boron treatments, Δ of composite leaf samples of trees in Harvest 2 was more closely correlated with total tree fresh weight and total leaf area (Figure 4) than with any specific leaf location of trees in Harvest 1.

Wood tissue Δ

At the onset of the treatments, mean tree canopy height was 183 ± 9 cm. Hence, every tree trunk cross section sampled

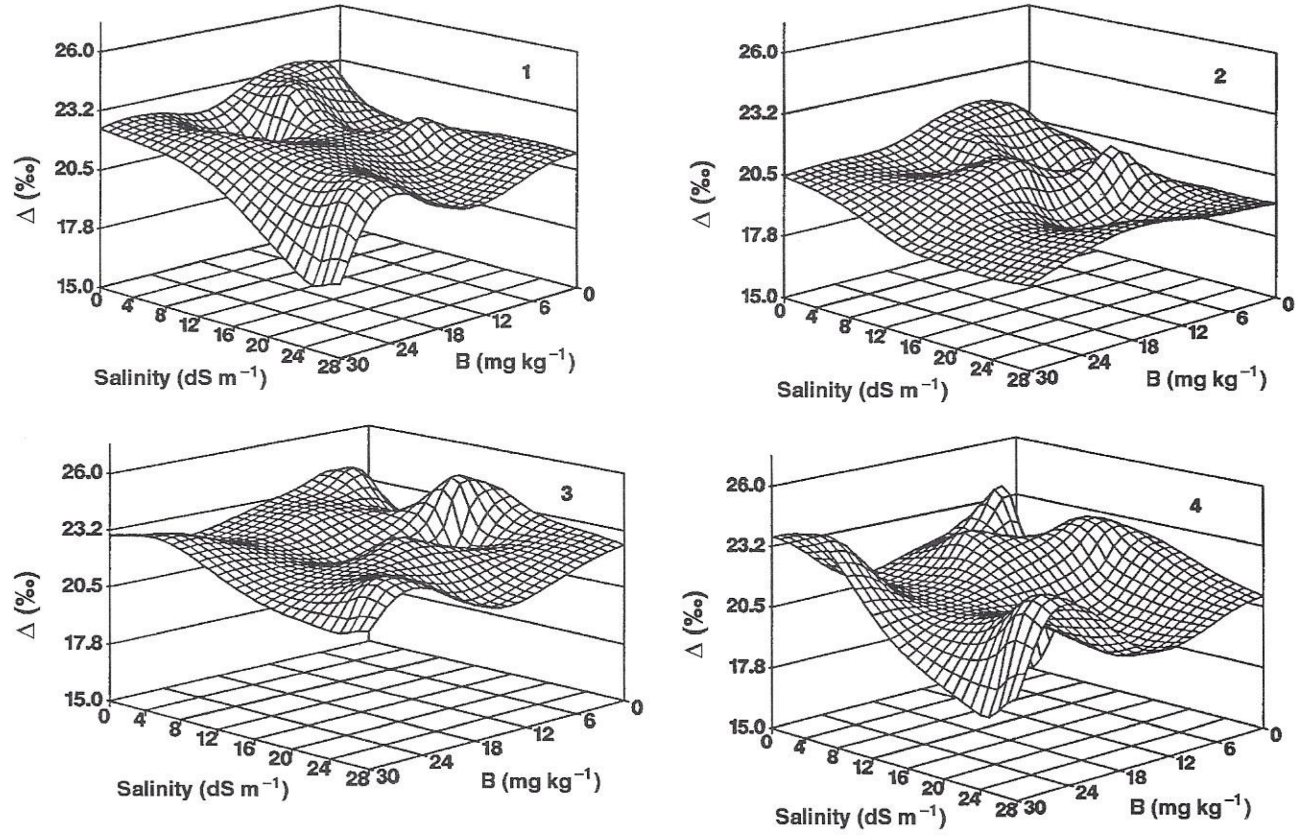

Figure 2. Spline surfaces ($n = 23$) for Δ as a function of boron concentration and salinity for leaves sampled at four different canopy positions (see Figure 1).

Table 1. Effect of B concentrations in the presence of low salinity (2.1 dS m^{-1}) on isotopic composition of leaves taken from four canopy positions of trees at Harvest 1 ($^{**} = P < 0.05$).

Leaf position	Equation	r^2
1	$\delta^{13}C = 0.02B_{sw} - 30.16$	0.10
2	$\delta^{13}C = 0.04B_{sw} - 28.76$	0.47
3	$\delta^{13}C = 0.07B_{sw} - 31.16$	0.89^{**}
4	$\delta^{13}C = -0.01B_{sw} - 30.16$	0.01

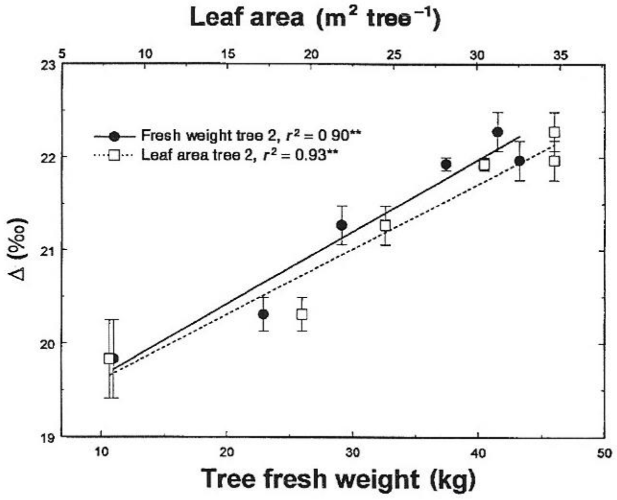

Figure 4. Linear regression of Δ of composite leaf samples taken from trees at Harvest 2 as a function of total leaf area and fresh weight.

1.4 m from the base was established before stress-induced differences in height were observed. Changes in DBH were influenced by treatment. When averaged across B treatments, increases in DBH over a 9-month period decreased with increasing salinity from about 30 mm at salinities up to 15 dS m^{-1} to 22 and 16 mm at salinities of 22 and 28 dS m^{-1}, respectively. There was a significant linear relationship between wood tissue Δ and increases in DBH for wood samples averaged over all three positions ($r^2 = 0.54$).

Isotopic composition of sapwood samples was lower than that of leaf samples. Wood samples from trees at Harvest 1 showed no overall difference in Δ attributable to sample position location, but a significant effect of salinity was observed in Position b. At Harvest 2, Δ differed significantly among all three wood sample positions and salinity significantly influenced Δ at each position (Figure 5). At each position, salinity and boron effects increased from Harvest 1 to Harvest 2 (Table 2), except at Position b where the effects were similar for trees subjected to salinity stress.

Transpiration efficiency and Δ

In trees at Harvest 1, long-term transpiration efficiency (*W*) was negatively correlated with Δ of leaf tissue sampled in Positions 1 and 3 only when averaged across boron treatments (Figure 6). In trees at Harvest 2, Δ of composite leaf samples was negatively correlated with *W* ($r^2 = 0.59$). The correlation between wood tissue Δ and *W* was higher for trees at Harvest 2 than for trees at Harvest 1 in all sample positions, except Position c where the correlation was similar (Table 3).

Salt tolerance and relative Δ

A relationship was developed for relative decreases in Δ as a function of salinity averaged across boron treatments. Relative discrimination was calculated as:

$$\text{Relative}\,\Delta = \Delta - \Delta_{min} / \Delta_{max} - \Delta_{min}, \quad (1)$$

where Δ is observed discrimination, Δ_{min} is the minimum Δ observed, and Δ_{max} is the fitted absolute maximum Δ of a par-

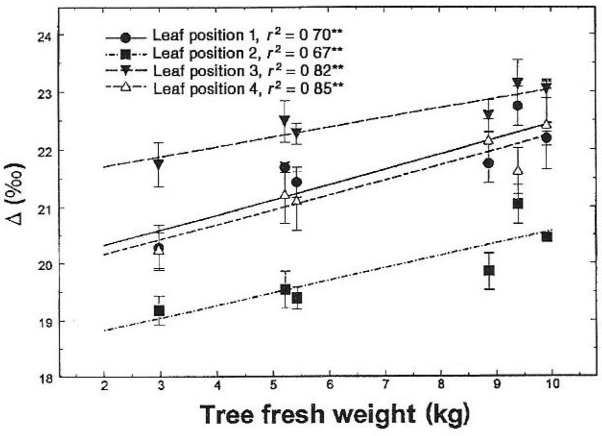

Figure 3. Linear regression of Δ sampled at four canopy locations as a function of total fresh weight for trees at Harvest 1 (** = $P < 0.05$).

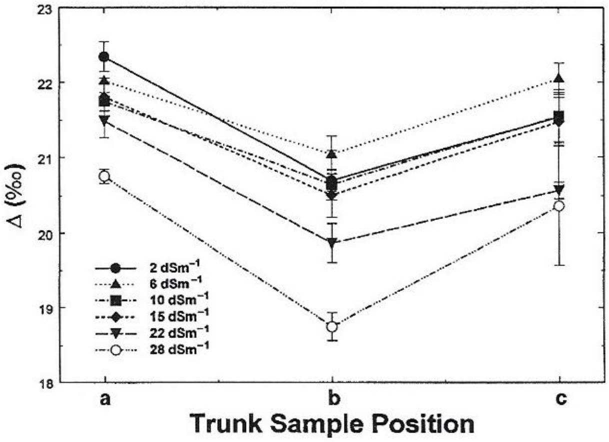

Figure 5. Isotopic discrimination (Δ) values of *E. camaldulensis* trunk wood tissue sampled at three radial locations in trees at Harvest 2 (see Figure 1).

Table 2. Probability of greater F ratio ($P \leq 0.01$ indicated by ***) for salinity and boron effects on Δ based on surface regression model for sapwood samples taken at three different locations from trees subjected to treatment for 223 (Harvest 1) and 333 (Harvest 2) days.

Factor[1]	Harvest 1 Sapwood position			Harvest 2 Sapwood position		
	a	b	c	a	b	c
Salt	0.1056	0.0007***	0.1637	0.0001***	0.0009***	0.0035***
Boron	0.3623	0.6379	0.8126	0.1771	0.3618	0.1067
r^2	0.37	0.64	0.30	0.74	0.78	0.59

[1] The test on a factor is a joint test on all the parameters involving that factor in the regression.

ticular tissue. The relative decrease in Δ as a function of salinity was estimated according to the salt tolerance equation:

$$\text{Relative}\,\Delta = \Delta_{\max} / (1 + (C / C_{50}))^{p}, \quad (2)$$

where $\Delta_{\max}$ is the fitted maximum Δ, C is the salinity in dS m^{-1}, C_{50} is the salinity in dS m^{-1} where Δ is reduced by 50%, and p is an empirical shaping parameter (van Genuchten and Hoffman 1984). Relative Δ as a function of salt tolerance was compared with that derived from the same equation based on tree fresh weight. The fitted values for the C_{50} parameter based on fresh weight of trees at Harvest 2 and relative Δ for the leaf composite samples from trees at Harvest 2 (Figure 7) were similar (18.6 versus 18.5 dS m^{-1}, respectively). Similar C_{50} values were also observed based on relative Δ of wood samples from trees at Harvest 2 (18.8, 18.5 and 19.6 dS m^{-1} for Positions a, b and c, respectively). However, the shaping parameter increased from about three to four to eight for the a, b and c wood samples, respectively. Thus, relative Δ of wood tissue showed a steeper inflection with increasing salinity than would be the case for tree fresh weight or relative Δ of leaf composite samples.

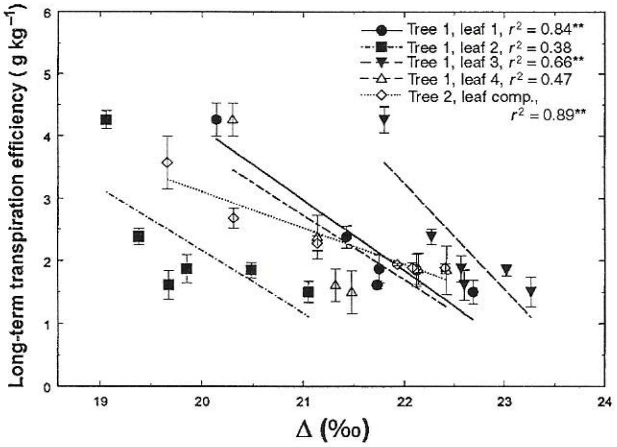

Figure 6. Linear relationships between estimated long-term transpiration efficiency (W) and Δ of leaves sampled at four different canopy positions for trees at Harvest 1 and Δ of composite leaf samples for trees at Harvest 2 (** = $P < 0.05$).

Discussion

Stable carbon isotope discrimination was predominantly influenced by salinity. Effects of high B concentrations on Δ were detectable only in older leaf tissue (leaf Position 3, see Figure 1) when salinity stress was low. As salinity increased, the influence of salinity on Δ dominated any effect of boron.

One possible explanation for the apparently small influence of boron may be sampling error due to the limited number of replications available in the outdoor lysimeter facility. Although the lysimeter facility limited the design to a pseudo-factorial study, these limitations were partially overcome with regression analysis and the exceptional control available to minimize variance within the facility. In a parallel study characterizing boron-related leaf injury in *Eucalyptus*, leaves of low branches proximal to the main trunk exhibited significant boron injury when trees were irrigated with water containing high concentrations of boron and low salinity; however, increased salinity significantly reduced B-induced leaf injury (Poss et al. 1999). If the mechanism resulting in decreased Δ with increasing boron concentration is related to B-induced reductions in photosynthetically active leaf area, then the cumulative stress effects on Δ might be reduced by the mitigating effects of salinity on boron injury. The observation that leaf and wood core Δ values were not reduced by boron at salinities greater than 2 dS m^{-1} or in other canopy leaf positions is consistent with such a mechanism. The finding that necrotic tissues associated with B injury were isotopically heavier than non-necrotic portions of the same leaf provides further evidence of a small injury-related reduction in discrimination in response to B. The positive effect of high B concentration on Δ in the composite leaf sample from Harvest 2 may be a statistical anomaly caused by the premature death of a tree in the 28 dS m^{-1} + 30 mg B l^{-1} treatment whose composite sample was not obtained.

The ability of Δ to integrate salinity and boron stress through time is apparent from the trends of increasing boron and salinity effects on Δ as stress duration increased. In addition, the finding that the isotopic composition of leaf tissue in trees at Harvest 1 was lighter in younger tissues that developed before salinity stress was induced and relatively heavier in tissues developed after salinization provides further evidence of time integration of salinity effects on Δ. Thus, leaves at the tips of branches (Positions 2 and 4) were isotopically heavier than leaves near the trunk (Figure 6). Radiation effects may provide

Table 3. Slope, intercept and correlation coefficients for Δ as a function of W for wood samples at three trunk diameter locations in trees subjected to salinity and boron stress for 223 (Harvest 1) and 333 (Harvest 2) days ($^{**} = P \leq 0.05$ and $^{***} = P \leq 0.01$).

Wood sample position	Harvest	Slope	Intercept	r^2
a	1	−0.58	14.85	0.03
	2	−1.06	25.38	0.86^{***}
b	1	−0.76	18.50	0.69^{**}
	2	−0.72	16.94	0.96^{***}
c	1	−1.69	37.99	0.87^{***}
	2	−0.86	20.56	0.81^{***}

an explanation for lower leaf Δ at branch tips compared with leaves near the trunk because lower C_i/C_a ratios would be expected.

On average, Δ was higher in leaf tissue than in wood tissue. This finding is consistent with the results of Francey et al. (1985) who observed an increase in Δ in branch tips compared with branchwood in huon pine trees. Similarly, leaves of juniper are isotopically lighter than wood tissues by about 2‰ (Leavitt and Long 1982). Francey et al. (1985) examined alternative explanations for this gradient in isotopic composition, including irradiance, maintenance respiration and translocation of photosynthate. The smaller difference in Δ between leaf and wood tissue in *E. camaldulensis* than that reported for huon pine or juniper may indicate that photosynthetic translocation and maintenance respiration effects on Δ values are smaller in eucalypt saplings relative to other tree species.

The Δ values for eucalypt leaves appear to reflect the conditions at the time the carbon was fixed in a particular tissue (Figure 3). Young leaves (Position 2) were exposed to salinity and boron stress throughout their development, as well as during periods of high evaporative demand. Conversely, older leaves (Position 3) were at least partially developed prior to treatment. Seasonal fluctuations in Δ, however, may not be as significant under well-watered conditions (Pate and Arthur 1998).

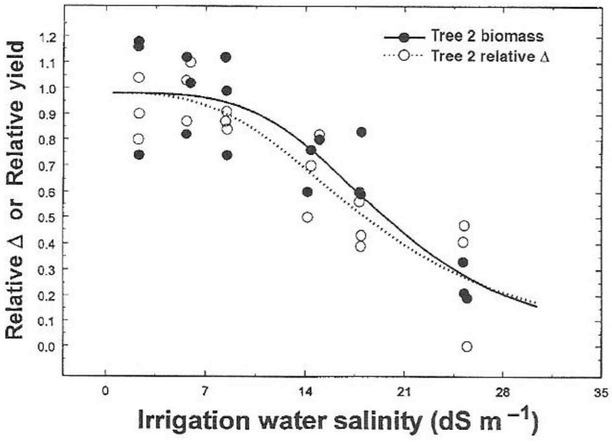

Figure 7. Salt tolerance functions based on decreases in fresh weight relative to the control (maximum fresh weight) and decreases in Δ relative to the control (maximum Δ). The C_{50} values, the electrical conductivity where both Δ values are decreased by 50%, were essentially equivalent.

Annual water use of trees at Harvest 2 ranged from over 1200 mm at low salinity to as little as 178 mm at high salinity. This is within the range of values reported in other studies, but more closely approximates conditions of intensive irrigation management than those of field or forest environments. Dryland eucalypt plantations in Victoria, Australia, which include *E. camaldulensis* utilizing shallow saline groundwater ranging from 1 dS m^{-1} to over 20 dS m^{-1}, have an annual water use of 300 mm (Morris et al. 1998). At another *E. camaldulensis* plantation near Perth, initially established with irrigation before relying on groundwater, transpiration of 230 to 350 mm per year was estimated from groundwater hydrographs and heat-pulse sap flow measurements (Salama et al. 1994). In a study conducted similarly to that at our sand tank facility, annual tree water use as high as 1045 mm was estimated in a Lake Albacutya provenance of *E. camaldulensis* irrigated with saline drainage water and fertilized with nitrogen and phosphorus (Sweeney and Stevens 1997).

Three provenances of *E. camaldulensis* subjected to water deficits in a pot experiment had transpiration efficiencies ranging from 1.1 to 2.1 mmol C (mol H_2O)$^{-1}$ (Hubick and Gibson 1993). Transpiration efficiency in our study had a comparable range (1.2 to 2.6 mmol C (mol H_2O)$^{-1}$). Salinity increased W in our study; however, biomass production of plants with high W was low. An inverse relationship between water-use efficiency and biomass production under saline conditions has also been observed by Medina and Francisco (1997) who compared the response of mangroves in coastal and riverine areas in Venezuela. Despite a lack of gas exchange data, our results not only support the coupling of high W with low Δ, but are also consistent with commonly reported decreased C_i/C_a ratios in leaves of salt-stressed plants (Seemann and Critchley 1985). As in other studies, we calculated W on the basis of aboveground production only (Olbrich et al. 1993).

Leaf Δ generally correlated better with salinity, boron, yield and W than did wood Δ. Possible explanations for this difference include carbon translocation, further fractionation when carbon is laid down as wood, and production of secondary metabolites (Park and Epstein 1961, Wilson and Grinsted 1977, Leavitt and Long 1982, Francey et al. 1985). Although wood Δ was related to DBH, the correlation was not strong. Because wood δ_p may vary across trunk cross sections and in different radial directions (Sheu and Chiu 1995), the use of cellulose extraction techniques might improve this relationship.

The ability to estimate salt tolerance from Δ of whole-plant tissue appears promising inasmuch as empirical salt-tolerance models can be applied similarly for Δ and biomass. Ansari et al. (1998) proposed that fitting parameters such as C_{50} to Δ may be even more suitable as a method for screening plants for salt tolerance than comparing mean Δ values between non-saline controls and saline treatments. We note that a limitation of the relative Δ technique proposed here is the assumption of a zero relative Δ result for the minimum value in the data set (the absolute minimum Δ). However, when fitting either relative Δ or yield as a function of salinity, the inclusion of "zero yield" or data from extremely stressed plants is useful (M. Th. van Genuchten, U.S. Salinity Laboratory, Riverside, CA, personal communication).

We conclude that the strong correlations between Δ, tree fresh weight, leaf area and W indicate that Δ is a useful parameter for evaluating whole-plant responses to salinity, and to a lesser degree, boron. Furthermore, coupled with other approaches, carbon isotope discrimination, which provides an integrated index of processes that are not easily measured or inferred from growth or final yield data alone, may help elucidate the mechanisms underlying salt tolerance of eucalypts.

Acknowledgments and notes

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