Leaf water relations of *Eucalyptus globulus* ssp. *globulus* and *E. nitens*: seasonal, drought and species effects

D. A. WHITE,[1,2] C. L. BEADLE[1,2] and D. WORLEDGE[2]

[1] *Cooperative Research Centre for Temperate Hardwood Forestry, Locked Bag No 2, Sandy Bay 7005, Tasmania, Australia*

[2] *CSIRO Division of Forestry, Locked Bag No 2, Sandy Bay 7005, Tasmania, Australia*

Summary   In August 1990, a 2-ha plantation was established in an area where rainfall (about 515 mm year^{-1}) was insufficient to meet evaporative demand. On nine occasions between September 1991 and April 1993, pressure-volume curves were constructed for irrigated and rainfed *Eucalyptus globulus* ssp. *globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden trees. During the experiment, rainfed trees experienced six periods when predawn water potential was significantly lower than that of irrigated trees. In early spring of 1991 and 1992, osmotic potentials at full turgor and turgor loss point in the irrigated *E. nitens* were significantly lower than at other times of the year, probably because of winter hardening. Water stress reduced osmotic potential and increased bulk elastic modulus in *E. nitens*, whereas the reverse occurred in *E. globulus*. However, treatment differences with respect to changes in osmotic and elastic properties were commonly overshadowed by interspecific differences. These were most apparent at the end of the sixth period of water stress when osmotic potentials at full and zero turgor were significantly higher and bulk elastic modulus and relative water content at turgor loss point were significantly lower in *E. globulus* than in *E. nitens*. We conclude that the drought-tolerance responses of *E. globulus* make it a more suitable species than *E. nitens* for establishment on sites where moderate water stress is experienced.

Keywords: drought tolerance, drought resistance, elastic modulus, irrigation, osmotic potential, relative water content, turgor.

Introduction

The hardwood plantation estate in Australia is 0.12 Mha and afforestation exceeds 13 kha year^{-1} (Australian Bureau of Agricultural and Resource Economics 1994). Most afforestation is in SE and SW Australia with the two fast-growing species, *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden. Because further expansion of the plantation estate in SE and SW Australia will necessitate establishment on drought-prone sites, an understanding of the relationships between growth and water use, and the physiological responses of *E. globulus* and *E. nitens* to water stress is needed to determine their relative suitability on these sites.

Several mechanisms of drought resistance have been described (Levitt 1972, Jones et al. 1981). When wood production is the primary objective, traits that allow growth to continue during periods of moderate drought are of most interest. Changes in turgor pressure provide a crucial link between changes in plant water status and many growth-related processes that are influenced by water deficit (Hsiao et al. 1976, Bradford and Hsiao 1982, McDonald and Stadenberg 1993). Turgor maintenance can be achieved through changes in osmotic potential or tissue elasticity (Tyree and Jarvis 1982). A decrease in osmotic potential results in greater turgor pressure at a given leaf water potential, whereas an increase in cell wall elasticity results in smaller changes in turgor pressure for a given change in relative water content. The capacity of a range of plant species, including eucalypts, to regulate osmotic potential (Clayton-Greene 1983, Bowman and Roberts 1985*a*, 1985*b*, Myers and Neales 1986, Abrams 1990) and cell wall elasticity (Cheung et al. 1975, Melkonian et al. 1982, Robichaux et al. 1983, Bowman and Roberts 1985*b*) in response to drought has been demonstrated.

The natural distribution of *E. nitens* is at high altitude (> 800 m asl) where it is regularly subjected to freezing temperatures (Pederick 1979), whereas *E. globulus* is found at low altitude (usually < 300 m, Kirkpatrick 1975). In plantations in southern Tasmania, *E. nitens* hardens to lower temperatures in winter than *E. globulus* (Hallam et al. 1989). We have tested the hypothesis that traits that confer cold tolerance on *E. nitens* render it more drought tolerant than *E. globulus* and more able to respond to water stress by adjustments in its tissue water relations. Osmotic and elastic properties of both species were investigated by pressure-volume analysis (Tyree and Hammel 1972) over a two-year period that included six drought cycles. Irrigated control plots were used to separate the effects of drought from those caused by seasonal changes.

Materials and methods

Study site

Measurements were made on leaves of *Eucalyptus globulus* ssp. *globulus* and *E. nitens* trees growing in a 2-ha experimental plantation located in a low rainfall (about 515 mm year^{-1})

area of Tasmania, approximately 2 km NE of Lewisham (42°49′ S, 147°36′ E). The plantation was established in August 1990 with three irrigated (I) and three rainfed (R) plots (replicates) each containing both species. In one I plot and one R plot, a nine-tree subplot (3×3) of each species was established in which several physiological variables were measured. A detailed description of the study site and experimental design is given in White et al. (1994a).

Soil and plant water status

Irrigation in the I treatment, which commenced on November 6 1991, was scheduled to maintain soil water deficit (Ψ_s) between 20 and 40 mm to promote adequate root development and to ensure that available water did not limit growth. In this way, seasonal changes in tissue water relations could be investigated and separated from those induced by drought. Soil water deficit was determined from neutron moisture meter readings of soil water content made regularly throughout the experiment. Trees in the R treatment were subjected to stress cycles that were separated by rainfall or supplementary irrigation.

At frequent intervals, single leaves were excised from each of the nine trees in the I and R subplots of both species to estimate predawn water potential (Ψ_{pd}). For periods between measurement of Ψ_{pd}, a water stress integral (S_Ψ) was calculated as described by Myers (1988) using a baseline of 0.2 MPa.

Sampling and rehydration

For each species, three trees per treatment were randomly selected from within each plot for examination of leaf water relations. On nine occasions between September 1991 and April 1993, a single leaf was excised from each of these twelve trees for pressure-volume (p-v) analysis (Tyree and Hammel 1972). Leaves were excised under de-ionized water and rehydrated in airtight containers in the dark for between 3 and 4 h (cf. Turner 1987, Parker and Pallardy 1987). Only the youngest fully expanded leaves from the top third of the crown were selected. Up to and including the sampling in May 1992 only juvenile leaves were used; thereafter, adult leaves were used.

Measurement and derivation of tissue water relations parameters

Pressure-volume curves were constructed by allowing leaves to dry on a laboratory bench while periodically measuring fresh weight (W_f) and water potential (Ψ_l). Leaves were weighed before (W_1) and after (W_2) Ψ_l was measured. Fresh weight was calculated as the average of W_1 and W_2. After measurement, leaves were dried to constant weight at 80 °C (W_d). Turgid weight (W_t) was estimated from a plot of Ψ_l versus W_f by extrapolation to $\Psi_l = 0$ (Davie et al. 1993). Relative water content (R^*) was calculated as $(W_f - W_d)/(W_t - W_d)$.

Estimation of tissue water relations variables

Osmotic potential at full turgor (π_s) and turgor loss point (π_p), relative water content at turgor loss point (R^*_p) and relative apoplastic water content (R^*_a) were derived from p-v curves (Tyree and Hammel 1972, Turner 1987). Bulk elastic modulus (ε) was calculated after Bowman and Roberts (1985b) as:

$$\varepsilon = \frac{\Delta P}{\Delta R^*}(R^*_x - R^*_a),$$

where R^*_x is the mean R^* over the calculation interval, ΔR^*, and ΔP is the change in turgor over the same interval.

Osmotic adjustment was calculated as the difference between mean π in the R and I treatments. Separate calculations were made at full and zero turgor for each measurement time.

Results were analyzed as a factorial with respect to treatment (I and R) and species (2^2). Separate analyses were conducted for π_s, π_p, $\Delta\pi$, ε_{max}, ε_s, W_d/W_t, R^*_p and R^*_a for each measurement time. The term $\Delta\pi$ is the difference between π_s and π_p, ε_{max} and ε_s are maximum ε and ε at full turgor, respectively. Two sample comparisons were conducted to test for seasonal changes between measurement times.

Water potential isotherms and the slope of the desorption isotherm

Water potential was plotted against relative water content and, for each tree, the slope of this desorption isotherm ($d\Psi_l/dR^*$) was determined for the region of positive turgor by linear regression. Two sample comparisons were used to test for significant seasonal, water stress and species effects on $d\Psi_l/dR^*$ in the region of positive turgor. This conservative approach was taken to avoid the problem of multiple points per observation (Snedecor and Cochran 1967, Draper and Smith 1981).

Results

Predawn water potential and cumulative water stress integral

A stress cycle was defined as any period when predawn water potential (Ψ_{pd}) of leaves in the R treatment was significantly ($P < 0.05$) lower than that of leaves in the I treatment. Six such cycles occurred during the study (Table 1, Figure 1a). In the I treatment, Ψ_{pd} remained above -0.5 MPa throughout the study (Figure 1a). At the end of the study on April 30, 1993, the cumulative stress integrals (S_Ψ) for the E. globulus and E. nitens trees in the R treatment were 229 and 225 MPa day, respectively (Figure 1b).

Seasonal variation in water relations of trees in the I treatment

In both years of study, osmotic potentials of trees in the I treatment increased from low values in early spring to high values in early summer (December) (Figures 2a and 2b). As summer progressed, π_s decreased slightly, whereas π_p tended to increase in E. globulus (Figures 2a and 2b). In early spring (September 17, 1991 and September 29, 1992), π_s and π_p in E. nitens were lower than at other times of the year and both parameters were significantly lower ($P < 0.05$) than in E. globulus (September 29, 1992 values for E. nitens were $\pi_s = -1.85$ MPa and $\pi_p = -2.45$ MPa and the corresponding

Table 1. Minimum values of mean predawn leaf water potential (Ψ_{pd}, MPa) in the R treatment for each of six stress cycles.

Cycle	Date	E. globulus	E. nitens
1	December 10, 1991	−0.59	−0.58
2	January 30, 1992	−1.24	−2.01
3	July 1, 1992	−0.57	−0.55
4	January 5, 1993	−1.48	−1.31
5	February 19, 1993	−0.88	−0.92
6	April 30, 1993	−2.37	−2.34

values for *E. globulus* were −1.32 and −1.80 MPa) (Figures 2a and 2b). On January 4, 1993, π_s in *E. globulus* was −1.29 MPa and increased to −1.11 MPa by April 13, 1993. During the same period, π_s decreased from −1.24 to −1.50 MPa in *E. nitens*.

There was no consistent pattern of seasonal change in bulk elastic modulus at full turgor (ε_s). In both species, the low

values of ε_s were around 4 to 5 MPa (Figure 2c); however, the high values were greater in *E. nitens* than in *E. globulus* (10 versus 8.5 MPa) (Figure 2c). In *E. nitens*, ε_s was significantly higher on September 29, 1992, December 24, 1992, and April 13, 1993, than at other times of the year. No significant seasonal changes in ε_s were evident for *E. globulus*. On September 29, 1992 and April 13, 1993, ε_s was significantly lower in *E. globulus* than in *E. nitens* ($P < 0.05$).

Throughout most of the study, values of $d\Psi_l/dR*$ in the region of positive turgor were between 10 and 12 MPa, and there was a tendency for *E. globulus* to have a higher water potential for a given relative water content than *E. nitens* (Figures 3a–i). On September 17, 1991 (Figure 3a) and September 29, 1992 (Figure 3f), $d\Psi_l/dR*$ was significantly higher for both species in both treatments than at other measurement times (Table 2).

Water stress

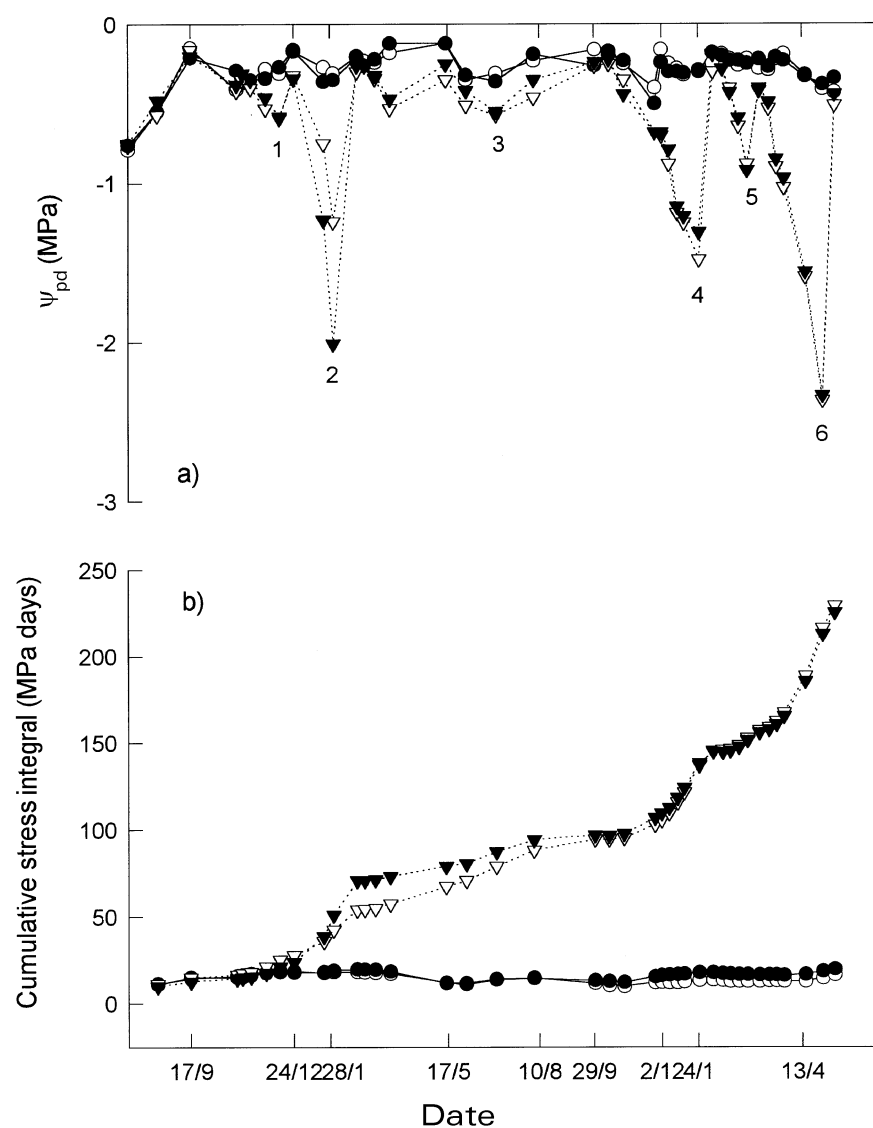Osmotic potential was usually lower in R trees than in I trees

Figure 1. (a) Predawn water potential, Ψ_{pd} and (b) cumulative water stress (S_Ψ) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) in the irrigated (circles) and rainfed (triangles) treatments from July 22, 1991 to April 30, 1993. The stress cycles are numbered 1 to 6.
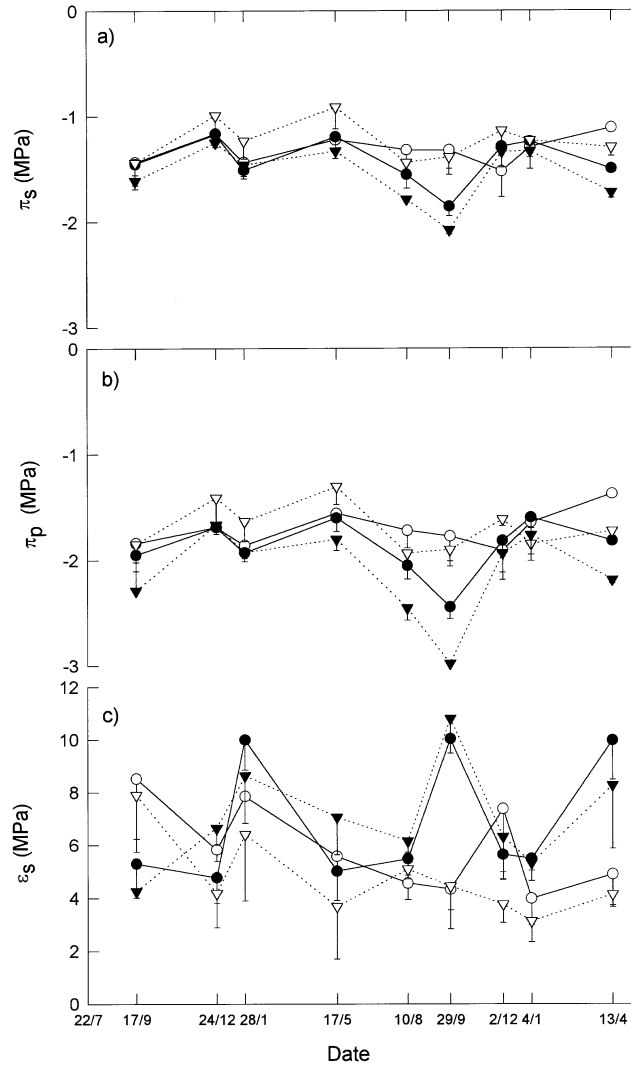
Figure 2. (a) Osmotic potential at full turgor ($\pi_s \pm$ SE), (b) osmotic potential at turgor loss point ($\pi_p \pm$ SE), and (c) bulk modulus of elasticity at full turgor ($\varepsilon_s \pm$ SE) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) in the irrigated (circles) and rainfed (triangles) treatments from September 17, 1991 to April 13, 1993.

nificant species by water status interaction for ε_s. In general, water stress reduced π_s and π_p in both species and increased ε_s in *E. nitens* and decreased it in *E. globulus*.

At no stage did water stress significantly influence the shape of the desorption isotherm (Figure 3). Even on April 13, 1993, when rainfed trees were experiencing significant soil and tissue water deficits for the sixth time in 18 months (Figure 1a), $d\Psi_l/dR^*$ in the region of positive turgor was not significantly affected by water stress (Table 2, Figure 3i).

Comparison of water relations of E. globulus and. E. nitens

Osmotic potentials at full and zero turgor were consistently lower in *E. nitens* than in *E. globulus* and were often lower in irrigated *E. nitens* than in rainfed *E. globulus* (Figures 2a and 2b). In April 1993, both π_s and π_p were significantly lower in *E. nitens* than in *E. globulus*. Trends in ε_s were less consistent than trends in osmotic potential, although rainfed *E. globulus* generally had the lowest ε_s. During stress cycles in January 1992 and April 1993, ε_s was higher in *E. nitens* (9.5 MPa) than in *E. globulus* (6.5 and 4.2 MPa).

On September 29, 1992 and April 13, 1993, mean $d\Psi_l/dR^*$ was significantly ($P < 0.05$ and $P < 0.001$, respectively) higher for *E. nitens* (18.1 and 14.6 MPa, respectively) than for *E. globulus* (14.7 and 9.2 MPa, respectively) (Table 2). At the same time, $d\Psi_l/dR^*$ beyond the turgor loss point was almost identical for the two species, although when $\Psi_l = \pi$ it was significantly higher for *E. globulus* than for *E. nitens* for any given R^*.

In general, *E. globulus* trees maintained positive turgor over a greater range of relative water contents than *E. nitens* trees and this difference was most apparent on April 13, 1993, when turgor loss occurred at an R^*_p of 0.87 for *E. nitens* and 0.79 for *E. globulus* (Figure 4a). At the same time, there was a reduction in dP/dR^* above $R^* = 0.95$ in *E. globulus*. As R^* fell from 1.0 to 0.95, turgor pressure was almost unaffected in *E. globulus* but was reduced from 1.6 to 1.2 MPa in *E. nitens* (Figure 4a). A plot of ε against π for April 13, 1993 showed a decline in ε above $\pi = 0.75$ MPa in *E. globulus* (Figure 4b). Values of ε_s were higher for *E. nitens* than for *E. globulus*, and higher in R than in I trees of *E. nitens* but higher in I than in R trees of *E. globulus*.

Discussion

Species was a more important determinant of drought response than cumulative water stress imposed during the experiment. We hypothesized that *E. nitens* would be more drought tolerant than *E. globulus*. The results did not support this hypothesis but indicated that *E. nitens* is more sensitive to drought than *E. globulus*. Moreover, traits that conferred cold tolerance on *E. nitens* facilitated desiccation avoidance rather than drought tolerance.

Seasonal variation in water relations of trees in the I treatment

No significant seasonal variation in π_s or π_p was observed in *E. globulus*. In contrast, on September 17, 1991 and Septem-

of *E. nitens*, whereas the reverse was found in *E. globulus* (Figures 2a and 2b). Maximum osmotic adjustment was observed on August 10, 1992, in *E. globulus* (−0.12 MPa) and on September 29, 1992, in *E. nitens* (−0.23 MPa).

During Stress Cycle 2 at the end of January 1992, when Ψ_{pd} was −1.24 and −2.03 MPa in rainfed *E. globulus* and *E. nitens*, respectively (Figure 1a), there was no significant effect of water stress on tissue water relations. On January 24 and April 13, 1993, at the end of Stress Cycles 4 and 6, respectively, $\Delta\pi$ was significantly higher in R trees than in I trees. Osmotic potential at full turgor was significantly lower at the end of Stress Cycle 6 in R trees than in I trees, but the effect of water stress on π_p was not significant (Figures 2a and 2b). On December 24, 1991 and January 4, 1993, ε_s was higher in irrigated than in rainfed *E. globulus*, whereas the reverse was true for *E. nitens*. This difference between the species resulted in a sig-
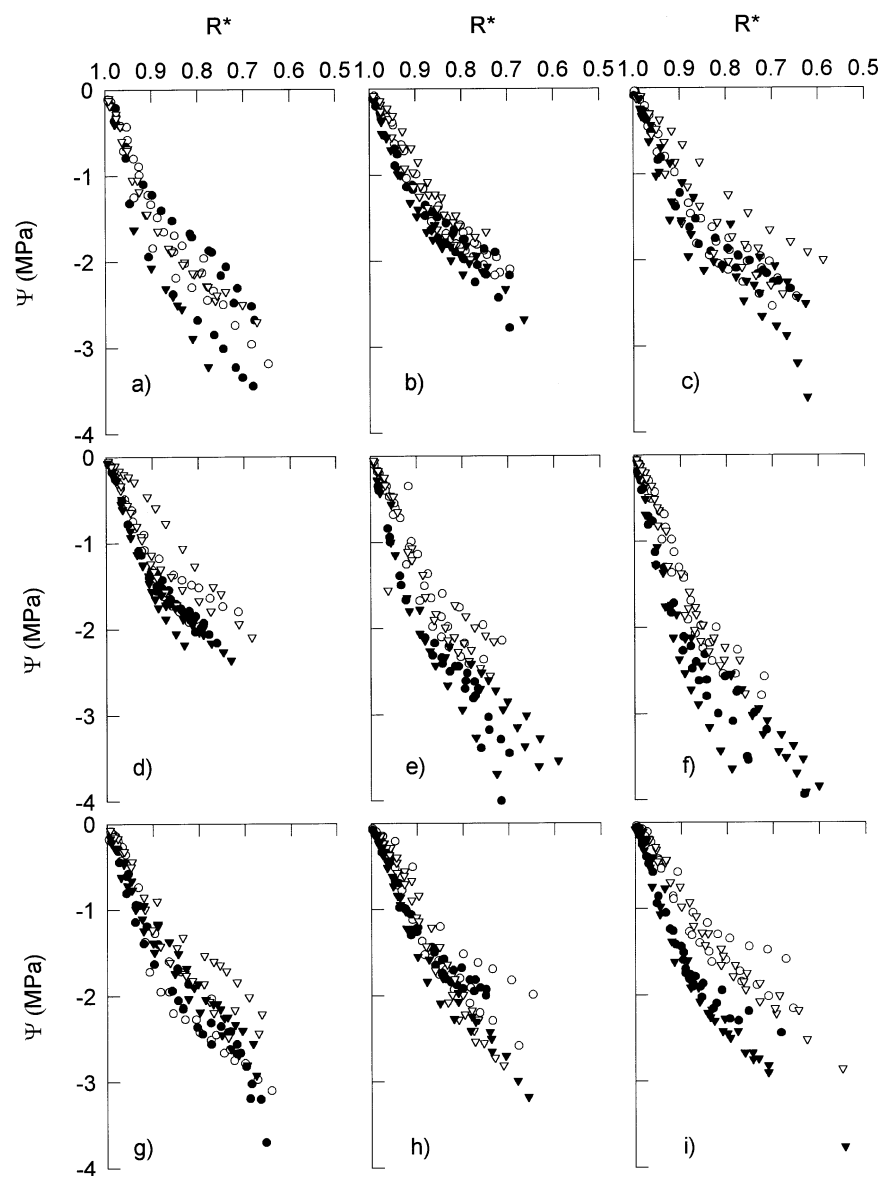
Figure 3. Leaf water potential (Ψ_l) versus relative water content (R^*) for *E.globulus* (open symbols) and *E. nitens* (closed symbols) in the irrigated (circles) and rainfed (triangles) treatments in (a) September 1991, (b) December 1991, (c) January 1992, (d) May 1992, (e) August 1992, (f) September 1992, (g) December 1992, (h) January 1993, and (i) April 1993.

ber 29, 1992, early spring in Tasmania, π_s and π_p were lower (significantly in 1992) in *E. nitens* than at other times of year. The seasonal osmotic adjustment in *E. nitens* was accompanied by significant increases ($P < 0.05$) in ε_s, $d\Psi_l/dR^*$ and $\Delta\pi$, all of which were associated with winter hardening. These findings are consistent with the natural distribution of *E. nitens*

on high-altitude sites subject to winter snow falls (Pederick 1979) and the distribution of *E. globulus* on sites below 300 m asl (Kirkpatrick 1975). Hallam et al. (1989) studied six *Eucalyptus* species, including *E. globulus* and *E. nitens*, and found little difference among them in frost hardiness at the end of May (late autumn), but by August (the end of winter) *E. nitens*

Table 2. Mean $d\Psi/dR^*$ (MPa) in the region of positive turgor by species and water status in September 1991, December 1991, September 1992 and April 1993.

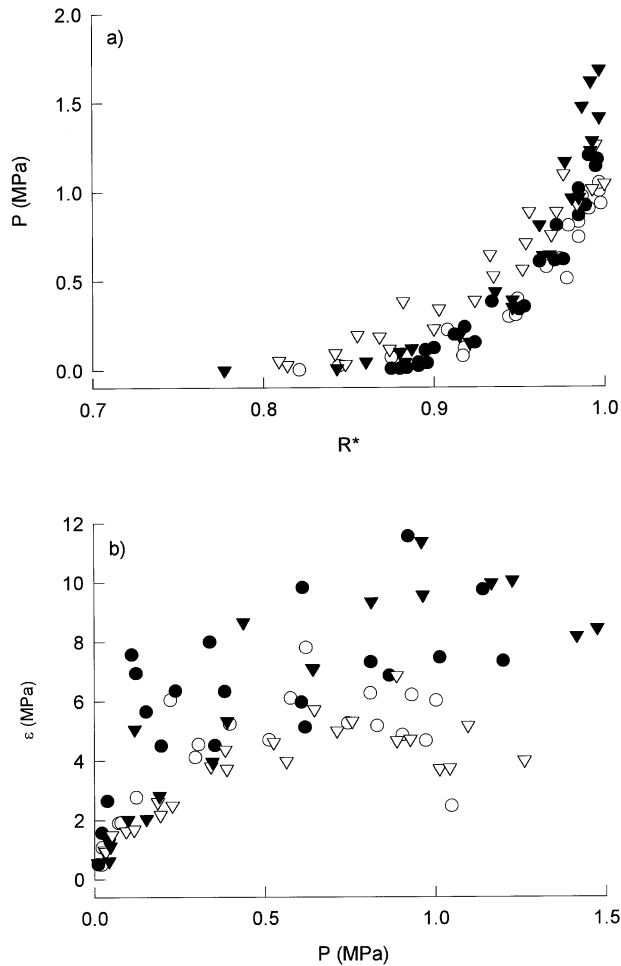| Treatment	Irrigated		Rainfed	
	E. globulus	*E. nitens*	*E. globulus*	*E. nitens*
September 1991	15.14	12.18	13.52	15.15
December 1991	10.65	10.36	10.11	11.88
September 1992	14.69	18.45	14.67	17.93
April 1993	9.72	14.10	8.71	15.09

Figure 4. (a) Turgor pressure (P) versus relative water content (R^*) and (b) bulk elastic modulus (ε) versus turgor pressure (P) for *E. globulus* (open symbols) and *E. nitens* (closed symbols) in the irrigated (circles) and rainfed (triangles) treatments in April 1993.

had hardened to a greater extent than *E. globulus*, and the degree of hardening between May and August was correlated with the minimum temperature experienced at the study sites. Frost is rare at the study site; however, eucalypts harden at temperatures just below 4 °C (Harwood 1980) and such temperatures were experienced during the study period. In several coniferous species, π is lowest at the end of winter or early spring and increases during the spring growth flush before declining again during the summer (Teskey et al. 1984, Ritchie and Shula 1984, Kubiske and Abrams 1991a, 1991b, Colombo and Teng 1992). Ritchie and Shula (1984) attributed the winter reduction in π_s and π_p of *Pseudotsuga menzeisii* (Mirb.) Franco needles (-2.3 and -3.8 MPa, respectively) to the accumulation of sugars and they attributed the summer minima (-2.5 and -3.5 MPa, respectively) to reduced symplasm volume. In contrast, there was no accumulation of osmotically active substances during winter in *Picea abies* (L.) Karst, and the observed reductions in π_s and π_p were attributed to a change in volume of the symplasm rather than to a change in solute content (Gross and Koch 1991). Because the magnitude of π at

any given R^* is directly proportional to solute content and inversely proportional to symplasmic volume (Tyree and Hammel 1972, Cheung et al. 1975), the observed decrease in π_s in *E. nitens* suggests an accumulation of solutes in the symplasm (Cheung et al. 1975). Increased W_d/W_t (results not shown) implies that part of the decrease in π_s was due to reduced symplasmic volume.

Water stress

After several cycles of drought, $\Delta\pi$ was significantly larger in R trees than in I trees, but neither π_s nor π_p was significantly influenced by water stress at any stage. There was no evidence of osmotic adjustment in either species when simultaneous p-v curves for I and R treatments were compared.

The absence of a pattern in osmotic or elastic adjustments in both *E. globulus* and *E. nitens* is consistent with recent reports (Munns 1988, Blake and Tschaplinski 1992) in which the adaptive significance of such adjustments is questioned, particularly in trees that store little water and where water uptake is driven almost exclusively by atmospheric evaporative demand (Schulte 1992). Thus, maintenance of gas exchange and elongation growth may not be closely correlated with turgor maintenance. For example, in wheat, stomatal closure in response to drying soil is independent of leaf turgor pressure (Gollan et al. 1986). Feng et al. (1994) concluded that leaf expansion is often poorly correlated with turgor pressure because cell wall properties are also altered in response to water stress. We found no evidence that tissue water relations acclimated to water stress in either species.

Differences in water relations between *E. globulus* and *E. nitens*

Throughout the study *E. globulus* tended to have lower ε_s, R^*_p and $d\Psi_l/dR^*$ and higher π_s and π_p than *E. nitens*. On January 28, 1992, and April 13, 1993, the effect of species on $d\Psi_l/dR^*$, R^*_p and π_s was significant ($P < 0.05$). Values of π_s varied between -1.1 and -1.4 MPa in *E. globulus* and between -1.1 and -2.1 MPa in *E. nitens*. The lowest value of π_s, when adjustments due to frost hardening were ignored, was -1.72 MPa. Values of π_s for the less mesic eucalypts *E. melliodora* A. Cunn. ex Schau. (-2.18 MPa) and *E. microcarpa* Maiden (-2.6 MPa) and *E. behriana* F. Muell., *E. microcarpa* and *E. polyanthemos* Schau. under well-watered (-1.74, -1.65 and -1.62 MPa, respectively) and water-stressed (-1.93, -1.98 and -2.14 MPa, respectively) conditions (Clayton-Greene 1983, Myers and Neales 1986) are more negative than those found here; however, our values are similar to those reported for *E. globulus* trees in Portugal (Correia et al. 1989). Ladiges (1975) reported a range of values for mature *E. viminalis* Labill., a mesic species, that are similar to those that we observed for *E. nitens*.

Differences in water relations between *E. globulus* and *E. nitens* were most pronounced near the end of the experiment on April 13, 1993, when $d\Psi_l/dR^*$ in the region of positive turgor was significantly greater for *E. nitens* than for *E. globulus* (Figure 3i). Thus for any given Ψ, R^* was significantly higher for *E. nitens* than for *E. globulus*. At the same time ε_s

was greater in *E. nitens* than in *E. globulus* and a reduction in R^* from 1 to 0.9 resulted in a corresponding reduction in turgor pressure of approximately 0.3 MPa in *E. globulus* and 1.8 MPa in *E. nitens* (Figure 4a). Stomatal conductance and growth were more sensitive to water stress in *E. nitens* than in *E. globulus* (White et al. 1994*a, 1994b*). Maintenance of high R^* at low Ψ_l in *E. nitens* therefore seems to be a means of avoiding desiccation, whereas in *E. globulus*, low ε facilitates maintenance of turgor over a wider range of R^* and allows *E. globulus* to tolerate moderate water stress. Feng et al. (1994) observed that the lower osmotic potentials in sudangrass than in spring wheat were associated with greater sensitivity of leaf expansion to water stress, and concluded that, in spring wheat, cell wall extensibility rather than osmotic properties adjusted in response to water stress. Robichaux et al. (1983) reported similar differences in the elastic properties of *Dubautia scabra* (DC.) Keck and *D. ciliolata* (DC.) Keck to those found for the eucalypts in our study. *Dubautia ciliolata* had a lower ε allowing it to maintain positive turgor at lower values of R^* than *D. scabra*.

In a study of variations in water relations among populations of *E. viminalis* Labill., seedlings from a low rainfall site had lower π, higher $d\Psi_l/dR^*$ and maintained transpiration at lower soil water contents than seedlings from more mesic environments (Ladiges 1974, 1975). Clayton-Greene (1983) reported higher values of $d\Psi_l/dR^*$ in the region of positive turgor for *E. microcarpa* (21.4 MPa) and *E. melliodora* A. Gunn. ex Schauer. (22.3 MPa) than for *Callitris columellaris* F.J. Muell. (13.0 MPa). Below R^*_p, $d\Psi_l/dR^*$ increased more in *C. columellaris* than in the eucalypts, indicating high desiccation resistance in *C. columellaris*. In *E. microcarpa* and *E. melliodora,* the high values of $d\Psi_l/dR^*$ in the region of positive turgor were associated with the maintenance of gas exchange at leaf water potentials as low as −5.5 MPa, whereas in *E. nitens* the same trait was associated with drought avoidance and low stomatal conductance (White 1994*b*). On April 13, 1993, there was no significant difference in the value of $d\Psi_l/dR^*$ below the turgor loss point between *E. globulus* and *E. nitens*; however, because of the higher slope above turgor loss point, the absolute value of water potential for any given R^* was significantly lower for *E. nitens* than for *E. globulus* (Figure 2i). This difference may result in greater resistance to desiccation in *E. nitens* than in *E. globulus* when exposed to severe water stress. The association of buffering by bound water with drought resistance reported by Gaff and Carr (1961) and Pook et al. (1966) seems less significant for *E. nitens* than resistance to desiccation resulting from elevated solute contents associated with cold tolerance.

Maintenance of positive turgor over a wider range of R^* by *E. globulus* than by *E. nitens* might be expected to result in higher growth rates in water-stressed *E. globulus*. Elongation growth is sensitive to changes in turgor pressure (Acevedo et al. 1971, Hsaio et al. 1976, Bradford and Hsiao 1982) and water stress resulted in a greater reduction in relative diameter growth in *E. nitens* than in *E. globulus* (White et al. 1994*a*). The drought-induced reduction in growth rate in *E. nitens* was probably mediated by a combination of lower stomatal con-

ductance and the effects of turgor pressure and cell wall elasticity on growth.

References

Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiol. 7:227–238.

Acevedo, E., T.C. Hsaio and D.W. Henderson. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631–636.

Attiwill, P.M. and K.A. Clayton-Greene. 1984. Studies of gas-exchange and development in a subhumid woodland. J. Ecol. 72:285–294.

Australian Bureau of Agricultural and Resource Economics. 1994. Forest products. Quarterly forest products statistics, March quarter 1994. Australian Bureau of Agric. and Resour. Econ., Canberra, 58 p.

Blake, T.J. and T.J Tschaplinski. 1992. Water relations. *In* Ecophysiology of Short Rotation Forest Crops. Eds. C.P. Mitchell, J.B. Ford-Robertson, T. Hinckley and L. Sennerby-Forsse. Elsevier, London, pp 66–94.

Bowman, W.D. and S.W. Roberts. 1985*a*. Seasonal and diurnal water relations adjustments in three evergreen chaparral shrubs. Ecology 66:739–742.

Bowman, W.D. and S.W. Roberts. 1985*b*. Seasonal changes in tissue elasticity in chaparral shrubs. Physiol. Plant. 65:233–236.

Bradford, K.J. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. *In* Encyclopedia of Plant Physiology, Volume 12b, Physiological Plant Ecology II, Water Relations and Carbon Assimilation. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, Berlin, pp 264–324.

Cheung, Y.N.S., M.T. Tyree and J. Dainty. 1975. Water relations parameters on single leaves obtained in a pressure bomb and some ecological interpretations. Can. J. Bot. 53:1342–1346.

Clayton-Greene, K.A. 1983. The tissue water relations of *Callitris columellaris, Eucalyptus melliodora* and *Eucalyptus microcarpa* investigated using the pressure-volume technique. Oecologia 57:368–373.

Colombo, S.J. and Y. Teng. 1992. Seasonal variation in the tissue water relations of *Picea glauca*. Oecologia 92:410–415.

Correia, M.J., F. Torres and J.S. Pereira. 1989. Water and nutrient supply regimes and the water relations of juvenile leaves of *Eucalyptus globulus*. Tree Physiol. 5:459–471.

Davie, A., K.A. Badcock and C.L. Beadle. 1993. 'Tiswat.Bas': a program to calculate simple water relations parameters from pressure chamber measurement. *In* Photosynthesis and Production in a Changing Environment. A Field and Laboratory Manual. Eds. D.O. Hall, J.M.O. Scurlock, H.R. Bolhar-Nordenkampf, R.C. Leegood and S.P. Long. Chapman and Hall, London, pp 456–462.

Draper, N.R. and H. Smith. 1981. Applied regression analysis, 2nd Edn. Wiley, New York, 709 p.

Feng, Y., X. Li and L. Boersma. 1994. Roles of osmotic adjustment and turgor potential in leaf area expansion. Physiol. Plant. 90:1–8.

Gaff, D.F. and D.J. Carr. 1961. The quantity of water in the cell wall and its significance. Aust. J. Biol. Sci. 14:299–310.

Gollan, T., J.B. Passioura and R. Munns. 1986. Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. Aust. J. Plant Physiol. 13:459–464.

Gross, K. and W. Koch. 1991. Water relations of *Picea abies*. I. Comparison of water relations parameters of spruce shoots examined at the end of the vegetation period and in winter. Physiol. Plant. 83:290–295.

Hallam, P.M., J.B. Reid and C.L. Beadle. 1989. Frost hardiness of commercial *Eucalyptus* species at different elevations. Can. J. For. Res. 19:1235–1239.

Harwood, C.E. 1980. Frost resistance of subalpine *Eucalyptus* species. I Experiments using a radiation frost room. Aust. J. Bot 28:587–599.

Hsiao, T.C., E. Acevedo, E. Fereres and D.W. Henderson. 1976. Water stress, growth, and osmotic adjustment. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 273:479–500.

Jones, M.M., N.C. Turner and C.B. Osmond. 1981. Mechanisms of drought resistance. *In* The Physiology and Biochemistry of Drought Resistance in Plants. Eds. L.G. Paleg and D. Aspinall. Academic Press, Sydney, pp 15–37.

Kirkpatrick, J. 1975. Geographical variation in *Eucalyptus globulus*. Bull. No. 47. Forestry and Timber Bureau, 64 p.

Kubiske, M.E. and M.D. Abrams. 1991*a*. Seasonal, diurnal and rehydration induced variation of pressure-volume relationships in *Pseudotsuga menziessii*. Physiol. Plant. 83:107–116.

Kubiske, M.E. and M.D. Abrams. 1991*b*. Rehydration effects on pressure-volume relationships in four temperate woody species: variability with site, time of season and drought conditions. Oecologia 85:537–542.

Ladiges, P.Y. 1974. Variations in drought tolerance in *Eucalyptus viminalis* Labill. Aust. J. Bot. 22:489–500.

Ladiges, P.Y. 1975. Some aspects of tissue water relations in three populations of *Eucalyptus viminalis* Labill. New Phytol. 75:53–62.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York, 697 p.

McDonald, A.J.S. and I. Stadenberg. 1993. Diurnal pattern of leaf extension in *Salix viminalis* relates to difference in leaf turgors before and after stress relaxation. Tree Physiol. 13:311–318.

Melkonian, J.J., J. Wolfe and P.L. Steponkus. 1982. Determination of the volumetric modulus of elasticity of wheat leaves by pressure-volume relations and the effect of drought conditioning. Crop Sci. 22:116–123.

Munns, R. 1988. Why measure osmotic adjustment? Aust. J. Plant Physiol. 15:717–726.

Myers, B.A. and T.F. Neales. 1986. Osmotic adjustment, induced by drought in seedlings of three *Eucalyptus* species. Aust. J. Plant Physiol. 13:597–603.

Myers, B.J. 1988. Water stress integral—a link between short-term and long-term growth. Tree Physiol. 4:315–324.

Parker, W.C. and S.G. Pallardy. 1987. The influence of resaturation method and tissue type on pressure-volume analysis of *Quercus alba* L. seedlings. J. Exp. Bot. 38:535–549.

Parker, W.C. and S.G. Pallardy. 1988. Leaf and root osmotic adjustment in drought-stressed *Quercus alba*, *Q. macrocarpa* and *Q. stellata* seedlings. Can. J. For. Res. 18:1–5.

Pederick, L.A. 1979. Natural variation in shining gum (*Eucalyptus nitens*). Aust. For. Res. 9:41–63.

Pook, E.W., A.B. Costin and C.W.E. Moore. 1966. Water stress in native vegetation during the drought of 1965. Aust. J. Bot. 14:257–267.

Ritchie, G.A. and R.G. Shula. 1984. Seasonal changes of tissue-water relations in shoots and root systems of Douglas-fir seedlings. For. Sci. 30:538–548.

Robichaux, R.H., K.E. Holsinger and S.R. Morse. 1983. Turgor maintenance in Hawaiian *Dubautia* species: the role of variation in tissue osmotic and elastic properties. *In* On the Economy of Plant Form and Function: Proc. Sixth Maria Moors Cabot Symp. Ed. T.J. Givnish. Cambridge University Press, London, pp 353–380.

Schulte, P.J. 1992. The units of currency for plant water status. Plant Cell Environ. 15:7–10.

Snedecor, G.W. and G.C. Cochran. 1967. Statistical methods. Iowa State University Press. Ames, Iowa, 593 p.

Teskey, R.O., T.M. Hinckley and C.C. Grier. 1984. Temperature induced changes in the water relations of *Abies amabilis* (Dougl.) Forbes. Plant Physiol. 74:77–80.

Turner, N.C. 1987. The use of the pressure chamber in studies of plant water status. *In* Proc. Int. Conference on Measurement of Soil and Plant Water Status. Utah State Univ., Logan, pp 13–24.

Tyree, M.T. and H.T. Hammel. 1972. The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. J. Exp. Bot. 23:267–282.

Tyree, M.T. and P.G. Jarvis. 1982. Water in tissues and cells. *In* Physiological Plant Ecology II, Encyclopedia of Plant Physiology, New Series, Vol 12 B. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler. Springer-Verlag, Berlin, pp 36–77.

White, D.A., C.L. Beadle, J.L. Honeysett and D. Worledge. 1994*a*. The effect of drought stress on height, diameter and leaf area index of *Eucalyptus globulus* and *E. nitens*. *In* Australian Tree Species Research in China. Ed. A.G. Brown. Australian Centre for International Agricultural Research Proc. No 48, Canberra, pp 71–76.

White, D.A., C.L. Beadle, J.L. Honeysett and D. Worledge. 1994*b*. Stomatal conductance of *Eucalyptus globulus* and *E. nitens* in irrigated and rainfed plantations. *In* Australian Tree Species Research in China. Ed. A.G. Brown. Australian Centre for Int. Agric. Res. Proc. No 48, Canberra, pp 56–63.