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Responses to water stress in two *Eucalyptus globulus* clones differing in drought tolerance

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Summary We evaluated drought resistance mechanisms in a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus* Labill. based on the responses to drought of some physiological, biophysical and morphological characteristics of container-grown plants, with particular emphasis on root growth and hydraulic properties. Water loss in excess of that supplied to the containers led to a general decrease in growth and significant reductions in leaf area ratio, specific leaf area and leaf-to-root area ratio. Root hydraulic conductance and leaf-specific hydraulic conductance decreased as water stress became more severe. During the experiment, the drought-resistant CN5 clone maintained higher leaf water status (higher predawn and midday leaf water potentials), sustained a higher growth rate (new leaf area expansion and root growth) and displayed greater carbon allocation to the root system and lower leaf-to-root area ratio than the drought-sensitive ST51 clone. Clone CN5 possessed higher stomatal conductances at moderate stress as well as higher hydraulic conductances than Clone ST51. Differences in the response to drought in root biomass, coupled with changes in hydraulic properties, accounted for the clonal differences in drought tolerance, allowing Clone CN5 to balance transpiration and water absorption during drought treatment and thereby prolong the period of active carbon assimilation.

Keywords: acclimation, allocation, hydraulic properties, root growth, water stress.

Introduction

Economically, *Eucalyptus globulus* Labill. is one of the most important members of its genus because of its high growth rate and superior pulp properties. More than 700,000 ha have been planted with *E. globulus* in Portugal. As a result of a combination of breeding programs and improved techniques for the rooting of cuttings, Portuguese plantations have recently been established with clones selected for their high growth rates, high pulp yield and environmental adaptability.

Portugal has a Mediterranean climate with a severe summer drought, even though winter rain may be abundant. To develop improved breeding programs, it is important to gain a better understanding of the physiological responses to drought of clones selected for drought tolerance. Plant responses to water stress involve morphological and biochemical changes that lead first to acclimation and later, as water stress becomes more severe, to functional damage and the loss of plant parts (Chaves et al. 2003). During the acclimation phase, water stress typically results in slower growth rates because of inhibition of cell expansion and reduced carbon assimilation (Osório et al. 1998*a*, 1998*b*). Aboveground plant growth can be further decreased by changes in carbon partitioning that favor root system development (Sharp and Davies 1979), mainly because root growth is less affected by drought than shoot growth (Sharp 1990, Hsiao and Xu 2000). A change in the balance between leaf surface (highly sensitive to drought) and root surface (less sensitive to drought) has obvious advantages for survival, because it permits water savings in relation to water uptake potential. Improved water balance also depends on the capacity to transport water through the plant from roots to leaves. As water stress increases in severity, plant survival depends on the maintenance of xylem integrity as a hydraulic conducting system (Sperry et al. 2002). Root and leaf-specific conductances are generally lower in drought-adapted species than in more water-demanding species (Nardini et al. 1999). There are also differences in xylem cavitation vulnerability to drought, which is lower (occurs at more negative water potentials) in drought-tolerant plants than in more mesophytic plants (Tyree and Ewers 1991, Tyree 1999).

Plant responses to drought depend heavily on the root-to-shoot balance; however, shoots and leaves have been studied in greater detail than roots. For the plant to acclimate to water stress and survive drought, roots have to maintain a viable water flow path along the xylem, and root cells have to withstand some water stress and grow into new unexploited soil to absorb water. Because the roles of root and leaf responses to drought in *E. globulus* have not been fully elucidated, we evaluated the relationship between water supply and demand and the hydraulic properties of two *E. globulus* clones differing in drought sensitivity. Specifically, we studied the drought responses of some physiological, biophysical and morphological plant variables, with particular emphasis on hydraulic properties and root growth.

Materials and methods

Plant materials and treatments

We selected a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *E. globulus*. Based on observations in field plantations subjected to summer drought, Clone CN5 has 29% higher survival and 41% higher growth rates (volume ha^{-1}) than Clone ST51. Rooted cuttings of both clones were grown in plastic containers filled with peat (60%) and Styrofoam beads (40%), and transplanted after 11 months to 10-l pots filled with a fine sandy soil. One month after transplanting, 32 cuttings per clone were transferred from the nursery to a controlled-environment greenhouse that provided a day/night temperature of 22/16 °C and relative humidity of about 60%. The mean reduction in solar irradiance in relation to outdoor conditions on sunny days was about 25% (Faria et al. 1996). Sixteen cuttings per clone were assigned to either a well-watered regime (WW; water supplied to equal transpirational losses) or a water-stress regime (WS; water supplied equal to 50% of transpirational losses). Each pot was enclosed in a dark plastic bag tied to the stem to prevent soil evaporation. The experiment lasted 7 weeks (September 9 to October 29, 2002). All plants were watered to runoff on the first day and then twice per week (Mondays and Fridays). To avoid effects caused by microenvironmental differences (light gradient), the plants were sorted by treatment and moved to the neighboring position every watering day.

Measurements

Transpiration rate in every plant per clone and treatment (n = 16) was determined by measuring differences in pot weight between successive waterings. Stomatal conductance (g_s) was measured in fully expanded leaves at midday (solar time) with a steady-state porometer (Li-1600, Li-Cor, Lincoln, NE). The leaf-to-air vapor pressure deficit during g_s measurements varied between 1.61 and 2.84 kPa. Leaf xylem water potential (predawn, Ψ_{pd}, and midday, Ψ_{md}) was measured with a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR). Measurements of g_s, Ψ_{pd} and Ψ_{md} were made on six plants per treatment (n = 6) four times during the experiment (Weeks 1, 3, 5 and 7). At Weeks 1, 5 and 7, stem xylem water potential (Ψ_x) was measured at midday in attached leaves (n = 6) that were sealed in aluminum bags at dawn (Jones 1992). Hydraulic conductances of the plant–soil system (K_{sp}) and leaf (K_l) were calculated on a leaf area basis, assuming Ψ_{pd} is an estimate of the soil water potential (Jones 1992, Saito et al. 2003):

$$K_{sp} = \frac{E}{\Psi_{pd} - \Psi_{md}} \text{ and } K_l = \frac{E}{\Psi_x - \Psi_{md}}$$

where E is transpiration rate ($m^3\ m^{-2}\ s^{-1}$) through the system measured between predawn and midday.

Plant biomass was evaluated at Weeks 1, 5 and 7 by destructively sampling five plants per treatment (n = 5). These plants were used to determine morphological parameters (height, diameter, number of branches, biomass partition, leaf area and root length). Specific leaf area (SLA) was calculated as the ratio between leaf area and leaf dry mass (DM), and leaf area ratio (LAR) was calculated as the ratio between total leaf area and total plant DM. All dry mass values were obtained after 48 h at 80 °C. Leaves and roots were scanned and leaf area and root parameters (length, diameter, area) were calculated with Delta T scan software (Delta-T Devices, Hoddeson, U.K.). Roots were assumed to be cylindrical and root surface area was calculated by multiplying the projected area by π.

Nondestructive measurements of leaf expansion on selected leaf blades (from the second leaf pair) were recorded every 3 days on six plants per treatment (n = 6), from Day 12 to Day 47 (one stem leaf per plant). When the selected leaves reached full expansion (during Week 5), the measurements began again with the youngest expanding leaves.

Root water flow

Root water flow was evaluated at Weeks 1, 5 and 7 in the same root systems as the biomass study (n = 5). Steady-state water flow rates in whole root systems (Q_v; $mm^3\ s^{-1}\ plant^{-1}$) were measured by the hydrostatic pressure method (Wan et al. 1999, Wan and Zwiazek 1999) with some modifications. A rigid plastic cylinder was inserted into a pressure chamber and filled with distilled water. The plant stem was cut 20 mm above the cutting end and the root system immediately immersed in distilled water in the pressure chamber. Samples were pressurized at 0.3, 0.4, 0.5, 0.6 and 0.7 MPa. Flow was measured by collecting the exudate for 5 min at each pressure in a pre-weighed capillary vial containing cotton wool that was placed over the cut stem protruding through the stopper in the pressure chamber. Volume flow density (J_v; $m^3\ m^{-2}\ s^{-1}$) was determined as a steady-state flow rate per unit of root surface area. Root hydraulic conductance (K; $mm^3\ s^{-1}\ MPa^{-1}$) was calculated as the slope of pressure versus flow rate where the relationship was linear. Because this method measures hydraulic conductance on branched systems with distal components present in parallel, hydraulic conductivity cannot be accurately calculated (Kolb et al. 1996). Measurements were standardized for the size of the root system by dividing K by the total leaf area of the plant, thereby obtaining the leaf-specific hydraulic conductance (LSC; $m\ s^{-1}\ MPa^{-1}$).

Data analysis

Data were subjected to two-way analysis of variance (ANOVA) to test for the effects and interactions of watering treatment and clone, using the STATISTICA (Version 6, 2001, StatSoft, Tulsa, OK) data analysis software system. All variables were tested for normality and homogeneity of variances. Differences were considered statistically significant at $P \leq 0.05$.

Results

Transpiration

Under well-watered conditions, E per plant increased throughout the experiment (Figure 1A). Well-watered ST51 plants, with their larger leaf area, exhibited a higher E per plant than the CN5 plants. However, on a leaf area basis, the clones had similar E values (Figure 1B). In water-stressed plants of both clones, E increased until Day 14, and then decreased until the end of the experiment (Figures 1A and 1B).

Plant water status and stomatal conductance

Plant water status was assessed by measuring Ψ_{pd} and Ψ_{md}. Well-watered plants of both clones maintained Ψ_{pd} at about –0.30 MPa throughout the experiment, whereas Ψ_{pd} of water-stressed plants declined throughout the experiment and, in Week 7, it fell to –1.71 ± 0.06 and –2.43 ± 0.27 MPa in CN5 and ST51, respectively. In both clones, the leaf water potential curves of the water-stressed plants can be divided into two phases (Figures 2A and 2B). In the first phase, moderate water stress developed slowly from the beginning of the experiment until Week 5. During the second phase, from Week 5 to Week 7, water stress became increasingly more severe.

Midday leaf water potential did not vary significantly in well-watered plants, whereas by the end of the experiment, it declined to –2.46 ± 0.05 and –3.26 ± 0.26 MPa in water-stressed plants of CN5 and ST51, respectively (Figure 2B). Not only were the differences between watering regimes statistically significant ($P < 0.001$), but there were also significant differences between clones. Clone CN5 had higher Ψ_{pd}

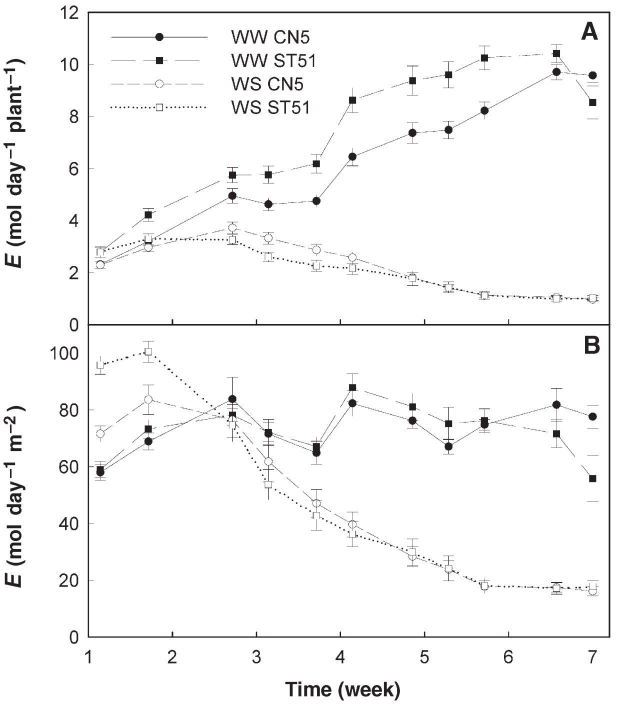

Figure 1. Leaf transpiration rate (E) expressed on a per plant basis (A) and leaf area basis (B) in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE (n = 11–16).

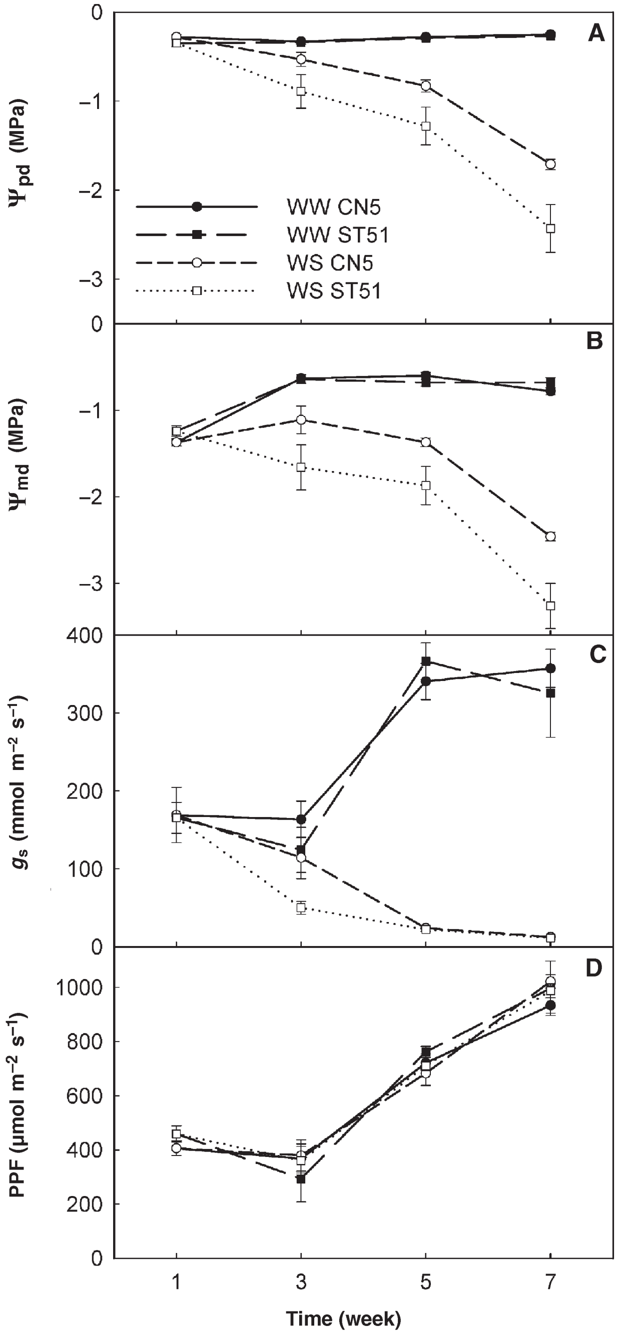

Figure 2. Predawn leaf water potential (Ψ_{pd}; A), midday leaf water potential (Ψ_{md}; B), midday stomatal conductance (g_s; C) and photosynthetic photon flux (PPF; D) in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE (n = 6).

Table 1. Total biomass, leaf area, number of branches, total root length, dry mass partitioning (percent of total biomass) and leaf growth analysis in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus* evaluated at the end of experiment (Week 7). Data are means ± SE ($n = 5$). Symbols: *, **, *** represent statistical significance at $P = 0.05$, 0.01 and 0.001, respectively; and ns = nonsignificant at $P = 0.05$.

Morphological characteristics	WW CN5	WW ST51	WS CN5	WS ST51	Significance of 2-way ANOVA		
					Clone (C)	Watering regime (W)	C × W
Total biomass (g)	15.4 ± 1.1	18.7 ± 1.6	9.2 ± 0.6	9.3 ± 0.4	ns	***	ns
Leaf area (m^2)	0.12 ± 0.007	0.16 ± 0.008	0.05 ± 0.005	0.05 ± 0.003	**	***	**
Number of branches	10.8 ± 0.6	10.0 ± 0.3	6.2 ± 0.7	5.6 ± 0.5	ns	***	ns
Total root length (m)	111 ± 10	121 ± 21	98 ± 13	59 ± 4	ns	*	ns
Dry mass partitioning							
Stem (%)	27.8 ± 1.5	23.8 ± 1.2	31.7 ± 1.3	35.4 ± 1.3	ns	***	*
Branches (%)	5.3 ± 0.22	6.4 ± 0.24	1.7 ± 0.63	2.8 ± 0.52	*	***	ns
Leaves (%)	51.4 ± 1.6	56.0 ± 1.1	46.8 ± 2.3	48.4 ± 1.3	ns	**	ns
Root (%)	15.5 ± 0.8	13.7 ± 1.2	19.8 ± 1.7	13.5 ± 0.8	**	ns	ns
Leaf growth analysis							
Leaf area ratio ($m^2\ kg^{-1}$)	8.1 ± 0.3	8.8 ± 0.5	5.8 ± 0.3	5.7 ± 0.3	ns	***	ns
Specific leaf area ($m^2\ kg^{-1}$)	15.6 ± 0.3	15.7 ± 0.6	12.4 ± 0.3	11.8 ± 0.4	ns	***	ns
Leaf area/root area	0.98 ± 0.10	1.12 ± 0.13	0.55 ± 0.12	0.76 ± 0.08	ns	**	ns

and Ψ_{md} than ST51 during the experiment ($P < 0.05$). Water-stressed ST51 plants exhibited a greater difference between Ψ_{pd} and Ψ_{md} than water-stressed CN5 plants until Week 5, indicating that they experienced more severe stress during the day.

The fall in Ψ_{pd} and Ψ_{md} in water-stressed plants of both clones was concomitant with a decline in g_s from 167 mmol $m^{-2}\ s^{-1}$ in Week 1 to about 12 mmol $m^{-2}\ s^{-1}$ in Week 7 (Figure 2C). Water-stressed ST51 plants displayed significantly lower g_s than water-stressed CN5 plants in Week 3 ($P < 0.05$). Well-watered plants of both clones had similar g_s that increased to about 342 mmol $m^{-2}\ s^{-1}$ at Week 7. The increase in the g_s of well-watered plants from Week 3 to Week 5 was probably associated with changing light conditions because it closely followed the PPF curve (Figure 2D).

Growth response

Water stress led to a general decrease in growth that was reflected in reductions in total biomass, leaf area, number of branches and total root length (Table 1).

Under well-watered conditions, Clone ST51 had a greater leaf area than Clone CN5 (Figure 3A), which explains its higher growth rate. Despite having similar leaf areas at the beginning of the experiment (Figure 3A), Clone CN5 had a greater total root length than Clone ST51 ($P < 0.05$). At Week 5, both clones displayed greater increases in root length in the water-stress regime than in the well-watered regime (59 and 16% in CN5 and ST51, respectively) ($P < 0.05$). Thereafter, water-stressed CN5 plants showed continual increases in root growth (32 and 66% at Weeks 5 and 7, respectively), whereas root growth ceased completely after Week 5 in water-stressed ST51 plants (Figure 3B).

At the end of the 7-week experiment, water-stressed plants of both clones had significantly decreased the proportion of biomass allocated to branches and leaves (Table 1). On the other hand, the water stress treatment caused an increase in the ratio of stem axis biomass to total biomass, particularly in ST51 (11.6%). In addition to differences in responses to water availability, the clones differed in biomass partitioning. The

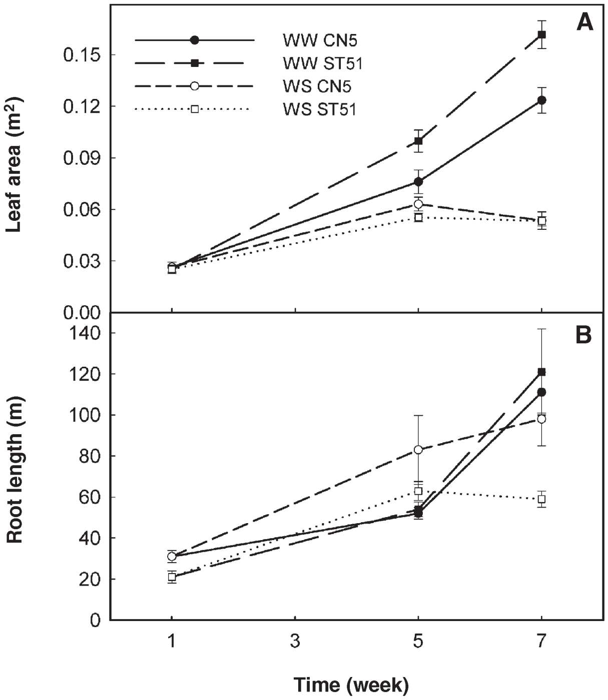

Figure 3. Total leaf area (A) and total root length (B) in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE ($n = 5$).

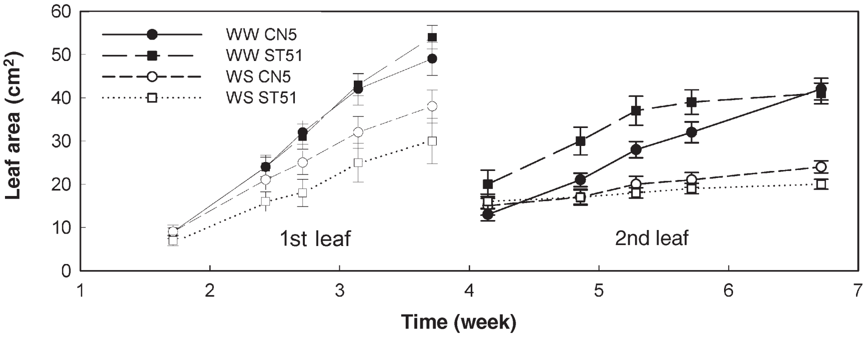

Figure 4. Leaf area expansion measured in the first and second leaves that appeared after the beginning of the experiment in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE ($n = 6$).

CN5 plants invested a larger proportion of total dry mass in roots than the ST51 plants (particularly water-stressed plants), whereas ST51 plants invested a larger proportion of total dry mass in leaves and branches, especially under well-watered conditions.

At Week 7, decreases in leaf area ratio and specific leaf area were observed in water-stressed plants of both clones, with no statistically significant clonal differences (Table 1). As a result of restrained leaf area growth and sustained root growth in response to drought (Figure 3), the leaf area/root area ratio decreased to 0.55 in CN5 and to 0.76 for ST51.

Leaf growth was strongly correlated with water supply (Figure 4). The effect of water shortage on leaf area expansion was detectable in the first phase of the experiment (up to Week 4), with a decrease of 24 and 44% in clones CN5 and ST51, respectively ($P < 0.001$). In this phase of moderate stress, leaf area expansion was 25% greater for water-stressed CN5 plants than for water-stressed ST51 plants. In the second phase (from Week 5 to Week 7), when severe water stress developed, leaf growth decreased by 44 and 53% in water-stressed plants of CN5 and ST51, respectively ($P < 0.001$).

Hydraulic properties

Root water flux (J_v) decreased from the beginning of the experiment, particularly in plants in the water stress treatment (Figure 5A), and was strongly correlated with root growth. The watering regime had a significant effect on J_v, with higher values for well-watered plants ($P < 0.001$).

Root hydraulic conductance (K) was reduced by soil water deficits in Weeks 5 and 7 ($P < 0.01$ and $P < 0.001$, respectively) (Figure 5B). Although there was no significant clone effect on K, there was a significant interaction between clone and treatment effects ($P < 0.05$), so that, by Week 7, ST51 plants exhibited the highest (+36%) and the lowest (–45%) K in well-watered and water-stressed conditions, respectively. At Week 7, both CN5 and ST51 water-stressed plants displayed a decrease in K (–27 and –35%, respectively) compared with values at Week 5.

Throughout the experiment, LSC decreased in plants in all treatments (Figure 5C). However, LSC declined in well-watered plants because of a large increase in leaf area, whereas it declined in water-stressed plants because of reduced K. During drought treatment, Clone CN5 maintained higher LSC than Clone ST51 (+43% at Week 5 and +79% at Week 7).

In well-watered plants, hydraulic conductance of the soil–plant system (K_{sp}) remained stable throughout the experiment, although Clone ST51 clone had higher mean values than Clone CN5 (0.54×10^{-7} versus 0.69×10^{-7} m s^{-1} MPa^{-1} in

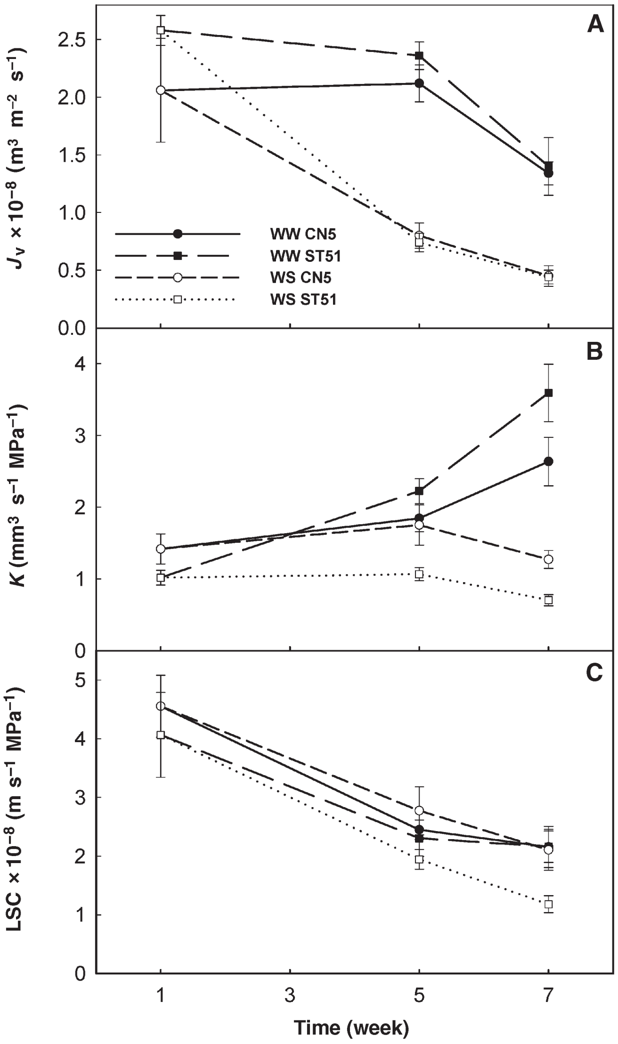

Figure 5. Root water flux (J_v; A), root hydraulic conductance (K; B) and leaf specific conductance (LSC; C) in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE ($n = 5$).

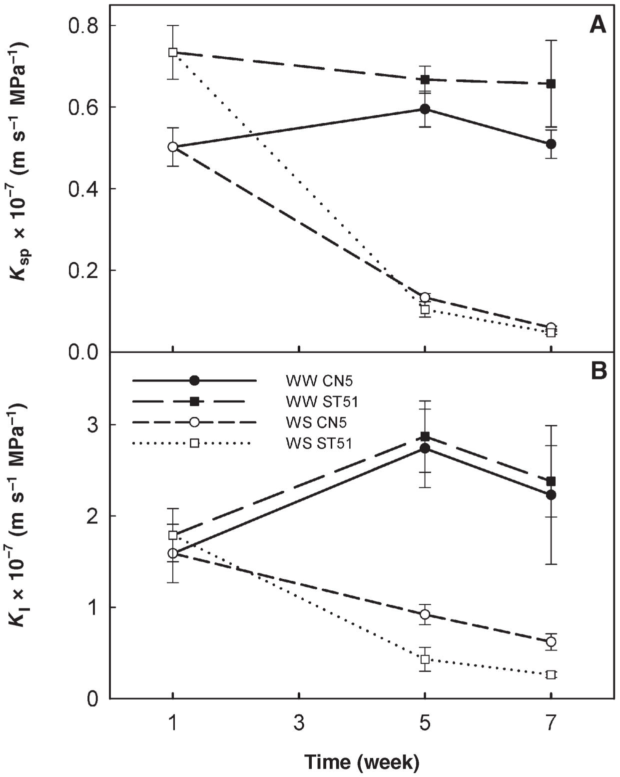

Figure 6. Hydraulic conductance of the soil–plant system (K_{sp}; A) and leaf (K_l; B) in well-watered (WW) and water-stressed (WS) plants belonging to a drought-tolerant clone (CN5) and a drought-sensitive clone (ST51) of *Eucalyptus globulus.* Data are means ± SE ($n = 6$).

CN5 and ST51, respectively) (Figure 6A). In both clones, K_{sp} decreased with increasing soil water stress at Weeks 5 and 7 ($P < 0.001$); however, water-stressed CN5 plants displayed a smaller decrease in K_{sp} in the first 5 weeks and maintained higher values until Week 7 than water-stressed ST51 plants (on average, +26%).

The development of drought stress led to comparable trends in leaf conductance (K_l) in both clones (Figure 6B). There were significant treatment differences in K_l at Weeks 5 and 7 ($P < 0.001$ and $P < 0.01$, respectively). Nevertheless, water-stress had a greater effect on K_l of ST51 plants compared with CN5 plants at both Weeks 5 and 7 (–54 and –58%, respectively).

Discussion

We observed a reduction of about 46% in mean total biomass growth in young container-grown *Eucalyptus* plants when water supplied to the pots was only 50% of plant water use. This treatment resulted in a 63% decrease in total leaf area and a 45% decrease in the ratio of leaf area to total biomass relative to values for well-watered control plants. In addition to the decrease in leaf area, stomata of water-stressed plants closed for longer each day, contributing to decreased growth as a result of reduced carbon assimilation (Figures 1 and 2C).

Acclimation to slowly declining soil water availability occurs before the onset of tissue dehydration and results in physiological and morphological adjustments that improve plant water balance (Pereira and Chaves 1993). We distinguished an initial period of slowly developing water stress during the first 5 weeks of treatment when the tested clones responded differently. Stomatal conductance in ST51 plants fell steeply in response to 3 weeks of moderate water stress, following which the plants entered a period of severe water stress. As a consequence, the plants had only limited time for drought acclimation. A plant's ability to prolong moderate stress or postpone severe stress and thereby maintain a more favorable leaf water status during the first phase of a drought may enable the plant to avoid damage by severe water stress later on. We observed that, in response to water stress, the drought-tolerant CN5 clone had a significantly smaller difference between Ψ_{pd} and Ψ_{md} than the drought-sensitive ST51 clone, leading to a more favorable leaf water status as a result of a higher water supply for a given stomatal conductance (Figure1). In addition, under drought conditions, CN5 plants had noticeably greater root length (Figure 3B) and rate of new leaf expansion (Figure 4) than ST51 plants. The maintenance of a continued higher growth rate in young leaves of CN5 plants under drought conditions compared with ST51 plants may have contributed to recovery of carbon assimilation after rehydration (data not shown), because the photosynthetic capacity of *E. globulus* is robust during periods of drought (Quick et al. 1992) and younger leaves are generally less affected by drought than older leaves (Pereira and Chaves 1993).

Until Week 5, increases in root length were greater in water-stressed plants than in well-watered plants of both clones (Figure 3B), indicating that water stress had less effect on root growth than on leaf growth (Sharp 1990, Hsiao and Xu 2000). Similar results were reported by Blum et al. (1983) and by McDonald and Davies (1996). Enhanced biomass partitioning to roots may result from a drought-induced reduction in the sink strength of the aboveground plant tissues, making more assimilates available for root growth.

Compared with the drought-sensitive ST51 clone, the drought-tolerant CN5 clone had a higher investment in root system development before drought was imposed (assessed on Day 1 of the experiment), suggesting that this characteristic partially accounts for the enhanced drought tolerance exhibited by this genotype. In addition, water-stressed CN5 plants showed continually greater root growth until Week 7, whereas root growth of water-stressed ST51 plants ceased completely after Week 5 (Figure 3B). Thus, we conclude that the initially larger root system of Clone ST51, coupled with its ability to rapidly increase the proportion of biomass allocated to the root, resulting in optimization of the relationship between transpiration area and absorption area under drought conditions, explains its superior drought resistance compared with plants of Clone ST51. Moreover, we predict that, in field conditions where soil volume is unrestricted, the benefits of a larger investment in root extension under drought conditions will be enhanced because Clone CN5 will be able to access as yet unexplored volumes of soil, resulting in increased water uptake.

Water transport in trees is regulated by the hydraulic conductance of the soil–root–shoot–leaf pathway. Because stomatal conductance and photosynthesis depend on the transport of water from soil to leaf to atmosphere, changes in whole-tree hydraulic conductance may affect gas exchange (Tyree and Ewers 1991, Hubbard et al. 1999). It is possible that, with the intensification of water stress after Week 5, a hydraulic limitation developed—mainly in Clone ST51—that considerably reduced young leaf expansion and root growth. During drought, ST51 plants displayed a greater restriction in water supply to leaves, with both lower K and LSC values (Figures 5B and 5C) and lower K_{sp} and K_l values (Figure 6) than CN5 plants.

Several studies have shown that changes in whole-plant hydraulic conductance affect g_s and photosynthesis (Bond and Kavanagh 1999, Wan et al. 1999, Brodribb and Field 2000, Hubbard et al. 2001). In our study, although midday g_s was low after Week 5 in water-stressed plants of both clones (Figure 2C), plants with a more limited water supply closed their stomata earlier in the day than plants with a greater water supply. When measured in the afternoon in Week 5, g_s of water-stressed ST51 plants was 45% lower than in water-stressed CN5 plants (data not shown), indicating a difference between the clones in hydraulic systems. In well-watered conditions, despite similar total root system length, Clone ST51 exhibited higher K and K_{sp} in both Weeks 5 and 7 compared with Clone CN5. This matches the general findings of lower root and shoot hydraulic conductances in drought-adapted species (Nardini et al. 1999). However, we cannot disregard the possibility that genotypic differences in root architecture influenced the hydraulic systems.We can assume that water-stressed plants were subjected to a certain loss in conductance as a result of embolism or cavitations, or both, given both the low Ψ_x values that were attained and the higher K values exhibited by well-watered plants throughout the experiment. At Week 5, for similar root system dimensions between clones (Figure 3B), water-stressed Clone ST51 displayed a significantly lower K (–52%), presumably as a result of cavitation. Compared with water-stressed CN5 plants, water-stressed ST51 plants displayed lower stem xylem pressures (–33% at Week 5) and lower K values. We speculate that, compared with Clone CN5, Clone ST51 suffered from a greater cavitation-induced loss in conductance, which took place before Week 5. Differences in vulnerability to cavitation have been associated with drought tolerance both between species (e.g., Tyree and Ewers 1991, Cochard 1992) and between genotypes of the same species (e.g., Tognetti et al. 1997, Vander Willigen and Pammenter 1998).

In summary, our data show that successful drought acclimation in *E. globulus* clones may be the result of different processes, including changes in root biomass coupled with changes in hydraulic properties of the root systems. A greater allocation of biomass to roots and higher hydraulic conductances made it possible to prolong the water-stress-free period for active carbon assimilation in the clone that was least susceptible to drought. These developmental changes, which maintained the balance between transpiration and absorption areas when soil water availability declined, seemed to be the key determinant of performance under drought conditions.

Acknowledgments

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