

Xylem cavitation, leaf growth and leaf water potential in *Eucalyptus globulus* clones under well-watered and drought conditions

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Abstract. Leaf growth, predawn leaf water potential (Ψ_{pd}), evapotranspiration, stem maximum permeability, and its percentage loss of hydraulic conductivity (PLC) were measured in rooted cuttings of selected clones of *Eucalyptus globulus* Labill. subjected to well-watered and drought conditions. Drought significantly reduced evapotranspiration, leaf growth and maximum permeability. *E. globulus* clones lost up to 70% of conductivity at values of Ψ_{pd} less negative than -1 MPa. PLC values higher than 85% could not be measured without causing leaf shedding. The coefficient related to the slope of the vulnerability curves ranged from 1.52–2.23. The lowest value was measured in the most drought-resistant clone, as estimated from field trials. Plants from this clone displayed higher drought-induced reductions in maximum permeability than plants from other clones, had significantly smaller leaves and maintained higher values of predawn leaf water potential as soil water content (SWC) declined.

Keywords: drought resistance, leaf growth, leaf size, leaf water potential, maximum permeability, xylem vulnerability to cavitation.

Introduction

Xylem cavitation during drought has been considered to be one of the most serious causes of productivity loss in drought-prone environments (Lo Gullo and Salleo 1993; Tognetti *et al.* 1998). The loss of hydraulic conductivity of the xylem is related to the degree of water stress in leaves and thus, to reduced cell expansion, stomatal conductance and photosynthesis (Tyree *et al.* 1993). Stomatal control has been related to cavitation threshold in several tree species (Cochard *et al.* 1996; Bond and Kavanagh 1999; Salleo *et al.* 2000). Jones and Sutherland (1991) suggested that plants may exhibit two different responses to water deficit: (1) stomatal conductance is reduced to avoid catastrophic cavitation and (2) stomatal conductance, and thus, transpiration, is maximized to obtain the highest production in the short term, and plants operate near the boundary of xylem safety. Both responses have been found in different tree species (Bond and Kavanagh 1999). Stomatal closure may reduce photosynthesis and thus, growth and productivity in the short term. Maintaining high stomatal conductance at the expense of some cavitation may result in the loss of distal organs (i.e. drought-induced leaf shedding) to ensure stem xylem safety and survival (Tsuda and Tyree 1997; Rood *et al.* 2000). This process has been called hydraulic

segmentation after Zimmermann (1983) and may cause a long-term loss of growth and productivity.

Xylem cavitation occurs when air enters water-filled xylem conduits through the inter-conduit pit membranes. The extent of xylem cavitation depends on (a) the balance between the rate of water loss by transpiration and the amount of water taken up by the roots and (b) several xylem traits such as the diameter and length of the xylem conduits and the flexibility of the pit membranes. Recent studies show an increasing body of evidence of variation in xylem vulnerability to cavitation according to environmental conditions, both among and within tree species (Cochard 1992; Franks *et al.* 1995; Tognetti *et al.* 1997; Kavanagh *et al.* 1999; Maherali and DeLucia 2000). Genotypic variation in xylem vulnerability to cavitation has been found among clones derived from crosses between different species (Neufeld *et al.* 1992; Pammenter and Vander Willigen 1998), but little is known about intra-specific differences among clones from a single tree species.

Eucalyptus globulus is one of the most widely-used species of the genus in forest plantation around the world (Eldridge *et al.* 1993), because of its rapid growth and pulping features, and it plays an important role in cellulose production in Spain. Survival and growth of *E. globulus* are

Abbreviations used: K_i , initial hydraulic conductivity; K_m , maximum hydraulic conductivity; PLC, percentage loss of hydraulic conductivity; SWC, soil water content; Ψ_{pd} , predawn leaf water potential.

strongly limited under Mediterranean climates. The use of morphophysiological traits in breeding for improved drought resistance has been considered worthy (Turner 1997) but it is not readily used in practice. In the scope of the breeding program established for *E. globulus* in Spain, we are working on a test for early selection of drought resistant clones using morphophysiological traits. We wanted to know whether xylem cavitation, estimated through the vulnerability curves, could be used as a selection trait in this test. Thus, the aim of this study was to investigate the variability in cavitation between drought-resistant and drought-sensitive *E. globulus* clones and its relationship to other components of drought resistance. For this purpose, rooted cuttings from four selected clones were grown in a greenhouse experiment and leaf growth, leaf water potential, evapotranspiration and xylem vulnerability to cavitation were assessed under well-watered and drought conditions.

Materials and methods

Plant material and growth conditions

Rooted cuttings were obtained from Empresa Nacional de Celulosas (ENCE), Spain. The four pure *Eucalyptus globulus* Labill. clones chosen for the present study (115.18, 115.7, 115.21 and 115.16) are currently used in commercial plantations in south-western Spain. Field trials established in south-western Spain showed that mean volume at age five years was highest in clone 115.16 and lowest in clone 115.21. Clones 115.7 and 115.18 exhibited an intermediate response (I. Cañas, ENCE, unpublished data).

Rooted cuttings were transplanted at the nine leaf pair stage to 3-L pots. Soil medium consisted of 1250 g (dry weight) of a 3/1 (v/v) peat/sand mixture. Ten rooted cuttings per clone were harvested at the time of transplanting (day 0) and leaf area and total dry weight were determined. At the same time, another 40 replicate cuttings of each clone were placed in a greenhouse following a randomized block design. Plant position was changed once a week to limit the influence of environmental heterogeneity. During the experiment, temperatures ranged from 10–27°C and maximum photosynthetically active radiation at the plant apex was 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (LI-185B, Li-Cor Inc., Lincoln, NE). Supplemental metal halide lamps provided a 13-h photoperiod. A water-soluble fertilizer (Peters 20:7:19) was applied periodically according to an exponential schedule, with a nitrogen relative addition rate of 0.045 $\text{g g}^{-1} \text{d}^{-1}$.

After a four-week acclimation period in the greenhouse, the plants were divided into two groups (twenty plants each) and two watering treatments were applied from this time (days 28–68). Every plant was periodically watered to a constant weight, in such a way that soil water content (% dry weight) was kept around 60% and 40% for plants in the well-watered and drought treatment respectively. Evapotranspiration (water loss by soil evaporation plus shoot transpiration) was estimated by weighing the pots once or twice a week.

Leaf growth

Non-destructive measurements of leaf growth were obtained weekly by drawing all the growing leaves of 15 plants per clone on tracing paper between days 7–68 of the experiment. These plants were randomly chosen; seven of them belong to the drought treatment and eight to the well-watered treatment. An Image Analyser (LI-3000, Li-Cor Inc.) was used to estimate leaf area from leaf drawings. New leaves of less than 5 cm^2 could not be drawn without causing some injury. These leaves

were just counted to calculate the average number of new leaves between consecutive measurements.

Cavitation measurements

Xylem embolism was quantified for stem segments by determining the hydraulic conductance (mass flow rate of water through the segment divided by the pressure gradient along the segment) of the xylem before and after the removal of air emboli by the flushing method (Sperry *et al.* 1988). Hydraulic conductivity was calculated as the hydraulic conductance multiplied by the length of the stem segment.

Hydraulic conductivity measurements started on day 68 and were carried out on 14–20 plants per clone and treatment. Plants were brought to the laboratory from the greenhouse the afternoon prior to hydraulic conductivity measurements, and kept in the dark, in a growth chamber at 20°C. The following morning, each plant was weighed with its container, and predawn leaf water potential (Ψ_{pd}) was measured in two leaves of the fourth–sixth whorl (counted from the apex) with a pressure chamber (PMS Instrument Co., Corvallis, OR). As juvenile *E. globulus* leaves are sessile, the main vein was used as a petiole by excising two pieces of the leaf lamina.

Afterwards, the stem of each rooted cutting was cut under water, just above the pair of leaves corresponding to the apex of the plant at the beginning of the experiment (that has been labeled). This way, the segment used in hydraulic conductivity measurements was grown entirely under controlled conditions. Leaves were cut off and the stem was cut under water up to 15 cm length and de-barked. The xylem segments were left under water for 15–20 min to release tensions, and afterwards both ends of each stem section were fitted with rubber gaskets under water and remained trimmed in water. All measured stem segments had diameters of 1.0–3.4 mm. Initial hydraulic conductivity (K_i) was determined by measuring the solution flow rate (kg s^{-1}) perfused through the segment at a pressure drop of about 0.006 MPa. The perfusing solution was 1‰ HCl in distilled water, degassed by agitating under vacuum and filtered to 0.2 μm . Maximum conductivity (K_m) was determined after pressurizing the solution through all the segments at 0.08 MPa for 30 min, which was determined to be sufficient to remove all embolisms, as longer perfusion did not result in additional increase in conductivity in previous measurements conducted with the same plant material. Percent loss of hydraulic conductivity (PLC) was calculated by $\text{PLC} = 100 \times (1 - K_i/K_m)$ and vulnerability curves were fitted to exponential sigmoidal equations ($\text{PLC} = 100 / \{1 + \exp[a(\Psi - b)]\}$). Cross-section diameters were measured at both ends of the stem segment and maximum permeability (Cochard 92) was calculated dividing K_m by the smallest stem section.

Statistical analysis

Data were subjected to analysis of variance (ANOVA). Variables were tested for normality and homogeneity of variances. All statistical comparisons were considered significantly different at $P < 0.05$. Simple linear regression was used to detect relationships between transformed variables.

Results

Transpiration and leaf growth

Plants of clone 115.16 had significantly smaller leaves than plants of the other three clones (Table 1). There were significant differences in leaf area among the clones, both at the beginning of the experiment (day 0, $P = 0.015$) and at the time of starting hydraulic conductivity measurements (day 68, $P < 0.0001$). The time course of leaf area expansion was fitted to an exponential curve (Fig. 1). The y -intercepts

Table 1. Mean size of the largest leaf (L_M , $\text{cm}^2 \text{leaf}^{-1}$) \pm standard errors, measured at the beginning of treatments (day 29), mean leaf area increment (ΔLA , $\text{cm}^2 \text{plant}^{-1}$) from day 29–41 and average number of new leaves (N) grown during the same period. $n = 7\text{--}8$ data per clone per treatment

Clone	L_M	ΔLA		N	
		well-watered	drought-treated	well-watered	drought-treated
115.7	23.35 ± 1.18	105.8 ± 6.5	92.5 ± 11.8	1.00 ± 0.4	1.14 ± 0.4
115.16	18.21 ± 0.92	65.9 ± 5.3	67.0 ± 7.1	1.20 ± 0.5	1.25 ± 0.5
115.18	22.64 ± 0.89	101.4 ± 10.2	79.6 ± 8.2	2.33 ± 0.3	1.14 ± 0.6
115.21	22.84 ± 0.90	100.5 ± 11.0	84.1 ± 6.1	2.33 ± 0.3	1.33 ± 0.7

differed among clones, but there were no significant differences in the slope among clones, indicating that clonal differences in leaf area were related to differences in the initial size of the plants. Significant differences between treatments in the parameters of the exponential curves were found only in clones 115.18 and 115.7. The highest decreases in leaf area in drought-treated plants relative to well-watered plants were measured in these clones (Fig. 1).

During the 12 d following imposition of treatments, increases in leaf area measured in drought-treated plants

were significantly lower than those measured in well-watered plants. During this period, the largest decreases in leaf area and the number of new leaves grown in drought-treated plants relative to well-watered plants were measured in clone 115.18 (Table 1).

Evapotranspiration of drought-treated plants decreased by up to 70–80% of that of well-watered plants 10 d after drought imposition (Fig. 2). During this period, soil water content of drought-treated plants remained above 47% (data not shown). There was a significant and positive relationship

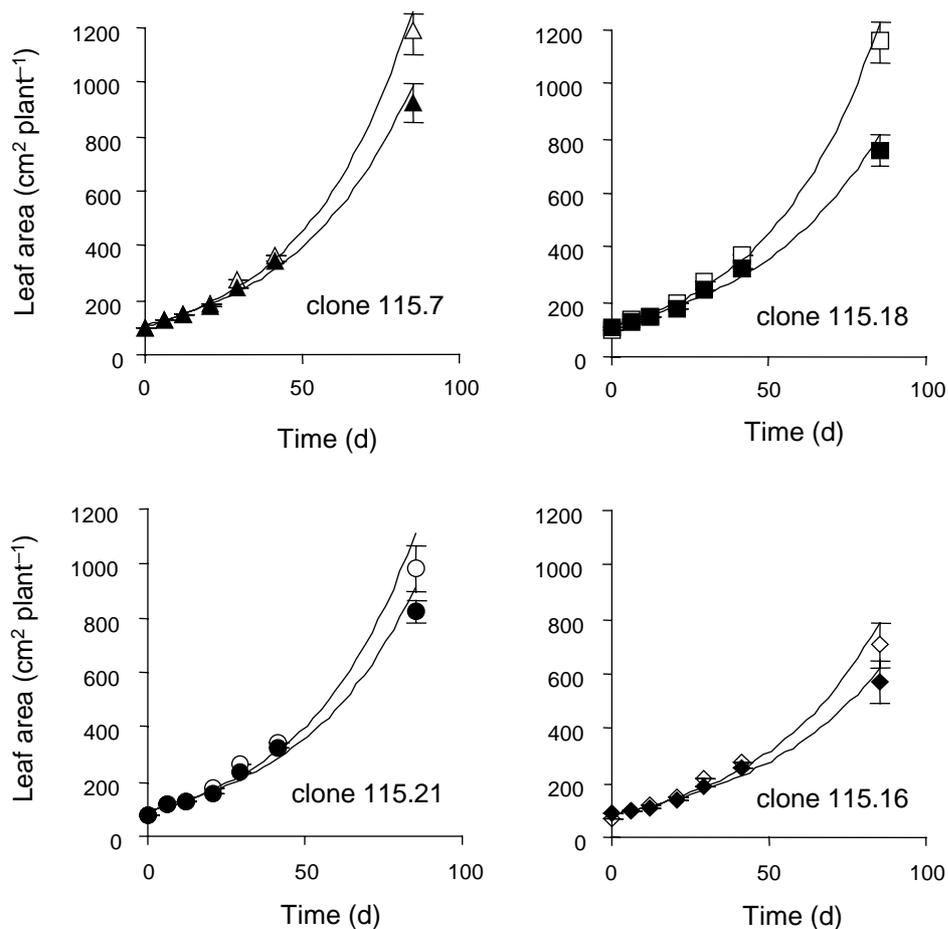


Fig. 1. Time course of leaf area expansion for the four clones and two watering regimes. Open symbols, well-watered plants; closed symbols, drought-treated. $n = 7\text{--}8$ data per clone per treatment.

between evapotranspiration and leaf area of well-watered plants (Fig. 3, $P < 0.0001$, $R^2 = 0.83$). The relationship was significant ($P < 0.0001$) but not as strong ($R^2 = 0.59$) for drought-treated plants. Plants from clone 115.18 displayed the highest drought-induced reductions in evapotranspiration related to well-watered plants of the same leaf area (Fig. 3).

Leaf water potential

Predawn leaf water potential (Ψ_{pd}) is plotted versus the soil water content of each containerized plant in Fig. 4. Data were pooled across treatments and fitted to the following model: $\Psi_{pd}^{-1} = A + B(\text{SWC})$ ($P < 0.0001$, $0.5 < R^2 < 0.9$ for all the lines). There were statistically significant differences ($P < 0.01$) among clones in both parameters (A , B) of the regression lines. The highest values of coefficient B were measured in clones 115.7 and 115.18 (Fig. 4), indicating that

steepest decrease in Ψ values as soil water content declined occurred in these clones. The highest values of Ψ_{pd} were measured in clone 115.16 under soil water deficit (SWC < 30%) (Fig. 4).

Hydraulic conductivity

Stems of *E. globulus* rooted cuttings experienced a sharp increase in loss of conductivity due to embolism at predawn leaf water potentials higher than -1 MPa (Fig. 5). For all clones combined, there were no significant differences between treatments in the parameters of the curves and thus, the data for each clone were pooled across treatments and grouped into Ψ_{pd} classes of 0.25 MPa to fit the vulnerability curves to an exponential sigmoidal equation (Table 2). Coefficient a is related to the water potential range over which conductivity is lost. It ranged from 1.52 (clone 115.16, least vulnerable) to 2.23 (clone 115.18, most

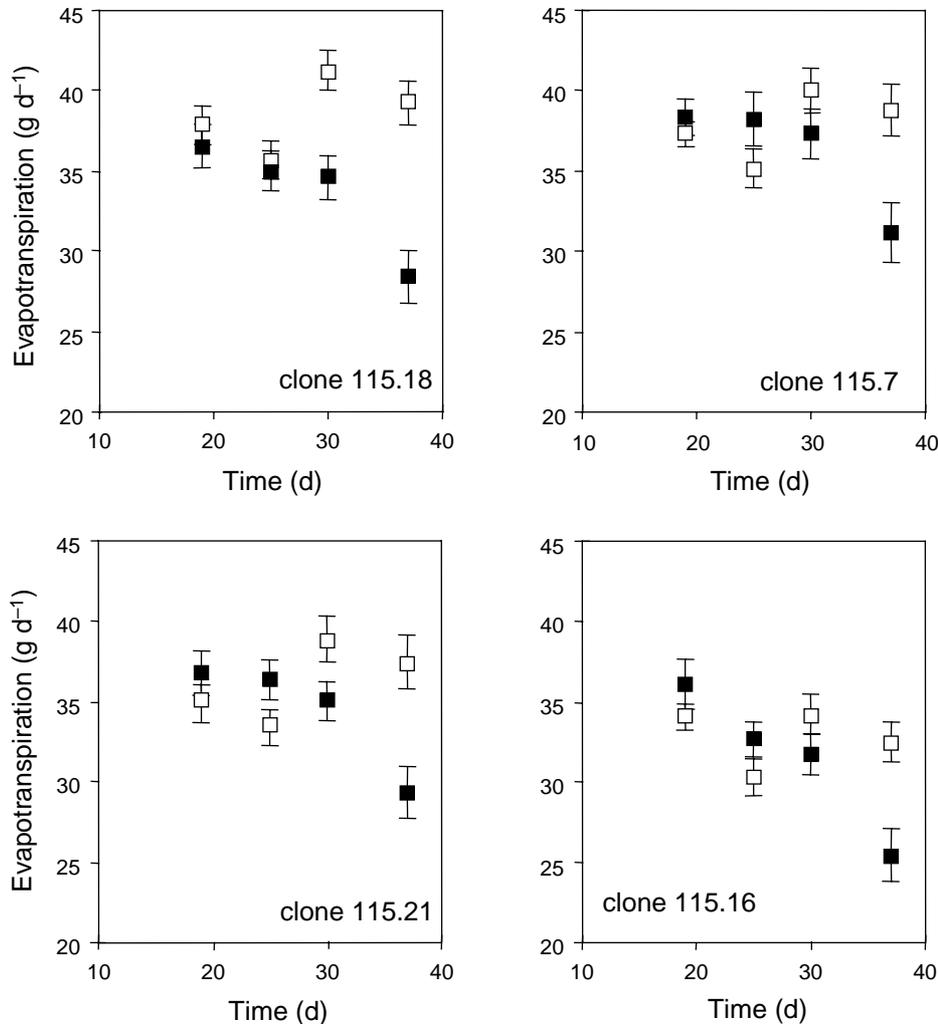


Fig. 2. Mean evapotranspiration of well-watered (open symbols) and drought-treated (closed symbols) plants. Treatments began on day 28. Vertical bars are standard errors. $n = 20$ plants per clone per treatment.

vulnerable) (Table 2). Coefficient b gives the water potential corresponding to 50% loss of conductivity. It ranged between -1.2 MPa (clone 115.16) and -1.02 MPa (clone 115.7) (Table 2). According to these data, clone 115.16 exhibited the least xylem vulnerability to cavitation. Differences among clones in both parameters were not statistically significant, however.

Maximum permeability was significantly lower in drought-treated plants than in well-watered plants and it was not significantly related to cross-section diameter. No significant differences were detected among clones, but it is worth noting that the highest drought-induced reductions in maximum permeability were measured in the most drought-resistant clone, as estimated from field trials (clone 115.16) and the lowest in the most drought-sensitive clone (115.21) (Table 3).

Discussion

Water shortage significantly decreased the amount of water loss by transpiration and leaf growth during the first two weeks after drought imposition. The most drought-resistant

of the clones tested, according to data from field trials, had significantly smaller leaves than the rest of the clones. A small leaf size has been related to high stomatal conductances and transpiration rates per unit leaf area in common bean (*Phaseolus vulgaris* L.) cultivars bred for cultivation in hot and dry regions (Mencuccini and Comstock 1999), and in Pima cotton (*Gossypium barbadense* L.) bred for increased yield and heat resistance (Cornish *et al.* 1991). Similarly, green ash (*Fraxinus pennsylvanica* L.) seedlings from a xeric habitat had smaller leaves than seedlings from more mesic habitats in a greenhouse experiment (Abrams *et al.* 1990).

The largest drought-induced decreases in transpiration and leaf growth were found in the clone that was most susceptible to xylem cavitation. Several studies have shown a wide variation in stomatal responses to drought among *Eucalyptus* species (Myers *et al.* 1997; Thomas and Eamus 1999; White *et al.* 2000). *E. globulus* has been reported to exhibit an intermediate stomatal sensitivity to drought (White *et al.* 2000). Our results show that both evapotranspiration and leaf growth decline at rather moderate levels of water deficit (SWC = 47%, estimated $\Psi_{pd} > -0.6$ MPa for all the clones). Leaf expansion depends on cell expansion, which is strongly influenced by turgor loss (Nardini 2002). Similarly, the amount of water lost by transpiration depends on the hydraulic resistances of the root and shoot (Tyree *et al.* 1993). Thus, early decreases in leaf growth and evapotranspiration may be related to the sharp increase in conductivity loss measured at moderate levels of water stress ($\Psi_{pd} < -1$ MPa).

The percentage of conductivity loss fell to 50% at a Ψ_{pd} of about -1.1 MPa. Similar results were observed for *E. grandis* by Pammenter and Vander Willigen (1998). This vulnerability profile has been considered to illustrate low tolerance to water stress (Kavanagh and Zaerr 1997) and is quite different from the vulnerability profiles obtained for several Mediterranean sclerophyllous trees by Salleo and Lo Gullo (1993). It has been suggested that 'non-conservative' species might maximize stomatal conductance at the cost of some cavitation (Jones and Sutherland 1991). This may lead to enhanced growth under water-limiting conditions, and can explain why *E. globulus* is the most productive species in south-western Spain, under a mild Mediterranean climate. In agreement with these findings, recent studies carried out on *Eucalyptus* have shown that trees with lower water-use efficiency were more productive than trees with high water-use efficiency (Bond and Stock 1990, Pita *et al.* 2001). Despite the rapid increase in conductivity loss experienced by *E. globulus* stems over a narrow range of leaf water potentials, a percentage of conductivity loss higher than 85% could not be measured in the present study. According to our previous experience, increasing water deficit may have caused leaf shedding and thus, a drastic reduction in transpiration, which may preserve the plant from catastrophic xylem cavitation (in fact we detected leaf shedding at final stages of drought in this study). Early leaf shedding under water stress has been

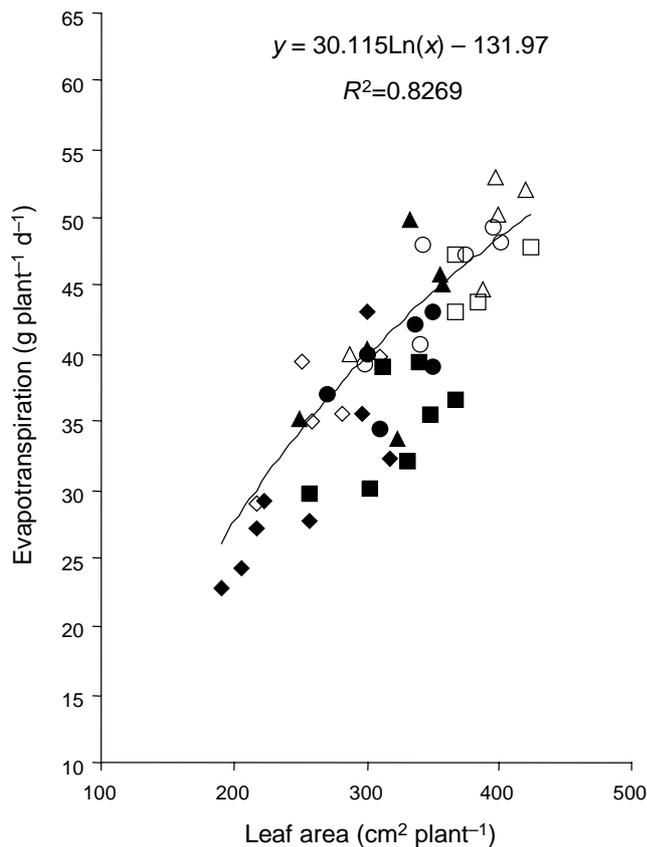


Fig. 3. Relationship between plant leaf area measured on day 41 and whole-plant transpiration measured two weeks after drought imposition (days 40–44). Open symbols, well-watered plants; closed symbols, drought-treated. Symbols refer to clones as follows: (\blacktriangle , \triangle) 115.7; (\square , \blacksquare) 115.18; (\circ , \bullet) 115.21; (\diamond , \blacklozenge) 115.16. The regression line has been drawn for well-watered plants.

widely documented in tree species (Pereira and Pallardy 1989) and recently related to cavitation threshold (Rood *et al.* 2000). Throughout cavitation and leaf shedding a small percentage of xylem conductivity is preserved, which is enough to allow survival even after losing all the living leaves in plants of similar size (Pita, unpublished observations).

Maximum permeability was significantly higher in well-watered than in drought-treated plants. This result shows a decrease in the efficiency of hydraulic transport by the

xylem in response to water shortage in the species. Similar results were obtained by Tognetti *et al.* (1997) in Aleppo pine (*Pinus halepensis* Mill.) seedlings and Vander Willigen and Pammenter (1998) in *Eucalyptus* clones growing in the field. This loss in conducting capacity may be related to a lower potential growth by means of a positive relationship between hydraulic efficiency of plant shoots and maximum diurnal stomatal conductance (Nardini and Salleo 2000). Eamus *et al.* (2000) suggested that water use may be limited,

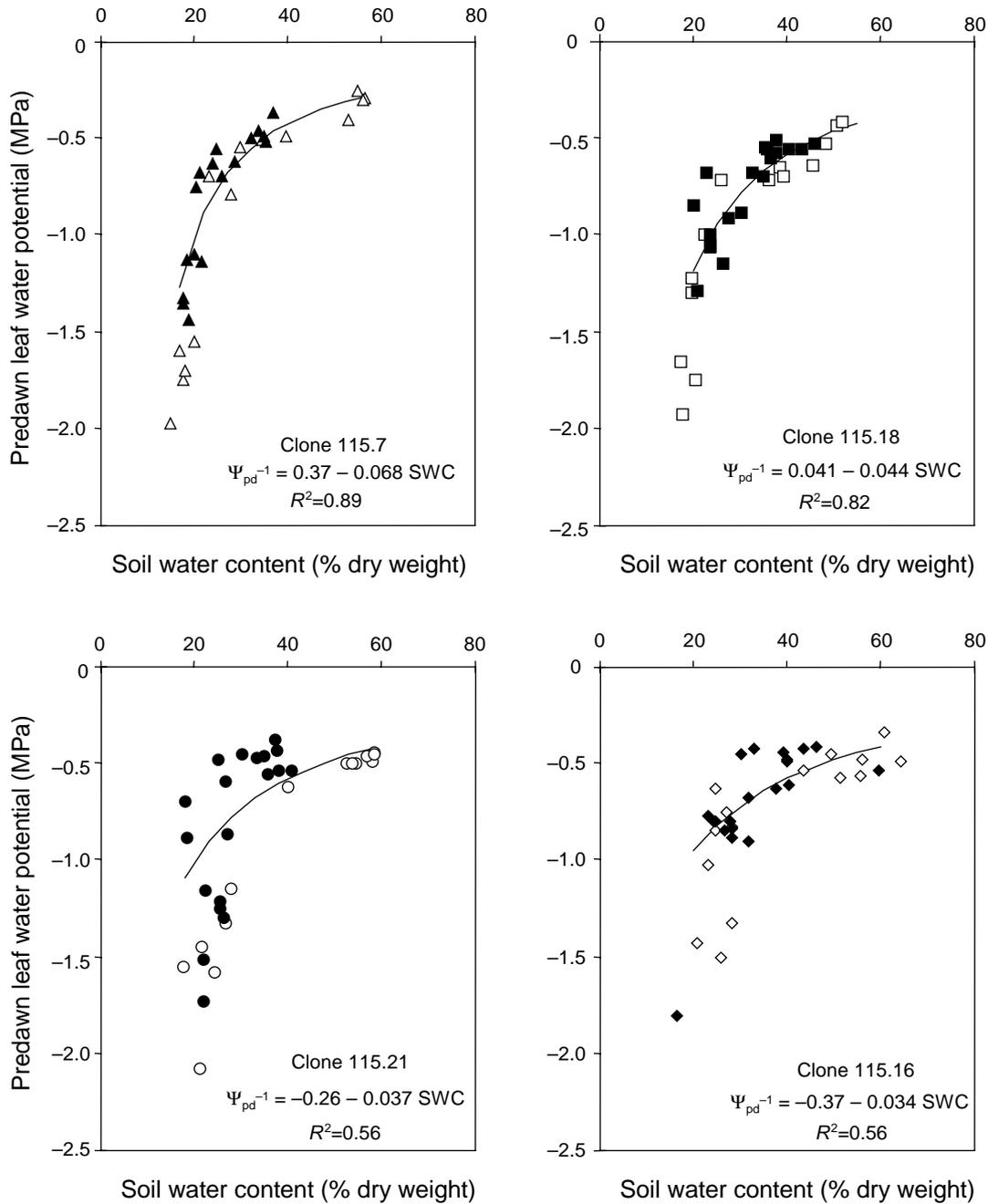


Fig. 4. Relationship between predawn leaf water potential and soil water content for the four clones and two treatments tested. Open symbols, well-watered plants ($n = 14-15$); closed symbols, drought-treated ($n = 17-20$).

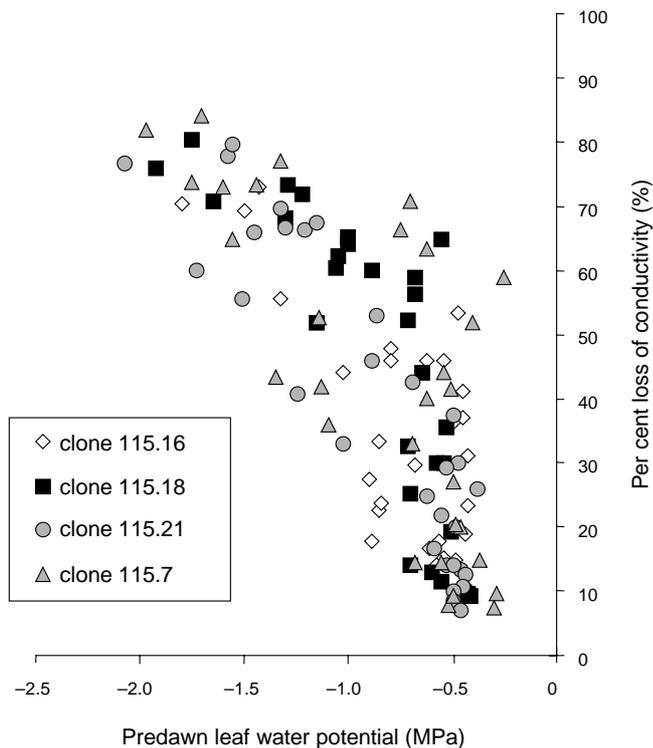


Fig. 5. Relationship between predawn leaf water potential and percent loss of conductivity in four *E. globulus* clones ($n = 31\text{--}35$ data per clone).

even during the wet season, by larger resistances to water flow in small xylem conduits formed during the dry season. Our results do not fully support these findings. Permeability and growth were lower in drought-treated plants relative to well-watered ones, but the lowest decrease in leaf growth under drought was measured in the clone that displayed the highest drought-induced decrease in permeability. Moreover, no significant differences in leaf-specific conductivity (stem conductivity/sustained leaf area) between clones were found in the present study, despite the large differences in total leaf area measured after growing the plants for 68 d. In agreement with this, Nardini (2002) found no relationship between hydraulic efficiency and shoot growth rate or adaptation to drought in several tree species.

Despite changes in maximum permeability with treatment, no significant differences between watering regimes were found in the coefficients of the vulnerability curves.

Table 2. Parameters of vulnerability curves fitted to an exponential sigmoidal equation: $PLC = 100/\{1 + \exp[a(\Psi - b)]\}$

Parameter	Clone			
	115.7	115.16	115.18	115.21
a	1.59	1.52	2.23	2.02
b	1.02	-1.20	-1.04	-1.14
R^2	0.97	0.95	0.76	0.89

Similar results were obtained by Pammenter and Vander Willigen (1998) in *Eucalyptus* clones, Maherali and DeLucia (2000) in desert and montane *Pinus ponderosa* Laws. trees and Alder *et al.* (1996) in adjacent populations of *Acer grandidentatum* Nutt. High permeability has been related to high vulnerability to cavitation (Sparks and Black 1999). However, a lack of correlation between permeability and xylem vulnerability to cavitation has been reported in several studies carried out both with single tree species (Kavanagh *et al.* 1999; Maherali and De Lucia 2000) and with several species (Cochard 1992). Xylem vulnerability depends on the pore size and flexibility of the inter-conduit pit membranes (Jackson *et al.* 1995; Sperry and Ikeda 1997; Tognetti *et al.* 1998), which may or may be not related to conduit size and maximum permeability.

The values of coefficient a in the exponential sigmoidal equation were of similar magnitude to those reported in branches of 7–8 year-old trees of four *Eucalyptus* clones (Pammenter and Vander Willigen, 1998). Coefficient a is related to the slope of the vulnerability curve. Thus, the range of water potentials over which conductivity is lost was similar in young *E. globulus* rooted cuttings and 7–8-year-old *E. grandis* \times *camaldulensis* hybrids. In agreement with this, Tyree *et al.* (1992) found similar vulnerability profiles in branches and seedlings or rooted cuttings of red oak (*Quercus rubra* L.) and eastern cottonwood (*Populus deltoides* Bart. Ex Marsh). Coefficient b gives the water potential corresponding to 50% loss of conductivity. Coefficient b values were lower in the present study than those reported by Pammenter and Vander Willigen (1998), most probably as a result of using predawn Ψ values in our study instead of actual Ψ .

Predawn leaf water potential has been considered a good index of soil water availability in the vicinity of roots. However, the relationship between Ψ_{pd} and Ψ_{soil} may be influenced by the hydraulic resistances in the xylem, which

Table 3. Mean stem maximum permeability \pm standard error measured in drought-treated and well-watered plants

	Stem maximum permeability ($\text{kg s}^{-1} \text{MPa}^{-1} \text{m}^{-1}$)			
	clone 115.7	clone 115.16	clone 115.18	clone 115.21
Drought-treated	4.03 ± 0.19	3.83 ± 0.31	4.02 ± 0.19	3.92 ± 0.24
Well-watered	4.62 ± 0.49	5.14 ± 0.40	4.78 ± 0.27	4.12 ± 0.25

may prevent soil–plant overnight equilibrium (Pallardy *et al.* 1991). Thus, the differences found in the parameters of the regression lines fitted to Ψ_{pd} and SWC data in the present study may reflect differences in the hydraulic system of the clones tested. Predawn leaf water potential decreased gradually over a broad range of soil water content values in control plants of clone 115.16. The highest values of Ψ_{pd} were measured in this clone as water availability decreased. Tuomela (1997) measured the lowest values of daily minimum leaf water potential in the most mesic provenances of *E. microtheca* in a greenhouse experiment. Similarly, Sun *et al.* (1995) found that xylem water potential decreased gradually in response to declining water availability in the more water-stress-tolerant *Nothofagus solandri* whereas it declined abruptly in *N. menziesii*. Thus, the shallow slope of the relationship between Ψ_{pd} and SWC found in clone 115.16 may reflect adaptation to drought. It is worth noting that the lowest Ψ_{pd} values were measured in well-watered plants in all the clones tested. This result may be related to higher transpiration in well-watered plants related to drought-treated plants. We hypothesize that it may be also related to higher stem permeability in well-watered plants. Plants grown in the absence of water deficits develop an excess conducting capacity that does not enhance drought tolerance. Decreasing stem permeability under drought conditions may decrease water availability to the leaves when water is not limiting, but it may prevent xylem pressure drop under mild water deficit. In agreement with this, the lowest Ψ_{pd} values were measured in drought treated plants in the clone that exhibited the smallest decrease in permeability under drought and showed the worst results in field plantations established in south-western Spain.

In conclusion, our results show that pure *E. globulus* clones differed in leaf size, leaf growth under drought and the rate of Ψ_{pd} decrease under drought. Although the present study has to be considered as preliminary, the range of the slopes of the vulnerability curves and clonal differences in maximum permeability decreases under drought suggest that hydraulic traits are likely to be used when searching for genotypic differences in drought resistance in the species. Moreover, the similarity of the vulnerability curves obtained from young rooted cuttings (this study) and branches from closely related genotypes (Pammenter and Vander Willigen 1998), together with the apparent lack of relationship between the vulnerability profile and the environmental conditions seem to support the use of xylem vulnerability to cavitation in breeding programs; whether it can be readily used, awaits further research.

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