



Hydraulic properties of *Pinus halepensis*, *Pinus pinea* and *Tetraclinis articulata* in a dune ecosystem of Eastern Spain

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Abstract

The hydraulic properties of *Pinus pinea*, *Pinus halepensis* and *Tetraclinis articulata* were studied in a coastal dune area from Eastern Spain. The measured variables include vulnerability to xylem embolism (vulnerability curves), hydraulic conductivity and carbon isotopic discrimination in leaves. Leaf water potentials were also monitored in the three studied populations during an extremely dry period. Our results showed that roots had always wider vessels and higher hydraulic conductivity than branches. Roots were also more vulnerable to xylem embolism and operated closer to their hydraulic limit (i.e., with narrower safety margins). Although it was not quantified, extensive root mortality was observed in the two pines during the study period, in agreement with the high values of xylem embolism (> 75%) predicted from vulnerability curves and the water potentials measured in the field. *T. articulata* was much more resistant to embolism than *P. pinea* and *P. halepensis*. Since *T. articulata* experienced also lower water potentials, safety margins from hydraulic failure were only slightly wider in this species than in the pines. Combining species and tissues, high resistance to xylem embolism was associated with low hydraulic conductivity and with high wood density. Both relationships imply a cost of having a resistant xylem. The study outlined very different water-use strategies for *T. articulata* and the pines. Whereas *T. articulata* had a conservative strategy that relied on the low vulnerability of its conducting system to drought-induced xylem embolism, the two pines showed regulatory mechanisms at different levels (i.e., embolism, root demography) that constrained the absorption of water when it became scarce.

Introduction

Tolerance of plants to drought is defined by several components (e.g., Rambal (1993)), including rooting extension and depth, the regulation of transpiration, and the water transport properties of the xylem. However, there is increasing evidence that hydraulic constraints within the xylem limit how different plant species cope with drought (Pockman and Sperry 2000; Sperry 2000). Under dry conditions, xylem water potentials tend to be very low. Eventually, a tension on the water column reaches a point where an air-water interface can be pulled through pit membranes into functional conduits by a process termed

air seeding (Zimmermann 1983). The resulting air bubbles tend to cause the cavitation of water, which is followed by the entry of air from surrounding tissues until the previously functional conduits become air-filled or embolized. Embolized conduits no longer contribute to water transport and, thus, the hydraulic conductivity of the xylem is reduced, causing a decrease in leaf water potential and, again, more embolisms. This cycle can become unstable ("runaway embolism", Tyree and Sperry (1988)), leading to a breaking of the hydraulic continuum between soil and leaves, and to branch (or plant) dieback (e.g., Rood et al. (2000)). Xylem embolism is thus an important ecological factor not only because it directly reduces

a plant's potential for gas exchange (Sperry et al. 1998) but also because of the limit it sets to the minimum water potential that the plant can tolerate.

Species in the genus *Pinus* tend to be more vulnerable to xylem embolism than most conifers. In addition to this, pines show little between-species variation in their vulnerability, with leaf water potentials around -3.5 MPa causing a 50% loss of conductivity in the stems of most species (Cochard 1992; Linton et al. 1998; Hacke et al. 2000a; Piñol and Sala 2000; Martínez-Vilalta and Piñol 2002 (in press)). This relatively high vulnerability to embolism is associated with an efficient stomatal control and water use (Linton et al. 1998; Rundel and Yoder 1998). In contrast, the family Cupressaceae, to which *Tetraclinis articulata* (Vahl) Mast. belongs, contains some of the most embolism-resistant species ever measured. In *Juniperus monosperma* and *J. ashei* from southern USA, for example, the water potential causing 50% embolism was ≈ -12 MPa (Pockman and Sperry (2000); W.T. Pockman et al., unpublished results). Within individuals, roots are usually more vulnerable to embolism than branches, both in angiosperms (Sperry and Saliendra 1994) and conifers (Linton et al. 1998).

Coastal dunes pose special problems to plant establishment, growth and survival (Ranwell 1972). In the Mediterranean region, low rainfall and high temperatures combine with the small water-retention capacity of sandy soils to establish the water-limited conditions that prevail in coastal dunes. The effects of soil porosity on plant water use have been discussed by Bristow et al. (1984) and Sperry et al. (1998). Water is retained by weaker capillary forces in coarse soils than in fine soils because of the larger pore spaces in the former. As a result, coarser soils lose more moisture and hydraulic conductivity at higher water potentials, and once the large pores are emptied only a small amount of water remains (Hillel 1980). Plants in sandy soils can potentially extract water at relatively high water potentials but, at the same time, the range of water potential over which soil water is available is narrower. This suggests that plants living in sandy substrates will show a greater physiological sensitivity to soil water potential than plants in fine-textured soils (Hacke et al. 2000a).

In this study we characterize the water relations of adult individuals of *Pinus pinea* L. (Stone pine), *Pinus halepensis* Mill. (Aleppo pine), and *Tetraclinis articulata* (Barbary thuja) in an area of coastal dunes during a dry period. The hypotheses we addressed were: (1) within a species, roots exist closer to their

hydraulic limit than branches of comparable size, (2) among species, pines are more vulnerable to xylem embolism than *T. articulata*, but because of the extremely dry conditions that are experienced periodically in the study area, (3) pines need other adaptations (e.g., high maximum hydraulic conductivity, high water-use efficiency) to compensate for the greater vulnerability of their xylem. An additional objective was to determine if for the species studied vulnerability to xylem embolism was more correlated with wood density than with xylem anatomy, as suggested by Hacke et al. (2001).

Methods

Study site and plant material

The studied populations are located at the Guardamar-La Marina area, Alacant, SE Spain ($38^{\circ}10'$ N, $0^{\circ}38'$ W). The dune system comprises a surface of 848 ha, and is one of the largest systems of coastal dunes in the Iberian Peninsula (Escarré et al. 1989). The climate is Mediterranean arid with a mean temperature of 17.5°C and an annual rainfall of 312 mm (average for the 1961–1990 period). The long-term average of potential evapotranspiration in Guardamar is 870 mm (Pérez 1994). Soils are sandy (sand > 99%) with predominance of the 0.05–0.2 mm grain-sizes (Escarré et al. 1989).

The study was carried out during the late spring and the summer of 2000. This period was extremely dry, with only 5 mm of rainfall between May and August. *P. pinea* and *P. halepensis* were sampled from the same mixed plantation (ca. 75 years old; Aldeguer et al. (1997)), whereas *T. articulata* was sampled from a more recent (ca. 17 years old) plantation within less than 1 km. The substrate of the two sites is almost identical (Jiménez-Ortiz 2001). Roots and branches for hydraulic measurements were sampled from the same trees; roots at a depth of ca. 25 cm, and branches from a fully exposed region of the crown. The cross-sectional area of the segments measured was similar for roots and branches (t-test; $t = 2.02$, $p = 0.358$).

Water potentials

Leaf water potentials were measured in July and August of 2000 with a pressure bomb (Model 3005, Soil-moisture Equipment corp., Goleta, CA, USA)

(Scholander et al. 1965). On each sampling date one branch tip from 6 different individuals per species was measured at predawn (0230–0400 solar hour) and at midday (1130–1300 solar hour). Predawn water potentials (Ψ_{pd}) were assumed to be in equilibrium with soil water potentials and were used to compare with the vulnerability curves of roots and establish their minimum safety margins (Hacke et al. (2000b); see the “Vulnerability to xylem embolism” section). For branches, the comparison was done with midday water potentials (Ψ_{md}).

Xylem anatomy and wood density

Tracheid diameters were measured on the same stem and root segments that had been used to establish vulnerability curves. Transverse sections (*ca.* 25 μm) were cut using a rotary microtome (Reichert, Vienna, Austria). The sections were stained with safranin (0.1%) to improve contrast and mounted in glycerol. The slides were viewed at 100 \times (branches) or 50 \times (roots) with a compound microscope (Olympus BH-2, Hamburg, Germany) attached to a monochrome video camera (JVC TK-1270, Yokohama, Japan) and a computer. Two to four representative regions from the outermost rings of each section, situated 90° apart, were captured in black and white format and analysed with a standard image analysis package. Within each image all open tracheids wider than 2 μm (stems) or 7 μm (roots) were sampled. These values were selected in each case to maximize the agreement between the visually identified tracheids and those selected by the computer. For each selected conduit the program determined the total cross sectional area and the perimeter. At least 500 conduits were measured from each section (the average was 1855 conduits).

Three variables were used to characterize the xylem anatomy of each species: the mean tracheid diameter (d , in μm), the mean hydraulic diameter (d_h , in μm), and the mean lumen area per cross sectional area of wood ($A_x:A_s$, in %). The hydraulic diameter was calculated assuming that hydraulic conductivity is proportional to the diameter raised to the fourth power. The following expression was used: $\sqrt{\sum d_i^4/N}$ (Tyree et al. 1994). A theoretical specific hydraulic conductivity was also calculated for each section exclusively from anatomy data using the Hagen-Poiseuille law. In order to do that the conductivity of all individual conduits was added and the total divided

by the area of the region measured. The resulting values were referred to the total cross-sectional area of the section.

Wood density was also measured on the same stem and root segments used for hydraulic measurements. Segments *ca.* 3 cm long were cut out of stems and roots, their bark was removed with a razor blade, and their fresh volume was determined by Archimedes' principle (Hacke et al. 2000b). Samples were then dried at 75 °C for 48 h and weighted. Wood density (D_w) was calculated as the ratio of dry weight to fresh volume. Preliminary measurements showed that for all species the effect of pith on density was negligible (much lower than the natural variability within a wood sample) and, thus, pith was not removed.

Hydraulic conductivity

Hydraulic conductivity was measured following Sperry et al. (1988). Segments *ca.* 20 cm long and with a diameter of 0.7 ± 0.2 cm were re-cut underwater from the sampled roots and branches. After removing the bark, their proximal ends were connected to a tubing system. The system was filled with a filtered (0.22 μm pore size) and degassed solution of HCl (pH = *ca.* 2). Hydraulic conductivity (K_h , in $\text{m}^4 \text{MPa}^{-1} \text{s}^{-1}$) was calculated as the ratio between the flow through the segment and the pressure gradient ($\Delta P = \text{ca.}$ 6 kPa). The flow was measured gravimetrically. To obtain the maximum hydraulic conductivity the measure solution was previously injected at *ca.* 100 kPa for 60 min. to remove all native embolisms from the segment. Specific hydraulic conductivity (K_s , in $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$) was calculated as the ratio between maximum hydraulic conductivity and mean cross sectional area of the segment (without bark); and leaf-specific conductivity (K_L , in $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$), as the quotient between maximum hydraulic conductivity and leaf area. Finally, the ratio between cross sectional area and leaf area ($A_S:A_L$, Zimmermann (1983)) of each branch segment was also calculated.

Vulnerability to xylem embolism

Vulnerability curves show the relationship between water potential (or pressure) in the xylem and percentage loss of hydraulic conductivity (PLC) due to embolism. The air injection method (Cochard et al. 1992; Sperry and Saliendra 1994) was used to establish the curves. This method has been validated for several species, including conifers (Cochard 1992;

Sperry and Ikeda 1997). In each run, six segments were put inside a pressure chamber with both ends protruding. Proximal ends were connected to the measuring circuit, and maximum hydraulic conductivity was measured. The pressure inside the chamber was then raised to 0.5 or 1 MPa, and maintained during 10 min. Next, the pressure was lowered to a basal value of *ca.* 10 kPa, and after 15 min. to allow the system to equilibrate, conductivity was measured again. The process was repeated for the following injection pressures: 0.5, 1, 1.5, 2, 3, 5 and 7 MPa (roots); and 1, 2, 3, 4, 6 and 8 MPa (branches).

Vulnerability curves were fitted with the following function (Pammenter and Vander Willigen 1998):

$$PLC = \frac{100}{1 + e^{a(P - P_{50PLC})}} \quad (1)$$

where PLC is the percentage loss of hydraulic conductivity, P is the applied pressure, P_{50PLC} is the pressure (i.e., $-\Psi$) causing a 50% loss of hydraulic conductivity, and a is related to the slope of the curve.

The fitted curves were used to calculate the safety margins at which each species (and tissue) was operating, in a way similar to Pockman and Sperry (2000); see also Hacke et al. (2000b). The safety margins were defined as the difference between the minimum water potential measured in the field (minimum Ψ_{pd} for roots and minimum Ψ_{md} for branches) and the water potential required to cause a 75 PLC (P_{75PLC}), calculated from the fitted equation.

$\delta^{13}C$ measurements

Carbon isotope discrimination was measured in leaves from the same branches used for hydraulic measurements, and was used as a proxy of integrated water-use efficiency (WUE, Farquhar and Richards (1984) and Ehleringer and Osmond (1989)). Since the studied populations were very close, differences in WUE due to microclimatic effects were negligible (Farquhar et al. 1989; Marshall and Zhang 1994). After drying, leaves were ground and sub-samples were separated to measure their carbon isotope composition. All analyses were carried out at the Serveis Científic-Tècnics of the Universitat de Barcelona with an elemental analyser Carlo Erba EA1108 (Milano, Italy) attached to a Delta C isotope mass spectrometer, and using a CONFLO II interface (Thermo Finnigan MAT, Bremen, Germany). The accuracy of

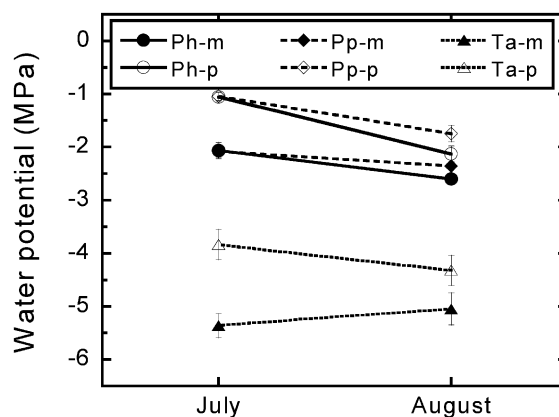


Figure 1. Pre-dawn (p) and mid-day (m) water potentials measured in *P. halepensis* (Ph), *P. pinea* (Pp) and *T. articulata* (Ta). The error bars represent standard errors ($n = 6$).

the measurements was 0.15 ‰. The relationship between carbon stable isotopes was expressed in relation to PDB (Pee-Dee Belemnite standard), and converted to discrimination ($\Delta = \delta^{13}C_{air} - \delta^{13}C_{plant}$), assuming that $\delta^{13}C_{air}$ was -8 ‰.

Results

Water potentials

Predawn and midday water potentials were much lower in *T. articulata* than in the two pines (Two-way ANOVA with repeated measurements; $F = 70.02$, $p \ll 0.001$ for predawn and $F = 113.99$, $p \ll 0.001$ for midday values) (Figure 1). Predawn water potentials decreased significantly between July and August for the three species ($F = 51.63$, $p \ll 0.001$), whereas midday values decreased only for the two pines and, hence, the global effect was not significant ($F = 3.10$, $p = 0.098$). The difference between midday and predawn water potentials was less in August for the three species ($F = 22.47$, $p < 0.001$).

Xylem anatomy and wood density

The between-tissue differences in xylem anatomy were always highly significant (Two-way ANOVA (species \times tissue), $p \ll 0.001$). Tracheid diameter (d), hydraulic tracheid diameter (d_h) and the $A_X:A_S$ ratio in roots always exceeded those in branches (Table 1 and Figure 2). The differences were more pronounced in the two pines than in *T. articulata* (see Figure 3 for a *P. pinea* example). In pines, wood density (D_w) was

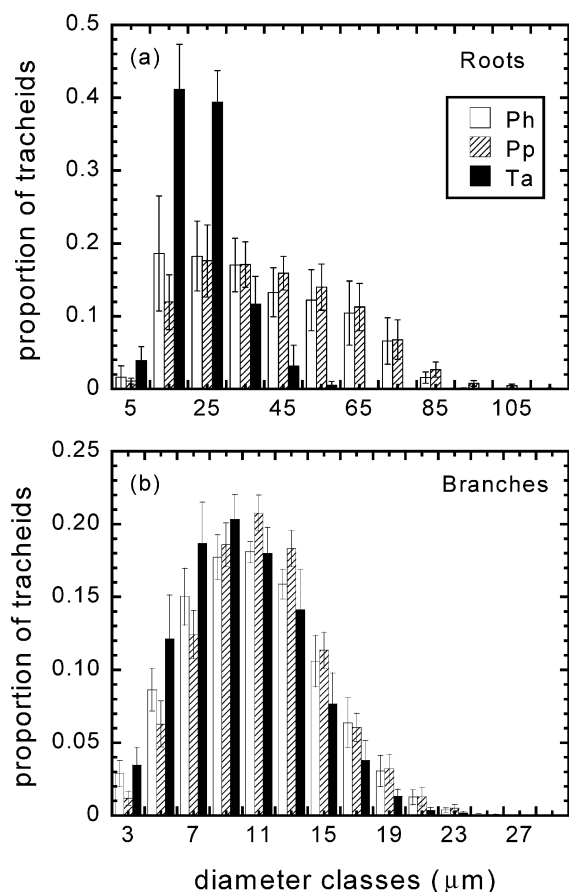


Figure 2. Tracheid-size distributions of roots (a) and branches (b) of the three studied species. Abbreviations as in Figure 1. The error bars represent standard errors ($n = 6-8$).

lower in roots ($p \leq 0.03$), whereas no difference between tissues was observed in *T. articulata* ($p = 0.876$) (Table 1).

Tracheids were narrower in the roots of *T. articulata* than in the roots of the two pines (Table 1 and Figure 2). The differences were significant for d (One-way ANOVA; $F = 5.73$, $p = 0.011$) and for d_h ($F = 7.41$, $p = 0.004$). In branches the pattern was the same, but the differences were smaller and not significant ($F = 1.99$, $p = 0.164$ for d ; $F = 1.63$, $p = 0.221$ for d_h). The percent of conducting area per cross sectional area ($A_x:A_s$) was higher in the two pine species than in *T. articulata* ($F = 13.11$, $p < 0.001$ in roots; and $F = 7.46$, $p = 0.004$ in branches). Wood density followed the opposite pattern, with higher values in *T. articulata* for both roots and branches ($p \leq 0.05$) (Table 1).

Hydraulic measurements and safety margins

Specific hydraulic conductivity (K_s) was higher in roots than in branches for the three species (Two-way ANOVA (species \times tissue); $F = 10.75$, $p = 0.002$) (Table 1). *P. pinea* had higher K_s than the other two species both for roots and branches, although the differences were (marginally) significant only in branches (One-way ANOVA; $F = 3.34$, $p = 0.058$). The differences in $A_s:A_L$ were not significant ($F = 2.29$, $p = 0.130$), but the larger values in *P. pinea* than in *T. articulata* (Table 1) combined with the higher K_s in *P. pinea* branches caused leaf-specific conductivity (K_L) to be significantly greater in *P. pinea* than in the other two species ($F = 5.44$, $p = 0.014$) (Table 1).

Roots were more vulnerable to embolism than branches (Figure 4). This was reflected in their P_{50PLC} values (Two-way ANOVA (species \times tissue); $F = 292.91$, $p \leq 0.001$) and in the slopes (a) of their vulnerability curves ($F = 13.74$, $p < 0.001$) (Table 1). *T. articulata* was more resistant to xylem embolism than the two pines (Figure 4), and showed higher P_{50PLC} for both roots and branches (Table 1). The vulnerability of the two pines was similar although *P. pinea* was slightly more resistant (Figure 4 and Table 1).

Safety margins were narrower for roots than for branches (Figure 5). Whereas the roots of the three species studied were predicted to loose more than 75% of conductivity during the study period (minimum $\Psi < -P_{75PLC}$), safety margins were always ≥ 2 MPa for branches. Among species the differences were not so pronounced: only *T. articulata* branches showed a safety margin (5.5 MPa) clearly wider than that of pines (around 2.5 MPa).

Trade-offs between wood properties

Combining species and tissues, tracheid diameter, specific hydraulic conductivity and wood density were all correlated with the pressure causing a 50 PLC (P_{50PLC} ; Figure 6). In all cases the best fits were obtained with power relationships. Resistance to xylem embolism increased with wood density ($r^2 = 0.77$, $p = 0.021$), and decreased with mean tracheid diameter ($r^2 = 0.84$, $p = 0.010$), and specific hydraulic conductivity (K_s). In this latter case, the relationship was better with theoretical K_s ($r^2 = 0.91$, $p = 0.003$) than with measured K_s ($r^2 = 0.73$, $p = 0.030$).

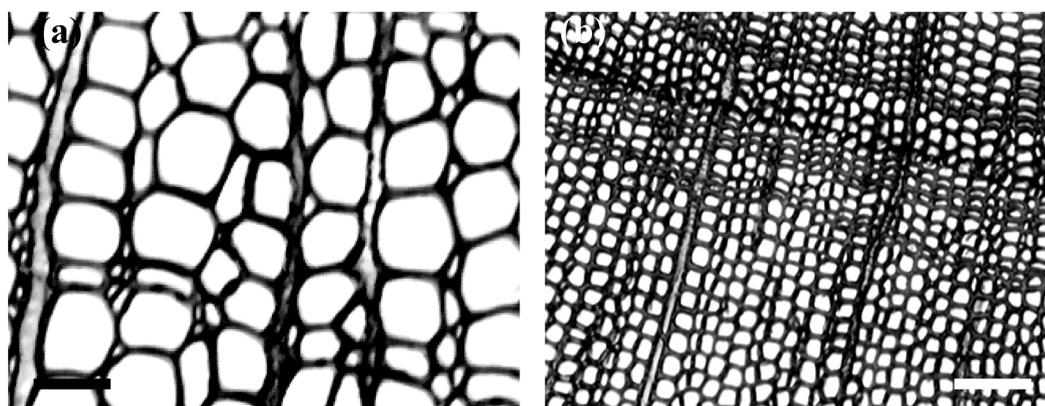


Figure 3. Photographs of representative sections of the xylem of a root (a) and a branch (b) from the same individual of *P. pinea*. The black/white bars in the lower part of the photographs have a length of 100 μm .

Table 1. Measured variables (means \pm standard errors) in roots and branches of *Pinus halepensis*, *P. pinea* and *Tetraclinis articulata*. Different letters indicate significant differences among species (lowercase for roots and uppercase for branches).

	<i>P. halepensis</i>		<i>P. pinea</i>		<i>T. articulata</i>	
	Roots	Branches	Roots	Branches	Roots	Branches
d (μm)	34.0 ^a \pm 5.2	9.4 [^] \pm 0.5	35.2 ^a \pm 3.9	10.1 [^] \pm 0.4	19.8 ^b \pm 1.6	8.6 [^] \pm 0.6
d_h (μm)	40.6 ^a \pm 6.0	11.3 [^] \pm 0.6	45.0 ^a \pm 4.7	11.7 [^] \pm 0.5	22.9 ^b \pm 1.9	10.3 [^] \pm 0.7
A_x:A_s (%)	30.5 ^a \pm 3.4	16.1 [^] \pm 1.6	32.5 ^a \pm 2.3	17.4 [^] \pm 0.8	16.8 ^b \pm 1.4	10.2 ^B \pm 1.6
A_s:A_L ($\times 10^4$)	–	7.59 [^] \pm 1.92	–	6.19 [^] \pm 0.53	–	3.64 [^] \pm 0.43
D_t (g cm^{-3})	0.416 ^a \pm 0.035	0.535 [^] \pm 0.031	0.377 ^a \pm 0.017	0.545 [^] \pm 0.024	0.632 ^b \pm 0.021	0.637 ^B \pm 0.022
K_S ($\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$, $\times 10^4$)	8.93 ^a \pm 3.02	1.52 [^] \pm 0.32	17.0 ^a \pm 5.63	3.51 [^] \pm 0.82	6.58 ^a \pm 2.43	1.63 [^] \pm 0.61
K_L ($\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$, (10^8))	–	9.54 [^] \pm 2.03	–	21.9 ^B \pm 4.81	–	5.78 [^] \pm 2.25
a	–5.40 ^a \pm 1.31	–0.97 [^] \pm 0.17	–2.80 ^a \pm 0.28	–0.72 [^] \pm 0.09	–1.79 ^a \pm 0.62	–1.36 [^] \pm 0.66
P_{50PLC} (MPa)	0.88 ^a \pm 0.10	3.11 [^] \pm 0.29	1.01 ^a \pm 0.14	3.65 [^] \pm 0.25	2.65 ^b \pm 0.46	8.55 ^B \pm 0.34
Δ %	–	16.1 [^] \pm 0.3	–	18.9 ^B \pm 0.2	–	16.1 [^] \pm 0.2

¹³C measurements

Carbon isotope discrimination (Δ) was higher in *P. pinea* than in the other two species (One-way ANOVA; $F = 36.49$, $p \ll 0.001$), among which no difference was found (Table 1). As air temperature and relative humidity were common for the three species, and for needle-leaved plants leaf temperature is often close to air temperature (Campbell and Norman 1998), vapour pressure deficit was similar at least for the two pine species. Thus, differences in Δ between the two pines presumably indicate long-term differences in C_i/C_a and in water use efficiency. The measured difference denotes a 26% lower water-use efficiency (integrated during needle life) for *P. pinea* (Farquhar et al. 1989).

Discussion

Large differences in the hydraulic architecture of above- and below-ground tissues have been repeatedly reported in the literature. Roots usually have wider conduits and higher K_S (Pallardy et al. 1995; Ewers et al. 1997) and are more vulnerable to xylem embolism. In fact, roots are not only more vulnerable but normally live closer to their hydraulic limit (i.e., with narrower safety margins; Hacke et al. (2000b)). Our results support all these findings (Figures 2, 3, 4 and 5). It is worth noting the extreme dimorphism between the anatomy of roots and branches that we have found in *P. halepensis* and *P. pinea*. For most species the mean conduit diameter in surface roots tends to be less than double the mean diameter in branches or stems of similar size (Ewers et al. 1997; Hacke et al. 2000b; Martínez-Vilalta et al. 2002 (in

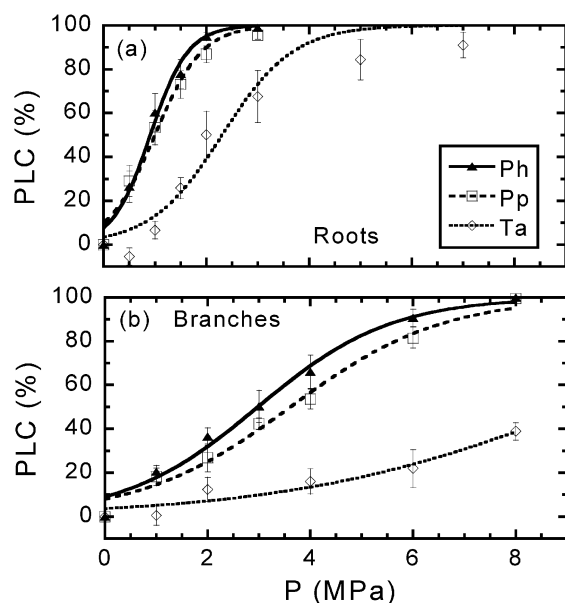


Figure 4. Vulnerability curves of roots (a) and branches (b) of the three studied species. Abbreviations as in Figure 1. The error bars represent standard errors ($n = 5-9$).

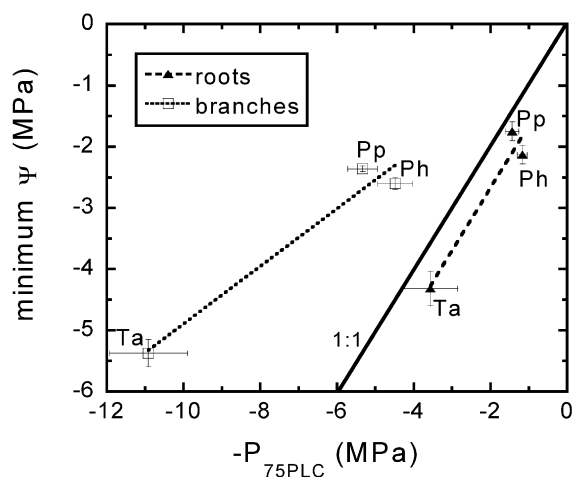


Figure 5. Relationship between the injection pressure that causes a 75 PLC ($-P_{75PLC}$) and the minimum water potential measured in the field. The 1:1 relationship and the linear regressions for roots and branches are also represented. Abbreviations as in Figure 1. The error bars represent standard errors.

press)). For the two pines in this study xylem conduits were almost four times larger in roots, reaching sizes that are exceptional among tracheid-bearing species (Zimmermann 1983). This might be a general character in pines, because Hacke et al. (2000a) found similar diameters in *P. taeda* roots from East USA, with a mean hydraulic diameter of ca. 49 μm (although their hydraulic means were calculated in a

slightly different way). Highly conductive roots have been also reported for *P. ponderosa* (Rundel and Yoder 1998).

It is also interesting to note that the roots of the three studied species were very close to (or beyond) their hydraulic limit during the summer drought of 2000. It should be noted, however, that *T. articulata* roots retained ca. 10% of its maximum conductivity at Ψ down to -7 MPa (Figure 4). Since predawn water potentials give an integrated measure over the entire "wet" rooting volume and we only sampled surface roots, it is likely that the actual safety margins were even lower than the calculated ones. During the sampling (summer 2000), a considerable amount of dead surface roots (depth=0–30 cm) was found. However, since root demography was not monitored it was not possible to establish a causal link between drought, xylem embolism and root mortality. High levels of xylem embolism in roots may be advantageous in order to hydraulically disconnect the roots that are in contact with the drier parts of the soil (e.g. near the surface) and in this way avoid losing water through them (Nobel and North 1993) and protect more valuable organs (Hacke et al. 2000a).

It has been shown that pines can use internally stored water when soil water is scarce (Borghetti et al. 1998). Although storage is normally considered to be primarily limited to aboveground tissues, some authors have proposed that *P. halepensis* roots can act as water-storing bodies (Schiller 2000). Low wood density is associated with high water storage capacity (Borchert 1994). It is thus possible that given the very low density of pine surface roots (Table 1), they have a significant role in water storage. The high vulnerability to xylem embolism of pine roots also suggests that this tissue may release water to the transpiration stream as a result of cavitation-refilling cycles (Zimmermann 1983; Holbrook 1995). When the soil dries and water potentials are too low for refilling to be possible, root tip mortality may result also in the net withdrawal of water from the affected roots (Schiller 2000).

As hypothesized, *T. articulata* was more resistant to xylem embolism than the two pines, which were notably similar (Figure 4). The among-species differences in vulnerability to embolism in this study were associated with differences in xylem anatomy and wood density: *T. articulata* also had smaller tracheids, lower hydraulic conductivity, and higher wood density; although the differences were not always significant (Table 1 and Figure 6). Our results agree with

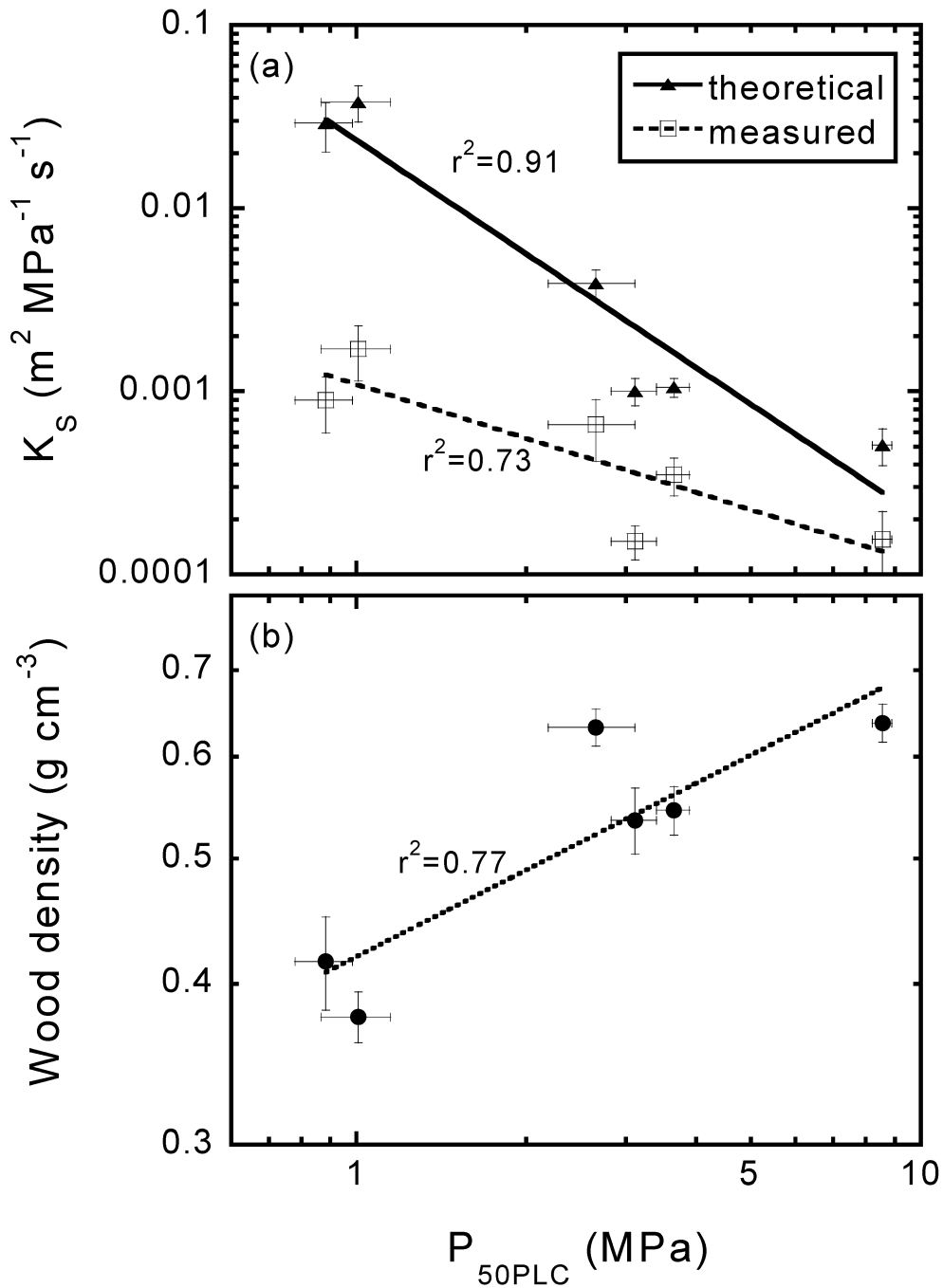


Figure 6. Power relationships between the pressure that causes a 50% loss of conductivity (P_{50PLC}) and theoretical specific hydraulic conductivity, and measured specific hydraulic conductivity (K_s) (panel a); and between P_{50PLC} and wood density (D_l) (panel b) for roots and stems of the studied species. Each symbol is the average for a given species and tissue. The error bars represent standard errors. Note that the scales are logarithmic.

those of Hacke et al. (2001) in that wood density seems to be linked to vulnerability to xylem embolism. Since higher wood density implies higher con-

struction costs, these results show a cost of having a resistant xylem (Hacke et al. 2001). However, in our case tracheid diameter and, in particular, specific hy-

draulic conductivity were even better correlates of xylem vulnerability than wood density (Figure 6), consistent with the existence of a trade-off between xylem conductivity and resistance to cavitation (Zimmermann 1983). Since hydraulic conductivity depends primarily on conduit size and the vulnerability to drought-induced xylem embolism depends on the size and structure of inter-conduit pit pores, the existence of this trade-off has been controversial (Tyree et al. 1994). Extensive reviews with conifers and non-conifers from around the world have shown that the negative relationship between conductivity and resistance to cavitation is rather weak (Tyree et al. 1994; Pockman and Sperry 2000). However, recent results suggest that hidden in the variability observed at the global scale there may be a relationship (or a group of relationships) between conduit diameter and pit-pore size, at least in angiosperms (Martínez-Vilalta et al. 2002 (in press)). Since tracheid diameter and wood density are correlated (Hacke et al. 2001), additional research, particularly on pit membrane characteristics, is required to clarify which are the fundamental relationships between xylem anatomy, wood density, and vulnerability to xylem embolism.

Despite the large differences in vulnerability to embolism between the pines and *T. articulata*, their safety margins were reasonably similar, particularly in roots (Figure 5). The reason for this is the different strategies that the species use to cope with drought. *T. articulata* has a conservative water-use, in which safety has a central role. The lower Ψ_{pd} found in this species, and also our own observations during the sampling of root segments, suggest that its root system is much less developed than in pines. This character has been related to low vulnerabilities to xylem embolism in the California chaparral (Davis et al. 1998). As we have already seen, great resistance to embolism is associated with low hydraulic efficiency and with higher construction costs.

At the other end of the spectrum, *P. halepensis* and *P. pinea* have high maximum hydraulic conductivities and high vulnerabilities to xylem embolism. Apparently, pines can extract water quickly when it is plentiful but need also mechanisms to limit water use when it becomes scarce. These control mechanisms exist at different levels, from roots to the conducting system and, probably, stomata. The relatively high water potentials and the extremely wide tracheids in surface roots suggest that at least some roots can access a reliable water reservoir. The main candidates are the water table and the subsurface condensation

of dew that takes place in dunes as a result of thermal oscillations (De Jong 1979; Barbour et al. 1989). Dew condensation has been shown to increase soil water content by *ca.* 1% per night in some dune ecosystems (Ranwell 1972). In the study site, temperature profiles show that dew condensation may occur at depths between 0 and 40 cm (Escarré et al. 1989). In their study on the influence of soil porosity on water use in *P. taeda*, Hacke et al. (2000a) predicted that, in sandy soils, there would be a shift to the use of deep water during surface drought. Although *P. pinea* has higher hydraulic conductivities in relation to the supported leaf area, and tends to have slightly lower vulnerabilities to xylem embolism (Table 1), safety margins are practically identical for both pines (Figure 5). We hypothesize that the hydraulic superiority of the xylem of *P. pinea* allows this species to have a less strict stomatal control than *P. halepensis*. This is consistent with larger Δ values measured in *P. pinea*.

We have shown that from the point of view of the hydraulic architecture, *T. articulata* is more resistant to drought than the two pines. This is consistent with the current distribution of the species studied: in N Africa, where most populations of *T. articulata* are located, this species is able to live in drier areas than both pines (Quézel 1980). If we consider that most models predict an increase in aridity in the Mediterranean region as a result of climate change (Palutikoff et al. 1994; Rambal and Hoff 1998), the ability of plants to cope with extreme droughts will be of increasing importance. In this context, the differences that we have found may be critical; not only because of the narrower safety margins in pines, but also because of the nature of their strategy to cope with drought. Their stress-avoider strategy, based on the protection of the vulnerable xylem by stomatal control or biomass allocation (Rundel and Yoder 1998), is presumably less capable of resisting extremely dry conditions than the intrinsically resistant xylem of the stress-tolerant *T. articulata*. In fact, extensive drought-induced mortalities have already been reported in NE Spain for another pine species (*P. sylvestris*), with a similar hydraulic architecture to *P. halepensis* and *P. pinea* (Martínez-Vilalta and Piñol 2002 (in press)).

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