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## Xylem hydraulic properties of roots and stems of nine Mediterranean woody species

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**Abstract** We studied the hydraulic architecture and water relations of nine co-occurring woody species in a Spanish evergreen oak forest over the course of a dry season. Our main objectives were to: (1) test the existence of a trade-off between hydraulic conductivity and security in the xylem, and (2) establish the safety margins at which the species operated in relation to hydraulic failure, and compare these safety margins between species and tissues (roots vs. stems). Our results showed that the relationship between specific hydraulic conductivity ( $K_s$ ) and resistance to cavitation followed a power function with exponent  $\approx -2$ , consistent with the existence of a trade-off between conductivity and security in the xylem, and also consistent with a linear relationship between vessel diameter and the size of inter-vessel pores. The diameter of xylem conduits,  $K_s$  and vulnerability to xylem embolism were always higher in roots than in stems of the same species. Safety margins from hydraulic failure were narrower in roots than in stems. Among species, the water potential ( $\Psi$ ) at which 50% of conductivity was lost due to embolism ranged between  $-0.9$  and  $<-8$  MPa for roots and between  $-2.0$  and  $<-8$  MPa for stems. Vulnerability to xylem embolism followed a pattern of: *Quercus ilex*=*Acer monspessulanum*=*Arbutus unedo*=*Sorbus torminalis*=*Cistus laurifolius*>*Cistus albidus*=*Ilex aquifolium*>*Phillyrea latifolia*>*Juniperus oxycedrus*. Gas exchange and seasonal  $\Psi$  minima were in general correlated with resistance to xylem embolism. Hydraulic safety margins differed markedly among species, with some of them (*J. oxycedrus*, *I. aquifolium*, *P. latifolia*) showing a xylem overly resistant to cavitation. We hypothesize that this overly resistant xylem may be related to the shape of the relationship between  $K_s$  and security we have found.

**Keywords** Drought · Hydraulic limits · Trade-off · Water transport · Xylem embolism

### Introduction

Water availability is one of the most important factors controlling the distribution of plant species at the global scale (Woodward 1987). The existence of a compromise between the ability to cope with water stress and the potential to grow at high rates under more favourable conditions explains, in part, why drought-tolerant plants tend to be displaced from mesic and humid habitats (Orians and Solbrig 1977). Although several characters related to drought-tolerance have been identified, plants with opposite attributes can coexist in the same water-stressed community. Despite the fact that single attributes are not very meaningful when considered alone, they usually combine in very specific ways to conform to a small array of character “syndromes” which can be considered typical of drought-tolerant plants (e.g. Davis et al. 1998). Again, the inter-dependence between attributes and the existence of trade-offs explains why the possibilities to combine attributes are limited (Reich et al. 1997; Stratton et al. 2000).

There is increasing supporting evidence that xylem embolism limits gas exchange (Sperry et al. 1998) and, in general, the ability of plants to cope with water stress (Pockman and Sperry 2000; Sperry 2000). Previous studies have shown that plants differ widely in their vulnerability to drought-induced cavitation and that this variation is associated with the range of water potentials ( $\Psi$ s) experienced in the field (Hacke et al. 2000; Pockman and Sperry 2000; Sperry 2000). As a result, the difference between the critical  $\Psi$ s causing catastrophic levels of xylem embolism and the minimum values under field conditions (i.e. safety margins; Tyree and Sperry 1988) tends to be small. This result suggests that there are disadvantages in having a xylem that is overly resistant to cavitation. The main disadvantage that has been proposed is the existence of a trade-off between hydraulic

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efficiency and resistance to xylem embolism (see below). Although the existence of a trade-off has not been consistently reported in the literature (e.g. Cochard 1992; Sperry and Sullivan 1992; Sperry et al. 1994), available evidence suggests a weak negative correlation between efficiency and security at the global level (Tyree et al. 1994; Pockman and Sperry 2000). Such a trade-off would have important evolutionary implications (Tyree et al. 1994). Alternatively, it may also be that there are direct advantageous effects of cavitation. Xylem embolism can be viewed as a control mechanism which, in connection with stomatal activity, regulates the amount of water extracted by the plant (Salleo et al. 2000).

The mechanism that causes drought-induced xylem cavitation also suggests the existence of a trade-off between conductivity and resistance to embolism. In angiosperms cavitation is supposed to occur when the pressure difference between adjacent air- and water-filled xylem conduits becomes large enough to pull the air-water meniscus through inter-conduit pores towards the water-filled conduit (Zimmermann 1983). The required pressure difference is inversely proportional to the diameter of the pores (Young-Laplace law). If this hypothesis is correct, the plant structural parameter that determines the vulnerability to drought-induced xylem embolism is the diameter of the largest inter-vessel pore. On the other hand, maximum hydraulic conductivity ( $K_h$ ) is normally assumed to be primarily related to the diameter of the conduits raised to the fourth power (Hagen-Poiseuille law; Tyree et al. 1994). Inter-conduit pores are very difficult to observe directly and most of the available data have been obtained using indirect methods (Van Alfen 1983; Jarbeau et al. 1995). In contrast, conduit diameters are much easier to measure and their distribution is usually reported in studies on plant water transport. If inter-conduit pores contribute substantially to xylem resistance (e.g. Calkin et al. 1986) and/or there is a positive relationship between the diameter of a conduit and the size of its larger pore, we would expect a trade-off between conducting efficiency (i.e. maximum conductivity) and security (i.e. resistance to embolism) in the conducting system. In particular, if the relationship between conduit diameter and the size of the largest pore of the conduit was linear, and assuming that specific hydraulic conductivity ( $K_s$ ) scales with the square of mean conduit diameter, we would expect a power relationship with exponent  $-2$  between  $K_s$  and a measure of mean vulnerability to xylem embolism. A linear relationship between conduit and pit pores sizes would naturally occur, for example, if the network of fibrils in the primary wall of pit membranes expands passively as the conduits grow. The assumptions of this model are more thoroughly explained in the Discussion.

The hypothesized trade-off between hydraulic efficiency and resistance to xylem embolism has also potential implications at the individual level. Since  $\Psi$  decreases from soil to leaves, it would be reasonable to expect also a gradient of hydraulic properties within plants. Indeed, vulnerability to drought-induced embolism tends

to be larger in roots than in stems or twigs (e.g. Sperry and Saliendra 1994; Sperry and Ikeda 1997). In agreement with the existence of a trade-off, the size of xylem conduits and  $K_s$  decrease also from roots to stems (Zimmermann 1983). Because of the differences in  $\Psi$ , the relevant question in comparing roots and stems is whether roots live closer to the critical  $\Psi$ s causing dangerous levels of xylem embolism. Some recent studies (e.g. Hacke et al. 2000) indicate that safety margins are indeed much narrower in roots, but yet little work has been done on root xylem (Sperry 2000).

Since differences in environmental conditions may introduce confounding effects in the relationships between hydraulic properties, we have focused on species coexisting in one single area. Few studies have compared the hydraulic architecture of more than three to four species within the same community (one exception is Pockman and Sperry 2000) and, to our knowledge, only one of them has included the study of root systems (Hacke et al. 2000). In this paper we describe the hydraulic architecture and the seasonal water relations of nine woody species from the same area in NE Spain. The studied community is known to be strongly limited by water availability (Rodà et al. 1999). We address the following hypotheses:

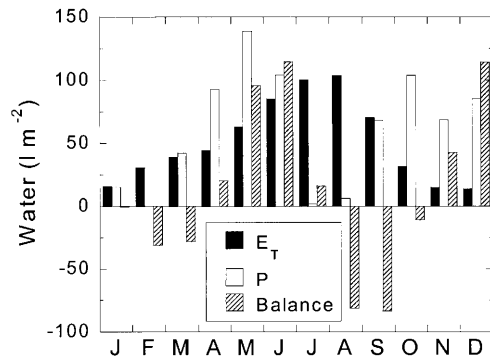
1. (a) Within species of a given community, there is a trade-off between hydraulic conductivity and resistance to cavitation; in particular, (b)  $K_s$  will be inversely proportional to the square of the pressure causing 50% embolism, in agreement with a linear relationship between conduit diameter and the size of the larger pore within the conduit.
2. Species experiencing lower  $\Psi$ s are also more resistant to cavitation. As a result, safety margins would tend to be more similar among species than either minimum  $\Psi$ s or cavitation resistance.
3. Within species, roots live closer to their hydraulic limit than stems.

## Material and methods

### Study site and plant material

The study site was located in the Prades Mountains, NE Spain (41°13'N, 0°55'E). The climate is Mediterranean, with a mean annual rainfall of 537 mm (1981–1995) and moderately warm temperatures (10.0°C mean at Prades, 1,000 m a.s.l.). Plants were sampled on south-facing upper slopes (approximately 1,000 m a.s.l.) of two adjacent valleys (Torners and Castellfollit). The substrate is fractured schist in the Torners area, and metamorphic sandstone in Castellfollit (Hereter and Sánchez 1999). Both valleys are covered by a similar evergreen oak forest (Table 1). We studied populations of nine woody species with different biogeographic origin, distribution, wood type and life-history traits (Table 2). In the following, species will be addressed by genus (except *Cistus*).

Transpiration and  $\Psi$  measurements were conducted during the spring and summer 2000 on four to six previously labelled individuals per species. Although the dry period during 2000 was relatively short, it was particularly dry, with only 8 mm precipitation between late June and early September (Fig. 1). Stem and root



**Fig. 1** Components of the stand's water balance from the field site at Torners valley during 2000. The data were obtained from a standard micro-meteorological station. Potential evapotranspiration ( $E_T$ ) was calculated using the Penman-Monteith equation.  $P$  Rain-fall,  $P - E_T$  cumulative balance,  $J$  January,  $F$  February,  $M$  March,  $A$  April,  $M$  May,  $J$  June,  $J$  July,  $A$  August,  $S$  September,  $O$  October,  $N$  November,  $D$  December

**Table 1** Plant density (stems  $\text{ha}^{-1}$ ) in two plots in the two studied valleys. Only adult individuals with diameter at 0.5 m of  $>2$  cm were counted

Species	Torners <sup>a</sup>	Castellfolit <sup>b</sup>
<i>Acer monspessulanum</i>	58	67
<i>Arbutus unedo</i>	1,175	0
<i>Cistus albidus</i>	<sup>c</sup>	2,133
<i>Cistus laurifolius</i>	<sup>c</sup>	0
<i>Ilex aquifolium</i>	$<30$	$<30$
<i>Juniperus oxycedrus</i>	67	67
<i>Phillyrea latifolia</i>	7,533	3,100
<i>Quercus ilex</i>	6,817	3,433
<i>Sorbus torminalis</i>	192	$<30$
Other woody species	558	1,367

<sup>a</sup> Area sampled=1,200  $\text{m}^2$

<sup>b</sup> Area sampled=300  $\text{m}^2$

<sup>c</sup> These two species were not detected in the inventories but were locally abundant in Torners

**Table 2** Some characteristics of the studied species. *Med* Mediterranean origin, *pMed* pre-Mediterranean origin, *C* conifer, *Dp* diffuse-porous, *Rp* ring-porous, *sRp* semi ring-porous, *E* evergreen, *ssD* summer semi-deciduous, *wD* winter deciduous, *Eur* Eurosibe-

Species	Abbreviation	Family	Origin <sup>a</sup>	Wood <sup>b</sup>	Leaf longevity	Distribution <sup>c</sup>
<i>Acer monspessulanum</i> L	Am	Aceraceae	pMed	Dp	wD	sMed
<i>Arbutus unedo</i> L	Au	Ericaceae	pMed	sRp	E	hMed
<i>Cistus albidus</i> L	Ca	Cistaceae	Med	Dp	ssD	MedR
<i>Cistus laurifolius</i> L	Cl	Cistaceae	Med	sRp	ssD	mMed
<i>Ilex aquifolium</i> L	Ia	Aquifoliaceae	pMed	Dp	E	Eur
<i>Juniperus oxycedrus</i> L	Jo	Cupresaceae	pMed	C	E	MedR
<i>Phillyrea latifolia</i> L	Pl	Oleaceae	pMed	Dp	E	MedR
<i>Quercus ilex</i> L. (ssp. <i>ilex</i> )	Qi	Fagaceae	pMed	Dp	E	hMed
<i>Sorbus torminalis</i> (L.) Crantz	St	Rosaceae	pMed	sRp	wD	sMed

<sup>a</sup> Data from Herrera (1992)

<sup>b</sup> Data from Baas and Schweingruber (1987)

segments at least 60 and 30 cm long, respectively, were collected from both labelled and adjacent plants during winter–spring of 2000 and the spring of 2001 for hydraulic and anatomy measurements. *Arbutus* stems were sampled both years and no significant difference between years was found in  $K_s$ , leaf-specific conductivity ( $K_L$ ), or the two parameters of the vulnerability curves (see below) ( $t$ -test,  $n=6$  stems per year,  $P>0.2$  in all cases). Roots were sampled at a depth of 15–40 cm. The maximum distance between sampled individuals was approximately 1.3 km.

#### $\Psi$ s and transpiration rates

Leaf  $\Psi$  was measured monthly between May and August 2000 with a pressure bomb (PMS Instruments, Corvallis, Ore.) (Scholander et al. 1965). For each sampling date shoot tips from the same four to six different individuals per species were measured at predawn (0200–0400 hours, solar time) and at midday (1100–1300 hours). Predawn  $\Psi$ s ( $\Psi_{pd}$ ) were assumed to be in equilibrium with soil  $\Psi$ s and were compared with the vulnerability curves of roots to establish its minimum safety margins (Hacke et al. 2000; see the ‘‘Vulnerability to xylem embolism’’ section). For stems, the comparison was done with midday  $\Psi$ s ( $\Psi_{md}$ ).

Leaf transpiration rate ( $E$ ) was measured in July and August 2000 on sun-exposed leaves of four individuals per species with a portable gas exchange system (LCA-4; ADC, Hoddesdon, Hertfordshire, UK). Plants were measured in the morning (0800–1000 hours), at midday (1100–1300 hours) and in the afternoon (1400–1600 hours). The natural inclination and azimuth of leaves/shoots was maintained during measurement. Absolute rates were corrected by the actual area of measured leaves, and expressed per area of one side of the leaf. Leaf area was determined in the laboratory using a leaf area meter (LiCor 3100 AM; LiCor, Lincoln, Neb.). Although porometer estimates of ‘‘in situ’’  $E$  are subject to error (McDermitt 1990), this is minimized in our case because we used the data only as a relative measurement. *Quercus* and *Phillyrea* were not measured.

#### Hydraulic conductivity

$K_h$  was measured following Sperry et al. (1988). Segments at least 20 cm long and with a diameter of  $6.6 \pm 0.4$  mm were re-cut underwater from the sampled roots and stems. After removing the bark, their proximal ends were connected to a tubing system. The system was filled with a filtered ( $\phi=0.22 \mu\text{m}$ ) and degassed solution of HCl (pH ca. 2).  $K_h$  ( $\text{m}^4 \text{MPa}^{-1} \text{s}^{-1}$ ) was calculated as the ratio between the flow through the segment and the pressure gradient. The pressure difference was ca. 6 kPa. The flow was measured gravimetrically. In order to obtain the maximum  $K_h$  the segments were flushed at high pressure (ca. 100 kPa) with the mea-

rian region, *hMed* relatively humid areas within the Mediterranean, *MedR* Mediterranean region, *mMed* mountain areas within the Mediterranean, *sMed* sub-Mediterranean areas

<sup>c</sup> Distribution according to Bolós and Vigo (1984–1995)

sure solution for 60 min to remove all native embolisms. The segments were flushed prior to the measurement of the vulnerability curve when the air injection method was used, and after each  $K_h$  measurement when the dehydration method was employed (see below).  $K_S$  ( $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$ ) was calculated as the ratio between maximum  $K_h$  and mean cross-sectional area of the segment (without bark); and  $K_L$  ( $\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$ ), as the quotient between maximum  $K_h$  and leaf area. The ratio between leaf area and mean cross-sectional area ( $A_L:A_S$ , Zimmerman 1983) of each branch segment was also calculated. Leaf area was measured with a leaf area meter (LiCor-3100).

To characterize the changes in the hydraulic pathway of whole plants associated with the summer drought, hydraulic conductance from soil to leaves ( $k_{S-L}$ , in  $\text{mmol m}^{-2} \text{MPa}^{-1} \text{s}^{-1}$ ) was also calculated from transpiration rates and  $\Psi$  measurements:

$$k_{S-L} = E / (\Psi_{pd} - \Psi_{md}) \quad (1)$$

### Vulnerability to xylem embolism

The air injection method (Cochard et al. 1992; Sperry and Saliendra 1994) was used to establish vulnerability curves, except in the case of *Quercus* stems, in which the dehydration method (Tyree and Dixon 1986; Cochard and Tyree 1990) was used. The two methods have been repeatedly compared and shown to give similar results (Cochard et al. 1992; Jarbeau et al. 1995; Sperry and Saliendra 1994). A different method was used for *Quercus* stems because initial measurements using the air-injection technique gave unreasonably high vulnerabilities in relation with the  $\Psi$ s measured in the field. This methodological problem with the air injection technique may be related with the very long vessels in *Quercus* stems: the average maximum vessel length was  $0.96 \pm 0.07$  m in *Quercus* ( $n=5$ ), whereas it was  $<0.60$  m for all the other species ( $n=3-4$ ; air-injection method, Zimmermann and Jeje 1981). Maximum vessel lengths were not measured in roots. However, we compared the vulnerability curves of roots of *Quercus* and *Phillyrea* in which segments had been cut to different lengths. The results showed that there was no significant difference between segments ca. 0.45 m long and segments ca. 0.20 m long [*t*-test comparing the two parameters of the curves (see below),  $n=3-5$  stems per species and size,  $P>0.4$  in all cases], suggesting that segment length was not critical in roots.

When using the air-injection method, six segments were inserted inside a pressure chamber, with both ends protruding. Proximal ends were connected to the measuring circuit, and maximum  $K_h$  was measured. The pressure inside the chamber was then raised to 0.1 MPa, and maintained for 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 at progressively higher injection pressures until the loss of conductivity was complete or a pressure of 8 MPa was reached. The percentage loss of  $K_h$  (PLC) after each pressure application ( $P$ ) was calculated by referring the conductivity after the treatment to the conductivity at 0.1 MPa:  $\text{PLC} = 100 \times [1 - (K_{h,P} / K_{h,0.1})]$ .

*Quercus* stems ca. 3 cm in diameter were collected from 12 different individuals to establish the vulnerability curves using the dehydration method. All stems were longer than 1.50 m. Immediately after cutting, stems were sealed in plastic bags with a humid paper towel and carried to the laboratory. Travel time was approximately 2 h. Once in the laboratory, three to five non-contiguous segments were labelled in each branch. One of them was immediately measured, and the rest of the branch was uncovered and allowed to gradually dehydrate for between 0.5 and 10 days before the percent loss of conductivity of the other segments was estimated. Immediately prior to cutting underwater the segment to be measured, leaf  $\Psi$  was measured in two distal shoot tips.  $K_h$  before and after perfusion with water at high pressure was then measured as described above. PLC was calculated as  $100 \times [1 - (K_{h,\text{after}} / K_{h,\text{before}})]$ .

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

$$\text{PLC} = \frac{100}{1 + e^{a \times (P - P_{50\text{PLC}})}} \quad (2)$$

where  $P_{50\text{PLC}}$  is the pressure (i.e.  $-\Psi$ ) causing a 50% loss of  $K_h$ , and  $a$  is related to the slope of the curve. The advantage of this function is that both parameters have a physiological meaning if we accept Zimmermann's (1983) air-seeding hypothesis.  $P_{50\text{PLC}}$  would be related to the mean of maximum (per conduit) pit-pore size, and  $a$  with the variance of these maximum sizes. A curve was adjusted for each segment, except in the case of *Quercus* branches, where a single curve was adjusted for all individual observations.

The fitted curves were used to calculate the safety margins at which every species (and tissue) was operating, in a way similar to that described by Pockman and Sperry (2000) (see also Hacke et al. 2000). The safety margins were defined as the difference between the minimum  $\Psi$  measured in the field ( $\Psi_{pd}$  for roots and  $\Psi_{md}$  for stems) and the  $\Psi$  required to cause a 75 PLC, calculated from the fitted equation. As we noted previously, we assumed that  $\Psi_{pd}$  equilibrates with soil (and root)  $\Psi$ , which is not always the case (Donovan et al. 2001).

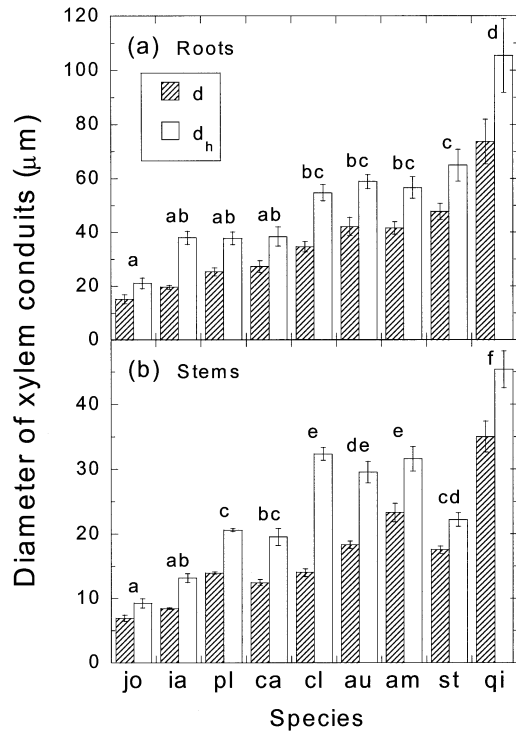
### Xylem anatomy

Conduit diameters were measured on at least four of the stem and root segments per species used to establish vulnerability curves. Transverse sections (ca. 25  $\mu\text{m}$ ) were cut using a rotary microtome (Reichert, Vienna). The sections were stained with safranin (0.1%) to improve contrast and mounted in glycerol. The slides were viewed at 50–100 $\times$  with a compound microscope (Olympus BH-2; Olympus, Hamburg) attached to a monochrome video camera (JVC TK-1270; JVC, Yokohama) 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 conduits wider than a given threshold were sampled. The threshold was selected for each species and tissue in order to maximize the agreement between the visually identified conduits and the ones selected by the computer. For each selected conduit the program determined the total cross sectional area and perimeter. At least 378 conduits were measured per species (the average per species was 2,133 conduits).

Three variables were used to characterize the xylem anatomy of each species: the mean conduit diameter ( $d$ ), the mean hydraulic diameter ( $d_h$ ), and the maximum conduit diameter. The hydraulic diameter was calculated by weighting each conduit according to its contribution to total  $K_h$ . The following expression was used:  $\sum d_i^5 / \sum d_i^4$  (Sperry et al. 1994). A theoretical  $K_S$  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 and corrected for pith area when necessary.

### Statistical analyses

The comparisons of parameters between tissues or among species were made using a one-way ANOVA followed by a honestly significant difference test. When comparing field parameters measured consecutively on the same plants [ $\Psi$ s, stomatal conductance ( $g_s$ ) and soil to leaf hydraulic conductivities], repeated measures ANOVAs were used. Model II regression [reduced major axis method (RMA), Sokal and Rohlf 1995] was used to compute the slope of the relationship between measured variables, because in all cases both the dependent and the independent variables were subject to error. Student *t*-tests were used to test if the calculated slopes were different to the ones predicted by our model. In doing that the SE of the RMA slope was approximated by the SE of the slope of the least squares regression. Variables were normalized when required. All analyses were carried out with the packages



**Fig. 2** Mean conduit diameter ( $d$ ) and mean hydraulic conduit diameter ( $d_h$ ) of roots (a) and stems (b) of the studied species. Note the different scale in (a) and (b). Different letters indicate significant differences in  $d_h$ s between species. Error bars are SEs. *Jo* *Juniperus oxycedrus*, *ia* *Ilex aquifolium*, *pl* *Phillyrea latifolia*, *ca* *Cistus albidus*, *cl* *Cistus laurifolius*, *Au* *Arbutus unedo*, *Am* *Acer monspessulanum*, *St* *Sorbus torminalis*, *Qi* *Quercus ilex*

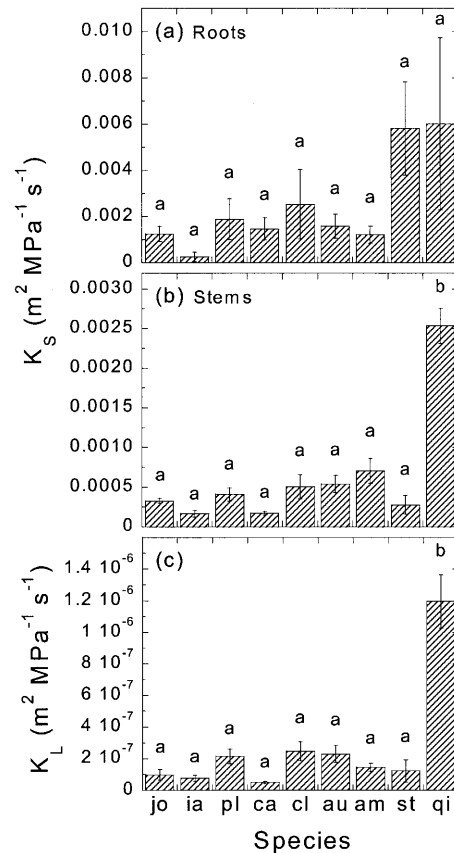
Statistica (version 5.95; StatSoft, Tulsa, Okla.) and SPSS (v. 10.0.6; SPSS, Chicago, Ill.).

## Results

### Xylem anatomy, maximum hydraulic conductivities and vulnerability to embolism

Both diameters and hydraulic diameters of the conduits were larger in roots than in stems (Fig. 2a, b). Among species, the conifer *Juniperus* and the angiosperm *Ilex* had the smallest conduit diameters, while *Quercus* was, by far, the species with the widest conduits (Fig. 2a, b).

As predicted by the differences observed between roots and stems in the hydraulic diameters of xylem conduits, measured  $K_S$  were always higher in roots (Fig. 3a, b). However, these differences were significant only for *Arbutus*, *Cistus albidus*, *Juniperus*, and *Sorbus*. Between-species differences in  $K_S$  were only significant for stems ( $P < 0.001$ ). Branch  $K_S$  was much higher in *Quercus* than in any other species (Fig. 3b). The  $A_L:A_S$  values ranged from  $1,403 \pm 322 \text{ m}^2 \text{ m}^{-2}$  for *Cistus laurifolius* to  $3,527 \pm 227 \text{ m}^2 \text{ m}^{-2}$  for *Cistus albidus*.  $A_L:A_S$  was only marginally different among species ( $P = 0.056$ ), with  $P > 0.1$  for all between-species comparisons. According-



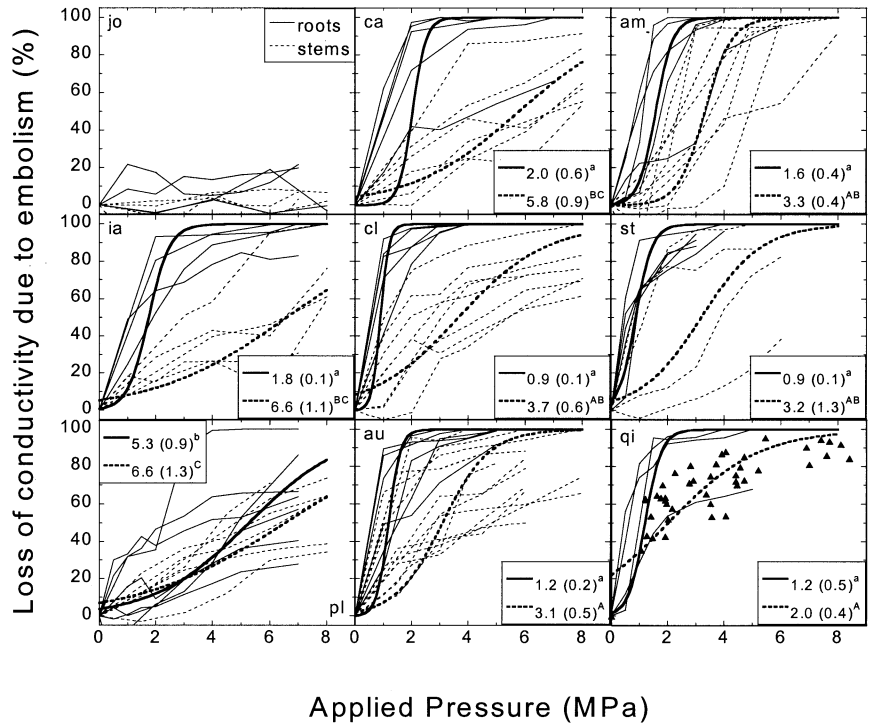
**Fig. 3** Mean specific hydraulic conductivities ( $K_S$ ) of roots (a) and branches (b), and leaf-specific hydraulic conductivities ( $K_L$ ) (c) of the studied species. Note the different scale in (a) and (b). Different letters indicate significant differences between species. Error bars are SEs. Species abbreviations as in Fig. 2

ly, the among-species differences in  $K_L$  ( $P < 0.001$ ) reflected primarily the variation in branch  $K_S$  (Fig. 3). Vulnerability to xylem embolism varied markedly between roots and stems (Fig. 4). Roots were generally more vulnerable than stems (Fig. 4). Roots were generally more vulnerable than stems, except for *Juniperus* (for which we were unable to establish complete vulnerability curves due to high resistance to cavitation) and for *Phillyrea*. The parameters of the fitted vulnerability curves, particularly  $P_{50PLC}$ , reflected between-tissue differences in vulnerability (Fig. 4). Among species, *Juniperus* was the most resistant and for both roots and stems we were unable to induce any significant decrease in conductivity for applied pressures up to  $-8 \text{ MPa}$  (Fig. 4). Of the rest of species, *Phillyrea* was the most resistant to xylem embolism; followed by *Ilex* and *Cistus albidus*. The other five species had similar, and clearly higher, vulnerabilities (Fig. 4).

### Seasonal patterns in water relations and hydraulic conductance

Although all the studied species shared the same habitat,  $\Psi_{pd}$  varied greatly among species (Fig. 5). The dif-

**Fig. 4** Vulnerability curves of roots and stems of all the studied species. The air-injection method was used in all cases except *Quercus* stems, in which the dehydration method was used. All the individual curves are shown, as well as the average fits (Eq. 2) (thicker lines). The pressure causing a 50% loss of hydraulic conductivity (MPa) is shown in the inserts. Different letters indicate significant differences between species ( $\alpha=0.1$ ). Species abbreviations as in Fig. 2



**Table 3** Summary of relationships between structural and functional xylem attributes of the species studied.  $\hat{\beta}_{RMA}$  is the slope estimated by reduced major axis (RMA) regression.  $P_{50PLC}$  Pressure causing a 50% loss of hydraulic conductivity,  $K_S$  specific hydraulic conductivity,  $d$  mean conduit diameter

Relationship	$r^2$	$\hat{\beta}_{RMA}$	$\beta_p$ (predicted)	$p$ ( $\hat{\beta}_{RMA} = \beta_p$ )
$P_{50PLC} = \alpha d^\beta$	0.71***	-1.20 (0.17)	-1.0	0.267
Theoretical $K_S = \alpha d^\beta$	0.87***	2.41 (0.23)	2.0	0.100
Measured $K_S = \alpha d^\beta$	0.83***	2.02 (0.22)	2.0	0.926
Theoretical $K_S = \alpha P_{50PLC}^\beta$	0.77***	-2.01 (0.26)	-2.0	0.979
Measured $K_S = \alpha P_{50PLC}^\beta$	0.53**	-1.68 (0.31)	-2.0	0.322

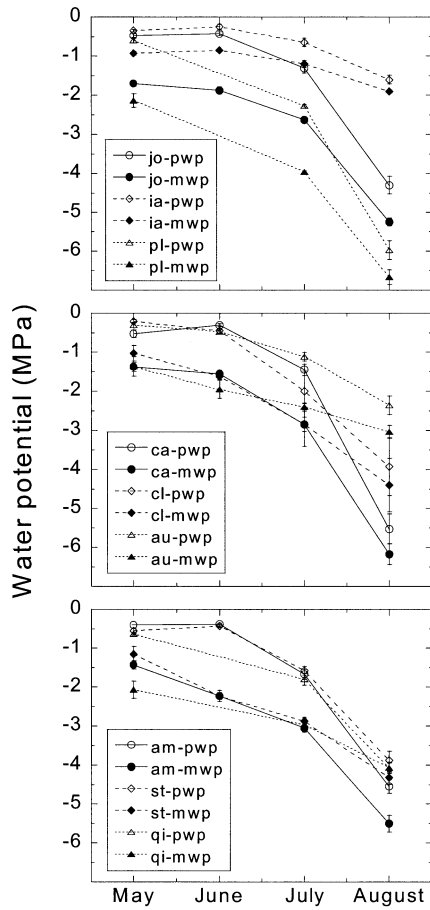
\*\* $P < 0.01$ , \*\*\* $P < 0.001$

ferences were particularly marked during the driest months, where mean  $\Psi_{pd}$  ranged from -1.6 MPa in *Ilex* to -6.0 MPa in *Phillyrea*. This wide range reflects large differences in the microenvironment or in the root system of the studied species. As expected, both  $\Psi_{pd}$  and  $\Psi_{md}$  decreased in all species from May to August ( $P < 0.03$ ). The difference between  $\Psi_{pd}$  and  $\Psi_{md}$  decreased in association with the progression of drought in the case of *Quercus* ( $P = 0.009$ ), whereas it remained approximately constant for all the other species ( $P > 0.07$ ).

Because in July morning and midday values of transpiration rates and  $g_s$  were similar for all species (data not shown), the maximum of the two values was used for all the comparisons. Maximum  $g_s$  ranged from  $0.035 \pm 0.004$  mol m<sup>-2</sup> s<sup>-1</sup> in *Juniperus* to  $0.124 \pm 0.047$  mol m<sup>-2</sup> s<sup>-1</sup> in *Cistus laurifolius*. This values were, at least for the more sensitive species, probably lower than the absolute maximum because water stress was already noticeable in July (Figs. 1, 4). In August, some species showed a decrease in  $g_s$  between morning and midday (data not shown), although the decline was only

significant in the case of *Arbutus* ( $P = 0.015$ ). For that reason, midday values were used to characterize August  $g_s$ . All species reduced  $g_s$  ( $P < 0.054$ ; Fig. 6a) and transpiration rate ( $P < 0.068$ ; data not shown) between July and August in association with the progression of drought (Figs. 1, 5). In three species (*Acer*, *Cistus albidus*, and *Juniperus*) stomata were almost completely closed in August. As predicted, the hydraulic conductance of the soil-to-leaves pathway ( $k_{S-L}$ ) also decreased in association with the drought for all species ( $P < 0.053$ ), except *Sorbus* ( $P = 0.328$ ) (Fig. 6b), which had probably lost a substantial part of the conductivity before July (Figs. 4, 5). Reductions in  $k_{S-L}$  ranged between 28.2% in *Ilex* and 82.7% in *Arbutus*.

The comparison between the pressure causing 75% embolism in the laboratory experiments ( $P_{75PLC}$ ) and the minimum  $\Psi$ s measured in the field showed that roots lived closer to their hydraulic limit than stems of similar diameter. Predicted PLCs in stems were >75% only for *Acer*, *Quercus* and *Sorbus*; whereas in roots they were >75% in all species except *Ilex* and *Phillyrea* (Fig. 7). The shape of the relationship between  $P_{75PLC}$  and mini-

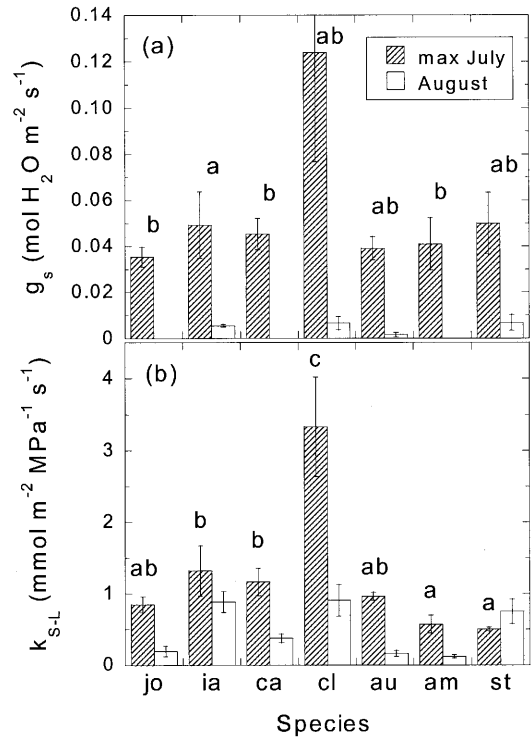


**Fig. 5** Seasonal patterns of predawn (*pwp*) and midday water potentials (*mwp*) for the nine studied species. Error bars are SEs. Species abbreviations as in Fig. 2

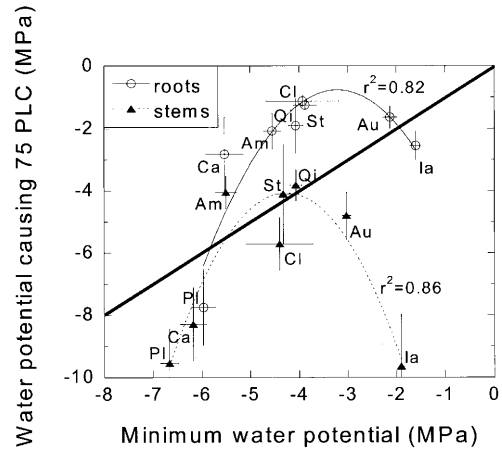
imum  $\Psi$  was parabolic rather than linear for both roots and stems, indicating that safety margins tended to be larger for species experiencing extremely high or extremely low minimum  $\Psi$ s (Fig. 7). The parabolic shape remained if  $P_{90\text{PLC}}$  or  $P_{95\text{PLC}}$  were used instead of  $P_{75\text{PLC}}$  (data not shown).

#### Trade-off between hydraulic efficiency and security

Combining species and tissues, the best fit between the pressure causing a 50% embolism ( $P_{50\text{PLC}}$ ) and  $K_S$  was obtained with a power function with exponent  $-2.01$  when  $K_S$  was calculated from conduit diameters (theoretical  $K_S$ ) or exponent  $-1.68$  when using the measured  $K_S$  (Fig. 8). These exponents were not significantly different from the predicted value of  $-2$  (Table 3). Consistent also with our hypothesis,  $K_S$  (both calculated and measured) scaled approximately with the square of mean conduit diameter ( $d$ ), and  $P_{50\text{PLC}}$  scaled approximately with  $d^{-1}$  (Table 3). In all cases the curves remained similar if roots and stems were segregated (data not shown).

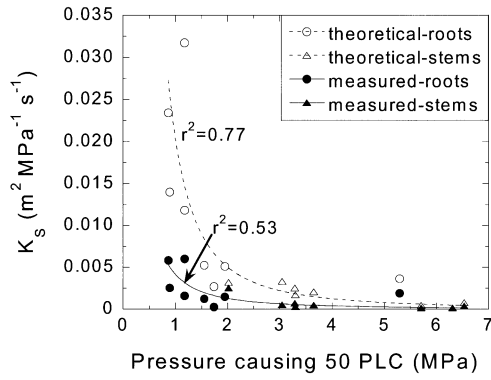


**Fig. 6** Maximum (July) and August values of stomatal conductance ( $g_s$ ; **a**) and soil-to-leaf hydraulic conductance ( $k_{S-L}$ ; **b**) for the studied species. Gas exchange was not measured in *Quercus* and *Phillyrea*. There was no significant difference in maximum  $g_s$  among species. In **a**, the same letter indicates non-significant differences in the percent reduction in  $g_s$ . In **b** different letters indicate significant differences in maximum (July)  $k_{S-L}$ . Error bars are SEs. Species abbreviations as in Fig. 2



**Fig. 7** Relationship between the minimum water potential experienced in the field and the water potential that causes a 75% loss of conductivity estimated from vulnerability curves. Root and branch values are independently fitted with a second-order polynomial regression. *Juniperus* is not included (see text). The straight line shows the 1:1 relationship. Error bars are SEs. Species abbreviations as in Fig. 2





**Fig. 8** Relationship between the pressure that causes a 50% loss of conductivity and the theoretical and measured  $K_S$  for roots and stems of the studied species. Each symbol represents a species' mean. *Juniperus* is not included (see text). Curves were fitted by reduced major axis regression on log-transformed data, and correspond to power functions with exponent  $\approx -2$  (see Table 3)

## Discussion

### Trade-off between hydraulic efficiency and security

Our results show that there is a trade-off between  $K_S$  and resistance to cavitation for the species studied (Fig. 8). A power relationship with exponent  $-2$  between  $K_S$  and the pressure causing a 50% embolism is to be expected if we assume that:

1. Xylem  $K_h$  is linearly proportional to the mean hydraulic diameter of the conduits ( $d_h$ , now calculated as  $\sqrt[4]{\sum d_i^4/n_c}$ , Tyree et al. 1994) raised to the fourth power:

$$K_h \propto d_h^4 \cdot n_c \quad (3)$$

where  $n_c$  is the number of conduits. If xylem area ( $A_X$ ) is proportional to  $d^2$  and  $n_c$ :

$$A_X \propto d^2 \cdot n_c \quad (4)$$

then,

$$K_S = K_h/A_X \propto d_h^4/d^2 \approx d^2 \quad (5)$$

provided that  $d_h \propto d$ . In our case, the coefficient of linear correlation between  $d_h$  and  $d$  using the mean values for each species was 0.996 (data not shown), indicating that this approximation is largely true.

2. The pressure that causes the cavitation of water inside xylem conduits is inversely proportional to the mean of the maximum (per conduit) size of pit pores ( $d_p$ ) (air-seeding hypothesis, Zimmermann 1983):

$$P_{50PLC} \propto 1/d_p \quad (6)$$

3. There is a linear relationship between the diameter of xylem conduits and the size of its larger pore:

$$d \propto d_p \quad (7)$$

The combination of Eqs. 5, 6 and 7 gives:

$$K_S \propto 1/(P_{50PLC})^2 \quad (8)$$

The first two assumptions are normally accepted, and are supported by our data. Therefore, our results are compatible with the hypothesis that there is an approximately linear relationship between vessel and pore sizes.

The shape of Fig. 8 helps to explain why a trade-off between xylem conductivity and resistance to cavitation has not been consistently reported in the literature (e.g. Cochard 1992; Sperry and Sullivan 1992; Sperry et al. 1994). Since the slope of the curve approaches  $-\infty$  or 0 for a substantial part of the relationship, the association between conductivity and resistance to cavitation is easily obscured by measurement error. Only when the studied species/tissues are in the central part of the relationship or a broad range of values is examined does the trade-off become apparent. The best fit was obtained by combining species and tissues, which suggests a general trade-off, independent of xylem type (Fig. 8). Obviously, what exists in real plants is a gradient of hydraulic properties from roots to terminal branches (Zimmermann 1983; Sperry and Saliendra 1994). However, it seems reasonable to concentrate on both ends of the pathway because they are the most likely to fail under extremely dry conditions (e.g. Alder et al. 1996). Pockman and Sperry (2000) also found a power relationship with a negative exponent between  $K_S$  of stems and mean cavitation pressure for 16 species from the Sonoran Desert. Tyree et al. (1994) and Pockman and Sperry (2000) found a weak relationship between conduit diameter and mean cavitation pressure using a large data set including woody species from all over the world. Their results imply a negative power relationship between  $K_S$  and mean cavitation pressure, although the exponent they obtained is less negative than the one predicted by our model. However, if the free parameter of the power relationship differs between functional xylem types or climatic regions, our model would predict a family of curves with exponent  $\approx -2$ . Our results suggest that hidden in the variability observed when considering the relationship at the global scale there is a relationship (or a group of relationships) between conduit diameter and pore size.

The relationship between  $K_S$  and  $P_{50PLC}$  can be viewed as a “cost” curve. In this context, a negative power relationship as seen in Fig. 8 has some important implications. Whereas in a linear trade-off the change in one variable per unit of change in the other (i.e. the slope of the relationship) is constant, in a negative power function it varies from  $-\infty$  to 0. When  $P_{50PLC}$  is small (highly vulnerable tissue) a small increase in  $P_{50PLC}$  would produce a large loss of  $K_S$ . In the other extreme of the curve (low vulnerability and conductivity tissue), any increase in conductivity would be at the expense of a large decrease in resistance to embolism. Conversely, a resistant species would obtain extra resistance (increase its  $P_{50PLC}$ ) at a very low cost in terms of conductivity, and vice versa. Only for the species/tissues situated in the central region of the curve is there an approximately linear trade-off between efficiency and security of the conducting system. The cost of cavitation resistance in terms of  $K_S$  should be considered together with its cost in terms

of wood density (Hacke et al. 2001). In both cases there are diminishing costs as cavitation resistance increases.

#### Vulnerability to embolism and drought resistance

For all the studied species, roots were closer to the hydraulic limit imposed by their vulnerability to xylem embolism than stems of similar diameter (Fig. 7). This seems to be a general characteristic of woody plants (Sperry and Saliendra 1994; Alder et al. 1996; Mencuccini and Comstock 1997; Linton et al. 1998; Kolb and Sperry 1999; Hacke et al. 2000). In fact, since  $\Psi_{pd,s}$  give an integrated measure over the entire “wet” rooting volume and we only sampled surface roots, it is likely that the actual safety margins of roots were even narrower than the calculated ones. Several arguments have been proposed to explain these narrow safety margins: (1) xylem embolism is easier to reverse in roots than in stems because positive or near-positive pressures are much more frequent in roots (e.g. Sperry and Saliendra 1994); (2) root xylem is easier to replace by new growth (e.g. Kolb and Sperry 1999); (3) roots are “cheaper” than stems or branches in terms of carbon investment (e.g. Hacke et al. 2000); and (4) under very dry conditions it may be advantageous to lose the parts of the root system that are in contact with the driest regions of the soil (e.g. Alder et al. 1996). There is an additional reason to expect higher levels of embolism in roots. Since roots are the tissue with higher  $K_s$ , their contribution to total plant resistance is small. In consequence, the impact of a fixed PLC on the conductivity of the whole plant is lower for roots than for any other tissue. In synthesis, it seems that surface roots function as valves responding to water availability: when the soil is wet they offer the least resistance to water transport; as the soil dries, they act as early sensors of water shortage, disconnecting the plant from the driest soil.

Among species, there was a good general correspondence between vulnerability to xylem embolism (Fig. 4) and drought tolerance of the studied species based on their distribution (Table 2). The five species that are distributed over relatively wet Mediterranean or sub-Mediterranean regions (*Acer*, *Arbutus*, *Cistus laurifolius*, *Quercus*, *Sorbus*) were the most vulnerable to xylem embolism. These species, with the exception of *Arbutus*, become scarcer as we move to southern, more arid areas in the Iberian Peninsula (Bolós and Vigo 1984–1995). A similar picture emerges when we compare the vulnerability curves with the  $\Psi$ s experienced in the field (Fig. 7). Six species (the same previous ones plus *Cistus albidus*) were predicted to retain <25% of the maximum  $K_h$  of roots at the peak of the drought. The fact that *Cistus albidus* was severely affected by xylem embolism is not surprising since it is a drought-deciduous species (see, for example, Kolb and Davis 1994). Only *Acer*, *Quercus* and *Sorbus* stems were predicted to experience high levels of xylem embolism in the field (PLC>25% in

August). Field observations indicated that *Acer* and *Sorbus* suffered higher levels of foliar senescence than any other species (except the summer-deciduous *Cistus*). However, senescence affected <25% of their leaf area (R. Ogaya, unpublished results). The case of *Ilex*, which is, according to its distribution, the less drought-tolerant of the species studied and, at the same time, one of the most resistant to xylem embolism (Fig. 4), deserves special attention. *Ilex* is an evergreen Eurosiberian species which, within the Mediterranean region, is restricted to the wettest and coldest areas (Castroviejo et al. 2000). We hypothesize that the hydraulic properties of *Ilex* are more related to the avoidance of freezing-induced xylem embolism in the cold areas where this species normally lives than to water stress. Since there is a direct link between the size of xylem conduits and their vulnerability to freezing-induced embolism (Tyree et al. 1994), the extremely narrow vessels of *Ilex* are not surprising. The fact that  $\Psi$ s never fell below  $-2$  MPa in this species, well above the values of deep-rooted species such as *Quercus* (Fig. 5), supports the idea that *Ilex* was able to grow only in the wettest microenvironments within the study area.

Despite the large differences in vulnerability to xylem embolism among species, all of them reduced  $g_s$  (Fig. 6a) and  $E$  (data not shown) to very low values. The reduction, however, was significantly lower in the embolism-resistant species *Ilex* (86%; Fig. 6a). Likewise, the reduction of  $g_s$  between late April and late July was lower in the embolism-resistant *Phillyrea* (80%) than in *Quercus* (90%) (R. Ogaya, unpublished results). Our results suggest that, at least for some species, stomatal closure during the drought was not only associated with the avoidance of hydraulic failure due to cavitation. This is particularly true in the case of *Juniperus*, which showed an acute reduction in  $g_s$  and  $E$  despite the fact it was predicted to experience negligible levels of xylem embolism. However, it should be considered that, since the relationship between  $K_h$  and  $\Psi$  is not linear, a plant may be very close to the critical transpiration rate causing hydraulic failure while maintaining a relatively wide safety margin in relation to the critical  $\Psi$  (e.g. Kolb and Sperry 1999). One caveat in our results is that we did not measure the changes in leaf area during the drought and, thus, we do not know how the changes in calculated  $k_{s-L}$  (Fig. 6b) translate in terms of specific hydraulic conductance over the soil-to-leaf pathway. Field observations indicated that all the studied species except *Ilex* and *Phillyrea* suffered partial defoliation (extensive in the case of both *Cistus* species) during late August.

In spite of the fact that the study area was relatively homogeneous, the species studied were extremely heterogeneous regarding their hydraulic properties. Using data from 73 species from around the world,  $\Psi$ s causing 50% embolism in stems ranged from ca.  $-1$  to  $-12.5$  MPa (Pockman and Sperry 2000). In this study we have measured values from  $-2$  to  $<-8$  MPa. An important part of this variation is associated with differences in the general ecology of the species (e.g. winter- and summer-deciduous species tend to be more vulnerable). However, there

are also substantial differences between ecologically similar species, such as *Phillyrea* and *Quercus*. In agreement with the higher vulnerability to xylem embolism of *Quercus*, this species has been much more severely affected by the episodes of extreme drought registered in NE Spain during the last decade (Peñuelas et al. 2000). In a context of increased aridity as the one predicted by the IPCC climate change models for the Mediterranean region (Houghton et al. 2001) and already observed in some areas of NE Spain (Piñol et al. 1998), these differences in vulnerability to xylem embolism and general hydraulic architecture can have important implications for plant survival (Martínez-Vilalta et al. 2002).

Unlike other studies (Hacke et al. 2000; Pockman and Sperry 2000), we have not found a linear relationship between vulnerability to xylem embolism and the minimum  $\Psi_s$  under field conditions. Instead, safety margins tended to be wider for species experiencing very high or very low  $\Psi_s$  (Fig. 7), contradicting our hypothesis that safety margins would be similar among species. Two questions are particularly relevant: why is xylem embolism so high in some species? And, if there is a trade-off between efficiency and safety of the conducting system (Fig. 8), why do some species have wide safety margins? In relation to the first question, we have to consider that the summer of 2000 was considerably drier than average. If xylem embolism (particularly in surface roots) acts together with stomatal control as a valve regulating water use during dry periods (Kolb and Sperry 1999; Salleo et al. 2000; Sperry 2000), substantial levels of embolism are probably commonplace during acute droughts. Regarding the existence of wide safety margins even during extremely dry conditions (e.g. *Ilex*, *Juniperus*, *Phillyrea*), the shape of Fig. 8 provides a possible explanation. For tissues that are very resistant to xylem embolism additional resistance would be obtained almost without cost in terms of  $K_s$ . In contrast, even a small increase in conductivity would be at the expense of a large decrease in resistance to embolism. It is likely that, in the field, this increase in  $K_s$  would be offset by the increase in xylem embolism associated with higher vulnerabilities. In that case, the parabolic relationship between embolism and minimum  $\Psi_s$  (Fig. 7) would be more related to historical reasons (phylogeny and biogeography of the particular species studied) than to a general parabolic relationship between the two variables. As discussed above, this could easily be the case for *Ilex*, which is the species that shows the largest departure from a linear relationship.

In conclusion, a negative power relationship between  $K_s$  and resistance to xylem embolism has been found. This is consistent with a linear relationship between vessel diameter and the size of its larger pore, and may explain macroscopic patterns such as the existence of species that are overly resistant to xylem embolism. In addition, the shape of the power curve may help to explain why a trade-off between xylem conductivity and resistance to cavitation has not been consistently reported in the literature.

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