

CHAPTER 3

Hydraulic properties of roots and stems of nine woody species from a Holm oak forest in NE Spain

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submitted

*But in the nature of things beauties are incompatible.
The spring cannot coexist with the autumn, nor day with night;
what is beautiful in a child is hideous in a man, and vice versa;
every age, every country, each sex, has a peculiar beauty,
finite and incommunicable; the better it is attained
the more completely it excludes any other.*

(G. Santayana, *The Sense of Beauty* (1896))

Resum

En aquest treball estudiem l'arquitectura hidràulica d'arrels i branques de nou espècies que conviuen a un alzinar del nord-est d'Espanya. Les espècies estudiades difereixen en les seves relacions filogenètiques, el seu origen biogeogràfic, el tipus de fusta i l'hàbit foliar. Per a cada espècie es va mesurar l'anatomia del xilema, la vulnerabilitat a l'embolisme induït per sequera, i la dinàmica estacional de les relacions hídriques. Les diferències en les propietats hidràuliques que vam trobar entre teixits són consistents amb els resultats obtinguts en estudis previs. El diàmetre dels conductes del xilema, la conductivitat hidràulica i la vulnerabilitat a l'embolisme van resultar majors a les arrels que a les branques. De resultes d'això, les arrels superficials operaven més a prop del seu límit hidràulic que les branques de diàmetre similar. Els nostres resultats també van mostrar grans diferències en les propietats hidràuliques entre espècies. La pressió a la qual es produïa un 50% d'embolisme va variar entre 1.3 i >8 MPa a les arrels i entre 3.1 i >8 MPa a les branques. De més a menys vulnerable a l'embolisme, les espècies estudiades eren: *Quercus ilex* = *Acer monspessulanum* = *Arbutus unedo* = *Sorbus torminalis* = *Cistus laurifolius* > *Cistus albidus* = *Ilex aquifolium* > *Phillyrea latifolia* > *Juniperus oxycedrus*. Totes les espècies van mostrar grans reduccions de la conductivitat estomàtica associades amb la progressió de l'eixut. Els marges de seguretat (definites com la diferència entre les pressions a les quals es produeix un 95% d'embolisme i els potencials hídrics mínims mesurats al camp) van resultar també molt diferents segons les espècies. Algunes d'elles (*J. oxycedrus*, *I. aquifolium*, *P. latifolia*) tenien un xilema desproporcionadament resistent a la cavitació. Vam trobar una relació no lineal negativa entre la conductivitat hidràulica i la resistència a la cavitació. La forma d'aquesta relació, una funció potencial amb exponent *ca.* -2, l'expliquem amb un model simple que assumeix una relació lineal entre el diàmetre dels vasos i la mida del seu porus més gran. Finalment, discutim les implicacions per la tolerància a la sequera del compromís que implica la relació anterior.

Abstract

The hydraulic architecture of roots and stems of nine woody species was studied in a Holm oak forest in NE Spain. The species studied differed in phylogenetic relationships, biogeographical origin, wood type and leaf-habit. Xylem anatomy, hydraulic conductivity, vulnerability to drought-induced xylem embolism, and seasonal water relations during a period of acute drought were measured. Between-tissues differences in hydraulic properties were consistent with previous findings reported in the literature. The diameter of xylem conduits, hydraulic conductivity and vulnerability to xylem embolism were always higher in roots than in stems. Surface roots were shown to live closer to their hydraulic limit than stems of similar diameter. Our results also showed large differences in hydraulic properties among species. The pressure at which a 50% of conductivity was lost due to embolism ranged between 1.3 and >8 MPa for roots and between 3.1 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*. All species showed large reductions in stomatal conductance associated with the progression of drought. Safety margins (defined as the difference between the pressure causing 95% embolism and minimum leaf water potentials under field conditions) differed markedly among species, with some of them (*J. oxycedrus*, *I. aquifolium*, *P. latifolia*) showing a xylem overly resistant to cavitation. A non-linear, negative relationship between hydraulic conductivity and resistance to cavitation was found when species and tissues were combined. The shape of this relationship, a power function with exponent *ca.* -2, is explained using a simple model that assumes a linear relationship between vessel diameter and the size of its larger pore. The implications of the trade-off implied by the above relationship are discussed in relation to drought tolerance of the species studied.

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 & 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 single attributes are not very meaningful when considered alone, they usually combine in very specific ways to conform 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 evidence supporting that xylem embolism limits gas exchange (Sperry *et al.* 1998) and, in general, the ability of plants to cope with water stress (Pockman & 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 experienced in the field (Hacke *et al.* 2000, Pockman & Sperry 2000, Sperry 2000). As a result, the difference between the critical water potentials causing catastrophic levels of xylem embolism and the minimum values under field conditions (*i.e.*,

safety margins, Tyree & 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 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 & 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 & 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). Under certain circumstances a decline in the conductivity of the xylem may allow the plant to draw the most water from the soil over the longest time (Sperry 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 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 is 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 has 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 pores, 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 pores 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. 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 within individuals. Since water potential 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 &

Saliendra 1994, Sperry & Ikeda 1997). In agreement with the existence of a trade-off, the size of xylem conduits and hydraulic conductivity decrease also from roots to stems (Zimmermann 1983). Because of the differences in water potential, the relevant question in comparing roots and stems is whether roots live closer to the critical water potentials causing dangerous levels of xylem embolism. Some recent studies (*e.g.*, Hacke *et al.* 2000) indicate that safety margins are 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 in species coexisting in one single area. Few studies have compared the hydraulic architecture of more than 3-4 species within the same community (one exception is Pockman & 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 limited by water availability (Rodà *et al.* 1999). We address the following hypotheses: (1a) within species of a given community, there is a trade-off between hydraulic conductivity and resistance to cavitation; in particular, (1b) specific hydraulic conductivity 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 water potentials are also more resistant to cavitation and, hence, safety

margins would be similar among species. (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, 1000 m asl). Plants were sampled in south-facing upper slopes (approximately 1000 m asl) of two adjacent valleys (Torners and Castellfollit). The substrate is fractured schist in the Torners area, and metamorphic sandstone in Castellfollit (Hereter & Sánchez 1999). Both valleys are covered by a similar Holm oak forest (Table 1). We studied populations of nine species with different biogeographic origin, distribution, wood type and life-history traits (Table 2).

Table 1. Plant density (stems ha⁻¹) in the two studied valleys. Only adult individuals with diameter at 0.5 m > 2 cm were counted.

Species	Torners ^a	Castellfollit ^b
<i>Acer monspessulanum</i>	58	67
<i>Arbutus unedo</i>	1175	0
<i>Cistus albidus</i>	^c	2133
<i>Cistus laurifolius</i>	^c	0
<i>Ilex aquifolium</i>	<30	<30
<i>Juniperus oxycedrus</i>	67	67
<i>Phillyrea latifolia</i>	7533	3100
<i>Quercus ilex</i>	6817	3433
<i>Sorbus torminalis</i>	192	<30
Other woody species	558	1367

^a Area sampled=1200 m².

^b Area sampled=300 m².

^c These two species were not detected in the inventories but were locally abundant in Torners.

Transpiration and water potential measurements were conducted during the spring and summer of 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 of precipitation between late June and early September (Figure 1). Stem and root segments at least 60 and 30 cm long, respectively, were collected from both labelled and adjacent plants during the winter-spring of 2000 and the spring of 2001 for hydraulic and anatomy measurements. *A. unedo* stems were sampled both years and no significant difference between years was found in specific hydraulic conductivity, leaf-specific conductivity, 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.

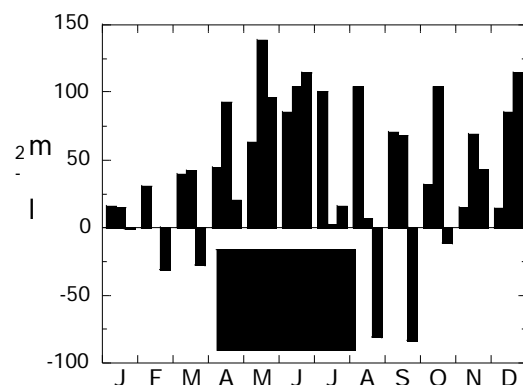


Figure 1. Meteorological data (E_T : potential evapotranspiration; P: rainfall; cumulative balance: $P - E_T$) from the field site at Torners valley during 2000. The data was obtained from a standard micro-meteorological station. E_T was calculated using the Penman-Monteith equation.

Table 2. Some characteristics of the studied species.

Species	Abbr.	Family	Origin ^a	Wood ^b	Habit ^c	Distr. ^d
<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	Med
<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	Med
<i>Phillyrea latifolia</i> L.	Pl	Oleaceae	pMed	Dp	E	Med
<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

^a Data from Herrera (1992). Med: Mediterranean origin, pMed: pre-Mediterranean origin.

^b Data from Baas and Schweinbruger (1987). C: conifer, Dp: diffuse-porous, Rp: ring-porous, sRp: semi ring-porous.

^c E: evergreen, ssD: summer semi-deciduous, wD: winter deciduous.

^d Distribution according to Bolós and Vigo (1984-1995). Eur: Eurosiberian Region, hMed: relatively humid areas within the Mediterranean, Med: Mediterranean Region, mMed: mountain areas within the Mediterranean, sMed: sub-Mediterranean areas.

Water potentials and transpiration rates

Leaf water potential was measured monthly between May and August 2000 with a pressure bomb (PMS Instruments, Corvallis, Oregon, USA) (Scholander *et al.* 1965). For each sampling date shoot tips from the same 4-6 different individuals per species were measured at predawn (0200-0400 h, solar time) and at midday (1100-1300 h). Predawn water potentials (ψ_{pd}) were assumed to be in equilibrium with soil water potentials 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 water potentials (ψ_{md}).

Leaf transpiration rate (E) was measured in July and August 2000 on sun-exposed leaves of 4 individuals per species with a portable gas exchange system (LCA-4, ADC Inc., Hoddesdon, Hertfordshire, UK). Plants were measured in the morning (0800-1000 h), at midday (1100-1300 h) and in the afternoon

(1400-1600 h). 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 one-sided leaf area. Leaf area was determined in the laboratory using a leaf area meter (LICOR 3100 AM, LICOR Inc., Lincoln, Nebraska, USA). 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. *Q. ilex* and *P. latifolia* were not measured.

Hydraulic conductivity

Hydraulic conductivity was measured following Sperry *et al.* (1988). Segments at least 20 cm long and with a diameter of 6.6 ± 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 ($\approx 0.22 \mu\text{m}$) 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 ($P \approx 6$ kPa). The flow was measured gravimetrically. In order to obtain the maximum hydraulic conductivity the measure solution was previously injected at high pressure ($ca.$ 100 kPa) for 60 min to remove all native embolisms from the segment. Specific hydraulic conductivity (K_S , in $m^2 MPa^{-1} s^{-1}$) 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 $m^2 MPa^{-1} s^{-1}$), as the quotient between maximum hydraulic conductivity 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, LICOR Inc., Lincoln, Nebraska, USA).

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 $mmol m^{-2} MPa^{-1} s^{-1}$) was also calculated from transpiration rates and water potential measurements:

$$k_{S-L} = \frac{E}{md - pd} \quad (\text{eq. 1})$$

Vulnerability to xylem embolism

The air injection method (Cochard *et al.* 1992, Sperry & Saliendra 1994) was used to establish vulnerability curves, except in the case of *Q. ilex* stems, in which the dehydration method (Tyree & Dixon 1986, Cochard &

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 & Saliendra 1994). A different method was used for *Q. ilex* stems because initial measurements using the air-injection technique gave unreasonably high vulnerabilities compared to the water potentials measured in the field, probably because of the very long vessels in this species. The mean maximum vessel-length in *Q. ilex* stems was 0.96 ± 0.07 m (N=5), whereas it was <0.60 m for all the other species (N=3-4; air-injection method, Zimmermann & Jeje 1981). Maximum vessel-lengths were not measured in roots. However, we compared the vulnerability curves of roots of *Q. ilex* and *P. latifolia* 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 longitude, $p > 0.4$ in all cases).

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 hydraulic conductivity was measured. The pressure inside the chamber was then raised to 0.1 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 at progressively higher injection pressures until the loss of conductivity was complete or a pressure of 8 MPa was reached. The percentage loss of

hydraulic conductivity (PLC) after each pressure application (P) was calculated by referring the conductivity after the treatment to the conductivity at 0.1 MPa: $PLC = 100(1 - (K_{h,P}/K_{h,0.1}))$.

Q. ilex stems from twelve different individuals were collected 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 two hours. Once in the laboratory, 3-5 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 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 water potential was measured in two distal shoot tips. Hydraulic conductivity before and after perfusion with water at high pressure was then measured as described above. PLC was calculated as $100(1 - (K_{h,after}/K_{h,before}))$.

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

$$PLC = \frac{100}{1 + e^{a(P-b)}} \quad (\text{eq. 2})$$

where b is the pressure (*i.e.*, -) causing a 50% loss of hydraulic conductivity, 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. Parameter b would be related with the mean of maximum (per conduit) pit-pore size, and a with the variance of this maximum size. The value of the parameters was obtained by least squares regression after linearization of equation 1. A curve was adjusted for each branch in the case of *Q. ilex* and for each segment in the other species/tissues.

The fitted curves were used to calculate the safety margins at which every species (and tissue) was operating, in a way similar to Pockman & Sperry (2000; see also Hacke *et al.* 2000). The safety margins were defined as the difference between the minimum water potential measured in the field (ψ_{pd} for roots and ψ_{md} for stems) and the water potential required to cause a 95 PLC, calculated from the fitted equation. In the same way, maximum specific hydraulic conductivity (K_s) values were combined with vulnerability curves and water potentials to predict the actual specific conductivities of roots and stems under field conditions (effective K_s). In doing that it was assumed that embolisms were noncumulative and, thus, our values are minimum estimates.

Xylem anatomy

Conduit diameters were measured on at least four of the stem and root segments used to establish vulnerability curves for each species. 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 50-100x 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 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 2133 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 considering that hydraulic conductivity is proportional to the diameter raised to the fourth power. The following expression was used: $\sqrt[4]{d_i^4/N}$ (Tyree *et al.* 1994). A theoretical specific hydraulic conductivity was also calculated for each section exclusively from anatomy data using the Hagen-Poiseuille law. 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 HSD test. When comparing field parameters measured consecutively on the same plants (water potentials, stomatal conductance and soil to leaf hydraulic conductivities), repeated measures ANOVAs were used. Correlations between different parameters were analysed using Pearson correlation tests. Variables were normalized when required. All analyses were carried out with the package Statistica (Version 5.5, StatSoft, Inc., Tulsa, OK, USA).

Results

Xylem anatomy, maximum hydraulic conductivity and vulnerability to embolism

Between-tissues differences in xylem anatomy were highly significant for all studied species ($p < 0.003$). Both diameters and hydraulic diameters of the conduits were larger in roots than in stems (Figures 2a and 2b). Among species, the conifer *J. oxycedrus* and the angiosperm *I. aquifolium* had the smallest conduit diameters, while *Q. ilex* was, by far, the species with wider conduits (Figures 2a and 2b).

As predicted by the differences observed between roots and stems in the hydraulic diameters of xylem conduits, measured specific hydraulic conductivities (K_s) were always higher in roots. However, these differences were significant only for *A. unedo*, *C. albidus*, *J. oxycedrus*, and *S. torminalis*. Between-species differences in K_s were only

significant for stems ($p < 0.001$). Branch K_S was much higher in *Q. ilex* than in any other species (Figure 3b). The $A_L:A_S$ values ranged from $1403 \pm 322 \text{ m}^2 \text{ m}^{-2}$ for *C. laurifolius* to $3527 \pm 227 \text{ m}^2 \text{ m}^{-2}$ for *C. albidus*. $A_L:A_S$ was only marginally different among species ($p = 0.056$), with $p > 0.1$ for all between-species comparisons. Accordingly, the among-species differences in leaf-specific conductivity (K_L) ($p < 0.001$) reflected primarily the variation in branch K_S (Figure 3). Vulnerability to xylem embolism varied markedly between roots and stems (Figure 4). Roots were generally more vulnerable than stems, except for *J. oxycedrus* (for which we were unable to establish complete vulnerability curves due to high resistance to cavitation) and for *P. latifolia*. The parameters of the fitted vulnerability curves, particularly the parameter b , reflected between-tissues differences in vulnerability (Figure 4). Among species, *J. oxycedrus* 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 MPa (Figure 4). Of the rest of species, *P. latifolia* roots and stems were the most resistant to xylem embolism; followed by *I. aquifolium* and *C. albidus*. The other five species had similar, and clearly higher, vulnerabilities (Figure 4).

Seasonal patterns in water relations and hydraulic conductance

Although all the studied species shared the same habitat, predawn water potential varied greatly among species (Figure 5). The differences were particularly marked during the driest months, where mean predawn water potential ranged from -1.6 MPa in *I. aquifolium*

to -6.0 MPa in *P. latifolia*. This wide range reflects large differences in the microenvironment or in the root system of the species studied. As expected, both predawn and midday water potentials decreased in all species from May to August ($p < 0.03$). The difference between predawn and midday water potential decreased in association with the progression of drought in the case of *Q. ilex* ($p = 0.009$), whereas it remained approximately constant for all the other species ($p > 0.07$).

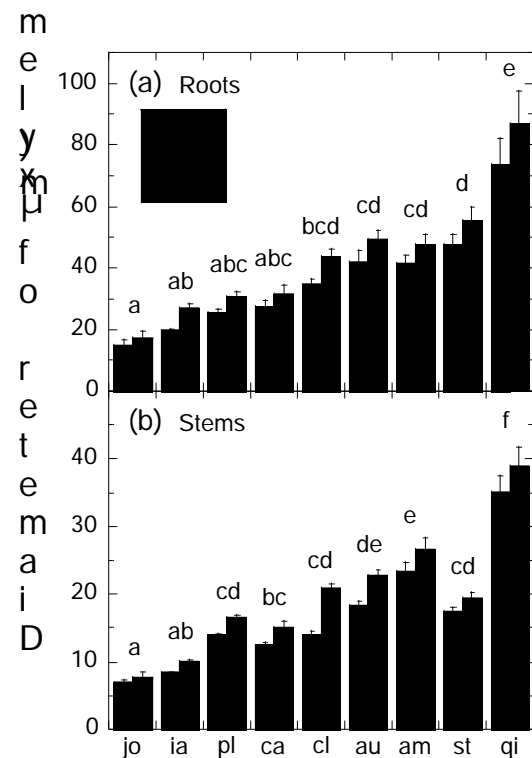


Figure 2. Mean conduit diameter (d) and mean hydraulic conduit diameter (d_h) of roots (a) and stems (b) of the studied species. Note the different scale in (a) and (b). Different letters indicate significant differences in hydraulic diameters between species. Error bars are standard errors. Species abbreviations as in Table 2.

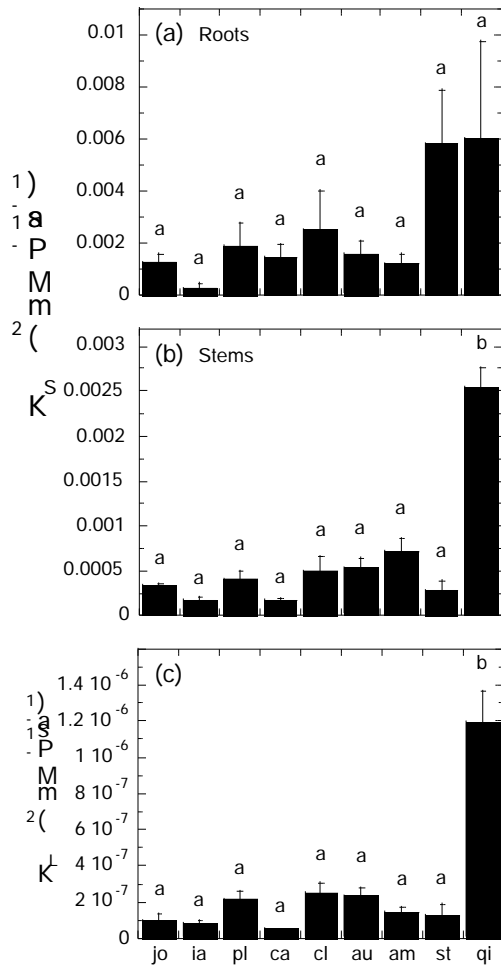


Figure 3. Mean specific conductivities (K_s) of roots (a) and branches (b), and leaf-specific conductivities (c) of the studied species. Note the different scale in (a) and (b). Different letters indicate significant differences between species. Error bars are standard errors. Species abbreviations as in Table 2.

Because in July morning and midday values of transpiration rates and stomatal conductance were similar for all species (data not shown), the maximum of the two values was used for all the comparisons. Maximum stomatal conductance ranged from $0.035 \pm 0.004 \text{ mol m}^{-2} \text{ s}^{-1}$ in *J. oxycedrus* to $0.124 \pm 0.047 \text{ mol m}^{-2} \text{ s}^{-1}$ in *C. 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 (Figures 1 and 5). In August, some species showed a decrease in stomatal conductance between morning and midday (data not shown), although the decline was only significant in the case of *A. unedo* ($p=0.015$). For that reason, midday values were used to characterize August stomatal conductance. All species reduced stomatal conductance ($p<0.054$; Figure 6a) and transpiration rate ($p<0.068$; data not shown) between July and August in association with the progression of drought (Figures 1 and 5). In three species (*A. monspessulanum*, *C. albidus*, and *J. oxycedrus*) 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 *S. torminalis* ($p=0.328$) (Figure 6b), which had probably lost a substantial part of the conductivity before July (Figure 7). Reductions in k_{s-L} ranged between 28.2% in *I. aquifolium* and 82.7% in *A. unedo*. Substantial declines in effective K_s (>25%) were predicted in both roots and stems for all species except *J. oxycedrus* and *I. aquifolium* (Figures 7a and 7b).

The comparison between the pressure causing 95% embolism in the laboratory experiments (P_{95PLC}) and the minimum water potentials measured in the field showed that roots lived closer to their hydraulic limit than stems of similar diameter (Figure 8). In stems, safety margins were >2 MPa for all species except *A. monspessulanum*; whereas in roots predicted PLCs were >95% in *A. monspessulanum*, *C. albidus*, *C. laurifolius*, *Q. ilex*, and *S. torminalis*. The shape of the relationship between P_{95PLC} and ψ_{min} was

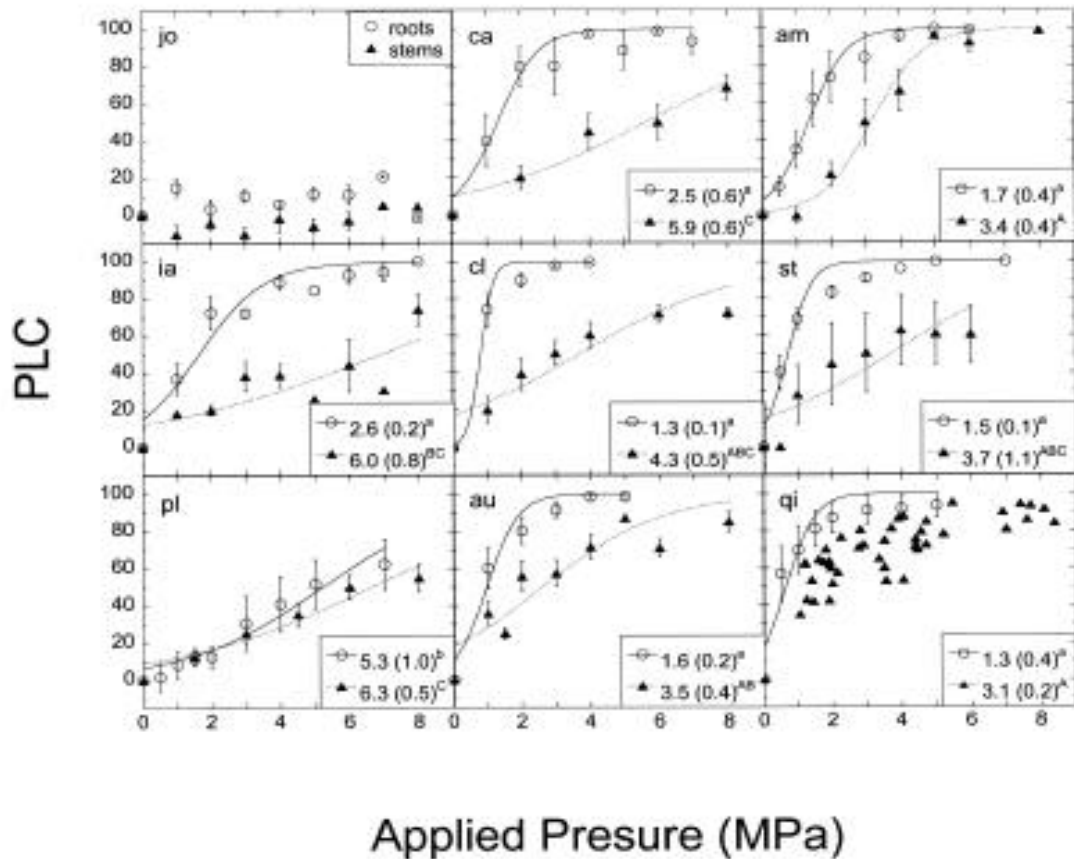


Figure 4. Vulnerability curves of roots and stems of all the studied species (PLC: percent loss of conductivity due to xylem embolism). The air-injection method was used in all cases except *Q. ilex* stems, in which the dehydration method was used. The values of the parameter b of vulnerability curves are shown in the inserts. Different letters indicate significant differences between species. Error bars are standard errors. Species abbreviations as in Table 2.

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 water potentials (Figure 8).

Trade-off between hydraulic efficiency and security

Combining species and tissues, the best fit between the pressure causing a 50% embolism (parameter b of vulnerability curves)

and specific hydraulic conductivity (K_s) was obtained with a power function with exponent -2.2 when K_s was calculated from conduit diameters (theoretical K_s) or exponent -1.5 when using the measured K_s . The correlation was highly significant in both cases ($p < 0.001$). When we fixed the exponent of the relationships to the hypothesized value of -2 , correlation coefficients remained almost identical (0.872 vs. 0.868 for theoretical K_s , and 0.743 vs. 0.742 for measured K_s). The curves remained also very similar if roots and stems were segregated (Figure 9). In that

case, the significances of correlations were always <0.05 for stems and 0.1 for roots. Consistent also with our hypothesis, K_S (both calculated and measured) was correlated with the square of mean conduit diameter (d) ($r = 0.85$, $p < 0.001$), and the parameter b of vulnerability curves was correlated with d^{-1} ($r = 0.80$, $p = 0.008$).

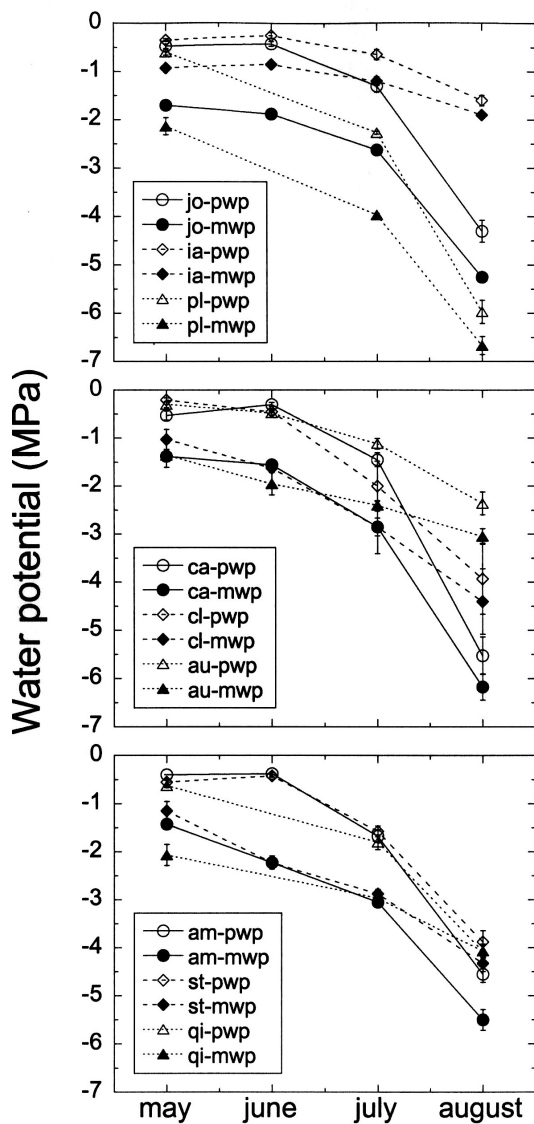


Figure 5. Seasonal patterns of predawn (pwp) and mid-day water potentials (mwp) for the nine studied species. Error bars are standard errors. Species abbreviations as in Table 2.

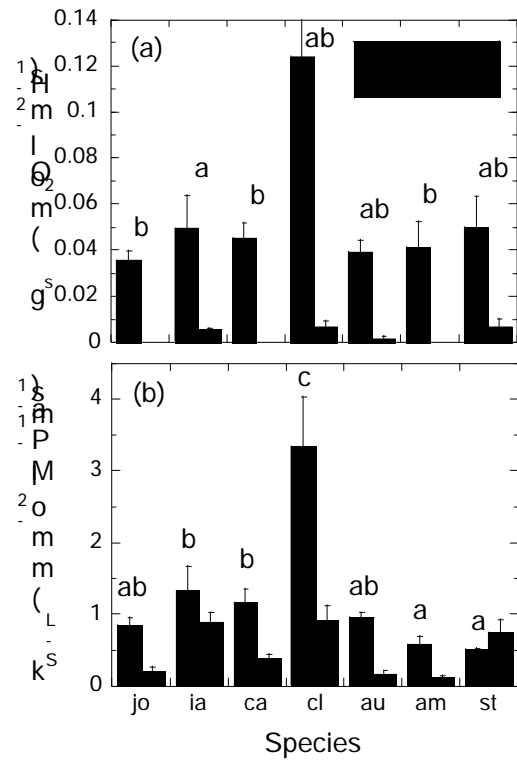


Figure 6. Maximum (July) and August values of stomatal conductance (g_s ; a) and soil-to-leaf hydraulic conductance (k_{S-L} ; b) for the studied species. Gas exchange was not measured in *Q. ilex* and *P. latifolia*. There was no significant difference in maximum g_s among species. In the upper panel (a), the use of the same letter indicates nonsignificant differences in the percent reduction in g_s . In panel b, different letters indicate significant differences in maximum (July) k_{S-L} . Error bars are standard errors. Species abbreviations as in Table 2.

Discussion

Trade-off between hydraulic efficiency and security

Our results show that there is a trade-off between specific hydraulic conductivity and resistance to cavitation for the species studied (Figure 9). 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 hydraulic conductivity is linearly proportional to the mean hydraulic diameter of the conduits (d_h) raised to the fourth power:

$$K_h = d_h^4 N_c \quad (\text{eq. 3})$$

where N_c is the number of conduits. If xylem area (A_x) is proportional to d^2 and N_c :

$$A_x = d^2 N_c \quad (\text{eq. 4})$$

Then,

$$K_s = \frac{K_h}{A_x} = \frac{d_h^4}{d^2} N_c \quad (\text{eq. 5})$$

Provided that $d_h = d$. 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):

$$b = \frac{1}{d_p} \quad (\text{eq. 6})$$

(3) There is a linear relationship between the diameter of xylem conduits and the size of its larger pores:

$$d = d_p \quad (\text{eq. 7})$$

The combination of equations 5, 6 and 7 gives:

$$K_s = \frac{1}{b^2} \quad (\text{eq. 8})$$

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.

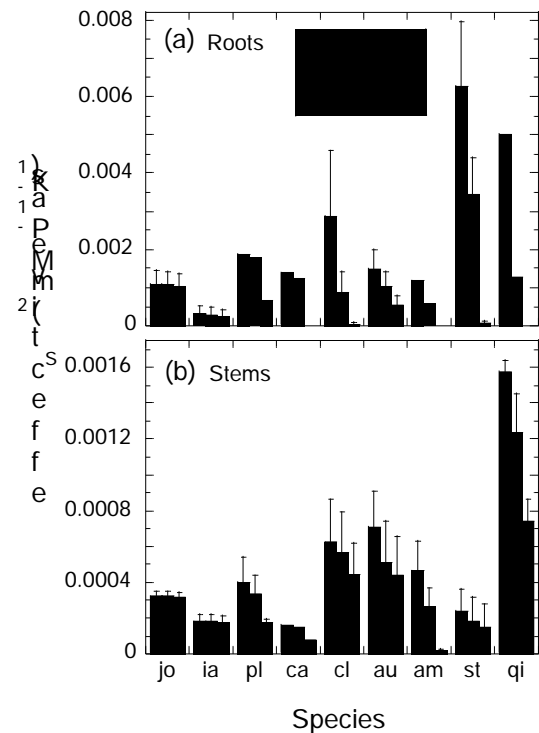


Figure 7. Values of specific hydraulic conductivity (effective K_s) estimated for roots (a) and stems (b) of the studied species during May, July and August. The values were calculated by combining maximum K_s and vulnerability curves obtained in the laboratory with the water potentials measured in the field on the same individuals. When laboratory and field measurements were not from the same individuals, the mean values for the species/tissue were used, and error bars are not shown. In the other cases, error bars represent standard errors. Species abbreviations as in Table 2.

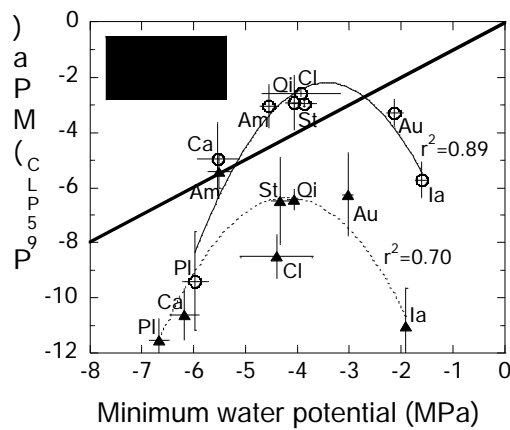


Figure 8. Relationship between the minimum water potential experienced in the field and the water potential causing a 95% loss of conductivity estimated from vulnerability curves. Root and branch values are independently fitted with a second-order polynomial regression. *J. oxycedrus* is not included (see text). The straight line shows the 1:1 relationship. Error bars are standard errors. Species abbreviations as in Table 2.

The shape of Figure 9 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 & Sullivan 1992, Sperry *et al.* 1994). Since the slope of the curve approaches - 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 the trade-off becomes apparent. The best fit was obtained combining species and tissues, which suggests a general trade-off, independent of xylem type (Figure 9). Obviously, what exists in real plants is a gradient of hydraulic properties from roots to terminal branches (Zimmermann 1983, Sperry & Saliendra 1994). However, it seems reasonable to concentrate on both ends of the path because

they are the most likely to fail under extremely dry conditions (e.g., Alder *et al.* 1996). Pockman & 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) used a power function to relate conduit diameter and mean cavitation pressure using stem data from 57 species from different regions. Although they obtained an exponent smaller than the one predicted by our model, their results also imply a negative power relationship between K_S and mean cavitation pressure. If the free parameter of the power relationship depends on environmental variables, our model would predict a family of curves with exponent *ca.* -2, one for each community. Part of the variability observed by Tyree *et al.* (1994) and Pockman & Sperry (2000) may be due to the fact that they were comparing a very heterogeneous group of species, exposed to different environmental conditions and selective pressures.

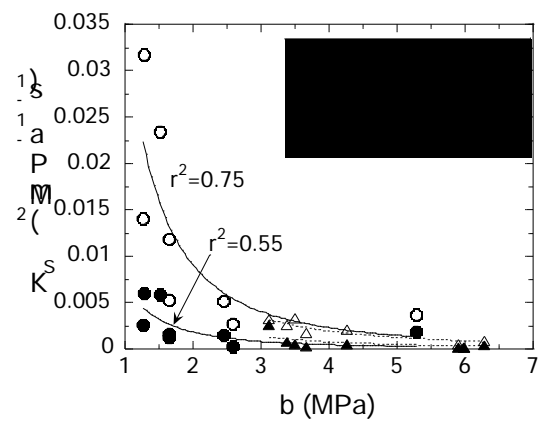


Figure 9. Relationship between the parameter *b* of the vulnerability curves and the theoretical and measured specific hydraulic conductivity for roots and stems of the studied species. Each symbol is a species mean. *J. oxycedrus* is not included (see text). Fitted curves are power functions with exponent -2 separating roots and stems. However, since the regressions are almost identical, the determination coefficients correspond to the correlation combining both tissues.

A negative power relationship as that of Figure 9 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 b is small (highly vulnerable tissue) a small increase in b 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. Only for the species/tissues situated in the central region of the curve there is an approximately linear trade-off between efficiency and security of the conducting system.

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 (Figures 7 and 8). This seems to be a general characteristic of woody plants (Sperry & Saliendra 1994, Alder *et al.* 1996, Mencuccini & Comstock 1997, Linton *et al.* 1998, Kolb & Sperry 1999, Hacke *et al.* 2000). In fact, 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 of roots were even lower than the ones calculated. 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 &

Saliendra 1994); (2) root xylem is easier to replace by new growth (*e.g.*, Kolb & 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 loose 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 hydraulic conductivity, 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 and disconnect the plant from the driest soil.

Among species, there was a good general correspondence between vulnerability to xylem embolism (Figure 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 (*A. monspessulanum*, *A. unedo*, *C. laurifolius*, *Q. ilex*, *S. torminalis*) were the most vulnerable to xylem embolism. These species, with the exception of *A. unedo*, become scarcer as we move to southern, more arid areas in the Iberian Peninsula (Bolós & Vigo 1984-1995). A similar picture emerges when we compare the vulnerability curves with the water potentials experienced in the field (Figures 7 and 8). Five species (the same previous ones substituting *C. albidus* for *A. unedo*) were predicted to

retain less than 5% of the maximum hydraulic conductivity of roots at the peak of the drought. The fact that *C. albidus* was severely affected by xylem embolism is not surprising since it is a drought-deciduous species (see, for example, Kolb & Davis 1994). Only *A. monspessulanum* stems were predicted to experience catastrophic levels of xylem embolism in the field. The case of *I. aquifolium*, 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 (Figure 4) deserves special attention. *I. aquifolium* 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 *I. aquifolium* 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 *I. aquifolium* are not surprising. The fact that water potentials never fell below -2 MPa in this species, well above the values of deep rooted species such as *Q. ilex* (Figure 5), supports the idea that *I. aquifolium* 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 (Figure 6a) and E (data not shown) to very low values. The reduction, however, was significantly lower in the embolism-resistant species *I. aquifolium* (86%; Figure 6a). Regarding the two species for which gas exchange was not measured in this study, the

reduction of stomatal conductance between late April and late July was lower in the embolism-resistant *P. latifolia* (80%) than in *Q. ilex* (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 *J. oxycedrus*, which showed an acute reduction in g_s and E despite it was predicted to experience negligible levels of xylem embolism. 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} (Figure 6b) translate in terms of specific hydraulic conductance over the soil-to-leaf pathway. Field observations indicated that all the studied species except *I. aquifolium* and *P. latifolia* 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, water potentials causing 50% embolism in stems ranged from *ca.* -1 to -12.5 MPa (Pockman & Sperry 2000). In this study we have measured values from -3 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 *P. latifolia* and *Q. ilex*. In agreement with the higher vulnerability to xylem embolism of *Q. ilex*, 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 climate change models for the Mediterranean Region (IPCC 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 (Chapter 7).

Unlike other studies (Hacke *et al.* 2000, Pockman & Sperry 2000), we have not found a linear relationship between vulnerability to xylem embolism and the minimum water potentials under field conditions. Instead, safety margins tended to be wider for species experiencing very high or very low water potentials (Figure 8), 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 (Figure 9), why some species have wide safety margins? In relation to the first question, we have to begin considering 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 & 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.*, *I. aquifolium*, *J. oxycedrus*, *P. latifolia*), the shape of Figure 9 provides a possible explanation. For tissues that are very resistant

to xylem embolism, even a small increase in hydraulic conductivity would be at the expense of a large decrease in resistance to embolism. It is likely that, in the field, this increase in hydraulic conductivity would be offset by the increase in xylem embolism associated with higher vulnerabilities. In that case, the parabolic relationship between embolism and minimum water potentials (Figure 8) 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 *I. aquifolium*, which is the species that shows the largest departure from a linear relationship.

If the negative power relationship between conductivity and resistance to embolism proves to be general for different plant communities, it will constitute an additional illustration that disparate ecophysiological behaviour among species may be governed by general underlying functional relationships, as suggested by the recent findings in Reich *et al.* (1997) and Stratton *et al.* (2000).

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