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## Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain

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**Abstract** Stem xylem features in two evergreen *Quercus* species (*Q. coccifera* and *Q. ilex*) and a deciduous one (*Q. faginea*) were analysed along an Atlantic-Mediterranean climatic gradient in which rainfall and winter cold experience strong variation. Mean maximum vessel diameter, vessel density, vessel element length, xylem transverse sectional area, Huber value (xylem transverse sectional area per leaf area unit), theoretical leaf specific conductivity (estimated hydraulic conductance per leaf area unit) and total leaf area were determined in 3-year-old branches. *Q. faginea* presented the widest vessels and the highest theoretical leaf specific conductivity while *Q. coccifera* showed the lowest total leaf area and the highest Huber value. Studied features did not exhibit significant correlations with mean minimum January temperature in any species but did show significant relationships with rainfall. In *Q. coccifera*, mean maximum vessel diameter, vessel element length and theoretical leaf specific conductivity increased with higher rainfall while vessel density decreased. Mean maximum vessel diameter and total leaf area in *Q. ilex* increased with precipitation whereas variables of *Q. faginea* did not show any significant trend. Results suggest that aridity, rather than minimum winter temperature, controls stem xylem responses in the studied evergreen species. *Q. faginea* traits did not show any response to precipitation, probably because this species develops deep roots, which in turn makes edaphic and topographic factors more important in the control of soil water availability. In response to aridity *Q. coccifera* only exhibits adjustment at a xylem level by

reducing its water transport capacity through a reduction of vessel diameter without changing the amount of xylem tissue or foliage, whereas *Q. ilex* adjusts its water transport capacity in parallel to the foliage area.

**Key words** Huber value · Mediterranean climate · Rainfall gradient · Winter temperature · Wood anatomy

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### Introduction

Hydraulic features of xylem are key elements in the water relations of plants and therefore in their final performance (Tyree and Ewers 1991). Xylem vulnerability and water flow resistance are dependent on xylem anatomy. For example, large vessels can transport a higher amount of water, but are also more prone to dysfunctions induced by embolisms than smaller conduits (Sperry et al. 1994; Tyree et al. 1994). The higher the number of vessels per unit of xylem area the lesser percentage of conductance is lost when the same proportion of vessels cavitates (Tyree et al. 1994).

When the high xylem structural diversity existing among woody plants (Fahn et al. 1986; Baas and Schweingruber 1987) is correlated with environmental variables several regularities appear (for instance, see Baas et al. 1983; Fahn et al. 1986), suggesting that environmental factors have acted as important selective forces in molding xylem structure (Wheeler and Baas 1993; Woodcock and Ignas 1994).

Plant features can vary within a species under different growing conditions (Woodward 1983; Castro-Díez et al. 1996), allowing species to maintain their fitness under an ample range of environmental conditions and resource availability. Among these plant features, foliar variation has long attracted the attention of scientists and there is an extensive literature dealing with their responses and their functional meaning (Chabot and Chabot 1977; Givnish 1979; Vitkowski and Lamont 1991). However, intraspecific xylem variation has been less studied in spite of its

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**Table 1** Sampling sites along the study area and their altitude, climatic characteristics and sampled species. (Province abbreviations: *Bi* – Vizcaya, *Hu* – Huesca, *Na* – Navarra, *Vi* – Alava, *Z* – Zaragoza)

Studied sites	Altitude (m)	Annual rainfall (mm)	Mean minimum January temperature (°C)	Mean maximum July temperature (°C)	<i>Q. ilex</i>	<i>Q. coccifera</i>	<i>Q. faginea</i>
1-Górliz (Bi)	170	1034	6.3	23.0	X	X	–
2-Arceniega (Vi)	260	1217	3.3	27.3	–	–	X
3-Mañaria (Bi)	220	1484	3.3	24.2	X	–	–
4-Nanclares de Oca (Vi)	520	774	1.2	27.8	–	X	X
5-Laguardia (Vi)	500	514	1.3	27.7	–	–	X
6-Lumbier (Na)	420	801	0.2	30.0	X	X	–
7-Jaca (Hu)	720	831	–1.2	28.2	–	–	X
8-Villanúa (Hu)	1030	1201	–1.2	28.2	–	–	X
9-Ejea de los Caballeros (Z)	570	450	2.8	32.5	X	X	X
10-Agüero (Hu)	680	686	0.0	29.6	–	–	X
11-Nueno (Hu)	710	731	1.3	28.8	X	X	X
12-Vedado de Peñafior (Z)	370	370	1.5	32.0	X	X	–
13-Sierra de Alcubierre (Hu)	580	452	1.9	32.1	X	X	X
14-Mediano (Hu)	500	891	–1.1	30.1	X	X	X
15-Sta. Liestra (Hu)	600	909	–2.8	29.7	X	–	–
16-El Grado (Hu)	470	627	–0.4	31.9	–	–	X
17-Olvena (Hu)	360	587	–1.3	32.9	X	X	–
18-Fraga (Hu)	250	409	0.9	31.1	–	X	–
19-Presa de Santa Ana (Hu)	370	455	0.3	32.2	X	X	X

importance to plant performance (Shumway et al. 1993). Recent studies in natural populations provide evidence that both aridity and low temperatures can influence xylem structure within a species (Xinying et al. 1988; Mencuccini and Grace 1995; Sperry et al. 1994), although the response patterns to the same environment can differ among species (Noshiro and Suzuki 1995). It has also been proposed that variations in vessel diameter and density can be related with different basipetal auxin gradients associated with the growth and ramification degree of branches (Aloni 1987).

The objective of this study is to analyse the variation of xylem anatomy in three *Quercus* species (*Q. coccifera*, *Q. ilex* and *Q. faginea*), differing both in growth form and ecology, along an Atlantic-Mediterranean gradient. In this area the two main plant limiting factors of the Mediterranean basin, i.e. summer drought and winter cold (Mitrakos 1980), experience strong variation. It is hypothesised that in response to an increase of aridity and continentality, xylem traits related with slow water consumption and with hydraulic security will be enhanced. We also inquire whether the three phylogenetically close species will respond in a similar way to the same environmental variation or whether, on the contrary, their structural differences will determine a different response.

## Materials and methods

### Study area and studied species

The study area is located in the NE quadrant of the Iberian Peninsula, extending from the Basque Atlantic coast to the middle Ebro Basin. Along this area there is a gradual reduction of precipitation and an increase of continentality from the Atlantic coast to the mid Ebro Basin. In the latter, annual rainfall hardly exceeds 350 mm, minimum winter temperature is close to 0 °C and mean maximum summer temperature reaches 33 °C. On the Atlantic coast precipitation is

around 1200 mm, mean minimum winter temperature is usually over 4 °C and mean maximum summer temperature does not exceed 25 °C (Table 1).

The studied species are *Quercus coccifera* L., *Q. ilex* L. and *Q. faginea* Lam. The former, an evergreen shrub, is the main component of the climax communities in the arid extreme of the gradient (Braun-Blanquet and Bolòs 1957). *Q. ilex* is an evergreen tree which includes two subspecies, both present in the study area: subsp. *ilex* and subsp. *ballota* (Desf.) Samp. in Bol. (*Q. rotundifolia* Lam.) (Amaral Franco 1990). The former is restricted to areas near the Atlantic coast and some moist and sheltered inner valleys, while the latter is the most important climatic tree in the Mediterranean part of the gradient. *Q. faginea* is a winter deciduous tree common in mature communities of the Eurosiberian-Mediterranean transitional belt.

### Study sites

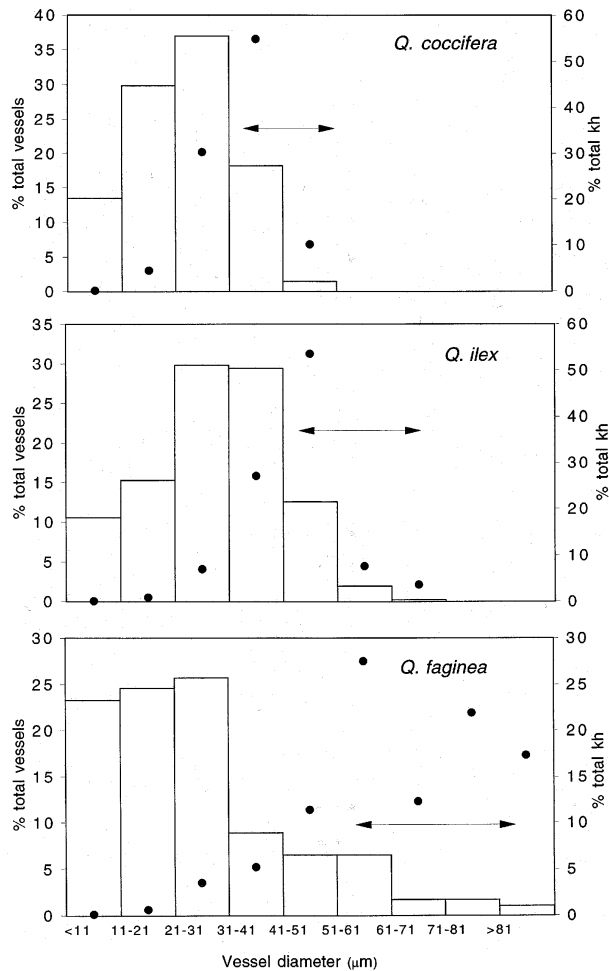
A total of 19 sampling sites, with similar geology, substratum and topography, were selected. Except for the “Vedado de Peñafior” population, which grows on a gypsum soil, the rest of the sites appear over limestones or marls. Altitudinal range varied from 170 m on the coast to 1000 m in the pre-Pyrenean range, although most of them were located between 300 and 700 m (Table 1).

The climatic profile of each site was established from the closest weather station of the National Meteorological Service. In some cases, rainfall and temperature data had to be extrapolated by altitudinal regressions from other nearby stations.

### Methodology

Sampling was made during July and August 1992. At each site we chose one plant of similar size per species and harvested two 3-year-old branches at a mid height on the southern side of the crowns. Then, shoots were cut into annual segments, fixed in FAA for 24 h and preserved in 70% ethanol. All the leaves sustained by each 3-year-old branch were stored in a freezer before measuring their total foliage area (FA) with a Delta-T image Analysis System (Delta-T Devices, Cambridge, UK).

Xylem was studied in the 3-year-old segments. Cross-sections of internodal areas were made with a sliding microtome (Anglia Scientific AS200, UK) and stained with safranin and fast green. Mean diameter of the 25 largest vessels (mean maximum vessel diameter, MxD) and



**Fig. 1** Frequency distribution of the different vessel diameter classes (histograms) and their contribution to the total theoretical  $K_h$  (closed circles) in the three *Quercus* species. Arrows indicate the range of the 25 largest vessels

vessel density (VD) of the whole section were measured with a micrometer and a grid placed in the microscope ocular. MxD was calculated as the average of major and minor axes of the vessel lumen. MxD was preferred instead of the mean vessel diameter because the hydraulic conductance of a stem is determined by the largest vessels (Zimmermann 1983; Tyree et al 1994; see also Fig. 2) and these are more prone to cavitate than smaller conduits (Lo Gullo and Salleo 1993; Sperry et al. 1994).

Vessel element length (VEL) was measured from xylem macerations of the same shoots used for transverse sections. Segments were cut to a match stick size after being debarked and treated with a 10% Jeffrey's solution (Johansen 1940). Macerated material was stained with safranin or Bismarck brown and mounted in distilled water. The length of 30 randomly chosen vessel members (vessel element length, VEL)

was measured excluding their tails, as it was considered that the functional meaning of this parameter is determined by the distance between the perforation plates.

In order to estimate the efficiency of the xylem to supply its foliage, a theoretical leaf specific conductivity (LSCt; sensu Tyree and Ewers 1991) was calculated as:

$$\text{LSCt} = K_h/\text{FA}$$

where  $K_h$  is the predicted hydraulic conductance ( $\text{mm}^4$ ) and was calculated as the sum of the fourth power diameters of the 25 largest vessels from each section. Biomass allocation between xylem and leaves in branches was assessed by the Huber value (HV), defined as the ratio between the cross section of the xylem, including the pith, (SA) and FA. It is assumed that in 3-year-old shoots all xylem is sapwood.

Branches from "Sierra de Alcubierre" populations (site 13 in Table 1) were used to determine the vessel diameter frequency distribution of each species. Diameter of all the vessels contained in photomicrographs of the whole section were measured and their  $K_h$  estimated (Fig. 1).

#### Statistical analysis

Regression analysis between stem xylem features and both mean annual precipitation and mean minimum temperature of the coldest month (January) was made to analyse xylem responses along the gradient. The linear model showed the best fits. Analysis of variance was used to assess differences between species.

## Results

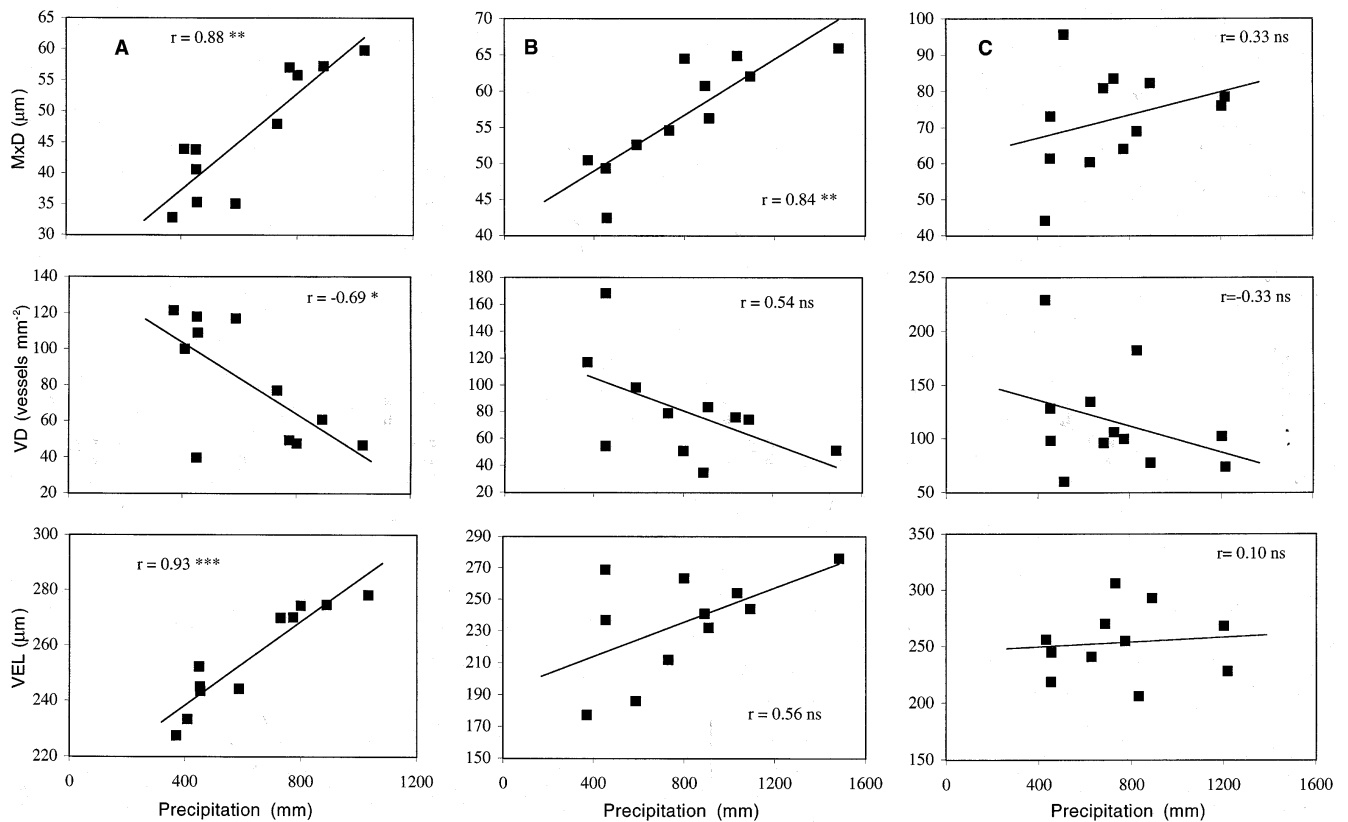
### Interspecific differences

*Quercus faginea* presented a ring porous wood whereas the evergreen species exhibited a diffuse porous type. All three developed distinct ring boundaries, solitary vessels and simple perforation plates. The frequency distribution of vessel diameter classes followed a normal pattern in *Q. coccifera* and *Q. ilex*, whereas *Q. faginea* presented a Poisson-type distribution due to the high number of small vessels (Fig. 1). In the three species, most of the estimated  $K_h$  was sustained by the highest vessel classes. Lower vessel classes ( $\leq 30 \mu\text{m}$ ) in *Q. faginea* and *Q. ilex* made up 75% and 55% respectively of the total number of vessels, but they only contributed 5% and 10%, respectively, to the total  $K_h$ , while in *Q. coccifera* lower vessel classes made up 70% of the total vessel population and contributed 35% to the total  $K_h$ .

*Q. faginea* showed the widest vessels and the highest LSCt of the three species, while MxD did not differ significantly between *Q. ilex* and *Q. coccifera*. This last species presented lower FA and invested more xylem tissue

**Table 2** Mean xylem and stem features in the three *Quercus* species (mean  $\pm$  1 SE). Same letters in a column indicate no significant differences ( $P \geq 0.05$ )

Species	MxD ( $\mu\text{m}$ )	VD (vessels $\text{mm}^{-2}$ )	VEL ( $\mu\text{m}$ )	HV ( $10^{-6}$ )	LSCt ( $10^{-9} \text{mm}^2$ )	SA ( $10^{-2} \text{cm}^2$ )	FA ( $\text{cm}^2$ )
<i>Q. coccifera</i>	46 $\pm$ 3 <sup>a</sup>	80 $\pm$ 10 <sup>a</sup>	254 $\pm$ 6 <sup>a</sup>	759 $\pm$ 87 <sup>b</sup>	11.1 $\pm$ 2.25 <sup>ab</sup>	10.5 $\pm$ 1.67 <sup>a</sup>	141 $\pm$ 16 <sup>a</sup>
<i>Q. ilex</i>	55 $\pm$ 3 <sup>a</sup>	85 $\pm$ 12 <sup>a</sup>	230 $\pm$ 9 <sup>a</sup>	330 $\pm$ 43 <sup>a</sup>	6.3 $\pm$ 0.99 <sup>a</sup>	13.6 $\pm$ 1.62 <sup>a</sup>	519 $\pm$ 99 <sup>b</sup>
<i>Q. faginea</i>	72 $\pm$ 2 <sup>b</sup>	116 $\pm$ 10 <sup>a</sup>	253 $\pm$ 9 <sup>a</sup>	216 $\pm$ 17 <sup>a</sup>	14.9 $\pm$ 1.81 <sup>b</sup>	12.0 $\pm$ 1.58 <sup>a</sup>	599 $\pm$ 88 <sup>b</sup>



per unit leaf area (higher HV) than the two tree species, whose HV did not differ significantly. No significant differences of VD, VEL and SA were observed between the three species (Table 2).

**Fig. 2** Relationship between MxD, VD, and VEL and the mean annual precipitation in *Q. coccifera* (A), *Q. ilex* (B) and *Q. faginea* (C). ns: not significant ( $P \geq 0.05$ ); \* $0.05 > P \geq 0.01$ ; \*\* $0.01 > P \geq 0.001$ ; \*\*\*  $P < 0.001$

#### Relationships between xylem features and climatic variables

None of the studied features in the three species showed significant trends with respect to the January mean minimum temperature (Table 3). In contrast, several attributes were correlated with rainfall. In *Q. coccifera*, MxD, VEL and LSCt showed a significant positive relationship with annual precipitation while VD presented a negative correlation. HV, FA and SA did not show any significant trend (Figs. 2–4).

In *Q. ilex*, MxD and FA were positively correlated with annual rainfall whereas HV appeared negatively correlated. VD, VEL, LSCt and SA did not present any significant correlation (Figs. 2–4).

None of the studied features in *Q. faginea* exhibited any significant relationship with precipitation (Figs. 2–4).

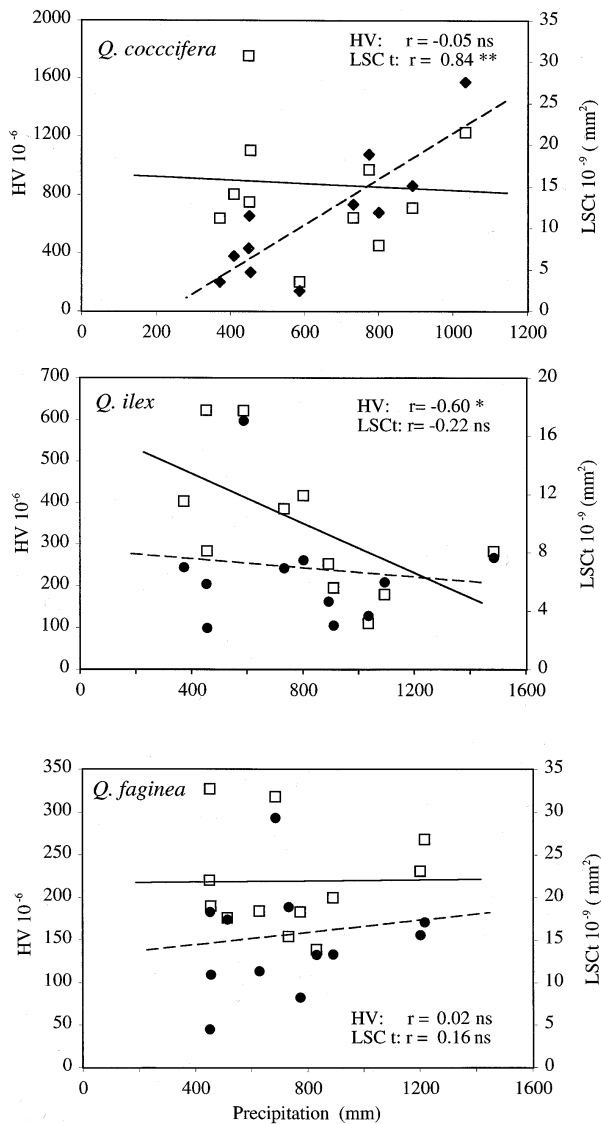
#### Discussion

The three species exhibited important differences in their xylem anatomy, the main one being between the evergreen (*Q. coccifera* and *Q. ilex*) and the deciduous species (*Q. faginea*). This latter shows a ring porous wood and develops larger vessels than the diffuse porous wood evergreen species, which present smaller vessels and are smaller plants with a higher degree of branching in accordance with Aloni's vascular adaptation hypothesis (Aloni 1987). According to the Hagen-Poiseuille law (Zimmermann 1983) water transport capacity is expected to be higher in

**Table 3** Pearson correlation coefficients of the regressions between xylem features and the mean January minimum temperature in the three *Quercus* species

	MxD	VD	VEL	HV	LSCt	SA	FA
<i>Q. coccifera</i>	0.30 ns <sup>a</sup>	-0.36 ns	0.21 ns	0.52 ns	0.07 ns	-0.42 ns	-0.41 ns
<i>Q. ilex</i>	0.32 ns	-0.08 ns	0.28 ns	-0.17 ns	-0.05 ns	0.30 ns	-0.05 ns
<i>Q. faginea</i>	-0.02 ns	-0.17 ns	-0.18 ns	0.35 ns	-0.09 ns	-0.08 ns	0.03 ns

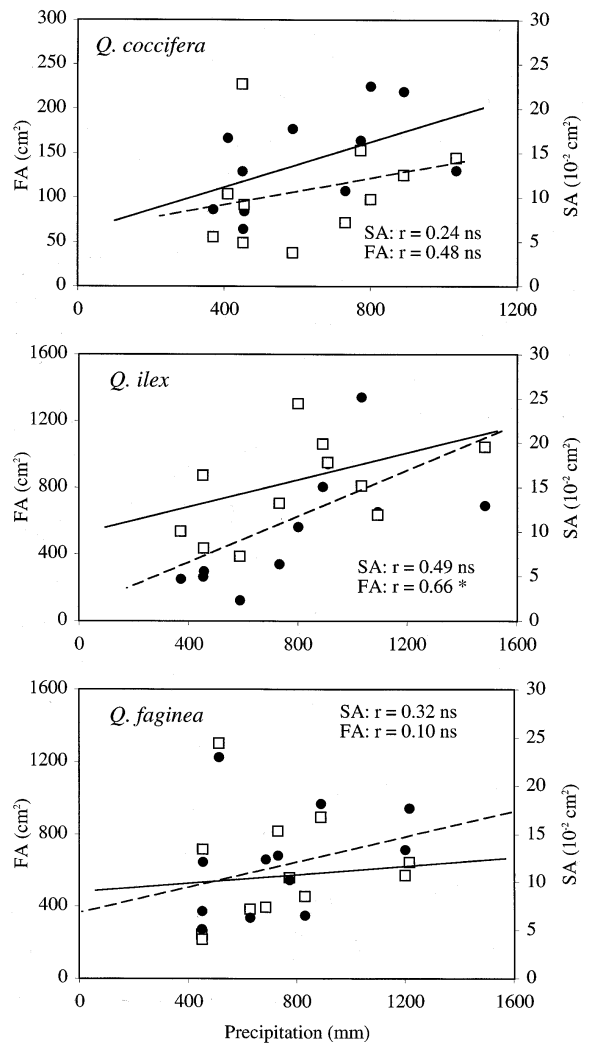
<sup>a</sup> ns  $P \geq 0.05$



**Fig. 3** Relationship between HV (open squares and continuous line) and LSCt (closed circles and broken line) and the mean annual precipitation in the three *Quercus* species. Statistical symbols as in Fig. 2

*Q. faginea* than in its evergreen relatives, while the narrower conduits of the latter would limit their flux rate, allowing plants to make a longer use of soil water reserves. In fact, other authors that compared deciduous and evergreen *Quercus* species found that the former exhibit higher sap velocity (Borghetti et al. 1992) and are more prone to cavitation (Tyree and Cochard 1996). Our results accord with the ecological distribution of the studied species: *Q. faginea* dominates in submediterranean areas where soils are deeper and water availability is higher, while *Q. ilex* and *Q. coccifera* prevail in the Mediterranean areas where soils are shallower and summer aridity is the main limiting factor for plant performance.

Biomass allocation patterns within branches differed between the trees and the shrub species. Total foliage area in *Q. faginea* and *Q. ilex* 3-year-old branches was



**Fig. 4** Relationship between SA (open squares and continuous line) and FA (closed circles and broken line) and the mean annual precipitation in the three *Quercus* species. Statistical symbols as in Fig. 2

almost four times that of *Q. coccifera*, no difference existing in the xylem transverse area. This means that *Q. coccifera* produces more wood per unit leaf area (higher HV) a feature which has been considered to improve plant water and nutrient storage capacity (Callaway et al. 1994) and to reduce the impact of xylem embolism (Tyree and Dixon 1986).

The wood anatomy of the studied species responded to the climatic gradient following different patterns. None of them responded to changes in winter temperature. Such a response was expected in *Q. faginea*, whose deciduous habit causes it to be inactive during the cold season, the new foliage being supplied by the embolism-free sapwood formed at the beginning of the growing season (Ellmore and Ewers 1986; Sperry et al. 1994). In contrast, the evergreen species, which have to maintain water supply to their foliage during winter, were expected to reduce xylem embolism vulnerability in the colder populations. In fact, *Pistacia lentiscus* and *Rhamnus alaternus*, two evergreen species from the same communities, presented an

increase in VD and a decrease in MxD, respectively, as a response to winter cooling (Castro-Díez 1996). The lack of response in the evergreen *Quercus* species could be due to a capacity to recover from embolism, as Lo Gullo and Salleo (1993) reported for *Q. ilex*.

The responses of the three *Quercus* species to precipitation gradient were different. Xylem features of *Q. faginea* did not correlate with mean precipitation, while those of *Q. ilex* and *Q. coccifera* did. Previous works on *Q. faginea*'s leaf morphology (Castro-Díez et al. 1996) and physiology (Acherar and Rambal 1992; Lansac et al. 1994) suggest that this species must depend on a reliable water supply to thrive in dry Mediterranean areas. Such an ability can be attained by developing deep roots which tap soil water reserves, as does *Q. pubescens* (Valentini et al. 1992), or by growing in valley bottoms or water storing substrata, as does *Q. faginea* in the arid places of the gradient (Montserrat G, personal observation). Both mechanisms allow a relative independence of the regional rainfall regime and can explain the lack of adjustment of *Q. faginea* xylem to the precipitation gradient.

In contrast, the evergreen species did respond to variations of rainfall, both reducing their MxD with aridity increase. As vessel size is a correlate of xylem conductance (Zimmermann 1983) the reduction of MxD could slow down water consumption and, therefore, avoid a fast depletion of soil water where this resource is scarce. Likewise, wider vessels in *Q. ilex* are more prone to water stress-induced embolism than narrower conduits (Lo Gullo and Salleo 1993) and, consequently, the reduction of MxD with aridity observed in both evergreen species may also diminish the risk of xylem dysfunction by water stress.

The rest of the observed trends differed between the evergreen species. *Q. coccifera* showed an increase of VD, a VEL shortening and a LSCt decline with aridity. The first response has been suggested to reduce the impact of embolism on xylem water transport, due to a greater redundancy of the water pathway (Zimmermann 1983; Tyree et al. 1994), while VEL shortening has been hypothesised to increase vessel member strength and prevent air bubble progress along them due to the constrictions located in the perforation plates (Carlquist 1988). The decline of LSCt was due to the reduction of MxD in absence of parallel changes in FA, indicating that plants from arid sites have a lower potential of water supply per leaf area unit. A similar response to aridity has been reported for other species and related to the control of the branch evaporative flux (Shumway et al. 1993).

Only *Q. ilex* experienced a significant increase of HV with increasing aridity, in agreement with the trends found in other plants (Shumway et al. 1991; Callaway et al. 1994; Mencuccini and Grace 1995; Kuuluvainen et al. 1996). This response was the result of a reduction in FA with a decrease of rainfall which was not paralleled by significant variations in SA. As mentioned before, an increase of HV can be considered to reduce the impact of xylem embolism (Tyree and Dixon 1986).

These data indicate that both evergreen species follow different strategies to overcome drought. In response to an

increase of aridity, *Q. coccifera* did not present a reduction of the transpiring surface nor significant leaf morphological adjustments (Castro-Díez et al. 1996), thus suggesting that this species regulates its water use mainly at a xylem level. In contrast, *Q. ilex* showed both xylem and foliar adjustments, as FA diminishes and specific leaf mass increases with aridity (Castro-Díez et al. 1996). Such a response indicates that *Q. ilex* relies on modifications of both xylem and foliage to adjust to the degree of aridity. This fact is reinforced by the lack of variation in LSCt along the gradient, which suggests an adjustment between the hydraulic properties of stems and the transpiring leaf surface supplied by them.

The results of this work demonstrate that phylogenetically close species can adopt different strategies to adjust to the same range of climatic conditions. Otherwise, leaf habit and plant structure appear to be key features conditioning the response patterns of the studied species. In this climatic gradient, water shortage appears to be the most important factor influencing xylem anatomy variations, while low winter temperature has less relevance. In response to an increase of aridity, *Q. faginea* does not show any clear response, since it probably achieves a relative independence from the regional rainfall regime by developing a deep root system and by habitat selection. *Q. coccifera* only exhibits adjustments at xylem level by reducing its conductance, whereas *Q. ilex* reduces both water transport capacity and the transpiring surface of its branches.

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