

Wood anatomy and hydraulic architecture of stems and twigs of some Mediterranean trees and shrubs along a mesic-xeric gradient

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Abstract Woody species populating the major Mediterranean ecosystems in the world are characterized by different levels of adaptation to the seasonal Mediterranean climate conditions. Many species of these ecosystems show wood features that allow high efficiency of transport when water is available, while maintaining hydraulic safety during drought periods. This study focuses on the anatomy of juvenile and mature wood of some species representative of continuous sequences of Mediterranean vegetation formations according to gradients of water availability, from xeric to relatively mesic: *Cistus monspeliensis* L., *Rhamnus alaternus* L., *Myrtus communis* L., *Pistacia lentiscus* L., *Olea europaea* L., *Quercus ilex* L., *Fraxinus ornus* L. and *Ostrya carpinifolia* L. Twigwood collected in Southern Italy was anatomically compared with the stemwood of the same species represented in the reference slide collection of the National Herbarium of the Netherlands (Lw). The “hydraulic distance” between the wood of main stems and twigs was estimated on the basis of suites of anatomical features related to water efficiency/safety. Although some attributes (i.e. porosity and type of imperforate tracheary elements) were similar in young twigs and older rings, other traits (i.e. vessel frequency and size)

evidenced the different hydraulic properties of twig and stemwood. The difference between juvenile and mature structures was large in the species of the mesic end of the gradient while it was relatively small in those more xeric. This tendency is in agreement with the habit gradient from medium-sized trees to small evergreen/drought deciduous shrubs according to decreasing water availability in Mediterranean vegetation types.

Keywords Juvenile wood · Mature wood · Mediterranean shrubs and trees · Quantitative wood anatomy · Water use strategies

Introduction

The Mediterranean climate is characterised by hot, dry summers alternating with cool, wet winters (Daget 1977; Nahal 1981). These climate features impose limitations on plant growth and are reflected in the vegetation-types dominating Mediterranean areas. The five Mediterranean regions of the world are considered open transitional zones between moist and arid ecosystems, and between temperate and tropical ones (di Castri 1981). They are dominated by a maquis vegetation type of scrub formations characterized by shrubs with evergreen, stiff and thick leaves (sclerophyll). Towards more xeric habitats, the vegetation changes into the garrigue where the scrub formations become lower, more open and scattered and with a major incidence of drought-deciduous species. On the other hand, along gradients of increasing water availability, Mediterranean shrublands are merged with evergreen sclerophyllous broad-leaved forests and with the deciduous mixed meso-xeric Mediterranean woodlands. It is commonly accepted that any separation between Mediterranean shrublands and

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other formations would be artificial because the intrinsic feature of the Mediterranean environment is its existence as a gradient of ecosystems (di Castri 1981).

Hydraulic architecture plays a fundamental role in the adaptive strategies of plants (Carlquist 1975, 1983, 1989; Zimmermann 1978, 1983; Baas and Carlquist 1985; Baas and Schweingruber 1987; Tyree and Sperry 1989; Tyree and Ewers 1991; Tyree et al. 1994; Hacke and Sperry 2001; Sperry 2003; Baas et al. 2004). Several authors have presented general ecological and phylogenetic trends in wood anatomy and suggested possible evolutionary mechanisms responsible for these trends (Baily and Tupper 1918; Carlquist 1975, 1980; Baas 1976, 1982; Baas et al. 1983, 2004; Ewers and Fisher 1991). From a functional viewpoint, attributes affecting conductivity, vulnerability to cavitation and mechanical strength, have been widely investigated (Zimmermann 1982, 1983; Ewers 1985; Salleo and Lo Gullo 1993; Lo Gullo et al. 1995; Wagner et al. 1998; Martínez-Vilalta et al. 2002; Sperry 2003; Hacke et al. 2006; Pittermann et al. 2006; Sperry et al. 2006; Jacobsen et al. 2007a, b). A usual approach to delineate ecological trends is the study of mature structures, while relatively few studies have been conducted on juvenile wood (Carlquist 1975; Baas 1976; Fahn et al. 1986; Gartner 1995, Fisher et al. 2007). However, notwithstanding their high variability, the study of juvenile structures is relevant since the most distal portion of branches plays a key role in the regulation of water relations and can offer the highest resistance to water flow (Yang and Tyree 1993).

The site of our study at Punta Tresino, Southern Italy, is characterized by a gradient of ecosystems starting from the more arid shrublands moving towards the deciduous mixed meso-xeric Mediterranean woodlands. Within the vegetation types encountered in the site, eight species were selected for the analysis as representative of a continuous sequence of vegetation formations according to a gradient of increasing water availability: *Cistus monspeliensis* L., *Rhamnus alaternus* L., *Myrtus communis* L., *Pistacia lentiscus* L., *Olea europaea* L., *Quercus ilex* L., *Fraxinus ornus* L. and *Ostrya carpinifolia* L.

Cistus species are typical of garrigue formations belonging to the autochthonous Tertiary-Mediterranean flora (Quézel 1978, 1985). They are seasonally dimorphic species as they develop short twigs with small leaves in summer (brachyblasts), and long twigs with large leaves in winter (dolichoblasts) (Aronne and De Micco 2001). Belonging to the Tertiary tropical flora, *M. communis* and *P. lentiscus* are both evergreen sclerophyllous shrubs common in Mediterranean woodlands, maquis and sometimes garrigue. Representative of these woodlands is also *O. europaea*, an evergreen tree cultivated in many regions since antiquity.

R. alaternus is an evergreen shrub or small tree recorded in the Mediterranean shrublands since the Tertiary (Raven

1973; Suc 1984). *R. alaternus* is also considered a typical member of the *Quercus ilex* sclerophyllous forest (Pignatti 1982): indeed within a given region, in specific altitudinal and bioclimatic zone, some types of maquis can evolve towards evergreen *Q. ilex* forests (Quézel 1981). *Q. ilex*, *F. ornus* and *O. carpinifolia*, are more mesic species of the mixed meso-xeric Mediterranean forest belonging biogeographically to the Holoartic or Eurasiatic elements. (Arambourg et al. 1953; Quézel 1985; Manos et al. 1999; Quézel et al. 1999). At present, *O. carpinifolia* and *F. ornus* are considered representatives of the deciduous forest of the Supra-Mediterranean Zone where species typical of maquis and garrigue vegetation are almost always situated between grasslands and forests (Quézel 1981).

Comparative studies in sites where sclerophylls, seasonally dimorphic and deciduous meso-xeric woody species co-occur, allow singling out various strategies that can be equally successful in a given environment.

This study reports on a comparison between the hydraulic architecture of twigwood of some Mediterranean trees and shrubs collected in the field along a mesic-xeric gradient and the stemwood anatomy of the same species studied from sections in an institutional reference slide collection (Lw) with the aim to clarify the “hydraulic distance” between the wood in main stems and twigs. It is realized that ideally one should study such structural “hydraulic” distances within the same living tree or shrub, but it was felt that using reference slides from normal mature stemwood provided close enough proxies for our purpose. Wood anatomical features were quantified through digital image analysis and are interpreted under ecological and functional perspectives in order to address two main questions: (a) how is the wood anatomy and hydraulic architecture of these Mediterranean trees and shrubs related to the mesic-xeric ecological gradient? (b) are these adaptive trends (safety/efficiency of water transport) equally or differently expressed in twig- and stemwood?

Materials and methods

Study site for sampling twigwood

Twigwood samples were collected from plants growing at the site of Punta Tresino (Parco Nazionale del Cilento e Vallo di Diano) on the Tyrrhenian Coast, southern Salerno, Italy.

The Tresino promontory presents low coastal hills of flysh-marls sandstone ranging from 0 to 200 m a. s. l. The climate is typical Mediterranean (Daget 1977; Nahal 1981) with an annual rainfall ranging between 800 and 1,000 mm, but with precipitation concentrated in autumn and winter, followed by a very dry summer. Grazing, fire and human impact heavily disturb the natural vegetation.

Along a mesic-xeric gradient, the main vegetation types pass from mesophilous woods to maquis dominated by a mosaic of shrub species, while restricted gap areas are colonised by annual herbaceous plants (therophytes). Along this gradient, eight species were selected: *Cistus monspeliensis* L., *Rhamnus alaternus* L., *Myrtus communis* L., *Pistacia lentiscus* L., *Olea europaea* L., *Quercus ilex* L., *Fraxinus ornus* L. and *Ostrya carpinifolia* L.

Samples were collected in summer 2001 at the end of the vegetative growth. As regards *C. monspeliensis*, long twigs developed in autumn/winter (longiblasts) were selected. Five plants per each species were sampled: per plant, five 1-year-old twigs were harvested for subsequent laboratory analyses.

Twigwood sample preparation for microscopy

Anatomy of twigwood was studied in 200 samples (5 twigs \times 5 plants \times 8 species), taken from the base of each twig. Samples were fixed in FAA (40% formaldehyde/glacial acetic acid/50% ethanol—5/5/90 by volume) for several days. Then, cross and longitudinal sections (15–25 μ m thick) were cut with a sliding microtome. Sections were stained with 2% Safranin O in water (Jensen 1962) and mounted with Canada Balsam.

Slide collections for stem wood anatomy

Stemwood anatomy was studied on wood samples from the NHN (National Herbarium of the Netherlands, Lw) complemented with samples from the slide collection given by Prof. F.H. Schweingruber (Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland) and used for his atlas of European Woods (Schweingruber 1990). All samples belonged to countries of the Mediterranean region and specifically to France, Greece, Israel, ex-Yugoslavia and Spain.

Digital image analysis and quantitative wood anatomy

Microphotographs of the twigwood and stem samples were obtained with a digital camera and analysed with the software program AnalySIS[®] 3.2 (Olympus).

Wood anatomy of twig and stems was described according to the sequence by Baas and Zhang Xinying (1986) with some modifications as follows:

- Porosity: diffuse-porous, semi-ring-porous, ring-porous, and/or in a radial or oblique to dentritic pattern.
- Vessel characteristics: frequency, grouping, mean Feret diameter of lumen (Feret diameter is the measured distance between parallel lines that are tangent to the cell's perimeter), ECD of lumen (the equivalent circle

diameter is the diameter of the circle having the same area as the measured cell), lumen area, wall thickness, type of perforation plate. Frequency (number of vessels per square mm) was determined by counting all vessels individually. Percentage of solitary vessels was calculated as the proportion of solitary vessels in relation to the total number of vessels (Wheeler 1986). In the case of twigwood, data regarding vessel size were calculated following the method by De Micco et al. (2006). For stemwood, measurements of vessel lumen were made in 5–15 rings per species, considering 15–30 vessels per ring. Total vessel area was calculated as percentage of total wood surface. Relative conductivity was calculated according to Van der Oever et al. (1981) and Zimmermann (1983) as the fourth power of the conduit diameter (ECD). To compare the species, absolute conductivity was estimated per each wood as the ratio between their own relative conductivity and the sums of the relative conductivities of all the species (Zimmermann 1983). Thickness of vessel walls was measured in both twigs and stems in at least ten elements per ring, carefully avoiding cell corners.

- Imperforate tracheary elements: presence/absence, type, presence of spiral thickenings.

Statistical approach and literature selection

All measured anatomical parameters were compared by means of ANOVA using SPSS statistical package (SPSS Inc., Chicago, IL USA). Data from twigwood and stemwood were kept separated and the one-way ANOVA was calculated on each group of data by using the anatomical parameters as variables and the species as factor. Before ANOVA, mathematical transformation of data was applied when necessary (i.e. percent values). LSD and Student–Newman–Keuls coefficients were used for multiple comparison tests ($p < 0.05$).

Data collected on stemwood from the slide collections were compared with those derived from various literature sources (Baas and Schweingruber 1987; Baas et al. 1988; Fahn et al. 1986; Grosser 1977; Hall 1952; Schweingruber 1990; Tippo 1938) and the InsideWood database (<http://insidewood.lib.ncsu.edu/search/>). Samples in the slide collection which gave data out of the range of variation commonly reported in literature were not considered in the further analyses aimed to evaluate and discuss the hydraulic distance between 1-year-old and older structures.

Results

Cross sections of twigwood and stemwood of the eight examined species are shown in Figs. 1 and 2. Images

illustrate an entire ring for each species. Figure 3 shows higher, identical magnifications of twig- and stemwood of four of the species. The same descriptions can be applied to stemwood and twigwood with small differences such as the tendency to the presence of smaller and more frequent vessels in twigwood. Moreover, in twigwood spiral thickenings in both vessels and fiber-tracheids were not easily detected and recurrent patterns in the arrangement of vessels were less clear. For example the dendritic vessel patterns in *Q. ilex* and *R. alaternus* were much clearer in stemwood than in twigwood. Major differences were found in ring-porous species where twigwood tended towards semi-ring-porosity rather than the outspoken ring-porosity of the mature wood. Below, very concise descriptions, focusing mainly on characters of the hydraulic system are given for each species. The species are arranged in the xeric-mesic gradient.

Cistus monspeliensis L. (Figs. 1a, b; 3a, b)

Wood diffuse-porous. Vessels small, rather frequent, mostly solitary. Vessels rounded to angular in cross section. Perforation plates simple. All ground tissue fibres with distinctly bordered pits common in radial and tangential walls (fiber-tracheids). Helical thickenings present in vessels and fiber-tracheids.

Rhamnus alaternus L. (Figs. 1c, d; 3c, d)

Wood diffuse- to semi-ring-porous. Vessels generally solitary or in short multiples or small groups forming a dendritic pattern. Vessels rounded to angular in cross section. Perforation plates simple. Vascular tracheids intergrading with narrow vessels present in the latewood. Helical thickenings distinct in vessel elements and vascular tracheids. Ground tissue fibres with simple to minutely bordered pits (libriform fibres).

Myrtus communis L. (Fig. 1e, f)

Wood diffuse- to semi-ring-porous. Vessels generally solitary, densely packed, angular to rounded in cross section. Perforation plates simple. All ground tissue fibres with distinctly bordered pits in radial and tangential walls (fiber-tracheids). Fine helical thickenings present in vessels.

Pistacia lentiscus L. (Fig. 1g, h)

Wood mostly semi-ring to ring-porous. Earlywood vessels are usually in a single row, rarely in multiple rows, and are very variable in diameter. In latewood, and throughout the ring where ring-porosity is not outspoken, vessels are

arranged in radial files or clusters showing sometimes a dendritic pattern. Perforation plates simple. Very narrow vessels sometimes intergrade with vascular/vasicentric tracheids. Helical thickenings present in narrow vessels. All ground tissue fibres libriform.

Olea europaea L. (Fig. 2a, b)

Wood diffuse-porous. Vessels generally in short to fairly long radial multiples, occasionally in clusters, rarely solitary, angular to rounded in cross section. Perforation plates simple. All ground tissue fibres libriform. Fine and faint helical thickenings present in narrow vessels.

Quercus ilex L. (Figs. 2c, d; 3g, h)

Wood diffuse-porous. Vessels generally large, solitary and rounded in cross section, sometimes in diagonal or dendritic pattern. Perforation plates simple. Both libriform fibers and fiber-tracheids present.

Fraxinus ornus L. (Figs. 2e, f; 3e, f)

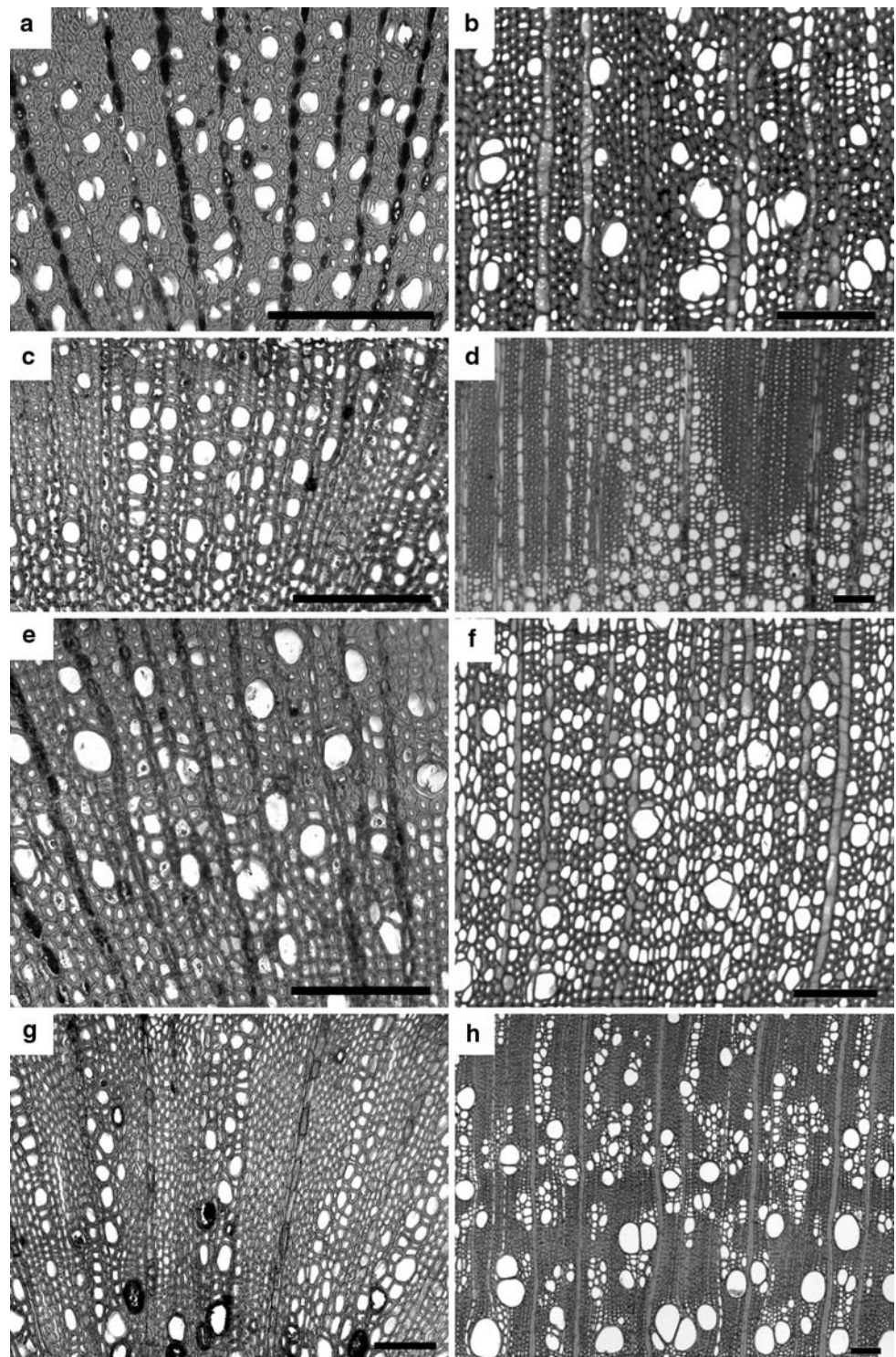
Wood ring-porous. In earlywood, vessels are generally solitary or loosely packed. Shape round to oval in cross section. In latewood, vessels are solitary or arranged in short radial files or small groups. Vessels are rounded in cross section. Perforation plates simple. Helical thickenings absent. All ground tissue fibres are libriform.

Ostrya carpinifolia L. (Fig. 2g, h)

Wood diffuse-porous. Vessels generally infrequent, in regular radial files. Vessels in the middle of multiples are square, while those at the ends are rounded to angular in cross section. Perforation plates simple. Fine helical thickenings present in vessels. All ground tissue fibres libriform.

Tables 1 and 2 summarize several quantitative features of stem and twigwood as well as data from the literature. Vessel frequency was higher in twigwood than in stemwood in all the species. Differences between species were highly significant ($p < 0.001$) in both young and mature structures. In stems, the separation of the species in groups (comparison tests using LSD and Student–Newman–Keuls coefficient) was more marked and reflected the distribution of the species in the studied area. In fact, *C. monspeliensis* was characterized by the highest value of vessel frequency, followed by *R. alaternus* that in turn showed frequency significantly higher than a group formed by *M. communis*, *P. lentiscus* and *O. europaea*. The remaining species showed the lowest frequencies.

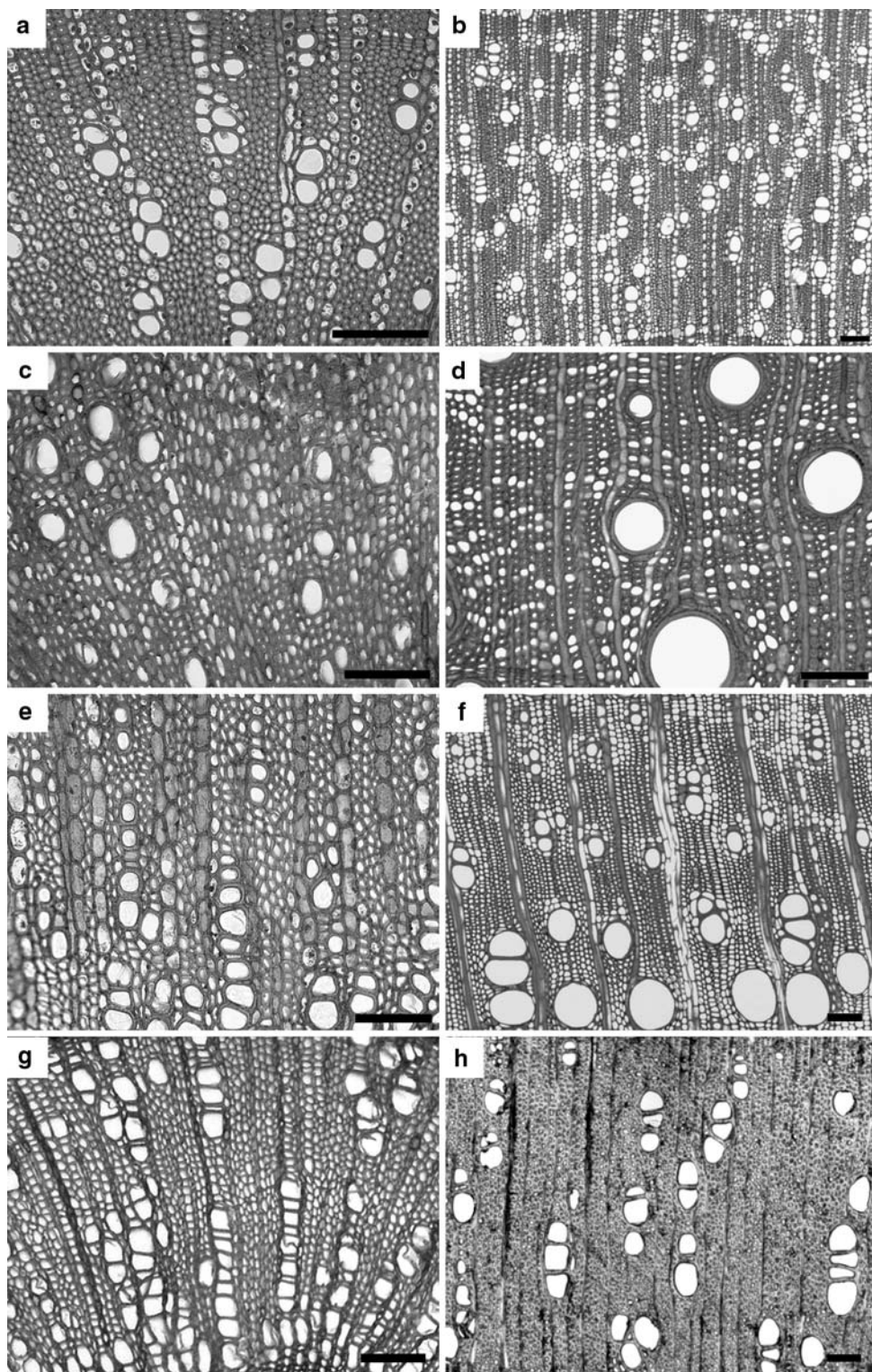
Fig. 1 Microphotographs of cross sections of twig- (a, c, e, g) and stemwood (b, d, f, h) of *C. monspeliensis* (a, b), *R. alaternus* (c, d), *M. communis* (e, f) and *P. lentiscus* (g, h). Entire rings are shown. Scale bar 100 μ m



Vessels were significantly larger in stem than in twigwood: mean Feret diameter calculated in stems was 1.45–6.48 times larger than in twigwood with the lowest ratio found in *M. communis* while the highest in *F. ornus*. Similarly, mean lumen area of vessels calculated in stems was 2.4–37.4 times larger than in twigwood. Vulnerability,

measured as mean Feret diameter of lumen divided by vessel frequency, showed values much lower than 1 (10^{-2} order) in twigwood of all the examined species. Also in stemwood of *C. monspeliensis*, *R. alaternus*, *M. communis*, *P. lentiscus* and *O. europaea*, vulnerability was lower than 1 (10^{-1} order), while it was more than 1 in the other

Fig. 2 Microphotographs of cross sections of twig- (a, c, e, g) and stemwood (b, d, f, h) of *O. europaea* (a, b), *Q. ilex* (c, d), *F. ornus* (e, f) and *O. carpinifolia* (g, h). Entire rings are shown. Scale bar 100 μ m



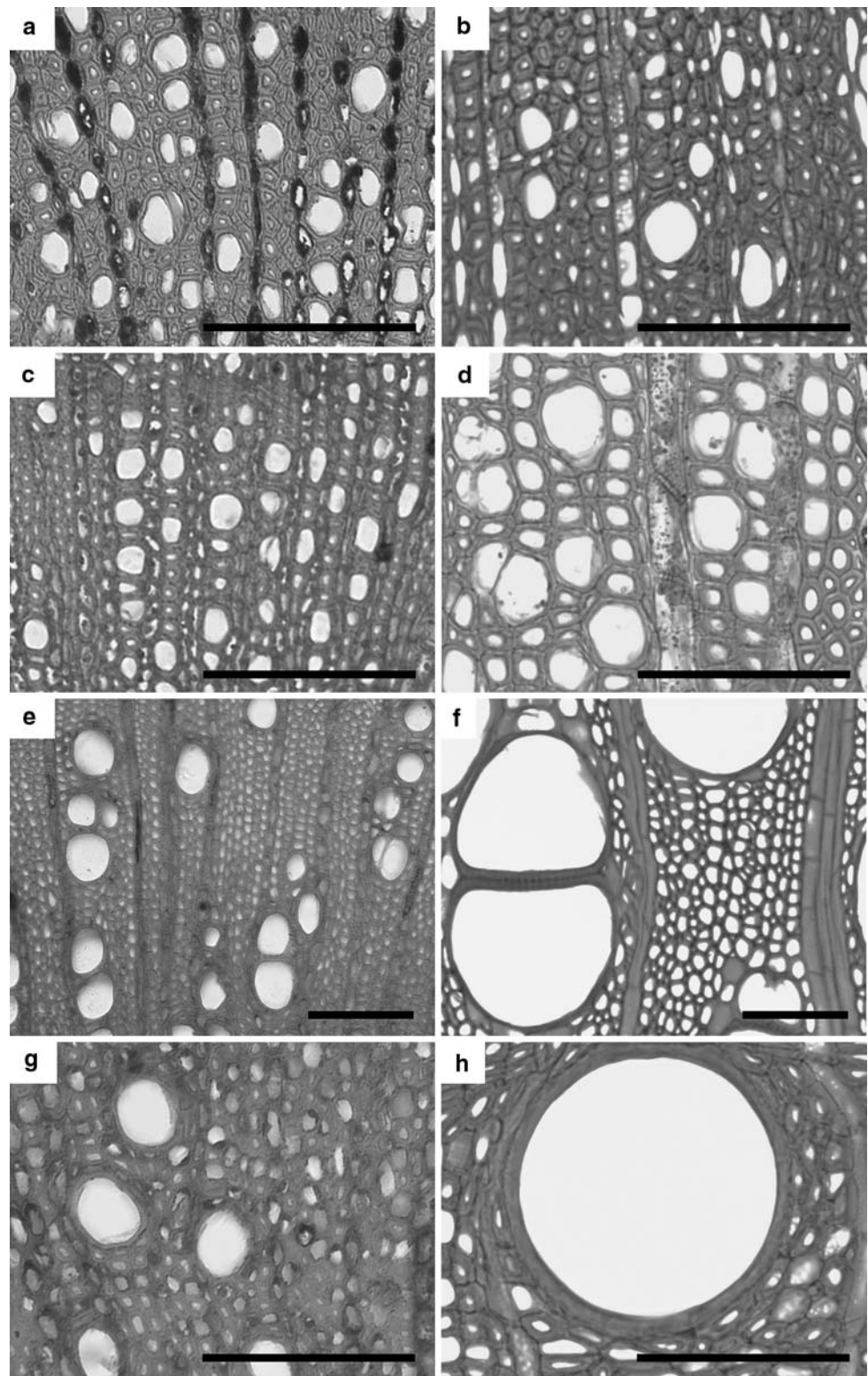
species, with maximum values in *Q. ilex* and earlywood of *F. ornus*.

Data measured in stemwood (Table 1) were comparable to ranges reported in literature (Table 2), though minor differences might be due to different ways of collecting the data by

various authors, to the variability between plants belonging to different environments within species, and to the variability between stems of different ages and diameters.

The “hydraulic distance” between species, and within species between stem and twigwood, was clearer

Fig. 3 Microphotographs of cross sections of twig- (a, c, e, g) and stemwood (b, d, f, h) of *C. monspeliensis* (a, b), *R. alaternus* (c, d), *F. ornus* (e, f) and *Q. ilex* (g, h). Twig- and stemwood are shown at the same magnification within species to highlight the “hydraulic distance”. Scale bar 100 μ m



considering the ECD (equivalent circle diameter) and calculating the relative flow rate (Table 3). For example, the ratio between the maximum (in earlywood of *F. ornus*) and the minimum (in *C. monspeliensis*) ECD measured in

stems was 5, but if relative conductivities were calculated, the ratio was much higher and became 650. The difference between conductivities of woods of more xeric and more mesic environments was reduced when young structures

were considered. Moving from young towards adult structures, relative conductivity showed a low increase in shrubs of more xeric areas (i.e. 5 times in *M. communis*) and a very high increase in trees of more mesic zones (i.e. 2,150 times in earlywood of *F. ornus*). However, the trend was not very distinct, since *P. lentiscus* was characterized by a higher increase than the more mesic *O. carpinifolia*.

Regarding total vessel area (Table 1), measured as the percent of wood occupied by vessels, some species showed higher values in twigwood than in the main stems, while in other species the opposite was true. *F. ornus* not only showed the larger increase of single vessel lumen area but also the larger increase of total vessel area.

Vessel grouping (Tables 1, 2) was highly variable between the studied species in both young and old stems. Moreover, vessel grouping tended to decrease in older wood in all the cases, except in *P. lentiscus* and *O. europaea*, and latewood of *F. ornus*.

Absolute vessel wall thickness showed a tendency to increase from young to mature wood with the exception of *C. monspeliensis* and *M. communis*. However, these two species showed only a small increase in vessel diameter moving from twigwood to stem.

Discussion

Mediterranean ecosystems represent interesting environments to study ecological trends in xylem anatomy, given that they are quite special in climatic conditions and support a wide diversity in growth forms. In general, trees show high efficiency in water transport (Baas and Schweingruber 1987), while many shrub species from Mediterranean regions have wood specialised for high conductivity when water is available (simple perforation plates, wide earlywood vessels, etc.), but also specialised for safety during drought periods (narrow latewood vessels, vasicentric tracheids, etc.) (Baas and Carlquist 1985; Fahn et al. 1986; Carlquist 1989). Furthermore, within the same plant form, the upper portions of plants have narrower and shorter vessels than the basal parts, so that most of the resistance to water flow of a shoot system is in the small diameter twigs (Scholander et al. 1965; Sastrapadja and Lamoureux 1969; Yang and Tyree 1993; Fisher et al. 2007).

The descriptive and quantitative analysis of xylem anatomy in the eight examined species highlighted a trend between juvenile and mature structures that resembles the tendencies found between shrubs and trees, basal and upper portions of plants, and are in agreement with observations made on other species for palaeoecological purposes (Poole 1994). In our analysis, when considering attributes such as porosity, presence of tracheids and of helical

thickenings, the traits were almost equally well expressed in young twigs and older stems. From a quantitative viewpoint, twigs were characterized by a xylem made of many more, narrower and generally more grouped vessels than stems, all attributes indicating a much safer hydraulic architecture.

Clear ring-porosity was manifest only in stems of *F. ornus* and in some rings of stemwood of *P. lentiscus*. However, in these species there was a tendency from ring-porosity towards semi-ring-porosity and diffuse-porosity in the safer young twigs. This phenomenon follows the trend indicating the decreasing of ring-porosity towards plant habits characterized by safer wood anatomy (Baas and Schweingruber 1987). Porosity, together with other traits, such as inter-vessel pitting, seems also to affect water transport efficiency and vulnerability to cavitation as shown recently by Hacke et al. (2006) who reported that increasing negative pressure causes an abrupt drop in hydraulic conductivity in ring-porous trees and vines, while it causes only a gradual decrease in diffuse-porous woods.

The frequency of vessels affects not only water transport efficiency but also safety. A very high frequency of conducting cells is generally referred to as redundancy: “superfluous” vessels are designed to permit conduction despite de-activation of a part of the tissue that can be caused by several factors (Zimmermann 1982; Carlquist 1989). Interestingly, the frequency of vessels increases moving from more mesic to xeric environments, from trees to shrubs and from tropical to Mediterranean species (Fahn et al. 1986; Carlquist 1989). In our study, the increase in vessel frequency along the mesic-xeric gradient was clearer in stem than in twigwood. According to the concept of redundancy, *C. monspeliensis* and *R. alaternus* would have the safest vascular system. *M. communis* and *P. lentiscus* showed quite low values of vessel frequency, comparable with those of more mesic species, as if this character would reflect their tropical origin and distribution (Quézel 1985; Raven 1973; Axelrod 1975; Yi et al. 2004). Notwithstanding the low vessel frequency in stemwood, the mesic *O. carpinifolia* also seemed to have high conductive safety because of the high vessel frequency, grouping and low vulnerability. Although its speculative nature due to the lack of an absolute hydraulic basis, the vulnerability index is commonly used to indicate adaptation to xeric (values <1) or mesic (values >1) conditions (Carlquist 1977, 1992; Psaras and Sofroniou 1999). In twigwood of the eight examined species, values of vulnerability of 0.01–0.06 accord with the occurrence of greater tensions in water columns at upper levels in terminal twigs than at lower levels in older branches and stems (Scholander et al. 1965; Poole 1994; Fisher et al. 2007). In stems, vulnerability marked a definite separation between trees of more mesic environment (*Q. ilex*, *F. ornus* and *O. carpinifolia*),

Table 1 Quantitative data of the twig- and stemwood measured in the examined species




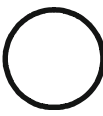


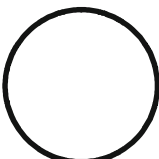










Sample	Habit	Vessel frequency (per mm ²)		Vessel mean feret diameter (µm)		Vulnerability index	Vessel lumen area (µm ²)		Wood area occupied by vessels (%)		Solitary vessels (%)	Presence of tracheids	Vessel wall thickness (µm)		Helical thickenings	
		x	se	x	se		x	se	x	se			x	se		
<i>C. monspeliensis</i>	b	s	1100	133 A	12.5	0.1 A	0.011	93	8 A	14.7	0.9 A	74.0	3.9 A	2.10	0.24 A	+
	s		243	13 a	24.4	0.3 a	0.101	442	13 a	7.7	0.8 ab	94.3	2.0 a	1.65	0.05 a	+
<i>R. alaternus</i>	b	s/t	1003	105 A	12.6	0.1 A	0.013	104	2 A	14.1	1.6 AB	57.0	2.8 B	0.92	0.06 B	+
	s		180	7 b	32.8	0.4 b	0.182	781	17 a	10.6	0.5 bc	77.8	1.8 c	1.93	0.04 b	+
<i>M. communis</i>	b	s	331	36 C	18.2	0.2 C	0.055	232	8 C	7.7	0.7 CD	73.0	3.6 A	1.97	0.32 A	+
	s		105	8 c	26.4	0.7 a	0.252	548	26 a	5.1	0.7 a	97.3	1.6 a	1.09	0.02 c	+
<i>P. lentiscus</i>	b	s/t	450	46 BC	20.7	0.2 E	0.046	281	14 E	10.1	0.9 BC	24.0	5.0 C	1.17	0.43 B	+
	s		105	13 c	78.9	1.7 e	0.752	4474	197 d	13.5	1.6 c	5.3	0.5 e	2.31	0.06 d	+
<i>O. europaea</i>	b	s/t	297	50 C	15.0	0.1 B	0.051	151	4 B	5.4	0.7 D	52.0	3.8 B	3.17	0.37 C	+
	s		81	3 c	45.1	0.5 c	0.556	1570	30 b	10.8	1.0 bc	25.8	3.4 d	3.17	0.04 e	+
<i>Q. ilex</i>	b	s/t	445	65 BC	20.8	0.2 E	0.047	260	16 E	10.4	1.1 ABC	75.0	2.7 A	2.34	0.66 A	-
	s		13	0 d	87.8	1.3 f	6.553	6121	176 e	9.0	0.5 ab	100.0	0.0 b	5.36	0.11 f	-
<i>F. ornus</i>	b	t	304	63 C	18.9	0.2 D	0.062	306	28 D	10.5	1.0 ABC	50.0	5.4 B	2.20	0.22 A	-
	s-e		20	2 d	122.7	2.1 g	6.137	11434	371 f	21.1	1.9 d	75.4	8.6 c	4.54	0.14 g	-
<i>O. carpinifolia</i>	b	t	813	237 AB	18.6	0.2 CD	0.023	224	14 C	14.2	1.0 AB	4.0	0.6 D	0.78	0.03 B	+
	s		38	1 d	56.4	1.2 d	1.468	2308	102 c	6.5	0.6 ab	35.5	5.6 d	2.76	0.06 h	+

Mean values (x), standard errors (se) and significance of ANOVA between species are reported. Different letters correspond to significantly different values after using LSD and Student–Newman–Keuls coefficients for multiple comparison tests ($p < 0.05$). “b” and “s” in sample are referred to “twigwood” and “stemwood”, “s” and “t” in habit are referred to “shrubs” and “trees”

Table 2 Quantitative and descriptive data of stemwood of the examined species, derived from various literature sources (Baas and Schweingruber 1987; Baas et al. 1988; Fahn et al. 1986; Grosser 1977; Hall 1952; Schweingruber 1990; Tippo 1938; the InsideWood database—<http://insidewood.lib.ncsu.edu/search/>)

	Vessel frequency (per mm ²)	Vessel tangential diameter (μm)	Vessel radial diameter (μm)	Presence of tracheids	Vessel wall thickness (μm)	Helical thickenings
<i>C. monspeliensis</i>	250–300	15–50 or 50–100	up to 60	+	3.00	+
<i>R. alaternus</i>	150	<50	up to 60	+	2.00	+
<i>M. communis</i>	100–125	50–100 or <50	up to 45	+	Thin to thick	+
<i>P. lentiscus</i>	120–160	15–100	170	±	2–4	+
<i>O. europaea</i>	40–100	50–100 or <50	up to 60	–	3–6	+
<i>Q. ilex</i>	5–20	100–200 or >200		+		–
<i>F. ornus</i>	10–40	60–280 20–90	up to 370	–	4.8	–
<i>O. carpinifolia</i>	20–140	50–100 or <50	30–110	–		+

Table 3 Mean vessel size and derived parameter of twig- and stemwood among the eight examined species

	<i>C. monspeliensis</i>	<i>R. alaternus</i>	<i>M. communis</i>	<i>P. lentiscus</i>	<i>O. europaea</i>	<i>Q. ilex</i>	<i>F. ornus</i> (earlywood)	<i>F. ornus</i> (latewood)	<i>O. carpinifolia</i>
Stem (vessel size)									
ECD (μm)	23.3	31.16	25.23	75.8	43.36	85.46	117.67	50.58	52.13
RC (μm ⁴)	294,730	942,735	405,200	33,012,379	3,534,737	53,339,821	191,718,055	6,545,085	7,385,007
%C	0.10	0.32	0.14	11.11	1.19	17.95	64.51	2.20	2.49
Branch (vessel size)									
ECD (μm)	11.4	11.47	16.44	18.64	13.93	19.01	17.28		16.4
RC (μm ⁴)	16,890	17,308	73,048	120,721	37,653	130,596	89,161		72,339
%C	3.03	3.10	13.10	21.65	6.75	23.42	15.99		12.97

Mean values are given only

ECD equivalent circle diameter, RC relative conductivity; %C percent conductivity

showing values greater than 1, and the other more xeric species having values of 0.1–0.7. In more mesic trees, vulnerability of stemwood was up to more than 100 times greater than that of twigwood. These ratios are much higher than correction factors between juvenile and mature wood discussed by other authors in *Betula*, *Populus* and *Aesculus* species (Poole 1994). High vulnerability of *Q. ilex* wood is in agreement with its sensitivity to aridity: although showing a plastic response to drought, mediated by changes of growth and wood features, after periods of severe drought this species probably suffers from widespread embolism which is responsible for dropping and reduced production of leaves (Corcuera et al. 2004). However, as demonstrated in several Mediterranean species, the response of plants to changing water availability

can be affected by other traits, such as root depth, root/shoot ratio, interaction with rootstocks, inter-vessel pitting and physiological adjustments (Villar-Salvador et al. 1997; Castro-Díez et al. 1998; Vilagrosa et al. 2003; Corcuera et al. 2004; Martínez-Vilalta et al. 2002; Trifilò et al. 2007). Considering all measured characters as a whole, *P. lentiscus* would be the species that maintains the best balance between safety and efficiency in adult wood. In this species, the increase of vessel diameter and associated increase of relative conductivity is in the range of species at the mesic end of the humidity gradient, while maintaining a vulnerability lower than one is typical of species at the xeric end of the gradient. It is demonstrated that, during drought, this species has an efficient stomatal control linked to a water-spending strategy allowing the

maintenance of its entire leaf biomass until the almost 100% loss of conductivity; moreover, its physiological behaviour facilitates the mechanisms of xylem refilling or the construction of new xylem after cavitation (Vilagrosa et al. 2003).

As expected, in this study, vessels in trees were larger than those in shrubs, in agreement with many reports in the literature associating vessel diameter with plant size (e.g. Carlquist 1966; Wallace 1986). There is also evidence for a trend of decreasing vessel element length and diameter with aridity (Carlquist 1966; Carlquist and Hoekman 1985) that was also found in the studied species with the exception of *P. lentiscus*. As a consequence, the hydraulic distance (considered as the ratio between relative conductivity of stem- and twigwood) was much lower in more xeric species than in more mesic ones with the exception of *P. lentiscus* that showed ratios not far from the more mesic *Q. ilex*. Nevertheless, vulnerability and relative conductivity are parameters without an absolute hydraulic basis but hypothetical concepts based on anatomical calculations. Efficiency and safety of the hydraulic system, however, depend on composite characteristics involving not only the size and frequency of vessels but also cell wall and pit membrane features and relationships between vessels, fibres and tracheids (Martínez-Vilalta et al. 2002; McCulloh and Sperry 2005; Sperry et al. 2006; Jacobsen et al. 2007a, b; Pratt et al. 2007). Regarding the relations between xylem cell types, recent investigations highlighted the importance of patterns in hydraulic architecture in determining efficiency of water transport and also demonstrated that the applicability of Murray's law is different in coniferous, diffuse-porous and ring-porous wood (McCulloh et al. 2004).

Vessel grouping is a widespread phenomenon in most woody species, especially those from the arid desert flora and Mediterranean species (Fahn et al. 1986; Carlquist 1989). In families, in which only libriform fibers are present, vessels are never entirely solitary (Carlquist 1984). The case of *O. carpinifolia* can be included among the species that compensate the lack of fiber-tracheids or tracheids with vessel grouping for safe water conduction. If a wood has tracheids, a background of conductive cells is ensured even during periods of extreme drought when vessels can be embolised. In a wood lacking tracheids, the three-dimensional pattern of the vascular system can be maintained through the selection for highly grouped vessels: if a particular vessel in a group fills with air, its intact neighbours can continue water supply to all the leaves (Carlquist 1984, 1989). In this respect, the woods of *F. ornus* and *O. europaea* showed the lower safety given that absence of conductive imperforate tracheary elements was associated with a medium to high percentage of solitary vessels. However, vessel grouping is a controversial

characteristic, because it could also favour the spreading of embolism by increasing total inter-vessel pit area (Hacke et al. 2006).

According to some authors, adaptation to drought also relies on vessel resistance to implosion, also defined as vessel strength and calculated as the square of vessel wall thickness divided by the diameter of the conduit (Young 1989; Hacke et al. 2001; Sperry 2003). Among the examined species, twigwood of all the species, except *O. carpinifolia* and *P. lentiscus*, was characterized by low vulnerability to implosion that is consistent with greater xylem tension in twigs. On the contrary stems showed low vessel strength with lower values in *P. lentiscus* and *M. communis* that behave similarly to the more mesic *O. carpinifolia* and *F. ornus*. *P. lentiscus* and *M. communis* have helical vessel wall sculpturing, but it is hard to envisage that these fine thickenings would considerably contribute to the mechanical strength of the vessels (cf. Carlquist 1975; Baas 1976; Baas and Carlquist 1985; Baas and Schweingruber 1987; Carlquist 1988).

The overall analysis of xylem anatomy of the eight species showed that they have various degrees of adaptation to severe drought periods. Twigwood in all species was characterised by many additive attributes favouring safety and the differences between species tended to be small, presumably because also the more mesic species have high safety demands in their terminal twigs. On the other hand, quantitative differences were amplified in mature wood with ratios depending on the plant habit and phenology and the position of the species along the humidity gradient. Consequently, the “hydraulic distance” between juvenile and mature wood differed among the species. Moving from more mesic versus arid areas there was a change in phenology from deciduous to evergreen and drought deciduous that was accompanied by an increase in the occurrence of attributes in wood anatomy allowing adaptation to drought conditions.

The increased hydraulic distance between stemwood and terminal twigwood in the xeric-mesic gradient in our study material is most probably due to two confounding, but in this case reinforcing factors: (a) the differences in plant size imply a greater absolute distance between terminal twigs and mature stemwood in mesic species, which—associated with ontogenetic and radial distance from the first formed secondary xylem—also causes a greater hydraulic distance; (b) the xeric end of the spectrum demands special adaptations to hydraulic safety, also in the stemwood, reducing hydraulic distance in these xeric species. In the material studied by us, these two confounding factors cannot be separated because of the mixed provenances of the twig- and stemwood samples. Future research on carefully sampled twig- and stemwood from the same plants should make it possible to separate the effect of plant

size from hydraulic xylem adaptation per se, minimising the effect exerted by other factors such as climatic conditions and nutritional state (Villar-Salvador et al. 1997). Moreover, such a sampling would allow to verify the applicability of Murray's law and to test the hypothesis that diffuse-porous species are less efficient than ring-porous ones, because the latter allows conduit area to increase distally without also increasing total xylem area (McCulloh and Sperry 2005). Whatever the results of such an analysis, the present study demonstrates once again the dual strategies of Mediterranean shrub and tree species for optimal safety and efficiency of their hydraulic architecture, co-depending on their position in a xeric-mesic gradient.

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