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Laurel forests in Tenerife, Canary Islands

I. Xylem structure in stems and petioles of *Laurus azorica* trees

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Abstract The general wood structure, vessel size and distribution along the stem xylem radius and in petioles were studied in *Laurus azorica* trees living in a Tenerife laurel forest. The fractions of volume occupied by dry matter, water and air in percentage of wood fresh volume were also studied. The wood showed a diffuse-porous structure, with solitary vessels or vessels somewhat clustered in small radially oriented groups. Vessels had a diameter ranging from 20 to 130 μm . This diameter was minimal close to the pith, increased more than 2-fold with age, and reached its maximum width close to the cambium. Vessel density decreased from 36 vessels mm^{-2} near the pith to about 13 vessels mm^{-2} near the cambium. Accordingly, the lumen area was small in young xylem close to the pith (0.0015 mm^2), reaching a value 5 times larger (0.007 mm^2) near the cambium than in the centre of the stem. Lumen area of vessels in petioles was about 1.5% of petiole cross-sectional area and thus much lower than in stems. Mean hydraulic diameter of these vessels was about 20 μm , and mean vessel density about 136 per petiole. There were only small differences in proportions of dry matter, water and air along stem radius. The relevance of each one of these fractions in the wood is discussed as evidence of the possible existence of a number of embolized vessels dispersed in the total functional cross-sectional area of the xylem.

Keywords *Laurus azorica* · Wood structure · Vessel distribution · Vessel lumen area · Wood water content

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Introduction

Study of wood structure is the first step in gaining knowledge of water transport efficiency through stems. Vessel size and distribution in the xylem have a very important functional significance (Zimmermann 1983; Aloni 1991; Sherwin et al. 1998; Jansen et al. 2000). The total stem cross-sectional area is not always involved in upward water transport. The weight of evidence indicates that the heartwood does not conduct water, and in mature trees, water moves upward in only a portion of the sapwood (Kozłowski and Pallardy 1997). Therefore, the determination of sapwood and heartwood area allows a better assessment of the conductive system efficiency in hydraulic studies. It also helps methodically when installing sensors for measuring the sap flow rate in stems, in particular when starting studies of tree species for the first time and even more so if they grow in unusual environmental conditions.

The amount and rate of sapwood and heartwood formation varies greatly with tree species, tree age, rate of growth and environmental conditions (Bamber and Fukazawa 1985). In a few species heartwood may never form at all (Kozłowski and Pallardy 1997). Sapwood and heartwood are clearly visible on wood cross-sections in most temperate woody species due to the difference in moisture content and light transmission between the two zones. The heartwood is often opaque while the sapwood is translucent (Kaufmann and Troendle 1981; Marchand 1984). Nevertheless the moisture content varies among species. In most gymnosperms and some angiosperms it is higher in sapwood than in heartwood while in some other angiosperms the opposite occurs (Cermák and Nadezhdina 1998). There are also many species where differences in moisture in either zone cannot be found (Kozłowski and Pallardy 1997), which makes its direct determination difficult.

Laurus azorica is an evergreen tree species whose distribution area is limited to the Canarian, Madeira and Azores archipelagos of the Macaronesian region (Hansen and Sunding 1993). Studies of wood structure of this

species are scarce. Oramas and De Roma (1967) give an overview of wood structures of Canary Island trees for the purposes of carpentry. Schweingruber (1990), in his Atlas of anatomy of European woods, includes pictures of *L. azorica* wood, mentioning that heartwood in this species is indistinct.

The aim of the present study was to obtain a better knowledge of morphological and anatomical features of the xylem in stems and petioles (considered as both “ends” of the aboveground conducting pathway), to assess the longitudinal (axial) characteristics of the water-conducting system of *L. azorica* trees. Therefore wood characteristics, number, size and distribution of vessels and moisture content along the stem radius were studied. The work was focused on obtaining a major structural background for a better understanding of sap flow measurements performed in this tree species growing in a cloudy laurel forest on the Canary Islands (Jiménez et al. 1996, 2000) and particularly on providing the morphological and anatomical data needed for the following study about the efficiency of tree hydraulic system in the same species (Cermák et al. 2002).

Materials and methods

Plant material and experimental site

The study was carried out on trees of different sizes [diameter at breast height (DBH) ranging from 90 to 240 mm] of *Laurus azorica* (Seub.) Franco, growing in the laurel forest on Agua García mountains, north-east of Tenerife, Canary Islands. The site is on a slight slope (12°) facing NNE, at an altitude of 820–830 m. The climate is humid Mediterranean with a dry period, from May to September, as can be seen in the climatic diagram (following Walter and Lieth 1967; Walter 1973) shown in Fig. 1. The average annual temperature was 14°C and annual precipitation was 733 mm. More details, such as highest recorded temperature (39°C), mean daily maximum of the warmest month (22.6°C), mean daily temperature change (7.0°C), mean daily minimum of the coldest month (6.9°C), and lowest recorded temperature (0.2°C), are mentioned in the legend. The dry period indicated in the climatic diagram, can be mitigated by high air humidity most of the time (annual mean relative humidity was 82%).

Historically, the site represented a laurel forest type with six tree species: *Laurus azorica* (Seub.) Franco, *Persea indica* (L.) K. Spreng., *Myrica faya* Ait., *Erica arborea* L., and two species of *Ilex*, *I. perado* Ait. ssp. *platyphylla* (Webb & Berth.) Tutin and *I. canariensis* Poir. All are evergreen and broadleaved species with the exception of *E. arborea*, which presents needle-like leaves. The stand regrew from the original one that was cut in the 1950s. More details about the site and forest stand were described in previous papers (Morales et al. 1996a, b, c).

Anatomy and physical properties of the conductive xylem

Density of xylem vessels ($D_{v,xyl}$) and distribution of anatomical vessel lumen diameters ($d_{lum,an}$) or radii ($r_{lum,an}$) in radial (rad) and tangential (tang) directions in stems were measured on two samples taken from opposite sides of four *L. azorica* trees at breast height (total eight samples). Light microscopy (magnification $\times 200$) was applied to observe slides from the wood cut with a microtome and stained with safranin fast green (Johansen 1940). Anatomical lumen area of conducting vessels was calculated as the ellipse:

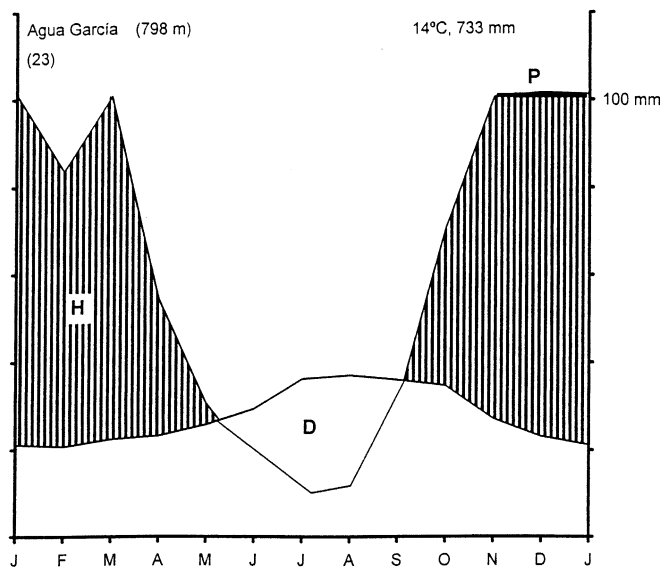


Fig. 1 Climatic diagram (according to Walter and Lieth 1967; Walter 1973) for the experimental plot in Agua García (Tenerife), at 798 m altitude (data from 23 years of observation). *Left axis* Mean monthly temperature (unit = 10°C), *right axis* mean monthly precipitation up to 100 mm (unit = 20 mm). *Abscissa* Months of the year. Dry period (D), humid period (H) and humid period with mean monthly precipitation above 100 mm (P). Average annual temperature 14°C. Annual precipitation of 733 mm. Highest recorded temperature (39°C), mean daily maximum of the warmest month (22.6°C), mean daily temperature change (7.0°C), mean daily minimum of the coldest month (6.9°C), lowest recorded temperature (0.2°C)

$$A_{lum,an} = \pi (r_{lum,an,rad} \times r_{lum,an,tang}) \quad (1)$$

Hydraulic lumen area, $A_{lum,hyd}$, was calculated from hydraulic mean radius of vessels, $r_{lum,hyd}$, in different diameter classes of vessels, i , along the cross-section of the xylem and expressed per unit of xylem area, A_{xyl} ,

$$r_{lum,hyd}^2 = \left(\sum n_i \times r_{lum,an,i}^4 / N \right)^{1/2} \quad (2)$$

where n_i is the number of vessels in each diameter class and N is the total number of vessels. All measured parameters were plotted against xylem radii expressed in percentage of total radii, in order to allow a better comparison of different size trees. Additionally, small samples of wood (5×5 mm in size) were macerated following the technique described by Purvis et al. (1966) so that the form of individual cells and perforations in cell walls could be seen better.

Vessel distribution in petioles

Vessels were also analyzed in *L. azorica* petioles in a similar way to the xylem of main stems. Leaves were sampled from the upper (sun leaves) and lower (shade leaves) canopy following the characteristic height pattern of the stand (Morales et al. 1996a) in five trees; five petioles of each tree and condition (sun and shade) were analysed. Distribution of vessels in the petiole according to their diameters and number per petiole were measured using a light microscope (magnification $\times 200$) on slides cut with a microtome. The anatomical and hydraulic lumen area of conductive vessels was calculated in the same way as for stems, based on the cross-sectional area of the petiole, A_{pet} .

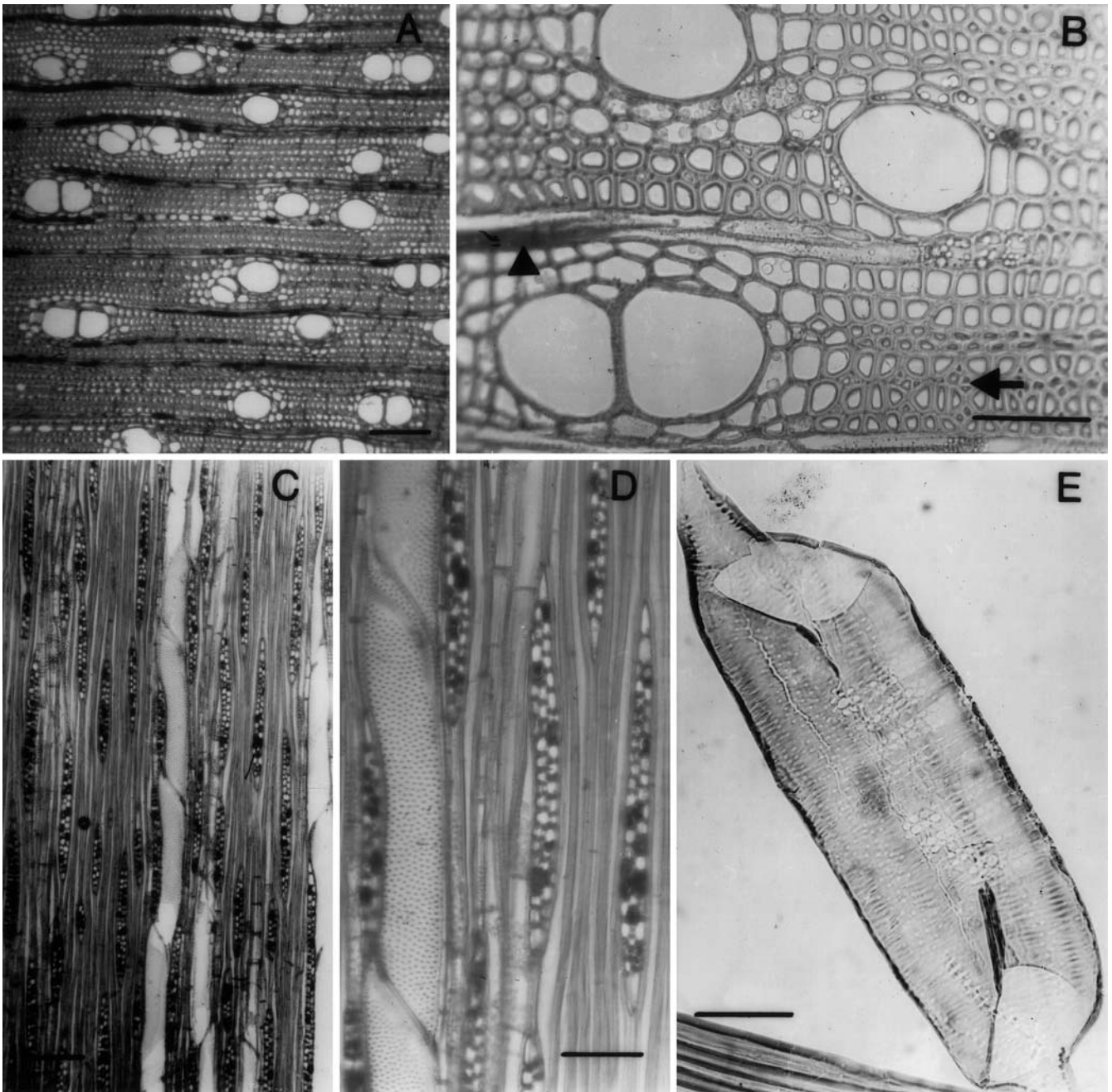


Fig. 2A–E Light micrographs of *Laurus azorica* wood. **A** General view of a cross-section showing the distribution of vessels with no significant differences in size along the growth ring, *bar* 200 μm . **B** Details of vessels with paratracheal parenchyma; *arrow* marks the position of the borderline between annual rings; granular masses in cells of pith rays are marked by an *arrowhead*, *bar* =100 μm . **C** General view of a longitudinal section, *bar* 200 μm . **D** Details showing a vessel member with two simple perforation plates; the fibres, some of them septated; and the pith rays with procumbent and upright cells, *bar* 100 μm . **E** A vessel member obtained by maceration. Note the alternate and large intervascular pittings and the opposite and elongated ones corresponding to the parenchyma cells, *bar* 50 μm

Wood physics

Fractions of wood volume (V) occupied by water (V_w), air (V_a) and dry matter (V_m) were measured in six *L. azorica* trees over a range of stem diameters (DBH=100–240 mm). Altogether 12 cores of wood taken from opposite sides of six tree stems with an increment borer (Suunto, Finland) were analysed gravimetrically after intersecting into a series of sub-samples several millimetres long, shortly after sampling (samples were protected in the meantime by wrapping in aluminum foil). A similar procedure was also applied on whole logs cut from main stems and branches of one additional sample tree, where cores were taken simultaneously.

Results

Xylem anatomy and distribution of vessels in stems and petioles

The wood of *L. azorica* is diffuse-porous, stem vessels are rather uniform in size and distributed through the growth rings; they are mostly solitary or in small radially oriented groups. Paratracheal parenchyma is irregular and often incomplete (Fig. 2A, B). Pith rays are 10–20 cells in height, 2–3 cells wide, heterogeneous, with the central part consisting of radially elongated cells (procumbent cells), while the upper and lower edges consist of vertically elongated (upright) cells (Fig. 2C, D). Libriform fibres with simple pits (partly septated) are of medium length (average range is 1,200–1,800 μm) and they usually retain their protoplasts (Fig. 2D). Cells of paratracheal parenchyma and pith rays have numerous globules that could be oil droplets representing stored lipids. Some of these cells are completely full of brown or red granular masses (Fig. 2B, D). Vessel elements are of medium length (average range 600–800 μm) and are connected through simple perforation plates that are overlapped by a very thin cell tip (the “tail” that is visible on macerated samples). The intervascular pittings are alternate and large; pits to parenchyma are opposite, large and elongated (Fig. 2E).

The anatomical diameter of vessels, $d_{\text{lum_an}}$, was within the range of 20–130 μm , the distribution curve was slightly asymmetrical and could be generalized by a log-normal equation (Fig. 3). The arithmetic mean anatomical diameter of stem vessels over the whole xylem cross-sectional area, A_{xyl} , of all sample trees irrespective of their size (DBH=150–240 mm) was 81 μm , and the mean hydraulic diameter, $d_{\text{lum_hyd}}$, was 90 μm . Mean density, $D_{\text{v_xyl}}$, was 19.7 vessels mm^{-2} of xylem cross-sectional area of stems at breast height.

Although no significant differences were found in the size of the earlywood stem vessels and the latewood vessels in growth rings, the diameter varied in the radial direction (Fig. 4). Vessel diameter, $d_{\text{lum_an}}$, was minimal close to the pith ($45.02 \pm 3.51 \mu\text{m}$), increased gradually more than twofold ($95.30 \pm 10.05 \mu\text{m}$), and reached its maximum width close to the cambium. The hydraulic diameter was obviously slightly higher than the anatomical one.

Vessel density, $D_{\text{v_xyl}}$, decreased from 36 vessels mm^{-2} close to the pith to about 13 vessels mm^{-2} near the cambium (Fig. 4). There was the strict inverse linear relation between vessel density (vessel mm^{-2}) and vessel diameter (μm) along the stem radius. The arithmetical mean anatomical diameter fits the relation: $d_{\text{lum_an}} = 137 - 2.98 \times D_{\text{v_xyl}}$; $r^2 = 0.99$; and for the corresponding hydraulic diameter the fit is $d_{\text{lum_hyd}} = 145 - 3.1 \times D_{\text{v_xyl}}$; $r^2 = 0.98$ (mean of three trees of diameters 150–240 mm).

Cross-section of stem vessels was usually slightly irregular (especially when contacting neighbouring vessels), but in most cases was in the form of an ellipsoid.

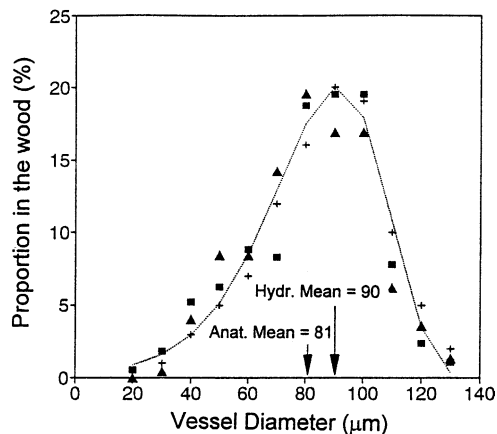


Fig. 3 Distribution of vessels within stem wood of *L. azorica* trees in the Agua García laurel forest experimental site. For each vessel diameter, three trees within a range of diameters are presented (DBH 150 mm filled squares, 200 mm plus sign, 240 mm filled triangles). Distribution of vessels (in % of total) was generalized by the log-normal equation in the form: $y = [a/(b-x)] \times \exp\{-[\ln(b-x)-c]^2/d\}$; where x is vessel diameter ($d_{\text{lum_an}}$) in μm ($a=1,500$, $b=163$, $c=4.35$, $d=0.15$)

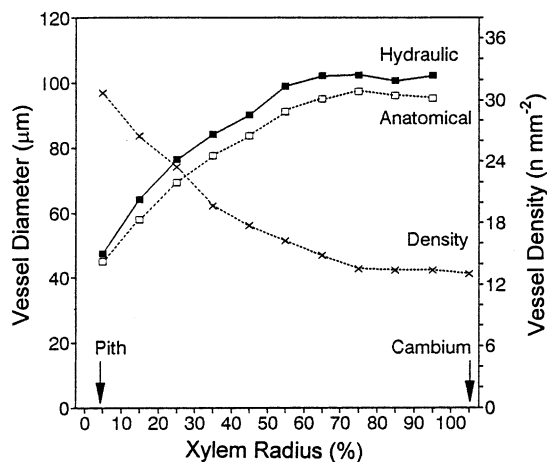


Fig. 4 Variation of vessel diameters (hydraulic and anatomical) and vessel density within the stem wood along xylem radius of *L. azorica* trees in the Agua García laurel forest experimental site. Data of mean values from five trees within the range of DBH=150–240 mm are shown (valid ± 5 –10%)

They were of a somewhat more rounded form when young and close to the pith (tangential diameter was 83% of radial diameter), gradually becoming a little more oblong towards the cambium (tangential diameter was 77% of radial diameter; Fig. 5).

According to the values of the diameters, the lumen area of stem vessels was small in young xylem close to the pith ($A_{\text{lum_an}} = 0.0015 \pm 0.0002 \text{ mm}^2$), increasing rapidly during tree development and reaching a value 5 times higher (about $A_{\text{lum_an}} = 0.007 \pm 0.0015 \text{ mm}^2$). At the same time, the proportion of lumen area of all vessels per xylem cross-sectional area, $A_{\text{lum_an}}/A_{\text{xyl}}$, was about 5%, close to the pith, and increased rapidly to slightly over 10% of xylem area in older tissues (Fig. 6). Lumen area

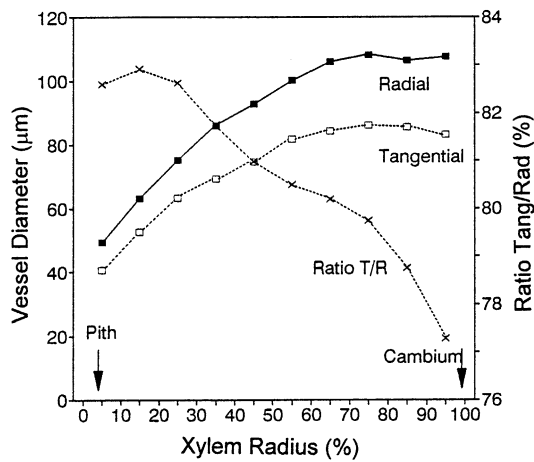


Fig. 5 Variation of anatomical vessel diameters in stems measured in radial and tangential directions, and their ratio along radius of *L. azorica* wood in Agua García laurel forest experimental site. Mean values from five trees within the range of DBH=150–240 mm are shown (valid ± 5 –10%)

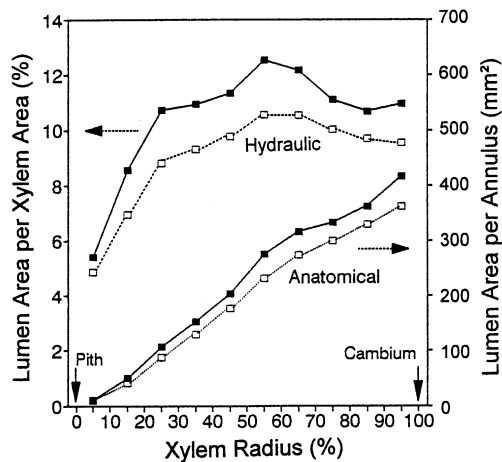


Fig. 6 Changes in vessel lumen area per annulus (width of each annulus is 10% of xylem radius), and lumen area in percentage of xylem area along xylem radius in stems of *L. azorica* trees in Agua García laurel forest experimental site. Mean values from five trees within the range of DBH=150–240 mm are shown (valid ± 5 –10%)

almost linearly increased when calculated for different annuli of unit width, which was a clear geometrical effect of an enlarging area of individual annuli with tree diameter.

The lumen area of vessels, A_{lum_an} , in petioles of *L. azorica* trees was much lower than in stems and represented only about 1.5% of the petiole cross-sectional area, A_{pet} . Vessels were concentrated in a crescent-shaped bundle on the cross-section (Fig. 7). There were minor differences in diameter of vessels between petioles of different depths in the canopy: Mean hydraulic diameter of sun leaves (18.6 μm) was only about 0.6% larger than that in shade leaves (18.5 μm), with a range of 5–25 μm (Fig. 8); but there were more vessels in petioles of shade leaves (118 and 153 vessels in sun and shade leaves re-

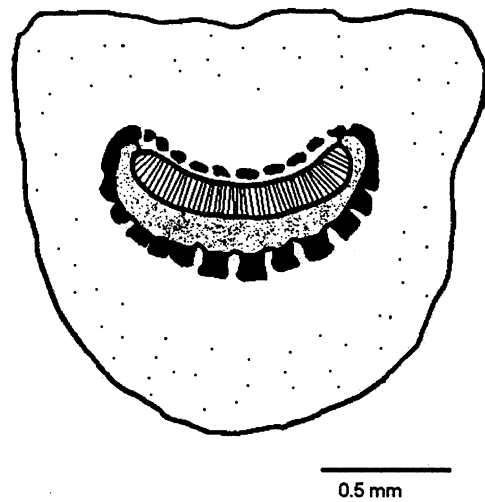


Fig. 7 Drawing of transverse section through the distal end of *L. azorica* petiole immediately below the lamina, showing a single crescentic vascular strand. White areas Parenchyma, sparsely stippled areas collenchyma, densely stippled areas phloem, hatched areas xylem, solid black areas sclerenchyma

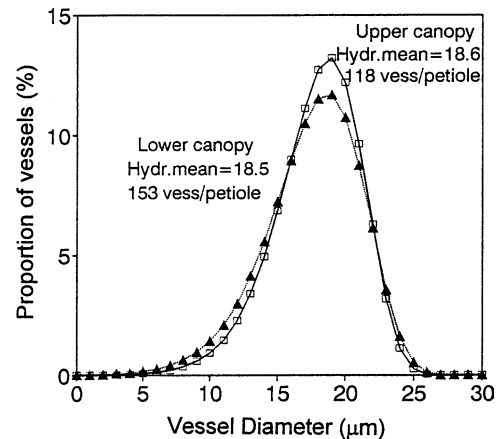


Fig. 8 Vessel distribution in petioles according to their hydraulic diameter of *L. azorica* trees in Agua García laurel forest experimental site, calculated separately for upper (sun leaves) and lower canopy (shade leaves). Mean hydraulic diameter was similar for sun and shade leaves (18.6 and 18.5 μm respectively). Total number of vessels per petiole was 118 and 153 for sun and shade leaves respectively

spectively), which confirms their somewhat larger potential when conducting water. Mean density for the whole crown was 136 vessels per petiole (number of vessels per petiole $D_{v_pet} = 249.3 - 8.75 \times \text{Height}$).

Fractions of xylem volume in tree stems

No clear differentiation between sapwood and heartwood was found, since no colour change or difference in light transmission could be observed along the stem fresh cores immediately after being taken. Bulk gravimetric analysis of xylem volume, done in whole cores (from the cambium to the pith) showed (Table 1) that the specific

Table 1 Physical parameters of *Laurus azorica* stem wood measured in 12 cores of six sample trees of different diameters at breast height (DBH), age 30–40 years, in Agua García experimental plot: Specific mass of fresh ($@_f$) and dry ($@_d$) wood (kg m^{-3}). Water content (WC) expressed in percentage of fresh ($\%_{f\text{mass}}$) or dry ($\%_{d\text{mass}}$) mass. Fractions of volume occupied by dry matter

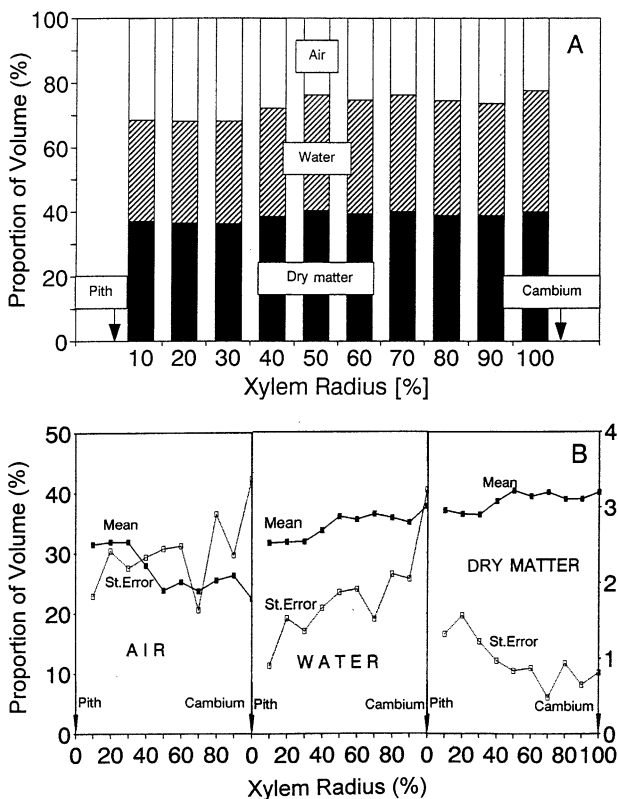
DBH (cm) ($\%_{xy}$)	$@_f$ (kg m^{-3})	$@_d$ (kg m^{-3})	WC ($\%_{f\text{mass}}$)	WC ($\%_{d\text{mass}}$)	V_m ($\%_v$)	V_w ($\%_v$)	V_a ($\%_v$)	Av. V_w ($\%_v$)	A_{lum}
9	908	612	32.6	48.5	39.7	29.4	30.9	17.4	10.2
10	901	512	43.1	75.9	33.3	38.8	27.9	26.8	10.2
15	941	592	37.2	59.1	38.4	35.0	26.6	23	9.7
16	1,010	605	40.1	66.8	39.1	39.0	21.9	27	9.6
20	871	552	36.6	57.6	35.7	30.6	33.7	18.6	9.5
24	973	613	36.9	58.5	39.7	36.2	24.1	24.2	9.8
Mean	934	581	37.8	61.1	37.7	34.8	27.5	22.8	9.8
\pm SE (%)	2.0	2.6	3.5	5.7	2.6	4.3	5.9	6.6	1.1

(V_m), water (V_w) and air (V_a) in percentage of fresh volume. Fraction of available water (Av. V_w), i.e. fraction of water when the bound water ($\sim 12\%_v$) was subtracted from the total. Total cross-sectional area of vessels (A_{lum}) in percentage of total xylem area (fraction of area is equal to fraction of volume)

Table 2 Fractions of volume occupied by dry matter (V_m), water (V_w) and air (V_a) in percentage of fresh volume, in different parts of a *L. azorica* tree, calculated using small pieces of wood in small and large branches. Logs and cores of the main stem were used in

order to calculate possible methodical errors. The fractions of total skeleton represented by small and large branches and main stem, are also indicated in percentage ($\%_{ske}$)

Part of tree	Diameter	V_m	V_w	V_a	$\%_{ske}$
Small branch	0.8	25.5 \pm 4.6	52.4 \pm 1.7	22.1 \pm 8.5	9.3
Large branch	4.1	25.7 \pm 3.2	34.2 \pm 4.3	40.1 \pm 5.7	22.1
Main stem (logs)	10.9	33.1 \pm 5.8	39.9 \pm 0.2	27.0 \pm 7.0	68.6
Mean/total	5.3	28.1 \pm 4.5	42.2 \pm 2.1	29.7 \pm 7.0	100
Main stem (cores)	10.9	33.3	38.8	27.9	



mass of fresh (i.e., wet under normal physiological conditions) and dry wood were $@_f = 934 \text{ kg m}^{-3}$ and $@_d = 581 \text{ kg m}^{-3}$ respectively. On average the wood contained around $38\%_{f\text{mass}}$ and $61\%_{d\text{mass}}$ of water when expressed as a fraction of fresh (f_{mass}) and dry mass (d_{mass}), with little variation (in general, about $\pm 5\%$ to $\pm 10\%$ of the mean) between trees of a large range of diameters. If expressed as fractions of fresh volume, the wood was constituted by dry matter ($38\%_v$: cell walls, dry constituents of living cells and other solid materials); water ($35\%_v$); and air or water vapour ($27\%_v$).

The fraction of volume occupied by dry matter, water and air in percentage of fresh volume, in different parts of the tree, can be seen in Table 2. The xylem water in small branches (diameter $< 10 \text{ mm}$) was greater (by about $1/3$) than in the main stem or large branches. No significant differences can be seen in values obtained for the main stem when logs and cores were used, respectively. When considering volume of the whole aboveground skeleton

Fig. 9 Fractions of dry matter, water and air in percentage of fresh volume ($\%_v$) within the radial profile of tree stems in *L. azorica* trees in Agua García forest experimental site. Fractions are shown in the upper part of the figure (A), representing samples from five trees analysed from opposite sides of stems (north-south, valid ± 5 – 10%). Trends of changes of proportions along the radius and the standard errors are shown in the lower part of B

of the tree, the small and large branches and the main stem represented about 10, 20 and 70%, respectively.

There were only small differences in the fractions of volume occupied by dry matter, water and air along radius in the stem xylem of *L. azorica*. Results expressed in relation to relative length of stem xylem radius (in percent of total) fit all trees irrespective of stem diameter (Fig. 9A). Dry matter showed least variation, mainly near the cambium (standard error decreased towards the cambium) (Fig. 9B). In contrast, the proportion of water slightly increased towards the cambium showing increasing variation in the same direction. The proportion of water in the pores was compensated by the proportion of air (Fig. 9B).

Discussion

L. azorica wood has the typical structure of diffuse porous stems. This structure has been found in other sclerophyll trees (Larcher 1995) living in more extreme Mediterranean conditions and allows them to survive during summer drought periods. *L. azorica*, as well as other trees living in the laurel forest, is considered a relic of the Tertiary Mediterranean flora now confined to the humid and warm regions of the Macaronesian archipelagos (among them the Canary Islands). But even under these general wet conditions there are periods with high evaporative demands (González-Rodríguez et al. 2001) so that insufficiently adapted trees might suffer cavitation.

Vessel diameter is the most significant contributor to the efficiency of water conduction, since according to the Hagen–Poiseuille equation, hydraulic conductance of capillaries is proportional to the fourth power of the radius (Zimmermann and Milburn 1982). Vessels of *L. azorica* are relatively small, on average about 81 and 90 μm in anatomical and hydraulic diameters, respectively, and they represent a rather safe conducting system due to their high density (about 20 vessels mm^{-2} , measured at breast height) and thus high total vessel number in stems. If vessels of a species are large, there are relatively few of them; therefore every failure blocks a larger percentage of the total path (Zimmermann and Milburn 1982). There is increasing evidence that vulnerability to cavitation induced by water stress is determined mostly by pit membrane porosity, not so much by large vessel diameter per se (Crombie et al. 1985; Sperry and Tyree 1988, 1990; Tyree and Ewers 1991; Holbrook and Zwieniecki 1999).

The conducting profile of stem wood of *L. azorica* trees shows strict radial regularities. Vessel diameter and density are allometrically closely (inversely) related (small dense vessels are close to the pith, their diameters increase and density decreases in direction to cambium). Vessels are slightly asymmetrical in their cross-section, showing a ratio of tangential/radial diameters of about 0.8. This radial (pith to bark) variation has been found in many species (Panshin and de Zeeuw 1980; Megraw 1985; Zobel and van Buijtenen 1989), and it is caused

because the wood produced by the cambium activity, increases in age with each growth ring (Gartner 1995).

Lumen area of vessels in petioles was about 1.5% of petiole cross-sectional area, thus much lower than stems. Mean hydraulic diameter of petiole vessels was almost 20 μm (almost the same in lower and upper canopy) and mean vessel density about 136 per petiole (about 30% higher in lower compared to upper canopy). These changes between leaves reflect changes in their general morphology according to the position in the dense canopy of the stand (Morales et al. 1996a).

From our bulk gravimetric analysis and comparing with literature data on different species (Esau 1965; Holbrook 1995; Kravka et al. 1999) it can be said that the *L. azorica* wood is rather heavy and well filled with water under physiological conditions. No color change or difference in light transmission could be observed along the fresh stem cores immediately after being taken, contrary to reports in other species (Kaufmann and Troendle 1981; Marchand 1984). This together with the fact that no significant changes in water content were found along the whole cross-sectional area of stem xylem (at least for trees up to 240 mm DBH, as can be seen in Fig. 9), confirms the statement of Schweingruber (1990) who could not distinguish sapwood and heartwood in this species.

It could be thought that significant errors were made during the estimation of water content since the vessels of *L. azorica* trees could be under high tension in normal conditions and so might have lost some of their water immediately, when the vessel walls were interrupted by the drill bit (Suunto increment borer) used for sampling the cores. Also a small amount of water could have evaporated from the wood surfaces during sample treatment in the laboratory. The ratio of the exposed vessel diameter to their length in the woody samples was over 1:10,000 for stem logs and less than 1:500 for the cores. Thus the small woody cores were much more vulnerable to water loss than stem logs. However, xylem water content estimated in stem logs was only about 1.1%_v higher than that in the cores of the very same tree (see Table 2); hence the difference is of little significance. This indicates that the loss of water due to the sampling technique was almost negligible in terms of total water content of the wood. It amounts to slightly more than 10%_v of the water contained within lumen of vessels in the worst case.

Most species with differentiated sapwood and heartwood contain about 10–12%_v water in the heartwood (Cermák and Nadezhdina 1998; Kravka et al. 1999). This water is bound, evidently strongly held by the physical forces in the xylem, and is not available for physiological processes (Zimmermann and Brown 1971). If we suppose the same fraction of inaccessible water (bound water \approx 12%_v) in the xylem of main stems of *L. azorica*, it can be concluded that 50%_v of in vivo total volume of wood was solid matter (that is, 38%_v of dry matter plus 12%_v of bound water), and 50%_v was free interstitial volume (that is, 23%_v of free water and 27%_v of air) (Fig. 10).

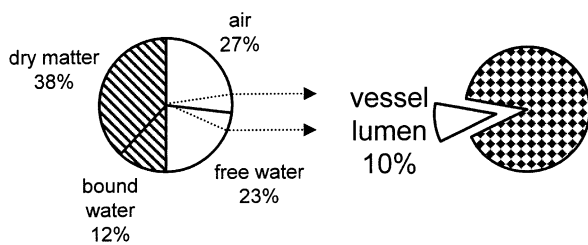


Fig. 10 Left Diagram showing proportions of air (27%), free water (23%), bound water (12%) and dry matter (38%) in a *L. azorica* stem (data taken from Table 1). Empty area represents the maximal free interstitial volume (50%). Dashed area represents the solid matter (50%) since part of the water is bound to dry matter (bound water) in living tissues. Right Diagram representing the proportion of anatomical vessel lumen (10%) in the total volume of wood. Looking to both diagrams it can be seen that there is enough free water to fill the total volume of vessels. However, considering that there is a great proportion of air, part of it must also fill the lumen of vessels, so that some of them must be embolized

Almost one-quarter (23%_v) of the wood volume is available water (i.e. not bound by strong physical forces). Therefore, *L. azorica* wood contains more than twice as much water as necessary to fill the vessels (total volume of anatomical vessel lumen occupied about 10%_v of the wood, see Fig. 10). The rest might be within fibres, cell walls and living cells, e.g. in paratracheal parenchyma and pith rays. However, this does not mean that the xylem is fully functional to conduct water. Considering that air occupies a quarter of wood volume (27%), such a percentage can certainly be associated not only with gas spaces in fibres and intercellular gaps but it might be the cause of embolization of vessels. (Embolized vessels are considered as only those that are fully air or water vapour filled but not those just containing some bubbles). This can be taken as indirect evidence that a certain percentage of stem vessels were probably embolized.

The summer dry period existing in the zone where the laurel forest grows (see Fig. 1) is mitigated by more or less persistent clouds that bring about high humidity. *L. azorica* wood is lacking adaptive xylem structures to a dry environment, unlike many Mediterranean species, such as vasicentric or vascular tracheids (Carlquist 1985). Besides, it has bigger vessels and lower vessel density per unit cross-sectional area than other Mediterranean species, like chaparral shrubs in California (i.e., 20 µm diameter and 299 vessels per mm⁻²; Carlquist 1989; Rundel 1995). *L. azorica* is inferior to such true Mediterranean species in terms of a highly drought stress-adapted xylem and would probably not endure severe summer drought conditions (Lösch 1993). Nevertheless, in some situations the evaporative demand of the laurel forest habitat can also be very high (Jiménez et al. 1996, 1999; Gonzalez-Rodríguez et al. 2001), and then vessels can suffer cavitation.

In ring porous trees, all functional vessels are in the last growth ring and so these trees have a smaller but more efficient wood functional area. This becomes obvious when the conducting area and the leaf area of differ-

ent species were plotted against each other (Pallardy 1989). This indicates a greater efficiency of the wide vessels of ring porous trees, requiring a much smaller functional xylem cross-section to supply an equivalent leaf area than either diffuse porous angiosperms or conifers. This confirms our statement that the whole cross-section of *L. azorica* diffuse porous wood can be functional, even when many individual vessels are embolized. It is supported experimentally by studies about patterns of the sap flow profile along the stem radius of *L. azorica* and other laurel forest trees (Jiménez et al. 2000) where in many cases the flow takes place over the whole cross-sectional area of xylem. Studies about vessel efficiency will provide us with a better knowledge of wood functioning in this species, and this will be the subject of our next study (Cermák et al. 2002). It would also be very interesting to learn something about “the other end”, the roots, in the future, since roots have a very important function, but we have strictly limited knowledge on laurel forest tree roots.

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