

Jan Cermák · M. Soledad Jiménez  
Agueda M. González-Rodríguez · Domingo Morales

## Laurel forests in Tenerife, Canary Islands

### II. Efficiency of the water conducting system in *Laurus azorica* trees

Received: 6 November 2001 / Accepted: 31 May 2002 / Published online: 16 July 2002  
© Springer-Verlag 2002

**Abstract** The efficiency of the conductive system in about 40-year-old *Laurus azorica* trees growing in a laurel forest was evaluated by comparing main stems and leaves (petioles) on the basis of theoretical sap flow values (1) calculated from vessel anatomy (taking vessels as ideal capillaries), (2) derived from measured dye velocity and (3) data taken from direct sap flow measurements. It was found that actual sap flow rate per wood area increases in stems from the pith towards the cambium. The outermost part of the stem is the most important part of the tree for conducting water. Maximum actually measured transpiration (sap flow rate) for the stand was practically identical to the theoretical rate calculated based on petiole anatomy, but it was about 45 times lower than that calculated based on stem anatomy. This illustrates the safety features of stem wood, which due to its high vessel density, is capable of transporting all the water required even when only a small area of its vessels is working. In the petioles, xylem is more efficiently used, but almost all vessels must work in order to supply water to leaves and any disturbance may cause leaf loss.

**Keywords** Laurel forest · *Laurus azorica* · Xylem sap flow · Efficiency · Water conducting system

#### Introduction

Knowledge of the functioning of the tree conducting system is a prerequisite for correct interpretation of sap flow data measured in forest stands. This study considers

efficiency of such a system in terms of actually measured sap flow deviations from those theoretically calculated from data on vessel anatomy along the stem radial profile. It also considers problems of proper scaling of sap flow data from individual measuring points in the stem to the whole tree (Cermák and Kucera 1990).

The radial profile of conducting pathways was examined in stems of many woody species from different viewpoints including the homogeneity of water supply to crowns, plant protection against insects or proper integration of sap flow rates to obtain correct data on whole plant water use (Kozłowski and Wignat 1963; Swanson 1971; Waisel et al. 1972; Edwards and Booker 1984; Hatton et al. 1990; Cermák et al. 1992; Cermák and Nadezhdina 1998; Jiménez et al. 2000; Nadezhdina et al. 2001).

The present study was intended as a background for long-term measurements of sap flow rate in *Laurus azorica* trees growing in a cloudy laurel forest on the Canary Islands (Jiménez et al. 1996). It is based on fundamental biometric studies already done at the same site (Morales et al. 1996a, b, c) and follows closely the previous anatomical analysis of the radial profile of conducting systems of stems and petioles (Morales et al. 2002). *L. azorica* is known as a species with no distinguishable sapwood and heartwood (Schweingruber 1990; Morales et al. 2002), which might complicate interpretation of measured data of sap flow. The true functional area of conducting xylem may differ significantly from that of sapwood if estimated by the usual methods (e.g. based on tissue water content or presence of living cells), as was shown in several contrasting species (Cermák and Nadezhdina 1998). To elucidate the functional situation along the stem radius, theoretically calculated properties of the conducting system were compared to those obtained by direct measurements using staining and stem heat balance sap flow rate measurement techniques. Both “ends” of the aboveground conducting pathway, the stem base and the petioles, were compared in order to assess the axial compartmentalization of the system (Zimmermann and Brown 1971).

J. Cermák  
Institute of Forest Ecology,  
Mendel's University of Agriculture and Forestry, Zemedelská 3,  
61300 Brno, Czech Republic

M.S. Jiménez · A. M. González-Rodríguez · D. Morales (✉)  
Departamento de Biología Vegetal. Universidad de La Laguna.  
38207 La Laguna, Tenerife, Spain  
e-mail: dmorales@ull.es  
Tel.: +34-922-318435, Fax: +34-922-318447

## Materials and methods

### The experimental site

The experimental site of the laurel forest is located in the Agua García mountains, on a slight slope (12°) facing NNE, at an altitude of 820–830 m, north-east Tenerife, Canary Islands, Spain. The climate of the site is humid Mediterranean. The natural mixed hardwood forest stand is composed of 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.). The stand is about 40 years old, regrown from sprouts after cutting the original forest; individual trees are probably 30–50 years old. More details about the site and forest structure have been given elsewhere (Morales et al. 1996a, b, c).

### Anatomy of vessels in the stem wood and in petioles

The anatomy of vessels in *L. azorica* stems and petioles measured in the same sample trees was described in Morales et al. (2002). The wood showed a diffuse-porous structure, with solitary vessels or vessels in small radially oriented groups with a diameter ranging from 20 to 130 µm. This diameter was minimal close to the pith, increased more than twofold with age, and reached its maximum close to the cambium. Vessel density had exactly the opposite pattern, decreasing from 36 vessels mm<sup>-2</sup> near the pith to about 13 vessels mm<sup>-2</sup> near the cambium. Accordingly, the lumen area was small in young xylem close to the pith (about 0.0015 mm<sup>2</sup>), increased rapidly during tree development, and stabilized at a value 5 times larger than at the beginning (about 0.007 mm<sup>2</sup>). Lumen area of vessels in petioles was about 1.5% of petiole cross-sectional area, thus being much lower than in stems. Mean hydraulic diameter of petiole vessels was only 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 the stem radius. This confirms the non-existence of heartwood in this species.

Application of a staining technique to the calculation of conducting xylem depth, and radial profile of sap velocity in stems

### The staining technique

The staining technique of Booker (1984) was applied to assess the depth of conducting xylem and the radial profile of sap velocity. For both purposes a 1% solution of a non-fixing dye (acid fuchsin in distilled water) was used as a tracer. Trees were stained during fine weather around midday using the modified technique of Cermák et al. (1984, 1992). A hole 8 mm in diameter was drilled into the tree stems through a small cylinder fastened at an angle of 45° to the vertical at the stem surface in a watertight manner applying an adhesive. The cylinder was filled with distilled water during treatment in order to prevent any air entering. The hole penetrating down to the centre of tree stems (to the pith) was quickly washed with ample water from the bottom up to remove any remaining woody particles. Then the dye was injected into the hole in the same way. The dye was partially diluted due to mixing with water remaining in the hole, but an uneven concentration of a non-fixing dye was not likely to influence the penetration time (Booker 1984).

### Assessing the depth of conducting xylem

The depth of conducting xylem (i.e. the point where the sap flow velocity reaches zero) was assessed in five trees covering the range of tree diameter at breast height (DBH). After exposure of tree stems

to the injected dye (10–15 min) in opposite sides of each tree, a core of wood was taken from the stem 2 cm above each injection point. Altogether ten samples were taken (two per tree). The depth of conducting xylem was analysed in the samples according to stained vessels visible on the cut and smoothed wood surface of the core.

### Assessing the radial profile of sap velocity

The radial profile of dye velocity was assessed with the same staining technique on a single tree (only a limited number of trees could be cut in the protected area of natural reserve), when the stained length of xylem was measured along the stem, and the time of exposure ( $t_{exp}$ ) was recorded. A required time interval (3–5 min in *L. azorica*) and suitable corresponding distance (over 500 mm, so that the lower cut could be made until the down-moving dye solution reaches the ground surface and the up-moving dye solution reaches the upper height), was previously assessed on the basis of published data on sap velocities (Zimmermann and Brown 1971; Hinckley et al. 1978). The stem was cut above and below the injection point of the dye after the exposure and recut immediately into a series of discs of known axial height (thickness about 20 mm, thinner close to the injection point). The stained area on the discs was recorded along the radii ( $r_d$ ). Stained spots within vessels along the radius of the most distant discs from injection point (the edge of the stained zone) were taken as markers for “high velocity”. Stained spots where it was not possible to distinguish actually stained and non-stained vessels (due to some local diffusion of the dye) were taken as markers for “low velocity”. The distance of stained points was related to the distance from the injection point (which consisted of the length of the hole when considering its radial depth,  $h_{inj}$ ), i.e. the sum of heights of cut discs (including the width of the saw cut); angle of the hole (its oblique position) and thus changes in position of each evaluated injection point with xylem depth were considered.

The recorded dye velocity ( $v_{rd}$ ) was calculated for every point (with the step of 5 mm) along the radius from the equation

$$v_{rd} = h_{inj} / t_{exp} \quad (1)$$

in directions up ( $vr_{du}$ ) and down ( $vr_{dd}$ ) from the injection point along the stem. Trying to approach the true sap velocity ( $v_{sap}$ ) the corrected dye velocity ( $v_{cd}$ , supposing that  $v_{sap} = v_{cd}$ ) was derived from the  $vr_{d}$  according to the procedure proposed by Kucera (in Cermák et al. 1992) using the equation in the form

$$v_{cd} = \frac{v_{rdu} \psi_c dL_u - v_{rdd} \psi_r dL_d}{dL_u \psi_c + dL_d \psi_r} \quad (2)$$

where  $dL_u$  and  $dL_d$  are distances from the injection point to the tree top and to the end of root of average length and  $\psi_c$ , and  $\psi_r$  are water potentials of leaves (measured by the pressure bomb – see Morales et al. 1996a) and roots (taken as close to that of soil at field capacity).

Actual sap flow rate ( $Q_{wv,i}$ ) for an individual stem annulus ( $i$ ) was derived from the estimated sap velocity (corrected dye velocity), considering the hydraulic lumen area of vessels ( $A_{h,lum,i}$ ) in that annulus:

$$Q_{wv,i} = v_{d,i} \times A_{h,lum,i} \quad (3)$$

of which total (velocity derived) sap flow rate per stems,  $Q_{wv,t}$ , was calculated as the total of all radii

$$Q_{wv,t} = \sum_{i=1}^n Q_{wv,i} \quad (4)$$

and expressed for the xylem cross-section area unit of the annulus,  $A_{ann}$

$$q_{wv,i} = Q_{wv,i} / A_{ann,i} \quad (5)$$

and mean for the entire stem (basal area)  $A_{bas}$  accordingly

$$q_{wv,t} = Q_{wt,v} / A_{bas} \quad (6)$$

#### Measurement of sap flow rates

The actual sap flow rate was measured using the tree trunk section heat balance technique with internal (electric) heating and sensing (Cermák et al. 1973, 1982; Kucera et al. 1977) using four pairs of compensating thermocouples (Cermák and Kucera 1981). A six-channel measuring device (model P-6, Ecological Measurement Systems, Brno, Czech Republic) was applied. Measuring points were located at breast height (1.3 m above ground) from two opposite sides of stems. Data on maximum actual sap flow rate for the stand applied for calculations in this paper were taken from our previous study (Jiménez et al. 1996) and represent the mean value from 10 days with the highest flow rates over the whole 1993 growing season.

Radial pattern of the sap flow rate was measured in two *L. azorica* sample trees with the same method as described above when electrodes were inserted along the whole stem radius above the pith. Six thermocouples at different depths along the radius, inserted in their polyvinylchloride tubing of 1.5 mm in diameter, were applied for measurements of temperature differences in order to prevent higher heat conductivity along the casting and to provide data representative of the corresponding individual annuli. The radial pattern of sap flow was measured supposing that the xylem is heated homogeneously between the electrodes in *L. azorica*, i.e. when we found homogeneous water content along stem radius ( $35 \pm 4.3\%_{vol}$  – see Morales et al. 2002) and also supposing a homogenous ion concentration in xylem tissues along the stem radius.

#### Calculated theoretical maximum of sap flow rate

Theoretical maximum sap flow rate ( $Q_{w,m}$ ) in stems and in petioles was calculated using the Hagen–Poiseuille equation. For this, the vessels were considered as ideal capillaries on the basis of vessel hydraulic radius ( $r_{vh}$ ), their density on a cross-section of xylem ( $D_v$ ), corresponding area ( $A$ , sapwood area or cross-section petiole area), a pressure gradient ( $dP/dL$ ), and viscosity of liquid water ( $\eta_w$ )

$$Q_{w,m} = \frac{D_v A_{sapw} \pi r_{vh}^4 dP}{8 \eta_w dL} \quad (7)$$

It was assumed that the length of the water pathway,  $L_v$  is equal to the height of the trees ( $L_v = ht = 15$  m). In view of a range of vessel diameters, the hydraulic mean radius of vessels,  $r_{vh}$  was taken into account (instead of the anatomical one,  $r_{va}$ ) in different diameter classes of vessels,  $i$ , on the cross-section of the xylem and expressed per unit of its area

$$r_{vh}^2 = \left( \sum n_i r_{va,i}^4 / N \right)^{1/2} \quad (8)$$

The driving force for the sap flow within the xylem,  $dP$ , was taken as the difference of water potentials between the leaf (yleaf) and the soil (ysoil),  $dP = yleaf - ysoil$ . Soil water content was rather homogeneous, somewhat below the field capacity during experimental days, and its mean water potential (ysoil) was taken as  $-0.2$  MPa, which was based on previous measurement of soil physical properties (see Morales et al. 1996b). Midday leaf water potential yleaf  $= -1.2$  MPa, corresponding to maximum sap flow rate, was taken into account. It was calculated on the basis of known vertical leaf distribution over the canopy (Morales et al. 1996a) by weighing corresponding values of yleaf measured in

different layers by leaf area in such layers. This value represented mean water potential over the whole canopy depth. Calculated  $dP/dL$  was taken as constant over the whole aboveground conducting pathway from the stem base to petioles.

#### Upscaling data from the organ to tree and stand levels

Data measured on the level of individual organs (stems and petioles) were upscaled to the level of mean tree and of the stand area unit on the basis of results in our previous biometric studies (Morales et al. 1996b, c). Basal area was applied for calculations on stems. Variables were expressed for stand area unit (1 ha = 10,000 m<sup>2</sup>), i.e. the unit commonly applied in European forestry as recommended by Philip (1994). Considering petioles (numbers of petioles,  $n_{p,j}$  = numbers of leaves) values for the whole crowns were calculated by summarizing values of all particular canopy layers (with 1 m steps) at different heights above ground. As in previously published papers we assumed that all species have a similar amount of foliage per basal area.

## Results

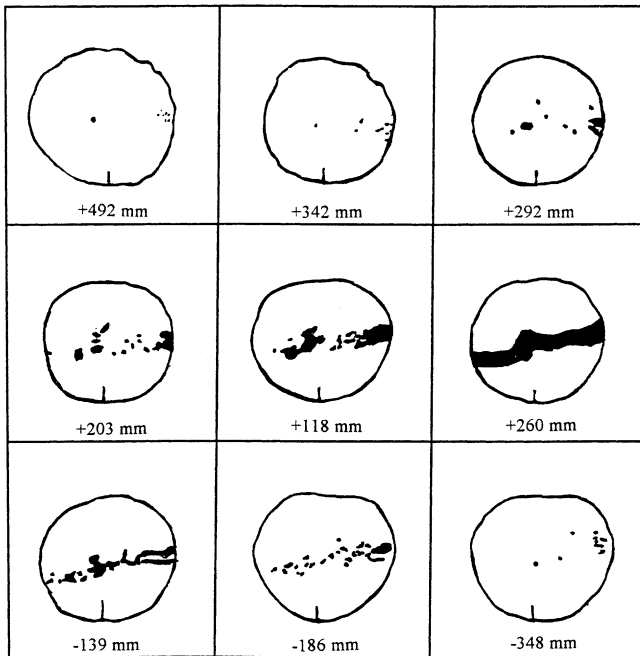
### Conducting systems in stems and petioles

Main parameters of the conducting system, calculated at the stem base and at the petioles on the basis of our previous biometrical and anatomical studies (Morales et al. 1996b, c, 2002) are given in Table 1. As shown by Schweingruber (1990), Oramas and De Roma (1967) and in the papers above cited, some other important laurel forest species have similar structures and properties to *Laurus azorica*; species with a different structure, like *Erica arborea*, comprised only a small fraction of the stand. Mean hydraulic diameter of stem vessels and mean stem vessel area in the mean tree of the laurel forest stand (DBH=160 mm, basal area=0.02 m<sup>2</sup>) were about 5 and 24 times larger than corresponding parameters in the petioles, respectively. The mean tree carried about 36,000 petioles, which served the same number of leaves with about 5,000,000 small vessels, subsequently served with about 400,000 bigger stem vessels. Total hydraulic vessel lumen area in the stem and petioles in the mean tree amounted to only 2,100 and 1,300 mm<sup>2</sup> respectively. Mean petiole cross-sectional area, total cross-sectional area of petioles and stems and total leaf area of a mean tree are also given in Table 1.

When considering the forest stand area unit (Table 1), almost 80,000 m<sup>2</sup> of corresponding leaf area was supported by almost 1,700 stems. They represented a basal area of 34 m<sup>2</sup> containing 700,000,000 bigger stem vessels, which served 61,000,000 petioles containing over 8,000,000,000 small petiole vessels. Total hydraulic lumen area for the stand area unit considering the stem base and petioles was 3.6 and 2.2 m<sup>2</sup> respectively. At the level of the forest stand, petiole cross-sectional area was 4.5 times higher than stem cross-sectional area. Allometric relations indicated (see Table 1) that the stem basal area was 7 times more efficiently used by the vessel lumen area than the petiole cross-sectional area. Each

**Table 1** Main parameters of the aboveground water conducting system of a mean *Laurus azorica* tree (DBH 160 mm, basal area 0.02 m<sup>2</sup>). Laurel forest stand and allometric relations are also included. The parameters below were calculated using anatomical data from Morales et al. (2002). Leaf parameters characterizing the same stand were taken from Morales et al. (1996b; this was done supposing that all species of the stand would have a similar leaf area per basal area). Mean leaf area was about 1,280 mm<sup>2</sup>. Total leaf area per stand was 7.77 m<sup>2</sup>m<sup>-2</sup>

Parameters	Petioles	Stem base
Mean tree		
Mean hydraulic diameter of vessels (mm)	0.0185	0.0905
Mean hydraulic vessel lumen cross-sectional area (mm <sup>2</sup> )	0.000269	0.006433
Total number of petioles per mean tree (petioles/tree)	35,826	***
Total number of vessels per mean tree (vessels/tree)	4,854,358	405,010
Total hydraulic vessel lumen area per tree (mm <sup>2</sup> /tree)	1,310	2,140
Mean petiole cross-sectional area (mm <sup>2</sup> )	2.47	***
Total cross-sectional area of mean tree (m <sup>2</sup> /tree)	0.0887	0.0199
Total leaf area of mean tree (m <sup>2</sup> /tree)	45.89	***
Forest stand area unit		
Density of petioles or stems in stand (units/ha)	60,652,600	1,693
Total cross-sectional area (m <sup>2</sup> /ha)	150.1	33.74
Total vessel density (10 <sup>3</sup> vessels/ha)	8,218,429	685,683
Total vessel hydraulic lumen cross-sectional area (m <sup>2</sup> /ha)	2.21	3.63
Allometric relations		
Vessel hydraulic lumen area per corresponding cross-sectional area (%)	1.47	10.8
Vessel density per leaf area (vessels/mm <sup>2</sup> )	0.1058	0.0088
Vessel density per mean leaf (vessels/leaf)	135.5	11.3
Total hydraulic lumen area of petioles per stem (%)	60.9	***
Vessel hydraulic lumen area per leaf area (%)	0.0028	0.0047
Vessel density per cross-sectional area (vessels/mm <sup>2</sup> )	54.75	20.32
Vessel hydraulic lumen area per mean leaf (mm <sup>2</sup> /leaf)	0.036	0.060
Leaf area per corresponding cross-sectional area (%)	51,753	230,249
Cross-sectional area per leaf area (%)	0.193	0.043
Basal area per total petiole cross-sectional area (%)	***	22.5
Total hydraulic lumen area of stem per petiole (%)	***	164.3
Total petiole cross-sectional area per basal area (%)	444.9	***

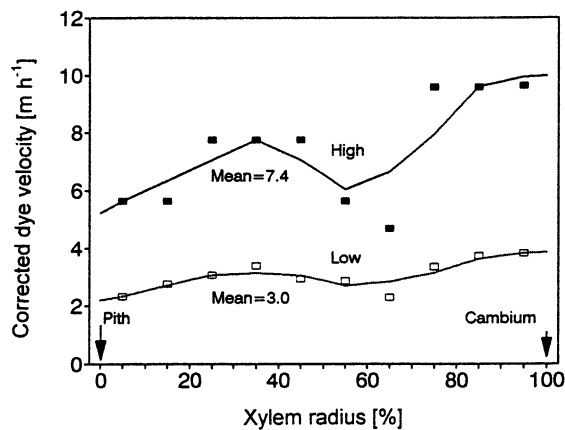


**Fig. 1** Pattern of stained wood in the stem of *Laurus azorica* experimental tree (DBH=111.4 mm) in the Agua García laurel forest experimental site, used for the staining experiment. The stained area is shown on disc surfaces cut from the stem at different distances above (positive numbers) and below (negative numbers) the injection point. Drill bit diameter =8 mm

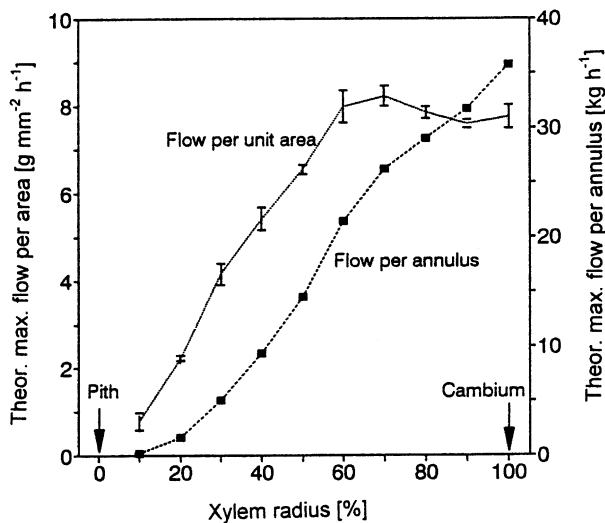
100 mm<sup>2</sup> of foliage was served by almost 11 petiole vessels and/or by almost one single stem vessel. Each leaf (mean leaf area =1,281 mm<sup>2</sup>) was served by 136 and 11 petiole and stem vessels, respectively (i.e. each large stem vessel served 12 small petiole vessels). Total hydraulic vessel lumen area in petioles reached only 60% of that in stems – which represented an almost negligible percentage of leaf area in stems and petioles of 0.005% and 0.003% respectively. Other significant relations are also given in Table 1.

#### Sap velocity and its radial pattern in stems

The staining method showed the path of flow up and down from the point of dye injection. Tracks of dye were apparent throughout the entire xylem area at short distances from the injection point (or line represented by the hole). Further from this point only small proportions of vessels were stained (Fig. 1). No clear results on sapwood depth were obtained when evaluating the cores of wood taken above the injection point. Therefore the radial profile of flow must be estimated on cross-cuts over the stem. The derived highest dye velocity (corrected  $v_d$ ) was almost 10 m h<sup>-1</sup>, and the mean value of high velocity along the conducting profile was about 75% of the maximum  $v_d$  with high variation especially in mid-radius (Fig. 2).



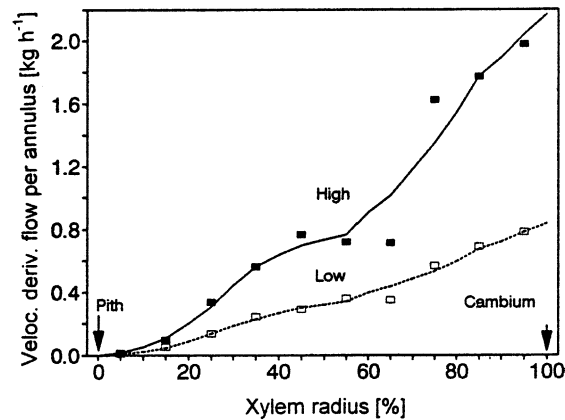
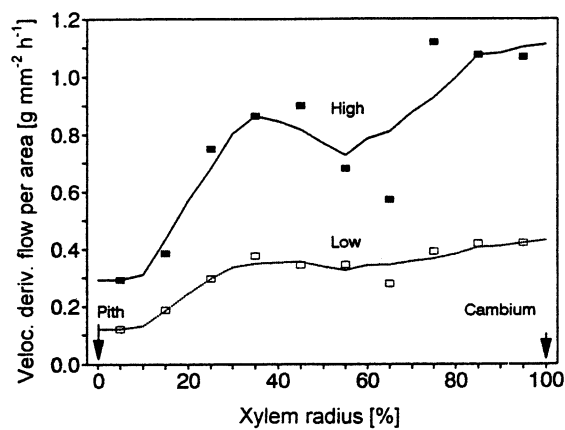
**Fig. 2** Radial profile of high and low dye velocity within the xylem of *L. azorica* experimental tree (DBH=111.4 mm used for the staining experiment; see Fig. 1) corrected for different distances and corresponding water potentials of tissues (oblique position of the hole was considered). Low velocity data on the xylem cross-sectional area close to the injection point may be somewhat impaired by diffusion of the dye



**Fig. 3** Radial profile of theoretical maximum sap flow rate (expressed for unit area and for different annuli) in *L. azorica* wood calculated from Hagen–Poiseuille equation for trees of different diameter (DBH=100–240 mm) and expressed for the mean tree of the stand (DBH=160 mm). Total sap flow rate (174.9 kg tree<sup>-1</sup>h<sup>-1</sup>) was calculated when summarizing flows in all annuli

#### Sap flow rate and its radial pattern in stems

The absolute values of calculated theoretical maximum sap flow rate in stems for the entire stand gave the extremely high value of approximately 33 mm h<sup>-1</sup> (this corresponds to a stand transpiration rate of 33 l m<sup>-2</sup>h<sup>-1</sup>, but this is not sap velocity). The radial pattern of theoretical maximum sap flow rate in stems (Fig. 3) showed an increasing trend from the pith towards the cambium, which is a similar pattern to the lumen area found during anatomical studies (see Morales et al. 2002). Variation of

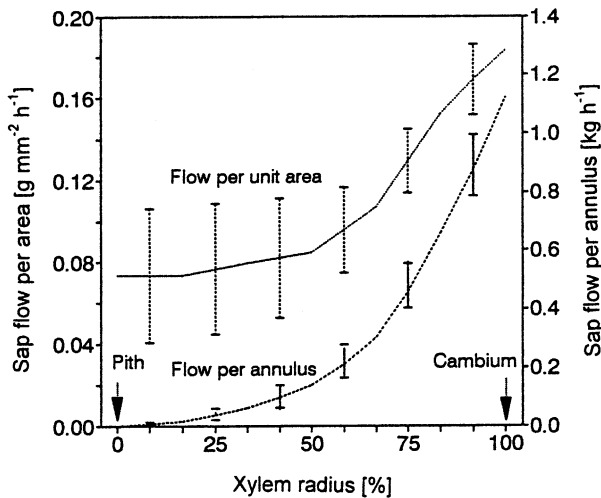


**Fig. 4** Radial profile of sap flow rate derived from velocity (measured by the staining technique, see Fig. 2) in *L. azorica* wood. *Upper* Flow per area. *Lower* Flow per annulus. Given values correspond to the mean tree of the stand (DBH=160 mm). The total low and high sap flow rates (6.8 and 16.7 kg tree<sup>-1</sup>h<sup>-1</sup> respectively) were calculated when summarizing flows in all annuli

data was small indicating that no significant differences in this pattern were found in trees of DBH in the range of 100–240 mm. The total sap flow rate expressed per annulus has a similar general radial pattern to that obtained when measuring actual flow density per sapwood area unit, but high flow density was apparent around 60–80% of the xylem radius.

Sap flow rate derived from measured dye velocity and approximately valid for the mean tree showed low and high sap flow rates of 6.8 and 16.7 kg tree<sup>-1</sup>h<sup>-1</sup>, which represent 3.9% and 9.5%, respectively of the theoretical maximum sap flow. The radial pattern of sap flow rate derived from estimated dye velocity differed with 1–3 being the minimum value close to the pith and the maximum near the cambium (Fig. 4 upper). The pattern of sap flow was slightly higher in mid-radius compared to sap velocity, due to a higher percentage of hydraulic vessel area, but depression of flow rate remains significant. However, this variation had a minor effect on the derived total sap flow rate for the whole tree (Fig. 4 lower).

The maximum value of actual sap flow (measured by the trunk heat balance method with direct electrical heating of tissues) when expressed for the mean tree of the



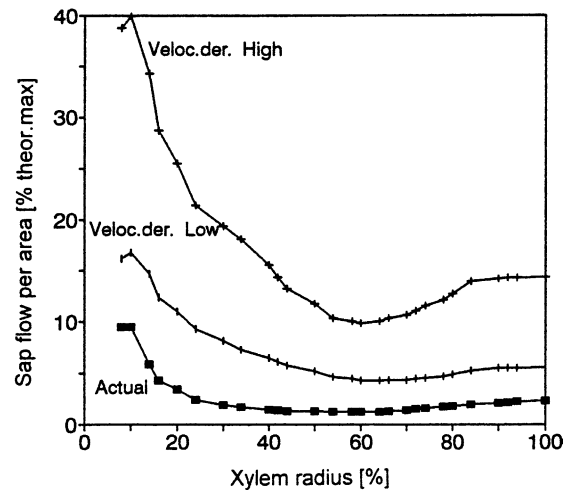
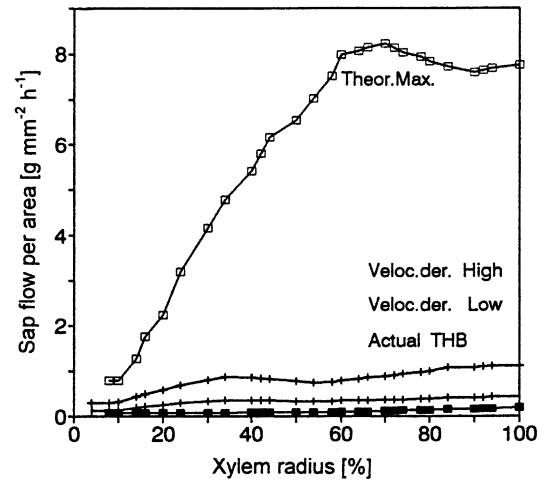
**Fig. 5** Radial profile of maximum daily sap flow rate measured using the tissue heat balance technique (expressed for unit area and for different annuli) in *L. azorica* wood (trees of DBH=150–220 mm). Given values represent the mean tree of the stand (DBH=160 mm). Total sap flow rate ( $3.9 \text{ kg tree}^{-1}\text{h}^{-1}$ ) was calculated when summarizing flows in all annuli

stand corresponded to about  $4 \text{ kg tree}^{-1}\text{h}^{-1}$ , which represented about 2.3% of the theoretical maximum sap flow rate or 58.6% and 23.9%, respectively, of sap flow rates derived from high and low sap velocities. The radial pattern of actual sap flow rate when expressed per unit of sapwood area also showed certain low values even in the oldest xylem at depths close to the pith and values more than twice as high in young xylem close to the cambium (with a rather high variation along the radius). Flow density per xylem area remained low until about 60% of xylem radius and then increased progressively up to the cambium. The total sap flow expressed per individual annulus was negligible close to the pith and reached much higher values close to the cambium in all sample trees with much less variation along the stem radius (Fig. 5).

Patterns of sap flow rate density per xylem area and also proportion of actual and theoretical flow, estimated by different methods, differ significantly along the stem radius. An error associated with the application of the fourth power of vessel diameter in the Hagen–Poiseuille equation could be involved in the above calculations of flow density, especially for high flow rates (Fig. 6 above). However, when the actual sap flow was compared to the theoretical one (Fig. 6, below), the general trend showed that a larger proportion of the narrow vessels close to the pith remained functional (up to the xylem radius of about 20–30%), while the proportion of functional vessels near the cambium decreased dramatically.

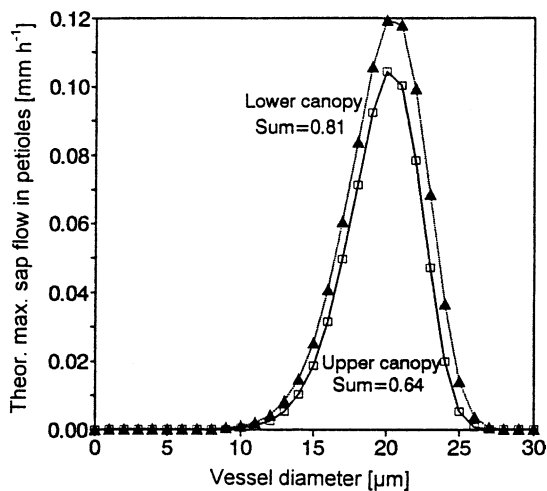
#### Comparison of sap flow rates in stems and petioles

Theoretical maximum sap flow rates through all petioles in the entire experimental forest stand (i.e. stand

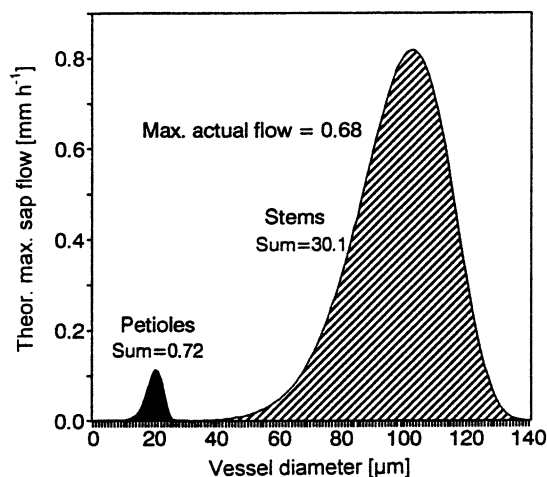


**Fig. 6** Above Radial profile of sap flow rate per unit of xylem area in *L. azorica* wood estimated by different methods (values characterize the mean tree of the stand, DBH=160 mm): Maximum theoretical sap flow calculated from distribution of vessel diameters (blank squares). Sap flow derived from sap velocity measured by the staining technique (high and low velocities at the same depths were considered, crosses and dashes respectively) and actual sap flow (dark squares) measured by trunk heat balance (THB) method. Below Radial profile of sap flow per area (estimated by the same methods as above) was expressed as a percentage of the maximum theoretical flow

transpiration) reached about  $0.72 \text{ mm h}^{-1}$ . This value was estimated less precisely than other hydraulic parameters owing to a high variation of leaf properties within the canopy (approximate error was about  $\pm 20\%$ ) and also differences in maximum flow rate associated with vessel distribution in the petioles in the lower and upper canopy (Fig. 7) and should be taken as a minimal estimate. Maximum theoretical sap flow rate for petioles (both given ranges are also associated with vessel distribution) represented only 2.2% of the maximum theoretical value calculated for the stems because the mean diameter of vessels in stems was five times larger (Fig. 8).



**Fig. 7** Theoretical maximum transpiration (derived from sap flow) for the stand calculated considering vessels of different diameter in *L. azorica* petioles from the lower (triangles, total=0.81 mm h<sup>-1</sup>) and upper canopy (squares, total=0.62 mm h<sup>-1</sup>)



**Fig. 8** Theoretical maximum stand transpiration (derived from sap flow) calculated for bases of *L. azorica* stems (30.1 mm h<sup>-1</sup>) and petioles (0.72 mm h<sup>-1</sup>) and expressed according to diameter distribution of vessels. These values are compared to maximum actual transpiration measured (0.675 mm h<sup>-1</sup>)

## Discussion

### Conducting systems in stems and petioles

General characteristics of stem conductive systems at the whole tree level have been well analysed (Zimmermann 1983), but there are not many detailed data on vessel distribution at the tree and stand level available. Data shown here for *L. azorica* contribute to increasing general knowledge in this area and were the basis for theoretical calculations in this work. The very large numbers that characterize amounts and distribution of vessels were simplified when considering only one (main) species and only the total hydraulic lumen area for the stand area unit.

Possible differences between laurel forest species were probably not important in the conclusions, because similar results were obtained in structurally quite different, ring-porous species of *Quercus robur* in floodplain forests of central Europe (Krejzar and Kravka 1998). Data of this type have been rarely applied in classical physiology, but they are especially needed for bio-physical calculations aimed at evaluation of the electrical environment and conducting systems in forest stands (Tributsch 1985).

### Sap velocity and its radial pattern in stems

In general, sap velocities obtained with the staining method should be treated with caution due to extremely large unnatural changes in hydraulic pressure conditions during the treatment as they change from high tension to atmospheric pressure (osmotic adjustment, etc; Nulsen and Thurtell 1978; Cermák et al. 1992). It is possible that some vessels can absorb the solution due to remaining tension caused by previous transpiration even if they are empty and actually non-conducting. Consequently, some overestimation of the estimated velocity may be expected, although calculated dye velocity was corrected according to water potential gradients up and down the stem. The evident high dye velocity in these vessels was more clearly defined, but the low dye velocity may be, at least partially, an artefact caused by local diffusion of the dye on the cut stem surfaces and cannot be taken as a sure indication of the flow. Variation of the velocity values along the radius with the higher ones close to the cambium has also been reported in willow (Cermák et al. 1984). There was an apparent significant depression of sap velocity in mid-radius parts of the xylem. This may be accidental (e.g. due to possible worsening in particular growing conditions leading to less well developed vessels during some years) or it may reflect different fractioning of flow rate to the upper and/or lower crown (Jiménez et al. 2000). No comparable data on sap velocity in *L. azorica* trees were found in the literature; nevertheless our results were close to published values of velocity (3–4 m h<sup>-1</sup>) in species with similar vessel diameters such as *Juglans* or *Salix* species (Zimmermann and Brown 1971; Cermák et al. 1984) and thus seem realistic.

### Sap flow rate and its radial pattern in stems

The calculated theoretical maximum sap flow rate fits if we consider vessels as ideal capillaries, but taking into account the contribution of perforation plates (simple in our case, Morales et al. 2002) to the overall stem vessel resistance. Based on similar studies (Schulte and Castle 1993a, b), it was estimated that they contributed to about 10% of sap flow reduction, so that the theoretical maximum sap flow rate was lowered to 30 mm h<sup>-1</sup>, still a very high value. When downscaled to the valid value for the mean tree of the stand this would correspond to about 175 kg tree<sup>-1</sup> h<sup>-1</sup>.

When considering the proportion of area of older (deep) and younger (shallow) xylem, it is clear that the deeper layers of xylem are quantitatively much less important in conducting water than the outermost layers, when the whole tree water supply is taken into account. This finding corresponds to the conclusions of another of our studies (Jiménez et al. 2000), which additionally pointed out the importance of individual variation.

Considering that sap flow values for the whole tree were obtained when summarizing flows in all annuli along the radial pattern measured by the sectoral trunk heat balance (THB) method, the above-mentioned results are important from the methodical viewpoint. When measuring the sap flow in a species where no clear conducting wood is visible or distinguishable, it is necessary to estimate correctly the proper depth for sap flow sensors (Cermák and Nadezhdina 1998). Our results confirm that the THB technique with internal electrical heating using electrodes inserted to the standard depth (50–60 mm according to the stem diameter and thermocouples) into the outer xylem layers is applicable in *L. azorica*. The sensors located at two different depths covered about 50–80% of stem radius and/or 80–90% of its basal sapwood area in the given range of stem diameters (Jiménez et al. 1996).

#### Comparison of sap flow rates in stems and petioles

There were great differences between actually measured stand sap flow rates and rates theoretically calculated in the base of stem and petioles (based on measured vessel area and density). Theoretical maximum flow in stems was about 42 times higher than that in petioles. The maximum measured actual value in stems reached about 93% of the theoretical maximum value calculated for petioles. This is within the estimated experimental error and thus both values can be taken as practically identical. A certain error may arise when considering an equal gradient along the whole conductive pathway, because this gradient may change significantly in second-order branches compared to the main stem, at least in some species (Kaibiyainen and Sazonova 1993).

Lewis and Boose's (1995) analysis showed that in general exact results are sometimes difficult to attain when applying the Hagen–Poiseuille equation and pointed out the need to clarify the causes of differences between the theoretical rates and the smaller measured volume flow rates in plant xylem. Overwhelming maximum theoretical flow rates compared to actual ones were not surprising, because they were calculated based on the assumption that all vessels are filled with water. In fact, the same assumption is accepted when applying various techniques based on pushing liquid water through xylem vessels (Tyree and Ewers 1991).

However we know from our previous experiments (see Morales et al. 2002) that a relatively large volume of air (or water vapour) is also present in vivo (27% of total volume of wood). The vessel lumen within the xylem repre-

sents 10% of the total volume of wood. It is probable that part of this volume could be air-filled (or water vapour filled). This means that a certain amount of vessels in stems are embolized and only some vessels are functional, although evidently sufficient for the plant to function. Ludwig (1952), for example, found that if vessels in stems were reduced up to 85% no wilting occurred. Even if this is an extreme value, a high percentage of completely embolized vessels could occur if empty parts of embolized vessels are combined with other parts still containing some water. In this case the vessels also remain non-functional. A much higher percentage of functional vessels in petioles (this percentage gradually increases from stem to branches and probably gradually further to twigs and leaves) is confirmed by previously found increasing xylem water content in branches (see Morales et al. 2002).

From our calculations it is evident that practically all vessels in petioles actually conduct water under conditions of high flow (their relatively large resistance is evidently one of the factors limiting total flow), while not nearly all the stem vessels actually conduct at the same time. This confirms the Zimmermann (1983) hypothesis that resistance to water flow in the water transport path increases away from the main stem. This was later confirmed by some other authors (e.g. Berninger and Nikinmaa 1994), based on branch area/stem area ratio measured along the stem). Irrespective of whether small vessels are included, leaves and petioles will suffer first from occasional drought stress and will be eventually shed to protect main stems against serious injury. Tyree et al. (1993) also pointed out a higher vulnerability of petioles than stems to water-stress induced cavitation.

It can be concluded that *L. azorica* wood, which has a large proportion of relatively small vessels, represents a rather safe conducting system. Due to its high vessel density it is capable of easily transporting all the water required under the prevailing habitat conditions, even during periods of high evaporative demands and when only some of the vessels are working. In the petioles, xylem is limited and more efficiently used. Practically the whole conducting system must work in order to supply water to leaves, and any disturbance will cause leaf decline.

**Acknowledgements** This work was performed on the basis of an agreement between the Universities of La Laguna (Spain) and Brno (Czech Republic). It was supported by DGICYT (Spanish Government) project no. PB94–0580 and “Viceconsejería de Educación” (Canarian Government). The stay of J. Cermák in Tenerife was financed through the agreement made between the University of La Laguna and Banco Santander. Thanks to Neil Abrey for his help with the English.

#### References

- Berninger F, Nikinmaa E (1994) Foliage area sapwood area relationships of Scots pine (*Pinus sylvestris*) trees in different climates. *Can J For Res* 24:2263–2268
- Booker RE (1984) Dye-flow apparatus to measure the variation in axial xylem permeability over a stem cross-section. *Plant Cell Environ* 7:623–628

- Cermák J, Kucera J (1981) The compensation of natural temperature gradient in the measuring point during the sap flow rate determination in trees. *Biol Plant* 23:469–471
- Cermák J, Kucera J (1990) Scaling up transpiration data between trees, stands and watersheds. *Silva Carelica* 15:101–120
- Cermák J, Nadezhdina N (1998) Sapwood as the scaling parameter – defining according to xylem water content or radial pattern of sap flow? *Ann Sci For* 55:509–521
- Cermák J, Deml M, Penka M (1973) A new method of sap flow rate determination in trees. *Biol Plant* 15:171–178
- Cermák J, Ulehla J, Kucera J, Penka M (1982) Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. *Biol Plant* 24:446–460
- Cermák J, Jenik J, Kucera J, Zidek V (1984) Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. *Oecologia* 64:145–151
- Cermák J, Cienciala E, Kucera J, Hallgren J-E (1992) Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiol* 10:367–380
- Edwards WRN, Booker RE (1984) Radial variation in the axial conductivity of *Populus* and its significance in heat pulse velocity measurement. *J Exp Bot* 35:551–561
- Hatton TJ, Catchpole EA, Vertessy RA (1990) Integration of sapflow velocity to estimate plant water use. *Tree Physiol* 6:201–209
- Hinckley TM, Lassioe JP, Running SW (1978) Temporal and spatial variations in the water status of forest trees. *For Sci Monogr* 20:1–72
- Jiménez MS, Cermák J, Kucera J, Morales D (1996) Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in *Laurus* trees and stand. *J Hydrol* 183:307–321
- Jiménez MS, Nadezhdina N, Cermák J, Morales D (2000) Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol* 20:1149–1156
- Kaibiyainen LK, Sazonova TA (1993) Variation of water potentials in the ‘soil-plant-atmosphere’ system, using Scots pine as an example (in Russian). *Lesovedenie* 3:41–47
- Kozłowski TT, Wignet CH (1963) Patterns of water movement in forest trees. *Bot Gaz* 124:301–311
- Krejarz T, Kravka M (1998) Sap flow and vessel distribution in annual rings and petioles of large oaks. *Lesn For* 44:193–201z
- Kucera J, Cermák J, Penka M (1977) Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol Plant* 19:413–420
- Lewis AM, Boose ER (1995) Estimating volume flow rates through xylem conduits. *Am J Bot* 82:1112–1116
- Ludwig RA (1952) Studies on the physiology of hadromycotic wilting in the tomato plant. *McDonald Coll Techn Bull* 20
- Morales D, González-Rodríguez AM, Cermák J, Jiménez MS (1996a) Laurel forests in Tenerife, Canary Islands: the vertical profiles of leaf characteristics. *Phyton* 36: 251–263
- Morales D, Jiménez MS, González-Rodríguez AM, Cermák J (1996b) Laurel forests in Tenerife, Canary Islands. I. The site, stand structure and stand leaf area distribution. *Trees* 11:34–40
- Morales D, Jiménez MS, González-Rodríguez AM, Cermák J (1996c) Laurel forests in Tenerife, Canary Islands. II. Leaf distribution patterns in individual trees. *Trees* 11:41–46
- Morales D, Jiménez MS, González-Rodríguez AM, Cermák J (2002) Laurel forests in Tenerife, Canary islands: I Xylem structure in stems and petioles of *Laurus azorica* trees. *Trees*: DOI 10.1007/s00468-002-0197-z
- Nadezhdina N, Cermák J, Ceulemans R (2001) Radial pattern of sap flow in woody stems related to positioning of sensors and scaling errors in dominant and understorey species. *Tree Physiol* (in press)
- Nulsen RA, Thurtell GW (1978) Osmotically induced changes in the pressure-flow relationships of maize root systems. *Aust J Plant Physiol* 5:469–476
- Oramas CP, De Roma LA (1967) Estudio de las principales maderas de Canarias. Instituto Forestal de Investigaciones y Experiencias. Ministerio de Agricultura, Madrid, pp 1–128
- Philip MS (1994) Measuring trees and forests. CAB International, Wallingford
- Schulte PJ, Castle AL (1993a) Water flow through vessel perforation plates a fluid mechanical approach. *J Exp Bot* 44:1135–1142
- Schulte PJ, Castle AL (1993b) Water flow through vessel perforation plates the effects of plate angle and thickness for *Liriodendron tulipifera*. *J Exp Bot* 44:1143–1148
- Schweingruber FH (1990) Anatomy of European woods. Haupt, Berne
- Swanson RH (1971) Velocity distribution patterns in ascending xylem sap during transpiration. Symposium on Flow – its measurement and control in science and industry. *Can For Serv Pap* 4:171
- Tributsch H (1985) Die Wasser-Zugspannung-Insuffizienz Hypothese zum Waldsterben. *J For Pathol* 15:237–246
- Tyree MT, Ewers F (1991) The hydraulic architecture of trees and other woody plants. *New Phytol* 119:345–360
- Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T (1993) Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant Cell Environ* 16:879–882
- Waisel Y, Lipschnitz N, Kuller Z (1972) Patterns of water movement in trees and shrubs. *Ecology* 53:520–523
- Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin Heidelberg New York
- Zimmermann MH, Brown CL (1971) Trees, structure and function. Springer, Berlin Heidelberg New York