Original article

Root and shoot hydraulic conductance of seven *Quercus* species

Andrea Nardini[a]*, Melvin T. Tyree[b]

[a] Dipartimento di Biologia, Università di Trieste, Via L. Giorgieri 10, 34127 Trieste, Italy
[b] USDA Forest Service, Northeastern Forest Experiment Station, 705 Spear Street, Burlington, VT 05402-0968, USA

Abstract – The root (K_R) and shoot (K_S) hydraulic conductances of seven different *Quercus* species, as well as the leaf blade hydraulic resistance (R_{LL}), were measured in potted plants with the aim of understanding whether a relationship exists between the hydraulic architecture and the general ecological behaviour of different species of this genus. The K_R values were scaled by dividing by root surface area (K_{RR}) and by leaf surface area (K_{RL}) and the K_S values were scaled by dividing by leaf surface area (K_{SL}). The likely drought-adapted species (*Quercus suber, Q. pubescens, Q. petraea*) showed lower K_{RL} and K_{RR}, lower K_{SL} and higher R_{LL} with respect to the known water-demanding species (*Q. alba, Q. cerris, Q. robur, Q. rubra*). The possible physiological and ecological significance of such differences are discussed. (© Inra/Elsevier, Paris.)

root hydraulic conductance / shoot hydraulic conductance / leaf blade resistance / *Quercus* / high pressure flow meter

Résumé – Les conductivités hydrauliques de la racine et de la tige de sept espèces de *Quercus*. Les conductivités hydrauliques de la racine (K_R) et de la tige (K_S) et la résistance hydraulique des feuilles (R_{LL}) des sept espèces de *Quercus* ont été mesurées avec pour objectif la compréhension de la relation qui existe entre l'écologie de l'espèce et son architecture hydraulique. Les valeurs des K_R ont été divisées par les surfaces des feuilles (K_{RL}) et des racines (K_{RR}), celles des K_S par les surfaces des feuilles (K_{SL}). Les K_{RR}, K_{RL} et K_{SL} des espèces adaptées aux environnements arides (*Q. suber, Q. pubescens, Q. petraea*) sont inférieures et leurs R_{LL} supérieures par rapport aux valeurs de celles adaptées aux environnements humides (*Q. alba, Q. cerris, Q. robur, Q. rubra*). Cet article se propose d'illustere ces différentces au plan physiologique et écologique.

conductivité hydraulique de la racine / conductivité hydraulique de la tige / *Quercus* / HPFM

1. Introduction

Many recent studies have reported the water relations of *Quercus* species [1, 3, 6, 18] with the aim of better understanding their different levels of adaptation to drought. A good correlation was found between vulnerability to cavitation in stems and drought tolerance [4, 8, 22]. Other studies show that hydraulic architectures of trees might be related to drought adaptation [2, 3, 23, 28].

A low hydraulic conductance in xylem is expected to cause a low leaf water potential, because leaf water potential at a given transpiration rate is determined by soil water potential as well as by root and shoot hydraulic conductance [16]. This means that the higher the root and/or shoot hydraulic conductance, the less negative would be the leaf water potential and the less severe would be the water stress suffered by the plant in terms of reduced cell expansion, protein synthesis, stomatal conductance and photosynthesis [15].

* Correspondence and reprints
salleo@univ.trieste.it

On the other hand, a high shoot hydraulic conductance (due to wide conduits) might increase vulnerability to cavitation, as suggested by some authors [10, 11] although questioned by others [21, 24]. As a consequence, it is still unclear whether a high hydraulic conductance of shoot and root can be of advantage to plants under water stress conditions.

To the best of our knowledge, only a few studies have appeared in the literature reporting measurements of the hydraulic conductance of whole root systems of *Quercus* species [12, 13]. Even less data have been reported from parallel measurements of root and shoot hydraulic conductances of different *Quercus* species.

In an attempt to find a relation (if any) between the root and shoot hydraulic conductances and the general ecological behaviour of different species of the genus *Quercus*, root and shoot hydraulic conductances were measured for seven oak species.

2. Materials and methods

The *Quercus* species used in this study were *Q. suber* L., *Q. pubescens* Willd, *Q. petraea* (Matt) Liebl, *Q. alba* L., *Q. cerris* L., *Q. robur* L. and *Q. rubra* L. These *Quercus* species were selected because they are representative of different levels of adaptation to drought, ranging from species well adapted to drought such as *Q. suber* to water-demanding species such as *Q. rubra*. In particular, *Q. suber* is a Mediterranean evergreen sclerophyll growing from the sea level up to 700 m in altitude [17]. *Q. pubescens* is a semi-deciduous species growing in calcareous soils between sea level and 1 200 m in altitude within the sub-Mediterranean climatic area (southeastern Europe [17]). *Q. petraea* is a European species growing in sub-acid soils between sea level and 1 000 m in altitude in Atlantic climate zones [17]. *Q. cerris* is a euro-Mediterranean species growing in acid soils with good water availability [17]. Finally, *Q. robur* is a

European species growing on nutrient-rich soils, with high water availability [17].

During a visit to the United States Department of Agriculture (USDA) Northeastern Forest Experiment Station (Burlington, VT, USA), preliminary measurements of root and shoot hydraulic conductance were performed in *Q. rubra* and *Q. alba*. Although both *Quercus* species have an American distribution area, they were added to the present study because they represent two cases of adaptation to different water availability.

Experiments were replicated on five to ten 3-year-old seedlings of each species. The seedlings were grown in pots. Dimensions of the seedlings are reported in *table 1* in terms of height (h), trunk diameter ($\varnothing_T$), total leaf surface area (A_L) and root surface area (A_R). Pots were cylindrical in shape with a diameter of 150 mm and a height of 250 mm. Seedlings of *Q. rubra* and *Q. alba* had been grown in pots since seed germination in the greenhouse of the USDA Forest Service, (Northeastern Forest Experiment Station, Burlington, VT, USA). Experiments on these two species were performed at the Northeastern Forest Experiment Station in July 1996. Seedlings of the other species, i.e. *Q. suber*, *Q. pubescens*, *Q. petraea*, *Q. cerris* and *Q. robur* were grown in the Botanical Garden of the University of Trieste (northeastern Italy). Experiments on these species were carried out in June 1997. All the seedlings were well irrigated with about 200 g of water supplied every 2 d.

Root (K_R) and shoot (K_S) hydraulic conductances of five seedlings per species were measured using a high pressure flow meter (HPFM) recently described by Tyree et al. [25, 26]. The HPFM is an apparatus designed to perfuse water into the base of a root system or a shoot while rapidly changing the applied pressure (P) and simultaneously measuring the corresponding flow (F) (transient mode [26]). The HPFM can also be used to perform steady-state measurements of shoot hydraulic conductance. In this case, the pressure applied to the stem is maintained constant at P = 0.3 MPa until a stable flow is recorded. In practice, it is never possible to keep

Table I. Height above soil (h), trunk diameter measured 50 mm above soil ($\varnothing_T$), total leaf surface area (A_L) and total root surface area (A_R) of plants used in this study. Means are given ± standard deviations ($n = 5$).

Species	h (m)	$\varnothing_T$ (mm)	A_L (m^2)	A_R (m^2)
Quercus suber	0.81 ± 0.14	4.8 ± 0.26	0.036 ± 0.010	0.066 ± 0.020
Quercus pubescens	0.45 ± 0.05	6.1 ± 0.21	0.049 ± 0.007	0.071 ± 0.011
Quercus petraea	0.68 ± 0.03	6.8 ± 0.90	0.062 ± 0.019	0.147 ± 0.081
Quercus alba	1.09 ± 0.20	9.4 ± 0.48	0.237 ± 0.041	–
Quercus cerris	0.38 ± 0.03	5.3 ± 0.29	0.026 ± 0.001	0.052 ± 0.013
Quercus robur	1.09 ± 0.18	8.5 ± 0.50	0.179 ± 0.051	0.374 ± 0.110
Quercus rubra	0.93 ± 0.28	9.2 ± 0.95	0.232 ± 0.095	–

flow and pressure perfectly constant, so it is best to refer to such measurements as quasi-steady state.

The HPFM technique was used in the transient mode for measuring root and shoot conductances, and in the quasi-steady-state mode for measuring leaf blade resistance (see later). The quasi-steady-state mode was not used on the roots because the continuous perfusion could cause accumulation of solutes in the stele by reverse osmosis, causing a continual decrease in driving force on water movement [25].

The pots were enclosed in plastic bags and immersed in water. The shoots were excised under water at about 70 mm above the soil, thus preventing xylem embolism. The HPFM was connected first to the base of the excised root system. The pressure was increased continually from 0.03 to 0.50 MPa within 90 s. The HPFM was equipped to record F and the corresponding P every 3 s. From the slope of the linear region of the relation of F to P it was possible to calculate root hydraulic conductance (K_R).

During K_R measurements, the shoots remained with the cut surface immersed in distilled water while enclosed in plastic bags to prevent evaporation. The base of the stem was connected to the HPFM and the stem was perfused with distilled water filtered to 0.1 μm at a pressure of 0.3 MPa for 1–2 h. After, leaf air spaces were infiltrated with water so that water dripped from the stomata of most leaves. The pressure was then released to 0.03 MPa and maintained constant for 10 min. Three to five transient measurements per seedlings were performed. From the slope of the linear relation of F to P, the stem hydraulic conductance (K_S) was calculated by linear regression of data. The pressure was then increased again to 0.3 MPa, and the hydraulic conductance of the shoot was measured in the quasi-steady-state mode.

The hydraulic resistance of leaf blade (i.e. the inverse of conductance) was also measured in the quasi-steady-state mode by measuring shoot hydraulic resistance after removal of leaf blades. Leaf blade resistance (R_L) was calculated from:

$$R_L = R_S - R_{S-L}$$

where R_S is the resistance of the leafy shoot and R_{S-L} is the resistance of the shoot after removal of the leaves.

During preliminary measurements made in Burlington (VT, USA), the agreement of transient versus quasi-steady-state measurements of shoot hydraulic conductance was tested on *Q. rubra* shoots of different basal diameter, using the same procedure described earlier.

A spurious component of the hydraulic conductance measurements when using the HPFM could be due to the elastic expansion of some components of the instrument such as tubing and connections [26]. Therefore, additional measurements of the relation of F to P were performed with the connection to solid metal rods. A linear relation of F to P with a minimal slope due to the intrinsic elasticity of the instrument was obtained. This slope was subtracted from the slope of the straight line relating F to P measured on the root or the shoot connected to the HPFM.

After each experiment, the A_L of the seedlings was measured using a leaf area meter (Li-Cor model 3000-A equipped with Li-Cor Belt Conveyor 3050-A). The total A_R of the seedlings was also estimated as follows: the soil was carefully removed from the root system under a gentle jet of water. The fine roots (< 2 mm in diameter) were then excised into segments 50 mm in length. The A_R of ten subsamples per species was calculated by placing the root segments (which were brown) into a glass box and covering them with a white plastic sheet to keep them in a fixed position while improving the contrast of the root images. The box was placed on a scanner (Epson model GT-9000 Epson Europe, The Netherland) connected to a computer. A program (developed by Dr P. Ganis, Department of Biology, University of Trieste, Italy) read the bit-map images and calculated the A_R. The root images were processed by the software and the A_R was obtained by multiplying the calculated area by π assuming the root segments as cylindrical in shape. Root subsamples were then put in an oven for 3 days at 70 °C to obtain their dry weights. A conversion factor between root dry weight and surface area was obtained. The whole root system was then oven-dried and the total A_R of each seedling was calculated. The A_R for *Q. alba* and *Q. rubra* seedlings was not measured.

K_R and K_S were both scaled by A_L so that root (K_{RL}) and shoot (K_{SL}) hydraulic conductances per leaf unit surface area were obtained. K_R was also divided by A_R, thus obtaining the root hydraulic conductance per root unit surface area (K_{RR}). Finally, R_L was multiplied by A_L, thus obtaining the leaf blade hydraulic resistance normalised by leaf surface area (R_{LL}).

3. Results

The relation of F to P as measured in the transient mode in roots and shoots was non-linear up to an applied pressure of 0.15 MPa, then became distinctly linear. The initial non-linearity was probably due to intrinsic elasticity of plant organs.

The root and shoot hydraulic conductances measured in the different *Quercus* species are reported in *figure 1*. Root hydraulic conductance per leaf unit surface area
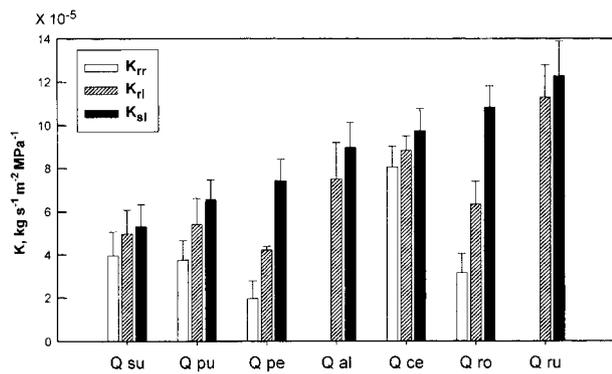
Figure 1. Root hydraulic conductance scaled by root surface area (K_{RR}, white columns), root hydraulic conductance scaled by leaf surface area (K_{RL}, dashed columns) and shoot hydraulic conductance scaled by leaf surface area (K_{SL}, black columns) as measured in different *Quercus* species. Q su: *Quercus suber*; Q pu: *Quercus pubescens*; Q pe: *Quercus petraea*; Q al: *Quercus alba*; Q ce: *Quercus cerris*; Q ro: *Quercus robur*; Q ru: *Quercus rubra*. Means are given ± standard deviations (*n* = 5).
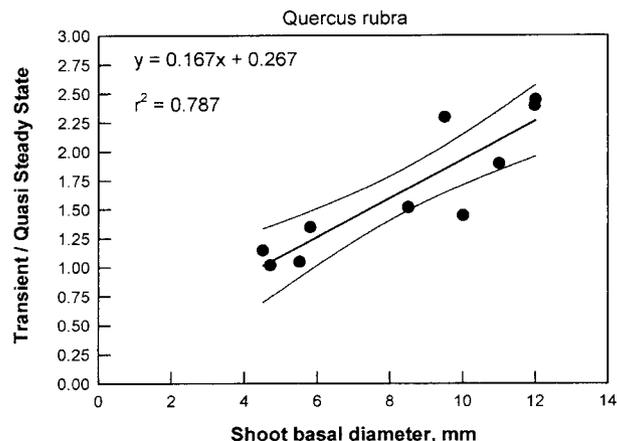

Figure 2. Relationship between transient to quasi-steady-state measurements of shoot hydraulic conductance and shoot basal diameter in *Quercus rubra*. The regression line is reported together with a 95 % confidence interval.

(K_{RL}, *figure 1*, dashed columns) ranged between 4.23 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1} for *Q. petraea* up to 11.29 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1} for *Q. rubra*. The drought-adapted species (*Q. suber, Q. pubescens, Q. petraea*) had lower values of K_{RL} (4.98, 5.41 and 4.23 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1}, respectively) than the mesophilous species (*Q. alba, Q. cerris, Q. robur* and *Q. rubra*; K_{RL} = 7.51, 8.83, 6.34 and 11.29 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1}, respectively). Student's *t*-test (*P* ≤ 0.05) revealed that *Q. suber, Q. pubescens* and *Q. petraea* were not significantly different from each other, but they were all significantly different from *Q. alba, Q. cerris, Q. robur* and *Q. rubra*. *Q. rubra* was significantly different from all the other species.

Root hydraulic conductance per root unit surface area (K_{RR}, *figure 1*, white columns) was approximately the same as root hydraulic conductance per leaf unit surface area (K_{RL}) in *Q. suber, Q. pubescens* and *Q. cerris* because root surface area approximately equalled leaf surface area. K_{RR} of *Q. petraea* and *Q. robur* were 46 and 50 % of K_{RL}, respectively, because the A_R of both species was approximately twice the A_L. The A_R of *Q. alba* and *Q. rubra* were not measured, so it was not possible to calculate the K_{RR} of these two species.

Shoot hydraulic conductance per leaf unit surface area (K_{SL}, *figure 1*, black columns) ranged between 5.32 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1} for *Q. suber* and 12.2 × 10^{-5} kg·s^{-1}·m^{-2}·MPa^{-1} for *Q. rubra*. The K_{SL} was found to

increase from the drought-adapted to the water-demanding species. A Student's *t*-test (*P* ≤ 0.05) indicated that the group of drought-adapted species (*Q. suber, Q. pubescens, Q. petraea*) showed significantly lower values than the water-demanding species (*Q. cerris, Q. robur, Q. rubra*). Generally, root and shoot hydraulic conductance were approximately equal in all species except in *Q. petraea* and *Q. robur*, whose K_{RL}s were 57 and 59 % of the corresponding K_{SL}s.

Shoot hydraulic conductance as measured in the quasi-steady-state mode was lower than the values recorded in the transient mode. The mean values of transient to quasi-steady-state ratio were 2.53 for *Q. suber*, 1.11 for *Q. pubescens*, 1.18 for *Q. petraea*, 1.60 for *Q. alba*, 1.83 for *Q. cerris*, 2.51 for *Q. robur* and 1.91 for *Q. rubra*. In *Q. rubra*, a good correlation was found between shoot basal diameter and transient to steady-state ratio; the transient to quasi-steady-state shoot hydraulic conductance ratio increased with basal diameter (r^2 = 0.787, *figure 2*).

The R_{LL} (*figure 3*) was found to range between 0.89 × 10^4 MPa s·m^2·kg^{-1} in *Q. rubra* and 3.68 × 10^4 MPa· s·m^2·kg^{-1} in *Q. robur*. R_{LL} tended to be higher in the drought-adapted species than in the water-demanding species, although the Student's *t*-test revealed that the differences were only slightly significant (*P* between 0.05 and 0.1). The only exception was *Q. robur*, which was significantly different from all the other species.

An interesting relationship was found between the general ecology of some of the species studied and the ratio of root dry weight to root surface area (RDW/A_R,
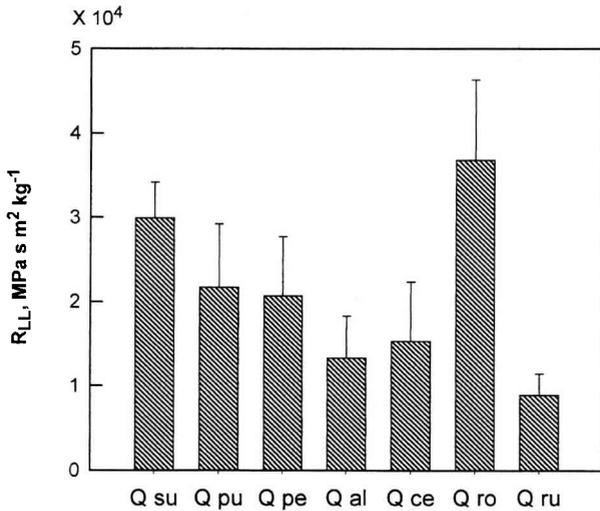
Figure 3. Leaf blade resistance scaled by leaf surface area (R_{LL}) measured in different *Quercus* species. The abbreviations for species are the same as used in *figure 1*. Means are given ± standard deviations ($n = 5$).
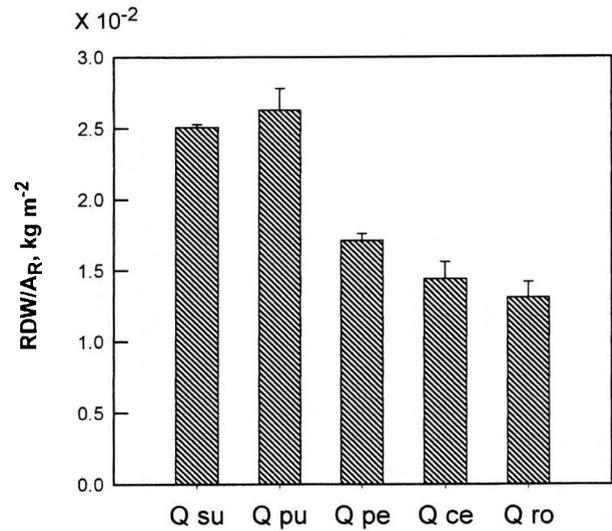

Figure 4. Root dry weight (RDW) to root surface area (A_R) ratio in different *Quercus* species. The abbreviations for species are the same as used in *figure 1*. Means are given ± standard deviations ($n = 5$).

figure 4). The two species better adapted to drought (*Q. suber* and *Q. pubescens*) showed significantly higher values of this ratio (2.51 and 2.63 × 10^{-2} kg·m^{-2}, respectively) than *Q. petraea, Q. cerris* and *Q. robur*, in which RDW/A_R was 1.71, 1.44 and 1.31 kg·m^{-2}, respectively. *Q. suber* and *Q. pubescens* were not significantly different from each other, but they were significantly different from all the other species; *Q. petraea* was significantly different from all the other species; *Q. cerris* and *Q. robur* were not significantly different from each other (Student's *t*-test, $P \le 0.05$).

4. Discussion

The K_{RL} and K_{SL} were of similar order of magnitude as reported for other tree species [23, 26, 27]. We found a general trend of K_{RL} and K_{SL} showing higher values in oak species typically growing in humid areas with respect to those adapted to aridity (*figure 1*). Species success in mesic sites may depend on rapid growth. Rapidly growing plants are better competitors for light and soil resources. Rapid growth is promoted when growing meristems are less water stressed. A high K_{SL} value will ensure rapid equilibration of shoots with Ψ_{SOIL} water potential at night which will promote rapid growth. A high K_{SL} value will also promote maximal values of $\Psi_{MERISTEM}$ water potential during the day. In arid environments where growth is usually slow because

of limited water availability, the ability to tolerate drought is more important than the ability to transport water rapidly. Hence, arid zone plants need to invest less carbon into shoot conductance and thus have lower K_{SL} values. Our data suggest that high root and shoot conductances are not physiological features conferring drought resistance to plants, at least in the genus *Quercus*. On the contrary, it seems that high K_{RL} and K_{SL} are important features allowing some species to compete more successfully in regions of high water availability, thus forcing low K_{RL} and/or K_{SL} species to migrate to habitats were water is less abundant and growth rate is less critical to survival.

In the present study, two alternative methods of scaling root hydraulic conductance were compared. K_R was normalised per leaf unit surface area as well as per root unit surface area. While in *Q. suber, Q. pubescens* and *Q. cerris* K_{RL} equalled K_{RR}, in *Q. petraea* and *Q. robur*, they did not. Scaling K_R by A_R is a more correct procedure when root physiology is under investigation. Scaling K_R by A_L seems to be more appropriate in an ecological context. In fact, K_{RL} is the expression of the 'sufficiency' of the root system to provide water to leaves [27].

Normalisation by A_L is sometimes more accurate than by A_R. Because of the difficulty in digging out whole root systems from the soil, the error that can be made when scaling K_R by A_R is intrinsically important and

would underestimate A_R. Moreover, the use of roots less than 2 mm in diameter for calculating A_R is rather arbitrary because it is still unclear what fraction of the root surface area is involved in water absorption. Therefore, we feel that scaling up K_R by A_L is much less subject to error when studying the hydraulic behaviour of whole root systems growing in the soil.

The observed difference between transient and quasi-steady-state measurements of shoot hydraulic conductance might be explained in terms of intrinsic elasticity of the stem as due to air bubbles in the xylem vessels. During transient measurements, air bubbles initially present in the xylem are continuously compressed as the pressure applied increases. This causes an additional flow that is recorded by the instrument, thus overestimating K_{SL}. During steady-state measurements the bubbles are completely compressed (and eventually dissolved) and the flow due to bubble compression does not affect the measurement. This seems to be confirmed by experiments performed on $Q. rubra$, showing that the discrepancies between transient and quasi-steady-state measurements are much more evident in larger and older stems. Older stems have more embolised vessels than younger stems. Our data would suggest that quasi-steady-state measurements of hydraulic conductance are more correct than transient measurements, at least in larger stems. However, it has been convincingly demonstrated that quasi-steady-state measurements of K_{RL} are affected by a number of problems (e.g. solute accumulation in the stele [25]); therefore, in roots it is preferable to measure K_{RL} in the transient mode. Roots contain less embolised tissue than shoots, thus transient measures of K_R are probably more accurate.

Tyree et al. [26] discussed the effect of elasticity and air bubbles on conductance measurements in shoots. The effect of air bubbles can be distinguished from the effect of elasticity, when the air bubbles are separated from the HPFM by a low hydraulic resistance, i.e. when the bubbles are present at the base of a shoot or in the connector between the HPFM and the shoot. Elastic effects cause an offset in the y-intercept of the plot of flow versus pressure, but elasticity has only a minor effect on slope (= hydraulic conductance). Air bubbles in the HPFM connector affect the slope at low pressure (0–0.2 MPa), but has a rapidly diminished contribution to the slope at higher pressure. The air-bubble effect reported here is a newly recognised phenomenon. When the hydraulic resistance for water flow from the base of the shoot to the air bubbles is sufficiently high, the effect of the air bubbles increases the slope (= conductance) over the whole range of applied pressure.

R_{LL}'s measured in the seven $Quercus$ species ($figure$ 3) were similar to those reported by Tyree et al. [23] for $Q. robur$, $Q. petraea$, $Q. pubescens$ and $Q. rubra$. R_{LL} includes vascular as well as non-vascular water pathways from the leaf base to mesophyll air spaces, but it is generally thought that the main hydraulic resistance is located in the non-vascular component of the path [20]. The higher the resistance to water flow, the larger should be the water potential drop in the guard cells of stomata during transpiration. This might cause stomatal closure under water stress conditions. A rapid and substantial drop in leaf water potential is advantageous in that it allows stomata to close before xylem water potential reaches the cavitation threshold [9]. Thus, differences in R_{LL} could account for the different capabilities of stomatal control of embolism observed in $Quercus$ species [5]. The higher R_{LL}s have been reported in the more drought-adapted species, with the exception of $Q. robur$. Field studies by Nardini et al. [14] show that $Q. suber$ (with a high R_{LL}) had good stomatal control of water loss under drought stress conditions while $Q. cerris$ (with a low R_{LL}) was unable to prevent water loss by stomatal closure.

The ratio of RDW/A_R ($figure$ 4) was higher in the drought-adapted species than in the water-demanding species. It is very likely that high values of this ratio are mainly due to roots with many small and very densely packed cells in the cortex. When the RDW/A_R ratio was plotted versus K_{RL} or K_{RR}, no significant correlation was found between the two parameters for the different species. It is generally thought that the main resistance to water flow in plant roots is located in the non-vascular pathway [7]. According to the 'root composite model' proposed by Steudle and Heydt [19], water migrates in the root across the apoplastic pathway at high transpiration rates. In this case, the resistance to water flow is mainly dependent on the overall length of the path, which does not change much when many densely packed cells are compared to somehow looser cortex cells. This could explain why a significant correlation could not be found between root conductance and root mass per unit surface area. An alternative explanation for the higher RDW/A_R ratio measured in drought-adapted species could be that these species might accumulate more starch in their roots.

In conclusion, our results indicate that significant differences in the stem hydraulic architecture of $Quercus$ species can account for their different ecological requirements, although further studies are needed to compare the physiological indices with species ecology. In particular, the case of $Q. robur$ deserves further investigation, because this species showed somewhat peculiar features when compared with other water-demanding $Quercus$ trees.

References

[1] Abrams M.D., Adaptations and responses to drought in *Quercus* species of North America, Tree Physiol. 7 (1990) 227–238.

[2] Acherar M., Rambal S., Comparative water relations of four Mediterranean oak species, Vegetatio 99–100 (1992) 177–184.

[3] Cochard H., Tyree M.T., Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism, Tree Physiol. 6 (1990) 393–407.

[4] Cochard H., Bréda N., Granier A., Aussenac G., Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl, *Q. pubescens* Willd, *Q. robur* L.), Ann. Sci. For. 49 (1992) 225–233.

[5] Cochard H., Bréda N., Granier A., Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism?, Ann. Sci. For. 53 (1996) 197–206.

[6] Epron D., Dreyer E., Long-term effects of drought on photosynthesis of adult oak trees [*Quercus petraea* (Matt) Liebl. and *Quercus robur* L.] in a natural stand, New Phytol. 125 (1993) 381–389.

[7] Frensch J., Steudle E., Axial and radial hydraulic resistance to roots of maize (*Zea mays* L.), Plant Physiol. 91 (1989) 719–726.

[8] Higgs K.H., Wood V., Drought susceptibility and xylem dysfunction in seedlings of 4 European oak species, Ann. Sci. For. 52 (1995) 507–513.

[9] Jones H.G., Sutherland R.A., Stomatal control of xylem embolism, Plant Cell Environ. 14 (1991) 607–612.

[10] Lo Gullo M.A., Salleo S., Wood anatomy of some trees with diffuse- and ring-porous wood: some functional and ecological interpretations, Giorn. Bot. Ital. 124 (1990) 601–613.

[11] Lo Gullo M.A., Salleo S., Different vulnerabilities of *Quercus ilex* L. to freeze- and summer drought-induced xylem embolism: an ecological interpretation, Plant Cell Environ. 16 (1993) 511–519.

[12] Nardini A., Ghirardelli L., Salleo S., Vulnerability to freeze-stress of seedlings of *Quercus ilex* L.: an ecological interpretation, Ann. Sci. For. 55 (1998) 553–565.

[13] Nardini A., Lo Gullo M.A., Salleo S., Seasonal changes of root hydraulic conductance (K_{RL}) in four forest trees: an ecological interpretation, Plant Ecol. 139 (1998) 81–90.

[14] Nardini A., Lo Gullo M.A., Salleo S., Competitive strategies for water availability in two Mediterranean *Quercus* species, Plant Cell Environ. 22(1999) 109–116.

[15] Nilsen E.T., Orcutt D.M., Physiology of Plants under Stress, John Wiley & Sons, Inc., New York, 1996.

[16] Pallardy S.G., Hydraulic architecture and conductivity: an overview, in: Kreeb K.H., Richter H., Hynckley T.M. (Eds.), Structural and Functional Responses to Environmental Stresses, SPB Academic Publishing, The Hague, the Netherlands, 1989, pp. 3–19.

[17] Pignatti S., Flora d'Italia, Edagricole, Bologna, 1982.

[18] Salleo S., Lo Gullo M.A., Sclerophylly and plant water relations in three Mediterranean *Quercus* species, Ann. Bot. 65 (1990) 259–270.

[19] Steudle E., Heydt H., Water transport across tree roots, in: Rennenberg H., Eschrich W., Ziegler H. (Eds.), Trees – Contributions to Modern Tree Physiology, Backhuys Publishers, Leiden, the Netherlands, 1997, pp. 239–255.

[20] Tyree M.T., Cheung Y.N.S., Resistance to water flow in *Fagus grandifolia* leaves, Can. J. Bot. 55 (1977) 2591–2599.

[21] Tyree M.T., Dixon M.A., Water stress induced cavitation and embolism in some woody plants, Physiol. Plant. 66 (1986) 397–405.

[22] Tyree M.T., Cochard H., Summer and winter embolism in oak: impact on water relations, Ann. Sci. For. 53 (1996) 173–180.

[23] Tyree M.T., Sinclair B., Lu P., Granier A., Whole shoot hydraulic resistance in *Quercus* species measured with a high-pressure flowmeter, Ann. Sci. For. 50 (1993) 417–423.

[24] Tyree M.T., Davis S.D., Cochard H., Biophysical perspectives of xylem evolution: is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction?, IAWA Bull. 15 (1994) 335–360.

[25] Tyree M.T., Yang S., Cruiziat P., Sinclair B., Novel methods of measuring hydraulic conductivity of tree root systems and interpretation using AMAIZED, Plant Physiol. 104 (1994) 189–199.

[26] Tyree M.T., Patiño S., Bennink J., Alexander J., Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field, J. Exp. Bot. 46 (1995) 83–94.

[27] Tyree M.T., Velez V., Dalling J.W., Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes, Oecologia 114 (1998) 293–298.

[28] Zimmermann M.H., Xylem Structure and the Ascent of Sap, Springer-Verlag, Berlin, 1983.