AZIMUTHAL VARIATIONS IN XYLEM STRUCTURE AND WATER RELATIONS IN CORK OAK (QUERCUS SUBER)

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SUMMARY

Azimuthal variations in xylem conductivity and transpiration can occur in trees and may be due to heterogeneity in environmental factors. In cork oak (Quercus suber L.), it can be hypothesized that such modifications may be more pronounced because the insulating layer of bark is harvested every 9–10 years, thus cambial cells will be exposed to fluctuations in the microenvironment. To investigate whether xylem structure and water relations differed around the stems of mature cork oak, sap flow per section and xylem structure were measured on the northern (N) and southern (S) sides of nine trees during three months in Portugal, using the Trunk Sector Heat Balance method. Crown size was measured on both sides of each tree and increment wood cores were extracted from the sites where sap flow was measured in five trees. Wood moisture content, earlywood (EW) vessel size and density were measured and theoretical hydraulic conductivity for individual vessels ($L_{th}$) was calculated along the N and S stem radial profiles. No significant differences in crown size between the two sides of the tree were found, but sap flow was higher on the S side of the tree in May only. No differences in wood moisture content were observed along the length of each wood core throughout the heartwood. Significant differences in vessel size occurred, with a greater diameter and surface area on the N side of the tree, and consequently $L_{th}$ was significantly greater. These conduit diameters on the S facing side of the tree may be smaller in response to a combination of signals and trade-offs due to the heterogeneous air and soil environment around the tree.

Key words: Wood anatomy, vessel lumina, hydraulic conductivity, sap flow.

INTRODUCTION

Portugal accounts for over 50% of the world cork harvest (FAO 1997). Cork is derived from the outer bark of the evergreen cork oak (Quercus suber L.), a Mediterranean species which is highly resistant to drought stress and elevated summer temperatures (Nardini & Tyree 1999; Ghouil et al. 2003; Otieno et al. 2006; Kurz-Besson et al. 2006).

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Nevertheless, in recent years the number of cork oak trees in Portugal dying through drought stress and stress related attacks by insects and fungi has increased (Brasier & Scott 2008). Although one of the mechanisms contributing to drought stress resistance is the presence of the thick, insulating layer of phellem, this phellem is harvested as cork every 9–10 years, thus placing trees under physiological stress. The effects of cork removal include increased water loss from the exposed surface, which may induce a decrease in stomatal activity and the death of the newly exposed inner bark tissues with subsequent formation of a traumatic periderm (see Silva et al. 2005). As a result, photosynthetic efficiency is reduced (Werner & Correia 1996). Although several studies have been carried out on the effects of climate on ecophysiology and growth of cork oak stands (Costa et al. 2002; Aranda et al. 2005), little information exists concerning the influence of very local environmental factors on water relations and xylem structure (Leal et al. 2006, 2007, 2008; Knapic et al. 2007).

In cork oak, most radial growth is linked to winter and autumn precipitation (Caritat et al. 2000; Costa et al. 2002). In the Mediterranean evergreen oaks Q. coccifera L. and Q. ilex L., maximal vessel diameter was positively regressed with mean annual rainfall (Villar-Salvador et al. 1997). However, in a more detailed study, earlywood (EW) vessel size in Q. petraea and Q. pubescens from a drought-prone site was largely governed by accumulated precipitation during the second half of the previous growing season, but at a mesic site, by spring precipitation of the current year (Fonti & García-González 2008). Cork oak is semi ring-porous in nature (Leal et al. 2007), therefore the size of vessels and their radial distribution along the stem radius are the most significant contributors to the theoretical hydraulic conductivity of wood ($L_{th}$) and hence water transport and efficiency along the whole water transport pathway (Ellmore & Ewers 1985). $L_{th}$ depends strongly on vessel diameter, as according to the Hagen-Poiseuille equation, hydraulic conductance of capillaries is proportional to the fourth power of the radius (Zimmermann 1983). Therefore, EW formed at the beginning of the growing season will largely determine the hydraulic architecture of the stem and any changes in EW structure as a result of external abiotic factors, e.g. drought or temperature, will be reflected in hydraulic conductivity and safety (Fonti & García-González 2004). In a typical sparse forest stand, which can be highly heterogeneous, variations in sunlight, temperature and water availability could therefore result in large inter- and intra-tree variability in EW vessel structure. However, tree density in cork oak stands is typically low, and mature trees are usually isolated with little competition from neighbours. Therefore, differences in environmental parameters, e.g. solar radiation, will be related to canopy orientation and azimuth (cardinal direction) rather than vertical gradient (Infante et al. 2001).

Several authors have suggested that physiological changes occur in trees subjected to uneven solar radiation levels around trees. Stokes et al. (1995) showed that in Picea sitchensis (Bong.) Carr., uneven irradiance levels resulted in asymmetric growth of both shoots and roots. Muth & Bazzaz (2002a) found that leaf number and canopy area were greater on the sides of Betula papyrifera Marsh. seedlings subjected to higher levels of photosynthetically active radiation (PAR). Muth & Bazzaz (2002b) also mapped tree canopies with regard to the heterogeneous light environments at the edges of six
experimental gaps and showed that the magnitude and precision of canopy displacement were generally greater for hardwoods than for conifers. With regard to xylem structure, Liese and Dadswell (1959) suggested that sunlight and temperature variations acting directly on the tree trunk can affect cell number and size. More significantly, recent work on *Q. ilex* has shown that sap flow density in mature trees was higher in the NE and NW orientations compared to that on the S side of the tree and differences were attributed to changes in spatial leaf area distribution, which were, however, not measured (Infante *et al.* 2001). These authors also suggest that the relationship between xylem conductivity and foliar transpiration will be reflected in long-term changes in sapwood vessel diameter and density in different orientations around the trunk.

If azimuthal variations in xylem conductivity and transpiration occur in trees, and are found to be due to heterogeneity in environmental factors around stems, it can be hypothesized that in cork oak such modifications may be more pronounced. In this species, the protective, insulating layer of bark is harvested every 9–10 years, thus the cambial cells will be exposed to fluctuations in the microenvironment, especially just after the harvest. Therefore, we carried out a study aimed at improving the understanding between xylem structure and water relations around the stems of mature cork oak in Portugal. Stem sap flow was measured at different positions around nine trees for three months. Increment wood cores were extracted from the sites where sap flow was measured in five trees and relative water content along the core was determined. Vessel size and density were measured using a light microscope on thin sections cut from wood cores. \( L_{th} \) was then estimated for individual vessels. Results are discussed with regard to the influence of xylem structure on hydraulic conductance in cork oak.

**MATERIALS AND METHODS**

**Experimental site characteristics**

The field plot was located near the town of Pinhal Novo, 35 km south-east of Lisbon and between the estuaries of Tagus (Tejo) and Sado in Portugal (38° 38' latitude and 8° 51' W longitude) at an altitude of 30 m. The climate at the field site is Mediterranean with an Atlantic influence. Total annual precipitation (average over 30 years) is 750 mm and occurs mainly in spring, winter and autumn (maximum in winter). Potential evapotranspiration ranged from 2–8 mm d\(^{-1}\) during the growing season (Nadhezhdina *et al.* 2008). Typical for a Mediterranean climate, summers are hot and dry with a high inter-annual variability of precipitation. The average temperature throughout the year is 16.1 °C, with an average minimum temperature in January of 5.3 °C and an average maximum temperature in August of 28.9 °C. A full description of geology and soil types in the region is given in Nadhezhdina *et al.* (2008).

The study site was a stand of 80-year-old cork oak (*Quercus suber* L.). Trees had been planted in rows 10 × 11 m apart, and had a density of 76 trees ha\(^{-1}\) in 2001 with some reduction in early 2003. The average canopy height was 10 m. The understorey was patchy and varied between dry grass and low shrubs, *e.g.* *Cistus* spp., which reached heights up to 0.4 m. Except for the study trees, cork was last harvested between 30/06/2003 and 12/07/2003 and before that in 1994.
Sampling procedure and sap flow measurements

Since healthy trees were needed for the study of sap flow, we used acoustic tomography to determine if any decay existed inside the stems. Twelve accelerometers were placed on the trunk of each tree at breast height (BH). Striking the tree with an impact device induced stress waves. The elapsed time for the signal to reach the other side of the tree and be detected by a second accelerometer was converted to a wave propagation speed, which gives information about the physical conditions inside the tree. Full methodology is described in Lorra & Kathage (2004). After sampling 30 trees, nine without any signs of decay were chosen for the study of sap flow. Mean diameter at breast height (DBH) was 0.42 ± 0.02 m (means are ± standard error). The mean crown radius was measured on the northern (N) and southern (S) sides of each tree.

Sap flow was measured in two cardinal directions (north and south) of each of the nine trees using the Trunk Sector Heat Balance method (THB, Čermák et al. 1973, 2004; Tatarinov et al. 2005). Sap flow sensors were inserted into the trunk at BH. Each sensor consisted of three electrodes inserted at the same height in parallel into sapwood, keeping the central electrode in a radial direction relative to the tree trunk. The electrodes comprised three stainless steel plates (25 mm wide and 1 mm thick), which were inserted into the sapwood at a depth of 0.02 m, which was approximately the depth of sapwood. A fourth plate of the same size was inserted 0.1 m below these electrodes. The temperature difference \(dT\) between the upper plates and the reference plate below was measured with copper-constantan (Cu-Cst) thermocouples placed into 1-mm-thin stainless steel hypodermic needles inserted in slots through the electrode axes. A constant heating power 0.6 W was supplied to the sapwood via the upper set of electrodes and the electric current running through the wood between the plates results in even heating between the plates according to equation 1:

\[
P = Q \cdot dT \cdot c_w + dT \cdot \lambda. \quad \text{[Equation 1]}
\]

where:

\[
Q = (P/dT \ c_w)_i - (P/dT \ c_w)_0 \quad \text{[Equation 2]}
\]

Variable \(P\) is the constant heat input power \([W]\), \(Q\) is the sap flow rate between the upper electrodes \([kg \cdot sec^{-1}]\), \(dT\) is the temperature difference between the upper (heated) and lower (reference) electrodes \([K]\), \(c_w\) is the specific heat of water \([J \cdot kg^{-1} \cdot K^{-1}]\) and \(\lambda\) is the coefficient of heat loss from the measuring point \([W \cdot K^{-1}]\). This heat loss is visible in the recorded flow data as the so called “fictive flow”, which can be calculated from the same input variables, but under conditions approaching that of zero sap flow (e.g., at night after prolonged rain). Full methodology and equations for calculating sap flow are given in Čermák et al. (1973, 2004) and Tatarinov et al. (2005).

Measuring points were protected against direct illumination and rain by covering the sap flow sensors with polyurethane foam, and sheets of aluminium and plastic tightened over slightly sanded stem bark. To avoid changing the microclimate of the stem, insulation was restricted to the sensors themselves, and not the surrounding stem surface, which was protected sufficiently by the thick bark. Data were measured every minute and recorded as means over 15 min intervals with a Campbell CR10 datalogger.
(Campbell Scientific Inc. NE, USA) for three months. All cables (between sensors and data loggers) were buried in a 0.05 m deep trench to protect them from animals. Data are presented as daily means averaged monthly from May to July 2003. Global radiation, $R_g$, (CM6B, Kipp and Zonen, Delft, Netherlands) was measured every minute and recorded as means over 15 min intervals during this period.

**Sampling of wood cores**

Five trees were randomly chosen from the 30 which had been examined using acoustic tomography and increment cores (5 mm in diameter) were extracted from breast height (BH) during the morning hours in early May, using a Suunto© wood corer. Two cores were extracted from due north and two from due south. The two cores taken at each position were 20 mm apart with one taken above the other. Each core was long enough to reach the stem pith; therefore the entire cross section of the stem was sampled. Cores were immediately wrapped in aluminium foil and plastic bags and were then transported to the laboratory and stored at 4 °C. With this method, water loss from samples should not be greater than approximately 10% (Morales et al. 2002). One core from each position was used for subsequent estimation of wood water content ($W_c$) and the second core was used for anatomical analysis.

**Wood water content ($W_c$)**

Wood water content ($W_c$) was measured using the method described in Kravka et al. (1999). Within 24 hours of extracting the wood cores, we measured $W_c$ along the length of the core. Both functional sapwood and heartwood were present in the core and could be distinguished by differences in colour. No dry transition zone occurred between the sap- and heartwood (Krejzar & Kravka 1998; Čermák & Kučera 1990). Samples 20 mm long were cut from the entire length of the core. The fresh mass ($M_f$) of each sample was determined using a balance with a resolution of 1.0 mg. The dry mass was obtained after drying in an oven at 80 °C for three days or until a constant dry mass ($M_d$) was attained. $W_c$ was calculated using:

$$W_c = \frac{M_f - M_d}{M_d} \quad \text{[Equation 3]}$$

**Microscopic analysis of vessel lumina**

Using the intact cores, 20-mm-long samples were cut from each core which corresponded to the segments in the cores used for determining $W_c$. Thin transverse sections (20 µm thick) were then cut from each segment in the radial direction, using a sliding microtome whilst the wood was still fresh. The thin sections were then mounted onto glass slides and stained with a solution of phloroglucinol (1,3,5-trihydroxybenzene) diluted in hydrochloric acid, which stains cell wall lignin a red colour (Chaffey 2002). The phloroglucinol solution was left for 1 min and samples were then washed with distilled water. Coverslips were placed on the sections to protect them.

Wood sections were examined using a light microscope at ×200 magnification. In order to scale the photographs processed by the software, a calibrated carbon lead was placed near the samples. Photographs were taken of the transversal surface of the wood
conducting vessels present in each annual growth ring. Several parameters were then measured using the image analysis software, WinCell© (Régent Instruments Inc., Quebec, Canada).

Maximum \((d_{\text{max}})\) and minimum \((d_{\text{min}})\) vessel lumen diameters were measured for earlywood (EW) within each growth ring. Hydraulic diameter \((d_h)\) of each EW vessel was then calculated using (Lewis 1992):

\[
d_h = \frac{1}{2} \times \frac{\sqrt{2d_{\text{max}}^2 d_{\text{min}}^2}}{d_{\text{max}} + d_{\text{min}}} \quad \text{[Equation 4]}
\]

Anatomical lumen area \((A_{\text{lum}})\) of conducting EW vessels was calculated as the ellipse:

\[
A_{\text{lum}} = \pi (d_{\text{max}} \times d_{\text{min}}) \quad \text{[Equation 5]}
\]

We calculated \(d_h\) and \(A_{\text{lum}}\) as opposed to weighted vessel diameter (Sperry & Sullivan 1992) so that minimum and maximum diameters were taken into account in the calculation of vessels with an elliptical shape. EW vessel density was obtained by counting the number of vessels per unit area of wood.

**Theoretical hydraulic conductivity \((L_{\text{th}})\) of single vessels**

The theoretical assessment of hydraulic conductivity \((L_{\text{th}})\) was carried out using the Hagen-Poiseuille equation (Equation 6, Zwieniecki et al. 2001) for all single vessels of EW along the stem core (mean per tree: \(n = 1315\) vessels on the N side and \(n = 1270\) vessels on the S side of the stem). \(L_{\text{th}}\) ignores the hydraulic resistance of end-walls, which account for the majority of the flow resistance, hence the calculated \(L_{\text{th}}\) is over twice as great as the actual conductivity \((L)\), and the proportionality between \(L_{\text{th}}\) and actual \(L\) is likely to be quite variable.

\[
L_{\text{th}} = \frac{r^4 \pi}{8 \eta} \quad \text{[Equation 6]}
\]

Where \(\eta\) is the viscosity of water \((1.002 \times 10^{-9} \text{ MPa s})\) at 20 °C.

**Statistical analysis**

Sap flow was analysed considering daily data recorded between 8-00 and 24-00 only. Mean daily sap flow was calculated using mean data from both the N and S sides of the trees and analysis of variance was used to determine if differences in mean sap flow existed between the months of May, June and July and between the N and S sides of the trees.

Vessel size and \(L_{\text{th}}\) data were tested for normality using an Anderson-Darling test. All data had normal distributions \((P > 0.05)\). Regressions were carried out to determine the relationship between crown radius and DBH on both N and S sides of the tree. The radial distance from the cambium was represented as a percentage of distance from the cambium in order to allow a better comparison of trees of different sizes. The relationship between mean \(W_c, A_{\text{lum}}, d_h\) and \(L_{\text{th}}\), between the N and S sides of the trees, was examined using analysis of covariance with depth of wood as a covariate.
RESULTS

**Site characteristics**

The mean crown radius on the N side of the tree was 4.8 ± 0.5 m and on the S side 5.4 ± 0.7 m. No significant differences in crown size between the two sides of the tree were found. No significant relationship was found between mean crown radius and DBH.

![Graph showing mean sap flow over time](image1)

Figure 1. Mean sap flow was higher in June and July than in May on the S side of cork oak stems. Data are means of daily sap flow ± standard error (n = 1 tree).

**Measurements of sap flow**

Mean sap flow at all times of the day was lower in May compared to June and July (Fig. 1). Between 12.00 and 18.00 h, mean sap flow ranged from 60–65 g.cm\(^{-2}.h^{-1}\) in May, increasing to 80–90 g.cm\(^{-2}.h^{-1}\) in June and July (Fig. 1). Mean sap flow was significantly greater on the S side of the tree during the month of May only (Fig. 2). On

![Graph showing mean daily sap flow](image2)

Figure 2. Mean daily sap flow was significantly higher on the S side (white bars) of cork oak stems compared to that on the N side (black bars) in May only \((F_{1,8} = 8.42, P = 0.02)\). Data are means ± standard error (n = 9 trees).
very sunny days, sap flow was higher on the S side of the tree until 14.00 h. Between
14.00 and 18.00 h, sap flow was similar on both sides of the tree, when the sun was
situated overhead. In the evening, sap flow was lower on the N side of the tree (Fig. 3).
On cloudy days, sap flow was similar on both sides of the tree (Fig. 3). A full detailed
analysis of seasonal sap flow results are presented in Nadhezhdina et al. (2008).

Wood water content ($W_c$)

Mean $W_c$ in all cores was $60.0 \pm 0.2\%$. No significant differences in $W_c$ in either
sapwood or heartwood were found either along the increment cores or between the N and
S sides of the tree, although sample length (20 mm) may have been too long to deter-
mine differences.

Microscopic analysis of vessel lumina

We observed precise boundaries between EW and latewood (LW) with regard to
vessel size. Wood was semi ring-porous to ring-porous and EW was characterized by
large lumina and LW by smaller lumina. The presence of tyloses (Cochard & Tyree
1990; Nardini et al. 1999) in vessel lumina was also observed but the quantity was not
measured.

Mean $A_{lum}$ decreased significantly from the cambium (30000 $\mu m^2$) towards the
pith (5000 $\mu m^2$). Significant differences in $A_{lum}$ were found between both sides of the
tree, with the S side having a significantly smaller $A_{lum}$ with regard to depth (Fig. 4a).
Mean vessel density was constant along the outer 50% of xylem depth, but increased
significantly towards the pith (Fig. 4b). Vessel density was not significantly different
between the N and S sides of the tree.
Hydraulic diameter and theoretical hydraulic conductivity ($L_{th}$) of single vessels

Mean hydraulic diameter ($d_h$) was $72.5 \pm 24.8$ µm and increased significantly from the pith to the cambium (Fig. 4c). When the N and S sides of the tree were compared, $d_h$ was similar in the outer wood between both sides of the tree but was significantly smaller towards the pith on the S side of the tree (Fig. 4c). Results show that the outer stem wood (up to 50% radial distance from cambium) had a significantly higher $L_{th}$ than inner wood (Fig. 4d). Except for wood in the outer 20%, $L_{th}$ was significantly higher in cores extracted from the N side of the tree compared to wood from the S side.
DISCUSSION

Results show that in cork oak, even when crown size does not differ around the tree, xylem structure can be influenced by the cardinal direction. In edge trees of plantations, crowns and root systems are often asymmetrical, which may be due to competition for space and light (Muth & Bazzaz 2002b; Cucchi et al. 2004). However, the cork oaks we studied were inside the plantation and planted at a low density, with little or no competition for space between the crowns. It is probable that crowns were asymmetrical with regard to gaps in the canopy, rather than cardinal directions, when the spacing was about 10 m. Muth and Bazzaz (2002a) found that leaf number and canopy area in Betula papyrifera seedlings were always greatest on the side of the tree with the highest PAR, and therefore grew towards gaps in the canopy. We did not measure gap size in the canopy of the cork oak plantation, nor the direction of greatest crown asymmetry; therefore these parameters would be useful to estimate in future studies. Kagawa et al. (2005) also showed through studies of pulse labelling and the distribution of $^{13}$C tracer in Cryptomeria japonica D. Don, that a given side of the stem is connected to different branches depending on the season. Nadezhdina (2010) demonstrated that water transport was integrated in the diffuse porous species Acer platanoides L. Large parts of the tree crown were supplied with water from the same root sector, therefore integration probably occurs through the cross-grained network of axial vessels. Thus studies of crown asymmetry may not necessarily reflect the exact nature of the internal hydraulic architecture of a tree.

Sap flow differed significantly between the N and S sides of the trunks during the month of May only, when EW is laid down. Sap flow was higher on the S side, which is in agreement with Loustau et al. (1998) and Kubota et al. (2005) who suggested that azimuthal variations were due to either xylem structure or were the result of differential solar heating (Granier 1987). However, more recent research has shown that root architecture can influence stem sap flow. Sap flow asymmetry near the stem base corresponds to different root distributions and rooting depths around the stem (Nadezhdina et al. 2002; Čermák et al. 2008). However, this asymmetry is less marked further up the stem (Čermák & Kučera 1990) and it is unlikely that a group of mature trees will possess the same asymmetric rooting patterns which similarly affect sap flow, although this has been observed in mature, leaning Pinus sylvestris L. subjected to strong prevailing winds (Čermák et al. 2008). To our knowledge, no studies of azimuthal sap flow have been combined with measurements of vessel size and hydraulic conductivity in oak trees. However, Infante et al. (2001) measured sap flow in three directions around the stem in Quercus ilex L. Results showed that sap flow was higher on the northeastern and northwestern sides than the S side of the tree. It was hypothesized that internal crown shading occurs during the day, affecting azimuthal sap flow. Also, if leaf water potentials differed depending on leaf orientation during drought, as found in some Quercus species (Hinckley et al. 1978), differences in leaf water potential could explain the lower transpiration rates of the S oriented leaves compared with leaves in other directions. Infante et al. (2001) also suggest that the lower sap flow measured in the S orientation could be explained as an adaptation of this part of the xylem to more...
severe water stress than in other orientations. David et al. (2007) demonstrated that *Q. ilex* possessed more effective drought avoidance and drought tolerance mechanisms than *Q. suber*, which may explain why we did not observe lower sap flow on the S side of the tree. *Quercus suber* is also regularly debarked, which may increase sensitivity to environmental signals and reflected in xylem structure.

Xylem structure in cork oak was semi ring-porous to ring-porous, with large EW vessels and smaller LW vessels. Variations in EW vessel size and density along the radial profile were similar to that of other oak species (Krejzar & Kravka 1998; Inside Wood 2004) and dicot woods in general. Significantly greater EW vessel \( A_{\text{cum}} \), \( d_h \) and \( L_{\text{th}} \) were found on the N sides of the trees compared to the S sides. As canopy structure did not change between both sides of the trees, another factor must exist which influences wood formation in springtime. The conduit diameters on the S facing side of the tree may be smaller in response to a greater potential for cavitation, as sap flow was higher during the period of EW formation and cell expansion. Smaller conduit diameter is one possible mechanism for achieving greater safety from cavitation, but vessels would have greater hydraulic resistivity. We calculated vessel \( L_{\text{th}} \), but this parameter does not consider the hydraulic resistance of end walls, which accounts for the majority of the flow resistance (Wheeler et al. 2005). In *Q. petraea* and *Q. pubescens* growing on a drought-prone site, EW vessel formation was found linked to the accumulation of reserves during the second half of the previous summer (Fonti & García-González 2008). Therefore, vessel size may be regulated in expectation of water demand, although the current year’s spring precipitation will likely also influence vessel expansion.

Other candidates for factors which affect xylem formation are water availability and variations in light and temperature (Fonti & García-González 2004). It is unlikely that spatial patterns in soil moisture content occur to such an extent as to differ significantly in cardinal directions around a tree (Barij et al. 2007), although root distribution and depth can result in asymmetric sap flow at the stem base (Nadezdina 2010). Uneven irradiation levels or temperature changes can affect wood formation, but very little information exists with regard to irradiation effects on wood formation. In thick-barked trees such as cork oak, light transmission would be extremely difficult. However, in this species, the insulating cork layer is harvested every nine years, therefore exposing the cambial region to direct environmental influences. With regard to temperature effects, recent evidence has shown that air temperature significantly influences xylem structure in trees (Gričar et al. 2007). Thomas et al. (2004) grew *Eucalyptus camaldulensis* Dehnh. at three temperatures for nine weeks at a constant vapour pressure deficit. Wood density was found to increase with higher growth temperature, and wood hydraulic conductivity per unit area decreased. Vessel area was also reduced at higher temperatures due to a decrease in vessel diameter. These authors showed that this phenomenon was due to water viscosity being sensitive to higher temperatures, therefore smaller or fewer vessels would be required to transport water to leaves at higher temperatures when water has lower viscosity (Roderick & Berry 2001). We did not measure wood temperature around the trunk of the cork trees we studied; however, Wieser (2002) found that sapwood temperature (measured at a depth of 0.01 m) was significantly greater on the S facing
side of 50-year-old *Pinus cembra* L. trees than on the N-facing side. Consequently, annual respiration was up to 13% higher on the south side of the trees. *Pinus* spp. are generally thick-barked, therefore in debarked cork oak, temperatures could be higher on the exposed S side of the tree, particularly when the sun is not overhead, thus affecting both xylem structure and water relations. However, Knapic *et al.* (2007) and Leal *et al.* (2008) showed that wood xylem structure differed little in old bark-harvested and never debarked *Q. suber* trees. These results indicate that it is necessary to carry out further research in this domain, to ensure that the scaling-up of stem respiration using data taken from one position in the tree is correct (Nadezhdina *et al.* 2002; Delzon *et al.* 2004), especially in thin-barked species, or species where the bark is removed as in cork oak.

No differences in wood *Wc* occurred along with radial distance from the cambium, even with regard to sap- and heartwood. Generally, it is thought that in coniferous trees, the water content in heartwood is usually lower than that for sapwood (Čermák & Nadezhdina 1998; Fromm *et al.* 2001) whereas in some hardwood species water content varies little between sap- and heartwood (Phillips *et al.* 1996; Fromm *et al.* 2001; Morales *et al.* 2002; Barij *et al.* 2007). However, it has been observed in other oak species, *e.g.*, *Quercus robur*, *Q. petraea* and *Q. pubescens*, that water content was lower in heartwood than in sapwood (Čermák, unpublished data). In our study, *Wc* did not differ between the N and S sides of the tree stems, although 20-mm sections may have been too long to register subtle differences. Similar results were also found in *Q. pubescens* by Barij *et al.* (2007) and Bucci *et al.* (2004), who suggested that xylem structure was a better indicator of stem storage capacity than saturated water content, as it reflects biophysical properties of the sapwood related to the efficiency of recharge and utilisation of stored water as well as the potential amount of stem water storage. We suggest therefore that in studies of hydraulic relations in trees, sap flow studies combined with xylem structure are more useful indicators of long-term water uptake than *Wc*.

In conclusion, differences in EW xylem structure occur around oak trees and are likely related to a variety of environmental signals. However, without a series of focused experiments, it is not easy to suggest which is the dominant, or limiting, factor affecting xylem growth. Most likely, a combination of signals and trade-offs in structure exist. In a species able to demonstrate a certain degree of plasticity in response to environmental signals, internal and local modifications will allow a more optimal regulation of water transport in a dry environment.

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