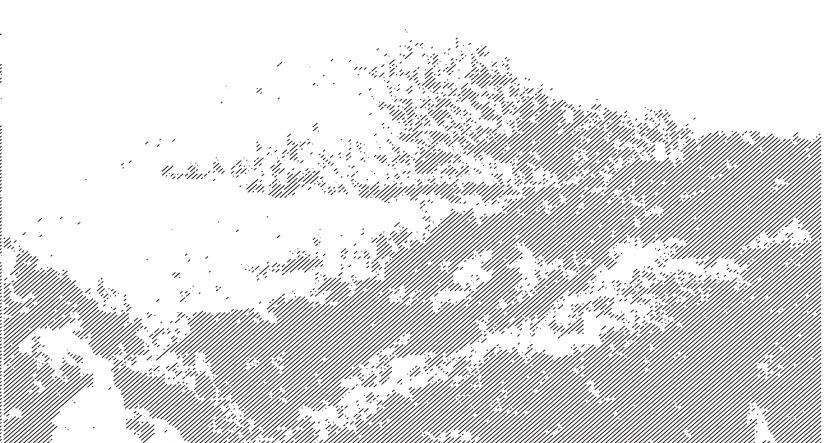**Measuring and modelling transpiration
of pine and oak forest stands
in a Mediterranean mountain area (Vallcebre, NE Spain)**

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3. Variation in the radial patterns of sap flux density in pubescent oak (*Quercus pubescens* Willd.) and its implications for tree and stand transpiration measurements.

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Abstract

Radial variation in sap flux density along the sapwood was assessed in several *Quercus pubescens* Wild. trees with the Heat Field Deformation method. Sapwood depth could be delimited by identifying the point of zero flow in radial patterns of sap flow, yielding tree sapwood areas which were 1.5-2 times larger than previous visual identifications on wood cores. These patterns varied among trees and diurnally, showing the higher sap flow close to cambium, but with a significant contribution from the inner sapwood, which was higher (up to 60% of total flow) during the early mornings and late in the day. Accordingly, the normalized difference between outer and inner sapwood sap flow was rather stable during the central part of the day, but showed a general decline in the afternoon. The distribution of sap flux density along the sapwood allowed us to derive correction coefficients for single-point heat dissipation sap flow measurements. We used daytime-averaged coefficients, which depended on the particular shape of the radial profile and ranged between 0.45 and 1.28. Therefore, corrected tree sap flow rates could be similar, higher or lower than previous estimations that did not consider this radial variation. Stand transpiration calculated using the new sapwood areas and radial corection coefficients was similar (year 2003) or about 25% higher (year 2004) than previous uncorrected values, and was 20-30% of reference evapotranspiration. We therefore showed how inaccuracies in determining sapwood depths and average sap flux density along the sapwood of ring-porous species could affect tree and stand transpiration estimates.

Resum

La variació radial de la densitat de flux de saba al llarg del xilema fou determinada en diferents arbres de *Quercus pubescens* Wild. utilitzant el mètode de Deformació del Camp de Calor (HFD). La fondària del xilema es determina identificant en els patrons radials de flux de saba el punt on el flux és nul. Utilitzant aquesta tècnica les àrees de xilema obtingudes foren entre 1.5-2 cops majors que les prèviament identificades visualment en els cores. Els patrons radials variaren entre arbres i diàriament, mostrant fluxos de saba majors prop del càmbium, però amb una contribució significant de la part interior del xilema, que fou màxima (fins al 60% del flux total) durant les primeres hores del matí i a les últimes del vespre. Conseqüentment, la diferència normalitzada entre el flux a la part exterior i a la part interior de l'albeca fou bastant estable durant les hores centrals del dia, però mostrà una disminució a la tarda. La distribució de la densitat de flux al llarg del xilema va permetre derivar uns coeficients de correcció per a les mesures de flux de saba puntuals obtingudes amb el mètode de dissipació tèrmica. S'utilitzaren com a coeficients promitjos diaris, que depenien de la forma de cada perfil radial i que variaven entre 0.45 i 1.28. Utilitzant aquests coeficients les taxes de flux de saba poden ser similars, majors o menors que les estimacions prèvies realitzades sense tenir en compte la variació radial. La transpiració del cobert, calculada utilitzant les noves àrees d'albeca i els coeficients de correcció radial foren similars (any 2003) o un 25% superiors (any 2004) que els valors previs no corregits, i representant un 20-30% de l'evapotranspiració de referència. Finalment es mostrà com les inexactituds en la determinació de la fondària d'albeca i de la densitat de flux mitjana al llarg d'aquesta en espècies de porus anellat pot afectar les estimacions de la transpiració a escala d'arbre i de cobert.

Introduction

Sap flow measurements in ring-porous trees face several methodological difficulties which pose significant uncertainties in the estimates of tree transpiration and subsequent extrapolations to tree and stand water use. Particularly, there are several critical issues in the application of the heat dissipation (HD) technique (Granier 1985; Granier 1987) in ring-porous species, largely due to the non-uniformity of sap velocity along the xylem (Clearwater et al. 1999). In these species, wide earlywood vessels in the most recent annual rings are responsible for most of the long distance water transport (Granier et al. 1994; Miller et al. 1980). Due to this particular xylem anatomy, oak trees usually show very narrow sapwood, which is difficult to identify visually or from changes in relative water content (Čermák and Nadezhdina 1998; Gartner and Meinzer 2005). Therefore, the identification of the depth where sap flow reaches zero in measured radial patterns of sap flow is recommended to identify the extent of conducting area in these species (Čermák and Nadezhdina 1998), an important parameter to extrapolate sap flux density measurements to trees and stands.

Deciduous *Quercus* spp. generally show a peak in sap flow close to the cambium and a sharp decrease with depth (Čermák and Nadezhdina 1998; Čermák et al. 1998; Granier et al. 1994). These large gradients of sap velocity can result in a serious underestimation of the average sap flow along the measuring length when using HD probes in oak species (Clearwater et al. 1999). On the other hand, assuming that sap flow measured in the outer xylem is uniform along the whole sapwood may result in a significant overestimation of the true flow, depending on the shape of the velocity profile (Nadezhdina et al. 2002).

Measuring sap flow at different depths or radial patterns with HD (Delzon et al. 2004; James et al. 2002; Phillips et al. 1996), heat field deformation (HFD) (Jiménez et al. 2000; Nadezhdina et al. 2002) or heat pulse velocity (HPV) methods (Hatton et al. 1990) and then relating this variability to a reference single-point probe in the outer sapwood (Lu et al. 2000), is a widely used procedure. These approaches do not incorporate temporal variations in sap flux density radial profiles, due to meteorological conditions, soil moisture or time of day (Čermák and Nadezhdina 1998; Phillips et al. 1996). However, according to Ford et al. (2004a), using a radial profile assessed during maximum flow rates to obtain the abovementioned corrections will not significantly affect daily sums of sap flow.

In this study we used a HFD multi-point sensor to measure radial variations of sap flow in mature *Quercus pubescens* Willd. trees growing in NE Spain. Long-term stand transpiration has been monitored with HD sensors in this stand since 2003. In a first approach to compute stand transpiration for the 2003 growing season, we determined hydroactive

sapwood by visual inspection and assumed a uniform sap flux density along the sapwood (Poyatos et al. 2005). The aims of this study were: (1) to assess radial variation in pubescent oak sap flow and its diurnal dynamics; (2) to use radial patterns to delimit sapwood depths; (3) to obtain correction coefficients to account for radial variation of sap flow and apply them to single-point heat dissipation measurements; and finally, (4) to apply the obtained corrections to estimate stand transpiration during 2003 and 2004 growing seasons.

Materials and methods

General site description and biometric characteristics of the stand

Field measurements were carried out in the Cal Barrol experimental plot, located in the Vallcebre experimental area (42º 12' N, 1º 49' E, 1100 m a.s.l.) in the Eastern Pyrenees (NE Spain). Climate is sub-Mediterranean, with an average air temperature of 7.3 ºC (measured at 1440 m.a.s.l.) and 924 mm of annual rainfall. (Gallart et al. 2002). The plot is characteristic of the climacic vegetation type in these Mediterranean montane areas (*Buxo-sempervirentis-Quercetum pubescentis*). *Quercus pubescens* is a winter deciduous or marcescent species which tends to hybridize with other *Quercus* species, resulting in a high variability in several morphological and ecophysiological traits (Himrane et al. 2004). Other woody species in the plot are *Prunus avium* L., *Fraxinus excelsior* L. and a dense understorey, mainly composed of *Acer campestre* L., *Buxus sempervirens* L., *Prunus spinosa* L., *Rubus spp.* and *Rosa spp.* The upper soil, which is formed by a loamy matrix and limestone boulders, is about 50 cm deep (Rubio 2005).

The experimental plot was located in a stand of about 1.2 ha. We selected a 10 m radius circular plot with a stand density of 987 trees ha^{-1} and a mean DBH of 21.1 cm. Pubescent oak density was 828 trees ha^{-1} and basal area was 32.5 m^2 ha^{-1} (99% of the total). Mean height of the stand was 10.6 m and maximum leaf area index (LAI$_{max}$) was 2.1 m^2 m^{-2}, obtained by allometry (Poyatos et al. 2005). Maximum age of the trees was about 70 years old.

Net radiation (NR-Lite, Kipp & Zonen, The Netherlands), air temperature and relative humidity (HMP45C, Vaisala, Finland), and wind speed (A100R, Vector Instruments, UK) were measured *ca.* 2 m above the canopy. Continuous soil moisture measurements (0-30 cm) with a water content reflectometer (CS616, Campbell Scientific, UK) began in May 2004. Weekly measurements of soil moisture (0-30 cm) by the TDR method (Tektronix 1502C, USA) were used to account for spatial variability of surface soil moisture (0-30 cm) at six locations in the plot and at two locations to assess soil water content in deeper soil

layers (30-50 cm). One of the probes was used to obtain a site-specific calibration for the reflectometer.

Heat dissipation (HD) *sap flow measurements*

Sap flow has been continuously monitored since May 2003 in 12 trees with heat dissipation probes (Granier 1985), installed at breast height, in the North side of each stem. Needles were inserted with a vertical separation of *ca.* 12 cm, and then covered with reflective material. Measurements were performed every 20 seconds and stored as 15-minute means in a data logger (DT500, DataTaker, Australia), which also recorded the meteorological data. Probes were 10 mm long, as the use of shorter probes minimizes the errors in estimating the average sap flow along the sensor, as demonstrated by Clearwater et al. (1999) and subsequently used in other studies concerning ring-porous oaks (Phillips et al. 2003). The original calibration (Granier 1985) was used to obtain the average sap flux density in the outer 10 mm of sapwood (v_{HD}).

Heat Field Deformation sap flow measurements

The heat field deformation method (HFD) was used to measure the radial patterns of sap flow during 2-7 days between July and October 2004 in nine trees which were also being monitored with HD probes (Table 1). An additional tree was also measured to cover a wider range of tree sizes for the derivation of the relationship between sapwood and basal area (Table 1). The HFD method is based on the changes in the spatial variation of the heat field around a linear heater placed in the tree's sapwood. Two temperature gradients mesured around the heater have been found to describe this heat field, dT_{sym} and dT_{asym} and allow for the calculation of sap flow (Nadezhdina et al. 1998). This technique has already been used in studies concerning radial patterns of sap flow (Jiménez et al. 2000; Nadezhdina et al. 2002) or long-term stand transpiration (Meiresonne et al. 2003). A recent study has shown the actual deformation of the heat field around the heater by moving sap using infra-red imagery (Nadezhdina et al. 2004) and an extensive validation against other estimates of transpiration is currently under way (Nadezhdina pers. comm.).

Table 1. Tree coding, diameter at breast height (DBH) and period of measurement of sap flow radial patterns, showing daytime averages, minimum and maximum values (in brackets) of vapour pressure deficit (*D*) and soil moisture (θ).

Tree	DBH (cm)	Measurement period (day of the year 2004)	θ (cm^3 cm^{-3})	D (kPa)
1	12.6	197-199	0.27 (0.27-0.28)	1.05 (0.69-1.40)
2	17.9	203-206	0.25 (0.23-0.25)	1.01 (0.21-1.68)
3	20.9	279-281	0.35 (0.34-0.36)	1.03 (0.38-2.02)
4	21.1	265-267	0.23 (0.22-0.23)	1.23 (0.61-1.86)
5	21.5	272-275	0.24 (0.22-0.40)	0.89 (0.16-1.65)
6	26.7	233-235	0.25 (0.24-0.25)	0.62 (0.04-1.41)
7	26.2	277-279	0.31 (0.29-0.35)	1.43 (0.52-3.82)
8	34.5	269-270	0.30 (0.29-0.30)	0.65 (0.07-1.50)
9	38.2	200-202	0.35 (0.32-0.43)	0.73 (0.12-1.45)
10 [a]	49.2	281-286	0.29 (0.27-0.30)	0.70 (0.11-1.63)

[a] This tree was not monitored with HD sensors but its radial pattern and sapwood area were measured to cover a wider range of tree sizes.

A multi-point HFD sensor (Dendronet, Czech Republic) with six measuring points and 8 mm spacing between them was inserted in the trees at breast height, in the same side where the Granier probes were installed, but far apart enough (about 10 cm) to prevent interferences between the measuring systems. Sensor readings were performed every 20 seconds and stored as 5-minute means in a data-logger (DT50, DataTaker, Australia). Only five points, though, could be recorded due to technical reasons. The first measuring point was located 3 mm inwards from cambium, hence, we had five estimates of sap velocity at 3, 11, 19, 27 and 35 mm inside the sapwood.

Sap flow per section (*q* in mm^3 mm^{-1} s^{-1}) was calculated using the following equation (Nadezhdina et al. 2006),

$$q = D_w \cdot \frac{(K + dT_{s-a}) \cdot Z_{ax}}{dT_{asym} \cdot Z_{tg}} \tag{1}$$

where

$$dT_{s-a} = dT_{sym} - dT_{asym} \tag{2}$$

dT_{sym} is symmetrical temperature difference (ºC), dT_{as} is asymmetrical temperature difference (ºC), dT_{s-a} is temperature difference (ºC) between upper points of symmetrical and asymmetrical thermocouple pairs (Equation 2), *K* is the value of dT_{s-a} under conditions of zero-flow, z_{ax} is axial distance between the symmetrical pair of thermocouples (30 mm), is z_{tg} tangential distance between the heater and the upper end of the asymmetrical pair of thermocouples (50 mm), and D_w is thermal diffusivity of fresh wood (mm^2 s^{-1}), assumed to have a value of $2.25 \cdot 10^{-1}$ mm^2 s^{-1}.

Sapwood depth (l_s) was then estimated extrapolating to zero flow the observed radial patterns of sap flow per section (Čermák and Nadezhdina, 1998). Third or fourth order polynomials were fitted to sap flux density radial patterns and then used to extrapolate the point of zero flow for each tree. Sap flux density (v_i, in mm^3 mm^{-2} sapwood area s^{-1}, or mm s^{-1} for brevity) for each measurement depth (mm), denoted by the subscript i, was calculated as:

$$v_i = \frac{q}{l_s} \tag{3}$$

We assumed that each TC junction sensed an 8 mm length interval, centered around the measuring point (Hatton et al. 1990), except for the shallowest point (which was only 3 mm inside cambium), and the deepest one, which we assumed representative of the sap flux density in the rest of the inner sapwood. Sap flow for the whole tree, Q, was integrated as follows:

$$Q = v_3 \cdot A_{s,3} + v_{11} \cdot A_{s,11} + v_{19} \cdot A_{s,19} + v_{27} \cdot A_{s,27} + v_{35} \cdot A_{s,35} + v_{35} \cdot A_{s,in} \tag{4}$$

Where v_i is sap flux density at each depth, $A_{s,i}$ is the corresponding annulus area with $A_{s,in}$ representing the conducting area beyond the influence of the last measuring point (deeper than 39 mm).

Analysis of diurnal variation in measured radial patterns of sap flow

The difference between outer flow, Q_o (represented by measuring points at 3 and 11 mm, i.e. the first 15 mm of sapwood) and inner flow Q_i (the remaining conductive sapwood) was normalized by total stem sap flow and expressed as a percentage (Q_{diff}), to investigate the diurnal variations in the radial profile of sap flow

$$Q_{diff} = \frac{Q_o - Q_i}{Q} \cdot 100 \tag{5}$$

We calculated a reference sap flux density (v_{ref}) in the outer 10 mm of sapwood from the weighted average of the two shallower junctions of the HFD sensor (3 and 11 mm inside cambium). According to the measuring length around each point (4 mm), the measuring point at 3 mm would be representative of the first 7 mm and the junction at 11 mm would account for the remaining 3 mm to cover the entire length of the Granier probe. Therefore we applied a 0.7 weighting factor for v_3 and a 0.3 weight for v_{11} to obtain the average flux density, and sap flux density obtained by the HD sensors (v_{HD}) could be equivalent to the weighted-average sap flow in the outer sapwood from HFD measurements (v_{ref}). We could only compare simultaneous values of v_{ref} and v_{HD} for two

trees throughout the measuring period due to malfunctioning or erroneous readings from the Granier probes.

To account for the particular sap flux density profile in each tree, we related sap flux density (v_i) in the five measuring points to v_{ref}, obtaining a radial correction coefficient for each depth, $C_{rad,i,}$ in which the subscript i indicates the corresponding depth in mm,

$$C_{rad,i} = \frac{v_i}{v_{ref}} \qquad (6)$$

which can be used to obtain an estimation of sap flow density at different depths ($v_{rad,,i}$) when only single-point HD measurements are available:

$$v_{rad,i} = C_{rad,i} \cdot v_{HD} \qquad (7)$$

Finally, integration of whole-tree sap flow was then done as in Equation (4), but replacing v_i for $v_{rad,i}$.

Stand transpiration

After correcting for sapwood area and radial variation of sap flow, the ratio between corrected sap flow on a sapwood area basis and sap flux density from Granier's equation was calculated for each tree. We then used this ratio as a coefficient (C) which accounted for the radial variation of sap flow and was applied directly to the sap flux density estimates from Granier sensors. Stand transpiration (E_c) for the 2003 and 2004 growing seasons was calculated assigning a different sap flow density to each diametric class (5 cm increment), obtained from the averaging of all the trees measured within that class. Transpiration of each class relative to total stand transpiration, calculated during periods with all diametric classes being measured, was used to fill the gaps whenever a diametric class was missing (i.e. due to sensor failure). Finally, stand transpiration was compared to the previous estimate without the corrections presented in this study (Poyatos et al. 2005) and to reference evapotranspiration (ET_0) obtained by the Penman-Monteith equation (Monteith 1965) with fixed surface resistance (Allen et al. 1998). To complete the data sets for missing values of E_c due to complete failure of sap flow sensors (one missing day in 2003 and two in 2004), we averaged the relative transpiration (E_c/ET_0) of the previous and following day and applied it to measured values of ET_0

Results

Meteorology during the measurement period

Meteorological conditions during the measurement period were mild (Table 1), compared to the extreme summer drought of the year 2003 (Poyatos et al. 2005). Although soil moisture in the first 30 cm of the soil reached 0.22 cm^3 cm^{-3}, which meant an equivalent in soil moisture deficit (SMD, Granier and Loustau, (1994)) of *ca.* 0.85, θ in the deeper horizons (30-50 cm) was always below (SMD less than 0.40).

Tree-to-tree variations in radial patterns

Sap flux densities were considerably higher in the outer xylem of *Q.pubescens* trees. Maximum v was 0.069 mm s^{-1} and 0.036 mm s^{-1} at the measurement points located 3 and 11 mm beyond cambium. The two innermost points, at 27 and 35 mm depth showed maximum values of v of 0.010 mm s^{-1}, and v at the depth of 19 mm showed peaked at 0.019 mm s^{-1}.

Radial patterns showed a great variability among trees (Figure 1), with sap flow peaks preferably recorded in the outer measuring point (Figure 1b, e, f, i) or the 11 mm deep point (Figure 1c, d, g, h, j). Only for tree 1, the smallest one, did sap flow peak at 19 mm depth (Figure 1a). The rate of decline in sap flux density with depth also varied, from steep declines (Figure 1b, e, f, i) to more gradual decreases (Figure 1d, g, h, j). In one case (Figure 1c), the pattern was comparatively flat and the sap flux density at a depth of 40 mm was still 40-60% of the maximum.

Estimation of sapwood depth

Sapwood depths of pubescent oak trees obtained from extrapolation of radial patterns of sap flow measured at midday (Table 2), as exemplified in Figure 2, spanned from 35 to 49 mm (20-65% of total xylem radius beginning from cambium), showing an increasing trend with DBH better described by a power relationship ($P = 0.040$). A power function between basal (A_b) and sapwood area (A_s) of each tree was also established ($A_s = 4.16*A_b^{0.66}$, $N = 10$, $P = 0.000$), which was be used to upscale tree-level sap flow to stand transpiration. Sapwood areas obtained with radial patterns of sap flow were 1.5-2 times larger than those estimated after visual inspection of wood cores in the field (Table 2). Obviously, the ratio between sapwood and ground area for the stand ($A_S:A_G$) is almost doubled using the new allometric relationship instead of the one in Poyatos et al (2005) between A_b and A_s (Table 2).
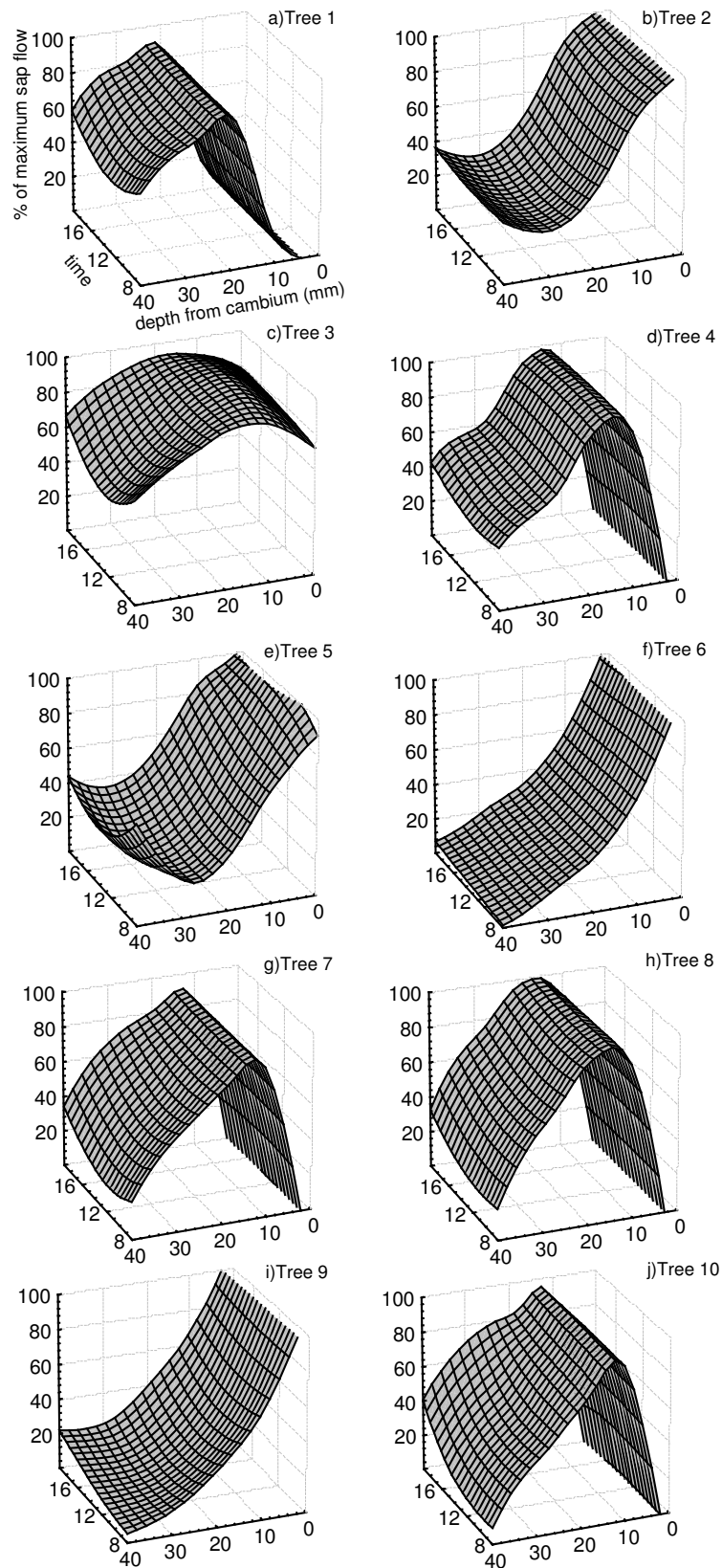
Figure 1. Diurnal variation (8:00-20:00 solar time) of representative radial patterns of sap flow in *Quercus pubescens*. The graphs show the fitted surface (distance-weighted least squares) to 15-min data throughout the entire measurement period for each tree (Table 1). Tree order as in Table 1.
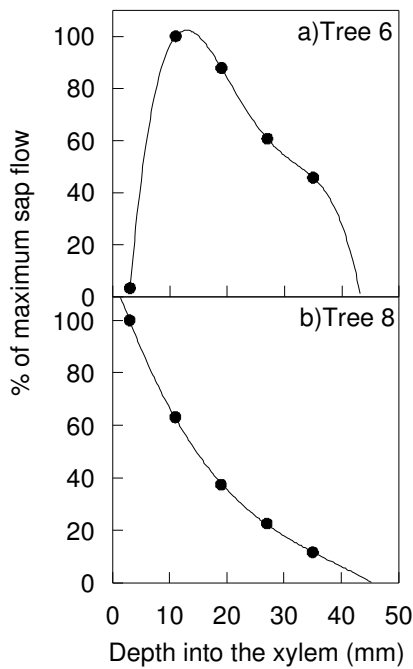
Figure 2. Two examples of sapwood depth estimation in two *Quercus pubescens* trees from radial patterns of sap flow. Black dots are HFD sap flux density measurements and lines are polynomial fits, used to extrapolate the point of zero flow.

Table 2. Sapwood areas obtained from visual field estimations and from radial patterns of sap flow for *Quercus pubescens* trees in the Cal Barrol plot, showing also the ratio between sapwood and ground area for the stand (A_S:A_G). The whole-tree radial correction coefficients (*C*) are also shown (see text for details).

Tree	Sapwood area (cm^2)		Ratio visual:radial pattern	*C*
	Visual estimation	Radial pattern of sap flow		
1	48	94	1.96	1.28
2	84	159	1.89	0.58
3	108	223	2.06	0.87
4	110	209	1.90	0.64
5	113	215	1.90	0.51
6	161	285	1.77	0.49
7	156	278	1.78	0.56
8	243	391	1.61	0.94
9	286	441	1.54	0.45
10 [a]	-	590	-	-
	A_S:A_G (m^2 ha^{-1})		Mean ± SE	
	9.7	17.3	1.82 ± 0.06	0.70 ± 0.09

[a] This tree was not monitored with HD sensors but its radial pattern and sapwood area were measured to cover a wider range of tree sizes.

Diurnal variations in radial patterns of sap flow

Diurnal variation was also observed on radial profiles of sap flow. Sap flux density in the inner xylem, expressed as a percentage of its maximum, was generally higher during the afternoon (Figure 1). This trend, which could be inferred by the upwards folding of the fitted surface, especially between 16:00 and 20:00 solar time, was observed for most, but

not all of the trees (Figure 1). In the outer xylem, sap flux density relative to its maximum value did not vary much along the day (Figure 1).

The normalized difference between outer and inner sap flow (Q_{diff}) was rather stable during the central part of the day, particularly in some cases (Figure 3b, d, j). Most of the trees, though, showed a slightly decreasing trend during the course of the day (Figure 3f, g, h) and others presented a steeper decline in Q_{diff} from 16:00 onwards (Figure 3c, e, i). For trees with a very pronounced peak profile (Figure 1a, e, f), the absolute contribution to total flow of the more internal sapwood was greater than the flow in the outer xylem (negative Q_{diff}) during most part of the day.

In general, Q_{diff} was positively correlated with D and R_n and negatively correlated with time of day (Table 3) for all the trees except for the largest one (tree 10). Some significant correlations were found between Q_{diff} and θ, but a consistent pattern did not emerge.
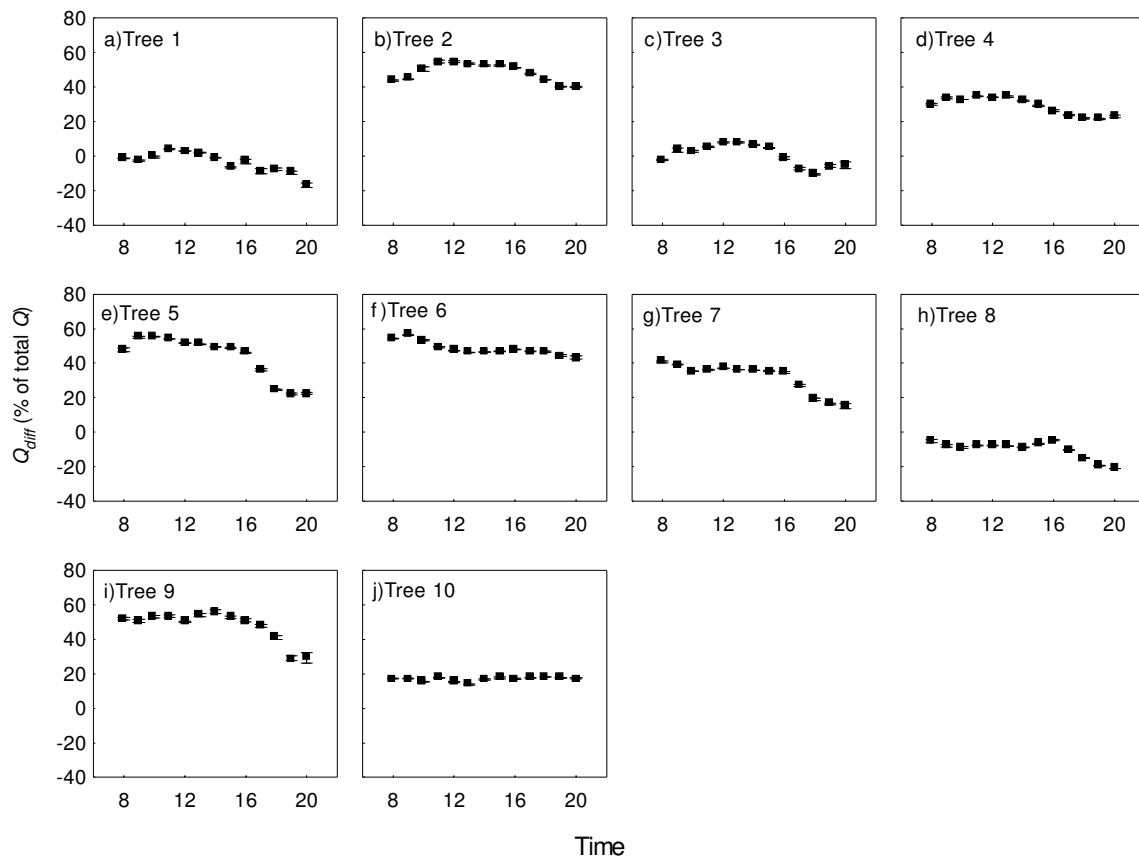

Figure 3. Diurnal variation of the difference between outer and inner sapwood sap flow normalized by total sap flow (Q_{diff}), in eight *Quercus pubescens* trees. Each point is the mean (±SE) of measurements taken within each hourly time step.

Finally, comparing the diurnal evolution of Q_{diff} with the magnitude of total stem flow, a clockwise hysteresis pattern could be observed for most trees, which showed that, for a

given rate of total flow, the relative contribution of the outer xylem was higher during the morning (Figure 4).
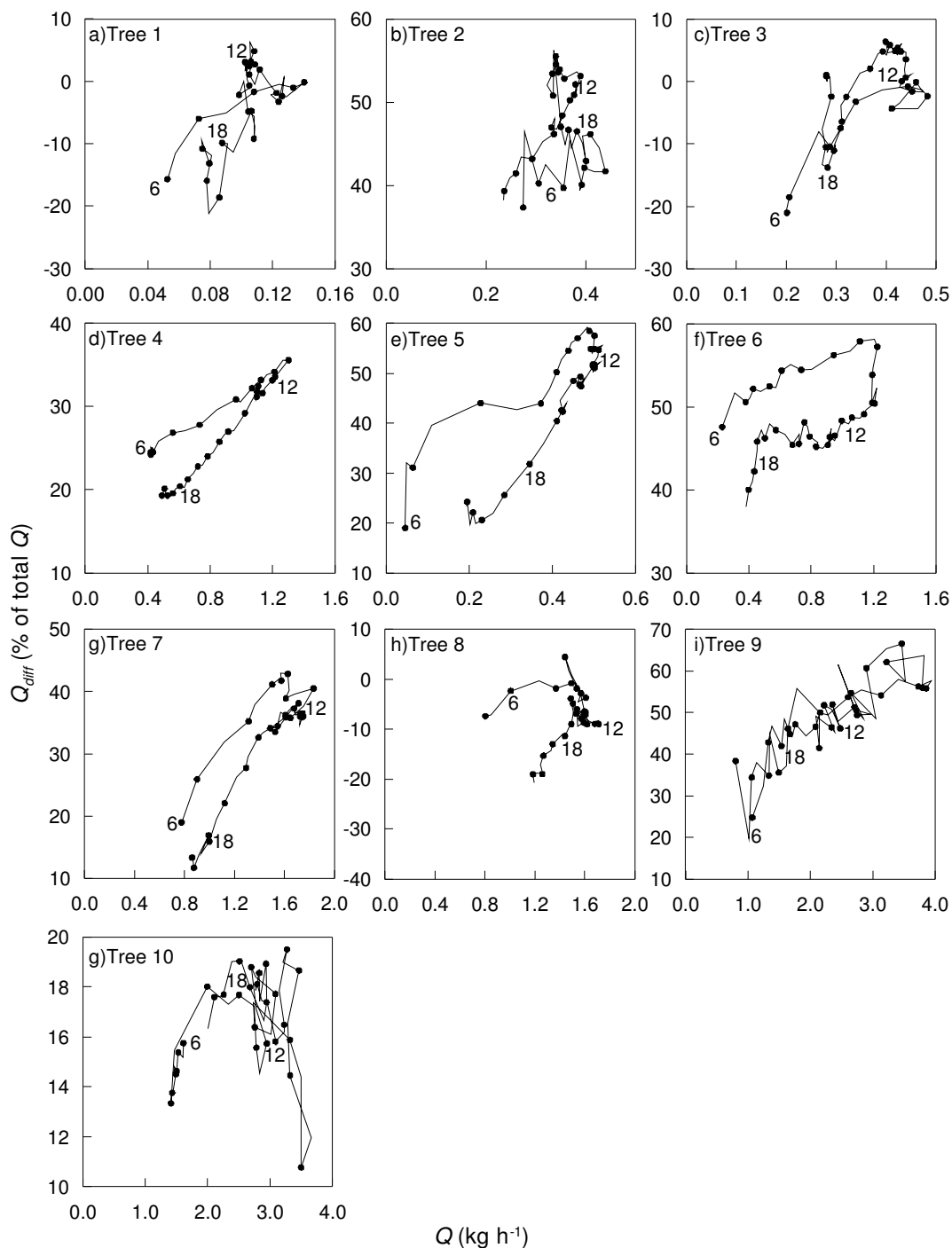

Figure 4. Difference between outer and inner sapwood sap flow normalized by total sap flow (Q_{diff}) as a function of total stem flow (Q) and time. Lines show 15-min data with data points drawn every 30-min. Numbers in the plots indicate solar time.

Table 3. Correlation coefficients between Q_{diff} (the difference between outer and inner sap flow normalised by total flow) and vapour pressure deficit (D), net radiation (R_n), soil moisture (θ) and solar time. Statistical significance at the 0.05 and 0.01 levels are marked by underlined and bold numbers, respectively.

Tree	D	R_n	θ	Time
1	**0.827**	**0.621**	**-0.674**	**-0.564**
2	**0.213**	**0.471**	0.093 [ns]	-0.154
3	**0.796**	**0.657**	**-0.380**	**-0.456**
4	**0.536**	**0.849**	0.177 [ns]	**-0.632**
5	**0.263**	**0.398**	-0.061 [ns]	**-0.444**
6	0.056 [ns]	**0.547**	0.124 [ns]	**-0.796**
7	**0.652**	**0.683**	0.171 [ns]	**-0.822**
8	0.071 [ns]	**0.438**	**0.675**	**-0.594**
9	**0.345**	**0.627**	**-0.306**	**-0.547**
10	**-0.372**	**-0.267**	-0.020 [ns]	0.068 [ns]

Radial correction coefficients

In the two cases (trees 5 and 9, Figure 5) that we could compare sap flux density in the outer 10 mm of sapwood as measured by the Granier probe (v_{HD}) and that estimated from v_3 and v_{11} (v_{ref}), very different results were obtained. Whereas for the first tree both values were rather similar (Figure 5c), for the second one, v_{HD} and v_{ref} differed greatly in daily dynamics and absolute value (Figure 5d). These differences were most important under higher D conditions (Figure 5b, d). For tree 9, v_{HD} was more similar to v_{11} than to the weighted average v_{ref} (Figure 5d).
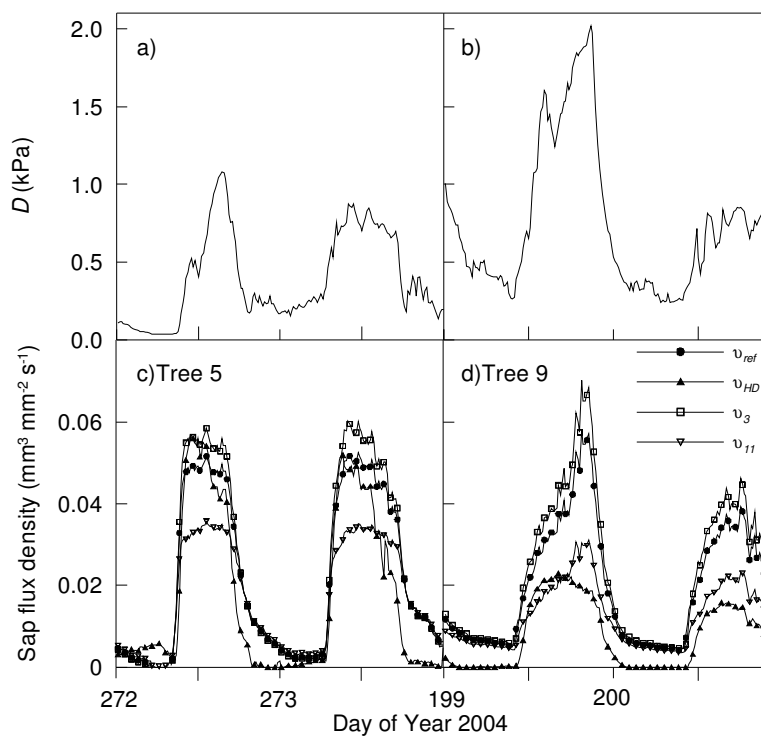

Figure 5. Sap flux density measured at 3 and 11 mm beyond cambium (v_3 and v_{11}, respectively), compared to the values of reference sap flux density (v_{ref}, estimated as a weighted average of v_3 and v_{11}, see text for details) and sap flux density obtained by the HD probes (v_{HD}).

As the radial patterns of sap flow were rather stable during the period of the day when most of sap flow occured (Figure 3), we used an average value of the radial correction coefficients ($C_{rad,i}$) under ample radiation conditions ($R_n > 200$ Wm^{-2}) to carry the corrections on sap flux density from Granier probes. These coefficients were lower and more variable with increasing depth (Figure 6).
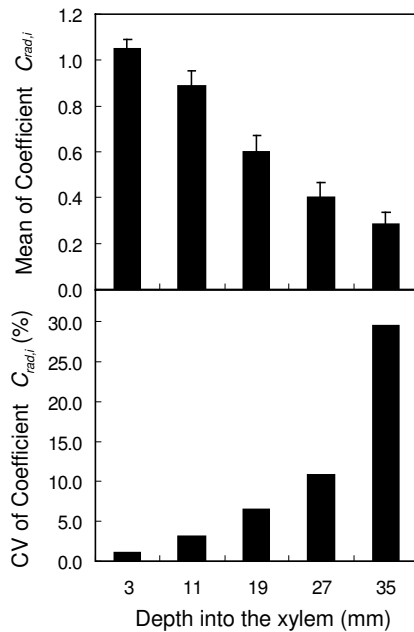

Figure 6. Mean (±SE) and coefficient of variation (CV) of sap flux density correction coefficients ($C_{rad,i}$) at different depths within the xylem.

Sap flow was then calculated with the A_s obtained from radial patterns (Table 1) and applying the coefficients $C_{rad,i}$. In two of the trees equipped with Granier probes, radial patterns were not measured and the mean value for all trees, except tree 1, which showed a very different pattern (Figure 1b), was used instead. The correction yielded different results depending on the shape of the radial profile. Radially corrected sap flow could be lower (Figure 7a) similar (Figure 7b) or higher (Figure 7c) than the original uncorrected values. These situations could be respectively related to three different radial patterns of sap flow: a steep decline of sap flow with depth (Figure 1i), a gradually decreasing one (Figure 1b), and lastly a rather flat profile (Figure 1h). Not accounting for radial variation of sap flow led to inflated sap flow estimates (Figure 7).

Figure 7. Two diurnal courses of stem sap flow rates (*Q*) calculated with raw HD data and visually estimated sapwood (closed circles), from raw HD measurements and sapwood areas obtained from radial patterns (crosses), and HD data corrected according to radial variation of sap flow and sapwood obtained from radial patterns (open circles). Data for three trees are shown.
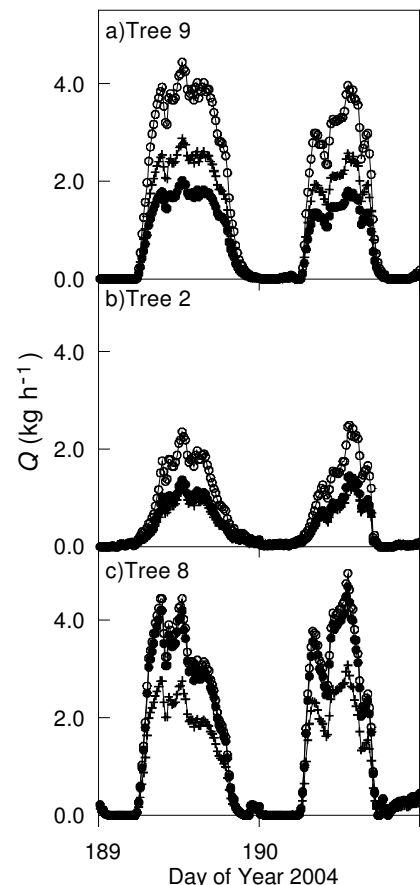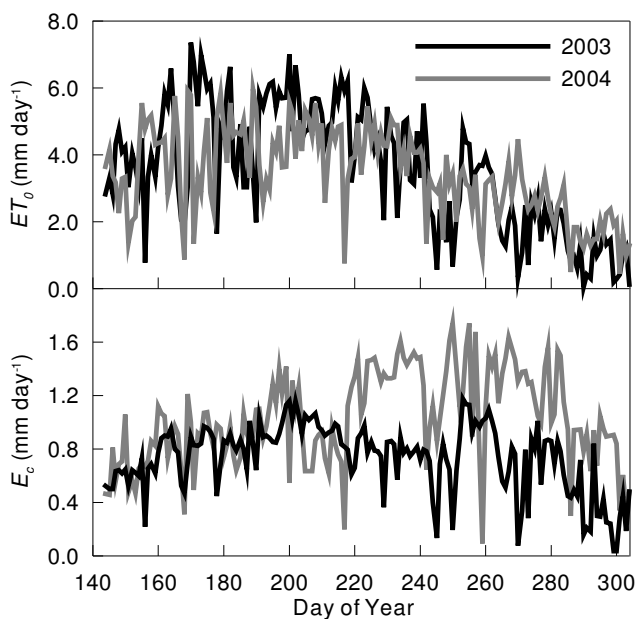
We assessed the effects on daily transpiration of assuming an average coefficient for daytime conditions by comparing the use of the average daytime coefficients as described in the paragraphs above, or the actual coefficients obtained when concurrent measurements of HD sap flow and radial patterns were available. At the 15-min time scale, the use of a daytime-averaged coefficient introduced errors of ca.+/-20%, but the overall impact on daily transpiration was low (2-4%).

Relating corrected values of sap flow on a sapwood area basis to raw data from HD sensors, a whole-tree correction coefficient to account for radial variation of sap flow within the stem (*C*) was obtained (Table 2), but we did not find a significant correlation between the value of *C* and DBH (P=0.25).

Stand transpiration

We applied the coefficients *C* to the single-point measurements with Granier sensors for the years 2003 and 2004 (Figure 8). Results from two growing seasons showed that canopy transpiration was 20-30% of reference evapotranspiration in the studied oak stand (Table 4). Considerable differences in E_c between years were observed during the last part of the summer (Figure 8).

Figure 8. Seasonal evolution of (a) reference evapotranspiration (ET_0) and (b) canopy transpiration (E_c) in the studied pubescent oak stand during two growing seasons (days 144-304, years 2003 and 2004).

Neglecting radial pattern coefficients and using visually determined sapwood areas resulted in estimates of E_c that were 75% lower than the corrected value for 2004, but no significant difference between corrected and uncorrected values was found for the year 2003 (Table 4).

Table 4. Canopy transpiration (E_c) and reference evapotranspiration (ET_0) for representative periods of 2003 and 2004 growing seasons (days 144-304). Uncorrected transpiration is calculated with visually estimated sapwood and without accounting for radial variation of sap flow. All values are in mm per growing season.

Year	Precipitation	ET_0	E_c (uncorrected)	E_c (corrected)	E_c/ET_0
2003	363.4	584.7	115.2	118.2	0.20
2004	483.3	553.5	131.3	164.1	0.30

Discussion

Radial patterns of sap flow in ring-porous oaks

Sap flow in ring-porous trees takes place predominantly in the outer xylem because earlywood vessels, much more efficient in water transport, are only functional in the outermost growth ring (Ellmore and Ewers 1986). However, flow can also occur in latewood vessels of older rings (Aloni et al. 1997). Our results on pubescent oak point at a significant contribution from deeper xylem layers (Figures 1, 3) as previously reported for this species (Čermák and Nadezhdina 1998) and other ring-porous deciduous oaks (Čermák et al. 1992; Granier et al. 1994). Indeed, we have found that up to 60% of the total flow can occur in the inner xylem (defined in this study as the portion of sapwood deeper than 15 mm from cambium), when Granier et al. (1994) found that up to 30% of the total flow occured from 11 mm inwards in a *Quercus petraea* (Matt) Liebl tree. The maximum values of sap flux density across the first 11 mm of sapwood in the former study (0.065 mm s^{-1}) are comparable to the maximum values of sap flux density we recorded in the shallowest measuring point (0.069 mm s^{-1}).

The inner xylem in ring-porous oaks may act as an hydraulic backup system when a disruption in the functionality of the current year earlywood vessels occurs (Granier et al. 1994). This could explain the significant contribution from deeper latewood vessels if drought-induced embolism takes place in the outer xylem. Measurements of hydraulic conductance in the same species and growing in a similar climate show that from July to November a 40% of total hydraulic conductance is lost due to drought-induced embolism (Nardini and Pitt 1999).

Sap flux density in a given point within the xylem depends on specific conductivity of the sapwood, the leaf area attached hydraulically to that portion of sapwood and the rate at which it is transpiring (Spicer and Gartner 2001). In deciduous species, there is no direct connection between leaves and inner, older xylem (Gartner and Meinzer 2005), therefore to explain the significant flow in this portion of the sapwood, water transport in the radial direction must take place. Earlywood vessels of the ring-porous *Fraxinus lanuginosa*

Koidz., have been recently shown to be efficiently connected through bordered pits with the latewood vessels of the previous growth ring (Kitin et al. 2004), confirming the existence of a pathway for radial movement of sap. Other recent findings also suggest that radial gradients of water potential may also play a role in determining the spatial patterns in stem water transport (Domec et al. 2006; James et al. 2003). Combining radial sap flow measurements and sapwood conductivity profiles (Spicer and Gartner 2001) in ring-porous species as recently done for a radial-porous evergreen oak (Hirose et al. 2005), should provide a better insight on the ultimate causes of radial variations in sap flow.

Estimation of sapwood depths from radial patterns of sap flow

Delimitation of sapwood depth using radial profiles of sap flow (Figure 1) is recommended for ring-porous species (Čermák and Nadezhdina 1998), in which wood relative water content may not be indicative of the true hydroactive xylem area (Gartner and Meinzer 2005). Nadezhdina et al. (2002) found that sapwood depths identified with radial patterns of sap flow corresponded well with the limit estimated by changes in xylem colour, but no ring-porous species were represented in this study. Visual identification of sapwood significantly underestimated the amount of hydroactive xylem area in a previous study, leading to very low sapwood areas (Poyatos et al. 2005). However, the resulting relationship we obtained in the present study between tree basal area and sapwood area is comparable to the one recently found in a *Quercus petraea* stand in montane areas of Central Spain under similar climatic conditions (Aranda et al. 2005).

Diurnal and tree-to-tree variations in radial patterns of sap flow

The general shape of the radial patterns showed in this study was similar to previous observations on the same species (Čermák and Nadezhdina 1998; Čermák et al. 1998), but the observed tree-to-tree variability suggests that other factors may have influenced the radial pattern of sap flow in trees. First, sap flow can also vary azimuthally around the trunk and we only measured the radial variation in one location (Loustau et al. 1998); however, radial patterns of sap flux density in *Quercus robur* L. showed little circumferential variation (Čermák et al. 1992). Second, radial pattern measurements were not taken concurrently in all the trees and therefore, variability in the shape of sap flux density within the trunk may have changed seasonally due to soil moisture or atmospheric conditions (Nadezhdina et al. 2002; Phillips et al. 1996). Finally, unrepaired

embolisms during the season may have changed the spatial patterns of xylem conductivity, affecting in turn, the radial profile of sap flow (Ford et al. 2004b). The information on factors influencing spatial variation of sap flow in ring-porous species is still relatively scarce.

The radial profile of sap flow varies diurnally in pubescent oak. There is increasing evidence of this fact for conifers and diffuse-porous species (Ford et al. 2004a; Ford et al. 2004b; Nadezhdina et al. 2002), but, to our knowledge, diurnal changes in radial patterns of sap flow in ring-porous trees are still poorly documented. There is proportionally more contribution from outer xylem, as defined in our study, to total stem flow during conditions of high evaporative demand. Recent findings in several *Pinus* species suggest that conditions of high evaporative forcing are responsible for the mobilization of water in the inner sapwood of pines (Ford et al. 2004b). Our results are thus more consistent with those showing that radial patterns of sap flow become sharper towards cambium with increasing evaporative demand (Nadezhdina et al. 2002). This pattern has been related to hydraulic connections between outer xylem and sun-exposed foliage (Jiménez et al. 2000; Nadezhdina et al. 2002). Studies on the connectivity between leaves and xylem in ring-porous species, as done for gymnosperms (Maton and Gartner 2005), should confirm this hypothesis.

The occurrence of drought-induced embolisms in earlywood vessels under conditions of high evaporative demand, would neither explain the observed pattern in this study, but the opposite (Granier et al. 1994). Embolism production and repair are increasingly regarded as highly dynamic processes even at the diurnal time scale (Clearwater and Goldstein 2005), and should therefore play a role in determining the spatial distribution of sap flux density. Finally, the increase in the relative contribution to total sap flow by the inner sapwood during the afternoon, could also be related to the refilling of sapwood tissue.

Radial correction coefficients

We shown that a weighted average of sap flux density of the two shallowest measurement points of the HFD sensor showed different relationships with average sap flux density measured by HD probes in two different trees. Large gradients in sap flux density along the probe length pose serious difficulties to estimate its average value by HD sensors (Clearwater et al. 1999). In addition, errors due to the unavoidable inaccuracies in the positioning of sensors may have lead to these discrepancies, which are more critical when steep gradients of sap flux density are present (Nadezhdina et al. 2002). As HD and HFD probes were place some centimeters apart, azimuthal variability of

sap flow could have also been responsible for this lack of correspondence between sensors.

A number of works have used similar approaches to correct single-point sap flow measurements according to radial variation of sap flow (Delzon et al. 2004; Köstner et al. 1996; Wullschleger and King 2000; Zang et al. 1996). In this study, whole-tree correction coefficients were applied directly to outer xylem sap flux density obtained by Granier probes in the first 10 mm of sapwood. However, we could not find a relationship between whole-tree coefficients and DBH or other biometric parameter as done in other studies (Delzon et al. 2004).

In the light of the significant variability observed among trees, it would have been difficult to generalize the observed radial patterns using a single equation with easily interpretable parameters. This has been previously done for conifers using a Gaussian-like curve (Ford et al. 2004b) or for a *Fagus* species using a Weibull function (Kubota et al. 2005). Double-Gaussian curves (Nadezhdina et al. 2002) may describe the variability in radial profiles shown in this work and therefore could be employed, but more measuring points along the xylem would be necessary to fit these curves.

Stand transpiration

Correcting for radial variation of sap flow and sapwood depths, estimates of stand transpiration were up to 25% higher than the results obtained using visually determined sapwood and assuming a uniform distribution of sap flux density along the sapwood (Poyatos et al. 2005). Corrected values of E_c showed that growing season E_c normalised by stand basal area was 3.6 and 5.1 m^3 m^{-2} basal area for 2003 and 2004 respectively, lower than the values found in a similar forest of the same species in Italy (*ca.* 7 m^3 m^{-2} basal area per growing season) (Čermák et al. 1998). In *Quercus robur* stands of different densities, growing season E_c divided by stand basal area was between 2.1 and 5.8 m^3 m^{-2} basal area, showing high interannual variation (Vincke et al. 2005). The mild meteorological conditions during the summer in 2004 compared to the extremely dry period in 2003 (rainfall was 42% higher in 2004, Table 4), resulted in a parallel increase in E_c (39% higher during 2004). Recent experiments have shown how E_c of a deciduous *Quercus* spp. forest was reduced by 23-32% when rainfall inputs were reduced by 33% (Wullschleger and Hanson 2006).

Although we could not validate our corrected estimates of E_c, we showed that once sapwood depth is accurately known, ignoring radial variation in stem sap flow would lead to significant overestimations of sap flow rates (Figure 7). In a recent study, neglecting the

radial pattern of sap flow was pointed as the cause of previous overestimations of stand transpiration in maritime pine (Delzon and Loustau 2005).

Conclusions

The general shape of the radial patterns of sap flow found in this study agrees with previous findings on the same species, although we observed a higher variability among trees. These differences may be attributable to the interference of azimuthal variability of sap flow due to crown irregularity, or to seasonal variation in radial distribution of sap flow. Sapwood depths estimated by extrapolation of radial patterns were higher than previous estimates by visual inspection, confirming the discrepancies between wood water content based estimates of hydroactive area and true conducting area in ring-porous trees. We did not find a clear correspondence between sap flux density measured by the HD probes and the calculated average using HFD measurements, which may be the result of uncertainties in the averaging of sap flux density by HD probes, azimuthal variation in sap flow or positioning errors when installing the probes.

Sap flow in the inner xylem, relative to total stem flow, tended to be higher during the early morning and late in the day, when evaporative demand is lower. This fact seems to contradict recent findings suggesting that high evaporative demand should mobilize water in the inner xylem in conifers and supports other studies pointing at the relevance of hydraulic connections between more exposed foliage and outer xylem.

Finally, the use of new sapwood areas obtained by radial patterns and the correction of HD sap flux density to account for radial variation, yielded results of stand transpiration which were up to 25% larger than previous uncorrected estimates. Given the high variability in radial patterns found across trees growing in the same plot, the assessment of these patterns in the same trees where long-term measurements are usually carried out, is recommended to scale-up single-point sap flow measurements in ring-porous species.

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