

Radial profiles of sap flow with increasing tree size in maritime pine

SYLVAIN DELZON,^{1,2} MICHEL SARTORE,¹ ANDRÉ GRANIER³ and DENIS LOUSTAU¹

¹ Unité-EPHYSE, INRA, 69 route d'Arcachon, 33612 GAZINET Cedex, France

² Corresponding author (delzon@pierroton.inra.fr)

³ Laboratoire d'Ecologie et Ecophysiologie Forestières, UMR INRA - Université Nancy I, 54280 Champenoux, France

Received December 15, 2003; April 18, 2004; published online September 1, 2004

Summary We investigated the radial variation of sap flow within sapwood below the live crown in relation to tree size in 10-, 32-, 54- and 91-year-old maritime pine stands (*Pinus pinaster* Ait.). Radial variations were determined with two thermal dissipation sensors; one measured sap flux in the outer 20 mm of the xylem (J_{ref}), whereas the other was moved radially across the sapwood in 20-mm increments to measure sap flux at multiple depths (J_i). For all tree sizes, sap flow ratios ($R_i = J_i J_{\text{ref}}^{-1}$) declined with increasing sapwood depth, but the decrease was steeper in trees with large diameters. Correction factors (C) were calculated to extrapolate J_{ref} for an estimate of whole-tree sap flux. A negative linear relationship was established between stem diameter and C , the latter ranging from 0.6 to 1.0. We found that neglecting these radial corrections in 10-, 32-, 54- and 91-year-old trees would lead to overestimation of stand transpiration by 4, 14, 26 and 47%, respectively. Therefore, it is necessary to account for the differential radial profiles of sap flow in relation to tree size when comparing tree transpiration and hydraulic properties among trees differing in size.

Keywords: correction factor, heat dissipation method, *Pinus pinaster*, sap flux, tree size effect.

Introduction

Sap flow measurements are widely used in ecophysiological field studies to estimate tree transpiration and investigate physiological and environmental controls on water use (Köstner et al. 1992, 1998, Swanson 1994, Čermák et al. 1995, Granier et al. 1996a, Granier and Bréda 1996, Oren et al. 1996, 1998, Wullschlegel et al. 1998). Meinzer et al. (2001) proposed that inaccuracies in the scaling up of transpiration to whole-tree and stand levels occur because of uncertainty in the hydroactive xylem area and the radial variation in sap flux, particularly in large trees with thick sapwood (Hatton et al. 1995). Sap flux is not uniform across the sapwood area because conducting properties vary widely during wood aging and therefore with depth in the stem (Miller et al. 1980, Edwards and Booker 1984, Čermák et al. 1992, Granier et al. 1994, Phillips et al. 1996, Jimenez et al. 2000, Nadezhdina et al. 2002). The assumption of a uniform profile of sap flux may therefore lead to a large bias when estimating whole-tree sap

flow from measurements made with a single sensor in the outer part of the xylem sapwood. Most methods for measuring sap flow, including the heat pulse (Swanson 1967, Cohen et al. 1985), stem segment heat balance (Čermák et al. 1984, Cienfiala et al. 1992, Jimenez et al. 1996) and heat dissipation methods (Granier 1985, Loustau et al. 1990, 1994, 1996, Granier and Loustau 1994, Meinzer et al. 2001), sample only a small portion of the radial profile in the sapwood.

Several attempts have been made to assess radial variability in sap flow across the sapwood. One approach involved positioning several sensors at different depths in the sapwood, and applying either the stem segment heat balance method (Čermák et al. 1982, 1992), heat pulse method (Edwards and Booker 1984, Edwards and Warwick 1984, Hatton et al. 1990, Pausch et al. 2000, Wullschlegel and King 2000) or thermal dissipation method (Granier et al. 1994, Phillips et al. 1996, Lu et al. 2000, James et al. 2002). A second approach was to assess the radial pattern of sap flow with a single sensor (Meiresson et al. 1999, Nadezhdina et al. 2002). Alternatively, a single sensor can be placed successively at different depths, an approach that has been applied successfully with the heat pulse methods (Dye et al. 1991, Zang et al. 1996, Wullschlegel and Norby 2001). Several methods have been used to integrate the sap flow values measured at different depths over the sapwood area. Hatton et al. (1990) established a method based on an area-weighted average of sap flux with increasing depth, and further improvements were incorporated by Pausch et al. (2000). Lu et al. (2000) proposed an integrative solution to estimate the whole-tree sap flow from outer sap flow measurements (0–20-mm depth) based on an exponential or linear relationship between sap flow and depth.

Our objectives were: (1) to determine the variation of sap flow along the stem radius of maritime pine trees (*Pinus pinaster* Ait.) by the thermal dissipation method; (2) to examine the size-related change in the radial profile of sap flow; (3) to develop a method for scaling sap flow from single outer measurements to the whole-tree; and (4) to quantify the errors that occur when sap flow is assumed to be uniform with sapwood depth. Our investigation was based on measurements of sap flow in a chronosequence of maritime pine stands located in southwest France. We characterized the variability in the radial profile of sap flow over a wide range of stem diameters.

Materials and methods

Stand description and sapwood measurements

Studies were carried out in four even-aged monospecific maritime pine stands located 20 km southwest of Bordeaux in the "Les Landes de Gascogne" forest in southwestern France. The climate of this region is temperate maritime with cool wet winters and warm dry summers. Mean annual temperature is 13 °C (1950–2000) and mean annual precipitation is 977 mm (1970–2000). The four stands were 10, 32, 54 and 91 years old and the characteristics of the trees in 2001 are shown in Table 1. Diameter 1.3 m above ground was obtained for each tree in the chronosequence from circumference measurements. Plant area index was measured with an optical system (DEMON, CSIRO, Canberra, Australia) and tree height (h) was measured with a Haglof hypsometer (Vertex type II, Forestor Instrument AB, Taby, Sweden) on a sample of 100 trees in each stand stratified according to tree basal area.

Diameter under the live crown (d_{LC}) was obtained from circumference measurements on 30 randomly chosen trees per stand. For these trees, we extracted one wood core from each stem, 0.5 m below the live crown, with an increment borer. We then separated the hydroactive part of the xylem (sapwood, which is more translucent) and measured the radii of heartwood and total wood. The cross-sectional sapwood area ($A_{S,LC}$) was calculated as the difference between the total wood and heartwood areas (under bark), assuming that the ratio of heartwood radius/total radius under the bark was equal in all directions.

Sap flow measurements

We used the original design of the thermal dissipation method (Granier 1985, 1987), i.e., a reference sensor comprising a pair of probes of 1.5 mm in diameter and 20 mm in length containing a copper-constantan (Cu-Cn) thermocouple and surrounded by a glass-coated constantan wire. The Cu-Cn thermocouples of the two probes were connected at the Cn lead, so that the voltage measured across the Cu leads represents the temperature difference (ΔT) between the probes. In addition, a new mobile sensor was designed for measuring sap flux at greater sapwood depths. This sensor was identical to the refer-

ence sensor, except that it was located at the end of a 140-mm-long needle. The thermocouple and the glass-coated constantan wire were inserted inside the needle to its tip. The probes were installed in the stem in previously inserted aluminium tubes, vertically separated at 130 mm. The upper probe was heated continuously with a constant power of 0.140 A, whereas the lower probe was unheated and measured wood temperature. Sensors were covered with an aluminum sheet to prevent exposure to rain and direct sunlight. The original equation relating the difference in temperature between probes to sap flux was applied (Granier 1985).

Maritime pine trees do not have continuous functional xylem across the entire radius at the base of the stem. Sap flow measured by thermal dissipation is underestimated when part of the probe does not contact the conducting xylem (Clearwater et al. 1999). Furthermore, maritime pine trees in southwestern France are characterized by large variability in sap flow in relation to azimuth at the stem base, because of the anisotropic distribution of sapwood hydraulic properties. Therefore, all sap flow measurements were performed at the base of the live crown as recommended by Loustau et al. (1998). A cherry picker with a 20-m boom was used to install sensors just below the live crown, and subsequently, access to the probes was obtained with a ladder.

There were two sensors in each tree: the reference sensor, which was at a fixed location in the outer 20 mm of the sapwood, and the mobile sensor, which measured sap flow at different depths along the sapwood radius (Figure 1). The mobile sensor was placed in the stem 1 m below the reference sensor at the same azimuth. Sap flux was measured at different radial depths by moving the two probes of the mobile sensor inward simultaneously in 20-mm increments. The mobile sensor was inserted at three to four depths in the stem of 10-year-old trees (0–20, 20–40, 40–60, 60–80 mm depth) and at five to six depths in larger trees. At each depth, measurements were carried out over 48 or 72 h to allow a correct determination of the maximum temperature gradient when flow was zero. The determination of a complete radial profile lasted 14–21 days depending on tree sapwood thickness.

Radial profiles of sap flow were determined on three trees in the 10-year-old stand and two trees in each of the 32- and

Table 1. Stand characteristics of the maritime pine chronosequence (reference year 2001). Values are means, standard errors are in parenthesis and sample sizes for biometric and radial profile measurements are described in the last two rows of the table. Plant area index was measured with an optical system (DEMON) and does not include the understory. Abbreviation: nd = no data.

Characteristic	Stand age (years)			
	10	32	54	91
Tree height (h ; m)	8.46 (± 0.08)	20.21 (± 0.11)	26.65 (± 0.11)	28.36 (± 0.26)
Diameter at breast height (DBH; m)	0.14 (± 0.0001)	0.30 (± 0.0001)	0.44 (± 0.0003)	0.51 (± 0.0004)
Tree basal area (g ; m ² tree ⁻¹)	0.016 (± 0.0002)	0.072 (± 0.0005)	0.153 (± 0.002)	0.213 (± 0.003)
Density (trees ha ⁻¹)	1180	500	250	155
Stand basal area (G ; m ² ha ⁻¹)	19.23	36.00	38.22	32.96
Plant area index (PAI; m ² plant m ⁻² ground)	3.41	3.04	2.51	1.85
Biometric measurements (trees)	637	1921	485	463
Radial profile measurements (trees)	3	2	2	nd

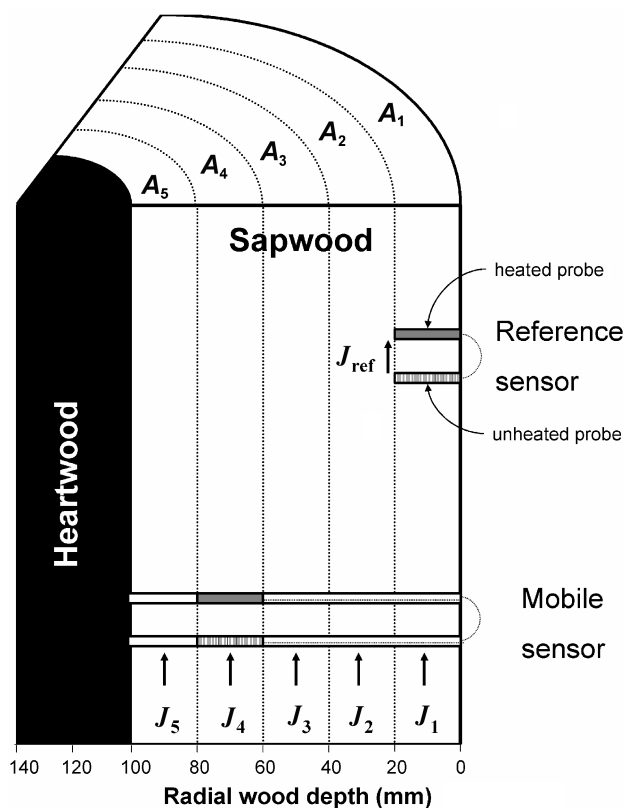


Figure 1. Schematic diagram of the location of the reference and mobile sensors and corresponding sapwood areas (A_{1-5}). The heated and unheated probes of the mobile sensor were moved inward in 20-mm steps at 48-h intervals. Sap flow J_{1-5} corresponds to measurements made by the mobile sensor and J_{ref} to the fixed reference sensor.

54-year-old stands (Table 2) during two measurement periods, September–October 2001 and September–November 2002. We compared radial profiles at two azimuths (east and north) in the same stem section of the largest 54-year-old tree. To avoid thermal interactions between adjacent sensors, sap flow was measured successively on each side. Data were taken every 10 s and 30-min averages were stored with a Campbell CR21X data logger and AM416 multiplexer (Campbell Scientific, Logan, UT). At the end of the experiment, wood cores

were extracted from the bark to the center of each stem and sapwood, and heartwood thicknesses were measured.

Local micrometeorological conditions were measured at the top of the canopy in each stand and soil volumetric water content was measured by both time domain reflectometry (TDR) and frequency domain reflectometry (FDR) techniques at four locations in each stand (for details, see Delzon et al. 2004). Maximum values of vapor pressure deficit (D_{max}) and photosynthetically active radiation (PAR) were about 2652 and 2183 Pa and 1319 and 1287 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in September–October 2001 and October–November 2002, respectively. All measurements were carried out under conditions of non-limiting soil water availability (soil water content at 0–0.8 m > 85 kg m^{-2} , corresponding to a soil water deficit of 40% (Granier and Loustau 1994)) to avoid heterogeneous water availability and differences in tree water status.

Water content and density

Relative wood water content (W_c) and wood density (D_w) were determined for 5.2-mm-diameter wood cores extracted just below the live crown from the eastern side of 10 additional trees in the 10-year-old stand, and from opposite sides (east and north) of seven additional trees in the 54-year-old stand. The cores were extracted in the morning and immediately placed in sealed plastic tubes in an ice-chest before transportation to the laboratory where all samples were stored at 4 °C. Dimensions of bark, sapwood and heartwood were determined, and 20-mm-long samples were cut from each core and the lengths and diameters measured with callipers to the nearest 0.01 mm. Fresh mass (M_F) of each sample was measured to the nearest 0.01 mg. Following these measurements, the samples were immersed in distilled water for 72 h to obtain the saturated mass of the wood (M_S). Then, dry mass (M_D) was determined by drying at 80 °C to constant mass. Relative water content (W_c) was calculated as:

$$W_c = \frac{M_F - M_D}{M_S - M_D} \tag{1}$$

Wood density (D_w) was obtained by dividing sample dry mass (M_D) by sample volume (V).

Table 2. Characteristics of the seven trees used for the radial sap flow measurements. Abbreviation: d_{LC} = diameter under the live crown (at measurement height).

Characteristic	10-year-old trees			32-year-old trees		54-year-old trees	
	1	2	3	1	2	1	2
Tree height (h ; m)	9.4	10.4	10.0	20.4	21.3	26.8	30.1
Diameter at breast height (DBH; m)	0.15	0.16	0.20	0.28	0.32	0.42	0.53
Measurement height (m)	1.5	1.5	2.0	12	10	13.5	15.5
d_{LC} (m)	0.14	0.15	0.17	0.15	0.21	0.27	0.34
Sapwood depth (mm)	52	50	74	55	60	82	88
Heartwood radius (mm)	9	11	4	4	19	20	74

Correction factors

To extrapolate sap flux from the fixed reference sensor to the entire sapwood area below the live crown, we calculated a correction coefficient (C) that accounted for both the radial sap flow profile and the area of the sapwood annulus sampled at each depth. First, we calculated the sum of sap flux for both reference ($\sum J_{\text{ref}}$) and mobile ($\sum J_i$) sensors during the measurement period (48 h) at each position. Then, we calculated a sap flux ratio (R_i) at each depth from the ratio of the sum of the sap flux measured by the mobile sensor ($\sum J_i$) to that of the fixed reference sensor ($\sum J_{\text{ref}}$) as:

$$R_i = \frac{\sum_0^{48} J_i}{\sum_0^{48} J_{\text{ref}}} \quad (2)$$

where i is the number of positions measured in the xylem.

Values of R_i were normalized by the value of the sap flow ratio at the first depth (R_1 , 0–20 mm), giving a range of values between 0 and 1. We calculated C from the sap flow ratio multiplied by an area-weighted mean, corresponding to the cross-sectional sapwood area (A_i) sampled at each sensor position, i , divided by the entire cross-conducting area (A) (Figure 1) as:

$$C = \sum_{i=1}^n R_i \left(\frac{A_i}{A} \right) \quad (3)$$

Results and discussion

Relationship between sapwood and tree size

The heartwood radius below the live crown increased with increasing stem diameter and ranged from 0 to 120 mm. Bark thickness varied between 4 and 20 mm and increased as stem diameter increased (data not shown). Conversely, sapwood thickness ranged from 35 to 95 mm, increasing slightly for $d_{\text{LC}} < 0.18$ m (Figure 2a). Moreover, variability in sapwood thickness increased with increasing stem diameter and showed no correlation for $d_{\text{LC}} > 0.18$ m, as has been reported for *Picea abies* (L.) Karst. where large variability in sapwood depth was found among trees of similar diameter (Kravka et al. 1999).

Sapwood area ($A_{\text{S,LC}}$) ranged from 0.005 to 0.08 m² and increased as a power function of d_{LC} , (Figure 2b) according to:

$$A_{\text{S,LC}} = k(d_{\text{LC}}^b) \quad (4)$$

where k and b are coefficients determined by nonlinear regression. This power relationship explained 97% of the observed variation in sapwood area. For the two younger stands, heartwood cross-sectional area was insignificant, whereas in the older stands, it ranged from 0.0015 to 0.042 m², according to stem size.

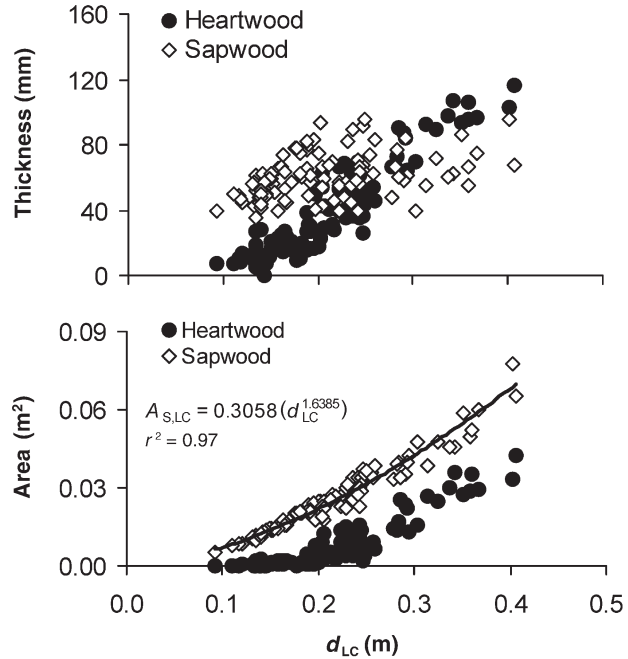


Figure 2. Relationship between stem diameter below the live crown (d_{LC}) and sapwood and heartwood thickness (a) and sapwood ($A_{\text{S,LC}}$) and heartwood area ($A_{\text{E,LC}}$) (b) as measured in a sample of 100 trees across the chronosequence.

Change in the radial profile of sap flow with tree size

In most cases, sap flow measured at different depths was linearly related to the flow measured at the reference location and the intercept was not significantly different from zero, as illustrated in Figure 3. The variance explained by the linear regression (r^2) decreased with depth in the sapwood, similar to the relationship in mango trees (Lu et al. 2000). In a limited number of cases, the relationship showed hysteresis, i.e., the sap flow ratio was not constant throughout the day, especially when sap flow was low in the morning and evening. To account for the time lags, we calculated the sap flow ratio as the sum of 2 or 3 days of measurements at the same depth. However, if the sap flow ratio was calculated only at a given time of day, the estimate of the correction factor may be inaccurate, e.g., when short-term measurements of radial profile were carried out by moving the sensor along the stem radius every 5 min. Nadezhdina et al. (2002) also reported that sap flow ratio changed with time and therefore errors could occur during scaling up to the whole tree when using data obtained from a single sensor in the outer sapwood, even if the radial profile corrections have been applied.

The mean radial profile of the sap flux ratio (R_i) measured on the eastern side of each tree was highly dependent on the depth in the sapwood, i.e., R_i decreased with increasing sapwood depth (Figure 4). Sap flux was higher in the outer part of the xylem for all tree ages, and no decrease at the outermost location of the profile was observed, except for the smallest tree where sap flux was greatest at a depth of 30 mm. Sap flux has often been reported to vary across sapwood, reaching a maxi-

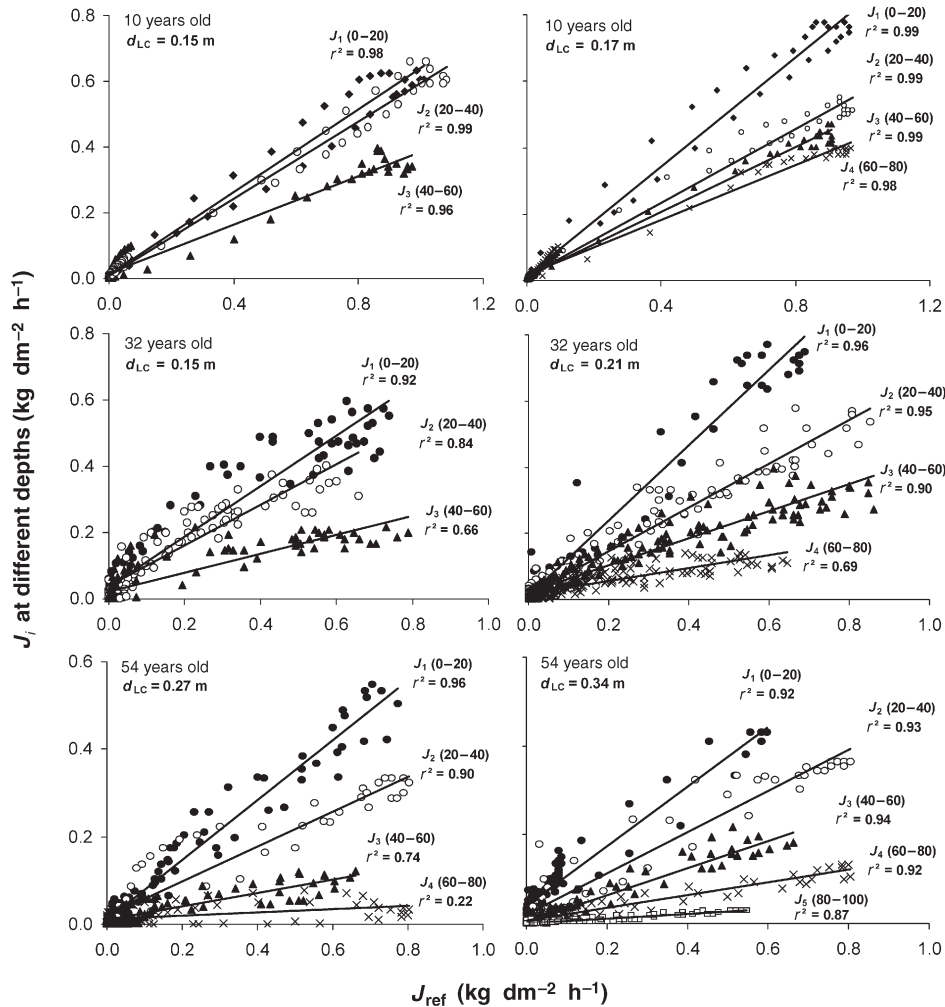


Figure 3. Relationship between half-hourly values of sap flux at various depths (J_i) and in the outer 20 mm (J_{ref} ; reference sensor) (r^2 values of the regressions are indicated on the graph). Each graph represents a full day of measurements.

imum at a depth of 10 to 20 mm from the cambium and decreasing toward the heartwood (Edwards and Booker 1984, Dye et al. 1991, Čermák and Nadezhdina 1998, Lu et al. 2000, Pausch et al. 2000, James et al. 2002, Nadezhdina et al. 2002), or declining along the entire xylem radius (Granier et al. 1994, Becker 1996, Phillips et al. 1996, Schafer et al. 2000, Wullschlegel and King 2000, James et al. 2002). In this study, the probe was too long (20 mm) to detect any change in sap flow properties in the outermost sapwood. This could be examined further by reducing the probe length to 10 mm (James et al. 2002).

Radial profiles of sap flow changed with tree size (Figure 4). For smaller trees (10-year-old), the sap flow ratio at a depth of 20–40 mm (R_2) was close to the value of sap flow ratio of the outermost measurement (R_1), and practically the whole cross-sectional area of xylem was conducting sapwood. The value of R decreased toward the center of the stem, but did not decrease to less than 60% of the value of the outermost measurement. In contrast, for large trees, R decreased dramatically with increasing sapwood depth, falling to 20% of the value of the outermost measurement at the sapwood–heartwood boundary. These results were similar to those of Phillips et al. (1996) for

loblolly pine, where a 59% reduction in the daily sap flux occurred between the outer sapwood and sapwood at a depth of 20–40 mm depth. Similarly, Čermák and Nadezhdina (1998) found that the decline in sap flow with increasing depth in the sapwood was larger for large oak trees than for small oak trees. The sap flow ratio was zero in the heartwood (only in the largest tree) as observed by Čermák et al. (1992), Čermák and Nadezhdina (1998), James et al. (2002) and Nadezhdina et al. (2002). We did not observe zero flow in smaller trees because the heartwood was absent or negligible and so the measuring part of the probe was never fully inside the heartwood. It is noteworthy that we could not demonstrate a relationship between the shape of the radial profile of sap flow and the number of annual rings.

Azimuth variability

Radial profiles of sap flow were measured below the live crown on two sides of the stem of the largest tree. For both the east and north azimuths, the sap flow ratio showed a similar pattern with increasing depth in the sapwood (Figure 4, bottom panel, filled diamonds) and the correction factors were similar, $C = 0.614$ (east) and $C = 0.640$ (north). Other studies have

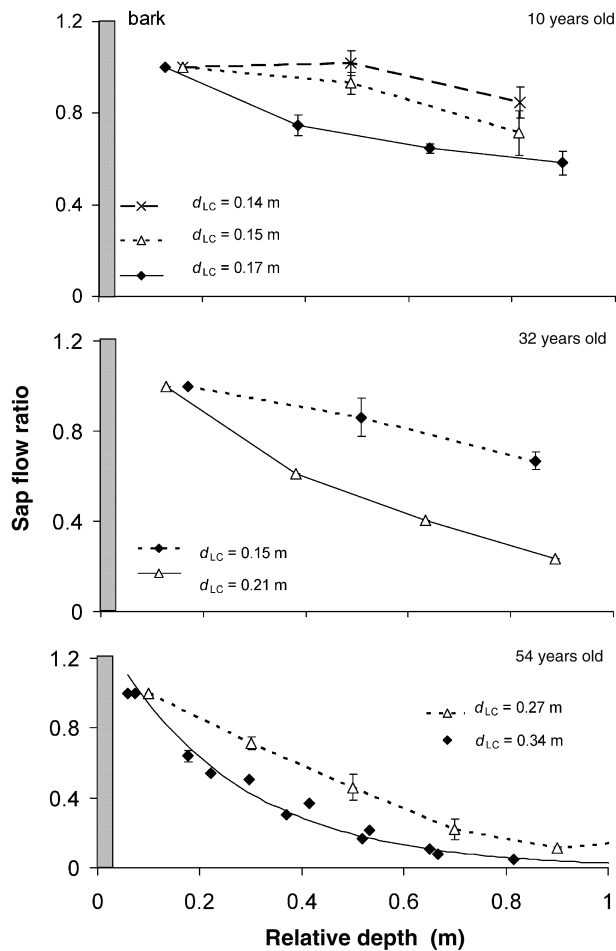


Figure 4. Sap flow ratio measured in the sapwood of each sample tree as a function of depth in the stems and expressed in relation to the relative depth in the xylem from bark to the center of the tree. Values for a given profile were measured on different dates and are means \pm SE ($n = 2-5$). Each profile was measured on the eastern side of each tree, except for the 54-year-old stand, where \blacklozenge = sap flow ratio was measured on opposite sides (east and north) of the stem of the biggest tree. Abbreviation: d_{LC} = diameter below the live crown.

shown that azimuthal variability in radial profiles of sap flow is large at the base of the stem, so several measurements around the stem are required for accurate estimates of whole-tree transpiration (Miller et al. 1980, Lu et al. 2000, James et al. 2002). Nevertheless, Loustau et al. (1998) found low variability of sap flow measured below the live crown with respect to azimuth, in contrast to high variability measured at the base of the stem. Therefore, our results also support the theory that variability in radial profiles of sap flow with respect to azimuth may be neglected when estimating whole-tree sap flow, provided that sap flow measurements are made below the live crown.

Correction factors

Variations in the area-weighted sap flow ratio ($R_i(A_i/A)$) with increasing depth in sapwood for all trees in each stand are

shown in Figure 5. Both the larger area of conducting sapwood and the higher sap flow rate close to the bark explain the greater contribution of the outer xylem to whole-tree sap flux. Conversely, sap flow in the innermost sapwood annuli (greater than 60 mm depth) contributed little to whole-tree sap flux, as observed by Dye et al. (1991), Lu et al. (2000) and James et al. (2002). The outer 20 mm annulus of sapwood accounted for 55, 42 and 53% of the total tree sap flux for the 10-, 32- and 54-year-old stands, respectively. Thus, for all tree size classes, measurement of sap flow ratio across the outer 60 mm of sapwood is sufficient to estimate more than 90% of the whole-tree transpiration.

To extrapolate whole-tree sap flux from continuous sap flow measurements at a single position (0–20-mm depth) below the live crown, C was determined for each tree on several dates (Figure 6). Values of C ranged from 0.6 to 1.0 for the large and small trees, respectively. To apply the correction to tree and stand sap flux estimates, we established a linear regression between C and d_{LC} : $C = -1.7643d_{LC} + 1.1936$, $r^2 = 0.90$. There was no significant relationship between C and sapwood thickness (data not shown). These values of C are similar to those derived by the heat pulse methodology in previous studies. Zang et al. (1996) used movable heat pulse sensors and estimated correction factors between 0.56 and 1.02 for two *Eucalyptus globulus* Labill. trees, but did not report tree diameter or sapwood thickness. Based on experiments by Granier et al. (1996b), Köstner et al. (1996) used a correction factor that depended on sapwood thickness and had a mean value of 0.86. Only Wullschlegel and King (2000) carried out replicates of radial profile measurements of sap flow as in this study. They estimated the fraction of sapwood functional in water transport for 20 yellow-poplar trees and obtained an index similar to our correction factor. Their values varied from 0.49 to 0.96, but they found no clear relationships with sapwood thickness or stem diameter. In yellow-poplar forest stands, stems are cleared of lateral branches up to a considerable height, and so measurements carried out at the base of the crown could have reduced the observed variation in the correction factor and revealed clearer links with tree dimensions.

We calculated the error introduced when ignoring sap flow profile pattern, i.e., assuming a uniform sap flow density along

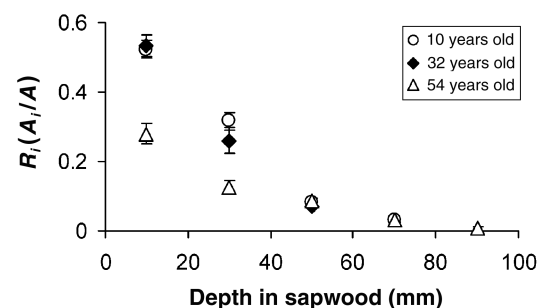


Figure 5. Radial profile of area-weighted sap flow ratio ($R_i(A_i/A)$), with increasing depth in sapwood. Values are means of all trees per stand \pm SE.

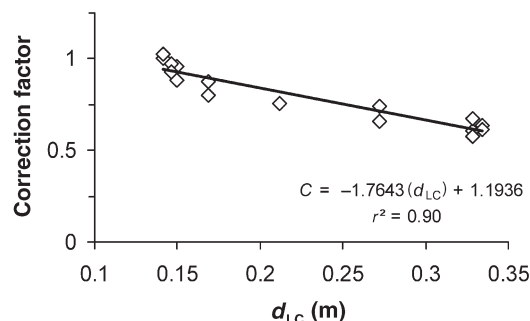


Figure 6. Relationship between the correction factor (C) and diameter measured below the live crown (d_{LC}) for each tree at several dates and azimuthal directions.

the sapwood radius as follows. We used Equation 4 to calculate a weighted sapwood area for each stand from the sum of sapwood areas corrected for C in each tree. We then estimated stand transpiration, multiplying this weighted stand sapwood area by the mean sap flux measured continuously on seven trees per stand. We did not scale using basal area distribution because we found no relationship between sap flux and tree dimensions within each stand (S. Delzon, unpublished data). Neglecting the radial correction in the 10-, 32-, 54- and 91-year-old trees would have led to overestimation of stand transpiration by 4, 14, 26 and 47%, respectively. These overestimates were slightly larger than the values obtained by Irvine et al. (2002) (17% for a 50-year-old *Pinus ponderosa* Dougl. ex Laws. stand). Thus, radial variation in sap flux is an important source of error in the scaling process for trees with wide sapwood. The assumption of a constant radial profile of sap flow (Granier and Loustau 1994, Loustau et al. 1996, Martin et al. 1997) can introduce systematic bias into estimates of both tree and stand water use, particularly in older coniferous stands.

Several replicate measurements were performed on the sample trees on different dates ($n = 2-5$ in 2001 and 2002) and yielded similar values of sap flow ratio (Figure 4) and correction factors (Figure 6). Therefore, even though we did not investigate the entire range of environmental conditions, we concluded that C was unaffected by meteorological changes and this method could replace the use of permanent sensors at multiple sapwood depths. Because measurements were carried out only on maritime pine, we do not know if the correction factor we determined for this species is applicable to other species; however, our method of determining a correction factor is applicable to other species.

Variation of wood properties within the stem

Profiles of wood density with xylem depth in the 10- and 54-year-old stands followed similar patterns (Figure 7a), showing a large decrease with increasing depth in the sapwood (D_w ranged between 500 and 400 kg m⁻³) and low constant values in the heartwood (decreasing from 0 to 50 mm depth for the 10-year-old stand and from 0 and 80 mm depth, but not beyond, for the 54-year-old stand). Values were close to those

previously published for loblolly pine (Megraw 1985), and the decline with radial depth was similar to that observed by Phillips et al. (1996). The decrease in wood density may be attributed to changes in ring width during the tree's life cycle, i.e., larger rings with a lower density occur in the stem center with thinner rings in the outermost part of the sapwood. Moreover, the first 12 growth rings of maritime pine trees counting from the stem center are composed of juvenile wood that has a lower density than adult wood (Dumail and Castera 1997).

Values of relative water content decreased with increasing xylem depth for trees in the 54-year-old stand. In the young stand, relative water content at a depth of 30 mm was higher than at 10 mm and both values were higher than W_c deeper than 50 mm (Figure 7b). For old trees, relative water content in the heartwood did not vary with depth ($W_c = 0.17\%$) and were lower than values for the sapwood (mean $W_c = 0.42\%$). Previous studies also reported a decrease in water content with sapwood depth (Waring and Running 1978, Phillips et al. 1996). Moreover, in coniferous trees, water content is usually lower in heartwood than in sapwood and invariant with diameter class (Bamber and Fukazawa 1985, Kravka et al. 1999). Panshin and Zeeuw (1980) reported that relative water content was less variable in heartwood than in sapwood, and concluded that there is little water movement within the heartwood. It is noteworthy that the profiles of relative water content paralleled the radial profile of sap flow. Čermák and Nadezhdina (1998) also reported that the radial pattern of sap flow was related to xylem water content for two coniferous trees (*Pinus pinea* L. and *Pinus sylvestris* L.), but not for several other species, e.g., poplar. Nevertheless, to our knowledge, no study has yet shown a cause-and-effect relationship between the radial pattern of sap flow and relative water content (Wullschleger and King 2000).

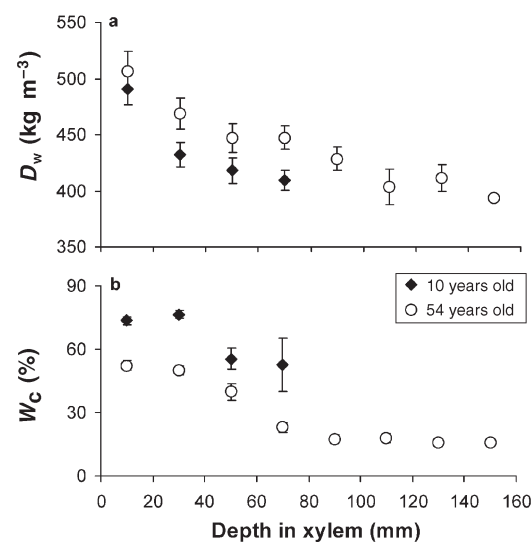


Figure 7. Radial patterns of mean wood density, D_w (a), and relative water content, W_c (b), as a function of radial depth in tree stems of two maritime pine stands aged 10 ($n = 10$) and 54 years ($n = 7$). Bars are standard errors.

The decline in sap flow with radial depth was greater for old (large) trees, even when the change in sapwood thickness with age was small, ranging between 50 and 90 mm. Phillips et al. (1996) and James et al. (2003) showed that the radial profile in sap flow was strongly correlated with the specific conductivity of the xylem. Previously, we found that whole-tree hydraulic conductivity decreases with increasing tree size, and this may explain the greater decline in sapflow with increasing xylem depth in large trees compared with small trees (Delzon et al. 2004). Moreover, Wullschleger and King (2000) speculated that sap flow would decline with increasing sapwood depth, but not because of age-related effects on hydraulic conductivity. They suggested that the old xylem that conducted water to the first branches when the tree was young no longer participates in the transport process to foliage once the older branches have become shaded or died.

Conclusions

We established a simple method for scaling sap flow measurements to estimate sap flux on a sapwood cross-sectional area basis using a correction factor. The value of C (1.0–0.6) was linearly related to stem diameter (142–335 mm) and can be used to predict transpiration in maritime pine over a large range of tree sizes.

We confirmed the need to account for variations in radial profiles of sap flow and showed that ignoring the profile within the sapwood introduces bias into sap flux calculations and thus estimates of transpiration and stand water use. This bias increased with increasing stem diameter from 5% for the young stands to 47% for the oldest stand we measured. Thus, uncorrected single probe measurements cannot be used to estimate sap flux of stands comprising different stem sizes or tree ages.

We used a new sensor based on the heat dissipation technique (located at the tip of a 140-mm-long needle), which was mobile and allowed us to characterize sap flux with increasing depth in sapwood. This enabled us to determine radial profiles based on the ratios of sap flow at different depths (mobile sensor) to the flow at the outermost location (reference sensor located at a depth of 20 mm). We recommend that measurements of radial profile should be integrated over at least one day, if such data are used to scale sap flow from a single location to the whole tree.

Acknowledgments

This work was supported by the EC Environment and Climate Research Programme CARBO-AGE project (contract ENV4-CT97-0577), and the senior author's doctoral fellowship by INRA and the French public institute ADEME. We thank Alexandre Bosc, Annabel Porté and Mark Bakker for multiple discussions and Andy Kowalski and David Whitehead for their help with the English.

References

Bamber, R.K. and K. Fukazawa. 1985. Sapwood and heartwood: a review. *For. Abstr.* 46:567–580.

- Becker, P. 1996. Sap flow in Bornean heath and dipterocarp forest trees during wet and dry periods. *Tree Physiol.* 16:295–299.
- Čermák, J. and N. Nadezhkina. 1998. Sapwood as the scaling parameter—defining according to xylem water content or radial pattern of sap flow? *Ann. For. Sci.* 55:509–521.
- Čermák, J., J. Ulehla, J. Kučera and M. Penka. 1982. Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. *Biol. Plant.* 24: 446–460.
- Čermák, J., J. Jenik, J. Kučera and V. Zidek. 1984. Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. *Oecologia* 64:145–151.
- Čermák, J., E. Cienciala, J. Kučera and J.E. Hallgren. 1992. Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiol.* 10:367–380.
- Čermák, J., E. Cienciala, J. Kučera, A. Lindroth and E. Bednarova. 1995. Individual variation of sap flow rate in large pine and spruce trees and stand transpiration: a pilot study at the central Nopex site. *J. Hydrol.* 168:17–27.
- Cienciala, E., A. Lindroth, J. Čermák, J.E. Hallgren and J. Kučera. 1992. Assessment of transpiration estimates for *Picea abies* trees during a growing season. *Trees* 6:121–127.
- Clearwater, M.J., F.C. Meinzer, J.L. Andrade, G. Goldstein and N.M. Holbrook. 1999. Potential errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree Physiol.* 19:681–687.
- Cohen, Y., F.M. Kelliher and T.A. Black. 1985. Determination of sap flow on Douglas-fir trees using the heat-pulse technique. *Plant Cell Environ.* 4:391–397.
- Delzon, S., M. Sartore, R. Burrell, R. Dewar and D. Loustau. 2004. Hydraulic responses to height growth in maritime pine trees. *Plant Cell Environ.* In press.
- Dumail, J.F. and P. Castera. 1997. Transverse shrinkage in maritime pine juvenile wood. *Wood Sci. Technol.* 31:251–264.
- Dye, P.Y., B.W. Olbrich and A.G. Poulter. 1991. The influence of growth rings in *Pinus patula* on heat pulse velocity and sap flow measurement. *J. Exp. Bot.* 42:867–870.
- Edwards, W.R.N. and R.E. Booker. 1984. Radial variation in the axial conductivity of *Populus* and its significance in heat pulse velocity measurement. *J. Exp. Bot.* 35:551–561.
- Edwards, W.R.N. and N.W.M. Warwick. 1984. Transpiration from a kiwifruit vine as estimated by the heat pulse technique and the Penman-Monteith equation. *N.Z. J. Agric. Res.* 27:537–543.
- Granier, A. 1985. A new method of sap flow measurement in tree stems. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. For. Sci.* 42:193–200.
- Granier, A. 1987. Sap flow measurement in Douglas fir stems using a new thermal method. *Ann. For. Sci.* 44:1–14.
- Granier, A. and N. Bréda. 1996. Modelling canopy conductance and stand transpiration of an oak forest from sap flow measurements. *Ann. For. Sci.* 53:537–546.
- Granier, A. and D. Loustau. 1994. Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71:61–81.
- Granier, A., T. Anfodillo, M. Sabatti, H. Cochard, E. Dreyer, M. Tomasi, R. Valentini and N. Bréda. 1994. Axial and radial water flow in the trunks of oak trees: a quantitative and qualitative analysis. *Tree Physiol.* 14:1383–1396.
- Granier, A., P. Biron, N. Bréda, J.Y. Pontailler and B. Saugier. 1996a. Transpiration of trees and forest stands: short- and long-term monitoring using sapflow methods. *Global Change Biol.* 2:265–274.

- Granier, A., P. Biron, B. Köstner, L.W. Gay and G. Najjar. 1996b. Comparison of xylem sap flow and water-vapour flux at the stand scale and derivation of canopy conductance for Scots pine. *Theor. Appl. Clim.* 53:115–122.
- Hatton, T.J., E.A. Catchpole and R.A. Vertessy. 1990. Integration of sapflow velocity to estimate plant water use. *Tree Physiol.* 6: 201–209.
- Hatton, T.J., S.J. Moore and P.H. Reece. 1995. Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: measurement errors and sampling strategies. *Tree Physiol.* 15:219–227.
- Irvine, J., B.E. Law, P.M. Anthoni and F.C. Meinzer. 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. *Tree Physiol.* 22:189–196.
- James, S.A., M.J. Clearwater, F.C. Meinzer and G. Goldstein. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol.* 22:277–283.
- James, S.A., F.C. Meinzer, G. Goldstein et al. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* 134:37–45.
- Jimenez, M.S., J. Čermák, J. Kučera and D. Morales. 1996. Laurel forests in Tenerife, Canary Islands: the annual course of sap flow in *Laurus* trees and stand. *J. Hydrol.* 183:307–321.
- Jimenez, M.S., N. Nadezhdina, J. Čermák and D. Morales. 2000. Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol.* 20:1149–1156.
- Köstner, B., E.-D. Schulze, F.M. Kelliher et al. 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia* 91:350–359.
- Köstner, B., P. Biron, R. Siegwolf and A. Granier. 1996. Estimates of water vapor flux and canopy conductance of Scots pine at the tree level utilizing different xylem sap flow methods. *Theor. Appl. Clim.* 53:105–113.
- Köstner, B., A. Granier and J. Čermák. 1998. Sapflow measurements in forest stands—methods and uncertainties. *Ann. For. Sci.* 55: 13–27.
- Kravka, M., T. Křezar and J. Čermák. 1999. Water content in stem wood of large pine and spruce trees in natural forests in central Sweden. *Agric. For. Meteorol.* 98/99:555–562.
- Loustau, D., A. Granier and F. El-Hadj Moussa. 1990. Seasonal variations in sap flow in a maritime pine stand. Evolution saisonniere du flux de seve dans un peuplement de pins maritimes. *Ann. For. Sci.* 47:599–618.
- Loustau, D., P. Berbigier, P. Roumagnac, C. Arruda-Pacheco, J.S. David, M.I. Ferreira, J.S. Pereira and R. Tavares. 1996. Transpiration of a 64 year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. *Oecologia* 107:33–42.
- Loustau, D., J.C. Domec and A. Bosc. 1998. Interpreting the variations in xylem sap flux density within the trunk of maritime pine (*Pinus pinaster* Ait.): application of a model for calculating water flows at tree and stand levels. *Ann. For. Sci.* 55:29–46.
- Lu, P., W.J. Muller and E.K. Chacko. 2000. Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. *Tree Physiol.* 20: 683–692.
- Martin, T.A., K.J. Brown, J. Čermák et al. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. *Can. J. For. Res.* 27:797–808.
- Megraw, R.A. 1985. Wood quality factors in loblolly pine. The influence of tree age, position in tree, and cultural practice on wood specific gravity, fiber length, and fibril angle. Tappi Press, Atlanta, GA, 88 p.
- Meinzer, F.C., G. Goldstein and J.L. Andrade. 2001. Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiol.* 21:19–26.
- Meiresonne, L., N. Nadezhdina, J. Čermák, J. Van Slycken and R. Ceulemans. 1999. Transpiration of a poplar stand: model calibration and validation by soil water and sap flow measurements. Modelling of transport processes in soils at various scales in time and space. International Workshop of EurAgEng's Field of Interest on Soil and Water, Leuven, Belgium, pp 406–415.
- Miller, D.R., C.A. Vavrina and T.W. Christensen. 1980. Measurement of sap flow and transpiration in ring-porous oaks using a heat pulse velocity technique. *For. Sci.* 26:485–494.
- Nadezhdina, N., J. Čermák and R. Ceulemans. 2002. Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors. *Tree Physiol.* 22:907–918.
- Oren, R., R. Zimmermann and J. Terborgh. 1996. Transpiration in upper Amazonia floodplain and upland forests in response to drought-breaking rains. *Ecology* 77:968–973.
- Oren, R., N. Phillips, G. Katul, B.E. Ewers and D.E. Pataki. 1998. Scaling xylem sap flux and soil water balance and calculating variance: a method for partitioning water flux in forests. *Ann. For. Sci.* 55:191–216.
- Panshin, A.J. and C.D. Zeeuw. 1980. Textbook of wood technology, 4th Edn. McGraw-Hill Book, New York, 772 p.
- Pausch, R.C., E.E. Grote and T.E. Dawson. 2000. Estimating water use by sugar maple trees: considerations when using heat-pulse methods in trees with deep functional sapwood. *Tree Physiol.* 20: 217–227.
- Phillips, N., R. Oren and R. Zimmermann. 1996. Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant Cell Environ.* 19:983–990.
- Schafer, K.V.R., R. Oren and J.D. Tenhunen. 2000. The effect of tree height on crown level stomatal conductance. *Plant Cell Environ.* 23:365–375.
- Swanson, R.T. 1967. Improving tree transpiration estimates based on heat pulse velocity measurements. *In Proc. 14th IUFRO Congress, Munich, Germany, Vol. 1, Section 10–12, pp 252–263.*
- Swanson, R.H. 1994. Significant historical developments in thermal methods for measuring sap flow in trees. *Agric. For. Meteorol.* 72: 113–132.
- Waring, R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant Cell Environ.* 1:131–140.
- Wullschleger, S.D. and A.W. King. 2000. Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiol.* 20:511–518.
- Wullschleger, S.D. and R.J. Norby. 2001. Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air CO₂ enrichment (FACE). *New Phytol.* 150:489–498.
- Wullschleger, S.D., F.C. Meinzer and R.A. Vertessy. 1998. A review of whole-plant water use studies in trees. *Tree Physiol.* 18: 499–512.
- Zang, D., C.L. Beadle and D.A. White. 1996. Variation of sapflow velocity in *Eucalyptus globulus* with position in sapwood and use of a correction coefficient. *Tree Physiol.* 16:697–703.