

Radial patterns of sap flow in woody stems of dominant and understory species: scaling errors associated with positioning of sensors

NADEZHDA NADEZHINA,^{1,2} JAN ČERMÁK¹ and REINHART CEULEMANS³

¹ Institute of Forest Ecology, Mendel University of Agriculture and Forestry, Zemedelska 3, 61300 Brno, Czech Republic

² Author to whom correspondence should be addressed (nadezdana@mendelu.cz)

³ Department of Biology, University of Antwerpen, UIA, Universiteitsplein 1, B-2610 Wilrijk, Belgium

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Summary We studied sap flow in dominant coniferous (*Pinus sylvestris* L.) and broadleaf (*Populus canescens* L.) species and in understory species (*Prunus serotina* Ehrh. and *Rhododendron ponticum* L.) by the heat field deformation (HFD) method. We attempted to identify possible errors arising during flow integration and scaling from single-point measurements to whole trees. Large systematic errors of –90 to 300% were found when it was assumed that sap flow was uniform over the sapwood depth. Therefore, we recommend that the radial sap flow pattern should be determined first using sensors with multiple measuring points along a stem radius followed by single-point measurements with sensors placed at a predetermined depth. Other significant errors occurred in the scaling procedure even when the sap flow radial pattern was known. These included errors associated with uncertainties in the positioning of sensors beneath the cambium (up to 15% per 1 mm error in estimated xylem depth), and differences in environmental conditions when the radial profile applied for integration was determined over the short term (up to 47% error). High temporal variation in the point-to-area correction factor along the xylem radius used for flow integration is also problematic. Compared with midday measurements, measurements of radial variation of sap flow in the morning and evening of sunny days minimized the influence of temporal variations on the point-to-area correction factor, which was especially pronounced in trees with a highly asymmetric sap flow radial pattern because of differences in functioning of the sapwood xylem layers. Positioning a single-point sensor at a depth with maximum sap flow is advantageous because of the high sensitivity of maximum sap flow to water stress conditions and changes in micro-climate, and because of the lower random errors associated with the positioning of a single-point sensor along the xylem radius.

Keywords: correction factors, integration, multi-point sensor, *Pinus*, *Populus*, potential sapwood, *Prunus*, random errors, *Rhododendron*, sapwood, single-point sensor, spatial variation, systematic errors, temporal variation.

Introduction

Transpiration of large or dominant trees usually comprises the main water balance component in forest hydrology. The measurement of sap flow provides a widely applicable method of estimating forest transpiration (Campbell 1991, Swanson 1994, Čermák 1995, Čermák and Nadezhina 1998a, Köstner et al. 1998, Wullschleger et al. 1998), whether undertaken by means of the heat pulse (Swanson 1967, Cohen et al. 1985), stem segment heat balance (Čermák et al. 1982, 1984, 1998a, Cienciala et al. 1992, Jiménez et al. 1996), heat dissipation (Granier 1985, Loustau et al. 1998, Meinzer et al. 2001) or heat field deformation (Čermák et al. 1998a, Nadezhina and Čermák 1998, Meiresonne et al. 1999, Čermák and Nadezhina 2000) method. Successful application of each of these methods depends on knowledge of the conducting systems of the trees, namely the depth of the sapwood and the radial pattern of sap velocity along the xylem radius. Both sapwood depth and the radial sap flow pattern vary widely among species and individual trees as well as within trees (Whitehead and Jarvis 1981, Čermák et al. 1984, 1992, Čermák and Nadezhina 1998b, Wullschleger et al. 1998). Hatton et al. (1995) concluded that measurement of sap fluxes of individual stems is the greatest potential source of error in estimating stand transpiration, because if large measurement errors occur at the tree level, they are propagated when the data are scaled up to the stand level. For this reason, it is important to position sensors correctly and ensure that the sap flow data are representative of the whole tree before further scaling the data to the forest stand level (Čermák and Kučera 1990, Oren et al. 1998, Clearwater et al. 1999, Wullschleger and King 2000).

Sap flow rates are rarely uniform across the sapwood area (Swanson 1971, Miller et al. 1980, Edwards and Booker 1984, Čermák et al. 1984, 1992, Granier et al. 1994, Phillips et al. 1996, Loustau et al. 1998, Jiménez et al. 2000, Lu et al. 2000). To account for nonuniform sap flow rates in stems, one approach has been to position several sensors at different depths below the cambium when using the stem segment heat balance method (Čermák et al. 1982 and subsequent studies), the heat

pulse method (Edwards and Warwick 1984, Hatton et al. 1990) or the thermal dissipation method (Phillips et al. 1996, Lu et al. 2000). Moveable probes (Zang et al. 1996, Wullschleger and Norby 2001) provide an alternative for sampling many points along a stem radius; however, this method requires special instrumentation and an increased measurement time such that temporal variations could influence the results. Moreover, accurate determination of sapwood depth can be made only with sensors able to distinguish zero flow at the edge of heartwood. This may be a problem for the heat pulse technique, which is not sensitive to low flows (Barrett et al. 1995, Becker 1998), or for any other technique where it is necessary to subtract some assessed constants (e.g., max ΔT or “fictitious flow”) to characterize non-flow heat losses. Multiple-point sensors based on the heat field deformation (HFD) method (Nadezhdina et al. 1998) allow high resolution of non-uniform sap flow measurements along the xylem radius and are able to determine zero sap flow accurately at the edge of the sapwood–heartwood boundary.

Sap flow values representative of the whole tree can be calculated by integrating the sap flow pattern around the stem, treating the stem as circular, because the range of natural elliptical eccentricities in tree stems is usually rather small (Hatton et al. 1992). Approaches used to integrate sap flow, and thereby minimize errors associated with scaling data from single-point measurements to the whole tree, include polynomial integration methods (Cohen et al. 1981, Edwards and Warwick 1984, Green and Clothier 1988), the weighted average technique (Hatton et al. 1990, 1992, Wullschleger and King 2000) or their modifications (the zero-step and zero-average methods; Pausch et al. 2000).

Additional random scaling errors can occur as a result of the imprecise positioning of single-point sap flow sensors, i.e., when we suppose that we know the exact depth of the sensor, but in fact its position is shifted. The depth of the sensor in the sapwood is usually estimated by taking small bark samples with a bark-gauge or on the basis of the mechanical resistance of tissues measured with a penetrometer. However, such measurements are imprecise because of the difficulty of distinguishing between uniformly hard tissues (as sometimes the phloem and young growing xylem) and by small natural variations in the xylem surface (Zimmerman and Brown 1971, Lin and Hu 2000).

Our objective was to improve understanding of the variation in sap flow in the whole tree and of the associated errors when scaling sap flow from routine single-point measurements to

the whole-tree level. We studied high- and low-transpiring species contrasting in wood anatomy and social position to identify potential errors that could be important during the scaling procedure. The study was not intended to provide general indications of species-specific radial patterns of sap flow, but rather to illustrate the degree of variability in radial patterns of sap flow in individual trees.

Materials and methods

Experimental sites, forest stands and sample trees

Coniferous and broadleaf species at two sites were selected for sap flow studies. A sparse 68-year-old plantation of Scots pine (*Pinus sylvestris* L.) with a dense understory of broadleaf trees (*Prunus serotina* Ehrh.) and shrubs (*Rhododendron ponticum* L.) was studied in Brasschaat (Campine region), 15 km northeast of Antwerpen (51°19' N and 4°31' E, altitude 16 m). Additional details about the site have been described by Čermák et al. (1998b). An individual, rapidly transpiring poplar tree (*Populus canescens* L.) was studied in the woodlands on the campus of the University of Antwerpen in Wilrijk, 5 km south of Antwerpen (51°10' N and 4°24' E). The main biometrical parameters of typical sample trees of each species are presented in Table 1.

Identifying the sapwood depth

Sapwood was distinguished from heartwood based on xylem water content and wood color. The volumetric fractions of water (water volume expressed as a percentage of fresh volume of samples) and solid matter were estimated in 5.2-mm diameter wood cores obtained with a Pressler's borer (Suunto, Vantaa, Finland). Samples were taken from opposite sides of stems and immediately placed in aluminum foil, taken to a field laboratory and cut into small pieces of measured length and analyzed gravimetrically. Dry mass was determined after drying for 48 h at 80 °C. Volume of solid matter was calculated by dividing sample dry mass by the volumetric mass of dry substance (1.54 g cm⁻³). The fractions of solid matter and water were calculated by dividing by the sample volume. Wood color was determined by visual inspection of the same wood cores.

Measurement of sap flow

Sap flow was measured by the HFD method with linear radial heating (Nadezhdina and Čermák 1998, Nadezhdina et al.

Table 1. Stem diameter at breast height (DBH), xylem radius, sapwood depth and age of sample trees.

Tree species	Age (year)	DBH (cm)	Xylem radius (cm)	Sapwood depth	
				(cm)	(%)
<i>Populus canescens</i>	17	22.8	10.6	8.0	75
<i>Pinus sylvestris</i>	68	28.7	12.5	7.1	57
<i>Prunus serotina</i>	19	15.3	6.7	5.0	75
<i>Rhododendron ponticum</i>	18	7.3	3.2	3.2	100

1998). We used a multiple-point sensor to determine the variable pattern of sap flow along the xylem radius of tree stems and a single-point standard sensor for routine measurements of sap flow during long-term studies. Each sap flow sensor consisted of a heater (insulated resistance wire) and two sets of differential thermocouples (symmetrical and asymmetrical) measuring temperature differences, ΔT_{sym} and ΔT_{asym} , around the heater (Figure 1). Both the heater and the thermocouples were placed in stainless steel hypodermic needles with an outer diameter of 1.2 mm. Each needle of the multiple-point sensor contained six thermocouples, 5 to 15 mm apart in different versions of the sensor (see Figure 1). Needles with thermocouples were from 45 to 95 mm long, the needle containing a heater was 15 mm longer. Needles of the standard sensor contained only one thermocouple placed at the end of each needle. Typically the temperature data were measured every minute and recorded as means over 15-min intervals (occasionally over 1-min intervals) with a data logger (Unilog and Environmental Measuring Systems, Brno, Czech Republic).

Changes in the heat field around the linear heater caused by moving sap and varying properties of the conductive system were characterized by the ratio of the measured temperature differences ΔT_{sym} and ΔT_{asym} . Constants relating this ratio to the sap flow included basic geometry of the measuring point and physical properties of the conductive system (Nadezhdina et al. 1998).

Integration of sap flow to the whole-tree level

To integrate sap flow data from multiple points in the stem to the whole tree, the mean radial pattern of sap flow was first estimated based on measurements from at least two (up to four) opposite sides of the stem per sample tree. The depth of the actual sapwood (corresponding to the edge of the heartwood) was identified on the records as the point where sap flow approached zero. In some cases (e.g., in young trees or *Rhododendron* shrubs), when the sap flow did not reach zero near the pith, the whole xylem was taken as the sapwood. In a few trees with extremely deep sapwood (beyond the reach of sensors), the location of the heartwood boundary was estimated on the

basis of changes in the volumetric relative water content (RWC) where possible (i.e., if it decreased significantly in the inner xylem layers). We also noted changes in xylem color.

Sap flow data, originally expressed as sap flow per sapwood area, i.e., the sap flow density, q_i ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) for a point i on the xylem radius, were converted to sap flow for individual annuli, Q_i , corresponding to particular radial depths by multiplying q_i by the area of such annuli, A_i . Sap flow for the whole tree, Q_t , was integrated by summing all individual flows per n individual annuli in the tree:

$$Q_t = \sum_{i=1}^{i=n} Q_i A_i \tag{1}$$

To integrate sap flow over the whole sapwood depth, generalized radial patterns (integration curves) were derived from a series of measuring points by a polynomial or by a combination (mostly of two) of Gaussian curves minus a constant (g):

$$q_i = a \exp[-b(R_{\text{xyl}_i} - c)^2] + d \exp[-e(R_{\text{xyl}_i} - f)^2] - g \tag{2}$$

where q_i and xylem radius, R_{xyl_i} , were each expressed as a percentage of their maxima.

The single-point sensors were placed on the same side of the stem and at a known depth (position along stem radius, r_i) according to the previously measured radial pattern of sap flow. We always measured sap flow on at least two opposite sides of a stem and then averaged the data. The ratio of sap flow rate integrated for the whole tree, Q_t , and sap flow density, q_i (which was measured by the multiple-point sensor providing that one of its points is at the depth of a future single-point sensor) was taken as the point-to-area scaling coefficient, K_{i-t} , i.e.:

$$K_{i-t} = Q_t / q_i \tag{3}$$

Typical values of K_{i-t} depend on species and tree size and are usually of the order of tens to hundreds.

If multiple-point sensor data from several sides of a stem are averaged, it is also necessary to average the corresponding single-point sensor data. Mean sap flow measured by the radial sensors from different (more than two) sides, Q_{bar} , was compared with mean sap flow measured by the radial sensors from two opposite sides, Q_s , where single-point sensors were installed later. Their ratio was then calculated and used as the circumferential scaling coefficient, K_{s-t} :

$$K_{s-t} = Q_{\text{bar}} / Q_s \tag{4}$$

Typical values of K_{s-t} are small: Q_{bar} and Q_s usually differ by about 10% (some extremes are exceptional, see Čermák and Kučera 1990, Čermák et al. 1992). The effect of stem variation is similar for single-point and multiple-point sensors: $K_{s-t} = 1$, if Q_t and q_i were measured only from two opposite sides.

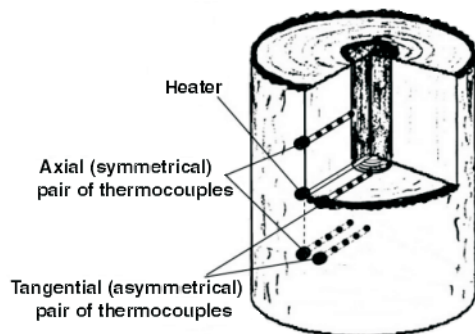


Figure 1. Schematic diagram of the front view of a multiple-point sap flow sensor installed in a tree stem for use with the heat field deformation method.

When combining the point-to-area scaling coefficient and the circumferential coefficient, K_{i-t} and K_{s-t} , we get the total scaling coefficient, K_{scal} . This coefficient directly converts mean values of sap flow density measured at a selected depth by a pair of single-point sensors, q_s , to the values of sap flow integrated by the multiple-point sensor for the whole tree:

$$Q_t = q_s K_{scal} \quad (5)$$

Systematic scaling errors attributable to assumption of uniformity of sap flow over sapwood

The systematic error in sap flow density, d_{sys} , characterizes the deviation of sap flow measured by the single-point sensor installed at a certain depth, when it is assumed that sap flow is uniform over the entire sapwood area. Values of d_{sys} were calculated for individual points on the radius (annulus), i , with the step of $dR_{xyl} = 5\%$ of stem xylem radius. Equal q_{i-uni} for all annuli were multiplied by the corresponding sapwood area, A_i , and summed to give tree total sap flow, Q_{t-uni} , as in the case of the calculation for the multiple-point sensor (see Equation 1). The systematic positioning error corresponds to:

$$d_{sys} = Q_{t-uni} / Q_t \quad (6)$$

Random errors attributable to uncertainties in positioning a single-point sensor

The random error of sap flow density, d_{ran} , characterizes the unknown deviation in sap flow values that arise because it is impossible to determine the exact position of a particular single-point sensor along the xylem radius (Figure 2). The depth of the sensor in the sapwood below the cambium is measured from the smoothed outer bark surface and the error in this measurement (dR_{xyl} assessed to about ± 1 mm) is caused by natural variations in xylem surface and bark thickness. The value of d_{ran} is calculated as a mean deviation of sap flow at points distant by dR_{xyl} on both sides from the depth of measurements.

Results

Determining the actual depth of sapwood

Scots pine Radial patterns of sap flow in individual Scots pine stems were limited by the cambium on the outer side and by the heartwood on the inner side of the sapwood. Potential depth of sapwood was around 7 cm (Table 1, Figure 3A). Water content was higher in the sapwood (about 25 to 30%_{vol}) than in the heartwood (about 12 to 15%_{vol}). Wood color was brighter in sapwood than in heartwood, especially in fresh cores.

Poplar Potential depth of poplar sapwood was about 8 cm (Table 1, Figure 3B). Relative water content (RWC) in poplar sapwood was similar to that in pine sapwood, but in contrast to pine, the RWC was much higher in the heartwood reaching about 60 to 80%_{vol}. Heartwood was easily distinguished from

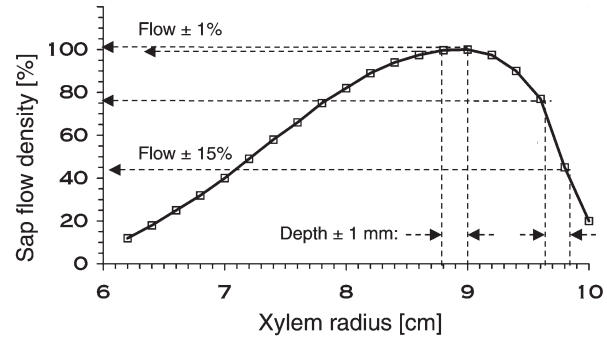


Figure 2. Hypothetical radial pattern and random errors in sap flow measurements associated with inaccurate positioning of single-point sensors (assuming an error in positioning at a certain depth of ± 1 mm). Each value represents the theoretical value of sap flow with a step of 2 mm in xylem radius.

sapwood by its darker color.

Cherry The potential depth of cherry sapwood was around 5 cm (Table 1, Figure 3C). A darker greyish transition zone occurred in sapwood, followed by a dark brown zone deeper in the xylem (closer to the pith) in contrast to the bright light color of the outer xylem (closer to the cambium).

Rhododendron No differences in RWC or wood color between sapwood and heartwood were found in *Rhododendron* shrubs.

Radial pattern of sap flow in stems

Scots pine In Scots pine, maximum flow density occurred at a depth of about 85 to 95% of the xylem radius (Figure 3A). There were no sap flow data available below 60% of the xylem radius, thus the heartwood radius reaching about 40% of the xylem radius was approximated according to RWC and wood color (Table 1).

Poplar Heartwood occupied only a small fraction (around 25%) of the xylem radius in the poplar stem as shown in an example of a medium-sized tree (Figure 3B). The radial pattern of sap flow was highly variable with three peaks. A peak with a maximum sap flow was observed far from the cambium (around 80–85% of the xylem radius) and a very low sap flow was recorded in the outermost sapwood layers.

Cherry In cherry, sap flow was characterized by three distinct zones occurring at different depths (Figure 3C). Maximum sap flow occurred beyond about 70% of the xylem radius with a sharp peak at about 80%, and a low sap flow was recorded just below the cambium, similar to that observed in poplar. This zone was visible in the wood cross sections and in the cores as a layer of light yellow wood. In the deeper zone of

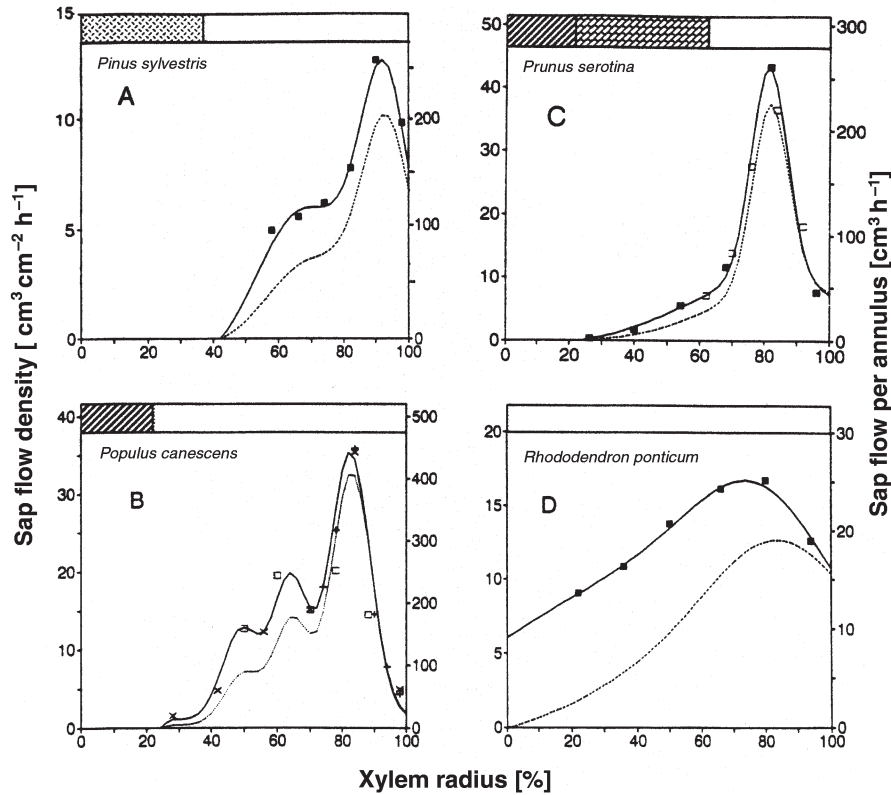


Figure 3. Radial patterns of sap flow in stems of two dominant overstorey (A, B) and two understorey (C, D) tree species, measured at midday on sunny days. Xylem color is shown schematically in the upper part of each graph: hatched = dark brown heartwood, reticulated = greyish-brown transition zone, dotted = slightly darker heartwood, and white = undifferentiated xylem. Measured values of sap flow density are shown, and the radial pattern was approximated by curve fitting (solid line). The dotted line represents sap flow per annulus calculated with a step of 2% of the xylem radius. Radial patterns of sap flow in poplar (*Populus canescens*; B) and in cherry tree (*Prunus serotina*; C) were recorded with three and two sensors, respectively.

the sapwood, between about 25 and 70% of the xylem radius (visible on the cores as darker greyish wood), sap flow was much lower and decreased gradually to zero. No flow was observed in the dark brown heartwood occurring beyond a depth

equal to about 25% of the xylem radius.

Rhododendron In *Rhododendron*, which had no visibly differentiated heartwood, the entire stem cross-sectional area was

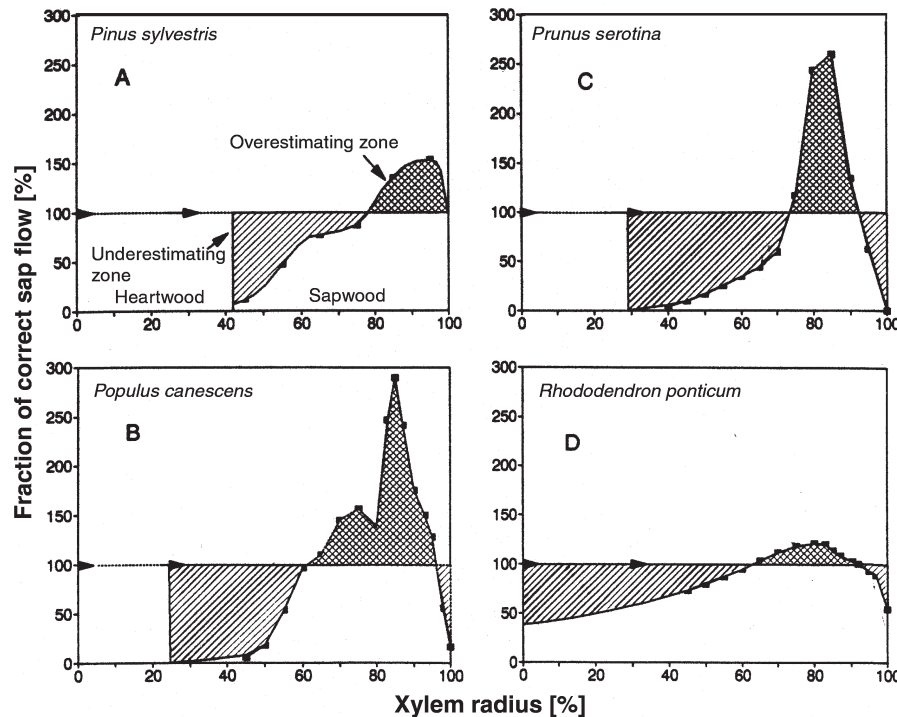


Figure 4. Possible systematic errors in sap flow rate measurements with single-point sensors positioned at one depth in overstorey (A, B) and understorey (C, D) tree species with different radial patterns of sap flow. The correct value of sap flow (100%) was taken as the value calculated by integrating the entire radial sap flow pattern measured with a multiple-point sensor. The curves represent sap flows measured by single-point sensors and calculated assuming uniform sap flow density over the entire sapwood. Zones of sapwood where the sensor was theoretically located and the corresponding errors are indicated by crosses. Shading: crosshatched = overestimated values; hatched = underestimated values).

conducting with maximum sap flow at xylem depth around 70% of the xylem radius (Figure 3D).

Errors in sap flow measurements with single-point sensors, assuming a uniform flow over the whole sapwood

We used the radial flow pattern as a standard to evaluate the magnitude of possible systematic errors caused by ignoring nonuniform sap flow across the sapwood. When measured under the same environmental conditions, sap flow was greatly overestimated (up to almost 300%) when single-point sensors were placed in the outer to middle sapwood, and it was greatly underestimated (up to 100%) when single-point sensors were placed in the inner sapwood, or in shallow layers (close to the cambium). Such large errors were observed in dominant specimens of forest overstory species (Figures 4A and 4B) and in tall understory species (Figure 4C). In contrast, smaller errors in the estimation of sap flow were observed when the pattern of sap flow over sapwood depth was more homogeneous, e.g., in the small understory species (Figure 4D).

Integration of nonuniform sap flow over the whole sapwood

Cyclic temporal variation in the ratio of sap flow density between any two points or any point along the stem radius (q_i) and mean sap flow density, q_{bar} , existed between day and night at different xylem depth of the Scots pine stem (Figure 5, lower panel). This variation was pronounced when measure-

ments were made under conditions of high evaporative demand and unlimited water supply after rains (Days 224, 225 and 243 in Figure 5). Some uncertainties in the calculation of the q_i/q_{bar} ratio occurred when sap flow approached zero (Days 234 and 240 in Figure 5). Relationships between sap flow density at any measurement point along the stem radius and sap flow per tree were nonlinear for the whole observation period because of differences in the conducting activity of the sapwood layers with time (Figure 6A). When only daytime observations were considered (as was done by Zang et al. 1996), relationships between q_i and sap flow per tree were linear but with different r^2 values (between 0.44 and 0.91), indicating the influence of different sapwood layers on whole sap flow (Figure 6B). The daytime q_i/q_{bar} ratio was more or less constant during the period of continuously hot weather with no rain (Figure 7), except for the sapwood layer with maximum sap flow density (measuring point at the depth of 14 mm), where a gradual decrease in sap flow density was recorded (cf. Days 224–233 in Figure 5).

Measurement time and the radial pattern of sap

Figure 8 illustrates changes in the amounts of sap flow occurring in different sapwood layers on 3 days with different environmental conditions taken from the period shown in Figure 5. Radial patterns of sap flow were derived from short-term measurements made with the multiple-point sensor at midday on each of the three days (when a peak of flow was recorded on the first two days and during rather low flow on the third

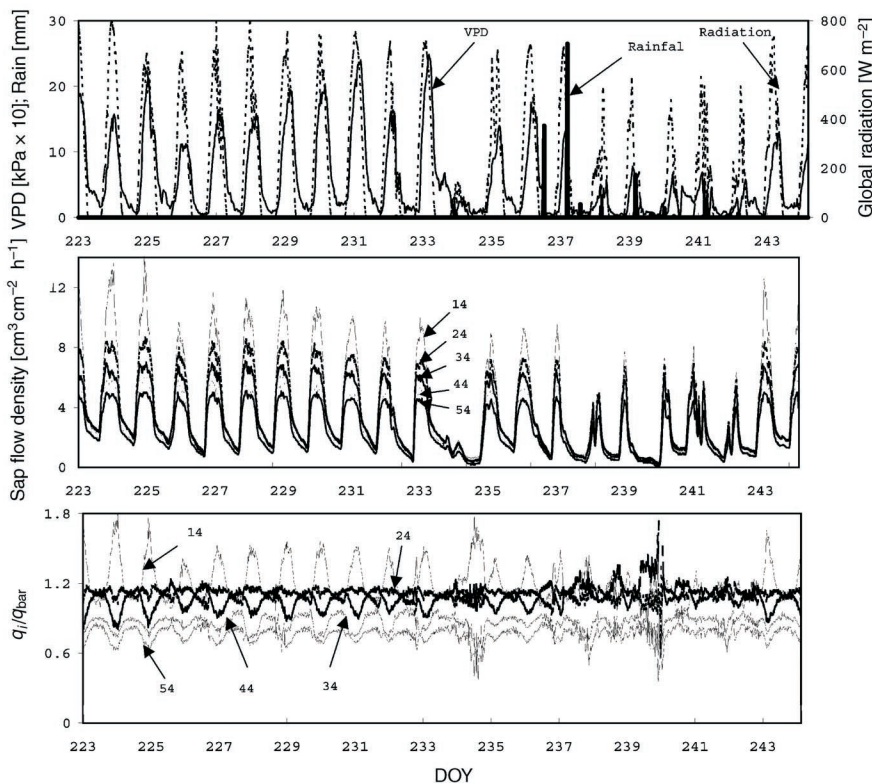


Figure 5. Dynamics of meteorological parameters (upper panel), sap flow density measured by the multiple-point radial sensor in a Scots pine tree (middle panel) and the ratio of sap flow density between any measured points and their mean, q_i/q_{bar} . Meteorological data were provided by Stijn Overloop (Institute for Forestry and Game Management, Geraardsbergen). Numbers indicate the depth of the measuring point below the cambium (mm). Values of sap flow density at a depth of 4 mm were similar to those at a depth of 24 mm and are not presented. Abbreviations: DOY = day of year; and VPD = vapor pressure deficit.

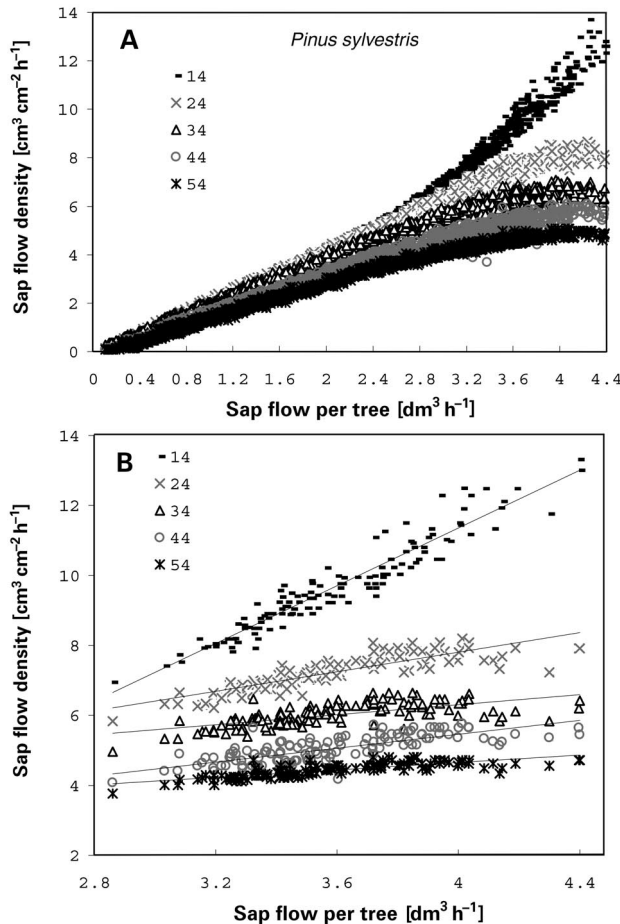


Figure 6. Relationships between sap flow calculated for the whole tree and sap flow density measured at different depths below cambium in the stem of a Scots pine tree (see Figure 5) over the whole measurement period (A) and for the period from DOY 224 to 233 under stable weather conditions (B; only daytime data from 1200 to 1500 h were included in this analysis). Numbers indicate depth of the measuring point below the cambium (mm).

cloudy day). Three integration procedures and corresponding integration curves (marked by the letters *a*, *b* and *c* in Figure 8) were used to compare data integrated from measurements made with a single-point sensor placed at the depth of maximum sap flow with the data recorded by the multiple-point sensor (Figure 9). The comparison based on the type *b* integration was superior, because it gave intermediate values with some overestimates and some underestimates for measurements during periods of high and low evaporation demand, respectively. The underestimates and overestimates were high when the comparisons were based on integrations of types *a* and *c*, respectively. These findings were confirmed when the integration curves derived from the three integration procedures were compared with the daily radial pattern data (measured from 1200 to 1500 h) for the period with clear weather (Days 224–233). The type *b* integration curves approximated real values (92%), whereas the types *a* and *c* integration curves gave significant underestimates (–19%) and overestimates

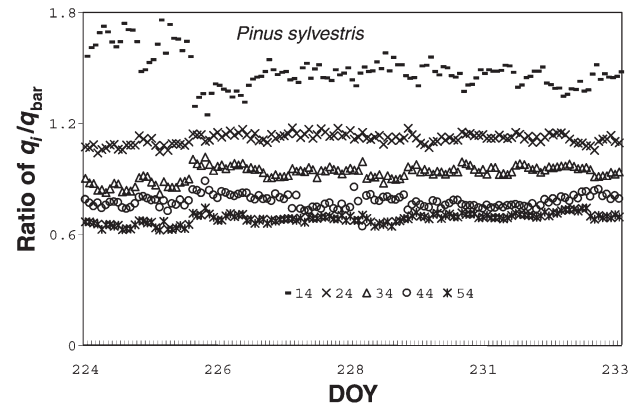


Figure 7. Dynamics of the ratio of sap flow density between any points along the stem radius and their means measured at different depths below the cambium in the stem of a Scots pine tree over the period from DOY 224 to 233 under stable weather conditions (see Figures 5 and 6). Only daytime data (1200–1500 h) were included in this analysis. Numbers indicate depth of the measuring point below the cambium (mm). Abbreviation: DOY = day of year.

(16%), respectively. The results changed significantly, however, when we compared data over the whole observation period (Days 224–244): the type *c* integration curve approximated the real data, whereas types *a* and *b* integration curves resulted in significant underestimates of –30 and –20%, respectively.

Evaluation of positioning errors of single-point sensors along the xylem radius

Generally, errors of 0.5–1.0 mm in the positioning of single-point sensors cannot be avoided. These positioning errors caused negligible scaling errors (around 1% per 2 mm depth) when the single-point sensor is placed in the flat zone of the sap flow radial pattern. Positioning errors can lead to significant scaling errors (up to 30% per 2 mm depth), however, if the sensor is located on the steep slope of the corresponding curve (Figure 10).

Discussion

Sapwood depth (expressed as percent of xylem radius) is related to tree size and tree age (Čermák and Nadezhkina 1998b). Depth of the outer, wetter xylem zone in young and old trees reaches about 45 and 30%, respectively, of the xylem radius in Norway spruce, and about 60 and 50%, respectively, in Scots pine from central Sweden (Kravka et al. 1999). Our Scots pine data (57% of the xylem radius) are in agreement with these published results. Sapwood was deeper in the poplar tree (75% of the xylem radius), which was much younger than in the Scots pine tree. A dark zone of xylem is typically larger in mature poplars than in young poplars (Balaban 1955). It is unclear, however, whether the zone delimits the heartwood within physiological limits (by impregnation with secondary metabolites) or whether it reflects, for example, a

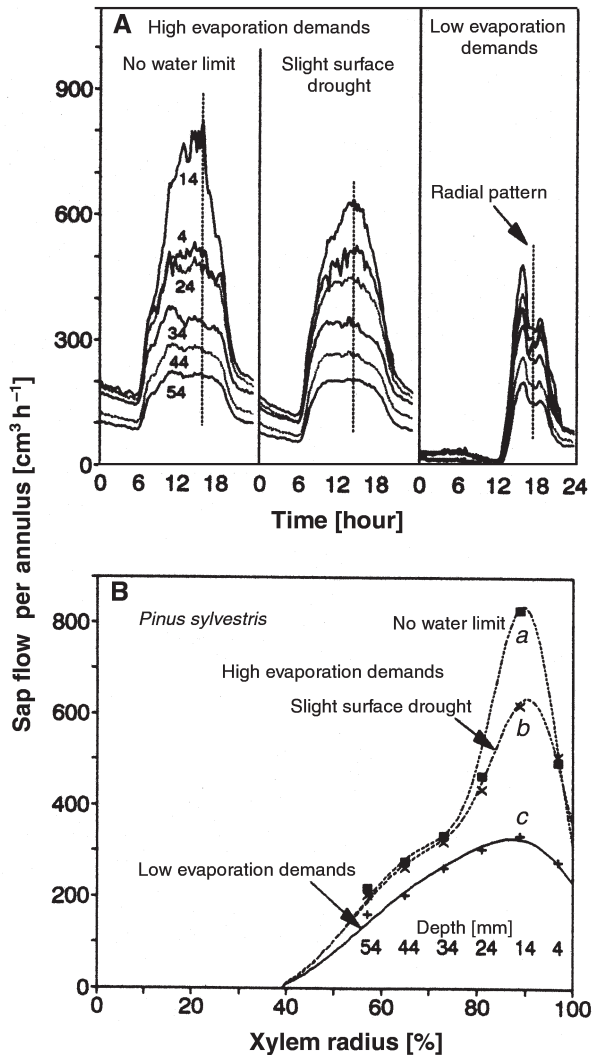


Figure 8. Changes in the radial pattern of sap flow per annulus in Scots pine (calculated for depth of each annulus equal to 8% of xylem radius) under different soil water conditions and evaporative demand. Vertical lines across diurnal courses of sap flow per annulus (A) indicate times for which the radial patterns are shown (B). Numbers indicate depth of the measuring point below the cambium (mm). Letters *a*, *b*, and *c* indicate three different radial patterns of sap flow per annulus corresponding to particular integration curves, calculated for terms marked by vertical lines in Panel A.

higher activity of bacteria as a precursor of infection by fungi (Cerny 1976). In the understory species, sapwood depth was about 75% of the xylem radius in cherry trees, as in poplar. All of the xylem was hydroactive in *Rhododendron*. The depth of the sapwood estimated from the radial sap flow profiles agreed well with the depth of the xylem zone determined by differences in water content or changes in wood color. Nevertheless, the conductive functions of the active sapwood differed significantly within a tree. In Scots pine, the position of maximum sap flow was more variable in the outer sapwood layers than in the deeper sapwood layers. Sap flow per annulus was shifted

slightly toward the cambium when compared with sap flow per area, especially in the inner sapwood, indicating that the most important part of the sapwood was the outermost layer (80–100% of the xylem radius).

In poplar, we observed pronounced changes in sap flow at different xylem depths. A similar pattern has also been observed in other tree species (Miller et al 1980, Dye et al. 1991, Čermák and Nadezhina 1998*b*, Lu et al. 2000). The peaks in sap flow observed beyond the maximum q_i probably reflected the positioning of the sensor within the wide annual rings of poplar (sometimes > 1 cm); i.e., in either earlywood or latewood and thus a high or low water conducting zone. Sap flow per annulus had a similar pattern as sap flow density in poplar. Because of low sap flow close to the cambium and a second peak of flow density in the inner sapwood, the most important part of the sapwood for whole tree water use occurred in the inner layers of xylem at a depth of 60–90% of the xylem radius.

The radial pattern of sap flow density in cherry was similar to that in poplar, but only in the outer xylem layers without any secondary peak in the inner sapwood. The most important part of the sapwood was at a depth of 70–90% of the xylem radius. There were pronounced differences in the shape of the curves characterizing sap flow density and sap flow per annulus in *Rhododendron*. Although sap flow density was high near the pith, it was quantitatively unimportant because the conducting area (cross-sectional area of the corresponding annuli) was close to zero. The more or less uniform radial pattern of sap flow over the whole xylem in *Rhododendron* effectively increased the sapwood conducting zone by up to 40% (at a depth of 60–100% of the xylem radius).

Although the potential sapwood was relatively deep in the studied species (57–100% of R_{xyl}), the most important part of the active sapwood was narrow (20–40% of R_{xyl}). A single-peak radial pattern of sap flow is reported to occur around the middle sapwood in pine and spruce (Swanson 1967, Čermák et al. 1992), whereas various patterns of radial flow have been observed in most broadleaf species (Čermák et al. 1984, Phillips et al. 1996, Čermák and Nadezhina 1998*b*, Jiménez et al. 2000, Lu et al. 2000), as was observed in our study (Figure 3). In our study trees, the position of maximum flow changed over the range of 75–92% of the xylem radius. Hence, installation of single-point sensors at the same fixed depth (e.g., around 20 mm) could represent another source of error.

Each of the six thermocouples embedded in the radial multiple-point sensor was able to record sap flow rate in a small area close to the thermocouple. Pronounced temperature differences were consistently measured over short distances along the xylem radius. No changes in the recorded data at different sapwood depths occurred when the needles with thermocouples were moved along the stem radius or when sensors with different distances between the thermocouples were used, provided that the other needles were installed in the same holes in stems under stable weather conditions (see Figures 3B and 3C). This confirms the reproducibility of the sap

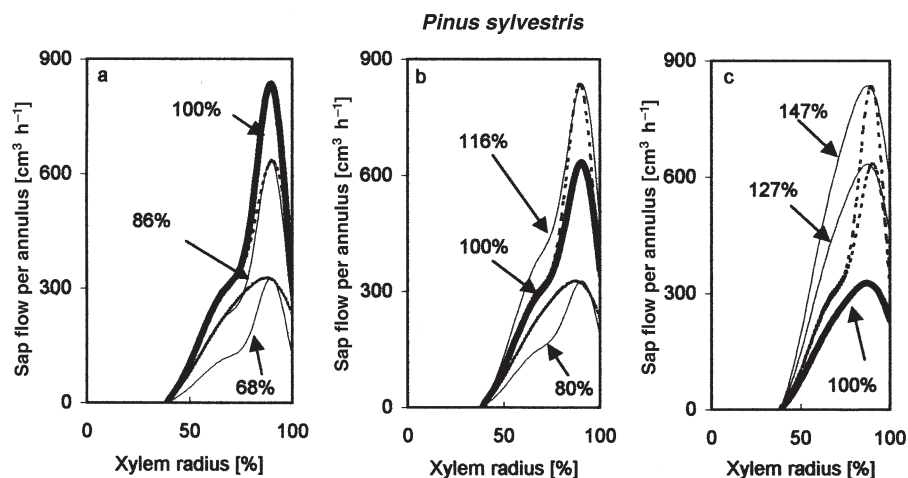


Figure 9. Effect of integration procedure on sap flow integration from single-point measurements with a sensor installed at the depth with maximum sap flow (curves for days with different weather conditions, see Figure 8). The integration curve obtained from radial profile measurements on a particular day and used in the recalculation of data obtained on the same day with a single-point sensor is shown by the thick line and labeled 100% in each panel. The dashed lines indicate the real radial patterns measured with a multiple-point sensor on each day and formally repeated in each panel from Figure 8B. The thin full lines indicate the theoretical radial patterns obtained by applying the same integration curve for the particular

day (marked by the thick full line) for integration of data from single-point sensor for the other two days. The percentage values above and below 100% indicate the possible magnitude of scaling errors between the real and theoretical radial patterns.

flow measurements by the HFD method and the reliability of the radial flow patterns. The HFD sensors have a short response time: 1–3 min is sufficient for each measurement when

moving the needles along the stem radius. The short measurement period is possible because the heater is separated from the thermocouples and thus remains untouched when replac-

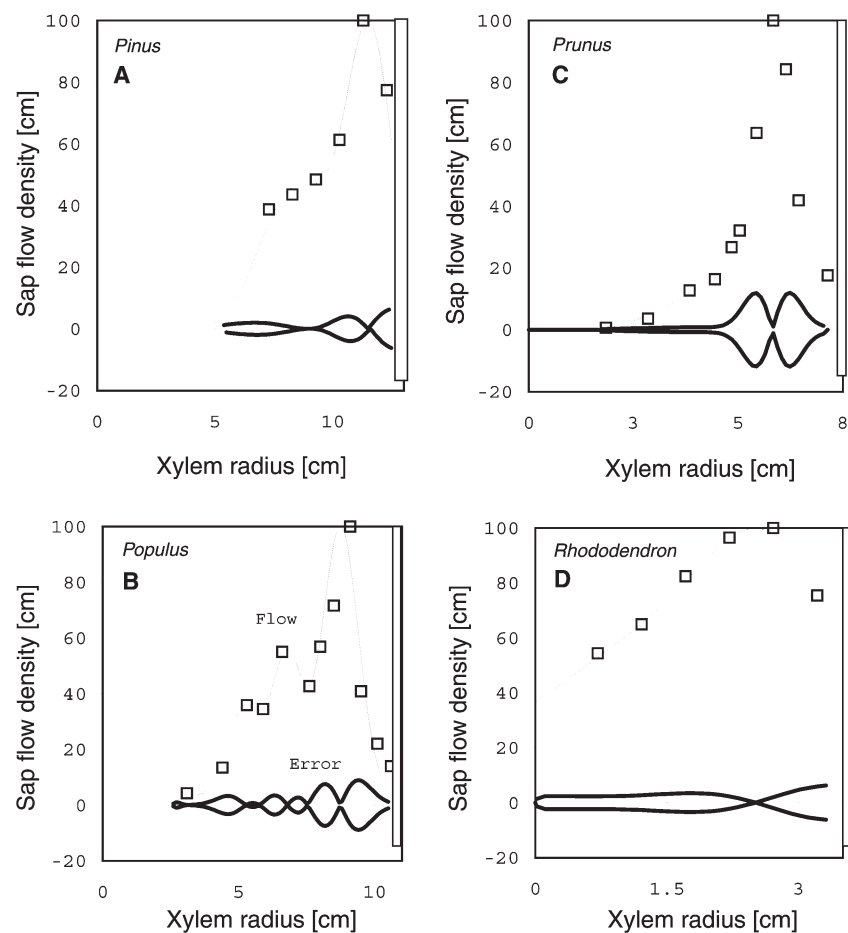


Figure 10. Possible random errors in sap flow measurement associated with inaccurate positioning of single-point sensors (assuming a positioning error of ± 1 mm) in overstorey (A,B) and understorey (C,D) woody species.

ing or moving the needles with thermocouples, hence the heat field is undisturbed and there is no need to wait for the new heat equilibrium to be reached. This allows rapid determination of the radial flow patterns of all trees chosen for further measurements by a single-point sensor.

Errors arise during integration or scaling flow from single-point measurements to whole trees when it is assumed that sap flow is uniform with sapwood depth (cf. Jiménez et al. 2000). The magnitude of such errors is mainly dependent on the width of the sapwood zones with peak sap flow rates. In general, the largest errors (–90 to 300%) occur when the width of the sapwood zone with peak sap flow is narrow and distant from the cambium (e.g., poplar and cherry), whereas smaller errors (–90 to 150%) arise when the width of the sapwood zone with peak sap flow is wider or closer to the cambium (e.g., Scots pine). The smallest errors (–60 to 120%) occur when sap flow has a wide peak (e.g., *Rhododendron*). Theoretically, no errors occur when sensors are, by chance, placed where the measured flow is close to the mean sap flow (the “correct value lines” as shown in Figure 4).

Significant errors occurred during scaling of data obtained by single-point sensors to the whole tree, even though we had previously determined the sap flow radial pattern by short-term measurements with multiple-point sensors. Thus, the assumption that the ratio of sap flow between points within a stem (used as the correction factor for flow integration) is constant is debatable (Zang et al. 1996), because both temporal and spatial variations of sap flow exist simultaneously. Furthermore, spatial variations in sap flow in the stem include both radial and circumferential ones. Therefore, the correction coefficient should include both radial (K_{r-i}) and circumferential (K_{s-i}) corrections. We found high linear correlations between sap flow measured at any two points at similar depth below the cambium from different sides of the stem under non-limiting soil water conditions, which agrees with results reported by Zang et al. (1996) and Lu et al. (2000). Although the ratio of sap flow between measured points around the stem circumference was almost constant with little evidence of temporal variation (authors’ unpublished data), this was not the case for the radial variation of sap flow. The ratio q_i/q_{bar} , which characterizes differences in the proportion of flows at different sapwood layers, changed with time (Figure 5). High temporal variation was observed in the sapwood layer with maximum sap flow rate, which is connected to sun-exposed leaves. Sap flow in the outer sapwood layers often connects sun-exposed foliage with surface roots (Nadezhdina and Čermák 2000, and unpublished data). For this reason, the zone with maximum sap flow is more sensitive to drought (when the upper soil layers dry out) and to changes in evaporation demand than inner (deeper) sapwood layers. Low sap flow rates in the outermost xylem layers, which were similar to the rates in the deep layers of the sapwood, may reflect an undeveloped conducting system in young sapwood, as shown earlier for conifers (Mark and Crews 1973). We hypothesize that long-term records of the ratio of q_i in some sapwood layers to q_{bar} or to sap flow in

the whole tree, measured by the radial profile sensor, could be used as an indicator of tree water stress.

The effect of time of measurement on sap flow data used to determine the radial pattern of sap flow was found to limit the influence of temporal variations on the point-to-area correction factor. Among the procedures used to integrate sap flow data obtained with a single-point sensor placed at the depth of maximum sap flow examined, we found that the *c*-type integration procedure produced values closer to those obtained with the multiple-point sensor. This finding can be explained by comparing the curves obtained by the three integration procedures with the sap flow data measured over a day (Figures 8A and 8B). Type *a* curves were observed only during short periods (around 2 h) on days with high evaporative demand. Type *b* curves were recorded during periods with higher soil water deficit and on days with fine weather during morning and evening hours. Type *c* curves, which were observed on cloudy days, more closely approximated the data recorded every day from late evening to early morning than did type *a* and *b* curves, indicating that about 70% of the curves obtained during a long-term study would be of type *c*. Therefore, we do not recommend making short-term measurements of sap flow radial patterns during periods when peaks in sap flow are expected if the data are to be used subsequently to scale sap flow from point measurements to the whole tree.

Random errors attributable to errors in the positioning of the single-point sensor along the xylem radius were higher in smaller trees exhibiting a narrow peak of sap flow, when the single-point sensor was located on the steep zone of a radial pattern (cherry: $\pm 15\%$; poplar: $\pm 10\%$). Although this kind of error is unavoidable, it can be minimized by positioning single-point sensors at the depth of maximum flow. This solution may not be applicable to ring-porous trees, however, because a steep radial pattern often occurs just below the cambium.

Conclusions

The assumption that sap flow is uniform over the whole sapwood depth results in a major error when scaling sap flow measured by a single-point sensor to the whole tree. Even when nonuniform sap flow over the sapwood has been taken into account, additional errors in scaling arise because of uncertainties in the positioning of sensors below the cambium and differences in environmental conditions between those prevailing when the radial pattern was determined over the short term and when the single-point measurements were made over the long term. We found high temporal variation in the correction factor along the xylem radius used for sap flow integration. Short-term measurements of the radial pattern of flow in the morning and evening hours during sunny days are recommended if such data are being used to scale sap flow from single-point measurements to the whole tree. Measurements at these times help minimize the influence of temporal variations on the point-to-area correction factor, which were especially pronounced in trees with a high asymmetry of radial sap flow pattern and differing functionality of the sapwood xy-

lem layers. Positioning a single-point sensor at the depth of maximum sap flow is advantageous (1) because of the high sensitivity of maximum sap flow to changes in environmental conditions, and (2) because of the lower random errors associated with positioning a single-point sensor along a xylem radius. Routine long-term measurements with multiple-point sensors determining the radial flow pattern seem the best way to eliminate most of the scaling errors.

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