Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees

STAN D. WULLSCHLEGER and ANTHONY W. KING

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831-6422, USA

Summary   Canopy transpiration and forest water use are frequently estimated as the product of sap velocity and cross-sectional sapwood area. Few studies, however, have considered whether radial variation in sap velocity and the proportion of sapwood active in water transport are significant sources of uncertainty in the extrapolation process. Therefore, radial profiles of sap velocity were examined as a function of stem diameter and sapwood thickness for yellow-poplar (*Liriodendron tulipifera* L.) trees growing on two adjacent watersheds in eastern Tennessee. The compensation heat pulse velocity technique was used to quantify sap velocity at four equal-area depths in 20 trees that ranged in stem diameter from 15 to 69 cm, and in sapwood thickness from 2.1 to 14.8 cm. Sap velocity was highly dependent on the depth of probe insertion into the sapwood. Rates of sap velocity were greatest for probes located in the two outer sapwood annuli (P1 and P2) and lowest for probes in closest proximity to the heartwood (P3 and P4). Relative sap velocities averaged 0.98 at P1, 0.66 at P2, 0.41 at P3 and 0.35 at P4. Tree-specific sap velocities measured at each of the four probe positions, divided by the maximum sap velocity measured (usually at P1 or P2), indicated that the fraction of sapwood functional in water transport (f_S) varied between 0.49 and 0.96. There was no relationship between f_S and sapwood thickness, or between f_S and stem diameter. The fraction of functional sapwood averaged 0.66 ± 0.13 for trees on which radial profiles were determined. No significant depth-related differences were observed for sapwood density, which averaged 469 kg m^{-3} across all four probe positions. There was, however, a significant decline in sapwood water content between the two outer probe positions (1.04 versus 0.89 kg kg^{-1}). This difference was not sufficient to account for the observed radial variation in sap velocity. A Monte-Carlo analysis indicated that the standard error in estimated mean f_S declined rapidly with increasing sample size. At $n = 10$, the coefficient of variation in mean f_S was 7% and at $n = 15$ it was slightly less than 5%. These observations indicate that radial variation in sap velocity is an important, albeit often overlooked, source of uncertainty in the scaling process. Failure to recognize that not all sapwood is functional in water transport will introduce systematic bias into estimates of both tree and stand water use. Future studies should devise sampling strategies for assessing radial variation in sap velocity and such strategies should be used to identify the magnitude of this variation in a range of non-, diffuse- and ring-porous trees.

Keywords: canopy transpiration, forest water use, heat pulse, Monte-Carlo analysis, radial profile, sapwood area, scaling.

Introduction

There is widespread interest in the use of sap velocity measured on single trees to derive estimates of canopy transpiration and forest water use (Swanson 1994, Granier et al. 1996*b*, Wullschleger et al. 1998). Such extrapolation requires not only accurate measurements of sap velocity, but also detailed inventories of stand-level attributes including tree domain, defined either by distance between stems or crown area (Hatton and Vertessy 1990), basal area, leaf area or sapwood area (Hatton et al. 1995). Each of these attributes has been used with varying success to estimate canopy transpiration and the hydrologic balance of forested watersheds (Hatton et al. 1995, Jiménez et al. 1996, Loustau et al. 1996, Vertessy et al. 1997, Cook et al. 1998). However, in practice, few studies use more than a single attribute to extrapolate sap velocity to the canopy scale. Many investigators currently describe areal rates of forest water use as the product of sap velocity and stand sapwood area (Teskey and Sheriff 1996, David et al. 1997, Hogg et al. 1997, Saugier et al. 1997, Alsheimer et al. 1998). Allometric relationships between stem diameter or circumference and sapwood area are typically established based on increment cores or stem disks taken across a range of size classes. Total sapwood area is estimated by applying these equations to inventory-based assessments of individual tree diameter or circumference in a stand (Vertessy et al. 1995, Loustau et al. 1996, Saugier et al. 1997, Vertessy et al. 1997, Wullschleger et al. 2000).

Although extrapolations based on sapwood area are conceptually simple, estimates of tree and forest water use derived in this manner are subject to uncertainties (Smith and Allen 1996, Köstner et al. 1998). Foremost among these uncertainties is the actual proportion of sapwood functional in water transport. Previous studies have shown that radial variation in sap velocity clearly exists in many woody species (Dye et al. 1991, Čermák et al. 1992, Becker 1996, Phillips et al. 1996, Oren et al. 1999), with sap velocities being greatest in outer

sapwood and progressively lower with increasing proximity to heartwood. Zang et al. (1996) conducted a study of two 3-year-old *Eucalyptus globulus* spp. *globulus* (Labill.) trees and reported that, on average, only 78% of the sapwood was active in water transport. Variability among the two trees studied was, however, high. Yet many investigators who derive rates of canopy transpiration based on sapwood area frequently fail to report whether radial gradients were present in the species studied (Granier et al. 1996*a*, Hogg et al. 1997, Martin et al. 1997), or assume *a priori* that such variation does not exist (Loustau et al. 1996). Studies that do recognize radial variation as an important consideration in extrapolating sap velocity to the canopy scale, often use only limited measurements (one to two trees) to quantify this parameter (Cook et al. 1998, Wullschleger et al. 2000). To our knowledge, only one study has evaluated the magnitude and significance of sampling errors associated with radial gradients in sap velocity (Hatton et al. 1995).

Our objective, therefore, was to assess radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar (*Liriodendron tulipifera* L.). Yellow-poplar is a diffuse-porous species native to temperate deciduous forests throughout the eastern United States. It has several desirable characteristics from the perspective of measuring sapwood area: stem diameter is symmetrical, sapwood thickness is uniform around the stem circumference, and sapwood thickness increases with stem diameter. In the present investigation, sapwood is defined as the region between the cambium and heartwood. In yellow-poplar, the interface between sapwood and heartwood is easily distinguished based on coloration. This definition sets an upper boundary on the potential cross-sectional area of sapwood for conducting water. We hypothesized that the fraction of sapwood functional in water transport ($0 < f_S < 1$) would be less than one, and that f_S would furthermore decrease as stem diameter and sapwood thickness increased. The compensation heat pulse velocity technique was used to quantify sap velocity at multiple depths (4) in the sapwood of 20 trees (Hatton et al. 1990). Observed patterns of sap velocity are discussed in terms of stem diameter and sapwood thickness, and are evaluated as a source of sampling error when extrapolating rates of forest water use from measurements of sap velocity.

Materials and methods

Site description and sapwood analysis

Two adjacent watersheds (Site 1 and Site 2) were selected within the U.S. Department of Energy's National Environmental Research Park (NERP), Anderson County, TN (35°58′ N and 84°17′ W) for the study of sap velocity in yellow-poplar. Site 1 and Site 2 are both north-facing watersheds and occupy 5.1 and 13.2 ha, respectively. Slopes across the two study sites range between 14 and 45%. Yellow-poplar, red maple (*Acer rubrum* L.) and scattered sugar maple (*Acer saccharum* Marsh.) are prevalent on lower mesic slopes at both sites, whereas chestnut oak (*Quercus prinus* L.) and isolated loblolly pine (*Pinus taeda* L.) are more prevalent on the upper drier slopes. Overstory basal area is 22.3 m^2 ha^{-1} at Site 1 and 24.9 m^2 ha^{-1} at Site 2. Mean annual rainfall (30-year average) at a nearby (1 km) weather station on Walker Branch Watershed is 134 cm and mean temperature is 14.4 °C (Hanson et al. 1998). Soils at the sites are mapped as Fullerton (Typic Paleudults) and characterized as deep, well-drained cherty soils that formed in residuum of dolomite (USDA 1981).

Fifty-five trees (26 from Site 1 and 29 from Site 2) were selected for measurements of stem diameter, bark thickness, sapwood thickness and sapwood area. Stem diameter at breast height (1.3 m) was measured with a diameter tape. Bark and sapwood thickness were determined at two to five locations around the stem circumference by drilling 1.3-cm holes through the bark and to the bark–sapwood interface. This transition was identified based on an assessment of color, texture and water content. An electronic caliper (Brown and Sharpe Mfg. Co., North Kingstown, RI) was used to measure bark thickness, and sapwood thickness was measured with a ruler on a core extracted with a 0.5-cm increment borer. Color differences were used to identify the boundary between sapwood and heartwood. Cross-sectional sapwood area was calculated from stem diameter, and mean bark and sapwood thickness. Sapwood areas were fitted to the equation (Vertessy et al. 1995):

$$A_S = kD^B, \tag{1}$$

where A_S is sapwood area (cm^2), D is measured tree diameter at breast height (cm), and k and B are coefficients as determined with nonlinear regression techniques.

Tree selection and sap velocity measurements

From the original 55 trees, 10 trees from each of the two sites (20 trees total) were selected for measurements of tree height, crown area and radial variation in sap velocity (Table 1). Tree heights were measured with a hand-held clinometer (Suunto USA, Carlsbad, CA), and crown areas were calculated from vertical projections of the crown perimeter.

The (compensation) heat pulse velocity technique (SF-300, Greenspan Technology Pty. Ltd., Warwick, Queensland, Australia) was used to determine sap velocity at four depths in the sapwood. Each probe consisted of two thermistors, one 10 mm upstream and one 5 mm downstream from a central heater. Thermistors and the heater were housed in 2-mm diameter stainless-steel tubing. Insertion depths were calculated so that thermistors of each probe were optimally located within concentric annuli of equal sapwood area (Hatton et al. 1990). This method was used to ensure that sap velocities measured at any probe position were representative of sap flow through (in this study) 25% of the cross-sectional sapwood area (Figure 1). Probe positions were, for convenience, identified as P1, P2, P3 and P4 beginning with the outermost position (P1) and progressing to the probe closest to the heartwood (P4). Holes for the four probes were drilled with a 1.98-mm bit. A drill guide was used to ensure that the holes were properly spaced and parallel. Probes were located at a height of 1.3 m and were po-

Table 1. Characteristics of the 20 yellow-poplar trees on which estimates of sap flow velocity were determined. Stem diameter, tree height, sapwood thickness, sapwood area, and projected crown area were measured directly for each tree.

Tree no.	Diameter (cm)	Height (m)	Sapwood thickness (cm)	Sapwood area (cm^2)	Crown area (m^2)
2	57	38	11.5	1476	99
5	44	32	9.2	901	38
7	66	37	12.8	1981	119
8	20	25	4.3	187	11
12	37	35	7.1	586	38
14	26	25	4.5	279	45
17	52	34	10.4	1193	91
18	35	28	6.9	539	33
20	52	38	10.2	1184	81
26	43	36	8.9	835	91
27	69	35	14.8	2227	119
32	34	27	6.2	477	26
42	30	28	5.7	376	17
45	39	37	7.9	684	36
46	46	33	9.5	960	48
47	38	31	7.7	642	24
48	20	24	3.0	135	11
51	41	30	8.3	753	31
52	32	29	5.8	414	14
55	15	18	2.1	75	14

sitioned on the northern side of the tree. Data loggers were programmed to provide a heat pulse for 1.4 s and measurements at each of four sapwood depths were recorded every 20 min. The availability of multiple heat pulse units made it possible to measure from 1 to 4 trees at a time. Sap velocity
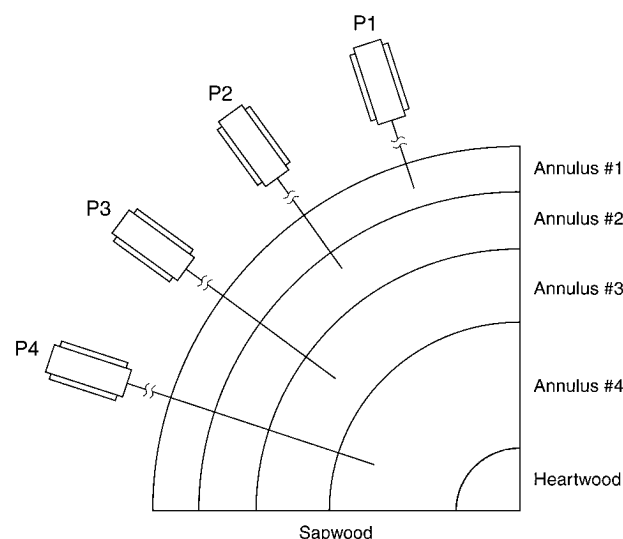

Figure 1. A schematic diagram showing probe placement in the weighted average technique for integrating point estimates of sap velocity from sensors placed at four depths into the sapwood conducting annulus (Hatton et al. 1990).

measurements for each tree were made for at least 4 days. All measurements of sap velocity were made between May 25 and July 4, 1998.

Heat pulse velocity was estimated as outlined by Barrett et al. (1995) and all estimates were corrected for probe implantation effects based on an assumed wound diameter of 2.2 mm (Swanson and Whitfield 1981). Sap velocity (V_s) was calculated from corrected heat pulse velocity (V_h) based on Equation 3 of Barrett et al. (1995):

$$V_s = \frac{V_h \rho_b (C_w + m C_s)}{(\rho_s C_s)}, \qquad (2)$$

where C_w is the specific heat capacity of sapwood, C_s is the specific heat capacity of sap, ρ_b is the density of wood, ρ_s is the density of sap, and m is sapwood water content. Sapwood density (kg m^{-3}) and m (kg water kg^{-1} dry sapwood) were determined separately for each of the four probe positions. Heat pulse and sap velocity nomenclature and units of expression are consistent with Edwards et al. (1996).

The fraction of sapwood functional in water transport (f_S) was calculated for each tree as the sap velocity measured at positions P1 through P4, divided by the maximum sap velocity measured at one of the four probe locations (usually at P1 or P2). Our estimate of f_S based on four fixed probe installations is conceptually similar to the correction coefficient calculated by Zang et al. (1996) with two fixed and one moveable heat-pulse probe.

Statistical analysis

Differences in ρ_b and m with sapwood depth were examined by one-way ANOVA and pair-wise Tukey's Studentized Range (HSD) tests (SAS, Cary, NC). Errors associated with sample size (n) in calculations of f_S were estimated by random unstratified Monte Carlo sampling with replacement from the data set of 20 trees. One hundred random samples at each value of n (2 to 20) were used to obtain an estimate of standard deviation (standard error) and coefficient of variation for the population mean.

Results

Among the 55 original trees selected from Sites 1 and 2, stem diameters (dbh) ranged from 15 to 69 cm (Figure 2A). Bark thickness varied between 0.8 and 3.0 cm, and generally increased as stem diameter increased (data not shown). Sapwood thickness was also a strong function of stem diameter and ranged from 1.9 cm for one of the smallest trees to 14.8 cm for one of the largest trees (Figure 2A). Sapwood thickness was uniform around the circumference of a given tree. Five replicate cores taken from Tree 27 (dbh 69 cm) revealed that the thickness of sapwood varied by no more than 1.4 cm (14.2 compared with 15.6 cm). Coefficients of variation for sapwood thickness ranged from 0.9 to 21.8%, and across all 55 trees averaged less than 10%.

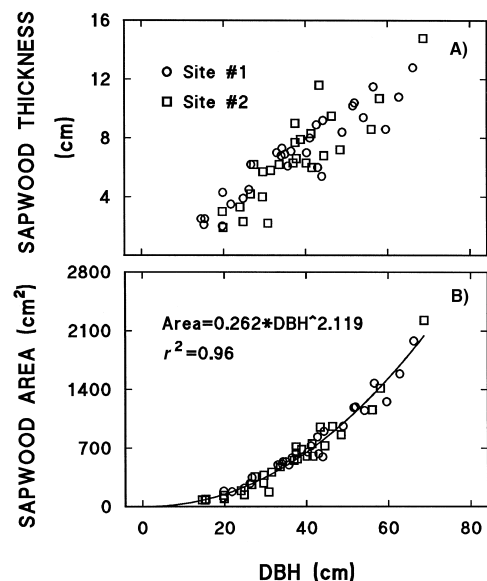Sapwood area, defined as the cross-sectional area between

Figure 2. Relationships between measured stem diameter (dbh) and (A) sapwood thickness and (B) cross-sectional sapwood area for 55 yellow-poplar trees.
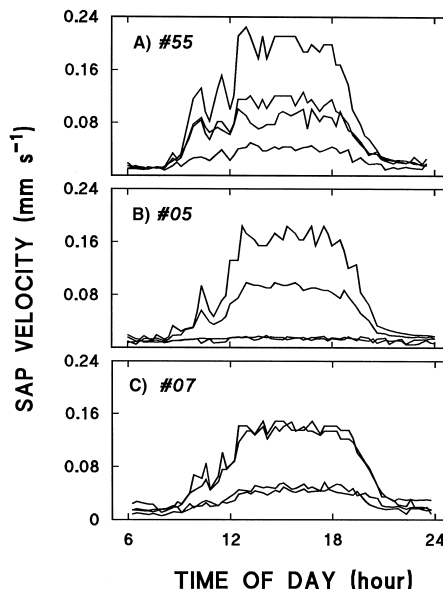

Figure 3. Diurnal variation in sap velocity measured at four sapwood depths in three yellow-poplar trees with stem diameters ranging from 15 to 66 cm. Measurements of sap velocity were made on June 12, 1998.

the inner bark surface and the outer heartwood, varied with stem diameter (Figure 2B). Sapwood area ranged from 75 to 2227 cm^2 and averaged 658 cm^2 across the 55 trees. Sapwood areas could be estimated from a power function-based regression (Equation 1). Such a regression indicated that stem diameter at breast height explained 96% of the observed variation in sapwood area (Figure 2B).

Rates of sap velocity were highly dependent on the depth of probe insertion into the sapwood (Figure 3). Sap velocity was greatest for probes located in outer sapwood annuli (P1 and P2) and lowest for the probes in closest proximity to the heartwood (P3 and P4). These depth-dependent differences were evident during early morning and late afternoon, but were most pronounced at midday when rates of sap velocity approached and often exceeded 0.16 mm s^{-1} (Figure 3). Sap velocity–depth profiles for mid-afternoon (1200–1600 h) and nighttime (2200–0200 h) periods corroborated the strong decline in velocity with increasing sapwood depth (Figure 4). These velocity–depth profiles were variable, as were nighttime rates of sap velocity during what should have been periods of low to zero flow. Several trees, including Tree 45, had appreciable rates of nighttime sap velocity especially in the outermost (P1) sapwood (Figure 4E). The limit of detection for sap velocity at night was 0.016 mm s^{-1} (data not shown).

Variation was also examined for ρ_b and m in relation to sapwood depth. No significant depth-dependent changes were observed for ρ_b (Figure 5A). Wood density varied from 385 to 518 kg m^{-3} and averaged 469 kg m^{-3} across all four probe positions. There was a clear decline, however, in m between the two probe positions P1 and P2 (Figure 5B). Water content at the outer P1 position averaged 1.04 kg kg^{-1} compared with 0.89 kg kg^{-1} at positions P2, P3 and P4.

Tree-specific sap velocities across the four probe positions indicated that f_S varied between 0.49 and 0.96 (Figure 6). There was no relationship between f_S and sapwood thickness, or between f_S and stem diameter (data not shown). The fraction of functional sapwood averaged ($\pm$ 1 SD) 0.66 $\pm$ 0.13 for the trees on which radial profiles were determined. A Monte Carlo analysis of the f_S data set indicated that the standard error in estimated mean f_S declined rapidly with increasing sample size (Figure 7B). At $n = 10$, the coefficient of variation in mean f_S was 7%, and at $n = 15$, it was slightly less than 5% (Figure 7C).

Whole-tree sap flow (Q) increased with increasing stem diameter (Figure 8). Estimates of Q for each of the 20 trees mea-
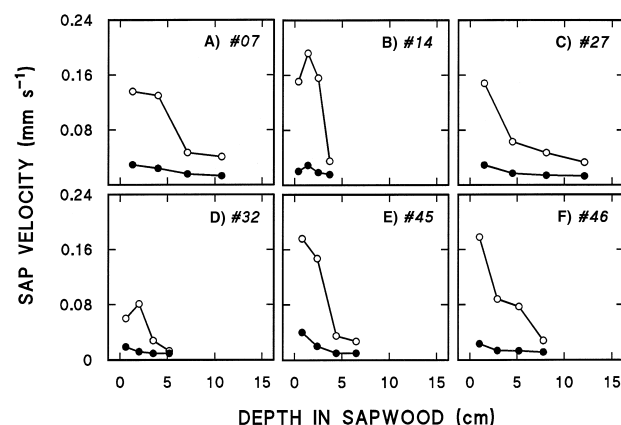

Figure 4. Variation of sap velocity with depth in sapwood during periods of peak (1200–1600 h) and minimum (2200–0200 h) sap flow.
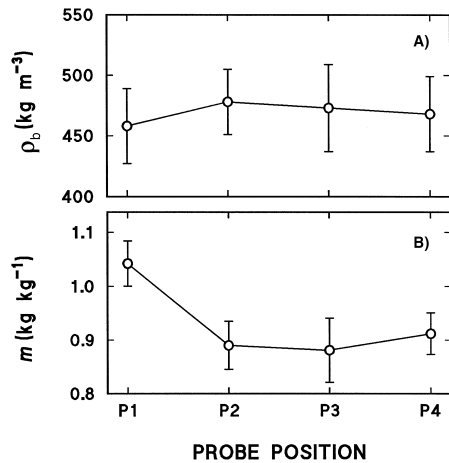
Figure 5. Depth-dependent variation in (A) sapwood density (ρ_b) and (B) sapwood water content (m). Data are the means ($\pm$ SE) of 20 trees.

Figure 7. Results of a Monte Carlo analysis showing the relationships between (A) mean f_S ($\pm$ SD), (B) standard error of the mean, and (C) coefficient of variation as a function of sample size.

sured in this study ranged from 28 (Tree 55) to 675 kg day^{-1} (Tree 27) and averaged 223 kg day^{-1} for the entire data set. Partitioning whole-tree sap flow to the four sapwood annuli indicated that, for the largest tree measured in this study (Tree 27), approximately 502 kg day^{-1} was moved in the two outermost sapwood annuli (measured by P1 and P2) and 173 kg day^{-1} in the two innermost annuli (measured P3 and P4). Sap flow measured at P1 alone accounted for almost 52% of total whole-tree Q or 353 out of 675 kg day^{-1} (data not shown).

Discussion

Sap velocity exhibits substantial variation in relation to sapwood depth (Cohen et al. 1981, Dye et al. 1991, Čermák et al. 1992, Becker 1996, Oren et al. 1999). Although not a universal observation, rates of sap velocity in many non-, ring- and diffuse-porous species are several-fold higher in outer sapwood compared with inner sapwood. This decline in sap velocity with sapwood depth prompted our hypothesis that the fraction of sapwood functional in water transport would decrease as either stem diameter or sapwood thickness increased. Köstner et al. (1998) put forth a similar hypothesis when they argued that
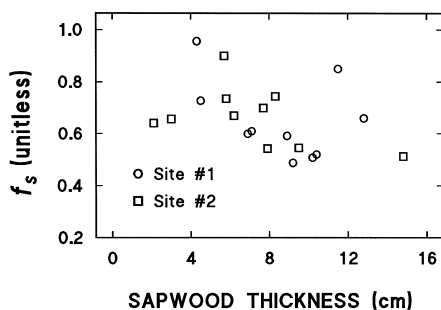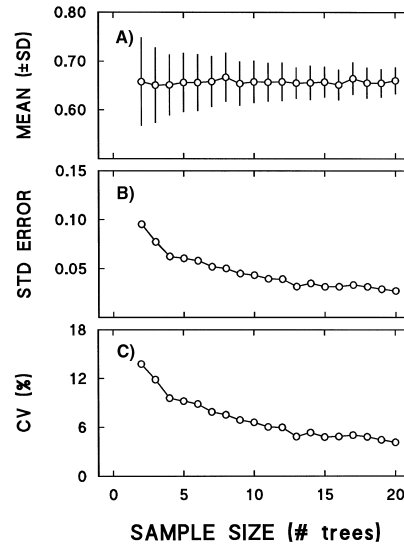
sapwood thickness or number of growth rings was a key contributor to radial variation in sap velocity. In our study, rates of sap velocity showed a progressive decline as probes were inserted deeper into the sapwood. However, no relationship was observed between f_S and sapwood thickness. Relative sap velocities averaged across all study trees were 0.98 at P1, 0.66 at P2, 0.41 at P3 and 0.35 at P4. This radial profile is similar to those derived with heat pulse methodology for the diffuse-porous species *Citrus sinensis* L. (Cohen et al. 1981), for *Eucalyptus globulus* ssp. *globulus* Labill. (Zang et al. 1996) and for several trees of a dipterocarp and heath forest (Becker 1996). It contrasts, however, with an apparent lack of radial variation in sap velocity for the diffuse-porous tree *Liquidambar styraciflua* L. and for the ring-porous hardwood *Quercus alba* L. (Phillips et al. 1996). These authors speculated that the constant heat-flow method (Granier 1987) used in their study to measure sap velocity probably underestimated the magnitude of radial variation, because zones of hydroactive sapwood were not adequately represented along the entire length of (in
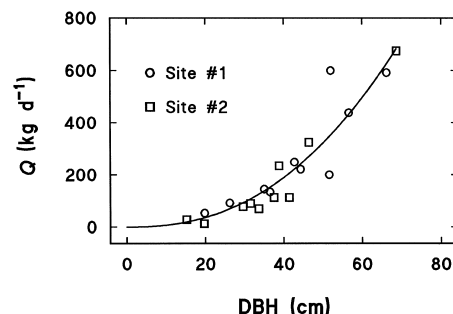
Figure 6. Tree-to-tree variation in the fraction of functional sapwood (f_S) plotted as a function of sapwood thickness for the 20 trees measured in this study.

Figure 8. Whole-tree water use (Q) for 20 yellow-poplar trees expressed as a function of measured stem diameter (dbh).

their case) a 20-mm-long measurement probe. Clearwater et al. (1999) recently reported that depth-dependent variation in sap velocity might be difficult to detect with constant heat-flow probes because these devices do not accurately integrate sap velocity along their lengths. Clearwater et al. (1999) used a simple model to examine the errors associated with nonuniform rates of sap velocity. They reported that sap velocity could be underestimated by 8% in diffuse-porous trees and by up to 45% in ring-porous trees if moderate to steep gradients in sap velocity were present along the length of the measurement probe. Technical limitations such as these must be considered when results are either compared among studies or when field experiments are conducted to quantify radial variation in sap velocity.

Despite a decline in sap velocity with increasing sapwood depth, we were unable to identify the cause of this depth-dependent variation. Wood density measured at each of the four probe positions varied little or increased only slightly with increasing sapwood depth, whereas m decreased on average from 1.04 to 0.89 kg kg^{-1} between the two outermost probe positions (P1 and P2). According to Equation 2, this 15% decline in m would contribute to an approximate 10% reduction in estimated sap velocity. Such a decline cannot alone explain the substantial gradient observed for sap velocity in relation to sapwood depth. Phillips et al. (1996) were similarly unable to establish cause-and-effect relationships between relative water content, wood specific gravity and radial profiles of sap velocity in *Pinus taeda* L. saplings. It was suggested that a change in wood specific gravity from outer (0–20 mm) to inner (20–40 mm) sapwood marked a zone of transition between mature and juvenile xylem. Phillips et al. (1996) used published information on tracheid length and lumen diameter to suggest that the hydraulic conductivity of juvenile xylem in pine might be 40% less than that of mature sapwood. They speculated that low hydraulic conductivity of juvenile, relative to mature, xylem was the likely cause of radial variation in sap velocity with sapwood depth. Such a conclusion is in general agreement with earlier research (Mark and Crews 1973, Miller et al. 1980, Čermák et al. 1992), although Dye et al. (1991) offered an alternative explanation for why heat-pulse velocity declines in xylem near the center of stems. They argued that the innermost xylem forms early in the life of a tree and functions as the primary conduit for the supply of water to young branches. These branches die or become shaded, however, as a tree gets older and heat-pulse velocity declines with increasing sapwood depth not because of age-related effects on hydraulic conductivity *per se*, but because older xylem simply no longer participates in the supply of water to transpiring surfaces. A series of pruning or shading experiments designed to alter radial profiles of sap velocity through either the removal or shading of lower branches could determine the validity of this hypothesis.

Because estimates of f_S are needed for the accurate extrapolation of sap velocity measured on individual trees to the canopy scale (Köstner et al. 1998), a major objective of our study was to determine the proportion of sapwood functional in water transport. Unfortunately, few studies adequately quantify the extent of radial variation in sap velocity for the species in question and estimates of f_S are seldom provided. Zang et al. (1996) used a combination of fixed and moveable probes to estimate the fraction of functional sapwood in two *E. globulus* trees and reported values that ranged between 0.61 and 0.94 (*C* in their Table 4). A re-analysis of depth–velocity profiles for three Bornean heath and dipterocarp trees indicated that f_S varied from 0.51 to 0.82 (wet and dry seasons combined) and averaged 0.67 (Becker 1996). Granier et al. (1996c) reported a radial correction factor of 0.86 for Scots pine (*Pinus sylvestris* L.) and Köstner et al. (1996) indicated that this factor was a function of sapwood thickness. No details, however, were provided to substantiate either the shape or significance of this functional relationship. Our results with yellow-poplar are in general agreement with many of these investigations, and further emphasize the uncertainties associated with the assumption that all sapwood is functional in water transport (Loustau et al. 1996). This statement applies to trees of all diameter classes, but especially to young saplings, because in many species the total cross-sectional area of a stem (or branch) may visually appear to be entirely sapwood. We have observed this in red maple, where the transition between sapwood and heartwood is difficult to detect, yet estimates of f_S nevertheless averaged 0.74 (Wullschleger et al. 2000).

Tree-to-tree variation in f_S for the twenty yellow-poplar trees measured in our study was high. Estimates ranged from a low of 0.49 to a high of 0.96, although an average estimate of 0.66 compares favorably with values obtained in other studies (Becker 1996, Zang et al. 1996). Some of the observed variation in f_S was no doubt a result of sampling trees that differed not only in stem diameter, but also in sapwood thickness, number of growth rings and age. A less variable estimate of f_S might have been possible if we had restricted our analysis to trees of similar diameter. Nonetheless, the substantial variation that we observed in f_S highlights a source of uncertainty or error not often fully considered when extrapolating sap velocity rates to the canopy scale. Hatton et al. (1995) showed that radial integration of sap velocity to a rate of sap flow for an individual tree was a major source of error when estimating transpiration for a box poplar (*E. populnea* F.J. Muell.) woodland. The methodology used by Hatton and Vertessy (1990), Hatton et al. (1995), Vertessy et al. (1995) and Vertessy et al. (1997) has the advantage that at least four heat-pulse probes were routinely used per tree for the sampling of sap velocity with depth and (often) bole quadrant. Because of the cost and complexity of the heat pulse technique, the less-expensive thermal dissipation probe is being increasingly used for the measurement of sap velocity. Users of this approach often install only a single probe per tree and, although careful to quantify tree-to-tree variation in sap velocity, often fail to either quantify or report variation in f_S (Loustau et al. 1996, Hogg et al. 1997, Martin et al. 1997). If our study is representative of the uncertainty associated with tree-to-tree variation of f_S, then estimated transpiration rates for a hypothetical yellow-poplar stand having a sapwood area of 10 m^2 ha^{-1} and a midday sap velocity of

0.15 mm s^{-1} would average 0.36 mm h^{-1} with a 95% confidence interval of between 0.33 and 0.38 mm h^{-1}, assuming that f_S was measured on all 20 trees. The 95% confidence interval would increase to between 0.31 and 0.40 mm h^{-1} if 10 trees were measured and to between 0.26 and 0.45 mm h^{-1} if only two trees were measured. An expanded analysis of the uncertainties associated with tree-to-tree variation in sap velocity and radial gradients in sap velocity, similar to that conducted by Hatton et al. (1995), will be required before these techniques can be used to compare rates of water use between stands subjected to different forest management strategies (Bréda et al. 1995) and to distinguish between treatments ranging from salinity, imposed drought and elevated CO_2 concentration (Bréda et al. 1993, Ellsworth et al. 1995, Myers et al. 1998).

The importance of f_S in extrapolating sap velocity measurements to trees and stands underscores the need for more intensive investigations in this area. Our studies with a diffuse-porous tree indicate that considerable radial variation in sap velocity exists and emphasize that reliable estimates of f_S are critical to the scaling process. The use of multiple heat pulse units made it possible to measure up to four trees at a time, although it still took almost six weeks to sample 20 trees. Clearly, a more rapid method for measuring f_S is needed. A series of movable and fixed probes have been used to assess radial gradients in sap velocity for several species (Dye et al. 1991, Hatton et al. 1995) and Zang et al. (1996) have successfully used such an approach to quantify functional sapwood in a limited number of trees. We envision that a range of trees could be sampled each day by this technique. In addition to sampling more trees, the measurement errors associated with f_S could be further reduced by measuring sap velocity in smaller sapwood increments than would otherwise be possible with the equal-area approach (Hatton et al. 1990) used in our study.

Acknowledgments

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