

Variability in radial sap flux density patterns and sapwood area among seven co-occurring temperate broad-leaved tree species

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Summary Forest transpiration estimates are frequently based on xylem sap flux measurements in the outer sections of the hydro-active stem sapwood. We used Granier's constant-heating technique with heating probes at various xylem depths to analyze radial patterns of sap flux density in the sapwood of seven broad-leaved tree species differing in wood density and xylem structure. Study aims were to (1) compare radial sap flux density profiles between diffuse- and ring-porous trees and (2) analyze the relationship between hydro-active sapwood area and stem diameter. In all investigated species except the diffuse-porous beech (*Fagus sylvatica* L.) and ring-porous ash (*Fraxinus excelsior* L.), sap flux density peaked at a depth of 1 to 4 cm beneath the cambium, revealing a hump-shaped curve with species-specific slopes. Beech and ash reached maximum sap flux densities immediately beneath the cambium in the youngest annual growth rings. Experiments with dyes showed that the hydro-active sapwood occupied 70 to 90% of the stem cross-sectional area in mature trees of diffuse-porous species, whereas it occupied only about 21% in ring-porous ash. Dendrochronological analyses indicated that vessels in the older sapwood may remain functional for 100 years or more in diffuse-porous species and for up to 27 years in ring-porous ash. We conclude that radial sap flux density patterns are largely dependent on tree species, which may introduce serious bias in sap-flux-derived forest transpiration estimates, if non-specific sap flux profiles are assumed.

Keywords: annual growth rings, diffuse-porous, dyes, *Fagus sylvatica*, *Fraxinus excelsior*, Granier method, ring-porous, sap flow, Tilia, Weibull function.

Introduction

In forest ecosystems, transpiration estimates are frequently based on xylem sap flux measurements of individual trees assuming that the sum of the mass flow in tree stems equals total canopy transpiration with a short time lag (Kaufmann and Kelliher 1991). Total stem sap flow is estimated from the product of sap flux and the cross-sectional area of hydro-active xylem or sapwood (Granier 1985), but these estimates can result in large errors if radial xylem flux density profiles are

unknown and uniform sap flux across the entire sapwood is assumed.

In some tree species, the determination of sapwood depth is difficult. Several authors have reported that sap flux density reaches a maximum in the xylem adjacent to the cambium and decreases exponentially along the radial axis toward the inner xylem (Swanson 1967, 1974, Mark and Crews 1973, Miller et al. 1980, Dye et al. 1991, Čermák et al. 1992, Becker 1996, Phillips et al. 1996, Oren et al. 1999, Fernández et al. 2001, Nadezhdina et al. 2002, Ford et al. 2004a, 2004b, Kubota et al. 2005a, 2005b). Such a pattern has been reported in the widely distributed European species *Fagus sylvatica* L. For example, Köstner et al. (1998), Granier et al. (2000) and Schäfer et al. (2000) all reported an exponential decrease in xylem sap flux density from the outer to the inner sapwood of this species. However, the same pattern may not be characteristic of other temperate tree species.

The hydraulic conductivity of the xylem in tree stems is partly dependent on the seasonal rhythm of conduit formation. Trees with ring-porous sapwood such as oak and ash conduct water only in the outermost annual growth rings (Ellmore and Evers 1986, Granier et al. 1994). In conifers and diffuse-porous broad-leaved trees, sapwood area usually occupies a greater proportion of stem cross-sectional area and is composed of relatively narrow conduits (Čermák and Nadezhdina 1998) that are typically more resistant to water transport than the larger vessels of ring-porous trees. Sapwood is the portion of wood external to the heartwood that contains living parenchyma cells, stores carbohydrates and includes that part of the xylem that is active in the transport of water and solutes from the soil to the crown (IAWA 1964, Braun 1970). However, the hydro-active sapwood area is often difficult to quantify because of the lack of a clear border between active and inactive xylem. The amount of sapwood area and its conducting role varies with species, tree age and environmental conditions (Čermák and Nadezhdina 1998). In some tree species, sapwood and heartwood (the inner, nonconductive wood) can be distinguished easily by the darker color of the heartwood or a marked drop in tissue water content (Taylor et al. 2002). However, this is not true of all tree species and it may be true of some but not all individuals of a given species. It is often diffi-

cult, therefore, to estimate sapwood area on the basis of changes in color, water content or wood density across wood core samples (e.g., Köstner et al. 1998). Furthermore, sapwood cores may change color after the release of phenols and terpenes or after alteration of precursor substances such as phenolic glycosides (Taylor et al. 2002, 2007).

A widely used method for estimating the hydro-active sapwood area is to dye the xylem. Dye is injected into living trees or applied to stem discs obtained from harvested trees or to extracted wood cores. Certain dyes such as indigo carmine (Andrade et al. 1998, Meinzer et al. 2001), safranin (Granier et al. 1994), berberine chloride (Gessler et al. 2005) and fuchsin (Sano et al. 2005) are added to the transpiration stream and stain the cell walls of water-conducting tracheids and vessels. Other dyes are used to indicate differences in chemical properties between sapwood and heartwood. For example, bromocresol green is a pH indicator (Kutscha and Sachs 1962, Schäfer et al. 2000) and iodine-potassium iodide (Lugol's solution) is an indicator for starch (Vötter 2005). In the case of extracted wood cores, sapwood depth is usually determined at only a few points on the stem, and sapwood area is then calculated by extrapolation assuming a constant sapwood depth in all stem directions.

Dyeing of stem discs has the advantage over the use of wood cores that the whole cross-sectional sapwood area can be investigated, but the method is destructive, as is thermo-imaging (Granier et al. 1994). Computer tomography provides a non-destructive but costly technique for sapwood area determination (Habermehl et al. 1982a, 1982b, Rust 1999), and it may be limited in applicability to only a few stems in a stand. Based on a review of Granier's thermal heat dissipation probe method, Lu et al. (2004) concluded that the use of sap flux measurements may provide a suitable nondestructive method to localize the sapwood-heartwood boundary and thus to determine the sapwood area of trees. Sap flux is measured by the use of heat pulse probes (Granier et al. 1994, Hatton et al. 1995), the heat-field deformation technique (Nadezdina et al. 2002) or the constant-heating method (Phillips et al. 1996, Lu et al. 2000, Ford et al. 2004a). We applied the constant-heating method with heating probes at various xylem depths to analyze radial profiles of sap flux density in the sapwood of seven broad-leaved tree species differing in wood density and xylem structure. Our study aims were to (1) compare patterns of radial sap flux density between trees with diffuse-porous and ring-porous xylem anatomy; and (2) compare the size of the hydro-active xylem between ring-porous and diffuse-porous tree species by relating it to stem diameter. Our intention was to provide a basis for more accurate estimates of stand transpiration in mixed forests obtained from sap flux measurements made exclusively in the outermost sections of the sapwood.

Materials and methods

Study site

The study was conducted in a mixed temperate broad-leaved forest in the Hainich National Park (Thuringia, Central Germany). The forest stand is located in the northeastern part of

the National Park between 295 and 355 m a.s.l. (51°04' N, 10°30' E). European beech (*Fagus sylvatica*), linden (*Tilia sp.*), common ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.), sycamore maple (*Acer pseudoplatanus* L.), Norway maple (*A. platanoides* L.) and field maple (*A. campestre* L.) occur at different densities within the forest. Mean tree height varies between 27.9 m in the denser part of the forest (614 stems ha⁻¹) to 32.9 m in the less dense forest area (392 stems ha⁻¹).

Mean annual temperature of the study site in the years 1973–2004 was 7.5 °C (Deutscher Wetterdienst). Mean annual temperature in 2006 (9.4 °C, Meteomedia AG, 2006) was higher than the long-term mean. Mean annual precipitation in 2006 (518 mm, Meteomedia AG, 2006) was lower than the mean for the years 1973–2004 (590 mm, Deutscher Wetterdienst).

Sap flux profiles

Xylem sap flux was measured between August and September 2006, during which period, there was no precipitation. Mean vapor pressure deficit during the light phase varied between 5 and 15 hPa, total daily radiation ranged between 6 and 19 MJ m⁻² day⁻¹. Characteristics of the selected trees are presented in Table 1. We estimated the sapwood area of the trees by dye injection (see details below). Xylem sap flux was measured by the heat dissipation method (constant-heating method) introduced by Granier (1985, 1987). Pairs of 20-mm-long and 2.0-mm-diameter heating probes were inserted at a depth of 0–20 mm in the stem sapwood. For measurements at xylem depths of 20–40, 40–60 and 60–80 mm, longer needles with identical heating and sensing devices were driven into holes in the xylem having the same diameter as those drilled for the outermost (0–20 mm depth) sensors. The probes were manufactured according to Granier's original design (Granier, pers. comm.). The upper probe was constantly heated, whereas the lower probe was unheated and recorded the reference temperature of the wood. The electric current of the heating element was held constant at 0.12 A with a heating power of 0.2 W. All sensors were inserted at 1.3 m stem height into the sapwood on the north side of the trunk. To guarantee direct contact with the surrounding wood and uniform heat dissipation, the probes were encapsulated in aluminum tubes previously inserted into the stem. The probes were placed 10–15 cm apart to avoid thermal interference, due to heat dissipation from the upper heated probe. The sensors at insertion depths of 20–40, 40–60 and 60–80 mm were placed radially between the northern and western sides of the trunk in proximity to the 0–20 mm sensor. All probes were covered with an insulating polystyrene mat, which in turn, was covered with reflective foil and transparent plastic to minimize the influence of solar irradiance and air temperature.

For the ring-porous species, *Fraxinus excelsior*, a smaller sapwood depth was expected. Therefore, the outer probes had a length of only 10 mm, and additional probes were inserted at depths of 10–20 and 20–30 mm.

The temperature difference (ΔT) between upper and lower sensor probes was recorded every 30 s with a CR10X data log-

Table 1. Biometric characteristics of the 11 stems of seven broad-leaved tree species analyzed for sap flux density–xylem depths relationship in the Hainich forest. Abbreviations: DBH = diameter at breast height; A_B = basal area; A_S = sapwood area; and na = not available.

Species	Stem	DBH (cm)	Age ¹ (years)	Tree height (m)	Crown area (m ²)	A_B (cm ²)	A_S (cm ²)	A_S/A_B	Sapwood depth (cm)	Annual rings in sapwood
Diffuse-porous										
<i>Fagus sylvatica</i>	Bu28	28.7	108	27.2	16.5	647	484	0.75	7.2	73
<i>Fagus sylvatica</i>	Bu1	39.8	104	32.7	20.1	1244	906	0.73	9.6	70
<i>Carpinus betulus</i>	HBu4	48.7	149	26.7	88.6	1863	1289	0.69	10.9	85
<i>Tilia cordata</i>	Li17	27.1	na	22.8	26.5	577	454	0.79	7.3	na
<i>Tilia platyphyllos</i>	Li11	28.3	30	26.2	21.9	629	486	0.77	7.4	29
<i>Tilia platyphyllos</i>	Li1	46.2	62	33.2	39.7	1676	1044	0.62	8.9	40
<i>Acer pseudoplatanus</i>	BAh4	41.1	110	26.5	36.5	1327	1127	0.85	12.6	88
<i>Acer campestre</i>	FAh167	26.8	92	23.9	na	564	364	0.65	5.4	46
Ring-porous										
<i>Fraxinus excelsior</i>	Es8	14.0	50	14.3	17.7	154	15	0.10	0.3	5
<i>Fraxinus excelsior</i>	Es2	27.2	108	29.6	5.1	581	88	0.15	1.1	12
<i>Fraxinus excelsior</i>	Es14	52.9	81	31	46.1	2198	521	0.24	3.4	11

¹ Minimum estimated tree age. Annual rings were counted from wood cores taken at 1.3-m height.

ger (Campbell Scientific, U.K.) equipped with a 16/32-channel multiplexer (AM16/32, AM416, Campbell Scientific). Thirty-minute means were calculated from the 30-s readings and stored by the data logger. Temperature differences were converted to sap flux densities (J_s ; g m⁻² s⁻¹) based on Granier's empirical calibration equation (Granier 1985, 1987):

$$J_s = 119 \left(\frac{\Delta T_M - \Delta T}{\Delta T} \right)^{1.231} = 119 K^{1.231} \quad (1)$$

where ΔT_M is the maximum temperature difference when sap flow is assumed to be zero.

Sapwood area and diameter at breast height

Sapwood depth was determined during August 2006 for trees of *Fagus sylvatica*, *Carpinus betulus*, *Tilia cordata*, *Acer pseudoplatanus*, *A. platanoides*, *A. campestre* and *Fraxinus excelsior* with a minimum diameter at breast height (DBH) of 10 cm and a maximum diameter of 60 cm. Measurements were made on at least 12 trees per species that were not used for sap flux measurements (Table 2). Sapwood depth at breast height was estimated by a staining method (Goldstein et al. 1998, Meinzer et al. 2001). During the morning (0800–1100 h), when transpiration rates were expected to rise, a core to the center of the trunk was taken at 1.3-m height with a 5-mm diameter increment borer (Suunto Oy, Vaanta, Finland). Immediately after coring, a 0.1% indigo carmine-solution was injected into the hole, which was refilled when necessary. After 2 to 4 h, when the xylem sap should have moved upward in the active xylem, a second core was taken 3–5 cm above the injection point. The stained depth of the sapwood was determined based on the following criteria. Wood sections continuously colored by indigo-carmin and adjacent wood sections with at least two spots of dye were considered to be conducting sapwood. This border was taken as the maximum sapwood depth.

Sapwood area was then calculated as the area of the stem ring with the estimated sapwood depth.

The wood core removed to allow dye injection was used for analysis of annual tree ring diameter (I. Schmidt, unpublished data) using LINTAB and TSAP-Win software (RINNTECH, Heidelberg, Germany).

The wood cores were cut into 10-mm segments for wood density determination. Fresh mass was recorded immediately after core extraction. Dry mass was measured after drying at 70 °C for 48 h to constant mass. Wood density was determined from the mass and volume of the oven-dried 10-mm segments with volume being determined by caliper measurements of length and width at several points on the fresh wood segments.

Data analysis

The relationship between sapwood area as estimated by dyeing and DBH was approximated by the following power function according to Vertessy et al. (1995) and Meinzer et al. (2001, 2005):

$$A_s = a \text{DBH}^b \quad (2)$$

where A_s is sapwood area (cm²) and a and b are species-specific coefficients determined by regression techniques.

To analyze the change in J_s with sapwood depth, J_s was calculated from the data obtained at the four measuring depths (three for ash) in the xylem. By calculating daily means, we minimized time lag effects on J_s at different sapwood depths. Sap flux density tended to increase later in the morning, and decrease earlier in the evening, at increasing xylem depths. The time of peak J_s differed by up to 2 h among the xylem depths. The J_s data were normalized to the value observed at the outermost measuring point in the xylem (0–20 mm for diffuse-porous species with a midpoint at 10 mm, 0–10 mm for ash with a midpoint at 5 mm). The dependence of relative J_s on radial xylem depth (x) was described by a four-parametric

Table 2. Diameter at breast height (DBH), sapwood depth, mean number of annual rings in the hydro-active sapwood (absolute numbers) and mean annual ring width in seven broad-leaved tree species (minimum and maximum, or mean (standard deviation) of n stems per species).

Species	n	DBH (cm)		Sapwood depth (cm)		Annual rings in sapwood		Mean annual ring width in sapwood (mm)
		min.	max.	min.	max.	min.	max.	
Diffuse-porous								
<i>Fagus sylvatica</i>	19	13.1	57.9	3.6	13.3	25	73	2.02 (0.99)
<i>Carpinus betulus</i>	20	13.4	61.8	2.3	14.5	25	104	1.41 (0.71)
<i>Tilia cordata</i>	24	10.8	60.2	6.8	10.0	14	77	2.17 (0.88)
<i>Acer pseudoplatanus</i>	15	16.2	57.6	5.3	17.3	18	169	1.63 (0.74)
<i>Acer platanoides</i>	14	13.5	51.9	7.6	12.1	38	95	1.67 (0.61)
<i>Acer campestre</i>	12	13.1	42.3	1.7	11.8	29	68	1.18 (0.43)
Ring-porous								
<i>Fraxinus excelsior</i>	24	9.9	57.6	0.2	5.7	3	27	2.35 (1.39)

Weibull function (Kubota et al. 2005b):

$$J_s = \frac{c-1}{c} + a \left(\frac{c-1}{c} \right)^{\frac{1-c}{c}} \cdot e^{-\left(\frac{x-d}{b} + \left(\frac{c-1}{c} \right)^{\frac{1}{c}} \right)^c} \cdot \left(\frac{x-d}{b} + \left(\frac{c-1}{c} \right)^{\frac{1}{c}} \right)^{c-1} \quad (3)$$

where coefficient a characterizes the peak value of the function, the coefficients b and c determine the shape of the curve, and d is the xylem depth where maximum J_s is located.

Results

Species differences in radial sap flux density profiles

Radial patterns of J_s showed considerable variability among the 11 investigated stems of the seven tree species. In all stems, J_s peaked in the first 4 cm of the xylem directly adjacent to the cambium according to the radial sap flux density profiles modeled by four-parametric Weibull functions (Figure 1). However, radial J_s peaked in the youngest xylem elements in *Fagus sylvatica* (diffuse-porous) and *Fraxinus excelsior* (ring-porous) and decreased exponentially toward the inner sapwood, whereas radial J_s patterns in *Carpinus betulus*, *Acer pseudoplatanus*, *A. campestre* and *Tilia* sp. showed a hump-shaped curve with maximum values 2 to 4 cm beneath the cambium and lower values in the youngest xylem elements. All stems showed decreasing J_s with increasing xylem depth beyond the maximum in the modeled flux profiles, but the slope of the decrease differed markedly among species and among stems of different DBH classes. The difference in the location of maximum J_s among species is expressed by the value of d in the four-parametric Weibull function describing the radial J_s profiles. Coefficient d was < 0.5 or even negative in *Fraxinus excelsior* and *Fagus sylvatica*, but ranged between 1.9 and 3.4 in the other species (Table 3). In the *Tilia* species, radial patterns

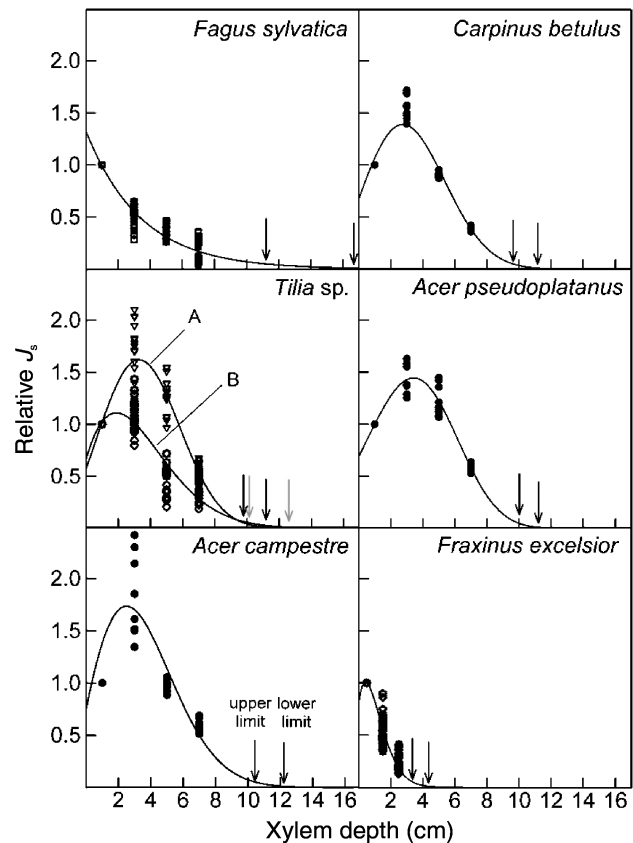


Figure 1. Xylem depth and mean daily sap flux density (J_s) normalized to the outermost measuring point. In all diffuse-porous species the outermost measuring point was at 1-cm depth, and in the ring-porous *F. excelsior* at 0.5 cm. Four-parametric Weibull functions were fitted to the data (solid lines). Values are means of 1–3 trees per species that were measured for between 8 (*A. campestre*, *A. pseudoplatanus*) and 22 (*F. sylvatica*) days. Sap flux density at the outermost measurement point is given a relative value of one and is the mean of up to 22 individual measurements. For *Tilia* sp. two stem size classes were analyzed separately (A = Li1: 46.2 cm, B: Li17, 27.1 cm and Li11: 28.3 cm). Arrows indicate the lower and upper limit (i.e. $J_s = 0.01$ or 0.05) of the transition zone from active to inactive xylem (*Tilia* sp.: A = black arrows, B = gray arrows) as estimated by modeled data from Weibull functions.

of J_s of large- and medium-diameter stems differed significantly: peak values occurred at about 3.5 cm from the cambium in the widest stem, but was within 2 cm of the cambium in the narrower stems (Figure 1, center row). Although J_s in Figure 1 is expressed relative to the outermost measuring point in the sapwood (at 1.0 or 0.5 cm depth), daily variation in patterns was observed, particularly in *Acer campestre*, where measurements on eight days yielded relative J_s values at a sapwood depth of 3 cm between 1.4 and 2.5 (Figure 1, bottom row). Temporal scatter of relative J_s was smaller in *A. pseudo-platanus* and *Carpinus betulus* which had a greater proportion of leaf area in the upper canopy of the stands than the sub-dominant individuals of *A. campestre*.

No distinct boundary between hydro-active and inactive xylem was detected within the 8-cm-wide flux profiles, indicating that J_s gradually approached zero flow with increasing xylem depth in all species. To estimate the hydro-active sapwood depth, we defined a relative $J_s = 0.05$ as the upper limit, and a relative $J_s = 0.01$ as the lower limit of the transition zone from active to inactive xylem based on the modeled J_s profiles. We obtained a mean sapwood depth of 11.2 cm (upper boundary) to 16.7 cm (lower boundary) for the *Fagus sylvatica* stems (Figure 1). The other diffuse-porous species had sapwood depths between 9.6 and 12.6 cm. The narrowest sapwood was found in the ring-porous species *Fraxinus excelsior* with an upper limit of 3.3 cm and a lower limit of 4.3 cm (Figure 1, bottom row). In the *Tilia* stems, there was only a minor difference in hydro-active xylem depth between the stem diameter classes (A: 46-cm DBH, B: 27–28-cm DBH) (Figure 1, center row).

In Table 4, we converted absolute xylem depth to relative depth by defining a relative J_s value of 0.01 as the boundary between hydro-active and inactive xylem (sapwood–heartwood boundary); this depth was set to 1. Accordingly, maximum J_s occurred immediately beneath the cambium in

Table 3. Coefficients of the four-parametric Weibull function describing the relationship between sap flux density (J_s) and xylem depth in the seven study species. For analysis, mean daily J_s normalized to the J_s at the outermost measuring point (=1) were used. For *Tilia*, the two similar species *T. platyphyllos* and *T. cordata* were pooled; however, stems of two diameter classes (A > 35 cm, B < 35 cm) were analyzed separately. Values are means of 1–3 stems per species (genus).

Species	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>r</i> ²
Diffuse-porous					
<i>Fagus sylvatica</i>	2.69	3.42	1.00	–2.44	0.95
<i>Carpinus betulus</i>	1.37	5.88	2.43	2.79	0.97
<i>Tilia</i> sp. (A)	1.62	6.35	2.71	3.28	0.93
<i>Tilia</i> sp. (B)	1.11	4.52	1.67	1.88	0.77
<i>Acer pseudoplatanus</i>	1.44	8.98	3.47	3.42	0.91
<i>Acer campestre</i>	1.74	4.86	1.94	2.50	0.79
Ring-porous					
<i>Fraxinus excelsior</i>	1.00	1.44	1.54	0.42	0.96

F. sylvatica, at a relative sapwood depth of 0.10 in *F. excelsior*, and at a relative depth of 0.15 to 0.30 in the other diffuse-porous species. Because of the differently shaped profiles of modeled radial J_s , relative J_s in the center of the hydro-active xylem (i.e., at a sapwood depth of 0.5) differed among species (*Fagus*: 0.11, *Fraxinus*: 0.28, *Tilia* sp. B: 0.39, *A. campestre*: 0.50, *Carpinus*: 0.77 and *Tilia* sp. A and *A. pseudoplatanus* > 1.00; Table 4).

Sapwood area determination

Sapwood area estimated by the dye method in 12 to 25 stems per species showed a highly significant relationship with DBH in each species (Figure 2). The coefficients of the exponential functions describing these relationships are listed in Table 5.

Table 4. Parameters characterizing the radial patterns of sap flux density (J_s) in the hydro-active xylem in seven tree species as estimated by modeled data from Weibull functions. Daily mean J_s was normalized to the flux at the respective outermost measuring point (= 1) to give relative values. Similarly, xylem depth was expressed in relative values (0 = cambium, 1 = transition from sapwood to inactive heartwood). Mean values of one to three stems per species (genus) are given. A relative J_s of 0.01 was used to define the sapwood–heartwood boundary. For the *Tilia* species, two size classes were analyzed separately (A = Li1: 46.2 cm, B: Li17, 27.1 cm and Li11: 28.3 cm).

Species	Relative J_s at different relative sapwood depths						Relative sapwood depth of maximal flux density	Relative J_s at maximal flux density
	1.0 ¹	0.75	0.5	0.25	0.01	0.0 ²		
Diffuse-porous								
<i>Fagus sylvatica</i>	0.01	0.03	0.11	0.39	1.26	0	< 0.01 ³	1.26–1.32
<i>Carpinus betulus</i>	0.01	0.15	0.77	1.37	0.69	0	0.25	1.37
<i>Tilia</i> sp. (A)	0.01	0.2	1.05	1.59	0.62	0	0.3	1.62
<i>Tilia</i> sp. (B)	0.01	0.08	0.39	0.99	0.73	0	0.15	1.11
<i>Acer pseudoplatanus</i>	0.01	0.22	1.03	1.41	0.72	0	0.3	1.44
<i>Acer campestre</i>	0.01	0.09	0.50	1.14	0.57	0	0.20	1.74
Ring-porous								
<i>Fraxinus excelsior</i>	0.01	0.06	0.28	0.78	0.86	0	0.1	1.00

¹ Sapwood–heartwood boundary.

² Cambium.

³ Close to cambium.

In all diffuse-porous species, a large proportion of the stem basal area was active in xylem sap flux. The mean sapwood area to basal area ratio in the diffuse-porous species varied from 0.66 in *A. campestre* to 0.88 in *A. pseudoplatanus*, when all stem diameter classes were pooled. The ring-porous species *F. excelsior* showed a smaller sapwood area to basal area ratio (0.21). Comparing diameter classes revealed a decrease in the ratio with increasing stem diameter. Weak DBH–sapwood area relationships were found in *F. excelsior* and *T. cordata* ($r^2 = 0.63$ and 0.65), whereas close relationships were found in *A. pseudoplatanus* and *A. platanoides* (0.90).

Table 2 lists the maximum and minimum number of annual rings in the hydro-active sapwood area of each species. In

A. pseudoplatanus, up to 170 annual rings apparently participated in sap flux in the thickest stems, whereas in the largest diameter *A. platanoides*, *F. sylvatica* and *T. cordata* stems, the hydro-active sapwood included a maximum of 75 to 95 rings (Table 2). As expected, the ring-porous species *F. excelsior* had a shallower sapwood (5.7 cm at the maximum depth) with a smaller number of annual rings (less than 27). The depth of hydro-active sapwood is not only a function of the time span of vessel operation, but also of ring width. We found considerable variation in mean ring width among species with particularly wide rings in *F. sylvatica* and *T. cordata* (> 2 mm wide) and relatively narrow rings in *A. campestre* and *C. betulus* (< 1.5 mm wide, Table 2).

Mean wood density of each species is given in Table 5. Among the diffuse-porous species, *C. betulus* and *F. sylvatica* had the highest mean wood densities (0.67 and 0.65 g cm⁻³, respectively) and *T. cordata* had the lowest (0.43 g cm⁻³). The ring-porous *F. excelsior* had a mean wood density of 0.59 g cm⁻³. All three *Acer* species had similar wood densities (0.59 – 0.60 g cm⁻³). No study species showed a significant change in wood density from the cambium toward the sapwood–heartwood boundary or beyond this point (data not shown).

Discussion

Sap flux density and sapwood depth

Various factors influence the radial patterns of xylem J_s in a tree stem, among them stem diameter, tree age, social status and species, and evaporative demand. In general, J_s decreases rapidly with increasing sapwood depth in temperate tree species (Cohen et al. 1981, Phillips et al. 1996). This is particularly evident in tall trees with large stem diameters, which position their leaf area in more exposed areas of the upper forest canopy and, thus, are forced to maximize hydraulic conductivity in the stem sapwood to meet the high demand of water consumed by transpiration. Failing to do so would mean a high risk of vessel embolism because of a drop in xylem water potential (Sperry et al. 1998, Koch et al. 2004). Jimenez et al. (2000) emphasized that leaf distribution within the crown has an important influence on radial sap flux density patterns, at least in dominant trees.

In our sample of six broad-leaved species, we found considerable variation in radial pattern of J_s among species, as is evident when comparing the modeled J_s profiles in Table 3. *Fagus sylvatica* was the only species to show an exponential decrease in J_s with sapwood depth; thus, maximum J_s occurred in the youngest xylem elements. This observation is in agreement with results for this species obtained by Granier et al. (2000), Hölscher et al. (2005), Köstner et al. (1998) and Schäfer et al. (2000). According to Hölscher et al. (2005), the decrease in J_s was particularly steep in large diameter stems, as in 140-year-old beech trees. This contrasts with results obtained by Gessler et al. (2005) who detected a less steep radial decrease in sap flux density in older (95-year-old) *F. sylvatica* trees than reported by Granier et al. (2000) for younger

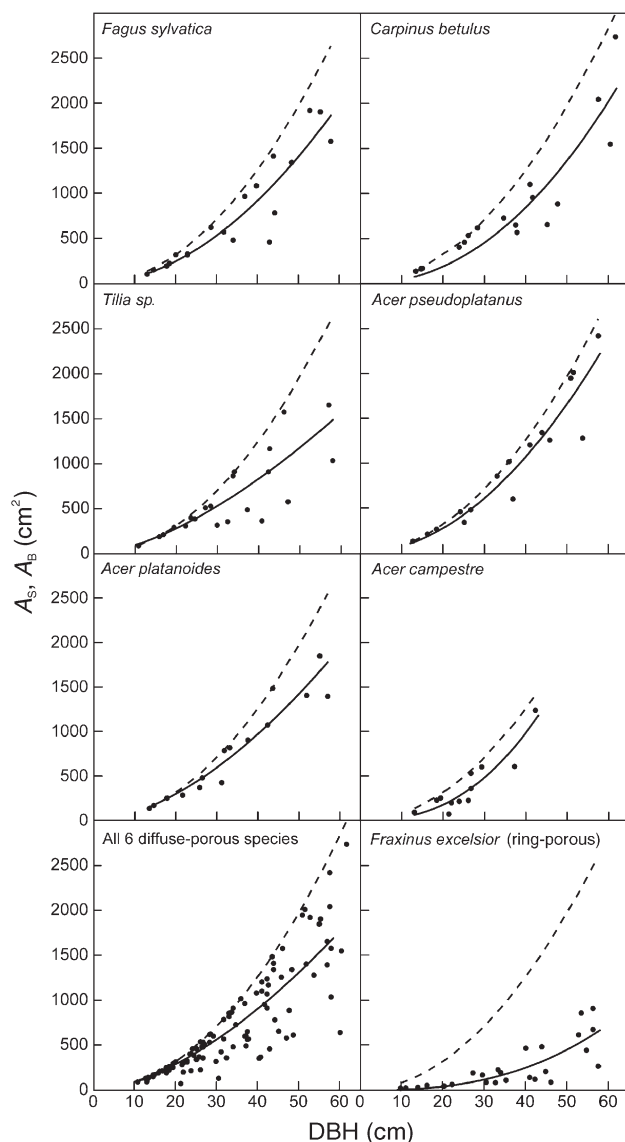


Figure 2. Relationships between stem diameter at breast height (DBH) and sapwood (A_S , solid lines) and basal area (A_B , dashed lines) in six diffuse-porous species and the ring-porous species *F. excelsior*. The relationships are described by power functions of the form $A = a\text{DBH}^b$.

Table 5. Coefficients of the power function (with coefficients of determination) describing the relationships between stem diameter at breast height and sapwood area ($A_S = aDBH^b$) in the seven tree species. Different letters indicate significant differences between species in wood density (Wilcoxon rank sum test). n_1 and n_2 are the numbers of trees sampled for A_S and wood density determination, respectively.

Species	n_1	a	b	r^2	Wood density (g cm^{-3})	n_2
Diffuse-porous						
<i>Fagus sylvatica</i>	19	0.778	1.917	0.86	0.65 (0.025) a	18
<i>Tilia cordata</i>	21	2.635	1.561	0.65	0.43 (0.063) c	21
<i>Carpinus betulus</i>	18	0.305	2.149	0.85	0.67 (0.024) a	11
<i>Acer pseudoplatanus</i>	16	0.754	1.967	0.90	0.59 (0.030) b	11
<i>Acer platanoides</i>	15	1.794	1.706	0.90	0.59 (0.032) b	7
<i>Acer campestre</i>	12	0.103	2.484	0.86	0.60 (0.015) b	2
All diffuse-porous species	101	1.151	1.801	0.75		
Ring-porous						
<i>Fraxinus excelsior</i>	25	0.013	2.671	0.63	0.59 (0.045) b	18

(32-year-old) beech trees. Our data and those of Schäfer et al. (2000) provide no evidence of a difference in the radial decrease in sap flux density between large and small *Fagus* stems.

Compared with *Fagus sylvatica*, the other species studied showed an initial increase in J_s from the youngest xylem elements toward older annual rings and then a decrease. In general, our results on radial J_s patterns were similar to those obtained in other temperate and subtropical tree species (e.g., Mark and Crews 1973, Hatton et al. 1995, Phillips et al. 1996, Jimenez et al. 2000, Lu et al. 2000, James et al. 2002, Nadezhdina et al. 2002, Ford et al. 2004a, Kubota et al. 2005a, 2005b). In the case of ring-porous *F. excelsior*, our regression model revealed a peak in J_s close to the cambium, i.e., in the second or third annual ring, which is similar to beech. However, our sensors could not give an accurate picture of J_s in the first mm beneath the cambium because the signal was integrated over the entire sensor length. Other methods of measuring J_s , for example, with heat pulse probes, are more appropriate for point measurements in one or two annual rings. In the diffuse-porous genus *Populus*, Edwards and Booker (1984), using heat pulse probes, observed maximum J_s in the second growth ring and lower J_s in the youngest (first) and third rings. Similarly, the highest J_s was reported in the second and third annual rings of 24-year-old *Pseudotsuga menziesii* (Mirb.) Franco trees (Domec et al. 2006).

In contrast, stems of *Carpinus*, *Tilia* and *Acer* showed maximum J_s at a xylem depth of about 3 cm, which corresponds to a growth ring age of about 15 to 30 years. Thus, J_s is comparatively low in the young, recently formed xylem elements and increases over years or decades to reach maximum values in these diffuse-porous species. However, differences in radial J_s patterns are not only related to species, stem size and tree age, but may also result from differences in measurement technique. For example, Gessler et al. (2005) used multi-point sensors where an overlap of neighboring heat fields can increase the uncertainty of measurement (Clearwater et al. 1999, Lu et al. 2000, James et al. 2002); however, Jimenez et al. (2000) found no significant interference among neighboring measurement points along their radial sap flow probe.

A further source of bias in radial sap flux data when only a single sap flow sensor in the outermost sapwood is used, is the diurnal variation in the radial profile of J_s . According to Ford et al. (2004a, 2004b; see also Nadezhdina et al. 2002), the radial profile of J_s in *Pinus* stems does change diurnally in response to daily variation in the evaporative demand. In the course of a day, the inner part of the xylem contributed more to J_s later in the day. Similarly, J_s was greater in the innermost sapwood on days when vapor pressure deficit was high. Finally, Nadezhdina et al. (2002) showed that changes in soil water content may influence radial J_s profiles and the size of hydro-active sapwood area. Such observations point to the capacity of trees to extend their hydro-active area on a daily or seasonal basis to accommodate changes in the demand for water transport. This may also indicate plasticity in the xylem and a capacity to overcome vessel embolism. *Fagus* species are unable to refill embolized xylem vessels as efficiently as other diffuse-porous species (Hacke and Sauter 1995, 1996, Sperry 1995, Améglio et al. 2004). This may explain the typical sharp decrease in J_s from the outer to the inner sapwood in *F. sylvatica*, and also in ring-porous *F. excelsior*.

To extrapolate the radial J_s profiles to different tree size classes, we suggest that the profiles be expressed in relative terms with maximum sapwood depth being set at 100%. By assuming that the radial J_s patterns are similar among the size classes of a species, this approach may yield the most realistic whole-tree transpiration estimates. Clearly, a set of species-specific sapwood area–DBH relationships and species-specific radial J_s profiles for different size classes of trees is required to accurately extrapolate mass flow in mixed stands, which makes this approach labor intensive.

Tree ring formation and hydro-active sapwood area

The dichotomy between diffuse-porous and ring-porous temperate tree species in the depth of the hydro-active sapwood is well documented (Wang et al. 1992). For example, Meinzer et al. (2005) found a sapwood-to-basal-area ratio of 0.15 in the ring-porous species *Quercus garryana* Dougl. ex Hook, and similarly low values in the North American conifers *Pseudotsuga menziesii* and *Thuja plicata* Donn ex D. Don. In contrast,

much higher ratios were observed in Central European diffuse-porous broad-leaved trees (0.78, Hölscher et al. 2005) and in 17 tropical trees (0.72, Meinzer et al. 2005). For 94-year-old *F. sylvatica* trees, Gessler et al. (2005) found a sapwood-to-basal-area ratio of 0.8, which matches well with our results for this species (0.76). Similarly, the other diffuse-porous species in our study had sapwood-to-basal-area ratios of 0.7 to 0.9, whereas a value of 0.21 was found for ring-porous *F. excelsior*. To ensure water flow to recently expanded foliage in spring, ring-porous trees produce earlywood composed mainly of large-diameter vessels. Such wide vessels are at greater risk of embolism than narrow latewood vessels, and they are thought to lose their capacity to transport water by the end of the first winter. No refilling occurs in these vessels during the following spring (Tyree and Zimmermann 2002). For example, the large vessels from the earlywood of ring-porous *Quercus alba* L. are dysfunctional after the year of formation (Miller et al. 1980), whereas small latewood vessels continue to function, or can be reactivated after each winter, and thus will continue to function for several years after ring formation (Granier et al. 1994). Because of the dependence of bud break on hydraulic capacity (Lechowicz 1984), ring-porous trees tend to produce new leaves later in spring than diffuse-porous trees.

Although our data generally support the above-mentioned concept of xylem function in diffuse- and ring-porous species, they provide a different insight into the maximum time span that xylem elements remain functional in the hydro-active sapwood. According to the radial J_s profile data, certain vessels seem to maintain their transport functions in ring-porous *F. excelsior* much longer than one or two years as is expected from general theory. For example, we measured significant sap flux in the outermost 3 cm of the sapwood of medium-sized ash stems (Figure 1) and counted five to 12 annual rings in the hydro-active sapwood (Table 1). Even if most vessels lose their functionality because of embolism after one year, a minority of xylem elements must remain active for several years in this ring-porous species.

Some diffuse-porous species recover conductivity through embolism reversal promoted by root pressure after winter freezing (Hacke and Sauter 1996), which plays no role in conduit refilling at tree heights above about 20 m. This recovery in conductivity may recur for several years in narrow vessels until irreversible embolism occurs (Utsumi et al. 1998). Our data from six diffuse-porous broad-leaved species indicate that certain xylem elements may fulfill transport functions in the older sapwood for as long as 100 years or more (see Table 2), even though they may be of marginal importance for mass flow during periods of peak flow. Sapwood parenchyma cells may be important in prolonging the active life of vessels. For example, Braun (1970) states that trees are able to maintain functional vessels if they have a high proportion of parenchyma cells in their sapwood, which act either as a protective shield against the diffusion of air into the xylem or by extracting air from the sap stream. This may hold true for *Tilia*, *Carpinus* and *Acer* species which have paratracheal contact parenchyma cells surrounding the vessels and wood rays within their woody tissue.

Fagus wood also contains paratracheal contact parenchyma cells, but only in short single-layer structures without shield formation. *Fraxinus* has contact parenchyma shields around the vessels with a high proportion of interfibrous parenchyma cells (Braun 1970).

How much water moves in a given sapwood ring depends partly on the transpiration rate of the foliage connected to that ring (Domec et al. 2006). In conifers with long-lived needles, these connections remain active for 3–5 years (Balster and Marshall 2000, Maton and Gartner 2005). Dye et al. (1991) hypothesized that the reduction in J_s along the radial sapwood profile of *Pinus* trees was the result of a decreasing participation of older xylem elements in the supply of water to transpiring surfaces. The initial hydraulic connection of early formed xylem as the primary conduit for the supply of water to young branches breaks when these branches die or become shaded. For deciduous broad-leaved species it is unknown how these connections are maintained or renewed each year with new foliage production or how relevant the connection to inner or to outer sapwood is.

No relationship between the reduction in J_s with sapwood depth and wood density was found in our sample. We observed no change in wood density with sapwood depth in the seven investigated species, nor did we find a relationship between wood density and number of annual rings in the sapwood. Similarly, other authors detected no general relationship between decreasing J_s and wood density (Phillips et al. 1996, Čermák and Nadezhdina 1998, Schäfer et al. 2000, but see Delzon et al. 2004).

In conclusion, the dye injection technique can give a first approximation of the size of the hydro-active sapwood area of tree stems. Our study revealed considerable variation in radial J_s patterns among seven co-occurring tree species. This variation is relevant for up-scaling from point measurements in the stem to the whole-tree and to the stand. Further investigations in a larger set of tree species and diameter classes are required to draw more general conclusions on possible relationships between tree functional types, xylem structural types and radial sap flux patterns.

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