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**Original article**

# Sapwood as the scaling parameter – defining according to xylem water content or radial pattern of sap flow?

Jan Cermak*, Nadezhda Nadezhdina

Institute of Forest Ecology, Mendel's Agricultural and Forestry University, 61300 Brno, Zemedelska 3, Czech Republic

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**Abstract** – Sapwood cross-sectional area is a simple biometric parameter widely used for scaling up the transpiration data between trees and forest stands. However, it is not always clear how the sapwood can be estimated and considered, which may cause scaling errors. We examined the sapwood depth according to xylem water content and more precisely according to radial patterns of sap flow rate in five coniferous and four broad-leaved species of different diameter, age and site conditions. Sapwood estimated by the two methods was almost equal in some species (e.g. *Cupressus arizonica*), but differed significantly in other species (e.g. *Olea europaea, Pinus pinea*). Radial pattern of sap flow rate is a more reliable indicator of sapwood then xylem water content for sap flow scaling purposes. Percentage of sapwood along radius changed with tree diameter and age. Sapwood also changes substantially under severe drought (e.g. in spruce, *Picea abies,* up to 1:3 in the course of several months). Sapwood should be used for upscaling sap flow data from measuring points to the whole trees and from trees to stands only for the period when it was actually measured, or the radial profile of sap flow should be measured continuously to avoid possible scaling errors. (© Inra/Elsevier, Paris)

**woody species / sapwood / radial pattern / sap flow / xylem water content / scaling**

**Résumé – Le bois d'aubier : paramètre de changement d'échelle défini en relation avec le contenu en eau du xylème ou avec le type radial de flux de sève ?** La surface de la section de bois d'aubier est un paramètre biométrique largement utilisé pour effectuer des changements d'échelle concernant la transpiration des arbres et des peuplements forestiers. Cependant, la façon dont le bois d'aubier est évalué peut être la cause d'erreurs dans les changements d'échelle. L'épaisseur du bois d'aubier est ici examinée en relation avec la teneur en eau du xylème et plus précisément en relation avec le type radial de densité de flux de sève (cinq conifères et quatre feuillus) de diamètre, âge et situation différents. Le bois d'aubier estimé à l'aide de deux méthodes

* Correspondence and reprints
E-mail: cermak@mendelu.cz

était presque identique chez quelques espèces (*Cupressus arizonica*) mais diffère significativement chez d'autres espèces (*Olea europaea, Pinus pinea*). Le type radial de densité de flux de sève est un meilleur indicateur de bois d'aubier que la teneur en eau du xylème pour un objectif de changement d'échelle du bois de sève. Le pourcentage de bois d'aubier sur un rayon varie avec le diamètre et l'âge de l'arbre. Le bois d'aubier change aussi substantiellement avec la sécheresse (*Picea abies*, dans une proportion de 1 à 3 en l'espace de quelques mois). Le bois d'aubier devrait être utilisé pour le changement d'échelle des flux de sève en mesurant à l'échelle de l'arbre entier et à l'échelle des peuplements, seulement pour la période pendant laquelle il a été de fait mesuré, ou bien le profil radial de densité de flux devrait être mesuré en continue pour éviter des possibles erreurs de changement d'échelle. 

**bois d'aubier / profil radial de flux de sève / teneur en eau du xylème / changement d'échelle**

## 1. INTRODUCTION

In rigorous anatomical studies, the sapwood 'splint' is considered as xylem containing living cells and the heartwood 'duramen' is that with dead cells, often impregnated with xylochromes, oleoresins, tannins and mineral compounds [2, 12]. According to usual physiological terminology, the sapwood or hydroactive xylem is the outer part of the xylem conducting sap and the heartwood or inactive xylem is the inner non-conducting xylem [4, 25, 29]. The fraction of water remaining in the heartwood (with a similar one also in the sapwood) is bound and cannot be used for tree metabolism; available water is that fraction of water which is found in tissues above the heartwood limit [34]. It can participate in the sap flow or serve as storage.

Sapwood cross-sectional area is a simple biometric parameter widely used for scaling the transpiration data between trees and forest stands. It is known that the extent of the conducting role of sapwood area is different according to species, ontogenetic phases and environmental conditions [16, 32]. There are many studies confirming strong allometric relations between sapwood area and other biometric parameters such as leaf area, e.g. [10, 15, 24, 33]; however, the functional role of sapwood area as a tissue supplying foliage with water is not always easy to evaluate, especially when comparing different species.

Sapwood area is principally large in coniferous and diffuse porous species with narrow tracheids or vessels (diameter about 0.05–0.1 mm) but small in ring-porous species with wide (diameter about 0.2–0.3 mm) and hydraulically very efficient vessels [3, 7, 35]. This fact makes it sometimes difficult to compare behaviour of different species especially in mixed forest stands when using only this parameter for scaling. Theoretical calculation of the sap flow, e.g. according to the Hagen-Poiseuille law, allows comparison of such species, but this is usually far too complicated (especially when considering that conducting elements are non-ideal capillaries, water flows through pits, etc.). That is why this approach is usually not used for scaling in routine studies.

This study was focused on evaluation of relations of sapwood depth and area and associated problems of upscaling sap flow data obtained in measuring points (which characterize radial sections of stems of different width given by the construction of sensors) to the whole trees. Several tree species contrasting in the conductive properties of their xylem and growing in distant sites were examined in order to cover large range of environmental conditions.

# 2. MATERIAL AND METHODS

## 2.1. Experimental sites

Altogether seven trees of Norway spruce (*Picea abies* (L.) Karst.) with diameters at breast height (DBH) ranging between 17 and 38 cm were studied in the plantation near the town of Rajec, southern Moravia at an altitude of 620 m (latitude 49°30'E and longitude 17°20'N). The stand was characterized as *Fagetum quercino–abietinum* with the presence of *Carex pilulifera* and a negligible number of herbal species connected with oligotrophic soils and raw humus. Oligotrophic brown forest loamy soil with decreased porosity in some places and high nutrient concentration in the humus layer and in the A-horizon was found. Depth of rhizosphere was around 60 cm, and in some places 120 cm. Long-term mean annual air temperature was 6.6 °C; mean annual precipitation was 683 mm (400 mm per growing period).

Scots pine, *Pinus sylvestris* L. (DBH = 28.6 cm) and three poplars *Populus interamericana,* cv. Beaupre (DBH = 46.2–48.7 cm) were sampled in Brasschaat, see [8] and in Balegem, Belgium, respectively [22]. In Brasschaat, the original climax vegetation (natural forest) was a *Querceto–Betuletum* [30]. The experimental plot was a pine plantation, 1.5 % slope oriented N.N.E, altitude 16 m. (51°18'33''E and 4°31'14''). Soil characteristics were moderately wet sandy soil with a distinct humus and/or iron B-horizon, umbric regosol or haplic podzol in the F.A.O. classification [1]. The groundwater depth normally ranged between 1.2 and 1.5 m and might be lower due to non-edaphic circumstances. In Balegem (coordinates: 50°55'7"E and 3°47'39"N) the experimental site was also flat (altitude 50 m) and located on the original orchard combined with meadow: moderately gleyic loamy soil with a degraded texture B-horizon, coarser with depth; an Ap-horizon of 30 cm FAO soil classification: glossaqualf [22]. The climate was moist subhumid (C1), rainy and mesothermal (B'1). Mean (over 28 years) annual and growing season temperatures for the region were 9.76 and 13.72 °C, precipitation was 767 and 433 mm, respectively.

*Olea europaea* L. (DBH = 19 cm), *Ficus carica* L. (DBH = 15.9 cm), *Cupressus arizonica* Green. (DBH = 20.7 cm), *Cupressus sempervirens* L.D. (DBH = 28.3 cm), *Pinus pinea* L. (31.5 cm) and *Quercus pubescens* Willd. (DBH = 8.9; 19.7 and 34.4 cm) were studied in central Tuscany, Italy, near the town of Radicondoli (latitude 43°15'3''N and longitude 11°03'29''E, altitude 550 m). The site was typical with loamy soil containing high to very high percentage of stones, mean annual and seasonal temperatures were 11.3 and 15.6 °C, precipitation was 621 and 540 mm, respectively.

## 2.2. Methods of measurement and data evaluation

The sap flow rate in spruce was measured using the tree trunk heat balance technique applying bulk internal (direct electric) heating [4, 5, 18]. Five stainless steel electrodes and four pairs of compensating thermocouples arranged in different depths within sapwood [6] were used. In all other species we used the heat balance method based on linear radial heating of tissues and sensing of temperature [23], applying dataloggers made by Environmental Measuring Systems & UNILOG, Brno, Czech Republic. A series of six thermocouples arranged in different distances (from 5 to 15 mm) were placed in stainless steel hypodermic needles 1.2 mm in outer diameter. More points of sap flow along the radius were obtained under stable conditions, when the needles were radially shifted during measurements.

Depth of conducting wood and corresponding area was estimated from the radial profiles of sap flow, taking into account the point where the sap flow approached zero. Sap flow rate for the whole tree was obtained, when individual points of radial pattern of sap flow per area (splained by the exactly fitting curve) were multiplied by the corresponding areas of annuli and summarized. For spruce, only sap flow data integrated over the sapwood by the measuring system were at our disposal. That is why the radial pattern of flow was approximately calculated using these totals and the previously estimated form of radial pattern in this species [7]. In general, the sap flow rate integrated for the whole trees according to directly measured radial pattern of flow per area was compared with the mean flow data characterizing individual sapwood layers (as if using only one thermocouple within a sensor placed at a different depth characterizing a certain layer) when multiplied by corresponding sapwood area. Each layer was measured 1) over 20 % of sapwood depth and 2) separately over 50 %. For this purpose, sapwood was distinguished from heartwood the classical way, i.e. according to xylem water content.

The volumetric fraction of water (water volume, $V_w$ expressed in percentage of fresh volume of samples, $V$) and specific dry mass (dry mass, $M_d$ estimated after drying for 48 h at 80 °C, divided by sample volume, $M_d/V$) was estimated on the wood cores sampled by the Pressler's borer (Suunto, Finland) from two opposite sides of stems at breast height (1.3 m). Cores were placed in aluminium foil immediately after sampling and analysed gravimetrically, after being cut into small pieces, within a few hours. The volumetric fraction of water was applied to estimate the depth of sapwood (and corresponding areas), here taken as xylem tissues, which differ in their hydration from heartwood.

## 3. RESULTS AND DISCUSSION

### 3.1. Radial pattern of xylem water content

Sapwood and heartwood are woody tissues usually containing higher and lower amounts of water, respectively, but this is not always the case. We found in spruce almost 60 $\%_{vol}$ in saturated xylem tissues (during early spring) and about 10–11 $\%_{vol}$ in heartwood (*figure 1*), which corresponds to our previous results [17]. Sapwood was relatively deeper in larger trees (up to 60 % of xylem radius, $r_{xyl}$) and shallower in smaller trees (up to 20 % of $r_{xyl}$) of even age. Sapwood was slightly deeper on the southern side (as shown by its relation to stem diameter at breast height: $y = 0.175x$; $r^2 = 0.92$; SE = 0.45) and more shallow on the northern side of stems ($y = 0.187x–0.94$; $r^2 = 0.78$; SE = 0.93). The radial pattern of water content differed completely in fast growing and vigorous poplars, where we found less water in the sapwood (25–30 $\%_{vol}$), whereas much more water was found in the heartwood (60–80 $\%_{vol}$) (*figure 1B*).

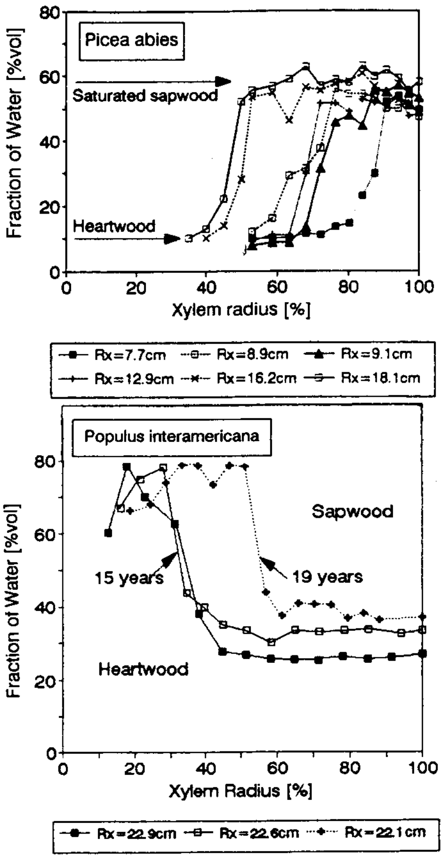


**Figure 1.** Radial xylem water content (volumetric fraction of water) in species representing contrasting pattern. Six Norway spruce (*Picea abies* (L.) Karst.) and three poplar (*Populus interamericana,* cv. Beaupre) trees were shown. All spruce trees of large diameter range were about 80 years old, poplar trees were of almost identical diameter, but of different age. Sapwood was saturated in spruce (early spring values), while that of poplar sampled in late summer was not saturated.

### 3.2. Radial pattern of water content and sap flow in different species

We found a variable radial pattern of sap flow in species with very different radial pattern of xylem water content (*figure 2*). In all given figures, splaining curves fitted measured points with $r^2 > 0.99$, thus exactly characterizing the patterns. Sapwood water content was very low in poplars (about 20 $\%_{vol}$) compared to that in the heartwood (almost 80 $\%_{vol}$), but sap flow took place over the whole sapwood (peaking at about 70–90 % of stem radius). There were almost no differences in xylem water content between sapwood and heartwood in *Olea europaea* (mean value of about 40 $\%_{vol}$); however, higher sap flow rates were limited to sapwood (peaking close to cambium) and lower rates were observed in a wide transition area towards heartwood (below 40 % of stem radius). The fraction of available water in *Ficus carica* increased more than two-fold from pith towards cambium (40–70 $\%_{vol}$) and no distinctive heartwood was identified here this way. This roughly corresponds to sap flow, which demonstrated a peak in the outer part of the xylem, corresponding to sapwood, but at a lower level remained also in the inner part of the xylem (also below 40 % of stem radius). The heartwood border identified from sapwood water content was almost the same as that identified on the basis of radial sap flow rate in Scots pine trees. However, water remained almost at the same level (about 25 $\%_{vol}$) through sapwood, while the sap flow pattern showed

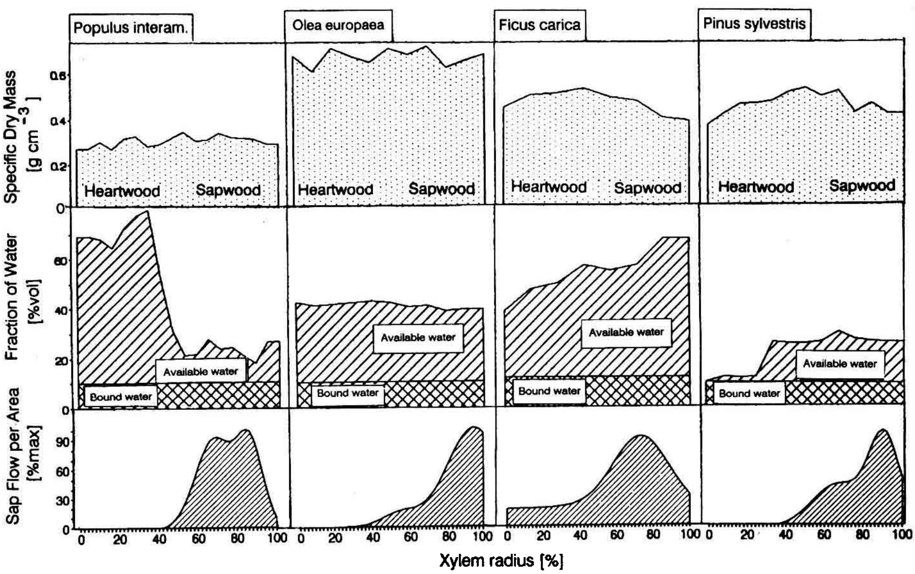


**Figure 2.** Xylem specific dry mass, water content (volumetric fraction of water) and sap flow rate per area (in percentage of its maximum) in species showing very contrasting radial pattern of all measurement parameters: american poplar (*Populus interamericana* cv.Beaupre) as an example of species with higher water content in heartwood then in sapwood, *Olea europaea* L. with almost equal water content in heartwood and sapwood, *Ficus carica* L. with gradually increasing water content towards sapwood and *Pinus sylvestris* L. with larger water content in sapwood then in heartwood.

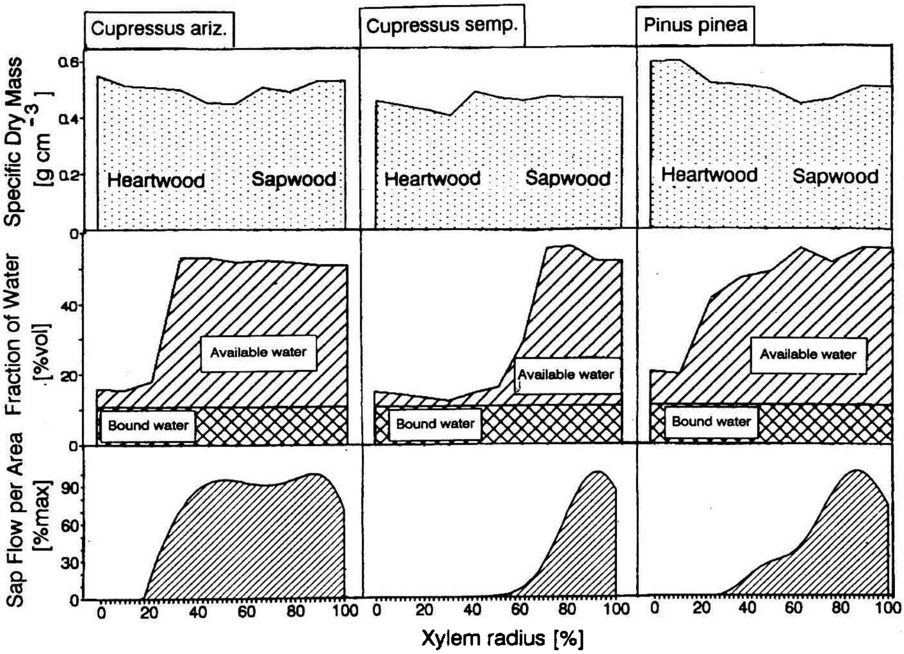


**Figure 3.** Radial pattern of specific dry mass, xylem water content (volumetric fraction of water) and sap flow rate per area (as a percentage of its maximum) in species with higher water content in sapwood then in heartwood, but different patterns of sap flow. Sap flow occurring virtually over the whole sapwood is demonstrated in the example of *Cupressus arizonica* Green.; sap flow occupying the prevailing part of the sapwood is shown in *Cupressus sempervirens* L.D. and sap flow occurring only over part of the sapwood is represented by the example of *Pinus pinea* L.

peak values at about 90 % of the stem radius.

Different pattern of sap flow rates were also found in other conifer species which all have distinctive differences in xylem water content between heartwood (15–20 $\%_{vol}$) and sapwood (around 50 $\%_{vol}$). *Cupressus arizonica* is an example of a tree with a radial pattern of sap flow very closely related to that of xylem water content (although it is not so close on the other side of the same stem). But even under such conditions, the sapwood does not conduct water uniformly across its whole area. Differences between sapwood areas estimated by both the methods mentioned are still more pronounced in other trees in the study, as shown by the example of *Cupressus sempervirens* and *Pinus pinea* (*figure 3*).

The radial pattern of sap flow per area differs from that calculated for corresponding annuli. The importance of outer xylem layers for sap flow rate is increasing owing to increasing area of the annuli from the pith to cambium (if an equal width of annuli is considered). The differences between both totals are rather small in species with shallow sapwood, but are substantial in species with deep sapwood (*figure 4*).

It is clear from the above results that sapwood area estimated on the basis of changes in xylem water content is partially related to conducting area, which should be applied for scaling the sap flow rate from measuring points (usually representing certain sections of sapwood) to the whole trees. However, the relations are not always straightforward. A very variable pattern of sap flow rate in different species indicates that for scaling purposes it is necessary to integrate properly the actual radial profile of sap flow measured per area and consider accordingly the conducting areas of corresponding annuli. Rather small differences in the radial pattern of sap flow per area and per annuli in shallow sapwood species make it technically easier to integrate the flow compared to that in deep sapwood species. Specific dry mass as a parameter sometimes used to indicate conducting properties of woody tissues and xylem water content can sometimes be used as an indicator of conductivity, but this is also not always reliable, if large differences between xylem tissues are not considered.

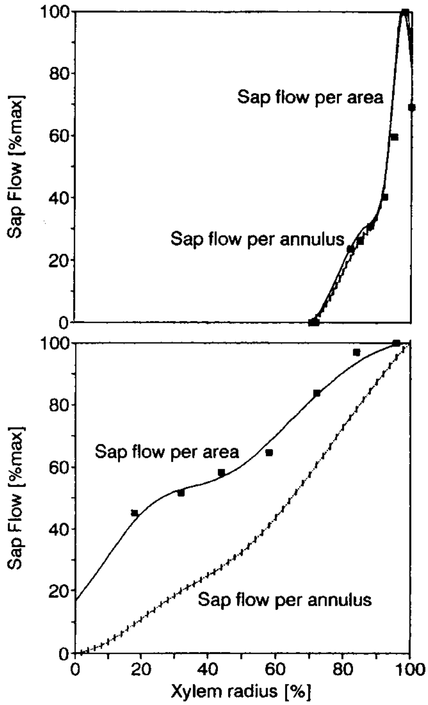


**Figure 4.** Radial profile of sap flow calculated per unit area and that calculated per entire area of corresponding annuli in trees with relatively shallow (A) and deep sapwood (B).

### 3.3. Changes in radial pattern of sap flow with tree diameter and age

The radial pattern of sap flow rate changes with tree size and age irrespectively of the specific dry mass and xylem water content (*figure 5*). Practically the whole cross-sectional area of xylem was conductive in young oak (*Quercus pubescens*) trees, even when high flow rates per area occurred only close to the cambium. However, sapwood area decreased dramatically in older trees, reaching up to only 30 % of the xylem radius in adulthood. Similar and lower percentages of conducting xylem in different oak species were reported by Phillips et al. [27]. In pedunculate oak (*Quercus robur*) growing in floodplain forests we found the sapwood depth to be about 60 % of the xylem radius in young trees (DBH = 8 cm) with the most important flows up to 16 % [7]. In adult trees (DBH = 30 cm) the visible sapwood reached about 19 % of the xylem radius there and the conductive sapwood about 15 %, with the most important flows up to only 4 %. As demonstrated in our related unpublished results, the larger part of the deeper layers in sapwood was active only in suppressed *Q. robur* trees, even when they were relatively large (those with little summer growth, which produced only low density earlywood composed of medium-sized vessels). However, one or two annual rings with very large vessels were usually most active and eventually another one or two showed very

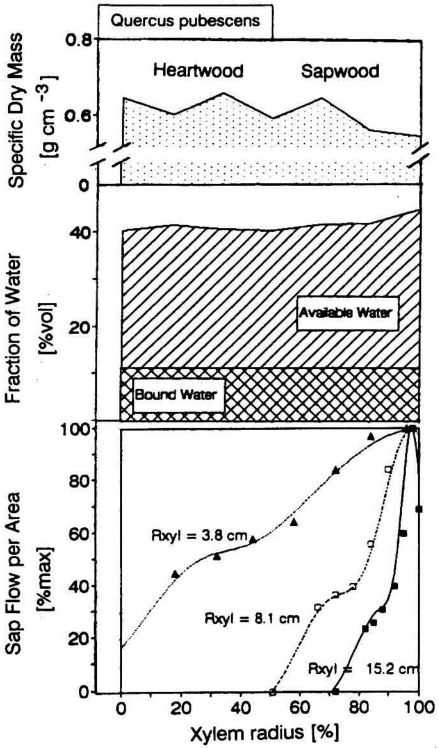


Figure 5. Radial pattern of specific dry mass, xylem water content (volumetric fraction of water) and sap flow rate per area (as a percentage of its maximum) in oak trees (*Quercus pubescens* Willd.) of different age (10–40 years) and stem diameter at breast height.

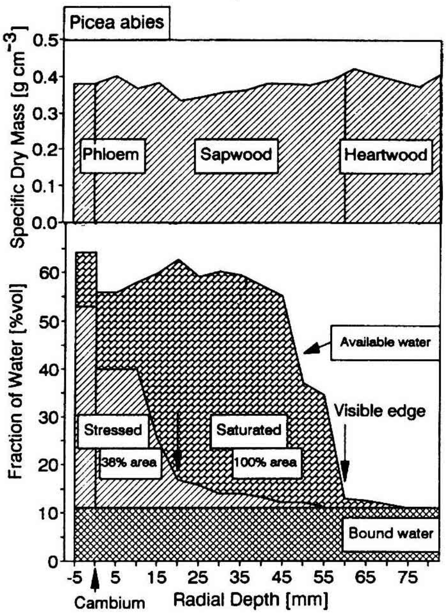


Figure 6. Xylem specific dry mass and tissue water content (volumetric fraction of water) along stem radius at breast height in large spruce tree (*Picea abies* (L.) Karst.) with xylem diameter of 31 cm under conditions of saturated tissues in early spring and after a period of severe drought in late summer. The visible edge of sapwood corresponding to higher xylem water content is marked by arrows. Bound water was taken as the percentage of water held in the heartwood (~11 %vol) and available water as that above this value.

little activity in the main canopy trees, which was also confirmed by other studies [18].

### 3.4. Changes in radial water content and total sap flow under drought

Saturated xylem water content compared to that under drought was shown only on one large spruce (*figure 6*), although the situation was similar in the other six sample trees already presented in the above (see *figure 1A*). There were no significant differences in specific dry mass of xylem along stem radius. Under saturated conditions, water content reached maximum (around 60 $\%_{vol}$) approximately at the centre of the sapwood, slightly closer to the cambium (at 20–30 mm). Water content was lower by about 5 $\%_{vol}$ near the cambium as well as at the same distance to the heartwood, where it decreased abruptly to the heartwood, which was characterized by an almost constant water content of about 10–11 $\%_{vol}$ down to the pith. (Phloem water content was about 65 $\%_{vol}$ at the same time.) Under drought in late summer the sapwood depth decreased down to about 1/3 of that in saturated tissues; sapwood area in largely dehydrated tissues decreased to about 38 % of that in saturated tissues (see *figure 2*). The fraction of xylem water decreased under drought to about 40 $\%_{vol}$ in the uppermost layers (at a depth of 0–1.2 cm beneath the cambium, thus down to only 8 % of the xylem radius). Mean fraction of xylem water when calculated over the entire depth of sapwood reached only 19 $\%_{vol}$. Phloem water decreased to about 53 $\%_{vol}$. There was no change in the heartwood water.

Since no radial pattern of sap flow was measured in the experimental spruce, we assumed that it had an approximately Gaussian-like pattern under good water supply as shown previously [7, 21, 30]. But it is clear that there must be a corresponding dramatic change in the radial pattern under drought compared to that in saturated conditions, if the sapwood area decreased 2.6 times (see *figure 6*). Considering total sap flow per tree, or relative transpiration (daily total of sap flow divided by PET), its seasonal course increased by about 20 % during May and June indicating development of foliage and reached about 75 % of PET at its seasonal maximum. However, this trend was reversed from June to August under the impact of continuous severe drought, when the relative transpiration decreased by about half (*figure 7*). Considering a decreasing area of sapwood, this indicates that the outer part of the sapwood was about one third more efficient in conducting water compared to its inner part. Similar results were obtained for *Pinus taeda* during drought by Phillips et al. [27], who reported that the ratio of the daily integrated flux density in the inner to outer xylem decreased with soil moisture from 0.44 to 0.36.

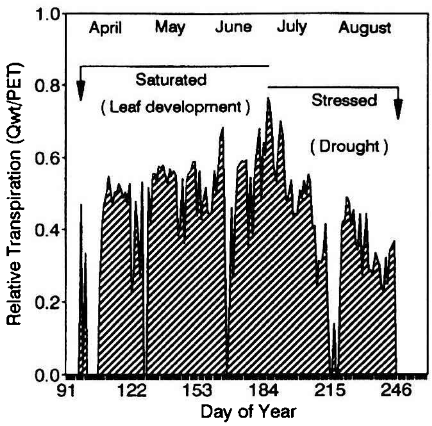


**Figure 7.** Seasonal course of relative transpiration in large spruce tree *(Picea abies* (L.) Karst.) near Rajec, southern Moravia, calculated as the ratio of daily totals of actual transpiration (the sap flow) to potential evapotranspiration, both considered for projected crown area unit. Periods of rather mild and dry weather are marked with horizontal lines. Arrows indicate sampling period of sapwood applied for estimation the radial xylem water content.

Our results on xylem water content in spruce generally correspond to the data found for this species in other sites [17]. The radial profile of xylem water content is not directly related to the radial profile of sap flow and the outer xylem – sapwood with higher water content represents the potential conducting area only. However, it is clear that the flow cannot take place in the xylem where there is no free water (i.e. in the xylem containing only bound water – see *figure 6*) and thus decreasing sapwood area must lead to decreasing sap flow. A similar situation indicating the importance of changes in the soil water supply for stem hydraulics has already been confirmed for broad-leaf species [9]. Under high evaporation demand, water is of course extracted from all stem tissues, although our results show that under long-term drought, water is extracted presumably from deeper layers of the sapwood. In contrast, dendrometer records reflect extraction of water from the outermost part of the last annual ring and phloem [11, 13, 26]. This means that only part of the water extracted from xylem is associated with volume changes of the tissues. Older xylem located deeper in the stems is rigid and does not significantly change in volume under physiological conditions, although it contains and provides a significant amount of water when necessary. The volume of the spruce stem can return almost to its original value after drought [14] and reverse embolism may occur by refilling tracheids in the absence of positive pressure [28]. Water storage in outer tissues is more readily replaced by rehydrating (night) flow, while deeper layers of sapwood remain mostly empty in the long-term (and eventually rehydrate more slowly) owing to higher radial xylem resistances.

### 3.5. Scaling errors caused by neglecting the radial pattern of flow

Rather large scaling errors may occur if the thermocouple applied in a sap flow sensor represents only one point along the xylem radius (one depth within the sapwood) and the calculated value of sap flow is upscaled for the whole tree supposing that equal sap flow rate occurs over the entire sapwood area. The actual situation depends on the intergrating depth covered by the sap flow sensor and the position of the sensor along the radius. Comparing all sample trees under study showed the magnitude of possible scaling errors (*table I*). Sensors placed, for example, in the outer half of the sapwood mostly overestimated total tree sap flow (by about 10–40 %) and those placed in deep inner layers of sapwood always underestimated it (by about 40–80 %). Such errors can be much larger under drought.

### 3.6. Assumed effect of climate changes on radial patterns

Decreased sap flow rates occurred at a small distance towards the pith from the peak value in almost all trees under study irrespectively of their species, size, age and location (see *figures 2–4*). Such a decrease corresponds to about five annual rings, which indicates that some unfavourable change in growing conditions occurred approximately between years 1987 and 1991 over Europe. The small number of sampled trees analysed here does not allow general conclusions, but it seems that detailed measurements of the radial pattern of sap flow can be applied as an alternative field method for estimating the impact of climatic change on woody vegetation.

## 4. CONCLUSIONS

1) Sapwood may contain a higher percentage of available (free) water than heartwood or the same percentage or heartwood may contain a higher percentage then sapwood (within the approximate range 10–60 $\%_{vol}$). For some species it is impossible to distinguish between sapwood and heartwood only according to water content in woody tissues.

2) Sapwood cross-sectional area is a somewhat problematic parameter when used alone for upscaling sap flow data from measuring points to whole trees. Depth of the actually conducting sapwood (estimated according to the radial pattern of sap flow) may approach the depth of sapwood. Sapwood estimated according

**Table I.** Total sap flow rate for whole trees calculated from data measured at one point along the radius only (single sapwood layer), but multiplied by the total sapwood area (estimated according to xylem water content). Data are given as a percentage of flow totals estimated from directly measured radial patterns of flow (= 100 %) for different species. High sap flow data from seasonal maximum (corresponding to deep, saturated sapwood) and low flow from the period of severe drought are given for spruce (deep and shallow sapwood was considered under drought; radial profile of sap flow was reconstructed here only).

| Species | Xylem radius (cm) | Sapw. depth (cm) | Radial sapwood layers (% sapwood depth from cambium) 0–20 | 21–40 | 41–60 | 61–80 | 81–100 | 0–50 | 51–100 |
|---|---|---|---|---|---|---|---|---|---|
| *Populus int.* | 18.9 | 12.0 | 82.5 | 161.0 | 148.0 | 61.5 | 1.8 | 127 | 55 |
| *Oliva europ.* | 9.6 | 9.6 | 162.7 | 95.6 | 39.4 | 14.1 | 2.5 | 111 | 15 |
| *Ficus* | 7.7 | 7.7 | 102.3 | 149.4 | 73.3 | 35.8 | 31.6 | 116 | 42 |
| *Quer. pub. Big* | 15.2 | 4.6 | 213.9 | 94.0 | 68.8 | 36.3 | 9.3 | 137 | 32 |
| *Quer. pub. Medium* | 8.1 | 4.0 | 180.5 | 106.1 | 72.7 | 51.0 | 14.7 | 129 | 41 |
| *Quer. pub. Small* | 3.8 | 3.8 | 123.2 | 101.8 | 77.3 | 64.9 | 37.9 | 105 | 57 |
| *Cupress. ariz.* | 9.8 | 8.0 | 105.8 | 107.4 | 107.8 | 100.5 | 48.9 | 107 | 81 |
| *Cupress. semp.* | 13.5 | 6.8 | 169.5 | 146.3 | 74.9 | 22.6 | 3.9 | 141 | 26 |
| *Pinus sylv.* | 12.5 | 9.0 | 165.5 | 115.8 | 81.2 | 32.0 | 3.6 | 129 | 30 |
| *Pinus pinea* | 13.1 | 10.4 | 153.7 | 127.9 | 60.5 | 31.7 | 4.8 | 125 | 27 |
| *Picea Sat. Deep* | 17.6 | 6.0 | 21.6 | 144.7 | 182.0 | 127.7 | 53.9 | 103 | 109 |
| *abies Dry. Deep* | 17.6 | 6.0 | 286.3 | 175.1 | 38.7 | 25.6 | 10.0 | 192 | 22 |
| *Dry. Shall* | 17.6 | 2.0 | 109.4 | 66.9 | 14.8 | 9.8 | 3.8 | 73 | 8 |

to xylem water content or a change in wood colour only is not reliable enough for scaling purposes, because the sapwood does not conduct water uniformly across its whole area.

3) The radial pattern of sap flow should be considered when upscaling data from measuring points (usually representing certain stem sections of different size) to the whole trees. It is best to measure the radial pattern (using more sensors along xylem radius) continuously or at least to determine the radial position of a smaller number of representative thermocouples applied for routine studies on such a basis.

4) We confirm that fraction of sapwood area in xylem cross-sectional area is large (up to 100 %) in young trees and decreases with tree age.

5) High seasonal dynamics of tissue water content and the associated radial profile of sap flow during drought may lead to significant scaling errors if the sapwood area is estimated, e.g. under conditions of good soil water supply and applied also to the possible period of drought.

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## REFERENCES

[1] Baeyens L., Van Slycken J., Stevens D., Description of the soil profile in Brasschaat, Internal research paper, Institute for Forestry and Game Management, Geraardsbergen, Belgium, 1993, 17 p.

[2] Balaban K., Wood Anatomy, SZN Praha, 1955, 220 p. (in Czech).

[3] Braun H.J., Handbuch der Pflanzenanatomie. Funktionelle Histologie der sekundaren Sprossachse, Gebruder Borntrager, Berlin, 1970, 190 p.

[4] Cermak J., Deml M. Penka M., A new method of sap flow rate determination in trees, Biol. Plant.(Praha) 15(3) (1973) 171–178.

[5] Cermak J., Ulehla J., Kucera J., Penka M., Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions, Biol. Plant.(Praha) 24(6) (1982) 446–460.

[6] Cermak J., Kucera J., The compensation of natural temperature gradient in the measuring point during the sap flow rate determination in trees, Biol. Plant.(Praha) 23(6) (1981) 469–471.

[7] Cermak J., Cienciala E., Kucera J., Lindroth A., Hallgren J.-E., Radial velocity profiles of water flow in stems of spruce and oak and response of spruce tree to severing, Tree Physiol. 10 (1992) 367–380.

[8] Cermak J., Riguzzi F., Ceulemans R., Scaling up from the individual trees to the stand level in Scots pine: 1. Needle distribution, overall crown and root geometry, Ann. Sci. For. 55(1–2) (1998) 63–88.

[9] Cohen Y., Moreshet S., Fuchs M., Changes in hydraulic conductance of citrus trees following a reduction in wetted soil volume, Plant, Cell Environ. 10 (1987) 53–57.

[10] Dean T.J., Long J.N., Variation in sapwood area – leaf area relations within two stands of lodgepole pine, Forest Sci. 32(3) (1986) 749–758.

[11] Dobbs R.C., Scott R.M., Distribution of diurnal fluctuations in stem circumference of Douglas-fir, Can. J. For. Res. 1(2) (1971) 80–83.

[12] Esau K., Plant Anatomy, J.Wiley & Sons, Inc., New York, 1965 (Mir, Moscow, 1969).

[13] Hinckley T.M., Bruckerhoff D.N., The effects of drought on water relations and stem shrinkage of *Quercus alba*, Can. J. Bot. 53 (1975) 62–72.

[14] Jackson G.E., Irvine J., Grace J., Xylem cavitation in Scots pine and Sitka spruce saplings during water stress, Tree Physiol. 15(12) (1995) 783–790.

[15] Kaufmann M.R., Troendle C.A., The relationship of leaf area and foliage biomass to sapwood conducting area in four subalpine tree species, Forest Sci. 27 (1981) 477–482.

[16] Kramer P.J., Kozlowski T.T., Physiology of Woody Plants, Academic Press, New York, 1979, 811 p.

[17] Kravka M., Cermak J., Water storage in stem wood of large pine and spruce trees in central Sweden natural forests, Europ. Geophys. Soc., Proc. XX General Assembly, Annales Geophysicae, Part II, Oceans, Atmosphere, Hydrology & Nonlinear Geophysics, vol. 13,C-504, suppl.II, Hamburg, Germany, 1995.

[18] Krejzar T., Kravka M., Sap flow and vessel distribution in annual rings and petiols of large oaks, Lesnictvi (1998) in press.

[19] Kucera J., Cermak J., Penka M., Improved thermal method of continual recording the transpiration flow rate dynamics, Biol. Plant.(Praha) 19(6) (1977) 413–420.

[20] Lu P., Biron P., Granier A., Cochard H., Water relations of adult Norway spruce (*Picea abies* (L.) *Karst.*) under soil drought in the Vosges mountains: whole-tree hydraulic conductance, xylem embolism and water loss regulation, Ann. Sci. For. 53(1) (1996) 113–121.

[21] Mark W.R., Crews D.L., Heat-pulse velocity and pordered pit conditions in living Engelmann spruce and lodgepole pine trees, For. Sci.19 (1973) 291–296.

[22] Meiresonne L., Nadezhdina N., Cermak J., Van Slycken J., Ceulemans R., Transpiration of a monoclonal poplar stand in Flanders (Belgium), Agric. For. Meteorol. (1998) in press.

[23] Nadezhdina N.E., Cermak J., Heat balance method and combined sensor with linear radial heating, U.S. Patent and Trademark Office, P.A. No.69055, June 30, 1997.

[24] O'Hara K.L., Valappil N.I., Sapwood-leaf area prediction equations for multi-aged ponderosa pine stands in western Montana and

central Oregon, Can. J. For. Res. 25(9) (1995) 1553–1557.

[25] Panshin J.R., de Zeeuw C., Textbook of Wood Technology, Vol.1, Structure, Identification, Uses and Properties of the Commercial Woods of the United States and Canada, McGraw-Hill, Toronto, 1970, 705 p.

[26] Panterne P., Burger J., Cruiziat P., Modelling the variation of water potential within a woody axis cross-section, CR Acad. Sci. III-Vie 318(11) (1995) 1119–1124.

[27] Phillips N., Oren R., Zimmermann R., Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species, Plant, Cell Environ. 19 (1996) 983–990.

[28] Sperry J.S., Nichols K.L., Sullivan J.E.M., Eastlack S.E., Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska, Ecology 75(6) (1994) 1736–1752.

[29] Stewart C.M., Excretion and heartwood formation in living trees, Science 153 (1966) 1068–1074.

[30] Swanson R.H., Velocity distribution patterns in ascending xylem sap during transpiration, in: Symposium on Flow – Its Measurement and Control in Science and Industry, Canadian Forestry Service paper No.4/2/171, 1971, 11 p.

[31] Tack G., van den Bremt P., Hermy M., Bossen van Vlaandren: Een Historische Ecologie, Davidsfonds, Leuven, Belgium, 1993, 320 p. (in Dutch).

[32] Waring R.H., Running S.W., Water uptake, storage and transiration by conifers: a physiological model, in: Lange O.L., Kappen L., Schulze E.-D. (Eds.), Water and Plant Life, Springer-Verlag, Berlin, 1976, pp.189–202.

[33] Waring R.H., Gholz H.L., Grier C.C., Plummer M.L., Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms, Can. J. Botany 55(11) (1977) 1474–1477.

[34] Zimmermann M.H., Brown C.L., Trees, Structure and Function, Springer-Verlag, Berlin, 1971, 336 p.

[35] Zimmermann M.H., Xylem Structure and the Ascent of Sap? Springer-Verlag, Berlin, 1983, 144 p.