

Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing

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Summary

Trunk-tissue heat balance, volumetric and staining methods were used to study xylem water flow rates and pathways in mature Norway spruce (*Picea abies* (L.) Karst.) and pedunculate oak (*Quercus robur* L.) trees. The radial profile of flow velocity was confirmed to be symmetrical in spruce, i.e., maximum flow velocity was in the center of the conducting xylem and tailed with low amplitude (about 30 cm h⁻¹) in the direction of the cambium and heartwood. Variability around the trunk was high. In contrast, in oak, the radial profile of flow velocity was highly asymmetrical, reaching a peak of about 45 m h⁻¹ in the youngest growth ring and tailing centripetally for about 10 rings, but variability around the trunk was less, under non-limiting soil water conditions, than in spruce. In spruce, the flow rate increased abruptly within seconds when the tree was severed while immersed in water, and then decreased gradually, showing significant root resistance. We conclude that water flow through an absorbing cut surface differs from the flow higher in a tree trunk because of the presence of hydraulic capacitances in the conductive pathways. The staining technique always yielded higher estimates of flow velocity than the non-destructive tree-trunk heat balance method.

Introduction

Long-term studies of transpiration and water transport in mature forest trees can provide important information about tree ecophysiology and forest hydrology (Huber and Schmidt 1936, Swanson 1975, Čermák et al. 1976, 1982, Čermák 1986, Hinckley et al. 1978, Čermák and Kučera 1987). When working with new material it is desirable to become familiar with its particular properties. For applications of the tree-trunk heat balance (THB) method, an understanding of the properties of the stem conductive systems and pathways is particularly important.

The aim of the present study was to develop this understanding for Norway spruce (*Picea abies* (L.) Karst.) and pedunculate oak (*Quercus robur* L.) trees. To test the THB method for planned long-term measurements, a short-term destructive volumetric technique was used in a spruce tree. This approach has previously been applied in other species (e.g., Rychnovska et al. 1980, Cohen et al. 1981, Čermák et al. 1984, Edwards and Booker 1984, Čermák and Kučera 1990, Olbrich 1991). Tree-trunk heat balance methods allow the detection of a very fast response to abrupt changes in water flow such as occur when a tree is severed (Čermák and Kučera

1991). Staining (or water injection) techniques, which date back two centuries in water pathway studies (Hales 1731), remain a valuable tool (Cohen 1974, Edwards and Jarvis 1981, 1982) and were used in this study. The objective of this investigation was not to analyze the general features of tree conductive systems, which are already well documented elsewhere (Boucherle 1840, Hartig 1855, MacDougal 1925, Arcikhovskiy 1931), but to verify such features in pedunculate oak and Norway spruce trees.

Materials and methods

Plant material

Several Norway spruce and pedunculate oak trees were studied with different techniques in two localities. The spruce trees were growing at the research plot in Skogaby, located 30 km from Halmstad in southwestern Sweden (the Skogaby Project, Umeå Agricultural University) and the oak trees were growing at the research plot near Lednice in Czechoslovakia—southern Moravia (the Lednice Project, Brno Agricultural University). The site in southwestern Sweden has an acid till soil and a homogenous and relatively healthy young stand of Norway spruce, growing in association with *Quercetum*, *Calluna vulgaris*, and *Rubus caesius*. The climate is characterized by a high annual precipitation (1100 mm) and a mean temperature of around 7.8 °C. The site in southern Moravia is a floodplain forest on the niveau of the Dyje river with deep alluvial soils. The forest is composed mostly of pedunculate oak in association with *Ulmeto-Fraxinetum carpineum* (Zlatník). The climate is relatively warm and dry with a mean annual temperature of 9 °C and precipitation of 525 mm.

The two experimental Norway spruce trees were 23 years old and had diameters at breast height (dbh) of 11.0 and 16.4 cm (bark and phloem thickness 3 mm) and heights of 10.5 and 13.8 m, respectively. The average stand height was 13.5 m and the average dbh was 13.0 cm. The young (30 years old) experimental oak tree had a dbh of 8 cm and a height of 9 m. The old (about 100 years old) experimental oak tree had a dbh of 30 cm and a height of 29 m, both the young and old oak trees were growing near the southern edge of the stand. Several additional trees of similar size were analyzed in both species.

Trunk-tissue heat balance method

Xylem water flow was measured by the trunk-tissue heat balance (THB) method with internal (direct electric) heating as described by Čermák et al. (1973, 1982) and Kučera et al. (1977). In the Norway spruce trees, the measuring points, which consisted of three stainless-steel electrodes and a battery of four compensating thermocouples (Čermák and Kučera 1981), were located on the opposite sides (east–west) of the spruce trunk at a height of 1.3 m. The entire lower end of the trunk was insulated with 30-mm thick, polyurethane foam surrounded by a cylindrical aluminum plate (0.5 mm thick) and covered with watertight plastic foil fastened to

the bark surface above the measuring point. After the experiment, it was confirmed that the electrodes penetrated the conductive part of xylem. The heartwood boundary was identified by a significantly lower xylem water content—about 10% (by volume) in the heartwood versus 30–50% in the sapwood (Figure 1). The actual depth of conductive xylem was about 20–30 mm (its cross-sectional area, $A_{cx} = 68 \text{ cm}^2$) and represented about 10–12 of the total of 18 growth rings at the given height. Results of the THB method were tested against volume flow measured directly using the destructive volumetric method.

A staining method was used to detect the conductive pathway and velocity profile in the cross section of the Norway spruce trunk in the severing experiment.

Severing technique

Xylem water flow rate was measured for about 12 h before the tree was severed. The severing procedure started shortly after noon on a relatively warm and sunny day (Figure 2a). The tree was stabilized in the vertical position with a rope fastened to the upper trunk and to the boles of three surrounding trees. A crossbar was mounted on the lower trunk to allow manipulation of the bole after cutting. The tree was severed at its trunk base within a few seconds using a handsaw, while washing the cut with water simultaneously. Immediately after cutting, the base of the tree was placed in a barrel of water and recut, underwater, about 30 cm above the first cut. Thus, assuming that under low flow velocities all embolized tracheids were removed, entry of additional air was prevented.

***Picea* D.B.H. = 11 cm**

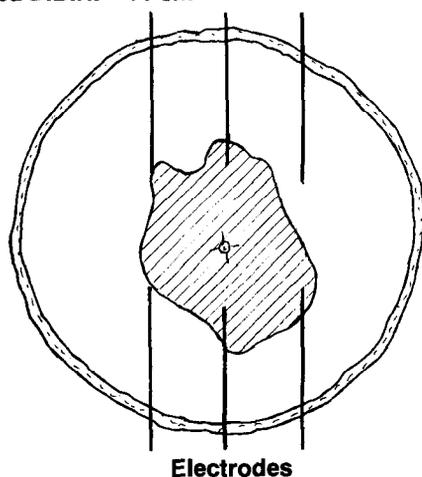


Figure 1. Sapwood and heartwood areas in a cross-section of a Norway spruce trunk through the measuring point of xylem water flow using the THB method. Sensors (electrodes and thermocouples) were located on opposite sides of the tree: east (upper) and west (lower) before the exact sapwood depth and area ($A_{cx} = 68 \text{ cm}^2$) were known. The heartwood border was assessed by its significantly lower water content.

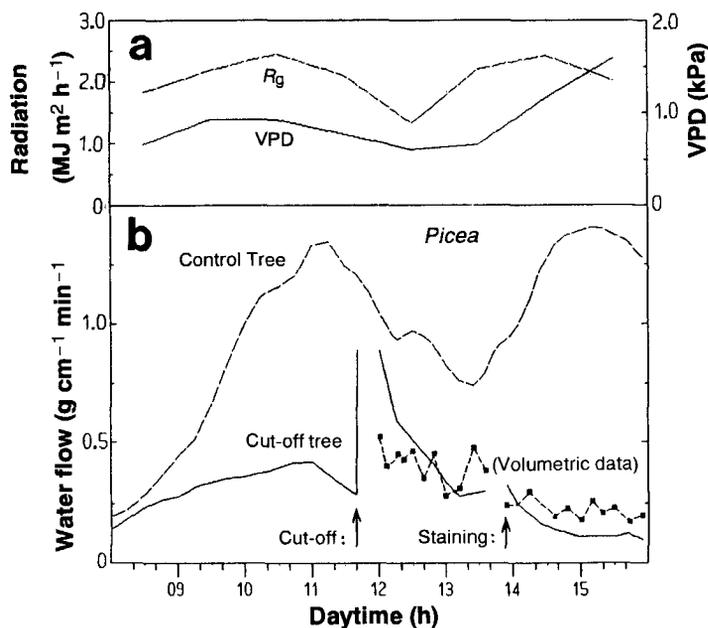


Figure 2. Diurnal courses of (a) saturation vapor pressure deficit, global radiation and (b) xylem water flow rate in experimental and control Norway spruce trees on June 20. The times of severing and subsequent staining are marked with arrows. Points indicate individual volumetric readings.

Volumetric technique

Immediately after recutting, the cut end of the tree was placed in a small pot (all the time immersed in water). The pot was then filled with water to its upper edge, which was taken as a reference level. To replace water absorbed by the tree, the pot was refilled every 5 min for the next 4 h. In this way volume flow data were obtained for 2 h for comparison with the THB data.

Staining technique

The staining experiment was started by filling the pot with dye solution (0.5% acid fuchsin) and refilling it every 5 min for 2 h. This moment was taken as the start point of staining. Refilling the pot with dye solution then continued for exactly two hours. Finally, the tree trunk was severed above the THB measuring point to eliminate absorption by the tree crown. The rest of the trunk was then removed from the pot and, starting at the basal end, immediately cut into 5-mm thick discs until the dye traces in the xylem became invisible. Eighteen discs were obtained. Every disc was orientated in position and photographed. The stained area visible on the discs was later evaluated from slides as a matrix of points to reconstruct the conductive pathway and the velocity (v) profile of water flow in the conductive xylem. This was calculated from the axial distances (summarized length of discs, DL) and the time interval of dye movement ($D_t = 120$ min), $v = DL/D_t$.

Another method of point staining was used in several specimens of oak and spruce. A dye solution was injected into an opening made through the conductive xylem by a borer as described previously (Čermák et al. 1984). In this case a small metal cylinder, soldered to a plate at an angle of 45° , was sealed to the bark surface with an artificial resin. The dye solution was then added to the cylinder and a hole was drilled quickly (2 seconds) into the xylem through the liquid, so that the dye penetrated the xylem while protected against air entry. After exposure for 1–2 min for oak and 10–20 min for spruce, the tree crowns were cut off and the remainder of the trunks were cut into discs and evaluated for the velocity profile as described previously. The diameter of borer used gives the size of the radial segment of stained conductive xylem (about 1 cm thick).

Results and discussion

Evaluation of the severing technique

The experimental conditions used, i.e., an initial cut in the open air and a second one immediately following in water have been validated (Roberts 1977, 1978) for coniferous species. Aspiration of pits evidently prevents air embolisms travelling along the whole trunk length from the cut surface (Gregory and Petty 1973). It is unlikely that resin from opened ducts would significantly block tracheids because of the relatively low resin content in Norway spruce and the short duration of the experiment. An uneven dye concentration was not likely to influence the results either, because Booker (1984) found that the penetration time was independent of the concentration of a non-fixing dye. The airtight dye injection technique using pure solutions completely eliminated such difficulties.

The response of xylem water flow to severing

At the beginning of the Norway spruce severing experiment, the xylem water flow rate (Q_{wt}) reached about $0.55 \text{ kg tree}^{-1} \text{ h}^{-1}$ (i.e., 0.3 g min^{-1}) when calculated per 1-cm long segment of stem circumference (Figure 2b). The xylem water flow rate, as measured by the THB method at a trunk height of 1.3 m, responded within seconds to the severing of the tree trunk close to the ground. It abruptly more than doubled, reached a peak within a few minutes, and then decreased gradually during the following four hours—the duration of the experiment. A change in radiation (partial cloud cover, Figure 2a) may have affected the response of Q_{wt} to severing because there was an effect of cloud cover on the Q_{wt} of the control tree. However, in both the control and the severed trees, there was only a slight response of Q_{wt} to increased radiation when the clouds disappeared after two hours. Xylem water flow rate decreased continuously in the severed Norway spruce (Figure 2b). This may have been caused by impurities present in the water (which was not filtered as recommended by Edwards and Jarvis (1981)), e.g., microorganisms or small particles of saw dust produced when the tree was cut, which could have interfered with absorption at the cut surface.

The xylem water flow rate in a Norway spruce tree can be described on the basis of the difference between root and leaf water potentials (Ψ) and appropriate resistances (R). If soil water is ignored (soil water potential as indicated by tensiometers placed within several meters of the study tree was about -0.02 MPa (P.-E. Jansson, personal communication)), we can write

$$Q_{wt} = \frac{\Psi_{leaves} - \Psi_{roots}}{R_{roots} + R_{trunk} + R_{leaves}}.$$

This relationship might change during the severing experiment if Ψ of water in the pot (which can be taken as zero) replaces Ψ_{roots} , or if R of the water pathways changes.

The value of R_{trunk} should decrease with increasing xylem water content at the tree base after immersion of the cut end of the trunk in water (Roberts 1977). In contrast, R_{leaves} was reported to increase in cut Norway spruce twigs, if they were immediately immersed in water after detachment (Lange et al. 1986). However, both of these changes should take place gradually and their magnitude should be relatively small during the first few minutes after severing. The original whole-tree resistance to flow was abruptly and dramatically changed by elimination of R_{roots} . The increase in Q_{wt} after severing was significantly higher in our experiment than that reported by Roberts (1978), who found rather small R_{roots} in the same species confirming previous findings of Hellkvist et al. (1974) on Sitka spruce. Roberts (1977) concluded that the value of R_{roots} represents about one half of the total tree resistance in pine. However, Roberts' conclusion was based on changes in Ψ_{leaves} or Ψ gradients at the root surface during longer time intervals than those studied here. Other experiments with a severed oak tree (Čermák and Kučera 1990) showed a 7% increase in the original Q_{wt} value, after an initial decline for about half an hour. This implies that R_{roots} is much lower in severed oak than in severed Norway spruce.

Quantitative verification of THB method

The time courses of Q_{wt} in the Norway spruce tree estimated by both the THB and volumetric methods were similar, although individual estimates of water volume absorbed varied because of difficulties in determining the exact reference water level in the pot (Figure 2b). Data obtained with the THB method can thus be considered quantitatively valid at the whole-tree level. The sums of flow obtained during the period of measurements (4 h) reached about 2.4 and 2.1 l tree⁻¹ as estimated by the volumetric and THB methods, respectively, i.e., the THB method underestimated Q_{wt} by 11%. The higher values of Q_{wt} determined by the THB method at the onset of the experiment parallel the higher values of Q_{wt} determined by the volumetric method after one hour. The time interval studied was too short to allow definite conclusions about flow behavior. But it is clear that the flows determined by the THB and volumetric methods cannot be absolutely identical before stabilization, i.e., until any capacitances between the trunk base and the THB measurement point have equilibrated. This equilibration process should take longer in coniferous species with small

tracheids and large sapwood area than in species with big vessels and small sapwood areas like oak and *Eucalyptus*, where a similar experimental technique was used successfully (Cermák and Kučera 1990, Olbrich 1991).

Water flow velocity profile in tree trunks

The water and dye solution absorbed at the cut surface of the Norway spruce trunk (penetrating through tissues previously saturated with water) showed a remarkably variable velocity profile across the trunk. This was apparent on the photographed surfaces of discs redrawn in Figure 3 and is well illustrated in the computed three-dimensional picture (Figure 4), which shows the stained xylem in the trunk after exposure to dye, i.e., the dye velocity. The range of velocities observed across the trunk was about $10\text{--}35\text{ cm h}^{-1}$, but there were many small peaks and depressions throughout the conductive xylem. Zero velocities (no flow) were found close to the cambium as well as close to the heartwood, which occurred at a depth of 4–6 cm at the trunk base (with a xylem diameter of 16 cm, $A_{cx} = 111\text{ cm}^2$). All the water flow velocity data were within the range observed by others in Norway spruce (cf. Zimmermann and Brown 1971, Hinckley et al. 1978). The shape of the velocity profile in the radial plane can be roughly approximated to a Gaussian curve. Norway spruce is known to have a clockwise spiral pattern of flow (Rudinsky and Vité 1959, Coutts and Philipson 1976). The spiralling of the flow in the severed Norway spruce was apparent (see Figure 3), reaching an angle of only $3\text{--}6^\circ$, i.e., similar or lower than the values reported by Birot et al. (1971). Because the distance of the path observed was short, spiralling was neglected when illustrating the radial profile in Figure 4.

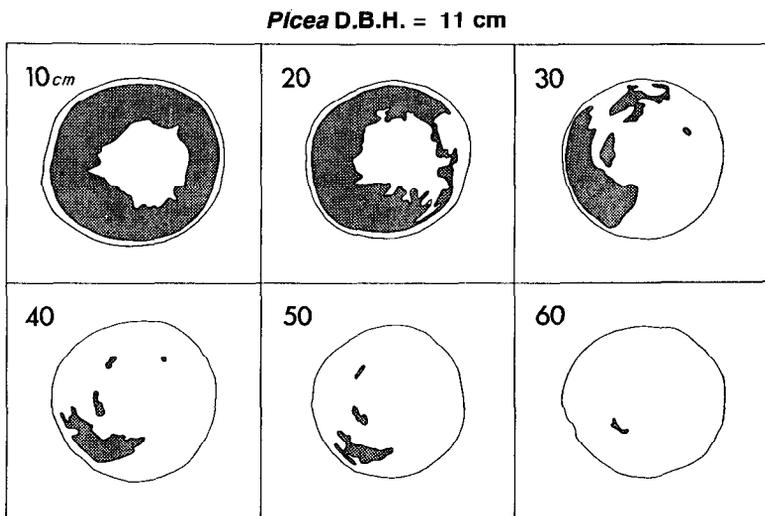


Figure 3. Stained xylem area as visible on discs from the trunk of the experimental Norway spruce at the end of the experiment, showing the conductive pathway of the water or dye solution. Numbers indicate the distance (cm) from the cut end of the trunk where the dye was applied.

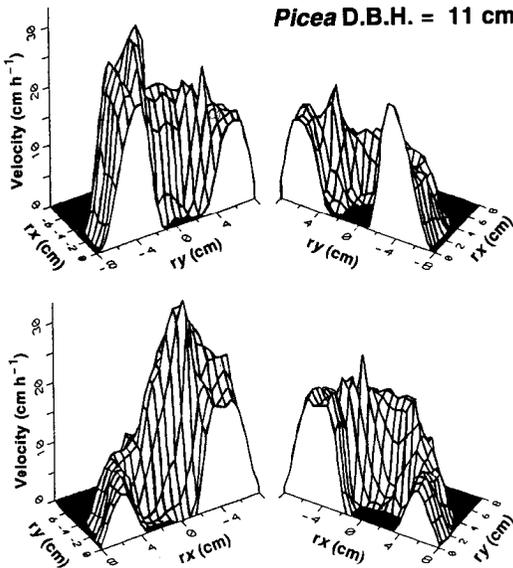


Figure 4. Acropetal velocity profile of a water or dye solution in a cross section of the basal part of the Norway spruce trunk (dbh = 11 cm; diameter at the base 16 cm, $A_{cx} = 111 \text{ cm}^2$). The velocity profile was derived from the stained areas visible on the discs (see Figure 3). The path length and time of exposure were computed from a simplified matrix of $5 \times 5 \text{ mm}$ only, neglecting the slight spiral pattern. Cross-sections through the radial profile in the west-east-west (upper part of figure) and north-south-north directions are given.

The mean value of velocity calculated in the spruce trunk, v' , was about 14 cm h^{-1} . This gives a total effective sapwood lumen area, A_{lum} , at the trunk lower end (when taking mean volumetric readings of $Q_{wt} = 441 \text{ cm}^3 \text{ tree}^{-1} \text{ h}^{-1}$), of $A_{lum} = Q_{wt}/v' = 31.5 \text{ cm}^2$. This means that the porosity of the lower trunk, P , is equal to $A_{lum}/A_{cx} = 28.4\%$. For the same period, the THB method at a height of 1.3 m gave mean values of Q_{wt} of about $304 \text{ cm}^3 \text{ tree}^{-1} \text{ h}^{-1}$. If the mean flow velocity at a height of 1.3 m is the same as in the lower trunk, then $A_{lum} = 21.7 \text{ cm}^2$ and $P = 32\%$. This value is only a little higher than the value of 28% obtained by gravimetric density analysis, indicating that the xylem at the trunk base was saturated with water under the experimental conditions (e.g., Heine and Farr 1973).

The radial profile of water flow velocity in Norway spruce confirms previous findings based on HPV techniques (e.g., Swanson 1967a, 1967b, 1971, Mark and Crews 1973), but contradicts the work of Sipchanov and Baurenska (1965), who used the staining technique in medium-aged Norway spruces and found maximal penetration in the outermost 1–2 growth rings only, tailing centripetally in an approximately exponential manner after 4–23 h of exposure to the dye.

Mark and Crews (1973) gave an excellent explanation of the Gaussian-like pattern of velocity in Engelmann spruce and lodgepole pine based on microscope studies. They found that bordered pits connecting tracheids in the area of peak water flow velocity (i.e., at a depth of 30–40 mm beneath the cambium) are not aspirated and

are only partially impregnated, and are thus maximally open. Pits located in the area of low flow in rings near the cambium are immature and nearly imperforate, whereas those in the area of low flow velocity deep within trees (i.e., 60–80 mm) have a high frequency of aspiration or nearly complete impregnation and thus for the most part block the flow. The formation of heartwood, which leads to slight decreases in leaf water potentials, can also be accelerated in diseased spruce trees by the formation of peroxides under the impact of pollutants (Richter et al. 1988). The velocity discussed here is that for the lumen in earlywood. Permeability of xylem is indirectly related to its specific gravity (Booker and Kinimonth 1978), so in dense latewood flow can hardly be detected.

Quite different velocities and patterns of flow were found in oak using the dye-injecting technique. Peak velocity was about 40 m h^{-1} in the latest growth ring in both the small (dbh = 8 cm) and large (dbh = 30 cm) oak trees, decreasing to zero at about 2 cm beneath the cambium in both cases (Figures 5 and 6). When compared with peak values (100%), the velocity decreased from approximately 25 to 5% within the following three to seven growth rings in the small oak tree and from 50 to 5% within three to nine growth rings in the large oak tree, which had 20 rings of visible sapwood. The decline in velocity with depth differed slightly on different sides of the same tree. Differences in flow velocities estimated by dye injection during the daytime and late at night were smaller than expected when compared with the flow rate of intact trees estimated by the THB method under similar conditions. Rather high velocities were observed in some trees analyzed during the second day of continuous rain. These observations confirm that, in both Norway spruce and oak, the flow is not driven by transpiration directly, but through the remaining water

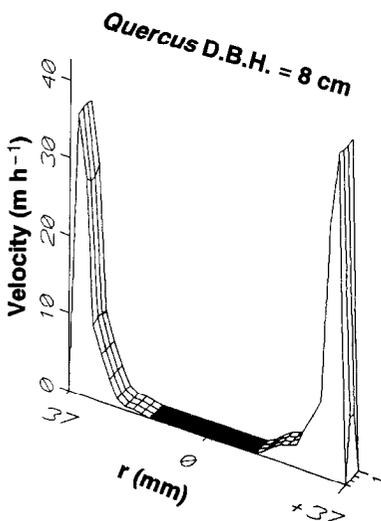


Figure 5. Acropetal velocity profile of a water or dye solution in a cross-section (north-south) of the basal part of a young oak trunk (dbh = 8 cm) as determined on discs obtained from the resampled tree trunk that had been stained by a dye-injection technique.

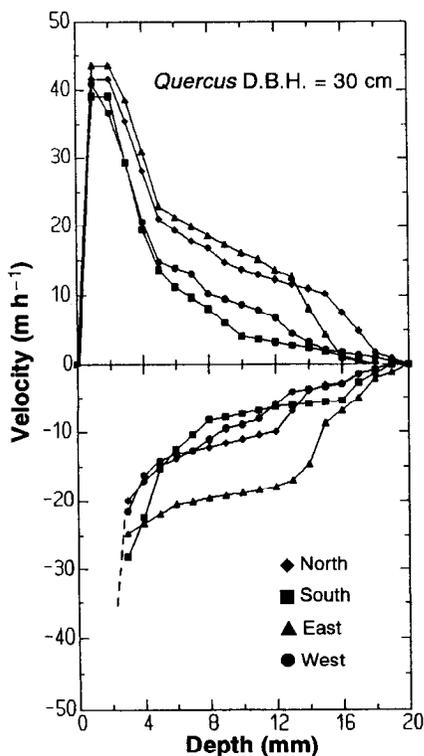


Figure 6. Acropetal and basipetal velocity profiles of a water or dye solution in the sapwood, at breast height, of a tall oak (dbh = 30 cm, visible sapwood depth = 25 mm) determined at the same time from four cardinal points from discs of a tree stained by a dye-injection technique. Peak basipetal values are missing because the dye entered the stump.

saturation deficit (or water potential gradient) of xylem tissues.

Oak, which is ring-porous, is known as a sectorial straight ascent species with very little or no spiral grain (Kozłowski and Winget 1963, Waisel et al. 1972, Miller et al. 1980). Very high water flow velocities in the latest growth ring of oak were described many years ago (Huber and Schmidt 1936, Kuntz and Riker 1955). Velocity profile variability (see Miller et al. 1980) occurs because almost all of the large vessels gradually fail as conductive units either as a result of the development of tyloses, which were observed in earlywood vessels in the 1-year-old growth ring of oaks, or as a result of cavitation events and embolism during melting of frozen water and desiccation in winter (Ikeda and Suzuki 1987, Sperry and Tyree 1988, Cochard and Tyree 1990). In the absence of functional large vessels, water can only flow through auxiliary water conducting units, such as small latewood vessels (Zimmermann 1964). However, the reported hydraulic resistance of these auxiliary vessels is 4–7 times higher than observed in this study. Thus, it is possible that, in oak, some of the large earlywood vessels continue to function for several years. This may be a result of the relatively mild climate in the region (J. Pivec, personal communication).

Minimal winter daily temperatures were apparently sufficient to freeze and subsequently embolize all earlywood but not all latewood vessels (Hobbs 1974, Bilanski and Tzeng 1980). Another reason for the observed variability in the velocity profile may be a methodological one: because the wood was not impregnated with special protecting solutions as recommended by Werner (1968), even non-fixing dyes can penetrate radially along the rays from the main conducting vessels and so simulate the axial flow. However, it is unlikely that this happened because the time of exposure to the dye was only about 1 minute. Tailing thus seems to be a real phenomenon.

The dye injection technique indicated that acropetal velocities were higher than basipetal velocities in the sapwood of Norway spruce, whereas velocities were almost the same in both directions in oaks, at least in older rings (see also Figure 6). The dye injection technique gave higher estimates of flow velocity and flow rate than the THB method, because of changes in the hydraulic parameters of the trunk as a result of severing. After injection of dye, flows in both directions were independent of each other, because the injection opening contains solution under atmospheric pressure. Pressure conditions in the conductive xylem before and after injection of stain are shown in Figure 7 (Kučera 1991, unpublished observations). For simplicity, a constant hydraulic resistance of conductive system from roots to leaves was assumed. Figure 7 shows the increase in the water potential gradient in the stem above the point of injection compared with the intact trunk under the same conditions. In contrast, the gradient below the point of injection in the direction of the roots changes in both magnitude and sign, causing a basipetal flow of water. Both gradients are of similar size, as indicated by the observed flow velocities. We conclude that the staining technique always overestimates the velocities of flow.

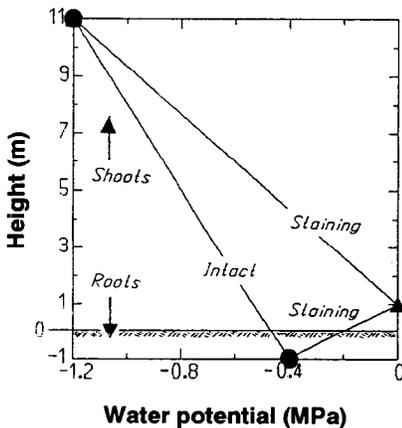


Figure 7. Relationship between water potential and height in a hypothetical tree with a constant hydraulic resistance along the whole conductive xylem. Values of root and shoot water potentials (●) are common marginal points of the relation. This is true when the tree is intact as well as when normal pressure conditions are changed at the point of injection of a solution with almost zero water potential (▲) (Kučera 1991, unpublished observations).

Conclusions

The xylem water flow rate in tree trunks is a sensitive indicator of the functional state of conductive xylem. It responds immediately to removal of root resistance, even if no embolisms appear in the tracheids after they have been opened in water. The course of xylem water flow rate in Norway spruce trees *in situ* might not be the same as the rate of absorption at the surface of a cut trunk immersed in water. Estimated velocity profiles are likely to be subject to error because of problems associated with unnaturally high changes in hydraulic pressure and remaining xylem water saturation deficits in the cut tissues. Radial velocity profiles in Norway spruce, which approximate a Gaussian curve with a low amplitude, differ substantially from those in oak, which are asymmetrical with peak values close to the cambium and reaching values up to two orders higher than in Norway spruce.

The destructive volumetric method can be used only for an approximate evaluation of other measurements in coniferous species, especially when the location of appropriate sensors is distant from the cut surface. Nevertheless, a simple staining method gives estimates of the conductive pathway of water and radial velocity profile of flow that are accurate enough for checking the correct position of sensors (i.e., depth of electrodes and thermocouples). Staining can also help to explain variations in xylem water flow rate in a trunk.

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