

Axial and radial water flow in the trunks of oak trees: a quantitative and qualitative analysis

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Summary

Axial water flow in the trunks of mature oak trees (*Quercus petraea* (Matt.) Liebl. and *Q. robur* L.) was studied by four independent techniques: water absorption from a cut trunk, sap flowmeters, heat pulse velocity (HPV) and thermomaging. Estimation of the total water flow with sap flowmeters, HPV and water absorption yielded comparable results. We concluded from dye colorations, thermograms and axial profiles of sap flow and heat pulse velocity that, in intact trunks, most of the flow occurred in the current-year ring, where early-wood vessels in the outermost ring were still functional. Nevertheless, there was significant flow in the older rings of the xylem. Total water flow through the trunk was only slightly reduced when air embolisms were artificially induced in early-wood vessels, probably because there was little change in hydraulic conductance in the root–leaf sap pathway. Embolization of the current-year vessels reactivated transport in the older rings.

Keywords: embolism, heat conduction, *Quercus petraea*, *Quercus robur*, sap flow, spatial variation, xylem.

Introduction

Axial water flow in the wood of temperate ring-porous species is restricted to either the last, or last few, annual rings (Longmann and Coutts 1974, Ellmore and Ewers 1986). Recent studies have demonstrated that the large early-wood vessels of temperate *Quercus* species are susceptible to frost-induced embolism (Cochard and Tyree 1990, Cochard et al. 1992, Sperry and Sullivan 1992, Bréda et al. 1993b). Because these species do not possess any mechanisms for repairing embolized vessels (e.g., root pressures), it could be that in regions where below freezing temperatures occur, axial water transport in the sapwood of *Quercus* species relies solely on vessels of the current-year ring.

To rely on such a small number of external vessels is highly precarious, because vessels are vulnerable to air embolism as a result of pathogen attacks, mechanical disruption, freezing or water-stress induced cavitation (Tyree and Sperry 1989). Furthermore, the finding that oak trees as well as other species can survive late spring frost seems inconsistent with the existence of only one ring of functional xylem

elements. Although the large early-wood vessels account for most of the hydraulic conductivity of the xylem (cf. Hagen-Poiseuille Law, Zimmermann 1983), the numerous short and narrow late-wood vessels and tracheids, which remain functional for many years, may play a significant role when the bigger vessels are dysfunctional (Zimmermann and Brown 1971, Zimmermann 1982, Gasson 1987). Preliminary experiments (Cochard and Tyree 1990) have demonstrated that small vessels and tracheids are able to maintain adequate water transfer in the xylem of small branches.

To obtain more information about the functioning of *Quercus* xylem and the role of small vessels and tracheids, we studied axial water flow in *Quercus petraea* (Matt.) Liebl. and *Q. robur* L., two climactic species in central Europe. Our objectives were (1) to compare different techniques for measuring sap transfer in tree stems, (2) to determine the path of the transpiration stream in the sapwood, and (3) to analyze the perturbations induced by embolization of early-wood vessels.

Materials and methods

Site and plant material

The experiments were performed in a mixed oak stand (*Q. petraea* and *Q. robur*) located in the Forêt Domaniale de Champenoux, France (48°44' N, 6°14' E, 237 m altitude). Stand density was 3644 stems ha⁻¹, mean height was 15 m, mean and maximal diameters at breast height were 8.6 and 17.5 cm, respectively, and age ranged from 30 to 40 years (see Bréda et al. 1993a for a detailed description of this stand). Most of the experiments were conducted on *Q. petraea* and some were repeated on *Q. robur*. At the end of each experiment, the studied trees were felled, and the apparent sapwood depth was assessed visually based on coloration in a transverse section.

Sap transfer techniques

Three techniques, water absorption, heat pulse velocity meters and radial sap flow-meters, were used to analyze sap transfer through the trunks.

(1) *Water absorption* Sap flow was estimated by measuring the absorption rate from a cut stem. A waterproof collar was sealed to the trunk at breast height, filled with distilled water filtered to 0.2 µm, and connected to a 30-l cylindrical reservoir with plastic tubing. All the sapwood was then exposed under water with a wood chisel. The reservoir was designed so that the water in the collar was maintained at a constant level ("Mariotte system" shown in Figure 1); the water flow from the reservoir to the collar thus equalled the water flow from the collar into the tree. This device allowed an estimation of the absorption rate with a precision of ± 5%.

(2) *Heat pulse velocity meters (HPV)* Sap velocity was assessed with miniature HPV meters. A temperature sensing probe, approximately 1.5 mm in diameter, was made by mounting three 1-mm diameter thermistors (type GB35J1, Fenwall Electronics Corporation, MA, USA) at 5-mm intervals in an epoxy resin. A heater, consisting of

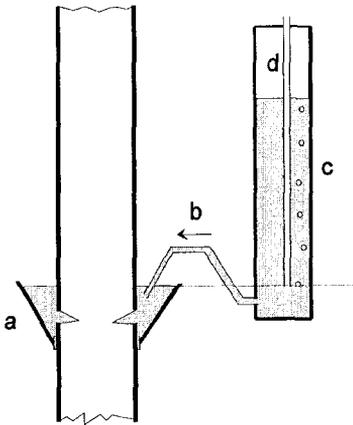


Figure 1. Schematic representation of the water flow device. Water flows from the closed tank (c) to the collar (a) through tube (b). Tube (d), which is open at both ends, allows air to enter the tank. The water pressure in the tank is at equilibrium with the atmospheric pressure at the bottom of tube (d), through which air enters the tank (horizontal line). Because the water level in the collar is maintained at this reference level, the change in water content in the tank equals absorption from the collar.

a 15-mm long and 1.5-mm thick constantan coil, was inserted 13 mm below the thermistor probe. Heat pulses were provided every 30 min, and the temperature of the thermistors recorded for 8 min following each heat pulse. The delay in appearance of the peak value of temperature was used to calculate the heat pulse velocity according to Cohen et al. (1981).

(3) *Radial sap flowmeters* These devices (described in detail by Granier 1985, 1987) measure the integrated sap flux density (F_d , $\text{dm}^3 \text{dm}^{-2} \text{h}^{-1}$) along a radius in the sapwood. Probes of 1.1 and 2.1 cm in length were used. Sap flow rate ($\text{dm}^3 \text{h}^{-1}$) was calculated as the product of sap flux density (F_d) and sapwood area at the measurement level.

We compared techniques (1) and (3) on an 11.1-cm diameter trunk of *Q. petraea* by placing a radial sap flowmeter 0.5 m above the collar of the Mariotte system. We used a 2.1-cm long probe to assess sap flow in the sapwood (1.8 cm of apparent sapwood). The experiment was run for one day. On the second day, an embolization experiment was performed on this tree (see below). Techniques (2) and (3) were compared on a 13.7-cm diameter trunk of *Q. petraea* (2.2 cm of apparent sapwood) by inserting both a flowmeter, with a 2.1-cm long probe, and a heat pulse velocity sensor at the same level. The concurrent measurements were recorded for eight days and then an embolization experiment was performed on this tree (see below).

Sap pathways

Sap pathways in the sapwood were characterized qualitatively by dye perfusion and thermoimaging and quantitatively by radial profiles of sap flow and heat pulse velocity.

(1) *Dye perfusion* Mariotte systems were adapted to four *Q. petraea* trunks (10 to 13 cm in diameter) as described above, and dye (basic fuchsin or safranin-O) was added to the water (5 g l^{-1}). After 6 to 24 h of absorption, the trees were felled and cut into 0.5-m long segments. The radial extension of coloration was assessed visually in each segment.

(2) *Thermoimaging* The principle of this technique is to assess with an infrared camera the temperature profile along a heated wire in contact with a sapwood radial section. In the active zones of the xylem, the heat dissipated by the heated wire is transferred by convection as a result of the ascent of sap. The thermograms therefore show thermal peaks corresponding to active rings. Two *Q. petraea* trees and two *Q. robur* trees were carved (Figure 2) according to the method described by Anfodillo et al. (1992, 1993) so that direct observation of a longitudinal surface about 25 cm in height was possible. A segment of 0.2-mm diameter nichrome wire was placed along this section in a small horizontal cut. The cut was filled with silicon grease to ensure contact between the wire and the surface throughout the section. The thermocamera (AGA 782 with a 20° field of view and 2 milliradian resolution, an 8–14 mm spectral response nitrogen-cooled sensor, and a 5° selected thermal range with 128 gray levels) was placed on a tripod at a distance of about 50 cm, allowing a geometrical resolution of $\pm 1 \text{ mm}$. The measurements consisted of a heating and a cooling phase. When a thermal steady state was reached, the heater was turned off and the cooling phase began. The cooling was faster in the most active tree rings, thus displaying the path of sap flow. Continuous recording on a videotape was done throughout the experiment. At the end of the procedure, the xylem in which the wire had been inserted was cut off and the tree ring thickness measured. Sapwood dimensions and the number of active rings were recorded from the digitized pictures.

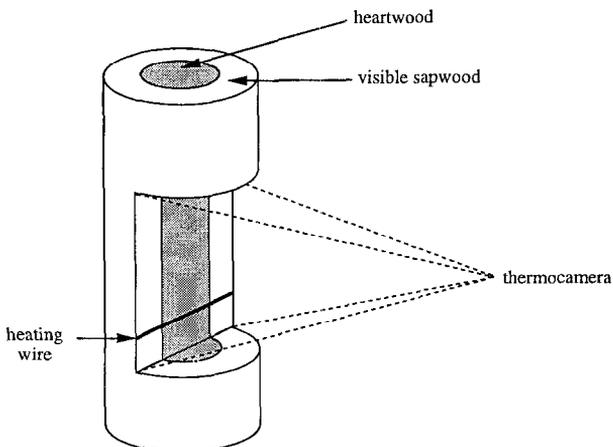


Figure 2. Scheme of the trunk preparation for the infrared observations.

(3) *Radial profiles* Sap flow profiles were obtained by using a set of three 1.1-cm long radial flowmeters inserted under the cambium of one *Q. petraea* trunk (11.9 cm diameter and 1.9 cm of apparent sapwood) at depths of 0 to 1.1 cm, 1.1 to 2.2 cm and 2.2 to 3.3 cm in the heartwood. The two deepest sensors were placed at the bottom of 8 mm diameter holes predrilled to limit heat transfer from the heated probes to the external wood. The flows were measured for eight successive days.

Heat pulse velocity profiles were obtained by placing the temperature probe just below the cambium of a 13.7-cm diameter trunk of *Q. petraea* so that the three thermistors measured the velocity 5, 10 and 15 mm below the cambium. Measurements were made for eight successive days.

Effect of vessel embolization

We studied the effects of vessel embolization on both sap flow and sap pathways. The effect on sap flow was assessed by adapting a Mariotte system and a radial flowmeter to a *Q. petraea* trunk. After the first day when the two techniques were compared (see above), the water in the collar was removed for 20 min, exposing all the sapwood to air. The exposure period was long enough to remove all the sap from the large cut xylem vessels without inducing cavitation in the other conduits. After 20 min, the water was returned to the collar.

After completion of the 8-day comparative study of the radial sap flowmeter and heat pulse velocity sensor methods, we analyzed the effects of xylem cutting on radial profiles of xylem sap fluxes. A reservoir was installed as described previously. The bark was removed on July 29, and water was provided on July 30. On August 6, the sapwood was cut under water with a wood chisel to a depth of about 20 mm over the entire circumference of the tree. Effects of both bark removal and wood carving on sap fluxes were analyzed separately.

The effect of vessel embolization on sap pathways in the wood was also assessed by thermoimaging. After a thermogram was obtained on a trunk set up as described above, the current-year annual ring was cut about 2 cm below the heated wire on both sides, and another thermogram was obtained by the same heating-cooling procedure.

Results

Comparison of techniques

Figure 3 shows the time course of water absorption, measured by a Mariotte system, and sap flow, estimated with a radial flowmeter. Cumulated fluxes between 0930 and 1800 h were 6.9 and 7.9 kg for absorption and flow measurements, respectively. Although the flowmeter overestimated total flow during the early morning and late afternoon, and underestimated it at midday, the integrated values obtained by the two methods were similar.

There was a good correlation between the diurnal time courses of sap flow and mean heat pulse velocity measured concurrently on the same stem for three successive days ($HPV = 0.147 + 0.084 \times \text{Sap Flow}$, $r^2 = 0.95$) (Figure 4). As usually

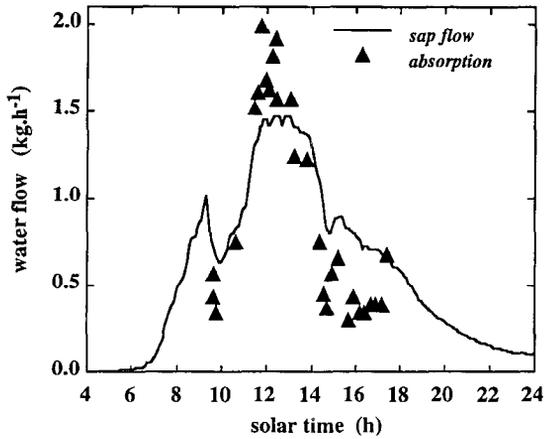


Figure 3. Comparison of time courses of sap flow (line) in a 13.7-cm diameter trunk of sessile oak computed from flowmeters inserted into the trunk, and of water absorption (\blacktriangle) from a reservoir during a sunny day.

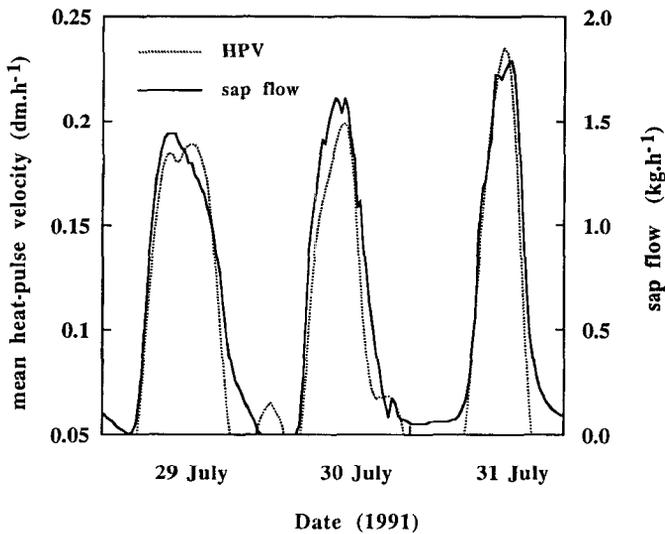


Figure 4. Comparison of diurnal time courses (July 29–31) of sap flow measurements (solid line) and mean heat pulse velocity (HPV) measurements (dotted line), calculated as the average of HPV at the three depths in the trunk of a sessile oak.

observed with HPV measurements, values at night remained at 0.05 dm h^{-1} , which corresponds to the velocity of conductive heat flow in wet wood.

Sap pathways in the xylem

Results from dye colorations were similar in the four sampled trees and for both dyes. Between 30 and 60 cm above the absorption point, the entire sapwood was colored,

but higher in the trunk, the coloration was restricted to the outer ring. Detailed examination revealed that only narrow vessels and tracheids were colored in rings more than one year old.

Figure 5 shows a representative radial profile of sap flow measured during a sunny day. Of total flow, 80% was located in the outer 1.1 cm of sapwood (corresponding to the first 5–6 annual rings), 13% in the 1.1- to 2.2-cm-deep sapwood layer and 7% in the 2.2- to 3.3-cm-deep sapwood layer. A comparable flow distribution along the radius was measured by the HPV technique with values of 58% at 5 mm (second ring), 27% at 10 mm (fifth ring) and 15% at 15 mm below the cambium (see July 29 in Figure 8).

Figure 6 shows a series of thermograms recorded on four oak trees: Q1 and Q2 denote a codominant and dominant *Q. petraea* tree, respectively, and Q3 and Q4 denote an intermediate and dominant *Q. robur* tree, respectively. The warmest zone adjacent to the heater appeared as a white line, whereas gray and black zones indicated the cooler and coolest surface temperatures, respectively. During the heating phase, we observed that rapid heat dissipation (i.e., water transport) was restricted to the last two tree rings in Q1 (Figure 6a), Q2 (Figure 6c) and Q3 (Figure 6e). Some significant differences in rates of dissipation were observed between the two sides of the trunk, indicating spatial heterogeneities in xylem sap fluxes in a given ring. Thermal peaks (white arrows) were higher in the left side in Q2 and Q3, and in the right side in Q1. During the cooling phase, the conducting tree rings cooled quickly, whereas the other rings and the bark remained warm for a long time (Figures 6b, 6d and 6f). The thickness of the conducting sapwood was about 0.5 cm in all of the trees (see Table 1). Tree Q4 (Figures 6g and 6h) displayed a

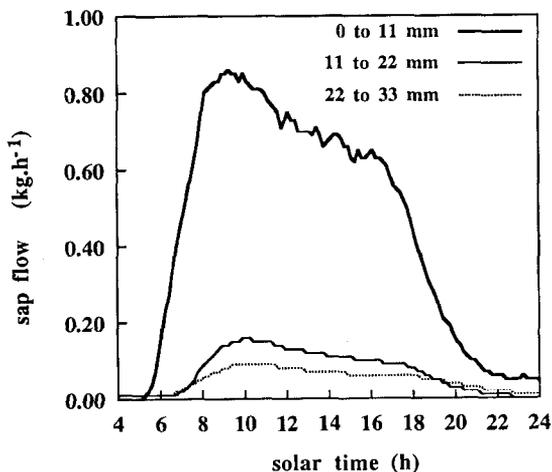


Figure 5. Diurnal time course of sap flow measured by three radial sensors inserted at depths of 0 to 11 mm (bold line), 11 to 22 mm (line), and 22 to 33 mm (dotted line) in the sapwood of a 11.9-cm diameter trunk of sessile oak (19 mm total apparent sapwood).

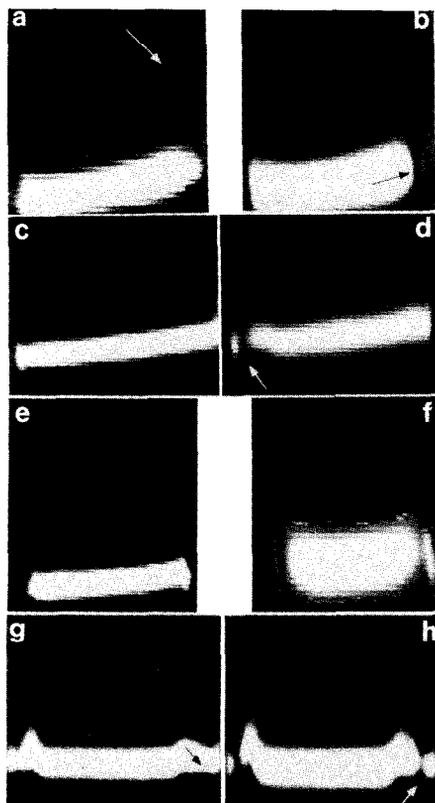


Figure 6. Infrared pictures of four oak trees. The pictures on the left side were taken during the heating phase; the pictures on the right side were taken during the cooling phase. Q1 (*Quercus petraea*): (a) the arrow shows the thermal peak on the right part of the stem, 5 min after the heater was turned on (1300 h); (b) 1 min after the heater was turned off. Q2 (*Quercus petraea*): (c) 3 min after the heater was turned on (1600 h); (d) 1 min after the heater was turned off, the white arrow shows that the outer rings cool first. Q3 (*Quercus robur*): (e) 2 min after the heater was turned on (1400 h); (f) 1 after min the heater was turned off. Q4 (*Quercus robur*): (g) 3 min after the heater was turned on (1200 h), the black arrow shows the indentation corresponding to the most active tree rings; (h) 1 min after the heater was turned off, the white arrow shows that the outer rings cool first.

slightly different behavior: most sapflow occurred in the outermost ring, although some xylem sap transport also occurred in the deeper rings.

Effect of embolization on sap flow and sap pathways

Figure 7 shows concurrent time courses of sap flow and water absorption when the xylem of a *Q. petraea* tree was temporarily exposed to air (arrows on the figure). During exposure to air, sap flow decreased rapidly but did not reach zero, probably because of the thermal inertia of the sapflow device. Ten min after the collar was refilled with water, both sapflow and water absorption increased and stabilized at 1 kg h^{-1} , only slightly lower than the values recorded the previous day when the

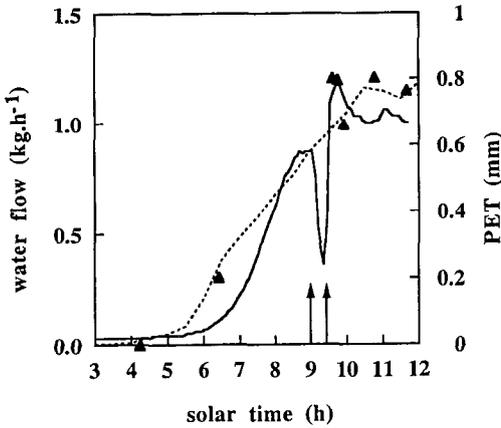


Figure 7. Comparison of diurnal time courses of sap flow (solid line) and water absorption (▲) before and after exposing the xylem to air for 20 min. The arrows show the times of exposure to air. The dotted line = Penman Evapotranspiration (PET).

xylem vessels were still functioning (cf. Figure 3). This is illustrated by the small effect of embolization on Penman Evapotranspiration (dashed line).

The radial profiles of water fluxes measured by HPV were modified by bark removal and the installation of a water reservoir (Figure 8). During the first day (July 29), the radial profile of xylem fluxes was as expected, with a larger velocity in the outer 5 mm of sapwood than in the inner layers. During the second day

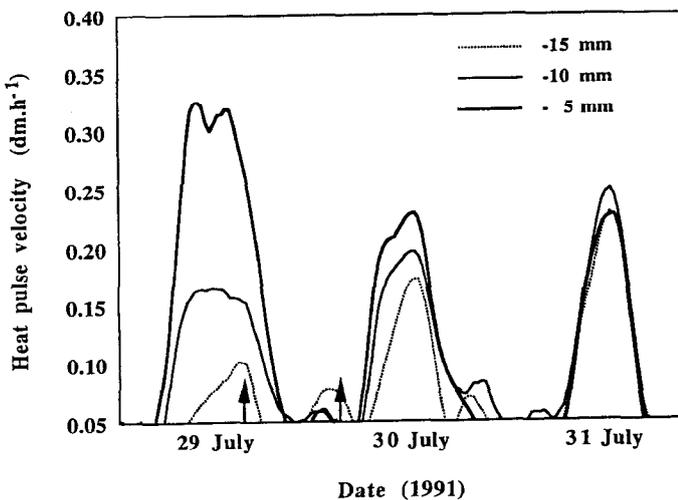


Figure 8. Diurnal time courses of heat pulse velocity measured at three depths (5 mm, bold line; 10 mm, line; 15 mm, dotted line) in the sapwood of a *Q. petraea* tree during July 29–31. July 29 = normal profile; July 30–31 = modifications induced by bark removal and installation of a water reservoir (indicated by arrows).

(July 30), however, we observed a decrease in the sap velocity in the outer layer and an increase in the inner layer, leading, on the third day (July 31), to similar velocities at the three depths. This axial distribution of water flow was maintained for the following nine days. We attributed this phenomenon to xylem damage and embolization caused by wounding of some of the large external vessels when the bark was removed.

After the current-year ring was cut, the thermal peaks became wider, revealing important changes in the path of sap fluxes (Figure 9). In trees Q1, Q2 and Q3, the number of conducting rings increased to 10 (Table 1). An indentation on both sides in the thermal peaks below the wire (Figures 9a, 9c and 9g) corresponded to a light-colored zone identified later as sapwood. Total velocity of sap under these conditions was greatly reduced, as indicated by the finding that cooling of the heated sapwood took twice as long as in trunks with an intact current-year ring (cf. Figure 6).

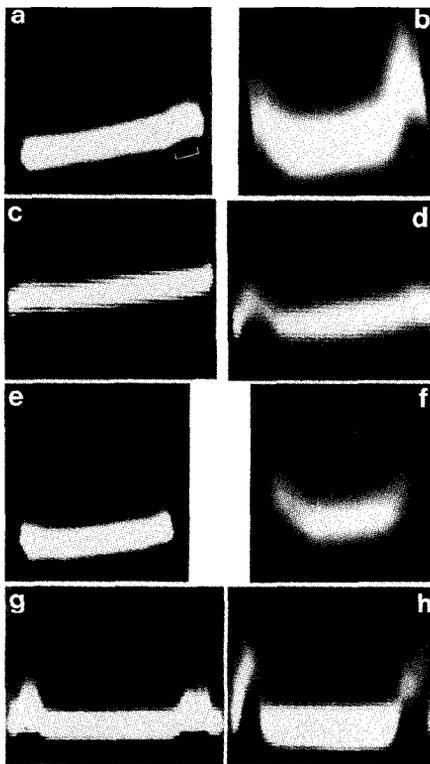


Figure 9. Infrared picture of four oak trees after cutting the external annual ring. The pictures on the left side were taken during the heating phase; the pictures on the right side were taken during the cooling phase. Q1 (*Quercus petraea*): (a) 2 min after the heater was turned on (1400 h), the white line shows the thickness of the sapwood; (b) 5 min after the heater was turned off. Q2 (*Quercus petraea*): (c) 4 min after the heater was turned on (1700 h); (d) 2 min after the heater was turned off. Q3 (*Quercus robur*): (e) 5 min after the heater was turned on (1700 h); (f) 5 min after the heater was turned off. Q4 (*Quercus robur*): (g) 3 min after the heater was turned on (1400 h); (h) 1 min after the heater was turned off.

Table 1. Dimensions of active sapwood and number of active tree rings in the trunks of four oak trees¹ as determined by infrared imaging. Values were recorded before and after a 3-mm cut was made in the external ring, 2 cm below the measurement area.

Tree	Diameter (cm)	Age (years)	Sapwood depth (cm)				Active tree rings			
			Before cutting		After cutting		Before cutting		After cutting	
			Left	Right	Left	Right	Left	Right	Left	Right
Q1	12.1	Unknown	≈0	0.5	≈0	2	–	2 (1)	–	10
Q2	15.7	Unknown	0.6	–	2.1	–	2	–	9	–
Q3	10.9	32	0.5	0.5	1.8	1.5	2	2	10	9
Q4	17.6	34	1.3	2.3	1.6	2.3	6	7	7	7

¹ Q1 and Q2 denote a codominant and dominant *Q. petraea* tree, respectively, and Q3 and Q4 denote an intermediate and dominant *Q. robur* tree, respectively.

During the cooling phase, the sap flux density profile became constant along the radius (Figures 9b, 9d, 9f and 9h).

Discussion

We compared measurements of sap flow rate based on two kinds of internal heating of the trunk (heat pulse and continuously heated flowmeters). Several papers have reported comparative studies of sap flow measurement devices where each technique has been calibrated independently with transpiration (gravimetric measurement for Lassoie et al. 1977, Swanson and Whitfield 1981, Cohen et al. 1981; water balance method for Granier 1987, Bréda et al. 1993a), but there have been no direct comparisons of these methods. Although the relationship between HPV and sap flow depends on the species (Cohen and Fuchs, 1989) and sapwood area of the tree stem (Sabatti et al. 1993), we found good agreement among the different sap flow methods, including the water absorption method. Radial flowmeters gave an accurate measurement of the total sap flow within the sapwood, and the short radial continuously heated probes detected the radial profile of sap flow. The HPV meters revealed a precise pattern of sap flux densities according to depth in the xylem, but despite the small dimension of the HPV probe, it was not possible to measure sap flow in a single ring, nor was this technique able to distinguish between early-wood and late-wood sap flow.

Although many studies have been conducted with dyes (Greenidge 1958, Holmes 1982), dyes can only successfully describe the sap pathway in the wood if they are freely transported by the water stream and if pressure gradients resemble those in intact plants. This is not the case for safranin and basic fuchsin. We think that these basic dyes are absorbed on the walls of the conduits and can travel further up the water stream only when all the fixation sites are saturated. This is illustrated by the finding that, although 30 l of dye solution was absorbed by some of the trees, the coloration barely reached the minor branches in the canopy. One meter above the absorption point, only the most external ring was colored, because the flow velocity

in the large early-wood vessels was higher than in the minor vessels and tracheids of the remaining rings. Because only the minor vessels and tracheids were stained in the deeper rings, we conclude that the large early-wood vessels were only functional in the current-year ring. Results from the sap flow and heat pulse velocity profiles (quantitative analysis) and the thermograms (qualitative approach) were consistent with these conclusions. Sap flow was more important in the external rings (0.5 cm below the cambium, e.g., second tree ring) than in the deeper layers of the wood. Nevertheless, we found that a significant flow (20 to 30% of the total flow) occurred in the deeper layers of the sapwood, indicating that more than one ring contributed to sap flow in the xylem of these *Quercus* trunks. This result is consistent with the observations of Cermák et al. (1992), who found a decrease in sap velocity from 50 to 5% within three to nine growth rings in a *Quercus* tree with 20 rings of visible sapwood. Because the probes were in contact with more than one ring, and because of passive heat dissipations from surrounding rings, we were unable, with these techniques, to measure sap flow in the first ring alone.

The infrared technique provided evidence of large differences in water transport between the two sides of a stem (cf. Anfodillo et al. 1992, 1993). Several papers (e.g., Swanson 1967, Lassoie et al. 1977) have reported that sap velocity changes according to the azimuth in the trunk, but that real differences in sap velocities may be confounded by the variability inherent in the HPV technique. Cermák et al. (1992) used a dye injection technique and found a more asymmetrical radial profile of flow velocity in a tall than in a small pedunculate oak tree. This difference could be due to the asymmetrical shapes of the crown and root system and the variable conditions around the trees (e.g., competition for light, water and mineral elements) causing an irregular thickness of tree rings along the section of the tree, or it could be an artifact induced by a slightly nonsymmetrical carving of the stem.

When the xylem of the trunks was exposed to air, sap was completely withdrawn from all the cut conduits, because the capillary forces that these conduits can sustain are too small to maintain water in the lumen (cf. Borghetti et al. 1993, Cermák and Kucera 1993). Because tracheids and late-wood vessels are shorter than early-wood vessels, many of them will be intact, but close to the cut surface, and will supply water to the entire network of smaller conduits when water is added to the collar.

Total sap transfer through the trunk was only slightly reduced by embolization of large vessels in the outer ring. Therefore, because at steady state, sap flow through the trunk equals evaporation from the leaves, the evaporation rate was only slightly changed after embolization, i.e., embolization had little effect on hydraulic conductance of the whole root-leaf sap pathway. The constancy of sap flow after embolization may be partly explained by the finding that the main resistances to water flow in the aboveground parts of *Quercus* species are located in the leaf blades (Tyree et al. 1993), the trunk resistance being very low. However, the primary explanation is that sap flow in the inner rings increased significantly after embolization, whereas it decreased in the outermost rings so that sap flow rate remained unchanged. We suggest that before embolization, the resistance to water flow was much lower in the

first ring, because of the functionality of the early-wood vessels, whereas after embolization, the resistances of all the rings were similar (cf. Canny 1991).

We conclude that, under normal condition, most sap flow occurs in the outermost annual ring where the large early-wood vessels are functional. Flow also occurs in the inner rings, but to a lesser extent. If, because of pathogen attacks, frost- or drought-induced embolism, or mechanical damage, the functionality of the early-wood vessels is disrupted, inner rings become activated so that the overall efficiency of the xylem is only slightly affected. In 1983, Zimmermann introduced the efficiency versus safety dilemma, namely that the large conduits of the xylem are more efficient for water conduction but are more vulnerable to damage than smaller vessels. The structure and function of the xylem in *Quercus* trunks provides an illustration of this dilemma. The large early-wood vessels assure the efficiency of the xylem, but, because of their high vulnerability to frost-induced embolism, they can only function for one year. The small vessels and tracheids are the safety component of the xylem. Their role is minor when conditions are favorable, but is critical when large vessels develop embolisms.

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