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Radial Variation of Sap Flow Densities in the Sap-Wood of Beech Trees (*Fagus sylvatica*)

By

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Summary

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The radial distribution of sap flow densities in the sapwood (0-14 cm) of c. 95-year-old beech trees has been determined with constant heating probes consisting of 7 thermocouples in line. Sap flow densities were constant up to a distance of 6 cm from the cambium but subsequently decreased with increasing distance. The radial gradient of sap flow densities in the sapwood was steepest during the day between 8:00 and 13:00 and lowest during the night. The implications of this gradient for the calculation of tree or stand sap flow and transpiration are discussed.

Introduction

Beech (*Fagus sylvatica* L.) is the most important deciduous tree species in natural forests of Central Europe (ELLENBERG 1992). In the past the area of distribution of this species has been forced back in favour of fast growing conifer species due to human activities. Recent forest management practices, however, are aimed to transfer uniform conifer monocultures to more structured species-rich forests by selective felling of adult trees and planting of beech seedlings (SCHÄFER 1995). Since the areal of beech is limited mainly by the water availability (ELLENBERG 1992) it has to be assumed that the consequences of anthropogenic climate change i.e. increasing temperatures (HOUGHTON & al. 1996) and enhanced

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periods of summer drought (ROECKNER 1992, RENNENBERG & al. 2004) have intensive effects on this species. Therefore, studies on the water balance of beech trees, promoted by recent management practices, are highly desirable.

Besides the determination of water potential and - more recently - the assessment of stable isotopes (e.g. ADAMS & GRIERSON 2001, KEITEL & al. 2003) the measurement of xylem sap flow is a useful technique for the description of the water balance of plants (VON WILLERT & al. 1995). Several sap flow techniques have been used to estimate the water flow in the trunks of trees (KÖSTNER & al. 1996). The most common methods are the heat balance techniques as described by CERMÁK & al. 1973 and KÖSTNER & al. 1996, the heat pulse method (BURGESS & al. 2000, BAUERLE & al. 2002), the heat field deformation method (ČERMÁK & al. 2004) and the constant heating technique introduced by GRANIER 1985, 1987. The system described by Granier is the most widespread at present as it has advantages in maintenance, relative low costs and a low electrical power demand (KÖSTNER & al. 1996). Thus, a high number of independent measurements is possible even in remote areas with limited power supply. With the constant heating method the sap flow density per area of sapwood is generally determined in the outermost 2 cm of the radius (GRANIER 1985). In order to calculate total tree and stand sap flow the flow density has to be multiplied by the sapwood area of the tree and the stand, respectively (GRANIER 1985). This calculation is only reliable if the sap flow density in the area of the sapwood where the measurements are performed is representative for the entire water conducting area. Several approaches have been used in the last few years in order to assess if radial gradients in sap flow density or velocity occur (JAMES & al. 2002, NADEZHDINA & al. 2002) and to correct whole tree or stand water use. Recently, GRANIER & al. 2000 reported that there were strong radial gradients in the sapwood of beech which have to be accounted for when scaling up from sap flow measurements in the outermost 2 cm to the tree or stand level.

The aim of the present study was to test a novel sensor type based on the constant heating technique with 7 thermocouples in series which allowed determining xylem sap flow densities in a distance of 0-2, 2-4, 4-6, 6-8, 8-10, 10-12 and 12-14 cm from the cambium. In addition, based on the results of GRANIER & al. 2000 we aimed at assessing if potential gradients in sap flow densities between inner and outer sap wood of beech - as one of the most important deciduous tree species in Central Europe - show diurnal patterns that have to accounted for when calculating tree or stand sap flow.

Material and Methods

Measurement of sap flow densities in the sapwood

Sap flow densities in the sapwood of c. 95-year-old beech trees were determined by the "constant heating" method of GRANIER 1985. The studies were performed at the field site "Höglwald" that is exposed to high loads of N (GÖTTLEIN & KREUTZER 1991, GEßLER & al. 1998, RENNENBERG & al. 1998).

Six trees with a circumference of 1.4 to 1.6 m, representative for the beech stand (ROTHE 1997), were equipped with a pair of identical sensors of 2 cm length, each. The sensors were installed in the outermost 2 cm of the sapwood of each tree at a height of 2 m above ground one upon the other with a distance of 15 cm in-between.

The radial profile of sap flow densities was measured with a pair of sensor probes each consisting of 7 thermocouples arranged in series, specially developed for this study (ProBit GmbH, Langenfeld, Germany). Each thermocouple was installed in the middle of a 2 cm section (Fig. 1). Pairs of these probes were placed into the sapwood of two beech trees with 1.6 m circumference each, with a vertical spacing of 15 cm. Xylem sap flow densities were measured in a distance of 0-2, 2-4, 4-6, 6-8, 8-10, 10-12 and 12-14 cm from the cambium.

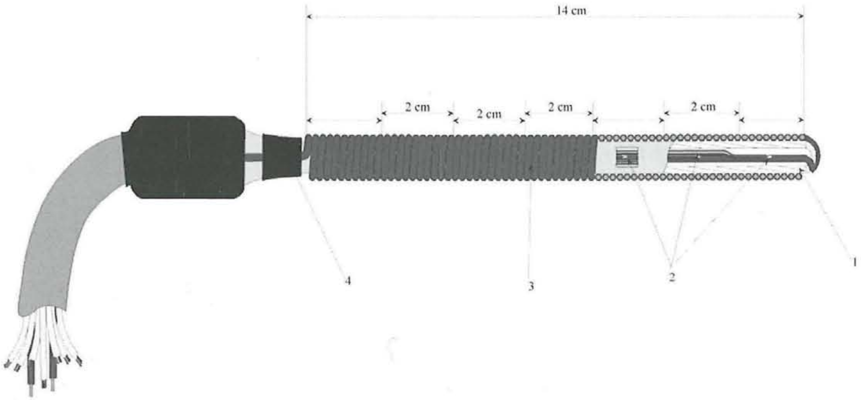

Fig. 1. Design of the probe consisting of seven thermocouples in line. (1: longitudinal section of the syringe (outer diameter 2 mm) containing the thermocouples; 2: copper-constantan thermocouples (one every 2 cm); 3: heating wire with Teflon isolation; 4: Fixation of the heating wire).

All sensors were made of copper-constantan-thermocouples with copper heating wiring. The upper sensors were constantly heated with a power of 5 mW per mm^2 of the sectional area of the sensor in direction to the sap flow (GRANIER 1985), the lower sensors remained unheated. The mass flow of water within the sapwood results in cooling of the heated sensor. The energy transferred from the sensor to the xylem sap depends on the amount of water passing the thermocouples per unit of time.

The differences in temperature between the two sensors were determined for calculation of sap flow densities. The maximum difference in temperature during the night or in the early morning was supposed to indicate the absence of sap flow (GRANIER 1985, KÖSTNER & al. 1996). Flow densities were calculated by equation 1 according to GRANIER 1985, 1987:

Equation 1:. $$u = 0.119 \cdot \left(\frac{(\delta T_m - \delta T)}{\delta T} \right)^{1,231}$$

where u is the sap flow density (l m^{-2} sapwood s^{-1}), δT_m is the maximum difference in temperature and δT is the actual temperature difference. Absolute sap flow densities summed up to half-hourly values were calculated for the six trees supplied with sensors of 2 cm length. For the radial distribution of flow densities, relative values were computed.

The radial pattern of sap flow measured with the probes with 7 thermocouples in series may be partially smoothed as a result of heat transfer through the metal of the needle (JIMÉNEZ & al.

2000). However, this heat transfer is dependent on the ratio of the longitudinal transfer through the thin walls of the probe to the tangential and radial transfer of heat from the massive surrounding wood, which has a much larger heat capacity than the probe. JIMÉNEZ & al. 2000 observed that heat transfer along a comparably designed probe did not alter measurements of radial gradients sap flow significantly.

Determination of the sapwood area of beech trunks

The sapwood area was determined by the displacement technique of GLAVAC & al. 1989 used to obtain xylem sap from trunks. A solution of berberine chloride was applied to displace the xylem sap of trunk sections of 6 representative beech trees from the same height (2 m) where the sensors had been installed. Infiltration of berberine chloride into the water conducting areas of the trunk resulted in staining of the sapwood area. A relationship between tree circumference at 2 m height (C) and sapwood area (SA) was established:

Equation 2: $SA = 47.05 - 5.73C + 0{,}104C^2$ ($r^2 = 0{,}87$)

The sapwood area per ha amounted to 32 m^2 i.e. to c. 80% of the total basal area (ROTHE 1997) of the adult beech trees at the field site.

Results

Figure 2 shows the mean values of sap flow densities in the outermost 2 cm of the radius of 6 beech trees from 09.06.1997 to 12.06.1997. The daily maximum of sap flow density was observed between 12:00 and 14:00 about 0.5 to 1 h after PAR maximum was reached. Minimum values were obtained between 4:00 and 6:00. The mean maximum sap flow density during the period shown amounted to 54 l m^{-2} sapwood per 0.5 h and was representative for the whole June (mean maximum value 52 l m^{-2} sapwood per 0.5 h (data not shown)).

Radial distribution of the relative sap flow densities in the sapwood of two beech trees of 1.6 m circumference is shown in Fig. 3. Deviation of sap flow densities between the two trees studied was 5 to 35 %. The width of the sapwood was calculated to be 16.6 cm when the sapwood area was estimated by equation 2. Sap flow densities did not decrease from the 0-2 cm to 4-6 cm. In a distance of 6-8 cm from the cambium sap flow densities amounted to 77 to 90% of the values measured in the outermost 2 cm of the sapwood and decreased with increasing distance from the cambium. This decrease was strongest in the morning until midday (8:00 to 13:00) when sap flow density in a distance of 12-14 cm from the cambium amounted to c. 30% of the value measured in the outermost 2 cm. This pronounced linear radial gradient of sap flow densities coincided with a steep increase of total sap flow densities in the morning until maximum of sap flow was achieved (Fig. 2). In the evening and during night when total flow densities were low (Fig. 2) the gradient in sap flow densities between the outer and inner part of the sapwood was less steep. Between 1:30 and 5:30 sap flow densities in a distance of 12-14 cm from the cambium amounted to 70 to 85 % of the fluxes determined in 0-2 cm distance.

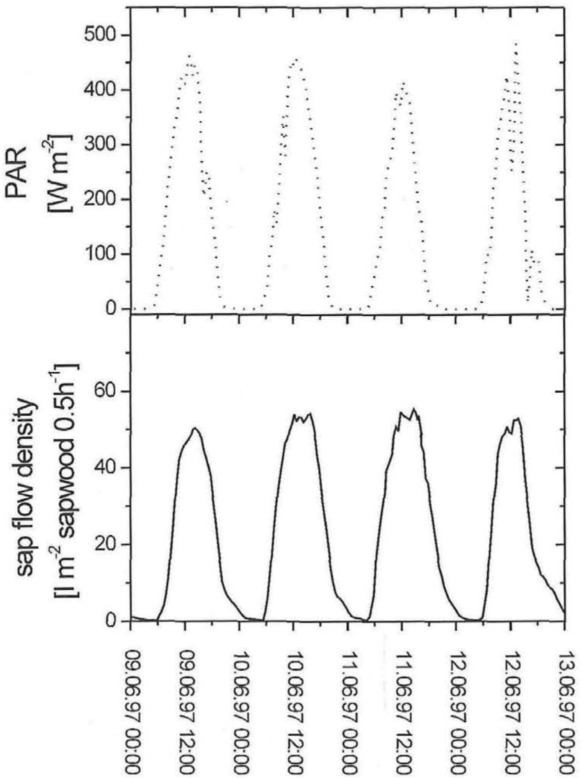

Fig. 2. Mean sap flow densities (—) from 6 adult beech trees measured in the outer 2 cm of the sapwood and diurnal courses of PAR (···) above the canopy. The flow densities were calculated as described in 'Materials and Methods'.

Discussion

Since berberine chloride staining showed that 80% percent of the basal area of the beech stand was able to conduct water and a significant radial gradient of sap flow densities in the sapwood was observed, a simple multiplication of the flow density measured in the outer part of the sap wood with the sap wood area of the tree or stand in order to calculate tree or stand sap flow, respectively, will lead to an overestimation of these parameters (NADEZHDINA & al. 2002). To show the extent of this overestimation the whole tree sap flow was estimated for beech trees with a circumference of 1.6 m (1) by multiplying the sap flow densities shown in Fig. 2 by the sapwood area calculated according to equation 2 and (2) by considering the radial variation of sap flow densities within the sapwood of the tree according to equation 3:

$$\text{Equation 3: } SF_t = \sum_{d=0-2}^{14-16} FD_t * F_{d,t} * SA_d$$

where SF_t (l per tree per 0.5 h) is the whole tree sap flow at the time t, FD_t the sap flow density in the outermost 2 cm of the sapwood, $F_{d,t}$ the factor describing the relation between the flow density in the interval d (2 cm increments) and FD_t as shown in Fig. 3, and SA_d the sapwood area of the interval d. Since the probes with 7 thermocouples in line which were used to determine the radial distribution of the sap flow densities did not cover the whole width of the sapwood (16.6 cm) $F_{d,t}$ for the last increment of d shown in equation 3 (d = 14-16) was calculated by regression analyses of $F_{4\text{-}6,t}$ to $F_{12\text{-}14,t}$. The inner 0.6 cm of the sapwood area was assumed not to differ in sap flow density compared to the segment d = 14-16 cm and was included in the calculation the whole tree sap flow. The half-hourly values were summed up to achieve daily sap flow rates.

The daily mean of whole tree sap flow during the period of time shown in figure 2 amounted to c. 135 l per tree and day when calculated by equation 3. Calculation of tree sap flow by simple multiplication of the flow density by the tree sapwood area resulted in a value of 183 l per tree and day, i.e. in an overestimation by c. 35%.

The results obtained with constant heating sensor probes with 7 thermocouples in line showed that a radial gradient in sap flow not only occurs in ring-porous tree species such as oak (CERMAK & al. 1992, GRANIER & al. 1994), but also in the diffuse-porous species beech. In beech trees with a much wider sapwood as compared to oak this gradient is, however, less steep than in ring-porous species where axial water flow is restricted to the last or the last few annual rings (ELLMORE & EVERS 1986). Comparable radial patterns were observed in tropical species with deep sapwood (JAMES & al. 2002). Different from our results GRANIER & al. 2000 observed a strong decline in sap flow densities within the outer 6 cm of the xylem. At c. 5 cm distance from the cambium, sap flow amounted to 25% of the maximum value of the outer xylem. The main differences between the beech trees assessed here and the individuals examined by GRANIER & al. 2000 are age and stem circumference. Whereas the trees in the present study where c. 95 years old with a circumference of 1.6m, the trees in the other study were 30 years and had a circumference at breast height between 0.09 and 0.65 m. Thus, we assume that trunk dimensions strongly influence the radial patterns of sap flow of a particular species.

The decrease in sap flow density with increasing distance from the cambium can be explained by the occurrence of embolisms especially in the wider vessels (SPERRY 1995) and by the formation of tyloses. Apparently, *Fagus* species are not able to refill embolized xylem vessels (SPERRY 1995, HACKE & SAUTER 1995, 1996, AMÉGLIO & al. 2004) as effectively as other diffuse-porous species, e.g. *Acer saccharum, A. pseudoplatanus, Betula occidentalis, B. penduala, Alnus crispa* and *A. incanata* do (SPERRY 1995, HACKE & SAUTER 1996).

During the diurnal course the gradient of flow densities between outer and inner xylem was most pronounced in the morning i.e. during that time of the day when transpiration driven xylem flow increases most intensively (Fig. 3). Comparable observations were made by FORD & al. 2004 with *Pinus taeda*. They also detected steepest gradients from the cambium towards the centre of the stem during the period of the most intensive diurnal increase in sap flow and less pronounced differences in the early morning and the late evening.

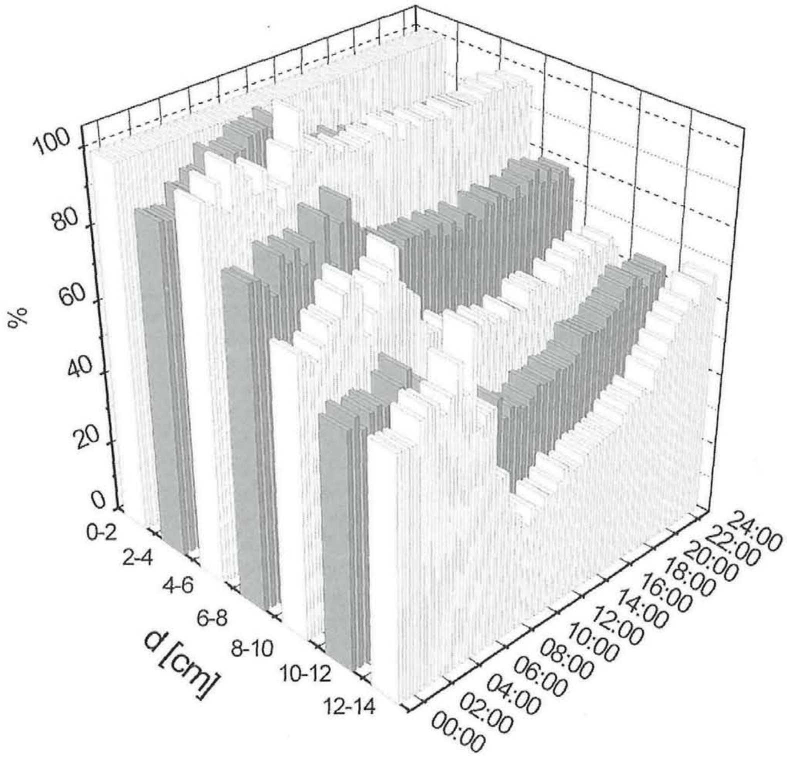

Fig. 3. Radial distribution of relative sap flow densities in the sapwood of beech trees depending on the time of day. Pairs of constant heating probes consisting of 7 thermocouples arranged in series were placed into the sapwood of two beech trees with a circumference of 1,6 m each. The values shown are means of measurements in both trees over a two month period (03.05.1998 - 30.06.1998) with a time resolution of 0.5 h. Flow densities of the outermost sensor (0-2 cm distance (d) from the cambium) were set 100% and the data of the other sensors were related to these values.

Water stored in the inner part of the xylem is supposed to be subjected to higher flow resistances (SPERRY 1995). When transpiration increases during the morning the water demand of the crown is likely to be met first by water with higher mobility i.e. the water in the outer xylem. During midday and in the afternoon when water pressure deficit of the air und thus, the driving force for transpiration and sap flow is high, the importance of the difference in flow resistance between outer and inner xylem becomes less important (FORD & al. 2004).

Additional studies on the radial distribution of sap flow densities in the sapwood of beech trees of different age and circumference classes are necessary in order to quantify the dependency of the radial gradient in sap flow densities from sapwood width and, thus to assess the variation depending on age and crown class of a tree (ČERMÁK & al. 2004, GRANIER & al. 2000). Quantitative information on this relation is crucial for the calculation of stand sap flow and transpiration of inhomogeneous beech stands from the measurements of flow densities by the 'Granier' technique.

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