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Estimates of Water Vapor Flux and Canopy Conductance of Scots Pine at the Tree Level Utilizing Different Xylem Sap Flow Methods

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With 5 Figures

Received November 10, 1994 Revised February 3, 1995

Summary

During the Hartheim Experiment (HartX) 1992 conducted in the upper Rhine Valley, Germany, three different methods were used to measure sap flow in Scots pine trees via heating of water transported in the xylem: (1) constant heating applied radially in the sapwood ("Granier-system"-G), (2) constant heating of a stem segment ("Čermák-system"-C), and (3) regulated variable heating of a stem segment that locally maintains a constant temperature gradient in the trunk ("Čermák/Schulze-system"-CS). While the constant heating methods utilize changes in the induced temperature gradient to quantify sap flux, the CS-system estimates water flow from the variable power requirement to maintain a 2 or 3 degree Kelvin temperature gradient over a short distance between inserted electrodes and reference point. The C- and CS-systems assume that all transported water is encompassed and equally heated by the electrodes. In this case, flux rate is determined from temperature difference or energy input and the heat capacity of water. Active sapwood area need not be determined exactly. In contrast, the G-system requires an empirical calibration of the sensors that allows conversion of temperature difference into sap flow density. Estimates of sapwood area are used to calculate the total flux. All three methods assume that the natural fluctuation in temperature of the trunk near the point of insertion of heating and sensing elements is the same as that where reference thermocouples are inserted.

Using all three systems, 24 trees were simultaneously monitored during the HartX campaign. Tree size within the

stand ranged between 18 and 61 cm circumference at breast height, while sample trees ranged between 24 and 55 cm circumference. The smallest trees could only be measured by utilizing the G-system. Sap flow rates of individual trees measured at breast height increased rapidly in the morning along with increases in irradiance and vapor pressure deficit (D), decreased slowly during the course of the afternoon with continued increase in D, and decreased more slowly during the night.

Ignoring potential effects introduced by the different methods, maximum flow rates of individual trees ranged between 0.5 and 2.5 kg H_2Oh^{-1} tree⁻¹ or 0.3 and 0.6 mm h⁻¹ related to projected crown area of trees and daily sums of sap flow for individual trees varied between 4.4 and 24 kg H_2O tree⁻¹ d⁻¹ or 1.1 and 6.0 mm d⁻¹. Maximum sap flow rates per sapwood area of trees varied least for the G-system (11–17 g cm⁻² h⁻¹) and was of similar magnitude as the C- (8–21 g cm⁻² h⁻¹) and CS-system (4–14 g cm⁻² h⁻¹).

Regressions of total tree conductance (g_t) derived from sap flow estimates demonstrated the same linear increase of conductance with increasing irradiance, however decrease of conductance with increasing D under non-limiting light conditions was different for the three systems with strongest reduction of g_t measured with the CS-system followed by the C- and G-system. This led to different estimates of daily sap flow rates especially during the second part of the measurement period.

Variation in sap flow rates is explained on the basis of variation in leaf area index of individual trees, heterogeneity in soil conditions, and methodological differences in sap flow measurements. Despite the highly uniform plantation forest at the scale of hectares, the heterogeneity in tree size and soil depth at the scale of square meters still make it difficult to appropriately and efficiently select sample trees and to scale-up water flux from individual trees to the stand level.

1: Introduction

Several xylem sap flow techniques have been used in recent years to estimate water fluxes in herbaceous plants and in trees. For trees with diameters larger than ca. 12 cm, Čermák et al. (1973) developed the constant-temperature-difference method to determine mass flow through a segment of the trunk of a tree. Granier developed a constant heating technique for estimating sap flux density, but the estimate must be empirically calibrated in order to relate temperature differences in the trunk to the mass of water flowing (Granier, 1985; Granier, 1987). Together with biometric information about tree size and distribution in the stand, xylem sap flow measurements allow the estimation of total forest transpiration (Granier et al., 1989; Kelliher et al., 1992; Granier et al., 1996, this issue). While micrometerological measurements integrate over large areas, xylem sap flow studies allow partitioning of the total flux to individual trees which may be of separate species, size, age or social position in the stand. At the same time, the variability in contributions of trees makes it difficult to select a small number of trees which truely represent stand level processes. Nevertheless, detailed knowledge of the dependence of stand conductance and transpiration rate on stand structure and climate factors are basically necessary to predict stand flux rates under changing conditions. The following investigation was conducted to provide information on variation in individual tree transpiration within the larger area of the Hartheim plantation site. The contribution of tree transpiration to stand water vapor fluxes was estimated and the relative performance of three commercially available xylem sap flow measurement instruments was compared.

2. Methods

2.1 Site Description

Studies were carried out in a 35-year-old Scots pine plantation (*Pinus sylvestris*) established on an old river terrace of the Upper Rhine Valley, ca. 20 km south-west of Freiburg/Germany (see Jäger and Kessler, 1996, this issue). Tree density, cumulative circumference, stem area and sapwood area were 3873 ha^{-1} , 1320 m ha^{-1} , $38 \text{ m}^2 \text{ ha}^{-1}$, $26 \,\mathrm{m^2 \, ha^{-1}}$, respectively. Leaf area index of trees determined optically with a leaf-area-meter around the towers (Joss, personal communication) was in accordance with LAI determined by biomass harvest of 5 trees in 1993 which was 2.8 (Sturm, personal communication). Tree height ranged between 10 and 14 m and tree circumference between 18 and 61 cm. The heterogeneous soil consisted of a small-scale mosaic of 15 to 80 cm deep sandy or loamy horizons above more stony river gravels (Sturm et al., 1996, this issue). The grass Brachypodium pinnatum, the sedges Carex alba and Carex flacca, and the moss Scleropodium purum dominated the understory with a total leaf area index of approximately 1.5 (Wedler et al., 1996, this issue).

2.2 Biometry of Sample Trees

A total of 24 Scots pine trees were used for sap flow measurements, located at various points up to a distance of 120 m apart. Tree circumference at breast height ranged between 24 and 55 cm; the smallest trees (24 and 28 cm circumference) were examined with the G-system. Radial sapwood depth of trees was between 2 and 6 cm. Sapwood area (swa) of the trees ranged between 42 and 228 cm² and was significantly correlated with circumference (c) $(swa = -67.65 + 3.97*c, r^2 =$ 0.97, n = 18; see Granier et al., 1996, this issue), projected crown area was between 1 and 7 m^2 , crown volume (cv), ranging between 1 and 15 m^3 was significantly correlated with crown area (ca) $(cv = -2.70 + 2.20^* ca, r^2 = 0.82)$, while tree height (h) ranged between 10 and 14 m and was less significantly correlated with circumference (h = $8.32 + 0.096 c, r^2 = 0.49$. However, for trees within the range of 38 to 55 cm circumference, which included most of the sample trees, these biometric correlations were weak due to high variation among individual tree structure in these size classes.

2.3 Xylem Sap Flow Methods

Three xylem sap flow techniques were used during HartX 1992 to monitor tree water flux: (1) The technique described by Granier (1985, 1987; "Gsystem"), (2) the technique of Čermák and coworkers (Čermák et al., 1973; Kučera, et al. 1977; "C-system") and the method of Čermák, as modified with respect to electronic control by Schulze (Electronic Lab of the University of Bayreuth; "CS-system"). Five trees were monitored with the G-system, 12 trees with the C-, and 7 trees with the CS-system.

Sap flow sensors of all systems were installed between breast height and 2m height of the tree and covered with foam and light reflecting foil to insulate the temperature field around the sensors from effects of the sun and convective heat loss.

2.3.1 Xylem Sap Flow Method According to Čermák

To measure xylem sap flow in large trees, Čermák and co-workers developed a heating technique which normally uses 5 steel plates as electrodes $(60 \times 25 \times 1 \text{ mm})$ inserted in parallel into the trunk with a separation distance of 20 mm (Čermák et al., 1973; Kučera et al., 1977). The electrodes span the entire water transporting sapwood. A commerical version of the technique (DMP AG, Hegnau-Volkdtswil, Switzerland) which was used during HartX supplies alternating current with a constant power of 1 Watt to the electrodes. The wood between the plates functions as a resistance and is heated by the current, while the steel plates remain cool. The power supply is regulated such that temperature differences > 5 Kelvin are avoided. Temperature difference due to heating of the flowing sap is measured with a thermocouple pair inserted first at the upper edge of the electrodes and for comparison approx. 15 cm below. In actuality, the thermocouple consists of a chain of 8 sensors that were also distributed to compensate for natural temperature fluctuations around the trunk area measured (Čermák and Kučera, 1981). Insertion length of the thermocouple probes differed with bark thickness and was around 30 mm. Mass flow of water is calculated according to the following (1):

$$E_{\text{tree}} = \frac{P \cdot k}{c_w \cdot (dT_{\text{max}} - dT)} \tag{1}$$

where E_{tree} is the sap flow rate per tree (kg s⁻¹ tree⁻¹), P is the heating power ($W = J s^{-1}$), c_w is heat capacity of water ($J kg^{-1} K^{-1}$), k is the dimensionless relation of measured segment length to total tree circumference, and dT is temperature difference between electrodes and reference point (K). Heat energy lost by conduction and convection from the trunk is estimated from the maximum temperature difference (dT_{max}) observed during the night when flow rates are lowest.

2.3.2 Xylem Sap Flow Method According to Čermák/Schulze

In contrast to the C-system the CS-system consists of a proportional-integrating-controller (UP Umweltanalytische Produkte, 80637 Munich, Germany) which maintains a given temperature difference (set-value normally 2 or 3 K) between the heated sapwood and a reference point. The power used to maintain the temperature difference is directly proportional to the sap flow rate and is calculated according to Čermák et al. (1973) with P as the variable and dT as the constant (2):

$$E_{\text{tree}} = (P - P_{\min}) \cdot \frac{k}{c_w \cdot dT}$$
(2)

where P_{\min} reflects heat loss due to conduction and convection which is determined during nights when sap flow is absent. During steady-state the applied power does not normally exceed 2 W (with a potential maximum of 20 W). The high timeresolution of the system allows investigations of high frequency fluctuations (<1 min.) in xylem sap flux (Hollinger et al., 1994). During the HartX period, 5 electrodes per system of the size $60 \times 15 \times 1$ mm were inserted up to 50 mm into the stem while depth of insertion of thermocouples was 40 mm. Flow rates were corrected over courses for natural temperature gradients measured without heating on May 19 and 20 for 3 and 4 sample trees, respectively.

2.3.3 Xylem Sap Flow Method According to Granier

The Granier-system is technically the simplest method which employs a pair of identically constructed probes (30–40 mm long, 2 mm diameter) with a 20 mm-zone of heating wire around a thermocouple (Granier, 1985, 1987). The two sensors are inserted radially into the trunk with a vertical spacing of 10 to 15 cm. The upper sensor is heated constantly with a 0.2 Watt direct current, and the temperature difference (dT) between the probes is monitored. Temperature differences have been related to the mass flow of water via an empirical calibration performed with trunk sections from several tree species. The relationship is similar for a variety of tree species (Granier, 1985). Similar to the assumption made with the C-system, maximum temperature difference is determined during nights when sap flow is assumed equal to 0. Local flow density is extrapolated to the total tree (E_{tree} , kg H₂O s⁻¹ tree⁻¹) by multiplying by estimated sapwood area (swa, m²) of the tree (3):

$$E_{\text{tree}} = 0.119 \cdot \left(\frac{(dT_{\text{max}} - dT)}{dT}\right)^{1.231} \cdot swa \tag{3}$$

where 0.119 (kg m⁻² s⁻¹) and 1.231 are empirical constants from the calibration.

To avoid overestimation of sap flux with the G-system due to decrease of sap flux density in sapwood beyond the measuring zone of 20 mm depth, the flux rates were additionally corrected accoring to findings of Lüttschwager and Granier (unpublished). In 1992, they measured sap flow density in 4 different depths of sapwood of a Scots pine tree of 66 cm circumference near Nancy/ France (Fig. 1). While sap flux density in up to 24 mm could be similar or was reduced by approx. 20%, flux density in up to 36 and 47 mm was reduced by approx. 40 and 85%, respectively. This is in accordance with an average reduction of approx. 50% in 20 to 40 mm depth (with high variation within individual trees) found by Lüttschwager (personal communication) in large Scots pine trees in Northern Germany and with measurements performed in 1993 at the Hartheim site by Sturm (unpublished). According to these findings, sap flux data measured with the G-system were multiplied by a correction factor depending on sapwood thickness, which was 0.86 on the average.



Fig. 1. Diurnal variation of sap flux density measured with short (12 mm long) sensors located at 4 different depth (0–12, 12–24, 24–36, 35–47 mm) in the sapwood of a *Pinus sylvestris* trunk at INRA/Nancy during a partly overcast day in June 1992 (data from D. Lüttschwager)

2.4 Climatic Data

Net radiation (R_n) , air temperature, and relative humidity from which vapor pressure deficit (D)was calculated, were measured above the canopy (data from R. Vogt and W. Wicke) at height 15.5 m above ground. Photosynthetic active radiation (PAR) was measured at height 30 m (data from U. Joss).

2.5 Estimation of Total Water Vapor Transfer Conductance

Conductance values for individual trees estimated directly from xylem sap flow rates and D represent the total water vapor transfer conductance (q_i) from the "average" stomata of the tree canopy to the measurement height of D which includes both aerodynamic (q_a) and stomatal components (q_a) Thom, 1972). Because g_a is usually an order of magnitude larger than g_c in coniferous stands, differences between g_t and g_c are small. During the HartX period, g_t values were ca. 5% lower than values of g_c from late morning to afternoon (Granier et al., 1996, this issue). For comparisons between trees, only g_t was evaluated, assuming similar behavior for g_t and g_c (Köstner et al., 1992). Total conductance of individual trees was calculated as follows (4):

$$g_t = k \cdot \frac{E_{\text{tree}}}{D} \tag{4}$$

Conversion factor $k = G_V \times T_K$; $G_V = \text{gas constant}$ stant of water vapor (4.62 m³ hPa kg⁻¹ K⁻¹), $T_K = \text{air temperature (Kelvin)}; D = \text{vapor pressure}$ deficit (hPa); $E_C = \text{transpiration rate per projected}$ crown area of trees (kg m⁻² s⁻¹).

For comparison of tree conductance as determined with the various sap flow methods, no time shift was undertaken to account for up to 1.5 h apparent difference between the morning increase in water vapor flux measured above the canopy and in tree sap flow at breast height (see Granier et al., 1996, this issue). However, for comparisons of canopy conductances at the stand level, the time lag in sap flux data must be considered. In our case the time shift increased maximum conductances determined via sap flux by a factor of ca. 1.6.

3. Results and Discussion

3.1 Hourly Changes in Tree Xylem Sap Flow Rates

During the measurement period from May 12–21, irradiance did not change greatly between days. Daily maximum half-hourly values of net radiation (R_n) ranged from 672 to 713 W m⁻² (PAR: 1.58 to 1.67 mmol m⁻² s⁻¹). A large vapor pressure deficit (maximum half-hour average, D_{max}) occurred on the first measurement days of the HartX period, increasing to 31 hPa. D_{max} decreased to 14 hPa at the end of the period. Hourly changes in tree sap flow rates monitored with the 3 different systems are shown in Fig. 2 for May 16, a typical day with high D_{max} (29 hPa) and May 17, a day with relative low D_{max} (21 hPa). Average flow rates per projected crown area of trees were not different for the G- and CS-system while higher sap flow rates were measured with the C-system. This was partly due to 4 trees studied with the C-system which had approx. 50% higher flow rates compared to trees of similar size measured with the other systems. Flow rates of the remaining trees assessed with the C-system were within the range of flow rates measured with the other systems. On May 17, average sap flow rates decreased by 14%, with



slower increase in flow rates during the morning. During the entire period of measurements, maximum hourly flow rates of individual trees ranged between 0.51 and 2.5 kg tree⁻¹ h⁻¹ or between 0.28 and 0.55 mm h⁻¹ related to projected crown area of trees. Maximum sap flow rates per sapwood area of trees varied least for the G-system (11 to $17 \text{ g cm}^{-2} \text{ h}^{-1}$) and were of the range of the C- (8 to 21 g cm⁻² h⁻¹) and CS-system (4 to 14 g cm⁻² h⁻¹). Lower variability in flow estimates obtained with the G-system obviously result from placing the sensing elements in the outer sapwood where flow density is most homogeneous.

Xylem sap began to flow at breast height approximately 1.5 to 2 h later than leaf transpiration in the crown which was measured via eddycorrelation above the forest canopy while dew evaporation was negligible (Gay et al., 1996, this issue; Granier et al., 1996, this issue). For an evaporation rate of $0.3 \,\mathrm{mm}\,\mathrm{h^{-1}}$, this time lag corresponds to ca. $0.5 \,\mathrm{mm}$ transpired water from the crown before sap flow at breast height had started. Assuming that an average tree (tree height 12 m, crown area $4.4 \,\mathrm{m^2}$, circumference at breast height 44 cm, sapwood depth 4 cm, available water in the xylem 60%) can store ca. 30 kg water in the stem which equals 6.8 mm, trees used ca. 7% of the

Fig. 2. Half-hourly course of net radiation (R_n) and photo-synthetic active radiation (PAR) vapor pressure deficit (D), xylem sap flow rate per projected crown area of trees according to the methods by Granier (G), Čermák (C), and Čermák/ Schulze (CS), and of average total water vapor transfer conductance (g_i) observed on May 16 and 17, 1992. Symbols for flux rates and g_i are averages of 5 (G-system), 12 (C-system), and 7 (CS-system) trees. Maximum standard error bars during timecourse are indicated

stored water in the morning before the onset of sap flow at breast height. This would indicate relatively moderate depletion of stored water since under extreme periods (dry or frozen soils) use of stored water in Scots pine can be as large as 50%(Waring et al., 1979). Moderate water stress was also indicated by predawn leaf water potentials of -0.6 to -0.8 MPa in contrast to low values of -1.5 MPa in the summer months (Sturm et al., 1996, this issue).

The time-course of total conductance was similar for the 3 systems on May 16 (Fig. 2). Conductance increased rapidly during the morning with maximum values between 10 and 11 h and decreased during the late morning and afternoon, with the most pronounced decrease observed with the CSsystem. On May 17, g_t remained high until midday before it decreased continuously during the afternoon. While maximum g_t was similar on both days when derived from the CS-system, g_t increased up to 30% on May 17 when derived with the G- and C-system. Thus, results from the different sap flow systems could lead to different interpretations of stomatal behavior of trees during these time-courses. While the CS-system indicates similar opening of stomata on both days, the G- and C-system suggest that stomata were more open on May 17.

Linear regression of g_t with respect to R_n or PAR in the morning gave similar results for trees measured with the three different systems ($g_t =$ $-0.547 + 0.011^* R_n; g_t = -1.258 + 0.005^* PAR;$ $r^2 = 0.77$). In contrast, decrease of g_t with increasing D during late morning and afternoon was different as observed with the various systems with the lowest conductances being obtained with the CS-system $(g_t = 7.90*10^{-0.016*D}; r^2 = 0.52)$ followed by the C- $(g_t = 11.05*10^{-0.018*D}; r^2 = 0.59)$ and G-system $(g_t = 17.01*10^{-0.022*D}; r^2 = 0.88)$ (Fig. 3). Besides individual tree variation, these differences can in part be explained by different sapwood depth over which the systems integrated flow. The depth of which sensors effectively measured were 2, 3 and 4 cm for the G-, C- and CS-system, respectively. Because diurnal and seasonal variations in flux density dependent on sapwood depth occur in Scots pine (Waring and Roberts, 1979), the general correction performed for the G-system may not have been sufficient to cope for all time dependent variation of flow in the inner xylem. The slope of the linear regression



Fig. 3. Relationship between the averages of total water vapor transfer conductance (g_t) derived from tree xylem sap flow rates of the G-, C-, and CS-system and net radiation (R_n) or photosynthetic active radiation (PAR) in the morning (above) as well as vapor pressure deficit (D) from late morning to afternoon (below) during the period of May 13–21, 1992. Symbols are averages of individual trees

between g_t and D obtained in this study with all measurements pooled, was more negative (-1.8) than previously reported for *Pinus sylvestris* (-0.9), but was similar to values reported for *Pinus radiata* (-1.5) and *Pinus contorta* (-2.2; Whitehead et al., 1984).

3.2 Changes in Daily Maxima of Xylem Sap Flow Rates

In Fig. 4, maximum sap flow rates on each day are compared for the three systems. Because no principle differences were found between the Cand CS-systems, values obtained with these methods are pooled. As assessed with the C- and CS-system, maximum transpiration rates increased from May 12 to May 16, and decreased continu-



Fig. 4. Changes in maximum daily net radiation (R_n) and vapor pressure deficit (D_{max}) , daily maximum tree transpiration per projected crown area for the G- and the average of the C- and CS-system (upper error bars indicate the C- and the lower error bars the CS-system), and of maximum total conductance of the G- and the average of the C- and CS-system during the measurement period from May 12 to 22, 1992. Symbols are averages of trees

ously from May 16 to May 22 in concert with maximum D. The maximum flow rates measured with the G-system exhibited less pronounced differences. While changes in maximum transpiration rates were significantly correlated with changes in maximum D during the measurement days for the C- and CS-system ($r^2 = 0.38$ and 0.65 for the C- and CS-system, respectively), no correlation was found for the G-system. This differential behavior again could be an effect of less measurement depth from which sap flow rates of the G-system were derived. Direct sap flow measurements in deeper sapwood than 2 cm with additional sensor probably would have improved the results.

Maximum tree conductance was not different between the C- and CS-system from May 13 to 16, however during the second part of the period when D_{max} declined, g_t values of the CS-system were lower except for May 19. Tree conductance derived from the G-system was similar to average g_t of the C- and CS-system from May 14 to 19, however was higher at the beginning and the end of the period in comparison to the C- and CSsystems. Maximum transpiration rate of approx. 0.3 mm h^{-1} and maximum canopy conductance of approx. 10 mm s^{-1} (g_t *1.6 for time shift) were comparable to those observed in a 40-year-old thinned Scots pine stand of similar stand sapwood area during August (Whitehead et al., 1984).

3.3 Variation of Individual Trees

The flux rate derived from the maximum number of measured trees (n = 24) was judged to be the "best estimate" to extrapolate to total stand transpiration. This "best estimate" plus an estimate of water flux from the forest floor (Wedler et al., 1996, this issue) of the tested day (16 May) differed 8% from above canopy water vapor flux rate (Granier et al. 1996, this issue). In order to evaluate the possible error in scaling up or averaging tree sap flux rates depending on the number of sample trees, e.g. the number of sap flow installations, the following test was performed. From random selections of sample trees between n = 1 and n = 24, average sap flux sums were computed and compared to the estimate derived from 24 trees (=100%) (Fig. 5). Because no dependence of sap flux densities on tree size within the range of sample trees was observed, all trees were treated equal. The test



Fig. 5. Deviation of average sap flux rate derived from different numbers (n = 1 to n = 23) of randomly selected sample trees from average flux rate derived from the maximum number of trees (n = 24, "best estimate"). The dotted line indicates deviation of $\pm 8\%$.

demonstrated high variation of estimates (20-60%)for sample collectives of less than 9 trees. For larger sample collectives between n = 9 and n = 20, maximum deviation of estimates was within $\pm 8\%$. Thus, due to individual tree variation an error of at least $\pm 8\%$ will normally be encountered with available instrumentation. Therefore, for the interpretation of differences between transpiration rates derived from the different methods with 5, 7, and 12 sample trees of the G-, CS-, and C-system, individual tree variation as an important factor influencing the interpretation has to be considered. For estimates of stand transpiration an additional source of error due to the scaling factor (e.g. cumulative sapwood area of the stand varied $\pm 15\%$ between 5 plots of 600 m²) has to be taken into account (cf. Granier et al., 1996, this issue).

4. Conclusion

Daily courses of tree water flux derived from the 3 different sap flow methods exhibited similar behavior during the period of measurements. Good coincidence in dependencies of total conductance on irradiance occurred between methods during early morning, while during late morning and afternoon total conductance was stronger reduced with increasing vapor pressure deficits for the CS-system, followed by the C- and G-system. Changes in daily maximum values of tree transpiration and conductance during the measurement period were more similar between the C- and CS-system in comparison with the G-system. In general, daily sap flow rates of all three systems were within the same order of magnitude. High variation in individual trees due to small-scale soil variability and relatively small sample collectives of the CS- and G-system were a further source of difference. Although the stand was homogeneous at a larger scale (100 m) with little variation in tree height, it was not at a small scale (m), especially in soil depth and potential rooting depth. This made it difficult to compare individual trees and to assess stand transpiration rate from individual measurements. Sample collectives of at least 10 trees were necessary to reduce the error of random tree selection to $\pm 8\%$.

In a practical sense the G-system has advantages in maintenance and relative low costs. Even when the sensors can only be used "one-way", higher numbers of sensors are affordable. The more expensive C-system is also a relative robust system which uses the largest heating elements and works best in trees with more than 40 cm circumference. The electronical CS-system has advantages in high time-resolution and in factors as controlled temperature difference and known wood resistance but it needs more servicing and the costs are relatively high. Depending on the type of sap flux investigations, the different methods are useful for particular studies or combinations of methods are advised.

Acknowledgements

We are grateful to John Tenhunen, Roland Vogt, Christian Bernhofer, and Dietmar Lüttschwager for valuable discussions. We thank Rainer Matyssek kindly allowing us to use six of his Čermák-systems and Stephan Reber for TDR sensors. Further we thank Annette Suske and Sabine Hahn for their help in the field and Gerhard Müller and Gerhard Küfner for their help in preparing the instruments. Financial support was provided from the German Bundesminister für Forschung und Technologie (BEO 51-0339476A).

References

- Čermák, J., Deml, M., Penka, M., 1973: A new method of sap flow determination in trees. *Biol. Plant.*, 15, 171–178.
- Čermák, J., Kučera, J., 1981: The compensation of natural temperature gradient at the measuring point during the sap flow rate determination in trees. *Biol. Plant.*, 23, 469–471.
- Gay, L. W., Vogt, R., Bernhofer, C., Blanford, J. H., 1996: Flux agreement above a Scots pine plantation. *Theor. Appl. Climatol.*, 53, 33-48.
- Granier, A., 1985: Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. Ann. Sci. For., 42, 193–200.
- Granier, A., 1987: Evaluation of transpiration in a Douglasfir stand by means of sap flow measurements. *Tree Physiol.*, **3**, 309–320.
- Granier, A., Bobay, V., Gash, J. H. C., Gelpe, J., Saugier, B., Shuttleworth, W. J., 1993: Vapour flux density and transpirations rate comparisons in a stand of Maritime pine (*Pinus pinaster Ait.*) in Les Landes forest. *Agric. Forest. Meteor.*, **51**, 309–319.
- Granier, A., Biron, P., Köstner, B., Gay, L. W., Najjar, G., 1996: Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine. *Theor. Appl. Climatol.*, 53, 115–122.
- Hollinger, D. Y., Kelliher, F. M., Schulze, E.-D., Köstner, B. M. M., 1994: Coupling of tree transpiration to atmospheric turbulence. *Nature*, **371**, 60–62.
- Jaeger, L., Kessler, A., 1996: The HARTX period May 1992 seen against the background of twenty years of energy balance climatology at the Hartheim pine forest. *Theor. Appl. Climatol.*, 53, 9–21.

- Kelliher, F. M., Köstner, B. M. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., Weir, P. L., Schulze, E.-D., 1992: Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest. *Agric. Forest. Meteor.*, **62**, 53–73.
- Köstner, B. M. M., Schulze, E.-D., Kelliher, F. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., Weir, P. L., 1992: Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia*, **91**, 350–359.
- Kučera, J., Čermák, J., Penka, M., 1977: Improved thermal method of continual recording the transpiration flow rate dynamics. *Biol. Plant.*, **19**, 413–420.
- Sturm, N., Reber, S., Kessler, A., Tenhunen, J. D., 1996: Soil moisture variation and plant water stress at the Hartheim Scots pine plantation. *Theor. Appl. Climatol.*, 53, 123–133.
- Thom, A. S., 1972: Momentum, mass, and heat exchange of vegetation. *Quart. J. Roy. Meteor. Soc.*, **98**, 124–134.
- Waring, R. H., Roberts, J. M., 1979: Estimating water flux through stems of Scots pine with triated water and phosphorus-32. J. Exp. Bot., 30, 459–471.

- Waring, R. H., Whitehead, D., Jarvis, P. G., 1979: The contribution of stored water to transpiration in Scots pine. *Plant, Cell and Environment*, 2, 309–317.
- Whitehead, D., Jarvis, P. G., Waring, R. H., 1984: Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. *Can. J. For. Res.*, 14, 692–700.
- Wedler, M., Heindl, B., Hahn, S. C., Köstner, B., Tenhunen, J. D., 1996: Model-based estimates of water loss from "patches" of the understory mosaic of the Hartheim Scots pine plantation. *Theor. Appl. Climatol.*, 53, 135-144.

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