Original article

Sapflow measurements in forest stands: methods and uncertainties

Barbara Köstner[a]*, André Granier[b], Jan Cermák[c]

[a]Department of Plant Ecology II, Bayreuth Institute for Terrestrial Ecosystem
Research (BITÖK), University of Bayreuth, 95440 Bayreuth, Germany
[b]Centre de recherches forestières, Inra, Champenoux, BP 35, 54280 Champenoux, France
[c]Institute of Forest Ecology, Mendel´s Agricultural and Forest University,
Zemedelska 3, CS-61300 Brno, Czech Republic

Abstract – This paper discusses the respective advantages and disadvantages of three sapflow techniques used for measuring tree transpiration in forests: heat pulse velocity, tissue heat balance (Cermák-Type), and radial flowmeter (Granier-Type). In the EUROFLUX programme, aiming at analysing and modelling water and CO_2 fluxes above European forests, the two latter techniques are used at several sites. These two techniques were compared on the same trees, and resulted in similar flux estimates. Principal problems of the methods are linked with the influence of natural thermal gradients in the trunks and with effects of heat storage and conduction within the tissue. Sapflow probes can be typically left in place during one vegetation period, without any apparent modification of water transfer properties of the xylem. Different sources of sap flux variability related to temporal and spatial scale are discussed. Accuracy of sapflow estimates at the stand level can only be achieved by appropriate sample size of flux measurements and structural scalars. In a homogeneous, untreated stand, the appropriate sample size is usually about ten but increases depending on species, conducting type of the xylem and spatial heterogeneity of the site. It is recommended to combine sapflow measurements with eddy covariance techniques in order to separate tree transpiration from total forest water vapor flux and to examine spatial heterogeneity of fluxes within forest stands. (© Inra/Elsevier, Paris.)

xylem sapflow methods / calibration / comparison / scaling / forests

Résumé – Mesure du flux de sève dans les peuplements forestiers : méthodes et incertitudes. Cet article analyse les avantages et les inconvénients respectifs des trois principales méthodes de mesure du flux de sève dans les arbres: les impulsions de chaleur, et les méthodes à chauffage continu : bilan d'énergie du xylème (Cermák) et fluxmètre radial (Granier). Ces deux

---
* Correspondence and reprints
E-mail: barbara.koestner@bitoek.uni-bayreuth.de

dernières techniques sont utilisées en routine sur plusieurs sites dans le cadre du programme Euroflux, qui porte sur l'analyse et la modélisation des flux d'eau et de CO_2 au-dessus des forêts européennes. Ces deux méthodes ont pu être comparées sur les mêmes arbres, et ont donné des résultats très proches. Les problèmes majeurs dans l'utilisation de ces méthodes sont liés aux modifications du signal par les gradients thermiques qui existent naturellement dans le tronc des arbres, et par les phénomènes de stockage et de transfert de la chaleur dans les tissus. En général, ces capteurs peuvent rester en place dans les troncs pendant une saison de végétation, sans influence apparente sur les propriétés de transfert hydrique de la zone du xylème mesurée. Les différentes sources de variabilité temporelle et spatiale des mesures de flux de sève sont discutées ; on constate en général que la variabilité intraarbre est du même ordre de grandeur que celle entre les arbres. La précision dans l'estimation de la transpiration à l'échelle de la parcelle dépend de la taille de l'échantillon pour les mesures de flux et de la variable de changement d'échelle. Le nombre de capteurs de mesure à mettre en œuvre pour avoir une estimation acceptable de la transpiration d'une population homogène est de l'ordre de 10, mais ce nombre peut augmenter selon l'espèce étudiée, le type de tissu conducteur et avec l'hétérogénéité de la parcelle. En conclusion, il est recommandé, dans ces projets de recherche sur la mesure des flux d'eau et de carbone dans les écosystèmes forestiers, de combiner les mesures de flux de sève à la méthode des corrélations turbulentes, pour pouvoir séparer la transpiration des arbres du flux total de vapeur d'eau, et pour analyser l'hétérogénéité spatiale des flux hydriques dans les peuplements forestier. (© Inra/Elsevier, Paris.)

flux de sève / étalonnage / comparaison / échelle / forêt

1. INTRODUCTION

Xylem sapflow techniques provide a mean at the tree level to estimate forest stand transpiration [37, 63]. Sapflow rates of trees scaled to forest canopy transpiration are used to compare tree transpiration in relation to water vapor flux from the forest floor and to total water vapor flux measured above the forest canopy [27, 35, 38, 51, 52, 80]. Total evaporation of a Scots pine plantation estimated from tree transpiration using different sapflow techniques plus forest floor evapotranspiration was not different from above-canopy surface evaporation and varied in the same range (mean coefficient of variation, CV = 13 %) as total water vapor fluxes measured simultaneously by several eddy-covariance systems above the canopy (CV = 16 %; see *table I*). Apart from comparative measurements estimating water vapor flux of forest stands, sapflow techniques demonstrate tree vegetation activity separately from total surface evaporation and conductance. Especially in old forest stands, tree transpiration is often found to be sig-

nificantly lower than expected from total evaporation rates [54, 55] and maximum tree stomatal conductance is only ca. 1/3 of maximum surface conductance [71]. Further, sapflow estimates demonstrate small scale heterogeneity of water fluxes due to stand parameters such as age, size, density of trees and species composition [2, 7, 22, 62]. Combined measurements of eddy covariance and tree xylem sapflow can also show coherent short-term fluctuations (10^{-3} to 10^{-2} Hz) of sapflow and atmospheric momentum, temperature and air humidity. Observations of emergent *Nothofagus* trees suggested that the maximum size of eddies to which the trees responded were ca. 100 m and according to the displacement events, fluctuations were best correlated among neighboring trees [46, 70].

Within the frame of EUROFLUX, long-term eddy-covariance measurements will be combined with tree sapflow monitoring at several experimental sites. Tree level estimates of water fluxes will aid us to 1) estimate the contribution of tree transpiration, 2) verify estimates of forest floor evapo-

Table I. Daily water vapor fluxes in a Scots pine plantation estimated by different approaches during the Hartheim Experiment (see [77]).

Date	$E_{soil+understory}$ (mm d⁻¹)		E_{tree} (mm d⁻¹)						$E_{surface}$ (mm d⁻¹)		
May 1992	Lysimeters	EC_blc	Model	G-syst. const.	C-syst. const.	C-syst. variable	OPEC	GIEC	CSEC	BREB	EPM
14	0.54	n.d.	n.d.	2.7	2.4	2.5	3.2	2.1	2.3	2.0	3.3
15	0.54	n.d.	0.61	2.5	2.4	2.4	3.4	2.6	2.8	2.5	2.9
16	0.52	n.d.	0.64	2.6	2.9	2.7	3.4	2.6	2.7	2.6	2.9
17	0.67	n.d.	0.65	2.4	3.3	2.1	2.8	2.7	2.8	2.1	2.7
18	0.53	n.d.	0.66	2.6	2.9	2.0	3.1	n.d.	2.7	2.4	3.1
19	0.49	0.50	0.66	2.7	3.0	2.0	2.8	2.1	n.d.	2.3	3.3
20	n.d.	0.49	0.64	2.5	2.9	1.6	2.7	2.3	n.d.	1.6	2.7
21	n.d.	n.d.	0.58	2.6	2.2	1.4	2.6	2.2	n.d.	2.0	2.6

May 1992	A_{day} (mm d⁻¹)	A_{night} (mm d⁻¹)	Mean E_{t+u} (mm d⁻¹)	Mean $E_{surface}$ (mm d⁻¹)	SD E_{t+u} (mm d⁻¹)	SD $E_{surface}$ (mm d⁻¹)	CV E_{t+u}	CV $E_{surface}$	n E_{t+u}	n $E_{surface}$	p
14	6.9	−0.4	3.1	2.6	0.18	0.59	0.06	0.24	3	3	0.251
15	7.1	−0.5	3.0	2.9	0.06	0.42	0.02	0.15	3	3	0.636
16	6.8	−0.7	3.4	2.9	0.13	0.46	0.04	0.16	3	3	0.199
17	6.7	−0.8	3.2	2.7	0.58	0.05	0.18	0.02	3	3	0.267
18	7.3	−0.8	3.2	2.8	0.50	0.32	0.16	0.12	3	4	0.385
19	7.3	−0.9	3.2	2.6	0.50	0.53	0.15	0.22	3	4	0.175
20	6.1	−0.8	3.0	2.3	0.63	0.51	0.21	0.23	3	4	0.217
21	6.6	−0.4	2.7	2.3	0.58	0.31	0.22	0.14	3	4	0.475

Evapotranspiration from the forest floor was estimated by lysimeters and modelled gas exchange (plus soil evaporation) areally scaled to the stand-level by patch type distribution of the understory [78] and measured by eddy-correlation below the tree canopy (EC_blc: Blanford, unpublished). Water use of trees was estimated by radial flowmeters according to Granier (G-system; n = 5), and by constant (n = 12) and variable (n = 7) heating THB-systems according to Čermák (constant/variable C-system) [38, 53]. Total surface evaporation was estimated by three eddy-correlation (EC) systems (one-dimensional propeller system, OPEC: three-dimensional Gill system, GIEC; one-dimensional Campbell Scientific system, CSEC), by a Bowen ratio energy balance system (BREB), and by the Penman-Monteith equation (EPM) parameterized for the Hartheim forest (see summary in Bernhofer et al. [6]). Total daily evaporation was about half of available energy (A) and not different between mean values of tree sapflow plus understory (E_t+u) and mean values of the EC-systems (May 14 to 17) or mean values of all E_surface estimates from May 18 to 21 (p-value of t-test for independent samples is shown; n.d. = not determined).

transpiration as the residual component of total stand and tree level fluxes, 3) examine spatial heterogeneity within forest stands, 4) assess temporal difference between soil water uptake and canopy evaporation, and 5) bridge missing data of above canopy measurements. For this purpose, appropriate sapflow methods, various methodological and technical assumptions and problems, as well as scaling procedures (cf. Jarvis [49]) are summarized. This paper addresses the current discussion on sapflow monitoring methods applied in forest stands (cf. Tenhunen et al. [75]).

2. APPROPRIATE METHODS AND TECHNIQUES

For continuous long-term measurements of xylem sapflow in trees two different thermal principles of sapflow methods are appropriate: the heat pulse velocity (HPV) and the tissue (THB) or stem surface (SHB) heat balance methods (for reviews see Cohen [25] and Swanson [74]). HPV methods (early descriptions in Huber and Schmidt [47], Marshall [60] and Swanson [73]) measure sap velocity by delivering heat pulses from an active electrode and registering temperature increase by thermocouples shortly above and below the pulsing electrode [24, 50, 74]. Absolute flux rates are estimated by transforming sap velocity to sap flux density (for definition of measures see Edwards et al. [30]) via specific wood density and multiplying flux density with conducting sapwood area. THB methods deliver heating current continuously to a volume of xylem tissue, which is either an undefined volume of tissue surrounding a needle-type sensor inserted radially into the stem [33 1, 48, 61, 76] or a better defined volume of tissue included between heating plates [26] or several heating elements placed in parallel into the xylem [16–18]. To derive sap flux density, an empirical calibration of temperature change versus the amount of water flowing can be used. In *figure 1* the rela-
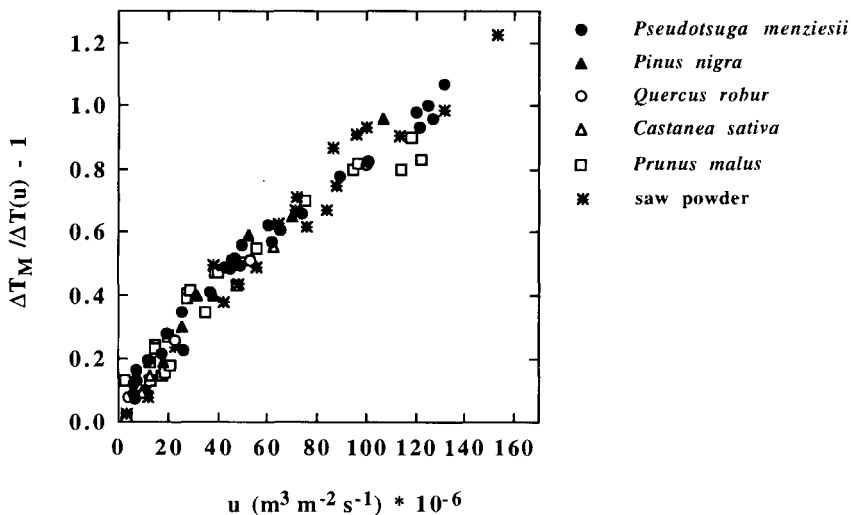

Figure 1. Calibration of the Granier radial flowmeter under laboratory conditions made on stem and branch segments of several tree species, plus in a sawdust column. The flow variable, called sap flux index, involves ΔT_M (maximum temperature difference between both probes of the sensor under zero flow condition) and the actual temperature difference $\Delta T(u)$ at a given flow rate u.

tionship between temperature change and flux density observed for stems of various tree species and an artificial stem (saw powder) are shown (cf. Granier [31]). Absolute flux rates are obtained by multiplying flux density with conducting sapwood area [31, 32].

In the other case, mass of water flowing through a defined volume of xylem tissue can be directly calculated via the physical heat capacity of water [16]. Heating power can be applied constantly while variable change of temperature difference is registered as analysed in detail by Kucera et al. [56]. Advantages of variable heating systems are due to the fact that accuracy does not depend on absolute flux rates and that the thermal equilibration rate between heated stem and surroudings remains constant [40]. Disadvantages of variable heating systems are connected with higher power requirements and higher costs of the equipment. SHB systems measure total stem water flux using a heating shield wrapped around the stem [4, 19, 57, 68, 72]. These systems use different approaches of calculating sapflow. They

have the advantage of an already integrated measurement of the total stem. Further, no heating elements need to be inserted into the wood. However, SHB systems are only appropriate for small stems or branches.

All methods require assumptions on heat losses due to conduction. Techniques according to Cermák using several heating plates or Granier using needle-type sensors are more adapted to measurements in large than in small trees. The first one measures sapflow within a larger xylem volume than the latter, which is more locally dependent on xylem fluxes within the small volume surrounding the sensor. Therefore, the Cermák-Type system, especially the electronically controlled, variable heating system, needs more energy for heating than the Granier-Type. Both systems can be powered by batteries. In field measurements, the techniques agree in the range of flux densities measured [54] and in the daily course of sapflow when both techniques are applied in parallel in the same tree (see *figure 2*). Comparisons were conducted in seven trees
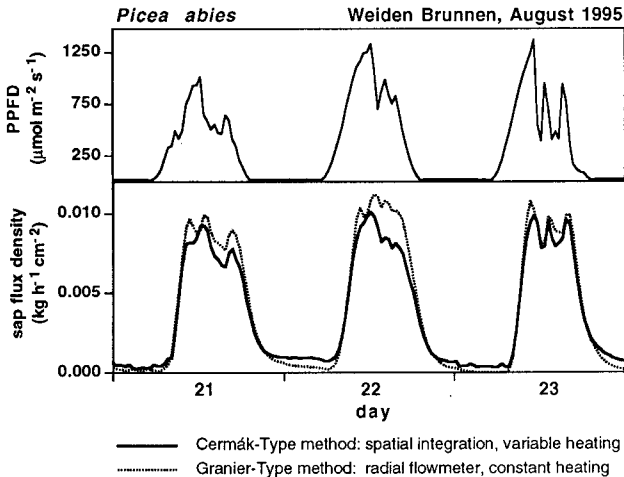

Figure 2. Daily courses of photosynthetic photon flux density (PPFD) and of xylem sap flux density measured with the variable heating system according to Cermák and the constant heating radial flowmeter according to Granier in the same trunk area of a 40-year-old Norway spruce (data from Alsheimer [1]).

during periods up to 60 days. Average difference in cumulative sapflow rate between the techniques was ± 9 %. No significant difference in daily flux rates of both techniques was found (*t*-test of paired samples). Flux rates measured by different techniques varied in the same range as flux rates measured by systems of the same technique within a tree [1].

Most users of sapflow techniques agree that there exists no unique technical solution for all tree sizes and all tree species. The techniques exhibit advantages or disadvantages in different directions [38, 74]. Tree xylem differs in conducting type, e.g. tracheids in conifers, diffuse- or ring-porous types in deciduous trees. For instance, Granier-Type systems, when used on species bearing narrow sapwood, such as *Fraxinus excelsior* (Granier and Peiffer, unpublished) showed an underestimation of the actual tree transpiration. Otherwise, when used in species with deep sapwood such as pine trees, sensors at different depths have to be used for an accurate estimate [37, 53, 62]. At the tree level, THB/SHB techniques are inherently more appropriate for quantification than HPV techniques. Uncertainties of HPV methods are associated with point sampling, probe separation, and estimation of wound diameter and volumetric water content [29, 44]. Otherwise, HPV systems are less affected by thermal imbalances, require lowest power supply and, therefore, may be left unattended for longer periods.

Commercial distributers of HPV-systems are for instance GreenSpan (Victoria, Australia) and IMKO GmbH (Ettlingen, Germany). THB or SHB systems according to Cermák and Kucera [16, 18, 54] using an electronic controller of both constant power or constant temperature difference are distributed by Kucera (Environmental Measuring Systems Inc., Brno, Czech Republic). THB-systems according to Granier [30, 31] are commercially distributed by UP GmbH (Land-

shut, Germany) and in a new technical version by Dynamax Inc. (Huston TX, USA).

3. TECHNICAL PROBLEMS ASSOCIATED WITH THERMAL PROPERTIES OF THE TISSUE

The quantification of sapflow with THB systems relies on the assumption that total heat dissipation by conduction of the wood and by convection of sapflow is known. Heat dissipation by conduction is determined as basic heating ($Q_{fictive}$, cf. Cermák et al. [17]) or as maximum temperature difference (ΔT_{max}, cf. Granier [32]) during periods when sapflow is absent (zero-flux). However, temperature sources other than heating sensors such as sun beams, temperature changes of the xylem water from root to above-ground levels, or effects of heat storage in the stem can affect the artificially established temperature gradients. Effects of heat storage in the stem or differences in heat conductance between day and night can falsify the zero-flux determination. Also, freezing of the xylem provokes troubles due to large heat exchanges during the freezing–sawing phases [69]. Therefore, in addition to means such as insulation material and compensating thermocouples [11], it is suggested that temperature control be introduced into heat balance methods [40, 79]. This seems practicable at least in small trees. Up to now, investigations in large forest trees have not been sufficient to assess the potential error of sapflow estimates related to heat storage effects. The correction of heat storage terms according to the results from an artificial tree model (acrylic glass filled with sawdust) as shown by Herzog et al. [45] does not seem appropriate because maximum flux densities obtained in the model tree reached only 20 % of realistic flux densities in coniferous trees. Considering successful comparisons of sapflow measure-

ments at the stand level, heat storage effects do not seem to be of major importance. However, improvements made on this subject could decrease variability in sapflow rates.

Problems of natural thermal gradients in the stem seem to be more pronounced when sapflow is measured close to the soil surface (especially in open stand conditions as in orchards or in thinned stands), where steep temperature gradients between trunk and soil usually develop. Natural temperature gradients in the stem are observed for minutes or hours when colder xylem water from roots passes the lower reference sensor and gradients decline again when the water reaches the upper sensor [18, 64]. During an experiment in an old Norway spruce stand in the Bayerische Wald/Germany, eight spruce and four beech trees were measured with a variable heating system (Cermák-Type). Natural temperature gradients were monitored between days of sapflow measurements [65]. Xylem sapflow rates were corrected according to natural temperature differences monitored between days of active sapflow measurements. On an hourly basis corrected sapflow rates related to uncorrected rates changed up to ± 25 % in spruce and up to ± 100 % in smaller beech trees. On a daily basis, average differences of corrected related to uncorrected sapflow rates amounted to ± 14 % in spruce and ± 25 % in beech. In most cases, the coefficient of variation (CV) of the daily rates could be reduced from ca. ± 20 % of the uncorrected to ± 10 % of the corrected flow rates. On the same day corrected flow rates of individual trees were both higher or lower than uncorrected ones. Therefore, the effect of correction on absolute flux rates was more or less compensated at the stand level and over periods of several days (Köstner et al., unpublished). Similar observations were made using the Granier system in a beech stand, corrections being made from the

natural gradients either measured during the previous days when sensors were not heated, or by using a switched power supply allowing the measurement of temperature difference between the two probes for 30 min under constant heating, and for 30 min without heating (Granier, unpublished).

The experience of many users of the Granier-Type sensor has shown that sensors can practically be used for one vegetation period or even longer. However, the injury of the cambium modifies its activity and probes may need to be replaced every year. This is also true of the Cermák-Type system. Although, histological investigations of wood tissue from *Picea abies* measured for one vegetation period by the variable heating system revealed that xylem damage and increased resin flow was confined to a few tracheid rows along the heating plates, cambium activity was seriously affected around and between the heating plates, obviously due to high electrical tension (up to 100 V; Köstner and Mehne-Jakobs, unpublished).

4. SCALING OF SAPFLOW MEASUREMENTS

The general question of accuracy of sapflow techniques refers both to the level of the sensed area or individual plant and to the level of plant stands. At the plant level, quite successful comparison studies of sapflow techniques with other independent methods (gravimetry, potometry, isotope tracing, porometry) could be demonstrated (e.g. Dugas et al. [28]), but conditions assessed during the comparisons (variation in sap flux density and conducting sapwood area, thermal properties of the tissue) may change in large trees and during long-term measurements. Sapflow measurements in large trees have to be proved at the stand level by comparison with micrometeorological flux

estimates. At the stand or watershed level, however, variability increases with an increase in spatial heterogeneity and additional sources of evaporation or transpiration. Also, stand-level sap flux estimates and eddy-correlation measurements or water balance methods do not refer to the same time and spatial scale. For instance, in a catchment study of Norway spruce, Peschke et al. [65] could show simultaneously the increasing phase-shifts in the diurnal oscillation of irradiance, leaf transpiration, trunk sapflow, trunk radius, soil matrix potential and runoff at the weir. Despite these difficulties related to temporal and spatial scales, comparative measurements derived from different scales are very useful for improving the quality of results and their interpretation and strengthening the plausibility of quantitative estimates.

4.1. From sensor to tree

Variation in xylem sap flux within trees depends on xylem structure and sapwood cross-sectional area. Sapwood depth and number of growth rings within sapwood are important factors affecting flux density [29]. Depending on site conditions and tree species, sapwood cross-sectional area within trees (and within the stand) may vary from rather regular (e.g. plantations, constant growing conditions) to very irregular (cf. Phillips et al. [66]).

Some sapflow techniques (HPV and Granier-Type THB) require the determination of cross-sectional sapwood area of trees. In most cases, sapwood depth can be determined by fresh cores showing differences in color or in transparency of sapwood and heartwood due to differences in water content. Radial profiles of sapflow velocity characterizing the conducting sapwood were determined by the staining technique in large willow, oak, eucalyptus and spruce trees [19, 20] showing a range

of velocity patterns including those rapidly declining from maximum close to cambium to the heartwood and those with maximum in mid sapwood (see summary in Phillips et al. [66]). Further, computer tomography [2, 41] can assess variability in sapwood cross-sectional distribution at the living tree and thermal imaging analysis [3] demonstrates changes in flux densities with sapwood depth.

As previously observed in oak species by a combination of short sapflowmeters with thermal IR-imaging [36], preliminary results from measurements in large diffuse-porous beech trees showed that flux density is exponentially reduced from outer to inner sapwood *(figure 3)*. No reduction in flux density up to a 4-cm sapwood depth was observed in two hardwood species (*Quercus alba, Liquidambar styraciflua*) by Phillips et al. [66]. Nevertheless, relationships of flux density and sapwood depth have to be investigated when total flux of trees with large cross-sectional sapwood area is estimated.

The trunk base of a tree often exhibits a more heterogeneous sapwood structure and geometry than higher parts of the trunk. Accordingly, azimuthal variation in stem sapflow usually decreases in an upward direction. Experiments on *Pinus pinaster* using two sets of four sensors inserted at two heights in the trunk showed CV in sap flux density of 35 % when sapflow was measured at 1.3 m, while CV decreased to 14 % when measured below live-crown [59]. Studies on spruce, larch, pine and beech confirmed dependence of such variation also on soil water supply - drought significantly increased variation in sapflow within stems [13, 21, 25]. In some species, infections by fungi decreased transpiration rate and increased variation in sapflow [14]. Hatton et al. [44] found the greatest potential source of error in scaling from sensor to tree. To estimate the flux rate of a single *Eucalyptus* tree (HPV method) 12 probes were needed to keep
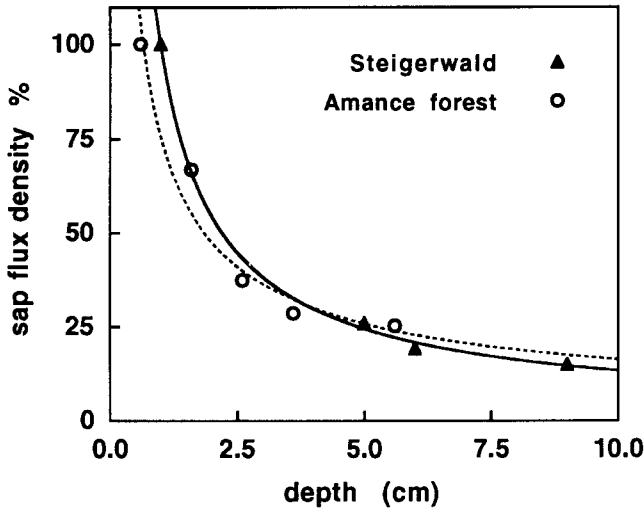
Figure 3. Variation in sap flux density measured using Granier-Type sensors (in % of maximum value) according to the depth below cambium, in one beech tree (data from Granier, Amance forest) and average variation in sap flux densities measured in seven beech trees of different size on one summer day (data from Schäfer and Köstner, Steigerwald).

the CV at 15 % when probes were placed randomly, while sample size could be reduced to six when the probes were stratified by depth and quadrant within the tree.

4.2. From tree to stand

In order to scale sapflow rates from tree to stand, the sampling strategy should be related to stand structure such as tree size and tree species distribution within the stand. If there is no information available, pre-studies are necessary to determine tree size distribution and tree/stand sapwood area and to assess the appropriate sample size or plot area. Structural scaling factors usually used are tree basal area, volume or tree circumference [11, 18], the tree sapwood area [37] or leaf area [43]. Cermák [10] could demonstrate that sapflow rates related to solar equivalent leaf area were less prone to systematic errors than flow rates related to stem or crown size parameters. In dry habitats, leaf area may be a worse scalar owing to pronounced changes in transpiration per leaf area during drought [44].

Within stand variability in sapflow depends on species distribution, stand structure and soil properties. For instance, increased variability between trees was observed during drought and after thinning [7] and in stands exhibiting symptoms of forest decline [37]. Scaling of fluxes should be based on an appropriate number of trees representing the spatial distribution of tree types or classes within a stand. A tree class can be related to dimension, social position, leaf area or vitality of tree species. In various monospecific stands, flux rates of sample means deviated from population mean in the range of ± 7 to 22 % for a sample size of 8 to 12 trees [22, 24, 25, 42, 53, 54, 58]. Oren et al. [62] report sample sizes

between 4 and 48 required for a CV of 15 % of mean sapflux in various coniferous and broad-leaved stands.

5. SAPFLOW MEASUREMENTS IN ROOTS AND BRANCHES

Sapflow measurements can be used to study repartitioning and temporal changes of water fluxes in branches or roots of trees. This allows investigations of spatial flux variation within the tree canopy or the root system. Differences in diurnal dynamics and specific sapflow occurred at the stem base compared to branches of a large willow tree. Within branches, sapflow rate increased from shaded to sun-exposed parts of the crown [19, 72]. Further, it was observed on spruce that the uppermost quarter of the crown (considering both length and needle dry weight) transpired as much as the residual crown below [15]. Similarily, it was shown on spruce, [1, 33] as well as on pine [61] that i) temporal variation in sap flux density was faster in branches than in the trunk, ii) higher flux density and higher flow rates were found in sun-compared to shade-exposed branches [19, 32, 72], and iii) increase in sapflow in the morning was earlier in branches than in the trunk. For a 40-year-old spruce tree, leaf transpiration, branch sapflow and stem sapflow at different heights are shown in *figure 4*. Whole branch transpiration was calculated by modelling light interception and gas-exchange based on porometer measurements at the branch tip (Falge, unpublished). Total needle biomass of the branch was about 0.5 kg_{dw}, which equalled a needle surface (total area) of ca. 7 m^2. Depending on the assumptions on needle clumping of the branch, both slightly higher or lower rates of modelled transpiration were obtained compared to measured branch sapflow. The time-lag between leaf transpiration measured at the branch tip and sapflow at the branch base

was more pronounced (ca. 70 min, *figure 4B*) than the time-lags between sapflow measurements at the branch base and different heights of the stem. This is explained by low absolute transpiriaton rates (max. daily rate ca. 0.1 kg h^{-1} branch^{-1}). During the first 70 min of the morning a total of only 0.02 kg branch^{-1} were transpired which equals about 10–20 % of the assumed capacity of easy available water in the branch.

For comparison of water fluxes in roots and in the trunk of an apple tree, sapflow was monitored in 14 main roots close to the trunk base [8, 9]. Good agreement was found between the sum of fluxes in roots and sapflow measured in the trunk. Furthermore, spatial variation in the rate of water absorbed by the roots was observed around the trunk. This distribution was modified after irrigation.

6. CONCLUSIONS

Within the context of physical and chemical environmental change, material fluxes in forest ecosystem became a focus of research. Xylem sapflow measurements in trees are increasingly used to identify the contribution of indivdual trees or the forest canopy to total water vapor flux measured concurrently by eddy-correlation. For this reason, methods and uncertainties of sapflow monitoring methods and scaling procedures applied in forest stands were described. From current knowledge we make the following conclusions.

For continuous long-term measurements of tree xylem sapflow both methodological principles, THB as well as HPV methods, are appropriate. While HPV methods show higher variation due to point measurements and higher relation of wound area to measured xylem tissue, integrative THB methods are more prone
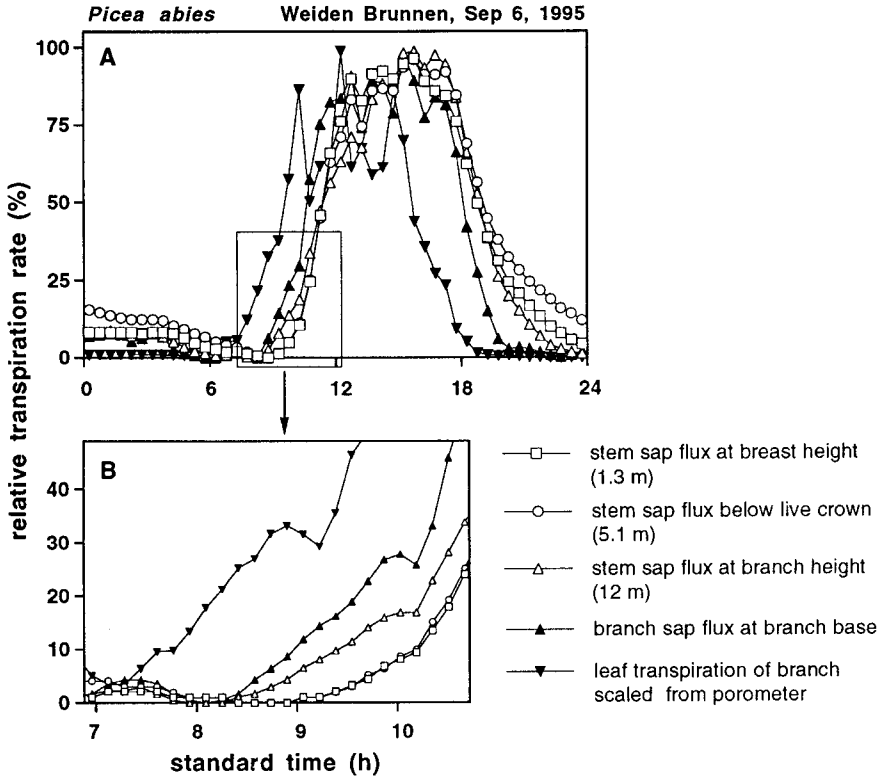
Figure 4. Comparison of relative transpiration rates (absolute flux rates related to maximum rate of the individual measurement) measured in different stem heights and in the base of a branch (A). Branch transpiration was estimated by leaf gas-exchange (porometer) at the tip of the branch and scaled to total branch by a model (Falge and Alsheimer, unpublished). Time-lag of initial fluxes was highest between branch tip and branch base (1 h) followed by stem sap flow at height of branch insertion (0.5 h) and stem sap flow below live crown and at breast height (0.5 h) (B).

to errors due to thermal imbalances, at least during shorter time-constants.

Problems of accuracy associated with thermal properties of the wood are not sufficiently investigated in large trees of various conducting types. More research is needed on this subject.

Accuracy of sapflow measurements scaled from sensor to tree can be proved by comparison with independent measurements. Such comparisons are usually limited by tree size.

Accuracy of sapflow estimates at the stand level can only be achieved by appropriate sample size of flux measurements and structural scalars. Analysis of water flux components derived from different levels of integration should be based on sound statistical evaluation.

Finally, flux programmes such as EUROFLUX are encouraged to include sapflow measurements in order to have a complementary, analytical tool for separating tree transpiration from total water

flux and assessing the range and dynamics in temporal variability and spatial heterogeneity of transpiration within the studied plot.

ACKNOWLEDGEMENTS

REFERENCES

[1] Alsheimer M., Charakterisierung räumlicher und zeitlicher Heterogenität von unterschiedlichen Fichtenbeständen (*Picea abies* (L.) Karst.) durch Xylemflußmessungen, Doctoral thesis, University Bayreuth, 1997.

[2] Alsheimer M., Köstner B., Falge E., Tenhunen J.D., Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany, Ann. Sci. For. 55 (1998) 103–123.

[3] Anfodillo T., Sigalotti G.B., Tomasi M., Semenzato P., Valentini R., Applications of a thermal imaging technique in the study of the ascent of sap in woody species, Plant, Cell. Environ. 16 (1993) 997–1001.

[4] Baker J.M., van Bavel C.H.M., Measurement of mass flow of water in the stem of herbaceous plants, Plant, Cell Environ. 10 (1987) 777–782.

[5] Berbigier P., Diawara A., Loustau D., A microclimatic study of the effects of drought on evapotranspiration in a maritime pine stand and its understorey, Ann. Sci. For. 48 (1991) 157–177.

[6] Bernhofer C., Gay L.W., Granier A., Joss U., Kessler A., Köstner B., Siegwolf R., Tenhunen J.D., Vogt R., The HartX-Synthesis: An experimental approach to water and carbon exchange of a Scots pine plantation, Theoret. Appl. Climatol. 53 (1–3) (1996) 173–183.

[7] Bréda N., Granier A., Aussenac G., Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quer-*

cus petraea (Matt) Liebl), Tree Physiol. 15 (1995) 295–306.

[8] Cabibel B., Continuity of water transfer in soil-plant system: the case of fruit trees, Agronomie 14 (1994) 503–514.

[9] Cabibel B., Do F., Thermal measurement of sap flow and hydric behavior of trees. 2. Sap flow evolution and hydric behavior of irrigated and non-irrigated trees under trickle irrigation, Agronomie 11 (1991) 757–766.

[10] Cermák J., Solar equivalent leaf area: an efficient biometrical parameter of individual leaves, trees and stands, Tree Physiol. 5 (1989) 269–289.

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

[12] Cermák J. , Kucera J., Transpiration of fully grown trees and stands of spruce (*Picea abies* (L.) Karst.) estimated by the tree-trunk heat balance method, in: Swanson R.H., Bernier P.Y., Woodward P.D. (Eds.), Proc. Forest. Hydrology and Watershed Measurements, Vancouver, Canada, August 1987, Publ. No. 167, IAHS-AISH, Wallingford, UK, 1987, pp. 311–317.

[13] Cermák J., Kucera J., Scaling up transpiration data between trees, stands and watersheds, Silva Carelica 15 (1990) 101–120.

[14] Cermák J., Kucera J., Changes in transpiration of healthy mature trees due to environmental conditions and of those with damaged water conductive system, in: Klimo E., Materna J. (Eds.), Proc. Cs MAB Natl. Comm-IUFRO Internat Workshop "Verification of hypotheses and possibilities of recovery of forest ecosystems", Beskydy Mt, Czechoslovakia, 4–8 Sept 1989, Agr. Univ. Brno, 1990, pp. 275–286.

[15] Cermák J., Kucera J., Extremely fast changes of xylem water flow rate in mature trees, caused by atmospheric, soil and mechanical factors, in: Raschi A., Borghetti M. (Eds.), Proc. CEC Internat Workshop "Methodologies to assess the impact of climatic changes on vegetation: Analysis of water transport in plants and cavitation of xylem conduits", 29–31 May 1991, Firenze, Italy.

[16] Cermák J., Deml M., Penka M., A new method of sap flow determination in trees, Biol. Plant 15 (1973) 171–178.

[17] Cermák J., Kucera J., Penka M., Improvement of the method of sap flow rate determination in adult trees based on heat balance with direct electric heating of xylem, Biol. Plant (Praha) 18 (2) (1976) 111–118.

[18] Cermák J., Ulehla J., Kucera J., Penka M., Sap flow rate and transpiration dynamics in

the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions, Biol. Plant (Praha) 24 (6) (1982) 446–460.

[19] Cermák J., Jenik J., Kucera J., Zidek V., Xylem water flow in a crack willow tree (Salix fragilis) in relation to diurnal changes of environment, Oecologia (Berlin) 64 (1984) 145–151.

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

[21] Cermák J., Matyssek R., Kucera J., Rapid response of large drought stressed beech trees to irrigation, Tree Physiol. 12 (1993) 281–290.

[22] Cermák J., Cienciala E., Kucera J., Lindroth A., Bednarova E., Individual variation of sap flow rate in large pine and spruce trees and stand transpiration: A pilot study at the central NOPEX site, J. Hydrol. 168 (1995) 17–27.

[23] Cienciala E., Lindroth A., Cermak J., Hallgren J.-E., Kucera J., The effect of water availability on transpiration, water potential and growth of *Picea abies* during a growing season, J. Hydrol. 155 (1994) 57–71.

[24] Cohen Y., Determination of orchard water requirement by a combined trunk sap flow and meteorological approach, Irrig. Sci. 12 (1991) 93–98.

[25] Cohen Y., Thermoelectric methods for measurements of sap flow in plants, in: Stanhill G. (Ed.), Advances in Bioclimatology Vol 3, Springer-Verlag, Berlin, Heidelberg, New York, 1994, pp. 63–89.

[26] Daum C.R., A method for determining water transport in trees, Ecology 48 (1967) 425–431.

[27] Diawara A., Loustau D., Berbigier P., Comparison of two methods for estimating the evaporation of a *Pinus pinaster* (Ait.) stand: sap flow and energy balance with sensible heat flux measurements by an eddy covariance method, Agric. For. Meteorol. 54 (1991) 49–66.

[28] Dugas W.A., Wallace J.S., Allen S.J., Roberts J.M., Heat balance, porometer, and deuterium estimates of transpiration from potted trees, Agric. For. Meteorol. 64 (1993) 47–62.

[29] Dye P.J., Olbrich B.W., Poulter A.G., The influence of growth rings in *Pinus patula* on heat pulse velocity and sap flow measurement, J. Exp. Bot. 42 (1991) 867–870.

[30] Edwards W.R.N., Becker P., Cermák J., A unified nomenclature for sap flow measurements, Tree Physiol. 17 (1996) 65–67.

[31] Granier A., Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres, Ann. Sci. For. 42 (1985) 193–200.

[32] Granier A., Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements, Tree Physiol. 3 (1987) 309–320.

[33] Granier A., Claustres J.P., Water relations in a Spruce (*Picea abies* L.) under natural conditions: spatial variation, Acta Œcol., Œcol. Plant 10 (1989) 295–310.

[34] Granier A., Loustau D., Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data, Agric. For. Meteorol. 71 (1994) 61–81.

[35] Granier A., Bobay V., Gash J.H.C., Gelpe J., Saugier B., Shuttleworth W.J., Vapour flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest, Agric. For. Meteorol. 51 (1993) 309–319.

[36] Granier A., Anfodillo T., Sabatti M., Cochard H., Tomasi M., Valentini R., Bréda N., Axial and radial water flow in the trunk of oak trees: a quantitative and qualitative analysis, Tree Physiol. 14 (1994) 1383–1396.

[37] Granier A., Biron P., Bréda N., Pontailler J.Y., Saugier B., Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods, Global Change Biology 2 (1996) 265–274.

[38] Granier A., Biron P., Köstner B., Gay L.W., Najjar G., Comparisons of xylem sap flow and water vapour flux at the stand level and derivation of canopy conductance for Scots pine, Theor. Appl. Climat. 53 (1996) 115–122.

[39] Grime V.L., Morison J.I.L., Simmonds L.P., Sap flow measurements from stem heat balances: a comparison of constant with variable power methods, Agric. For. Meteorol. 74 (1995) 27–40.

[40] Grime V.L., Morison J.I.L., Simmonds L.P., Including the heat storage term in sap flow measurements with the stem heat balance method, Agric. For. Meteorol. 74 (1995) 1–25.

[41] Habermehl A., Hüttermann A., Lovas G., Ridder H.-W., Computer Tomographie von Bäumen, Biologie in unserer Zeit 4 (1990) 193–200.

[42] Hatton T.J., Vertessy R.A., Variability of sapflow in a *Pinus radiata* plantation and the robust estimation of transpiration, Hydrology and Water Resources Symposium, Christchurch, New Zealand, 1989, pp. 6–10.

[43]   Hatton T.J., Wu H., Scaling theory to extrap-
olate individual tree water use to stand water
use. Hydrol. Proc. 9 (1995) 527–540.

[44]   Hatton T.J., Moore S.J., Reece P.H., Esti-
mating stand transpiration in a *Eucalyptus
populnea* woodland with the heat pulse
method: measurement errors and sampling
strategies, Tree Physiol. 15 (1995) 219–227.

[45]   Herzog K.M., Thum R., Zweifel R., Häsler
R., Heat balance measurements – to quantify
sap flow in thin stems only? Agric. For. Mete-
orol. 83 (1997) 75–94.

[46]   Hollinger D.Y., Kelliher F.M., Schulze E.-
D., Köstner B.M.M., Coupling of tree tran-
spiration to atmospheric turbulence, Nature
371 (1994) 60–62.

[47]   Huber B., Schmidt E., Eine Kompensations-
methode zur thermoelektrischen Messung
langsamer Saftströme, Ber. Dtsch. Bot. Ges.
55 (1937) 514-529.

[48]   Ittner E., Der Tagesgang der Geschwindigkeit
des Transpirationsstromes im Stamm einer
75-jährigen Fichte. Ecol. Plant. III (1968)
177–183.

[49]   Jarvis P.G., Scaling processes and problems,
Plant, Cell Environ. 18 (1995) 1079–1089.

[50]   Jones H.G., Harmer P.J.C., Higgs K.H., Eval-
uation of various heat-pulse methods for esti-
mation of sap flow in orchard trees: compar-
ison with micrometeorological estimates of
evaporation, Trees (1988) 250–260.

[51]   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., Evap-
oration, xylem sap flow, and tree transpiration
in a New Zealand broad-leaved forest, Agric.
For. Meteorol. (1992) 62, 53–73.

[52]   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.,
Transpiration and canopy conductance in a
pristine broad-leaved forest of *Nothofagus*:
an analysis of xylem sap flow and eddy cor-
relation measurements, Oecologia 91 (1992)
350–359.

[53]   Köstner B., Biron P., Siegwolf R., Granier
A., Estimates of water vapor flux and canopy
conductance of Scots pine at the tree level
utilizing different xylem sap flow methods,
Theor. Appl. Climatol. 53 (1996) 105–113.

[54]   Köstner B., Alsheimer M., Falge E., Geyer
R., Tenhunen J.D., Tree canopy water use
via xylem sap flow in an old Norway Spruce
Forest and a comparison with simulation-
based canopy transpiration estimates, Ann.
Sci. For. 55 (1998) 125–139.

[55]   Köstner B., Alsheimer M., Wedler M., Schar-
fenberg H.-J., Zimmermann R., Falge E., Joss
U., Tenhunen J.D., Controls on evapotran-

spiration in spruce forest stands, in: Tenhunen
J.D., Lenz R., Hantschel R., Eds., Processes
in Managed Ecosystems, Ecological Studies
(1998), in press.

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

[57]   Lindroth A., Cermak J., Kucera J., Cienciala
E., Eckersten H., Sap flow by the heat bal-
ance method applied to small size salix trees
in a short-rotation forest, Biomass and Bioen-
ergy 8 (1) (1995) 7–15.

[58]   Loustau D., Berbigier P., Roumagnac P.,
Arruda-Pacheco C., David J.S., Ferreira M.I.,
Pereira J.S., Tavares R., Transpiration of a
64-year-old maritime pine stand in Portugal.
1. Seasonal course of water flux through mar-
itime pine, Oecologia 107 (1996) 33–42.

[59]   Loustau D., Domec J.C., Bosc A., An analy-
sis of the spatial variability of sap flow den-
sity in maritime pine, Ann. Sci. For. (1998)
??–??.

[60]   Marshall D.C., Measurement of sap flow in
conifers by heat transport. Plant Physiol. 33
(1958) 385–396.

[61]   Nadezhdina N., Sazonova T.A., Kaibiainen
L.K., Specifications of the dynamics of sap
flows and water potentials in leaves of apple
trees under different water supply (in Russ),
8th All-Union Symp. on Water Regime,
Tashkent, 1984, p. 104.

[62]   Oren R., Phillips N., Katul G., Ewers B.E.,
Pataki D.E., Scaling xylem sap flux and soil
water balance, and calculating variance: a
method for partitioning water flux in forests.
Ann. Sci. For. 55 (1997) 191–216.

[63]   Pallardy S.G., Cermák J., Ewers F.W., Kauf-
mann M.R., Parker W.C., Sperry J.S., Water
transport dynamics in trees and stands, in:
Smith W.K., Hinckley T.H. (Eds.), Resource
Physiology of Conifers, Academic Press,
San Diego, New York, 1995, pp. 301–389.

[64]   Penka M., Cermak J., Deml M., Water trans-
port estimates in adult trees based on mea-
surement of heat transfer by mass flow, Acta
Univ. Agric. (Brno), Ser C, 42 (1973) 3–23.

[65]   Peschke G., Rothe M., Scholz J., Seidler C.,
Vogel M., Zentsch W., Experimentelle Unter-
suchungen zum Wasserhaushalt von Fichten
(*Picea abies* (L.) Karst.) Forstw Cbl 114
(1995) 326–339.

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

[67]   Poschenrieder W., Die Bestimmung der Tran-
spiration eines Fichtenaltbestandes (*Picea
abies* (L.) Karst.) mit der Konstant-Temper-

aturdifferenz-Methode unter Vergleich mit dem Eddy-Korrelationsverfahren, thesis, University Bayreuth (1992).

[68] Sakuratani T., A heat balance method for measuring water flux in the stem of intact plants, J. Agric. Meteorol. 37 (1981) 9–17.

[69] Saugier B., Granier A., Pontailler J.Y., Dufrêne E., Baldocchi D.D., Transpiration of a boreal pine forest measured by branch bags, sapflow and micrometeorological methods, Tree Physiol. 17 (1997) 511–519.

[70] Schulze E.-D., The regulation of plant transpiration: interactions of feedforward, feedback, and futile cycles, in: Schulze E.-D. (Ed.), Flux Control in Biological Systems. From Enzymes to Populations and Ecosystems, Academic Press Inc, San Diego, 1994, pp. 203–237.

[71] Schulze E.-D., Kelliher F.M., Körner C., Lloyd J., Leuning R., Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: A global ecology scaling excercise, Ann. Rev. Ecol. Syst. 25 (1994) 629–660.

[72] Steinberg S.L., McFarland M.J., Worthington J.W., Comparison of trunk and branch sap flow with canopy transpiration, J. Exp. Bot. 41 (1990) 653–659.

[73] Swanson R.H., Water transpired by trees is indicated by heat pulse velocity, Agric. Meteorol. 10 (1972) 277–281.

[74] Swanson R.H., Significant historical developments in thermal methods for measuring sap flow in trees, Agric. For. Meteorol. 72 (1994) 113–132.

[75] Tenhunen J.D., Valentini R., Köstner B., Zimmermann R., Granier A., Variation in forest gas exchange at landscape to continental scales, Ann. Sci. For. (1997).

[76] Vieweg G.H., Ziegler H., Thermoelektrische Registrierung der Geschwindigkeit des Transpirationsstromes, Ber. Dtsch. Bot. Ges. 73 (1960) 221–226.

[77] Vogt R., Gay L.W., Tenhunen J.D., Bernhofer C., Kessler A., Eds., HartX'92 - Vegetation-Atmosphere Coupling of a Scots Pine Plantation, Theor. Appl. Climatol. 53 (1996).

[78] Wedler M., Heindl B., Hahn S., Köstner B., Bernhofer C., Tenhunen J.D., Model-based estimates of water loss from 'patches' of the understory mosaic of the Hartheim Scots pine plantation, Theor. Appl. Climatol. 53 (1996) 135–144.

[79] Weibel F.P., Boersma K., An improved stem heat balance method using analog heat control, Agric. For. Meteorol. 75 (1995) 191–208.

[80] Zidek V., Actual and potential evapotranspiration in the floodplain forest, Ekologia (CSSR) 7 (1) (1988) 43–59.