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ORIGINAL ARTICLE

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Sap flow measurements with some thermodynamic methods, flow integration within trees and scaling up from sample trees to entire forest stands

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Abstract Sap flow measurement techniques and evaluation of data are reviewed. Particular attention is paid to the trunk segment heat balance (THB) and heat field deformation (HFD) methods based on 30 years experience. Further elaboration of sap flow data is discussed in terms of integrating flow for whole stems from individual measuring points, considering variation of radial patterns in sapwood and variation around stems. Scaling up of data from sets of sample trees to entire forest stands based on widely available biometric data (partially on remote sensing images) is described and evaluated with a discussion of the magnitude of errors, the routine procedure applicable in any forest stand and practical examples.

Keywords Evaluation of methods · Heat balance · Heat field deformation · Radial pattern of flow · Flow visualization

Introduction

Following the pioneering work of Huber early last century (Huber 1932), many types of sap flow measurement methods based on very different principles (e.g. thermodynamic, electric, magneto-hydrodynamic, and nuclear magnetic resonance) were described. However, only a few of them, particularly those based on thermodynamics, are widely used in the field (i.e. forests and orchards). For the methods based on thermodynamics measuring devices are commercially available. However, measurement of flow itself represents only the first part in sap flow studies. Additional important items to consider are evaluation of errors, integration of data measured by a certain sensor for the whole stems (e.g. Marshall 1958; Shackel et al. 1992; Hatton et al. 1990, 1995; Allsheimer et al. 1998; Clearwater et al. 1999; Nadezhdina et al. 2002a,b) and spatial variation of flow within trees (Čermák et al. 1984a, b, 1992; Čermák and Kučera 1990a,b; Granier et al. 1994; Čermák and Nadezhdina 1998a,b,c; Nadezhdina et al. 2002a,b). Another important issue to consider is the eventual scaling up of data from a series of sample trees to entire stands or even higher levels of biological organization, using biometric data (usually forest inventory based, e.g. Morikawa 1974; Čermák et al. 1978; Čermák and Kučera 1987, 1990a,b), hydrologic modelling (Meiresonne et al. 1999a,b; Oltchev et al. 2002a,b) or detailed remote sensing images (Balek et al. 1985a,b; Chiesi et al. 2002). This paper gives a brief overview of such problems and based on our own long term experience describes the routine procedure applicable in any forest stand and illustrates problems with corresponding practical examples.

Characteristics of main methods applied for sap flow measurements

The main methods developed for sap flow measurements (presented in chronological order) are: (1) Heat pulse velocity (HPV; Huber 1932; Huber and Schmidt 1936; Marshall 1958; Swanson 1970; Morikawa 1972; Cohen et al. 1981; Cohen 1993; Green and Clothier 1988; Green et al. 2003; Caspari et al. 1993). (2) Trunk segment heat balance (THB; Čermák and Deml 1974; Čermák et al. 1973, 1982; Kučera 1977; Kučera et al. 1977). (3) Stem heat balance (SHB; Sakuratani 1981, 1984; Baker and Van Bavel 1987). (4) Heat dissipation (HD; Granier 1985). (5) Heat field deformation (HFD; Nadezhdina et al. 1998; Nadezhdina and Čermák 1998). Detailed reviews of the above methods have been presented by Marshall (1958),

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Jones et al. (1988), Campbell (1991), Cohen (1993), Swanson (1994), Čermák (1995), Granier (1995), Edwards et al. (1996), Smith and Allen (1996), Braun (1997), Čermák and Nadezhdina (1998a,b,c), Gonzales-Altozano et al. (1998), Kostner et al. (1998), Wullschleger et al. (1998) and others. Theoretical analysis indicating goals and drawbacks of different methods and showing possible ways for their improvement have been presented by Marshall (1958), Pickard and Puccia (1972), Pickard (1973), Swanson and Whitfield (1981), Swanson (1983), Valancogne and Nasr (1989), Groot and King (1992), Barret et al. (1995), Grime et al. (1995a) and Nadezhdina (1998). Delta-T, UK (http://www.delta-t.co.uk) and Dynamax, USA (http://www.dynamax.com) are well known as suppliers of SHB and HD sensors, Greenspan (New Zealand) supplies HPV sensors.

Several research groups have focused their studies on comparison of results obtained when using different methods, which has also led to their eventual improvement (e.g. Penka et al. 1979; Rychnovská et al. 1980; Cohen et al. 1981; Čermák et al. 1984a; Schulze et al. 1985; Diawara et al. 1991; Hatton and Vertessy 1990; Kelliher et al. 1992; Kostner et al. 1992, 1994; Grime et al. 1995b; Zhang et al. 1997; Offenthaler and Hietz 1998; Schubert 1999; Lundblad et al. 2001). The majority of our experience with sap flow measurements is based on using the trunk section heat balance method and the heat field deformation method [see our cited papers and those, e.g. by Martin et al. (1997, 2000), Čermák et al. (1995, 1998), Hubbard et al. (1999), Cienciala et al. (1999, 2000, 2002), Bauerle et al. (1999), Lagergren and Lindroth (2002, 2004) and others]. Further improvements of some of these methods as well as some specific instrumental and other methodical features are therefore described in more detail in this paper.

Trunk heat balance method

The original THB method characterized by direct electric heating and internal sensing of temperature was originally designed for large trees (Čermák and Deml 1974; Čermák et al. 1973, 1976, 1982; Kučera 1977; Kučera et al. 1977). A section of a large tree trunk is heated from the inside by an electric current (supplied by electrodes) passing through the tissues. Heat is released more uniformly within the bulk xylem tissue and does not come through the thick bark. Both, power (*P*-which is directly proportional to sap flow) or temperature difference (d*T*-indirectly proportional) can be held constant by electronic circuits, while the other variable is recorded. Other ways of power control (e.g. such as changes in time of day) can bring significant errors due to heat storage in plant tissues. The electrodes, i.e. stainless steel plates (usually 25-mm wide and 1-mm thick) are pounded at short distances (about 2 cm) into approximately the depth of sapwood (therefore they are of different length). They are inserted in parallel into sapwood keeping the central electrode in a radial direction relative to the tree trunk. The power usually of 0.6-1 W is applied by 1 kHz alternating current separated from the ground. The temperature difference d*T* between upper heated plates and the reference ends about 10 cm below (usually up to 5 K) is measured by a battery of 1-mm thin needle thermo-sensors (usually thermocouples Cu-Cst).

This method calculates the heat balance of a defined heated space. Basically, the input energy has to be split between the conductive heat losses and the warming of water passing through, according to the following simple equation

$$P = Q\,\mathrm{d}T\,c_{\mathrm{w}} + \mathrm{d}T\,\lambda \tag{1}$$

where P is the heat input power (W), Q is the sap flow rate (kg s^{-1}), dT is the temperature difference in the measuring point (K), c_{w} is the specific heat of water (J kg^{-1} K^{-1}) and λ is the coefficient of heat losses from the measuring point (W K^{-1}). The physical principle is exact; the only question is the estimation of heat loss and the real heat field pattern in relation to the sap flow. There are two main types of set-ups where application is mostly based on stem diameter.

Most heat goes up with streaming water, but part of it (about 10-20%) is lost by heating stem tissues surrounding the measuring point. This heat loss (λ) considered in the applied equations is eliminated partially by the technical design of the measuring point (insulation by polyurethane foam and shielded against direct sun radiation), but nevertheless loss does take place. It changes mainly with the heat field pattern as it is changed with sap flow magnitude. In contrast, the influence of possible changes in water content of tissues, dM_{w} (a relation of dM_{w} to the total mass of tissue) is of little significance. The heat loss magnitude is clearly evident on the records of sap flow as a certain value of the so-called "fictitious flow" ($Q_{\mathrm{w.fic}}$), which is recorded even when the actual flow is zero (and under constant P, dT reaches its maximum). When calculating the actual sap flow (Q_{w}), it is necessary to subtract $Q_{\mathrm{w.fic}}$ (estimated periodically when the actual flow approaches zero, e.g. early morning after prolonged rain) from the recorded flow data ($Q_{\mathrm{w.rec}}$) (Eq. 2). However it is difficult to distinguish between "true" $Q_{\mathrm{w.fic}}$ and $Q_{\mathrm{w.fic}}$ plus a certain very low value of re-saturating flow, which almost always occurs in early morning and which can cause minor errors (more days should be taken into account).

$$Q_{\mathrm{w}} = Q_{\mathrm{w.rec}} - Q_{\mathrm{w.fic}} \tag{2}$$

Sensors have been gradually improved by modifying their geometry and arrangement during long-term application of the THB method. For example, three to five electrodes were applied, P or dT was kept constant and thermocouples were put in the xylem at the upper edge of electrodes or into their centre, reference ends of thermocouples were put into several or into a single point, etc. (equations are then modified accordingly). Measuring points are protected against direct illumination and against rain or stemflow by a special reflective insulation. Measuring points can be located anywhere on stems, but they are better more than 0.5 m above ground (usually 1.3 m), because steep temperature gradients occurring below this level can affect accuracy. The impact of such gradients can be compensated by application of additional pairs of thermocouples outside the heat field of the heater (Čermák and Kučera 1981, confirmed, e.g. by Silvestre and Ferreira 1998). A multi-channel battery-operated measuring system is commercially available from Environmental Measuring Systems (EMS), Turistická 5, 62000 Brno, Czech Republic (http://www.emsbrno.cz).

One of the simplest technical arrangements recently developed by EMS (see below) is as follows. In large trees, constant heating power (about 0.6 W) is supplied into the sapwood via a set of three electrodes. A fourth plate of the same size is hammered 10 cm below (Fig. 1). A battery of thermo-sensors inserted in slots through electrode axes measures the temperature difference of electrode temperatures. This variant of the THB enables better equalising of sapwood temperature (due to higher heat conductivity of the metal of electrodes) and minimises the impact of environmentally caused temperature gradients in radial direction (which may be more significant than those related to vertical temperature stratification).

The EMS firm also produces “baby” sensors (applicable for diameters 0.6-2 cm), which are a significantly improved version of those based on flexible external heating and sensing as described by Čermák et al. (1984b) and Lindroth et al. (1995). Heat is supplied by a resistance wire fastened to a soft resilient insulating tissue, assuring good contact even to non-cylindrical stem surfaces, even if a plant grows in diameter up to about 50% during the period of measurement. Temperature difference between heated and non-heated part of the measuring point (4 K) is kept constant and measured by thermo-sensors closely connected to xylem (Fig. 2) and controlled by variable power that is proportional to sap flow magnitude. Sap flow is calculated from the usual equation applied in the THB technique, but excludes the term for section size, when flow is measured for the whole small stem in this case. Heat losses are considered periodically as $Q_{\mathrm{w\_fic}}$ (see Eq. 2) the same way as described above. Close connection of thermocouples with the conductive xylem is important, because insulation properties of bark should be considered in order to get reasonable data (as mentioned in comments to SHB method). For example, McNabb and Hart (1962) found in elm branches differences in temperature above the heater reaching up to several degrees when bark was removed when compared with intact branches. Stone and Shirazi (1975) found that when applying surface heating through intact bark (2-mm thick) in small plants the sap velocity was lower by 25% when compared with the situation when the bark was removed.

HFD method

The heat field deformation method-as its name indicates-is based on measurement of deformation of the heat field around a needle-like linear heater, inserted in a radial direction into the stem. The frontal view of heat field looks like a symmetrical ellipse (due to different heat conductivities of the stem k_{st} in axial and tangential directions under zero flow and obtains a form of a gradually prolonging deformed ellipsoid under increasing flows). (The stem must be considered as a complex material consisting of xylem solid substance, water and air). The idea of the method occurred in 1991, when working with the “sap flow index” sensors (Nadezhdina 1989, 1992, 1999), and applied to apple trees (N. Nadezhdina 1998,

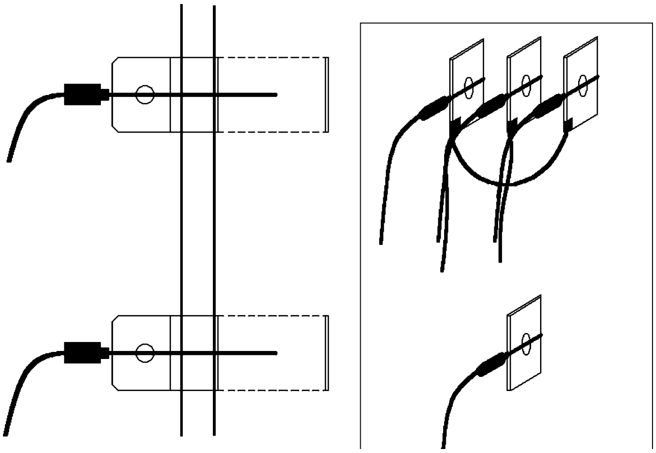

Fig. 1 Illustration of actual arrangement of simple sensors based on a recent EMS variant of the THB method. A series of three stainless steel plate electrodes (plus one reference) are pounded in the sapwood and a set of thermocouples in hypodermic needles (measuring temperature differences between upper and lower electrodes) inserted in their centres

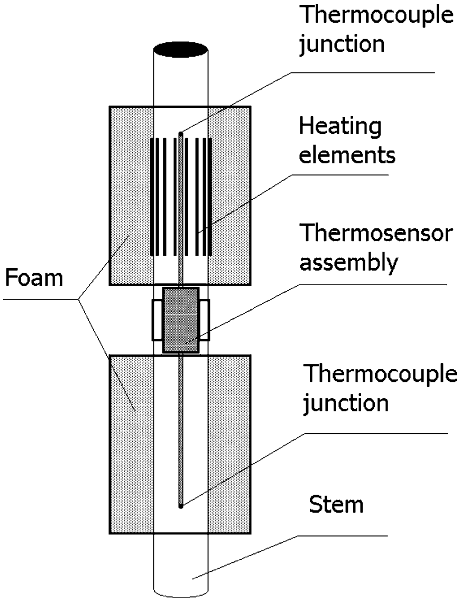

Fig. 2 Scheme of the EMS “baby sensor” for shoots or small stems

unpublished data). The method was further developed and tested quantitatively using the volumetric and the THB methods (Nadezhdina et al. 1998; Nadezhdina and Čermák 1998). Sap flow using the HFD method is calculated from the ratio of temperature gradients around the linear heater in axial (dT_{sym}) and tangential (dT_{as}) directions. These are measured by two pairs of thermocouples inserted (similar to the heater) in stainless steel hypodermic needles 1-1.2 mm in diameter. Experimentally, it was found that the above ratio is proportional to sap flow rate, Q_w (Nadezhdina 1998; Nadezhdina et al. 1998). Constants in the corresponding equation also include the geometry of the measuring point (k_{geom}), physical properties of the conducting system including stem heat conductivity (k_{st}) and specific heat of water (c_w).

$$Q_w = f\left[k_{geom}, k_{st}, c_w\left(\frac{dT_{sym}}{dT_{as}}\right)\right] \tag{3}$$

The HFD method can be fully exploited in large trees only when applying multi-point sensors, which allow measurements of radial patterns of sap flow (Čermák and Nadezhdina 1998a, 2002; Nadezhdina and Čermák 1998; Jimenez et al. 2000; Meiresonne et al. 1999a,b; Nadezhdina et al. 2001, 2002a,b; Čermák et al. 2001a,b; Oltchev et al. 2002a,b; Chiesi et al. 2002). The system is commercially available from EMS and Dendronet (dendronet@wo.cz).

Different variants of sensor geometry were tested during a continuous process of sensor improvement (Fig. 3). The common feature for all schemes is a presence of the axial pair of thermocouples measuring symmetrical temperature differences and allowing bi-directional (acropetal and basipetal) and very low flow measurements (Nadezhdina 1998, 1999). The tangential pair of thermocouples measuring asymmetrical temperature difference is responsible mostly for the magnitude of sap flow. The first two schemes (1) and (2) differ only by the positions of reference ends in both thermocouples. The axial temperature difference is measured directly by the axial pair of thermocouples in the first two schemes (from the left) showing sensor arrangement around the heater. The arrangement (2) with three needles only, i.e. with a common reference thermocouple T_{ref} (Fig. 3, middle) is preferable because it is easier to install, creates fewer wounds in stems and gives fewer errors due to incorrect positioning of needles. However, its manufacturing is more demanding especially in multi-point sensors. The last scheme (see Fig. 3, right panel) is a modification of the first version using two separate pairs of thermocouples. Symmetrical temperature differences are then calculated as the sum of both temperature differences measured by the upper and lower pair of thermocouples, assuming that temperatures in short (left and right) tangential distances (usually 5-10 mm) are equal on both sides of the heater. Advantage of this arrangement is that it is easier to manufacture and doubles the width of the measured stem section. However, it can increase the positioning error when more needles are installed in parallel.

Depth of thermocouples below cambium should be the same in all multi-point sensors installed in a particular stem (or even better in all sample trees in a stand). This simplifies and facilitates further integration of sap flow data from individual sensors to the whole tree level. For strictly parallel installation of particularly long needles (especially in deep-sapwood species) special tools must be applied. A template is fastened to the bark and a "drill bit holder", keeping the bit at a right angle to the smoothed bark surface. Correct distances between pairs of individual thermocouples in the needles (Z_{cor_ij}) should be used for calculating the sap flow in corresponding depths. This can be done more precisely according to measurement the angles of deviation (α_j) between particular thermocouple needles (j) and the heater needle. The distances, Z_{par_ij}, are expected to be valid at any depth in the needles if they are installed in strictly parallel positions. Deviated distances, Z_{dev_ij}, i.e. those occurring due to non-paralleled needles at corresponding radial depths from the bark surface (d_{br_ij}), are dependent on the tangent of deviation angles α. Therefore Z_{cor_ij} is derived from Eq. 4

$$Z_{corr\_ij} = Z_{par\_ij} \pm Z_{dev\_ji} = Z_{par\_ji} \pm d_{br\_ij} \times \text{tang}\,\alpha_j \tag{4}$$

Evaluation of THB and HFD methods

The THB method is very robust and provides reliable data during long-term measurements in trees with diameters over 15 cm in a range of tree species, sizes and environmental conditions. It has been applied as a standard when testing other methods (Offenthaler and Hietz 1998; Nadezhdina and Čermák 1998; Schubert 1999; Lundblad et al. 2001). Measured sections are spatially well defined in terms of released heat power, are rather wide (4-8 cm)

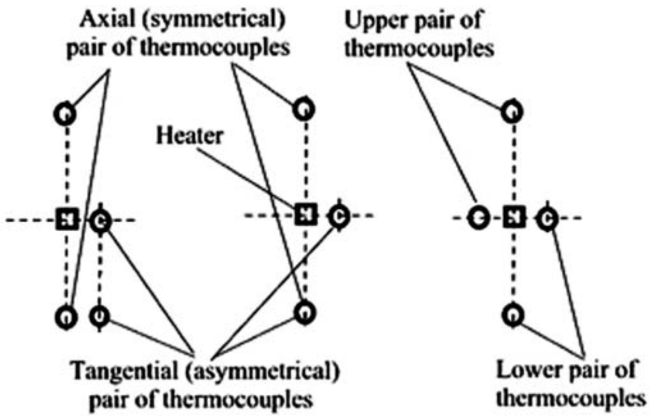

Fig. 3 Scheme of the HDF sensor: arrangements of thermocouples (*circles*) around the linear heater (*squares*)-frontal view: original version with two pairs of separated thermocouples (*left panel*) and later modifications: the same version two pairs of thermocouples, but with common reference end (the lowest needle: *middle panel*) and modified version with separate pairs of thermocouples arranged like "cross" around the heater (*right panel*). *Lines* show connections of particular thermocouples

and therefore represent significant parts of stems, especially when more of them are installed around them. The electrodes used in measuring points do not cause serious injuries to stems despite appearances. Electrodes have to be insulated in the highly electrical conductive phloem in order to focus the heating current only on the sapwood layer (Heimann and Kučera 1998). A single exception is ring-porous species with very narrow sapwood: there the additional heating of phloem can help to measure extremely high flow densities. The exact estimation of very low flow (values approaching the fictitious flow) is difficult, since it interferes with the changes of heat loss. However, recent arrangements by EMS have improved the measuring uncertainty in the range of small sap flows. Furthermore, due to the avoidance of any drilling the installation procedure is easier.

The defined power supplied into the sapwood faces a xylem resistance varying across two orders (roughly between 1,000 and 30,000 Ω) and therefore requires sophisticated electronic control of each individual gauge. As a result of heating a large xylem volume, the method needs a relatively high heating power in order to maintain a suitable artificial to environmental dT ratio. The variant of the measuring system with constant power P_{const} (thus 1/dT is proportional to flow) is simpler from an electronic point of view. If a power supply of about 0.6 W is used, the dT ranges between 0.5 and 5 K (higher at night). The variant using constant temperature difference dT_{const} (about 1 K) and variable power requires more complex electronics, but it has significantly lower average power consumption and has better dynamic properties (since the heat energy accumulated in xylem tissues does not change) (Kučera et al. 1977). This approach is also more suitable for use with a solar power supply.

Installation and dismantling of sensors require special tools. The THB measuring system has rather good dynamic properties (Čermák and Kučera 1991), although some inertia can occur. Due to the plane-like form of the electrodes the installation in stems with highly curved, spirally formed water conductive pathways (Kozlowski and Wignet 1963; Waisel et al. 1972; Harris 1989) may be difficult, since larger sapwood area may be cut then it corresponds to electrode thickness. Partially rotten stems with wet heartwood may cause problems. There might also be problems with installation in stems with very deep sapwood or in some tropical species with sapwood located deep inside stems or those with widely diffused vessels such as palms, where extremely long electrodes (difficult to insert in parallel) would be required.

The HFD method is extremely sensitive to very low flows, fast responding (minimum inertia occurs) and has unique capabilities for measuring the real vector of sap flow rate. This includes basipetal flows (Kunia 1955; McNabb and Hart 1962; Daum 1967) which occur, e.g. during rain events after periods of drought when shoots are absorbing intercepted water (Katz et al. 1989) or reversed flow in general (Sakuratani et al. 1999; Burgess et al. 2001; Brooks et al. 2002). Detection of basipetal as well as low night re-saturating flows is important, because they carry valuable information about plant water status. Multipoint HFD sensors contain series of thermocouples and therefore are especially suitable for measurements of radial patterns of flow in stems over a wide range of their diameters. Long sensors for very deep-sapwood require a relatively high power supply (up to 0.7 W). Resulting heat energy released in sapwood around the needle heater should be high enough to heat the tangential needle, but low enough to avoid tissue damage.

Installation of especially long needles in deep-sapwood species strictly in parallel must be always assured and checked and corrected distances between needles and heaters have to be applied when calculating the flow. HFD is relatively young and its theoretical analysis presently being done by several groups of physicists is not yet finished. Nevertheless preliminary comparative studies with other methods, either direct or indirect, are promising (Nadezhdina and Čermák 1998; Meiresonne et al. 1999a, b, 2002; Čermák et al. 2001a; Chiesi et al. 2002; Oltchev et al. 2002a,b). Thus further improvement of the method is expected. Some uncertainties were found during measurements of very high sap flow densities, e.g. those measured just below the crown of tall trees (N. Nadezhdina, unpublished data). This is a common problem in most methods working with needle-like heaters, if not compensated by a sophisticated calculation procedure.

For both these methods, proper installation of sensors required basic knowledge of the anatomy and physiology of the conductive systems in sample trees. THB sensors integrate the radial sap flow profile by technical averaging within the wide stem sections; multi-point HFD sensors integrate the profile by measuring flow in different depths. Fast growing large stems can grow over sensors during long-term measurements. This changes the relative position of sensors in sapwood and could affect results, if a sufficiently integrating technical system (as in new EMS devices) or multi-point sensors (the only sensors covering radial pattern in all cases) are not applied (Nadezhdina et al. 1998, 2002a,b; Čermák and Nadezhdina 1998a; Nadezhdina and Čermák 2000a, 2000b).

General evaluation of sap flow data

Integration of flow from individual sensors for the whole tree level

The interior of a tree is far from homogenous. As a tree grows, old knots, limbs, etc. are grown over and often not visible at the surface; flow divides around the knot leaving a non-conducting void immediately above and below. In general, it is not possible to avoid such areas. Careful attention to probe placement, correct sampling program and careful analysis of the collected data are the only ways to ensure representative data, free from bias (Swanson 1971). The variability in flow should be considered especially over the radial profile and over the circumference of trees at the same height (Čermák et al. 1992, 2003; Anfodillo et al. 1993; Phillips et al. 1996; Loustau et al.

1998; Lu et al. 2000; Nadezhdina et al. 2002a,b). Eventually it may be necessary to consider that specific flow and velocity may increase or decrease with height depending on species (Huber 1928). If water storage is not considered, data for the whole stem in the part below the crown without branches should be practically the same (Schulze et al. 1985; Čermák and Kučera 1991).

Wounding of stems by sensors can also be important for integration of flow within trees. Insertion of metal probes into holes drilled in the sapwood (even if narrow) causes interruption of conducting elements above and below the holes and partially also on their sides, where tyloses are formed. Ranges of damaged elements at distances 3-20 cm in axial direction and up to distances comparable to probe diameter in tangential direction have been reported. In order to avoid HPV measurement errors, corresponding correction factors for different species have been empirically derived (Swanson 1971; Swanson and Whitfield 1981; Green and Nicholson 1987; Jones et al. 1988; Green and Clothier 1988; Olbrich 1991). Similar situation also fits to HD and HFD needle-like sensors, whose diameter should be kept as small as possible. Electrodes applied in the THB method can cut more conducting elements if improperly installed, but few of them are interrupted, when they are well inserted in parallel to the grain (when elements are not cut but stand apart). This method uses much wider and better defined directly measured stem sections than other methods. Most of the conducting xylem tissues thus occur between several 20-mm distant and 1-mm thick electrodes and remain absolutely intact, therefore the relative importance of tissue wounding by sensors significantly decreases. Growth of the new annual ring is slightly stimulated during but especially after removing of electrodes, when scars can be formed in thin bark species.

Integration of sap flow within stems: radial pattern

Integrating the radial velocity profile is more important in some methods (especially those using needle-like heaters) than in others, where it is overcome by technical arrangements (e.g. internal sectional heating). Many authors (Edwards and Booker 1984; Green and Nicholson 1987; Phillips et al. 1996; Zang et al. 1996; Nadezhdina et al. 1998, 2002a,b; Čermák and Nadezhdina 1998a,c; Oren et al. 1998; Wullschleger and King 2000) measured the sap velocity or sap flow density and estimated the volume flux, q, in different radial depths below the cambium. Special caution must be taken in fast growing trees with wide annual rings, when using single-point sensors. Distinctive maxima and minima in sap velocity or density were found to correlate with early-wood and late-wood, which led to the recommendation that probe emplacement in such cases should be to randomly assigned depths in the sapwood (Dye et al. 1991). Small radial shifts of single-point sensors can cause very different results (Nadezhdina et al. 2002a,b).

The resulting flux profile could then be integrated over the sapwood cross-section area in order to calculate the total volume flow within the stem, Q_w. Hatton et al. (1990) described a practical method for integrating the radial profile: given a set of sap flow velocity estimates from n sensors placed in different depths of sapwood, the annular cross-section of a tree is divided into n concentric annuli such that inner radius r_k of annulus k occurs midway between sensors k and k+1, where k=1,2,3,...,$n$numbered from cambium. The information from each sensor k is weighted by the proportion (p_k) of the total sapwood conducting area, which it represents. The sap flow rate, Q_w is then given as the average of sap velocities, weighted by the area of sapwood associated with each sensor. This approach can also be used to estimate the optimum spacing of sensors, providing that each sensor should contribute equal information regarding the distribution of sap flow.

Similar integration of flow is achieved, when a generalising curve is first calculated from individual measuring points along the stem radius

$$Q_{wt} = \int_{r_h}^{r_c} 2\pi r q_I \, dr \qquad (5)$$

where q_I is the sap flux density at the radial depth I, r_c and r_h are the radii at the cambium and heartwood, respectively. The usual approach is to fit a least-square polynomial or other function (e.g. double-Gaussian) to a point sapwood conducting area and then to integrate this function across the sapwood conducting area and around the bole (Cohen et al. 1981; Green and Nicholson 1987; Green and Clothier 1988; Čermák and Nadezhdina 1998a; Nadezhdina et al. 2002a,b). Large errors can occur when radial pattern of flow is neglected (assuming uniform flow over the sapwood cross-section area). Placing single-point sensors at random depths can result in errors in the range of −50 to +300%, if by chance missing two available points, where correct data can be obtained (range of −100 to +140% is shown in the Fig. 4) (Nadezhdina et al. 2002a, b). The same authors showed that incorrect positioning of sensors with an error of only ±1 mm can lead to errors about ±1% in a rather flat radial pattern and about ±15% when this pattern is sharp. The above procedure fits for regular symmetrical stems, or at least such where averaging data from several sensors around stems does not cause significant errors.

Integration of sap flow within stems: number of measuring points around trees

A single measuring point per main stem is usually sufficient when applying the methods with external heating and sensing temperature around the circumference only in very small stems or shoots. Sapwood is usually more variable in large trees (Čermák et al. 1992, 2003;

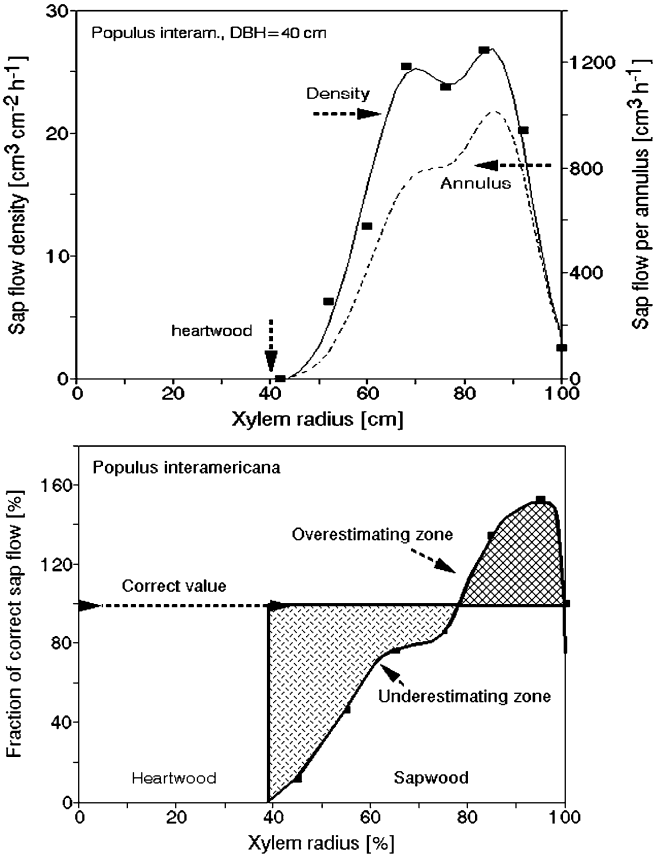

Fig. 4 An example of radial pattern of sap flow in the poplar stem measured with the multi-point sensor and potential errors, which may occur if applying a single point sensor. **a** *Curves* characterizing measured sap flow density (at individual points) and sap flow per annulus (after multiplying particular densities by corresponding sapwood areas) are shown. *Horizontal arrows* indicate appropriate scales for both *curves*, *vertical arrows* indicate the edge of heartwood. **b** Magnitude of potential errors when applying a single point sensor and assuming flow uniformity over the sapwood as depending on sensor position (according to Nadezhdina et al. 2002a, b). If the radial pattern of flow is not known in advance, placing the single-point sensor too shallow in the sapwood causes positive deviations of results (overestimation zone) and too deep in the sapwood negative deviations (underestimating zone). Correct positioning of a single point sensor (which should be located at the point where the curve intersects the 100% line) is only accidental

Čermák and Kučera 1990a,b; Gartner 1995; Saint-Andre 1998; Fromm et al. 2001), therefore more measuring points around stems should be used. This fits especially when applying techniques based on point measurements, i.e. those sensing the flow at the distance of only a few millimetres around (the HPV or heated needle probes). Fewer measuring points are necessary when using measuring systems, which include larger sections of sapwood (as THB). The number of required sensors (a range of 2-12 has been recommended) substantially depends on natural variation of conducting systems in stems and resulting variation of flow density (Lassoie et al. 1977; Miller et al. 1980; Cohen et al. 1985; Schulze et al. 1985; Čermák 1986; Čermák et al. 1986, 1992; Čermák and Kučera 1990a,b; Dye et al. 1991; Olbrich 1991; Jimenez et al. 2000). It is very important to distinguish natural variability of sapwood from measurement errors of applied sensors of course. Example of sap flow variation across stems based on measurements using 48-60 HFD sensors showed the importance of this issue (Čermák et al. 2003). A special visualization procedure gives the most informative results (Fig. 5). Multi-point radial patterns represent primary data here; "open stem" drawings enable better visualization of inner parts of stem, which are more difficult to see when a "3D network" image is constructed. 2D colour visualization (as suggested by Martinek, see the above cited paper) seems more instructive. Improved versions of a similar procedure allow a movie to be shown-color visualization of flow dynamics (Nečas 2003).

Integration of sap flow within trees, when measuring branches in the tree crown

Some trees or shrubs have almost no main stems suitable for installation of sensors. Then integration of sap flow measured in a series of tree branches is acceptable, although it requires a larger number of sensors. This approach was also applied, e.g. in large trees (in sites equipped with towers), where branches were spread over the whole crown (north and south orientation, heights between 40 and 60 m) (Fig. 6). Application of biometric parameters available on the branch and entire tree level is a prerequisite for this approach. This situation is rather rare in forest stands, where working with whole trees (and main stems) is preferable when scaling up for the stand level is required.

Scaling up from whole sample trees to forest stands

To estimate transpiration of forest stands or orchards on the basis of sap flow measurements in individual trees requires including a selected series of sample trees of different diameters, depending on the species, tree age, their health state and stand characteristics and also the method applied. Range of sample trees size should cover the actual range of experimental stands. Tree size distribution is also important, because characterisation of a mean tree is problematic especially in stands with a very wide range of tree sizes. It was found in many studies since late 1980s (Čermák et al. 1978) that dominant trees (accounting one-third of tree number) account for about two-thirds of the total stand water loss, medium trees about one-quarter of water loss and suppressed trees only about 5-10%. Therefore it is preferable to select sample trees according to special statistical procedures.

Selection of sample trees based on quantiles of total

When measuring transpiration in stands with large range of tree size there may occur problems with selection of representative size of sample trees, especially due to the occurrence of very small trees (it is not reasonable to use

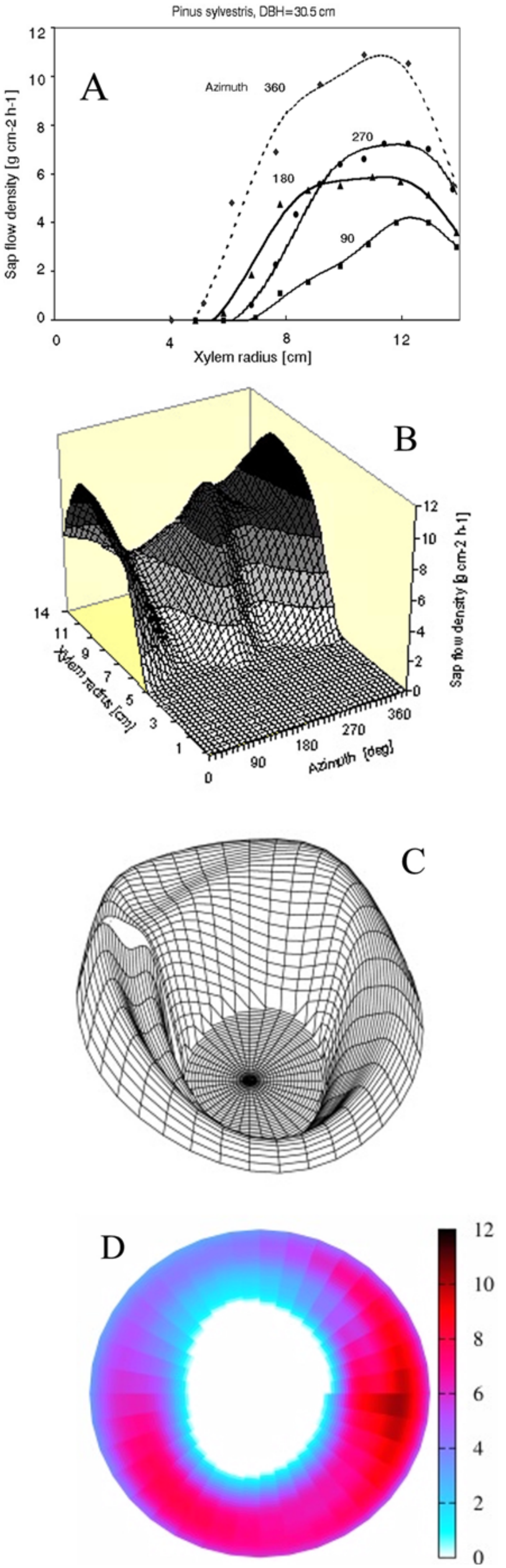

Fig. 5 Example of sap flow distribution across pine (*Pinus sylvestris* L.) stem measured by the HFD method using different visualization techniques-scales are identical in all sub-figures. **a** Radial patterns of flow measured from four stem sides (azimuths) using up to 12 sensors along each stem radius. **b** 3D visualization of the "open stem", when pith is shown as a line of the same length as cambium, where azimuths are marked. **c** 3D network visualization (it is difficult to show the scale when the image is in a general position). **d** 2D colour visualization (according to Martinek and Nečas, see Čermák et al. 2003) showing geometrically correct stem cross-section, where sap flow density is marked by *colors*

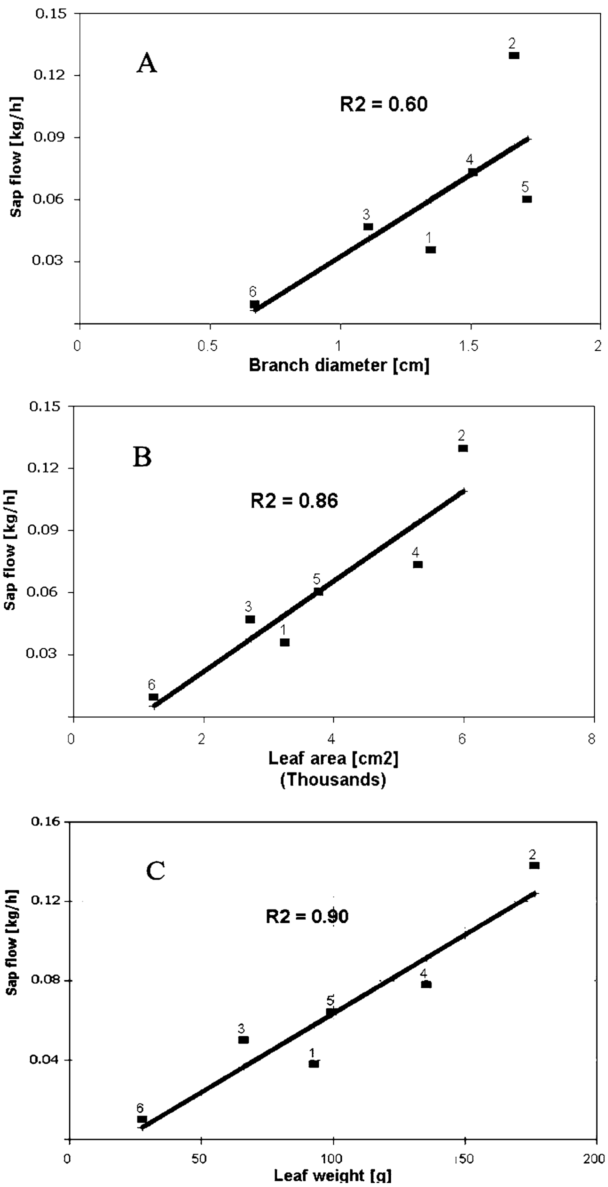

Fig. 6 Example of the "scaling curves" on the branch level (relationships between different branch biometric parameters and monthly totals of sap flow) used for integration of sap flow values to the entire tree from a series of representative branches (J. Kučera, unpublished data)

mean values calculated, e.g. from seedlings and large trees). The usual problem in such cases (i.e. estimating which trees should be considered as a sample and which not) can be overcome, e.g. with the "quantiles of total"

Table 1 Selection of sample trees at the experimental plot using quantils of total (Michalek and Cermak 1990) based on inventory of all trees at the plot. (Example of a biometric parameter: Basal area = Abas) Site: ....; Plot area: 3390 m^2; Number of sample trees to be measured: 12; Basal area per stand area unit: 33,4053 m2 ha-1; Sampled fraction of stand Abas: 33.4053/12 =2.7838 m^2

Species .... Tree No.	DBH [cm]	Basal area (Abas) [cm^2]	Cumulated Abas		Calculation the size of sample tree as quantil	Sample tree No:
			per plot area [cm^2]	per (1ha) stand area [m^2]		
1	3,5	10	10	0,0028	The smallest tree (=Min)	
2	4,2	14	23	0,0069		
3	4,4	15	39	0,0114		
4	4,5	16	55	0,0161		
5	4,8	18	73	0,0214		
6	5,0	20	92	0,0272		
7	5,0	20	112	0,0330		
8	5,2	21	133	0,0393		
9	5,2	21	154	0,0456		
10	5,3	22	176	0,0519		
11	5,3	22	198	0,0583	(Min+Samp.1)/2	Eventual
12	5,3	22	220	0,0648	0,0691	(Sample. 0)
⇒ 13	5,3	22	242	0,0713		
14	5,4	23	265	0,0781		
15	5,5	24	289	0,0851		
...	...	...	...	...	...	...
108	9,2	66	4610	1,3599	2.7838⁎0.5=1,3919	Sampl. 1
109	9,2	66	4677	1,3795		
⇒ 110	9,2	66	4743	1,3992		
111	9,2	66	4810	1,4188		
112	9,2	66	4876	1,4384		
...	...	...	...	...	...	...
215	12,0	113	13936	4,1109	2.7238⁎1.5=4,1757	Sampl. 2
216	12,0	113	14049	4,1442		
⇒ 217	12,0	113	14162	4,1776		
218	12,0	113	14275	4,2110		
219	12,0	113	14388	4,2443		
...	...	...	...	...	...	...
...	...	...	...	...	...	...
557	28,5	638	97656	28,8071	2.7838⁎10.5=29,2299	Sampl. 11
558	28,6	642	98299	28,9966		
⇒ 559	28,7	647	98945	29,1874		
560	29,2	670	99615	293850		
561	29,5	683	100299	29,5866		
562	29,7	693	100991	29,7910		
563	30,0	707	101698	29,9995		
564	30,5	731	102429	30,2150		
565	31,3	769	103198	30,4420		
566	31,5	779	103978	30,6719		
567	32,0	804	104782	30,9091		
568	32,0	804	105586	31,1463		
569	32,7	840	106426	31,3941		
570	33,0	855	107281	31,6464		
571	33,5	881	108163	31,9064	2.7838⁎11.5=32,0137	Sampl. 12
⇒ 572	36,8	1061	109223	32,2193		
573	38,5	1164	110388	32,5627		
574	39,0	1195	111582	32,9151		
575	46,0	1662	113244	33,4053		
⁎⁎⁎	⁎⁎⁎	⁎⁎⁎	Total=	33,4053		

statistical technique (Čermák and Kučera 1990a; Čermák and Michálek 1991). This technique calculates diameters of a series of sample trees of which each represent the same fraction of a selected biometric parameter. According to that technique all trees in the stand are sorted according to the selected biometric parameter characterizing the size of trees, B_{tree}, in an ascending manner and cumulative, B_{tree}, is calculated simultaneously (Table 1). Total value of the biometric scaling parameter of the stand, B_{stand}, is divided into the number of equal portions corresponding to the chosen number, k, of sample trees ($B_{port} = B_{stand}/k$). This number (e.g. k=12) is determined practically, e.g. by the number of channels of the measuring device available at the given site. The fractions (1 to k) when added subsequently in an ascending order and compared with cumulative B_{tree} characterize border values between fractions. The size of sample trees representing individual fractions is calculated using means of the fractions, i.e. B_{port} multiplied by factors: 0.5,1.5, ...,11.5 (always k-0.5). Resulting values are arranged along the column containing cumulative values of B_{tree}. Trees whose corresponding cumulative B_{tree} values of are nearest to the products of the above fractions (1 to k) and multiplying factors are taken as the best representing size of sample trees. True sample trees of corresponding diameter at breast height are found on the list of sorted individual trees and are identified in the field according to their fixed numbers. In practice, several trees of similar size for every portion were considered and one sample tree is selected from them in the field.

The inclusion of at least one additional small sample tree is recommended (e.g. "Sampl.0"); it usually shows practically negligible transpiration (which can thus be taken as zero) and its non-zero size can again help to anchor the "scaling curve" (the sap flow/biometric parameter relationships) near the origin. Eventual lack of values for small trees can be alternatively overcome by introducing fictitious values corresponding to "the smallest tree of the experimental stand" (representing the virtual border between growing and still just surviving trees, which evidently will die soon), even when it was not actually measured. This prevents overestimation of transpiration results calculated for tree sizes lower then mean tree of the stand (often frequent) and underestimation for sizes above the mean.

Scaling up based on biometric parameters

Scaling up is usually based on a relationship of sap flow to a selected biometric parameter. Usual forest inventory parameters can be used for this purpose, if no better ones are available (e.g. such based on detail leaf and illumination and root and soil water studies). This is the usual situation when working in the field outside a few especially well equipped research plots. Diameter at breast height or basal area are most commonly used. Some authors have used tree girth, but timber volume or sapwood basal area can be used as well (Denmead 1984; Owston et al. 1972; Morikawa 1974; Roberts 1977; Čermák et al. 1982; Čermák and Kučera 1987; Hatton and Vertessy 1990; Diawara et al. 1991; Vertessy et al. 1995, 1997; Allsheimer et al. 1998). Diawara et al. (1991) found it difficult to select one of three tested biometric parameters in sparse stands of even-aged pines. When testing seven biometric parameters in a hardwood stand, the sunlit (solar equivalent leaf area, derived from basal area and relative mean irradiance along the depth of the canopy) was found to be one of the best of simple parameters (Čermák 1989). Otherwise the leaf mass (M in g) seems to be also very suitable simple biometric parameter when integrating sap flow for the tree from its individually measured branches (see J. Kučera as mentioned above). This is because leaf mass incorporates both leaf area (A in m^2) and mass per area (MpA in $g\ m^{-2}$), therefore: M=A×MpA, which is important since MpA is almost a linear function of leaf irradiation in broadleaf as well as coniferous species (Čermák 1989, 1998; Sprugel et al. 1996).

Scaling up of physiological and/or silvicultural data from individual trees to forest stands has been generally applied in forestry especially in the case of growth and production (e.g. Korf et al. 1972; Philip 1994). In principle this is based on biometric parameters directly measurable on trees in the field, which characterize their size (B_{tree}). Such parameters must be directly measurable on a number of trees to represent a stand (e.g. stand area unit, 1 ha). Patterns of tree distribution within stands (proportion of trees of different size) and stand density (number of trees per stand area unit, N/ha) are applied in addition to characteristics of individual trees. Three approaches are possible: (1) the simplest way is to scale up physiological data according to the ratio of certain biometric parameters of sample trees and of the stand. (2) In more detailed studies, properties of mean trees of individual DBH classes are considered and number of trees in classes is used to characterize distribution of trees within stands. Especially in cases with large range of tree size, where it is desirable to focus more on larger trees in stands, a technique of quantiles of total (as described above) should be applied. (3) The other approach based on random sample tree selection along a transect line as applied in a boreal forest was described by Cienciala et al. (1999).

Scaling up based on the simple ratio of biometric parameters

The simplest way of calculating stand transpiration, Q_{stand}, is based on the total value of transpiration, Q_{tree}, measured in k sample trees and the ratio of values of a selected biometric parameter of sample trees B_{tree} and of the entire stand B_{stand} (e.g. 1 ha) considering the stand density of N (trees ha^{-1})

$$Q_{\mathrm{stand}} = fQ_{\mathrm{tree}} \frac{B_{\mathrm{stand}}}{B_{\mathrm{tree}}} \tag{6}$$

Such a way of scaling up can be also expressed as a linear regression line coming through the origin. Usually an overestimation of true values in small classes and underestimation in large classes can be expected. Scaling up based on simple ratios may be applied in cases of uniform stands (e.g. even aged plantations with limited range of tree size), in cases where available only very small number of sample trees to calculate reasonable regressions and also when high individual variation of Q_{tree} occur, e.g. due to environmental factors (e.g. drought) or due to the mechanical damage to the trees (Čermák et al. 1982; Čermák and Kučera 1990a; Hinckley et al. 1994).

Scaling up based on sap flow distribution in DBH classes

When possible, to avoid using the ratio of the transpiration total of all the sample trees and that of the stand (Owston et al. 1972; Čermák and Kučera 1987; Diawara et al. 1991), it was found better to apply a diameter class technique similar to that one common in forest inventory (Čermák et al. 1978, 1987, 1992; Čermák and Kučera 1987, 1990a) (Table 2). First the values of transpiration of mean trees $(Q_{\mathrm{mean}})_i$ of m individual DBH classes (usually with the step of 2 cm) are derived from regressions ("scaling curves") relating corresponding transpiration values of individual sample trees, Q_{samp}, to biometric parameters of such trees $(B_{\mathrm{tree}})_I$, e.g. basal area, illuminated leaf area, etc. (Fig. 7). The regressions are rarely linear, usually sigmoidal (e.g. Gompertz) or similar functions are applied (Eq. 7).

$$(Q_{\mathrm{mean}})_i = f(B_{\mathrm{tree}})_i \tag{7}$$

Transpiration of mean trees of individual diameter classes is calculated from the regressions. Stand transpiration is obtained when derived transpiration values for mean trees of individual classes are multiplied by numbers of trees in classes, n_i, and summarized for the stand area unit, 1 ha (Eq. 8).

$$Q_{\mathrm{stand}} = \sum_{i=1}^{i=m} (Q_{\mathrm{mean}})_i \times n_i \tag{8}$$

The scaling curve is calculated, e.g. for each individual day of the growing season or a certain longer period when soil water supply is constant. This helps to better distinguish possibe changing behaviour of different tree groups within stands during growing seasons (Fig. 7a). All species or different layers of the canopy (if any) must be evaluated separately (Fig. 7b). Scaling up technique based

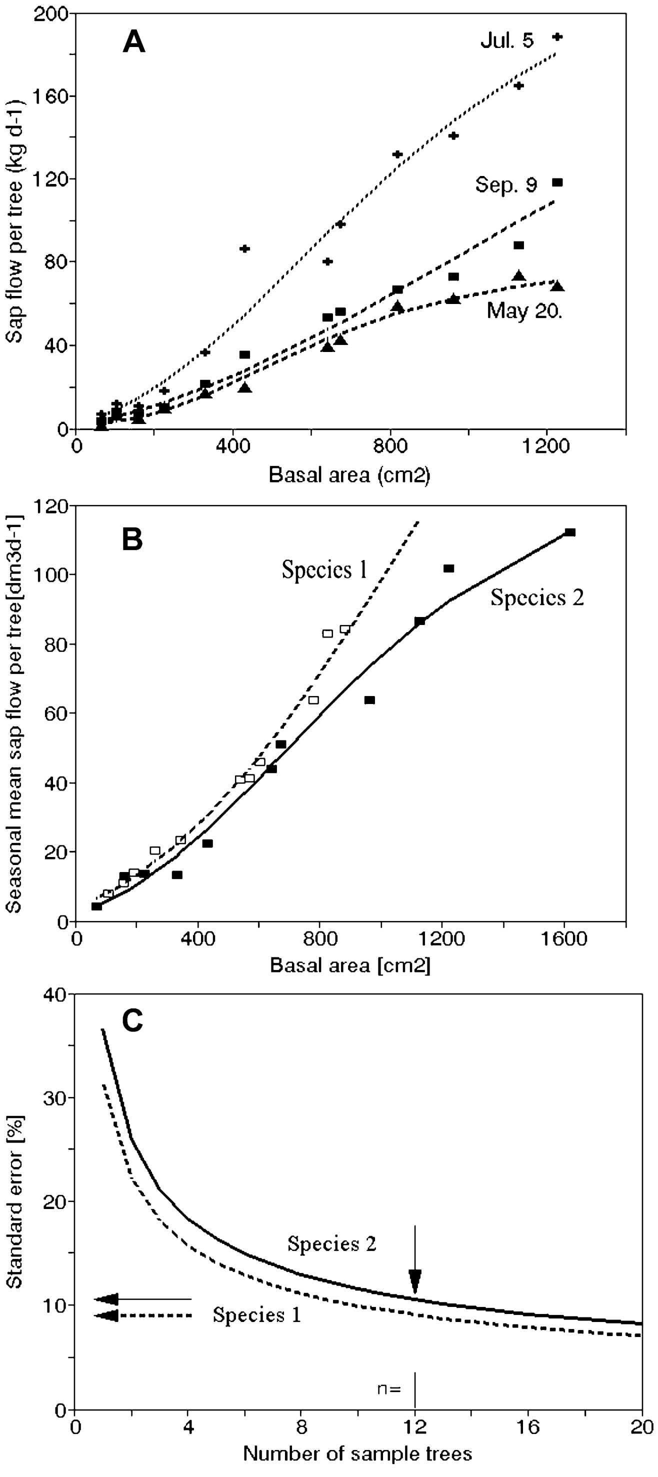

Fig. 7 Example of the "scaling curve" on the whole tree level. **a** Relationships between basal area and daily totals of sap flow for the set of sample trees measured on 3 days under different environmental conditions during the growing season. **b** Similar example of the scaling curves for two different species (mean values over the growing season are shown). **c** Magnitudes of corresponding scaling up errors for the two above species (*arrows* indicate values corresponding to selected number of sample trees, n=12)

Table 2 Example of the table applied for upscaling of sap flow data measured in sample trees to the forest stand area unit (1 ha)

Year: 2003				Site:					Species:					Comment:												
Measured days=				Biometric parameters of sample trees (e.g. 12 or more):										Generalizing data from individual sample trees to y=Qmean sample trees:				Biometric parameters of a stand ("i" DBH classes								
Sample tree No:		1	2	3	4	5	6	7	8	9	10	11	12					Class DBH (cm):	10	12	14	...	24	...	38	46
DBH (cm):		9,2	11,5	14,3	16,9	20,5	23,4	28,6	29,3	32,3	35,0	37,9	39,5					Basal area (cm2):	79	113	154	...	452	...	1134	1662
Basal area (cm2):		66	104	161	224	330	430	642	674	819	962	1128	1225	Equation (e.g. x=Abas):				Other parameter:	...	...	...	...	...	...	...	...
Other parameter:		...	...	...	...	...	...	...	...	...	...	...	...	Qmean=a∗exp[-b∗exp(-c∗x)]-d,				Tree/class (ni):	124	95	134	...	15	...	5	5
Date	Day of year	Measured daily sap flow data in sample trees Qsamp (kg/tree)												Values of coefficients				Summarized classes (=stand transpir.) mm/d	Daily sap flow data, Qclass (kg/class) derived from the generalizing equation, Qclass=Qmean∗ni							
														a	b	c	d									
Apr_1	91	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
2	92	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
3	93	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
May_20	140	1,4	6,1	4,4	9,7	16,7	19,8	39,5	42,4	59,0	62,5	13,7	68,4	77,5	4,5	0,00316	-0,2	0,58	312	335	680	...	399	...	343	379
Jul_05	186	6,5	11,9	10,5	18,2	36,5	86,7	80,3	98,0	1320	141,1	165,2	188,3	241,5	3,4	0,00211	6,5	2,27	874	958	1902	...	881	...	853	1058
Sep_09	252	3,6	7,8	7,3	10,1	21,6	35,3	53,2	56,2	67,0	72,8	88,3	118,6	248,8	3,2	0,0012	9,1	1,56	549	582	1112	...	445	...	502	759
...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Nov_13	317	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
14	318	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
15	319	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Seasonal mean=		4,1	8,7	7,3	12,3	22,4	43,8	50,9	63,5	75,4	86,3	101,6	112,1	Stand seasonal total=				272,3=Sum=	9,1	9,2	17,4	...	8,0	...	8,7	11,4

on sap flow distribution according to tree DBH is usually more realistic and accurate then that on simple ratio. The minimum scaling up error when applying reasonable sets of sample trees and proper integration technique can be between 5 and 10% in homogenous stands and 10-15% or more in heterogeneous stands (Fig. 7c). In any case selection of a sufficiently high number of sample trees is recommended.

Example of a simplified spreadsheet used for this calculation when applying basal area as the scaling parameter is demonstrated (in Table 2 and Fig. 8).

Scaling up based on remote sensing images

Another approach for scaling up sap flow data from sets of trees to stands or higher levels of biotic organization is to use remote sensing data, i.e. combination of spatial (remote) and temporal (ground based) methods (Balek et al. 1985a,b; Čermák and Kučera 1990a,b; Chiesi et al. 2002). An advantage of remote sensing is that it covers large spatial scales while ground-based measurement gives the dynamics of the processes. Acceptable relationships of actual transpiration to reflectance of foliage in tree canopies were found, e.g. in the near-infrared part of the spectra (band 7) or similar separately for broadleaf and coniferous species. If the whole study area including the suitably located sample trees is characterized by images taken at a suitable time, it is possible to scale up the data according to non-linear regression curves separately for each species (Balek et al. 1985a,b). Time shift between leaf transpiration and sap flow must be considered especially in trees with large water storage. This method seems promising especially for landscape level studies, but still needs to be better elaborated.

Scaling up based on hydrologic models

Evapotranspiration and transpiration of different vegetation types are at present well represented in many different SVAT models of different levels of complexity (e.g. Sellers et al. 1995; Kowalik et al. 1997; Pietsch et al. 2003). Simple "big-leaf" models usually require a limited number of parameters and can be used in global and regional scales. More sophisticated "distributed multi-layer" SVAT models require more input parameters with detail information about spatial distribution of key biophysical properties of vegetation. Models usually describe adequately the daily and even hourly transpiration in mixed stands under non-limiting soil water conditions, however, under limiting soil water conditions, the more sophisticated and complex models describe more accurately the responses of different tree species (Meiresonne et al. 1999a,b, 2002; Chiesi et al. 2002; Oltchev et al. 2002a,b); this seems a good perspective for future.

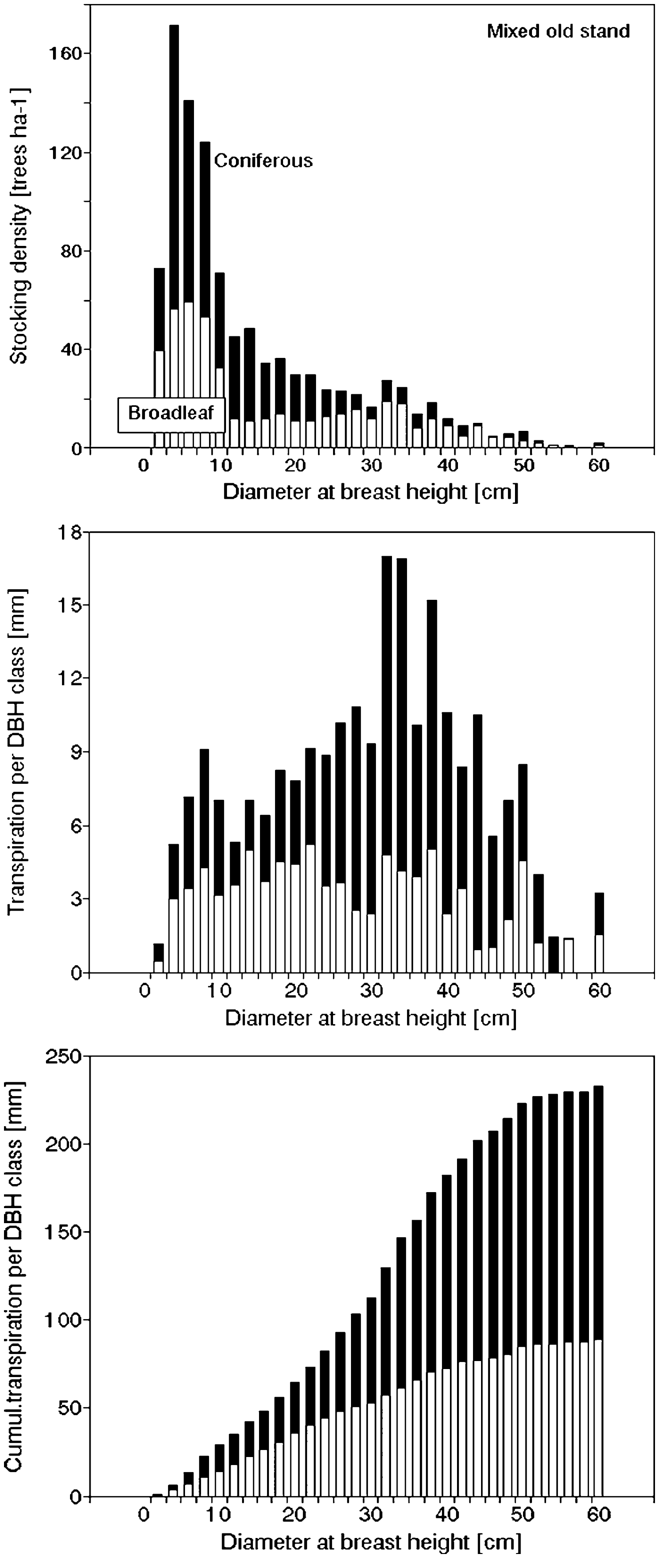

Fig. 8 Scheme of the results of the entire scaling up procedure applied for two tree species occurring in the same stand. **a** Input biometric data from forest inventory-stocking density, **b** resulting transpiration (daily totals of flow) calculated for all DBH classes in the given stand from the scaling curve, see Fig. 7 and stocking density and **c** cumulated transpiration of DBH classes (i.e. total transpiration of the entire stand) using seasonal totals

Conclusions

There are many different commonly used methods, which have to be applied with respect to the matter of analysis. We gained experience in long term studies of many tree and shrub species with THB and HFD methods not requiring calibration (which is usually difficult to achieve in a routine field work).

Methods applied for evaluating of measured flow data include integration of flow within trees and its scaling up from individual trees to the entire stands (when required). Integration of flow within trees should be done with respect to variation of flow across sapwood (i.e. simultaneously along stem radius and along stem circumference). This variation might be the source of largest errors when values representing whole trees are required and therefore estimates of whole tree sap flow should be based on measurement always using sufficiently large sets of sensors.

Scaling up from a series of individual trees to stands should be done with respect to existing natural variation between trees under given environmental conditions. Application of biometric parameters available at the individual tree and stand levels is suitable for this purpose. Remote sensing data represent another alternative for the future, more applicable to higher levels of biological organization.

Future developments will certainly bring even better methods, but natural flow variation should always be taken into account. There will still be reasons for using different measuring and evaluation techniques to match special demands.

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