Transpiration of trees and forest stands: short and long-term monitoring using sapflow methods

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Abstract

We show that sapflow is a useful tool for studies of water fluxes in forest ecosystems, because (i) it gives access to the spatial variability within a forest stand, (ii) it can be used even on steep slopes, and (iii) when combined with eddy correlation measurements over forests, it allows separation of individual tree transpiration from the total water loss of the stand. Moreover, sapflow techniques are quite easy to implement.

Four sapflow techniques currently coexist, all based on heat diffusion in the xylem. We found a good agreement between three of these techniques. Most results presented here were obtained using the radial flow meter (Granier 1985).

Tree sapflow is computed as sap flux density times sapwood area. To scale up from trees to a stand, measurements have to be made on a representative sample of trees. Thus, a number of trees in each circumference class is selected according to the fraction of sapwood they represent in the total sapwood area of the stand. The variability of sap flux density among trees is usually low (C.V. 10–15%) in close stands of temperate coniferous or deciduous forests, but is much higher (35–50%) in a tropical rain forest. It also increases after thinning or during a dry spell.

A set of 5–10 sapflow sensors usually provides an accurate estimate of stand transpiration. Transpiration measured on two dense spruce stands in the Vosges mountains (France) and one Scot's pine plantation in the Rhine valley (Germany) showed that maximum rate was related to stand LAI and to local climate. Preliminary results comparing the sapflow of a stand of *Pinus banksiana* to the transpiration of large branches, as part of the BOREAS programme in Saskachewan, Canada showed a similar trend.

For modelling purposes, tree canopy conductance (g_c) was calculated from Penman-Monteith equation. In most experiments, calculated canopy conductance was dependent on global radiation (positive effect) and on vapour pressure deficit (negative effect) in the absence of other limiting factors. A comparison of the vapour pressure deficit response curves of g_c for several tree species and sites showed only small differences among spruce, oak and pine forests when including understorey. Tropical rainforests exhibited a similar behaviour.

Keywords: canopy conductance, sapflow, transpiration, variability

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Introduction

This paper reports on the potential use of sapflow measurements for long-term studies (over months or years) of water fluxes in trees and forest ecosystems. Sapflow techniques are useful tools when combined with other methods, like eddy-correlation or energy balance over forest stands. It allows for the separation of the contribution by trees to the total water fluxes.

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Furthermore, sapflow measurement can be an alternative method for measuring tree transpiration, and in some cases it is the only method, e.g. on forest stands located on steep slopes, or on plots of very small size. Water content can change within trees during the day, or over longer periods when water stress occurs (see Jarvis 1975; Waring & Running 1978), causing a shift in the relationship between transpiration and sapflow. Nevertheless, sapflow is a good approximation of tree

transpiration, even if a time lag is often observed between both fluxes.

The following analyses are based on results obtained during several experiments under various climate conditions and on diverse species.

Current methods of measuring sapflow and intercomparison

There are four main methods of sapflow monitoring. Each of them has specific advantages, and all of them are based on heat diffusion in the xylem. Heat pulse velocity (HPV) is the oldest method (Hüber & Schmidt 1937), and is still used either on small plants or big trees. Swanson & Whitfield (1981) developed a theoretical correction for the perturbation due to the presence of the sensor in the wood, thus eliminating the problem of empirical calibration. This technique is particularly useful when analysing sapflow profiles in the trunks, because it uses local point measurements; integration over the conducting sapwood area is carried out using multi-point sensors. Cermak *et al.* (1973) developed an alternative system (TBH: Trunk Heat Balance, also called the Cermak method), which is well adapted to big stems. The main advantage of TBH is that sapflow is calculated from the energy balance of a sector of the hydroactive xylem.

Sakuratani's method (1981) and methods derived from it (Valancogne & Nasr 1993; 'Dynamax' system, Dynamax, Houston, TX. USA) use an external heating jacket. These techniques also give high accuracy and good absolute precision (energy balance) without calibration, but are limited to stems of small diameter (< 15 cm). One of us has developed a radial sapflow meter (Granier 1985, 1987b) for continuous measurements in trees. The system uses two 2-cm long cylindrical probes inserted in the sapwood of the tree. One of these probes is heated at a constant rate, while the other, about 15 cm apart, is not heated and remains at the wood temperature. The temperature difference between the two probes (ΔT), measured with thermocouples, is related to sap flux density (i.e. sapflow per unit of sapwood area F, $dm^3 \ dm^{-2} \ h^{-1}$) circulating in the sapwood. This relationship can be described by:

$$F = 4.28 . \left(\frac{\Delta T_M}{\Delta T} - 1 \right)^{1.23}$$

where ΔT_M is the temperature difference when there is no sapflow (night values).

This system integrates F along a radius in the sapwood of the trunk over the heated probe length (2 cm). For trees with a thicker sapwood, other sensors inserted at increasing depth in the trunk can be used. Total sapflow S is calculated as the product of F and the sapwood area
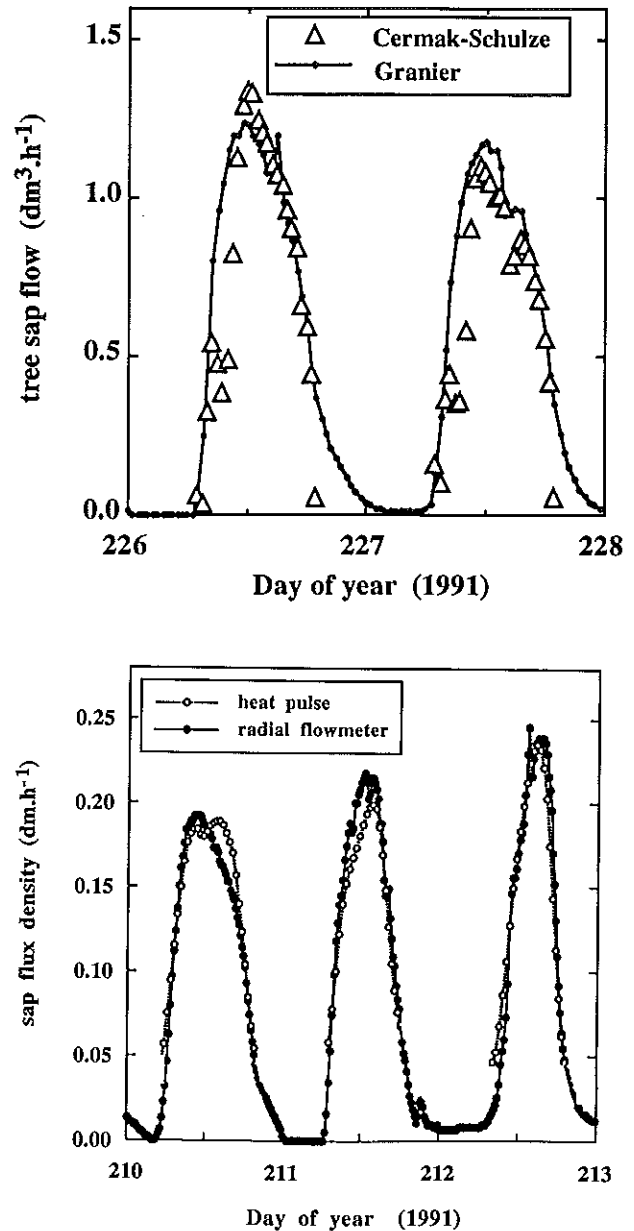

Fig. 1 (a) Comparison of sapflow in an oak tree (*Quercus petraea*) measured by means of the radial sapflow meter (Granier) and the trunk tissue heat balance (Cermak-Schulze), during two successive clear days. (b) Diurnal time courses of sap flux density measured by means of heat pulse velocity (average over 3 depths) and the radial flow meter in the trunk of a sessile oak (*Quercus petraea*) during 3 successive days in summer. Values of heat pulse velocity less than 0.05 dm h^{-1}, which are not reliable by this technique, were eliminated (from Granier *et al.* 1994).

of the tree. Most of the results presented here were obtained using this method.

Few experiments have attempted to compare different sapflow methods on the same trees at the same time.

Problems may arise due to thermal or electromagnetic interactions, because some methods use high voltage (e.g. Cermak et al. 1973), or large heating rates.

In an oak stand near Nancy, France (6°12 E, 48°41 N), we compared three of the above-mentioned methods during summer 1991, for two short-term experiments. Trunk tissue heat balance systems (derived from the Cermak method) were installed by B. Köstner (BITÖK, University of Bayreuth, Germany) on three oak trees, together with radial flowmeters. In the same plot, a comparison was made between radial flowmeters and three-depth HPV devices adapted from the system of Cohen & Fuchs (1989) by M. Sabatti (University of Viterbo, Italy) and working at –5, –10 and –15 mm in the hydroactive xylem of a 13 cm diameter sessile oak (see Granier et al. 1994 for further details).

In the first experiment, a good agreement was found for both daily pattern and absolute values of sapflow (Fig. 1a). Nevertheless, the Cermak technique occasionally displayed a faster decrease of sapflow in the late afternoon. This phenomenon could be due to a lower thermal inertia of the Cermak device; the heating system induces a lower temperature increase (1–2 °C) than that of the radial flowmeters (5–10 °C). A good agreement was also found in the second experiment. For sap flux densities calculated from average heat-pulse velocity (over the three depths) and measured with a radial sapflow meter during daylight hours (Fig. 1b). No consistent time lag between both methods was noticed here.

2 Scaling of sapflow from trees to stands

Scaling-up is often required in ecosystem studies in order to extrapolate local measurements to larger areas (see Jarvis & McNaughton 1986), but discrepancies between distinct space scales are often reported. For instance, whole-tree transpiration extrapolated from data obtained with a porometer is sometimes in good agreement with tree sapflow (Granier & Loustau 1994), but it often exhibits large discrepancies (see Meinzer et al. 1993).

Extrapolation of sapflow can be done at different spatial scales: from sensor to tree, from tree to stand, and even up to a regional scale.

2.1 From sensor to tree

There are several difficulties associated with scaling-up to a tree, these difficulties being largely species-dependent. For example, problems can arise when sapflow measurements are performed on a tree with deep sapwood (e.g. pine), or when a tree shows large azimuthal sapflow variations, as can be observed on

Depth in the sapwood:

—□— 0 to -12 mm
—○— -12 to -24 mm
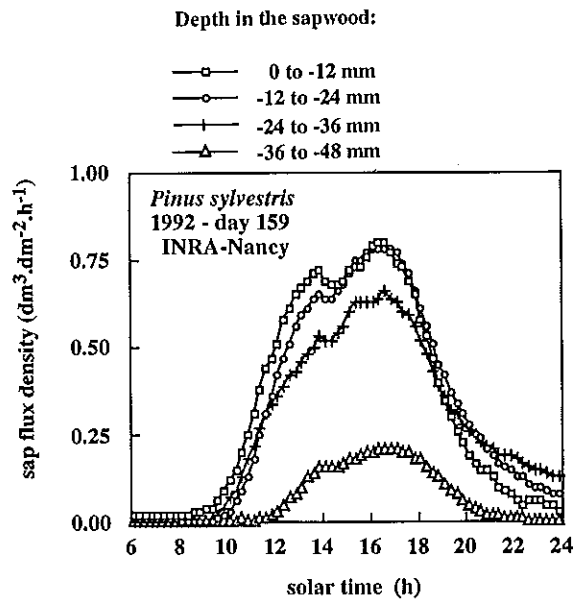—+— -24 to -36 mm
—△— -36 to -48 mm

Fig. 2 Diurnal course of sap flux density measured at 4 increasing depths in the trunk of a 19.8 cm diameter *Pinus sylvestris* in the forest of Amance (Nancy, France). Sapwood thickness was 4.9 cm (Lüttschwager and Granier, unpublished).

trees growing in coppices or in open conditions, such as orchards (Granier, unpublished results).

An experiment was carried out at Nancy over a 1 week-period (in collaboration with D. Lüttschwager, ZALF, Eberswalde, Germany) on a 20 cm-diameter Scot's pine (*Pinus sylvestris*) with 50 mm-thick sapwood. Four 12 mm-long sapflow meters were inserted at increasing depths into the sapwood in order to record the sap flux density profiles. Even when small day-to-day variations were observed in the general pattern, due to climatic conditions, quite constant sapflow rates were recorded from 0 to –36 mm, and a sharp decrease was found when approaching the sapwood–heartwood limit (Fig. 2). In this case, an extrapolation of the total sapflow was carried out, using one probe only, by integrating the observed sap flux density profiles within the trunk. Other species, such as oaks and ring-porous trees in general, exhibit very different patterns of water transfer within the sapwood. We have shown in oaks (*Quercus petraea*) that 80% of the sapflow was circulating in the outer 1 cm of sapwood of the trunk (the sapwood total thickness was 19 mm; Granier et al. 1994). It is, therefore, occasionally necessary to make preliminary experiments on the path of water transfer or on the azimuthal variations of sapflow within a tree stem.

2.2 From tree to stand

When extrapolating sapflow data from a few trees to a stand, the main problem is determining an appropriate
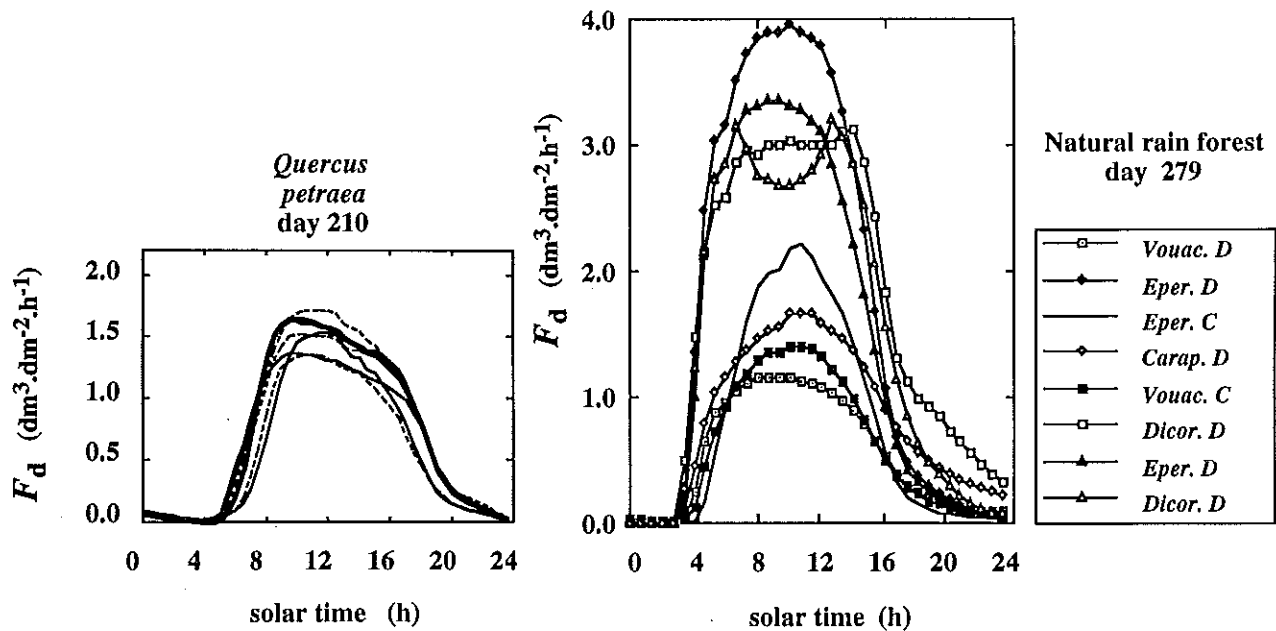
Fig. 3 Left: diurnal courses of sap flux density (F_d) measured on 7 codominant and dominant sessile oaks (*Quercus petraea*) during a bright day in a closed stand (Champenoux forest, France). From Bréda *et al.* (1993).

Right: diurnal courses of sap flux density measured on 8 dominant and codominant trees in the tropical rainforest at Paracou (French Guiana). Eper.: *Eperua falcata*, Vouac.: *Vouacapoua americana*, Dicor.: *Dicorynia guianensis*, Carap.: *Carapa procera*; D: dominant trees; C: codominant trees. From Granier *et al.* (1995).

sampling strategy; specifically, on how many and on which trees to work.

Most experiments show good relationships between sapflow and climatic factors (global radiation, vapour pressure deficit) for individual trees (Morikawa *et al.* 1986). However, these relationships can vary from one tree to another when comparing, for example, trees with different crown status (Bréda *et al.* 1993) or, more generally, from different tree species growing within the same stand (Schulze *et al.* 1985). For technical reasons, only a small number of trees (typically 5–10) is fitted with sapflow meters, and it is therefore important to quantify the among-tree variability so that it can be compared to easily measurable parameters at a stand scale. Figure 3 gives two contrasting examples of among-tree variability in diurnal sap flux densities. All measurements were performed below closed canopies on clear days. For oaks growing in Champenoux forest (Nancy, France), among-tree variability of sap flux density was very low: coefficients of variation ranged between 10% and 12% (Fig. 3). In this experiment (Bréda *et al.* 1993), trees were selected within a 0.25 hectare (50 m × 50 m) plot. By contrast, experiments performed in tropical rainforest (Paracou, French Guiana) showed much larger tree-to-tree variations in the sapflow rates (Fig. 3). Eight trees (of 4 different species) from the dominant and codominant crown classes were examined; coefficients of
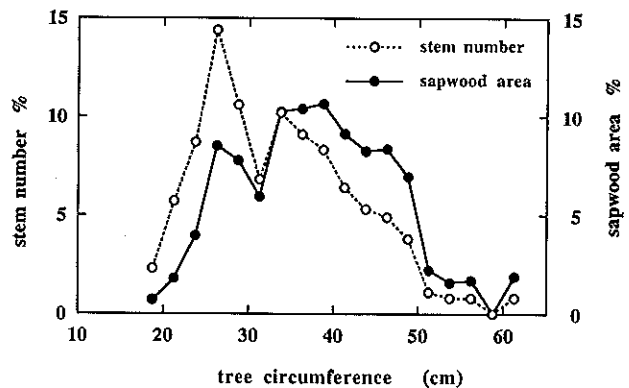

Fig. 4 Example of distribution of circumference classes in a Scot's pine stand, and proportion of stand sapwood area (A_i/A_T) in the classes (Hartheim forest, Germany).

variation ranged between 35% and 50%, depending on the day.

Table 1 shows the among-tree variability of sap flux density observed during various sapflow experiments. In temperate coniferous and broadleaved stands, this variability was generally low. The coefficients of variation ranged between 10 and 15%, and were much higher in the tropical rainforest. It was also shown, for a given species, that tree-to-tree variability increased after thin-

Table 1 Among-tree variability of sap flux densities, where n is the number of sapflow meters within each stand, CV is the coefficient of variation in the measurements (1) under optimal conditions (closed stand, no water stress) (2) (a) in a thinned stand, (b) under water stress.

species	n	CV% (1)	CV% (2)	references
Quercus petraea	8	11	37 (a)	Bréda *et al.* (1993, 1995)
Pinus sylvestris	5	9		Granier *et al.* (1996)
Pinus pinaster	7	15		Loustau, personal communication
Picea abies	8	13	50 (b)	Lu *et al.* (1995)
Tropical rainforest	8	40		Granier *et al.* (1995)

ning, due to the heterogeneity in microclimate produced by thinning (Bréda *et al.* 1995). Water stress also induces a differential response of trees. Dominant trees displayed a stronger decrease in transpiration than codominant or intermediate ones (Lu *et al.* 1995).

Stand sapflow (*T*) is calculated from individual tree measurements and from sapwood distribution in the stand:

$$T = A_T * \Sigma (F_i * p_i),$$

where A_T = plot sapwood area per unit of ground area $(m^2 ha^{-1})$, F_i = mean sap flux density of trees in the class of circumference i, A_i = sapwood area of the trees in the class of circumference i, and $p_i = A_i/A_T$.

Figure 4 shows the distribution of stem circumferences observed in a Scot's pine stand (Hartheim, Germany). Trees belonging to the 35–50 cm circumference classes are highly important because of their contribution to total sapwood area (A_i/A_T = 58%), even if the trees of the 20–35 cm circumference classes are more abundant in the stand. To optimize the sampling, the number of sapflow meters in each class must be proportional to p_i.

A way to check if there is a bias in the estimate of stand transpiration is to compare it with latent flux measured over the forest. In an experiment made in the Hartheim forest (Granier *et al.* 1996), which is a large pure forest located on a flat area (upper Rhine valley, Germany, 47°56′N, 7°37′E, altitude 201 m), sapflow was measured on six Scot's pines, while OPEC, an eddy correlation system (Blanford & Gay 1992) was used to measure water fluxes above the stand. Figure 5 shows a good correspondence between stand sapflow (*T*) and water vapour flux (λE). However, while both methods provided similar maximum rates and diurnal patterns, we observed a 90 min time lag for sapflow behind the vapour flux estimates. This observation has been frequently reported for several coniferous species, such as *Larix decidua* and *Picea abies* when comparing sapflow to transpiration estimated from cuvette measurements (Schulze *et al.* 1985). Furthermore, a time lag was also observed between sapflow measured at the base and the upper part of the trunks for *P. abies* and *Pseudotsuga*

menziesii (Granier 1987a; Granier & Claustres 1989). These lags are the consequence of changes in water storage within the trees. In the Hartheim experiment, after introducing a 90 min time lag between the two sets of data, we obtained a very satisfying correlation: T = 0.75 * λE (r^2 = 0.86).

The difference between vapour flux and sapflow was attributed to understorey transpiration, which was not measured with the sapflow meters. Similar observations were made in *Pinus pinaster* in Les Landes forest (SW France, 44°10′N, 0°46′W) during the HAPEX-MOBILHY programme where 25–30% of total vapour flux came from the understorey compartment (Granier *et al.* 1990). Other estimates of forest transpiration from sapflow measurements were done in the tropical rainforest (Granier *et al.* 1995). The relationship between daily values of forest sapflow and PET (Penman formula) was similar (ratio = 0.75) to that reported by Shuttleworth *et al.* (1984) in central Amazonia.

2.3. Comparison of sites

Projects are increasingly orientated towards large-scale monitoring and modelling of water and carbon dioxide fluxes. Experiments made in the REKLIP (REgio-KLIma-Projekts) programme were aimed at monitoring water fluxes and the energy balance over the Rhine basin in France, Germany and Switzerland. Sapflow was measured simultaneously in 3 locations: two experiments were carried out in young dense spruce stands located in the Vosges mountains, France (1000 m elevation, 48°12′N, 7°15′E), one was on a North-Eastern slope and the other on a Southern slope. The third experiment was in a Scot's pine plantation in the Rhine valley (Hartheim forest, Germany).

Figure 6 shows a 12-day time course of sapflow in the three stands during July 1994. The maximum rate of stand transpiration was about 0.5 mm h^{-1} in both spruce stands, but it was below 0.35 mm h^{-1} in the pine stand. These differences were probably related to leaf area index (LAI) which was about 6.5 for the spruce but only 2.9 for the pine stand. Leaf area index being low in the pine
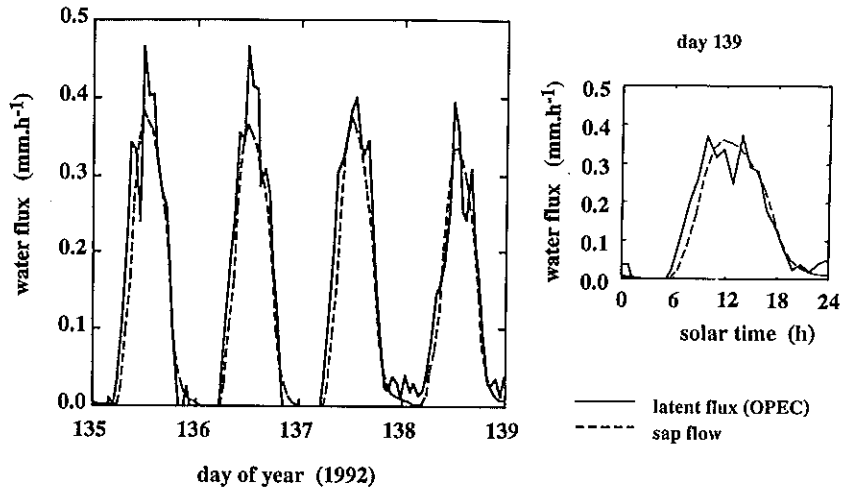
Fig. 5 Comparison of diurnal courses of stand sapflow and vapour fluxes (latent flux OPEC) over the Pinus sylvestris Hartheim forest (Upper Rhine valley, Germany). Sapflow measurements are shifted 1.5 hour. The right part of the figure shows a detail of one day of measurement. From Granier et al. (1996).
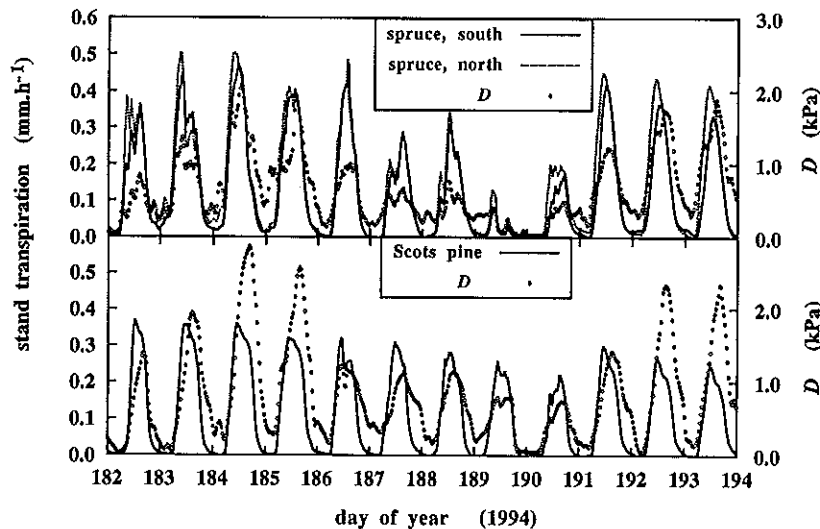

Fig. 6 A 12-day time course of stand sapflow measured in 3 forest stands, compared with vapour pressure deficit (D): in the Aubure watershed (Vosges, France) on spruces, on a north-east and on a south slope, and in the Hartheim forest (Upper Rhine valley, Germany) on Scot's pines.

stand, about 20% of total latent flux was attributed to the understorey vegetation, as estimated from transpiration chambers placed at ground level (Wedler et al. 1996).

Significant night sapflows, reaching up to $0.1 \, mm \, h^{-1}$, could be observed during the period from Days 182 to 185 (1 July to 4 July) in the two spruce stands, while it remained close to zero in the pine forest. This was due to differences in climate between the valley and the mountain. Night-time vapour pressure deficit reached 0.8–1.0 kPa in the mountains but rarely exceeded 0.3 kPa in the valley. Other differences in sapflow rates, due to climate can be seen in Fig. 6. For example on Day 189, the sky was clear in Hartheim but heavily overcast in the Vosges. Differences in diurnal time courses during clear days (Days 191–193) were related to slope orientation: north-east-exposed trees showed an earlier increase in sapflow compared with south-exposed trees. Neverthe-

less the course of sapflow was similar during the rest of the day.

2.4 Comparison with cuvette measurements

While sapflow is measured at the whole-tree level, cuvettes generally enclose a leaf or a branchlet only. Leaf chamber measurements make scaling-up difficult, and require large numbers of replicates. However, large branch chambers may be compared directly to sapflow. We have measured simultaneously the sapflow of five trees and the transpiration of two branches in a Pinus banksiana forest during the BOREAS programme (Prince-Albert OJP, 105°W, 54°N). The branches were enclosed in large transparent bags (volume: $0.25 \, m^3$) supplied with ambient air by a blower giving air changes of 13–14 volumes per minute. Every half-hour, the blowers were

Table 2 Sapflow experiments performed using the radial flowmeter method in different species, site and stand conditions: validation and problems

| Species	Location	Duration of experiment (days)	Stand	Validation	Remarks/ problems	References
Pinus pinaster	SW France	45	open (low LAI)	eddy correlation	abundant understorey	Granier *et al.* (1990)
		241		porometry		Granier & Loustau (1994)
Pseudotsuga menziesii	NE France	119	plantation	water balance		Granier (1987)
Picea abies	NE France-Mt	121	3 sites	water balance		Lu *et al.* (1995)
Abies bornmulleriana	NE France	116	plantation	water balance		Granier & Colin (1989)
Pinus sylvestris	Germany-Plain	12	plantation	eddy correlation		Granier *et al.* (1996)
Pinus banksiana	Central Canada	134	boreal forest	eddy correlation	xylem freezing	Granier, Saugier, Pontailler (unpublished)
Prunus domestica	S France	81	orchard		azimuthal heterogeneity	Granier, Valancogne (unpublished)
Quercus petraea	NE France	764	natural regeneration	water balance		Bréda *et al.* (1993)
Fraxinus excelsior	NE France	330	natural regeneration		narrow sapwood	Granier (unpublished)
Tropical rainforest	French Guiana	85	mixed		biodiversity	Granier *et al.* (1995)
Acacia albida	Burkina fasso	60	orchard		night transpiration	Roupsard (unpublished)
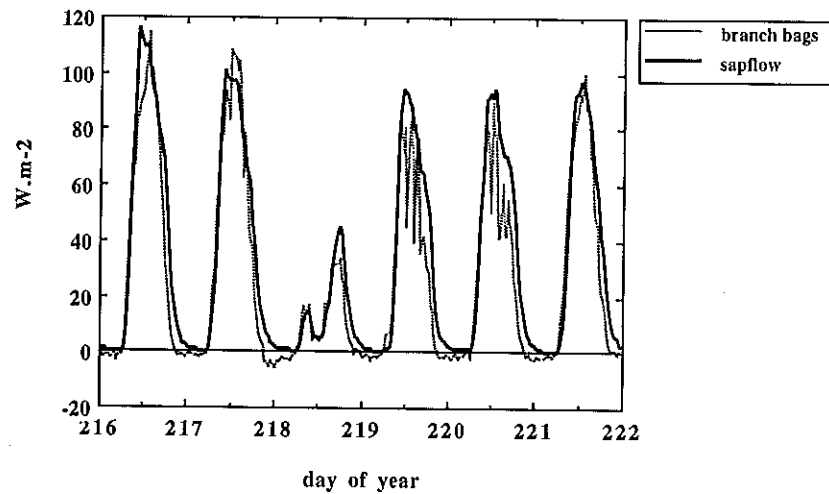
Fig. 7 Time course of transpiration measured with branch bags and of sapflow measurements during the BOREAS experiment. (*Pinus banksiana*, Saskatchewan, Canada). Tick marks on *x*-axis correspond to 00.00 hours local time.

shut off and the bags were closed for five minutes and used as cuvettes for gas exchange measurement (see Dufrêne *et al.* 1993). Simultaneously, two fans were activated inside each bag. Relative humidity and temperature were monitored inside the bags (Vaisala HMD 30 YB probe, Vaisala OY, Helsinki, Finland). Stand LAI was found to be close to 2.3 by another BOREAS group using a Li-Cor 2000 LAI meter (Chen 1996).

Figure 7 shows the parallel variation of sapflow and transpiration for six contrasting summer days. A 1-h time lag was applied between the two sets of data and the

agreement was excellent; the sapflow method exhibiting a little more inertia at sunset.

3 Estimation of tree canopy conductance

Canopy conductance (g_c) is a key parameter for modelling forest responses to climate factors, and can be derived from direct latent flux measurements using the eddy correlation method (Gash *et al.* 1989). In our experiments, tree canopy conductance was derived from the Penman–Monteith equation. This model assumes that the canopy
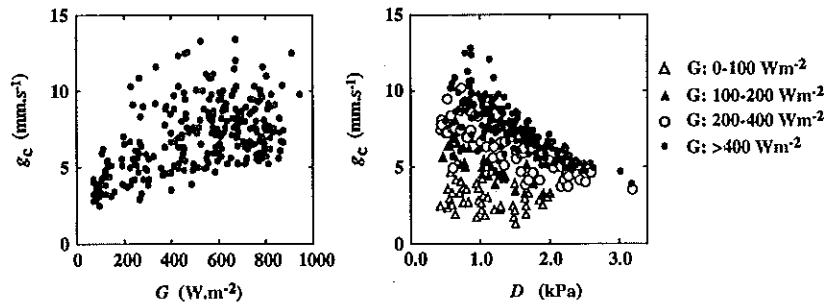
Fig. 8 Effect of global radiation G (left) and of vapour pressure deficit D (right) on forest canopy conductance calculated from sapflow for *Pinus pinaster* (HAPEX-MOBILHY programme, Les Landes forest, France). Four global radiation classes are shown.

can be considered as a single leaf characterized by only one value of conductance to water vapour, and that stand sapflow is equal to tree transpiration. Canopy conductance was calculated from stand sapflow and from climatic variables measured above the forest: net radiation, air temperature, vapour pressure deficit and windspeed (see Köstner et al. 1992). For species showing short-term water exchanges between the transpiration stream and the living tissues, it was assumed that stand sapflow represented the stand transpiration with a time lag behind the driving climatic factors. Therefore, a shift between both sets of data was introduced for calculating g_c. This time lag was about 1 h for oak (Granier & Bréda 1996), and 1.5 h for Scot's pine (Granier et al. 1996), indicating a larger water exchange capacity in coniferous than in deciduous species.

Canopy conductance is often related to climatic variability. Figure 8 shows g_c for a *Pinus pinaster* stand; g_c was dependent on global radiation (positive effect), and on vapour pressure deficit D (negative effect). Other parameters also had a direct influence on g_c water stress (Granier & Loustau 1994) and leaf area index. In the Nancy oak forest, a linear dependence of g_c on LAI was observed (Granier & Bréda 1996).

A comparison of canopy conductance for various forest ecosystems with respect to their response to D is given in Fig. 9. Little difference was observed between spruce and oak stands. Two spruce stands, one located in the Vosges mountain, and the other on a flat site near Nancy, exhibited exactly the same behaviour. When including understorey transpiration, g_c response of maritime pine to vapour pressure deficit, was not significantly different from the previous forest stands (data from Granier & Loustau 1994). Furthermore, the variation of g_c to increasing D for a tropical rainforest was in the same range as for the temperate forest ecosystems, even if it seemed a little more sensitive to D. This similarity between tropical and temperate forests was previously reported by Shuttleworth (1989). A pioneer tropical species (*Simarouba amara*, Fig. 9) growing in an even-aged plantation appeared to be more sensitive to atmospheric drought than the other tree species.
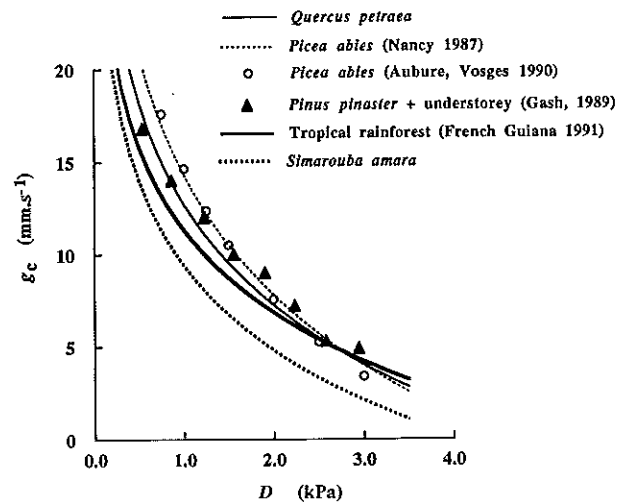

Fig. 9 Canopy conductance of various forest ecosystems, calculated from sapflow measurements, as a function of air vapour pressure deficit D, for a global radiation of 500 W m^{-2}.

The omega factor (Ω), which is calculated from the ratio of aerodynamic to canopy conductance, was proposed by Jarvis & McNaughton (1986). Lower Ω-values indicate a greater dependence of transpiration on D. Values of Ω are generally much higher in grasses (> 0.5) than in forest stands (Meinzer 1993). In most of our sapflow experiments, calculated Ω-values (Jarvis & McNaughton 1986) ranged from 0.1 to 0.3 during the daylight periods: 0–0.15 for *Pinus sylvestris* (Granier et al. 1996), 0–0.38 for the tropical rainforest (Granier et al. 1995), and 0–0.10 for *Quercus petraea* (Granier & Bréda 1996). This indicates a strong coupling between forest canopies and the atmosphere, g_c being, in general, much lower than aerodynamic conductance (10–50 times), except in the case of the tropical rainforest where windspeed is generally low and stomatal conductances are rather high.

Conclusion

Table 2 lists experiments that have used radial sapflow meters, plus the validation methods. The main problems

encountered were either linked with species-specific variation based on species or the extrapolation of results from trees to the stand.

At the tree scale, sapflow measurements give accurate estimates of transpiration. The method is suitable for long-term studies. In some of the experiments listed in Table 2, sapflow meters were operated for several months without any trouble. Nevertheless, if the annual radial growth had produced a wound response, it was necessary to replace the sensors on the same trees at a different location in the stem. Monitoring under natural conditions is relatively easy to implement and at moderate cost. When employed on a number of trees, sapflow measurements can be used to analyse the among-tree variability. This is not possible with vapour-flux methods that operate over the canopy.

At the stand scale, one of the major difficulties is associated with the extrapolation of measurements from trees to the whole stand. Despite apparent stand homogeneity, large local differences in stand density and in sapwood area are often found (Granier *et al.* 1996). Sapflow measurements provide a way to separate tree transpiration from total stand transpiration (Granier *et al.* 1990).

Sapflow measurements also offer a way to estimate canopy conductance, and to establish environmental controls of canopy conductance. The low values of Ω calculated in most of our experiments indicates a strong coupling between forest canopies and overhead atmosphere. This means that variation in forest transpiration is mainly due to changes in vapour pressure deficit and canopy conductance during the day. For modelling purposes, the relationships between canopy conductance and climatic factors may be re-introduced into the Penman–Monteith equation as a sub-model of evaporation from dry canopies.

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