[1] INRA Ecophysiologie forestière, Champenoux, Seichamps, France
[2] CEREG Université Pasteur, 3 rue de l'Argonne, Strasbourg Cedex, France
[3] BITÖK Universität Bayreuth, Bayreuth, Federal Republic of Germany
[4] School of Renewable Natural Resources, University of Arizona, Tucson, Arizona, U.S.A.

Comparisons of Xylem Sap Flow and Water Vapour Flux at the Stand Level and Derivation of Canopy Conductance for Scots Pine

A. Granier[1], P. Biron[2], B. Köstner[3], L. W. Gay[4], and G. Najjar[2]

With 6 Figures

Summary

Simultaneous measurements of xylem sap flow and water vapour flux over a Scots pine (*Pinus sylvestris*) forest (Hartheim, Germany), were carried out during the Hartheim Experiment (HartX), an intensive observation campaign of the international programme REKLIP. Sap flow was measured every 30 min using both radial constant heating (Granier, 1985) and two types of Cermak sap flowmeters installed on 24 trees selected to cover a wide range of the diameter classes of the stand (min 8 cm; max 17.5 cm). Available energy was high during the observation period (5.5 to 6.9 mm.day^{-1}), and daily cumulated sap flow on a ground area basis varied between 2.0 and 2.7 mm day^{-1} depending on climate conditions. Maximum hourly values of sap flow reached 0.33 mm h^{-1}, i.e., 230 W m^{-2}.

Comparisons of sap flow with water vapour flux as measured with two OPEC (One Propeller Eddy Correlation, University of Arizona) systems showed a time lag between the two methods, sap flow lagging about 90 min behind vapour flux. After taking into account this time lag in the sap flow data set, a good agreement was found between both methods: sap flow $= 0.745*$ vapour flux, $r^2 = 0.86$. The difference between the two estimates was due to understory transpiration.

Canopy conductance (g_c) was calculated from sap flow measurements using the reverse form of Penman-Monteith equation and climatic data measured 4 m above the canopy. Variations of g_c were well correlated $(r^2 = 0.85)$ with global radiation (R) and vapour pressure deficit (vpd). The quantitative expression for $g_c = f(R, vpd)$ was very similar to that previously found with maritime pine (*Pinus pinaster*) in the forest of Les Landes, South Western France.

1. Introduction

Water fluxes in forest ecosystems can be determined by means of several different approaches: water balance, vapour flux, or sap flow. One of the greatest difficulties encountered in unifying these approaches is linked to the differing spatial and time scales most appropriate to each methodology. Water vapour flux measurements over forests (via eddy correlation or Bowen ratio) typically provide average estimates for large areas (ha); the main weakness of these techniques is the inability to determine the exact origin of measured fluxes, since this changes depending on wind direction and wind speed. Sap flow techniques provide information at the individual tree scale (m^2). Thus, estimates of stand sap flow are directly dependent on local conditions which may vary over a short distance. Sampling design becomes of major importance when scaling-up from individual trees to the stand.

The work described here is part of a larger interdisciplinary research programme focusing on climate-vegetation interactions and simultaneously examining soil water, water flux from the forest understory vegetation, tree transpiration, and meteorological estimates of evapotranspiration. The first objective of the present study was

to conduct simultaneous measurements of xylem sap flow and of above-crown total water vapour flux. Such comparisons have been carried out previously by Granier et al. (1990) and Kelliher et al. (1992), and have allowed definition of the tree transpiration component of the total water flux. The second goal of the study was to determine relationships useful for modelling forest transpiration. Toward this end, measurements of sap flow were used to calculate forest canopy conductance (Köstner et al., 1992; Granier and Loustau, 1994), a key parameter that determines transpiration rate, since the aerodynamic conductance is in most cases not limiting for tree stands. The pine forest at Hartheim was chosen as an experimental site for the REKLIP international programme and for the comparison of methods, due to its exceptional homogeneity in structure and flat topography.

2. Material and Methods

This study was carried out in a Scots pine (*Pinus sylvestris* L.) plantation located in the Hartheim forest, Germany (47.56° N, 7.37° E, altitude 201 m). Trees were on average 12 m tall and 33 years old. Leaf area index (LAI) of the pines was estimated as approximately 2.9 (Joss and Graber, 1996, this issue). The understory consisted of a mosaic of patches with grass and sedge species (*Brachypodium pinnatum, Carex alba*, and *C. flacca*) as well as open patches with moss or bare soil. The total understory LAI was estimated to be approximately 1.5 (Wedler et al., this volume).

Sap flow was measured on 24 trees using 3 different methods: a) radial 2.1 cm long xylem sap flowmeters on 5 trees (Granier, 1985, 1987; method "G"), b) stem-tissue heat balance method on 12 trees (Cermak et al., 1973; method "C"), and c) a "modified" Cermak method, applying a constant temperature difference on 7 trees (Köstner et al.,

1992; method "CS"). Trees chosen for measurement of sap flow were located near the two meteorological towers and included a wide range of diameters between 8 cm (dbh) and 17.5 cm. Each applied method permitted us to calculate xylem sap flux density, i.e., sap flow per unit of sapwood area (litre $dm^{-2} h^{-1}$), which is proportional to vapour flux density on a leaf area basis, since for any given species growing in a closed stand, there is a linear relationship between leaf area and sapwood area (Grier and Waring, 1974).

Trees sap flow rate ($1 h^{-1}$) is calculated as the product of sap flux density and the sapwood cross-sectional area (*Sa*) of the tree at the sensor height. Scots pines, as other pines, have sapwood active in transport that is typically 3 to 5 cm thick, a much thicker layer than found in other conifers such as spruce or Douglas fir. Radial sap flow-meters (*G*) were only 2.1 cm long. Therefore, they did not obtain an average measure for flow within the entire sapwood, but only in the outer, most active past. From a previous experiment in which radial profiles of sap flux density were measured on Scots pine, we obtained a correction factor that permitted us to adjust downward the average measured sap flux density such that it was appropriate for the entire sapwood (further details are given in Köstner et al., 1996, this issue). The correction coefficient applied was 0.86.

To estimate *Sa* of the trees studied, a relationship was established between breast height circumference (C_{130}) and sapwood thickness measured on cores:

$$Sa(cm^2) = -67.65 + 3.97 {*} C_{130}(cm)$$

$$(n = 18, r^2 = 0.97) \tag{1}$$

Stand sap flow *SF* ($mm\, h^{-1}$) was extrapolated from individual measurements as:

$$SF = SA {*} Ju \tag{2}$$

Table 1. *Forest Inventories made in Different Plots*

Plot	1	2	3	4	5	all plots
Plot area (m2)	675	540	473	625	625	2938
Trees/plot	194	213	216	281	234	1138
Trees/ha	2874	3944	4566	4496	3744	3873
Circumference/ha (m)	1002	1274	1626	1482	1308	1320
Basal area/ha (m2)	30.00	34.97	43.91	42.1	38.9	38
Sapwood area/h (m2)	20.53	24.43	30.52	28.4	26.6	26

in which SA is the stand sapwood area per unit of ground area $(m^2 ha^{-1})$, and Ju is the average corrected sap flow density.

From an inventory made in the study plots (area sampled $= 2938 m^2$, see Table 1), SA was determined to be $26.1 m^2 ha^{-1}$.

During the observation period (from midday day of year (DOY) 133 through midday DOY 143, 1992), sensible heat flux was simultaneously measured over the pine forest with two OPEC (One Propeller Eddy Correlation) systems positioned at 17 m height. An OPEC system consists of a fine-wire thermocouple for sensing short term variations in air temperature, a propeller anemometer for sensing variations in vertical wind velocity, a net radiometer, and soil heat flux discs. The sensors were sampled at 2 Hz, and the sensible heat flux was computed every 30 minutes from the correlation between variations in temperature and vertical wind velocity. The measurements principles and frequency corrections for the OPEC system are described by Blanford and Gay (1992). The water vapour flux was calculated as a residual in the surface energy balance for each 30-minute period.

As proposed by Stewart (1988), we used the Penman-Monteith equation to calculate stand canopy conductance (g_c). This calculation was made half-hourly using climate data measured at 16 m height and the measurements of stand sapflow. Aerodynamic conductance was calculated from windspeed using the Monteith equation (1973). We also estimated g_c from the simplified equation of McNaughton and Black (1973), which is applicable when canopy conductance is much smaller then aerodynamic conductance.

3. Results

3.1 Comparison Between Sapflow and Water Vapour flux above the Forest

The sap flow measurements (ground area basis) were compared to latent heat flux measured by means of the OPEC systems Gay et al., 1995, this issue). Maximum rates of sapflow were approximately $0.33 mm h^{-1}$, i.e., $230 W m^{-2}$. A good general agreement between the integrated and up-scaling measures was found as shown in Fig. 1. However, while both methods provide maximum rates that are similar in magnitude and diurnal pattern, we observe a consistent time lag for sap flow behind the above-canopy vapour flux estimates. This phenomenon is apparently the consequence of non steady-state conditions and of time dependent redistribution of water within the trees. The apparent time lag was greater in the morning than during the late afternoon. This may partly be the result of dew evaporation in the early morning that is measured with the OPEC, while transpiration remained low.

Another observed difference is the occurrence of short term peaks in above-canopy vapour
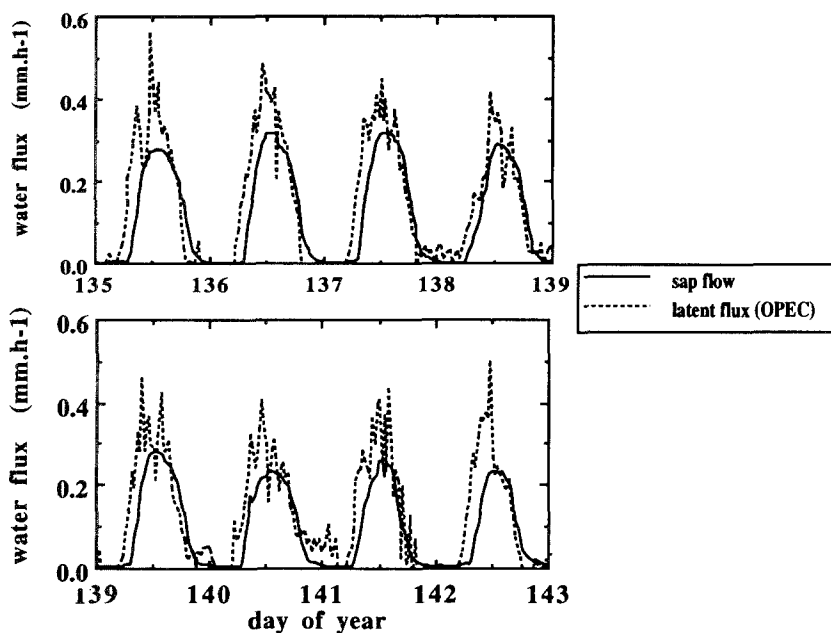

Fig. 1. Time courses of latent heat flux measured over the Hartheim forest with the OPEC systems and of stand xylem sap flow, computed as the mean value of the 3 methods (average of 24 trees, see text), during 8 consecutive days
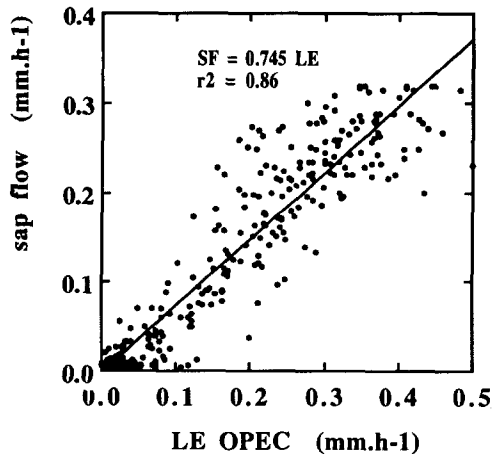
Fig. 2. Comparison of estimates of stand sap flow with latent heat flux measured with the OPEC systems. Data are 30 min averages. Sap flow estimates are shifted by 90 minutes to earlier time in the comparison

We plotted hourly daylight values of sap flow against vapour flux estimates (Fig. 2), introducing 1.5 hour time lag between both sets of data. Negative latent heat fluxes observed during the night were eliminated. A good correlation was observed between sapflow and vapour flux:

$$SF = 0.745 * \lambda E \quad r^2 = 0.86 \tag{3}$$

The difference between vapour flux and sapflow can be attributed to the understory transpiration, which was not measured with sap flowmeters. Wedler et al. (this volume) have estimated understory evapotranspiration equal to approximately 20% of stand transpiration.

Available energy was high during the observation period (5.5 to 6.9 mm day^{-1}), and daily cumulated sap flow on a ground area basis varied between 2.0 and 2.7 mm day^{-1} depending on climate conditions. Water fluxes evaluated by different approaches during the entire observation period are compared in Fig. 3, in which estimates of understory transpiration (Wedler et al., this volume) have been added to tree transpiration. The low day-to-day variation in water fluxes is explained in part by slight changes in weather conditions. Except on DOY 140, sap flow plus understory evapotranspiration and latent fluxes were in good agreement. Estimates ranged between 1.9 and 3.4 mm day^{-1}.

Daily evapotranspiration was evaluated by Tajchman et al. (1979) using the Bowen ratio method, 21 years before the present studies when the trees were only 3.2. m tall. ET varied between 0.61 and 3.9 mm day^{-1}. Sap flow estimated with

flux (OPEC), while monitored sap flow provided smooth response curves. The smooth response in sap flow is probably due to 1) the thermal inertia of the sensors, and 2) the hydraulic inertia of the trees, so that rapid changes in transpiration may not be transmitted to the base of the trunk. The OPEC estimates of the vapour flux were large and from the canopy to the atmosphere during daylight hours, and small and generally down into the canopy at night. A night time vapour flux into the canopy is often observed in association with dew formation, and the magnitude, though small, may be slightly overestimated by the OPEC system as a consequence of stable air conditions in the near-canopy layers.
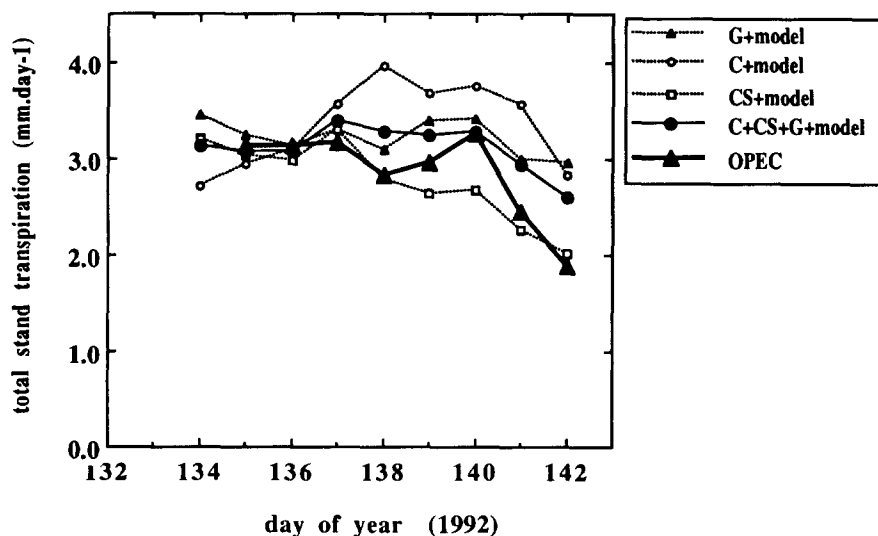

Fig. 3. Comparison of daily water fluxes estimated by different methods during the Hartheim experiment. Three sap flow methods are compared here: the heat balance of Cermak (C), the modified Cermak method (CS), and radial sap flowmeters (G). Estimated understory evapotranspiration is added to tree transpiration in order to compare flux rates with OPEC latent flux measurements over the forest

the C and CS systems exhibited a continuous decrease after DOY 135, while G estimates decreased only slightly and somewhat later. This observation could be related to water stress development in the trees equipped with C and CS systems, which were standing on a lower part of the plot that was characterized by shallower soil.

3.2 Canopy Conductance

For calculating canopy conductance, it was assumed that sapflow expressed on a ground area basis represented the stand transpiration with a 1.5 hour time lag behind the driving climatic factors. Figure 4 shows an example of diurnal variations of calculated canopy conductance on DOY 138. Highest values were observed before mid-day (11:00), increasing to $0.9 \, \mathrm{cm \, s^{-1}}$. Later, g_c decreased continuously, indicating a progressive stomatal closure during the afternoon. Diurnal variations in g_c were reported by Shuttleworth

(1989) for a variety of tree species, showing similar diurnal trends for both coniferous and broadleaved species. Over the observation period, daily maximum g_c ranged between 0.6 to $1.0 \, \mathrm{cm \, s^{-1}}$. With *Pinus pinaster*, Gash et al. (1989) also found similar diurnal variation in g_c (including the understory component), with maxima of about $1.3 \, \mathrm{cm \, s^{-1}}$ at 10:00 GMT. Estimates of g_c from the McNaughton-Black equation were very close to those obtained with Penman-Monteith formula (Fig. 4).

We have illustrated in Fig. 5 the effect of both global radiation (different classes) and of vapour pressure deficit (vpd) on canopy conductance estimated from the G systems. A strong decrease in canopy conductance occurs with increase in *vpd*; while g_c increases with increasing global radiation as reported by Stewart (1988) for *Pinus sylvestris* or Bréda et al. (1993) with *Quercus petraea*. Qualitatively, the same effects of global radiation and *vpd* are observed for leaf stomatal conductance (Jarvis, 1976).
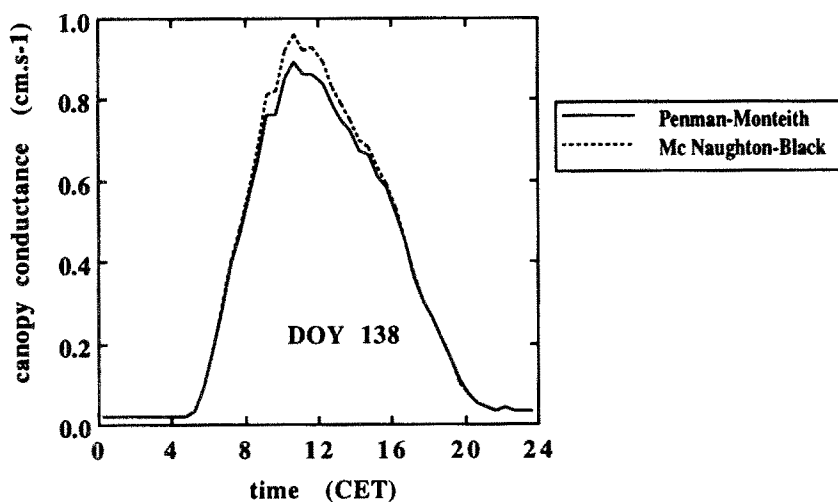

Fig. 4. An example of diurnal course of canopy conductance (g_c) estimated from sapflow measurements with a 90 minute shift to earlier time and climatic data using the reverse forms of Penman-Monteith and McNaughton-Black equations
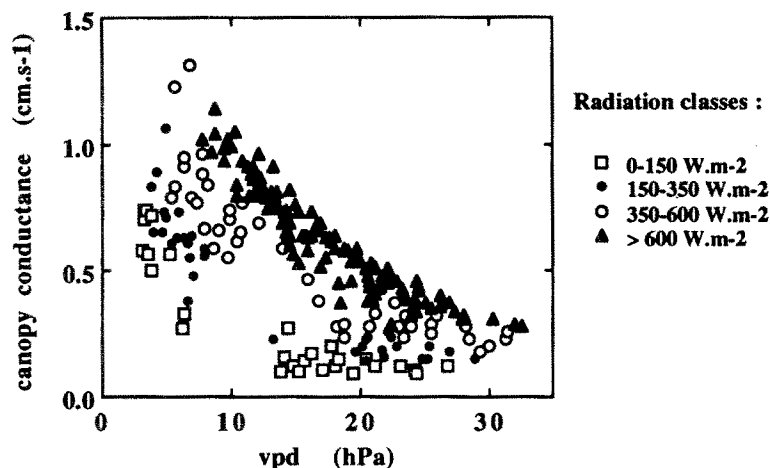

Fig. 5. Relationships between pine canopy conductance estimated from sapflow measurements (Granier method) and vapour pressure deficit, for different global radiation classes. Data are 30 min averages
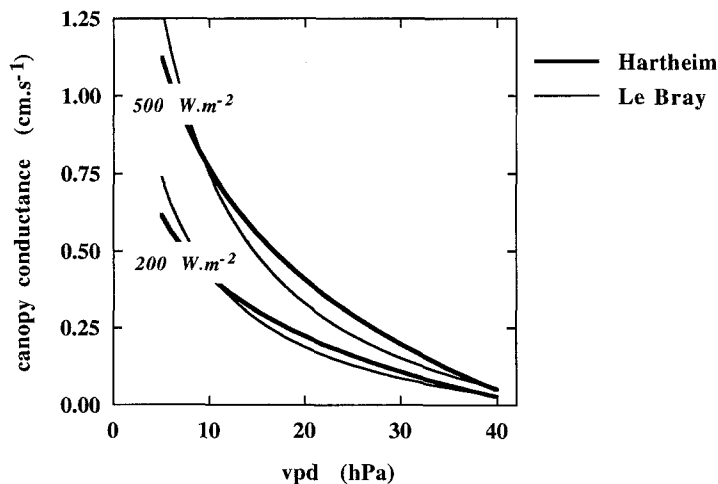
Fig. 6. Comparison between the non-linear regression relationships of canopy conductance vs. vapour pressure deficit (vpd) obtained at Hartheim on *Pinus sylvestris*, and in Les Landes forest on *P. pinaster* (data from Granier and Loustau, 1994). Results for two global radiation classes are presented here: 200 and 500 $W \cdot m^{-2}$

A non linear regression (Gauss-Marquardt algorithm) gave the following equation, calculated for *vpd* conditions below 3 hPa:

$$g_c = \frac{R}{R + 615} *(4.36 - 1.152\ln(\text{vpd})) \quad r^2 = 0.85$$

(4)

(units: g_c in cm s^{-1}, R in W m^{-2}, *vpd* in hPa)

This relationship is shown for two intensities of global radiation (200 and 500W m^{-2}) in Fig. 6 and compared with that obtained for maritime pine (*Pinus pinaster*) by Granier and Loustau (1994). The variations in g_c for both global radiation levels were remarkably close, indicating a similar behaviour of the two species with respect to the effects of climate on transpiration.

4. Discussion and Conclusion

One of the major difficulties encountered in comparing the methods applied at Hartheim is associated with extrapolation of measurements on trees to the stand. Despite apparent stand homogeneity, the inventories carried out in adjacent plots revealed large differences in stand density, in cumulative total circumference, and, hence, in sapwood area (see Table 1). Nevertheless, a very good general agreement was found between sap flow and eddy correlation methods both over the short term (hour) and for daily evapotranspiration. Differences between sap flow and above-canopy water vapour flux rates were observed in the morning and in the afternoon. Water exchanges between reservoirs in the trees is probably responsible for non steady-state water transport

from the roots to the leaves (Jarvis, 1975; Schulze et al., 1985).

This work illustrates the potentials that sap flow measurements offer in estimating forest transpiration, to derive canopy conductance, and to establish environmental as well as endogeneous time dependent controls on conductance. Latent heat flux estimated here was equal to approximately 47% of the available energy. These transpiration rates and latent heat fluxes are very comparable to those obtained with other pine canopies: Whitehead et al. (1983) found 0.3mm h^{-1} transpiration with *Pinus sylvetris*, Stewart (1988), 200W m^{-2} (i.e. 0.29mm h^{-1}); Gash et al. (1989) reported 185W m^{-2} with *P. pinaster* (i.e. 0.27mm h^{-1}), and Granier and Loustau (1994) 0.35mm h^{-1} with the same species. Such low transpiration rates are related more to low LAI in Pine stands (projected LAI about 2.5 to 3 in the above cited stands) than to low stomatal conductances. Bowen ratio measurements of Tajchman et al. (1979) made over the Hartheim forest in a younger stage showed that evapotranspiration utilized about 53% of the available energy under non-limiting soil water conditions, a value close to our estimates. The LAI of this stand has probably not changed during the period between these two experiments.

Short term variations of canopy conductance were highly correlated with global radiation and vapour pressure deficit variations. As seen in Eq. (4), a saturation plateau was not reached in the case of the increase in g_c with increasing global radiation as usually found for stomatal conductance, even at high radiation levels. This is probably due to the vertical distribution of foliage in the

tree crowns and gradual penetration of radiation to the lower canopy levels, leading to a progressive extension of light saturation levels for stomatal conductance of needles from top to bottom in the canopies. A strong negative effect of *vpd* on conductance was observed, indicating a high sensitivity of stomata to humidity as found with other conifers like *Abies* (Guehl et al., 1991).

Following the analytical approach of McNaughton and Jarvis (1983), the dependence of transpiration on canopy conductance and climatic variables may be expressed via the "Omega factor". In the present study, Ω ranged from 0 to 0.15 during the daylight period, indicating a strong coupling between canopy and the atmosphere. In other words, variations of stand transpiration are to a great extent explained by changes in vapour pressure deficit and canopy conductance during the day. Estimates of g_c from either the McNaughton-Black or Penman-Monteith equations were, therefore, very in close agreement.

For modelling purposes, the regression relationship between canopy conductance and climatic factors may be re-introduced into the Penman-Monteith equation as a sub-model of dry canopy evaporation and for predicting the combined effects of radiation and vapour pressure deficit on canopy transpiration. Water stress effects were not reported in this study, but strong drought developed later (June to August). Nevertheless, other measurements using OPEC systems showed a strong limitation of transpiration during this dry period (Gay et al., 1996, this issue and Köstner, unpublished data) as also reported by Granier and Loustau (1994) in a *P. pinaster* stand. These effects must be taken into account in generalizing such transpiration models.

References

Blandford, J. H., Gay, L. W., 1992: Tests of a robust eddy correlation system for sensible heat flux. *Theor. Appl. Climatol.*, **46**, 53–60.

Bréda, N., Cochard, H., Dreyer, E., Granier, A., 1993: Water transfer in a mature oak stand (*Quercus petraea*): seasonal evolution and effects of a severe drought. *Can. J. For. Res.*, **23**, 1136–1143.

Cermak, J., Deml, M., Penka, M., 1973: A new method of sap-flow rate determination in trees. *Biol. Plant.*, **15**, 171–178.

Gash, J. H. C., Shuttleworth, W. J., Lloyd, C. R., André, J.-C., Goutorbe, J.-P., Gelpe, J., 1989: Micrometeorological measurements in Les Landes forest during HAPEX-MOBILHYX. *Agric. Forest. Meteor.*, **46**, 131–147.

Gay, L. W., Vogt, R., Bernhofer, Ch., Blanford, J. H., 1996; Flud agreement above a Scots pine plantation. *Theor. Appl. Climatol.*, **53**, 33–48.

Gay, L. W., Vogt, R., Blanford, J. H., Kessel, A., 1996: The May–October energy budget of a Scots pine plantation at Hartheim, Germany. *Theor. Appl. Climatol.*, **53**, 79–94.

Granier, A., 1985: Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.*, **42**(2), 193–200.

Granier, A., 1987: Evalution of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol.*, **3**, 309–320.

Granier, A., Bobay, V., Gash, J. H. C., Gelpe, J., Saugier, B., Shuttleworth, W. J., 1990: Vapour flux density and transpiration rate comparisons in a stand of Maritime Pine (*Pinus pinaster* Ait.) in Les Landes forest. *Agric. Forest. Meteor.*, **51**, 309–319.

Granier, A., Loustau, D., 1994: Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. *Agric. Forest. Meteor.*, **71**, 61–81.

Grier, C. C., Waring, R. H., 1974: Conifer foliage mass related to sapwood area. *For. Sci.*, **20**, 205–206.

Guehl, J. M., Aussenac, G., Bouachrine, J., Zimmermann, R., Pennes, J. M., Fehri, A., Grieu, P., 1991: Sensitivity of leaf gas exchange to atmospheric and soil drought and water use efficiency in some mediterranean *Abies* species. *Can. J. For. Res.*, **21**, 1507–1515.

Jarvis, P. G., 1975: Water transfer in plants. In: de Vries, D. A., Afgan, N. G. (eds.) *Heat and Mass Transfer in the Plant Environment*. Part 1. Washington D. C.: Scripta Book Co., pp. 369–374.

Jarvis, P. G., 1976: The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. Roy. Soc. London*, **273**, 593–610.

Joss, U., Graber, W. K., 1996: Profiles and simulated exchange of H_2O, O_3, NO_2 between the atmosphere and the Hartheim Scots pine plantation. *Theor. Appl. Climatol.*, **53**, 157–172.

Kelliher, F. M., Köstner, B. M. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., Wier, P. L., Schulze, E.-D., 1992: Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest. *Agric. Forest. Meteor.*, **62**, 53–73.

Köstner, B. M. M., Schulze, E.-D., Kelliher, F. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., Weir, P. L., 1992: Transpiration and canopy conductance in a pristine broad-leaved forest of Nothofagus: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia*, **91**, 350–359.

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

Loustau, D., Granier, A., El Hadj Moussa, F., 1990: Evolution saisonnière du flux de sève dans un peuplement de Pins maritimes de 18 ans. *Ann. Sci. For.*, **47**, 599–618.

McNaughton, K. G., Black, T. A., 1973: A study of evapotranspiration from a Douglas-fir forest using the energy balance approach. *Water Resour. Res.*, **9**, 1579–1590.

McNaughton, K. G., Jarvis, P. G., 1973: Predicting effects of vegetation changes on transpiration and evaporation. In: Koslowski, T. T. (ed.) *Water Deficits and Plant Growth*, vol VII. New York, London: Academic Press, pp. 1–47.

Monteith, J. L., 1973: *Principles of Environmental Physics*. London: E. Arnold.

Schulze, E.-D., Cermak, J., Matyssek, R., Penka, M., Zimmermann, R., Vasicek, F., Gries, W., Kucera, J., 1985: Canopy transpiration and water fluxes in the xylem of the trunk *Larix* and *Picea* trees – A comparison of xylem flow, porometer and cuvette measurements. *Oecologia*, **66**, 475–483.

Shuttleworth, W. J., 1989: Micrometerology of temperate and tropical forest. *Phil. Trans. Roy. Soc. Lond. B*, **324**, 299–334.

Stewart, J. B., 1988: Modelling surface conductance of pine forest. *Agric. Forest. Meteor.*, **43**, 19–35.

Tajchman, S., Hädrich, F., Lee, R., 1979: Energy budget evaluation of the transpiration-pF relationship in a young pine forest. *Water Resour. Res.*, **15**, 159–163.

Wedler, M., Heindl, B., Hahn, S., Köstner, B., Bernhofer, Ch., Tenhunen, J. D., 1996: Model-based estimates of water loss from "patches" of the understory mosaic of the Hartheim Scots pine plantation. *Theor. Appl. Climatol.*, **53**, 135–144.

Whitehead, D., Jarvis, P. G., Waring, R. H., 1983: Stomatal resistance, transpiration, and resistance to water uptake in a Pinus sylvestris spacing experiment. *Can. J. For. Res.*, **14**, 692–700.

Authors' addresses: A. Granier, INRA Ecophysiologie forestière, Champenoux, F-54280 Seichamps, France; P. Biron and G. Najjar, CEREG Université Pasteur, 3 rue de l'Argonne, F-67083 Strasbourg Cedex, France; B. Köstner BITÖK Universität Bayreuth, D-95440 Bayreuth, Federal Republic of Germany; L. W. Gay, School of Renewable Natural Resources, University of Arizona, Tucson, Arizona, U.S.A.