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Water balance, transpiration and canopy conductance in two beech stands

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Abstract

Measurements of sap flow, vapour fluxes, throughfall and soil water content were conducted for 19 months in a young beech stand growing at low elevation, in the Hesse forest. This experiment is part of the Euroflux network, covering 15 representative European forests. Study of the radial variation of sap flow within tree trunks, showed a general pattern of sap flux density in relation to the depth below cambium. Among-tree variation of sap flow was also assessed, in order to determine the contribution of the different crown classes to the total stand transpiration. Stand sap flow and vapour flux, measured with eddy covariance technique, were well correlated, for half hourly as well for daily values, the ratios of the fluxes for both averaging periods being 0.77. A strong canopy coupling to the atmosphere was found, omega factor ranging between 0.05 and 0.20 relative to the windspeed. Canopy conductance variation was related to a range of environmental variables: global radiation, vapour pressure deficit, air temperature and soil water deficit. In addition to the effect of radiation and of vapour pressure deficit often found in various other tree species, here beech exhibited a strong reduction in canopy conductance when air temperature decreased below 17°C. The model of transpiration was calibrated using data measured in the Hesse forest and applied to another beech stand under mountainous conditions in the Vosges mountains (east France). Measured and modelled stand transpiration were in good agreement. ©2000 Published by Elsevier Science B.V. All rights reserved.

Keywords: Sap flow; Transpiration; Soil water content; Canopy conductance; Model; *Fagus sylvatica*

1. Introduction

Analytical studies of forest ecosystem functioning, and modelling of fluxes are of basic importance (see Tenhunen et al., 1998), because they constitute key data sets that are used for parameterisation of larger scale models, from watershed (hydrology) to the global scale (predicting weather and climate change), especially if those experiments cover several years, taking into account inter annual variation due to climate. There is an increasing interest in water and carbon fluxes at the canopy–atmosphere interface, due to the uncertainty linked with the perspective of climate change. Forests cover large areas and therefore have a major contribution to total energy and mass fluxes. On the other hand, management of forests is much less intensive than management of agricultural crops. Therefore, forests will be more directly influenced by the variations of climate. The European Union initiated the large scale programme EUROFLUX ('Long term carbon dioxide and water vapour fluxes of European forests and interactions with the climate system') to study the interactions between forests

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and the atmosphere, constituting a framework of 15 experimental sites located in various climatic zones, in 10 different European countries. The programme EUROFLUX is aiming at quantifying energy, water and carbon dioxide fluxes over forests stands representative of European forests, using eddy covariance (EC) as a common technique. A major objective is to derive parameters describing forest–atmosphere interface properties that can be used in larger scale models.

One of the tree species selected for the EUROFLUX programme, beech (*Fagus sylvatica* L.) covers large areas in Europe, extending from south England, France and north Spain in its western limit to Poland and Romania in the east. Latitudinal extension ranges from south Sweden to north Italy and Greece. In its northern area, beech is mainly found at low elevations, while in the southern part of Europe it is located at higher elevations (Tessier du Cros, 1981); in France, beech covers about 13 000 km^2 and plays an important economic and recreative role.

The present study took place in a young beech stand growing in the east of France, combining techniques working at different spatial and temporal scales. In particular, we combined eddy covariance with sap flow and classical water balance measurements over a 2-year period.

This work is aiming at a quantification of the different water and energy fluxes in the beech ecosystem, focusing on tree transpiration and on total evapotranspiration. The use of sap flow measurements allows the analysis of the variability in tree transpiration within the experimental plot, and to quantify the contribution of the different crown status to the total water flux. In this paper, tree transpiration, estimated from sap flow measurements, is compared to total evapotranspiration. Environmental and physiological control of stand evapotranspiration is then assessed using the variation of canopy conductance which is derived from climatic variables and from transpiration measurements. A big leaf model of beech transpiration, including the effects of radiation, vapour pressure deficit, air temperature and water stress, is parameterised. In a next step, this model is applied to another beech stand, differing in age, structure and site conditions, in order to analyse to what extend transpiration differs between beech forests, and to assess the possibility of a more general use of the model. This work is aiming at: (1) quantifying the different fluxes of water in the beech ecosystem, (2) analysing stand evapotranspiration in relation to climate, soil water content and tree phenology, concentrating especially on within and among-tree variation in sap flow, and on stand transpiration mechanisms, (3) deriving from the water flux measurements tree canopy conductance to water vapour, that can be extrapolated to other sites under different environmental conditions, and (4) validating a model of stand transpiration in a second beech stand differing in age, structure and environmental conditions.

2. Materials and methods

2.1. Sites and stands

The experimental plot was located in the state forest of Hesse, France (48°40′N, 7°05′E, elevation 300 m), which was mainly (90%) composed of beech. Other tree species (about 10% of the ground area) are *Carpinus betulus* L., *Betula pendula* (Roth), *Quercus petraea* (Matt.), and *Larix decidua* (Mill.). Due to canopy closure, understorey vegetation was very sparse and its contribution to the water balance was neglected in this study. Trees were on an average 30 years old when the study started, stand density was 3800 stems ha^{-1}, and basal area 19.6 m^2 ha^{-1}. Average tree height and circumference (at 1.3 m) were 12.7 m and 227 mm, respectively. The experimental plot covered 0.6 ha; it was located in the central part of a 65 ha area homogeneous, naturally established beech forest, ranging from ca. 10 to 16 m average height. Stem distribution in the plot is presented in Fig. 1. It shows an asymmetrical distribution, the smallest stems being much more numerous. Four tree classes were distinguished according to the crown characteristics (Table 1).

Three towers were installed: one (18 m height) was used for eddy covariance and microclimate measure-

Table 1
Circumference and height ranges of the four crown classes in the beech stand

Crown class	Circumference (mm)	Height (m)
Dominant	300–650	14.0–18.2
Codominant	200–299	11.9–14.0
Intermediate	170–199	11.0–11.8
Suppressed	90–169	7.6–11.0

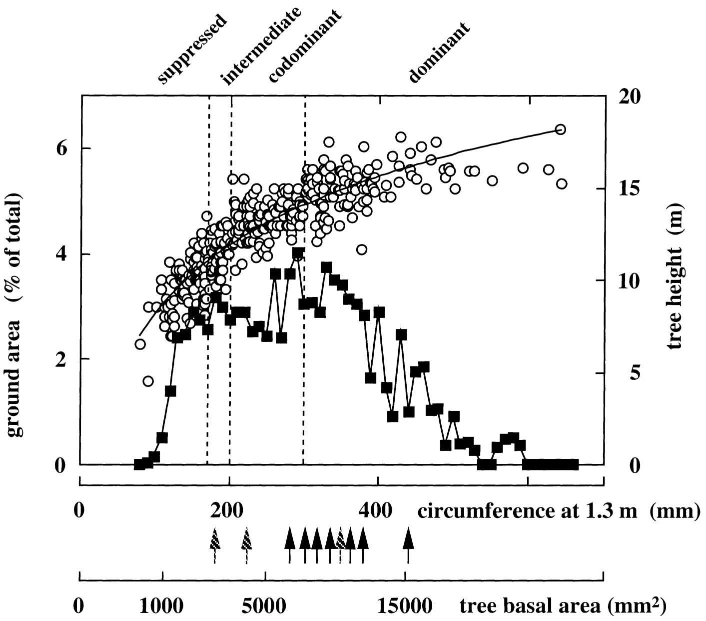

Fig. 1. Frequency of stem circumference at height of 1.3 m (squares) and tree height (open circles) in the Hesse forest. Vertical black arrows indicate circumference and basal area of the trees equipped with sap flow meters in 1996 and 1997. Grey arrows are for trees measured only in 1997.

ments, the two other (15 m) for ecophysiological measurements. A hut containing the data acquisition systems was located near the first tower. 60 sub-plots were delimited for geostatistical studies of soil and of vegetation. Nine of them were used for soil respiration measurements and 12 other for dendrometric measurements (growth, height).

The soil type was intermediate between a luvisol and a stagnic luvisol. Clay content ranged between 25 and 35% within 0–100 cm depth, and was about 40% below 100 cm. Most of the root biomass was located between 0 and 40 cm depth, however minor roots (diameter < 1 mm) were observed down to 150 cm depth in the soil (E. Lucot, personal communication). Annual precipitation was 820 mm, average annual temperature 9.2°C.

Some of the results obtained in the Hesse forest were compared to measurements performed in an older beech stand growing under mountainous conditions, in which sap flow and climate were recorded for 1 year, in 1995. This stand was located in the Aubure forest (Strengbach watershed, in the Vosges mountains, France, 48°12′N, 7°15′E), at 1000 m elevation on a sandy soil characterised by a poor mineral content and a low extractable soil water (ca. 100 mm). Average tree height was 22.5 m, trees were 120 years old, and stand density was 429 stems ha^{-1}. A more detailed description can be found in Biron (1994).

2.2. Leaf area index

Leaf area index (LAI) was estimated by means of two independent methods. Litter was collected during fall using forty-two 0.25 m^2-square litter traps. Dry mass of litter was measured weekly during the leaf-fall period, while a sub-sample of leaves was taken every 2 weeks for measuring the leaf specific area (Delta-T area meter, Cambridge, UK). An optical leaf area meter DEMON (CSIRO, Australia) was also periodically used on bright days when LAI was maximum, in July. Measurements were taken along seven transects approximately 25 m long across the plot. For both years, higher values of LAI were obtained with the leaf area meter than from litter collection, presumably because the DEMON leaf area meter also measures the visible fraction of the woody parts of the trees.

Table 2
Maximum leaf area index (in $m^2\,m^{-2}$) at the two experimental sites, as estimated by litter collection and by DEMON[a]

	Litter collection	DEMON
Hesse		
1996	5.7	6.1 (0.2)
1997	5.6	6.5 (0.5)
Aubure		5.7 (0.6)

[a] Standard deviation is indicated in brackets.

These estimates of LAI are presented on Table 2. The seasonal time course of surface area index (SAI) was assessed from the measurement of global radiation absorbed by the canopies, using the Beer–Lambert law and the LAI (litter). The extinction coefficient was estimated as 0.40. Time course of SAI was calculated on a daily time scale to reduce the effect of light distribution heterogeneity.

2.3. *Throughfall, stemflow and soil water content*

Forty-two standard raingauges were disposed on a grid over the experimental plot during the growing season 1997, allowing measurements of cumulated throughfall every 7 days. Throughfall was also measured automatically with two linear collectors (5.66 m × 0.17 m), each one being connected to a tipping bucket raingauge (ARG 100, Campbell Ltd., UK) and the data was recorded every 30 min. Because rainfall interception was calculated from throughfall as measured with the two automatic devices, we first calibrated them against measurements obtained from the 42 raingauges, for ten 1–7 day periods, each including at least one rain event. Throughfall from the two automatic systems was on average 4% lower than that measured with the 42 raingauges ($r^2 = 0.97$). A correction coefficient of 1.04 was therefore applied on half-hourly data obtained with linear collectors to calculate actual throughfall. Gross rainfall was measured with an automatic raingauge (Campbell, ARG 100, UK) located above the canopy, at 17.5 m height on the central tower. Because this raingauge may be influenced by wind, there could be some bias in the gross rainfall measurements and in rainfall interception estimates.

Spiral channels disposed around the trunks connected to reservoirs allowed stemflow measurement on seven trees of various circumference (ranging between 130 and 560 mm). Stemflow was measured every week, hence cumulating one or several rain events, during 6 months in 1997.

Soil water content was measured weekly using two techniques. During the years 1996 and 1997, volumetric water content (θ_{NP}) was measured with a neutron probe (NEA, Denmark) in eight aluminium access tubes: six tubes were 1.6 m long, and two tubes were of 2.6 m length. Five of these tubes were installed nearby the central part of the plot (Zone 1), while the other three were in the eastern part (Zone 2). This distinction was based on visual observation of soil cores showing a spatial variation in the soil characteristics within the experimental plot: in the central part, where most of the ecophysiological measurements were performed, soil was deeper and contained less clay (27.9%) than in the eastern part (34.3%). In 1997, a TDR device (Trase system, Soil Moisture, USA) was additionally used to measure soil water content (θ_{TDR}) in the superficial soil levels from twelve 0.4 m-long wave guides. A good agreement was found between neutron probe and TDR, when averaging humidity measurements from the neutron probe over the 0–0.4 m depth is

$$\theta_{NP} = 1.10\,\theta_{TDR} \qquad (1)$$

From the distribution profiles of water content over 2.6 m soil depth, we calculated relative extractable water (θ_e) in the soil as the ratio of actual extractable water to maximum extractable water (Black, 1979), the latter term being equal to the difference between maximum and minimum soil water content. Maximum water content was evaluated as the average of wettest profiles measured during winter and early spring. Minimum water content was estimated from water retention curves established at –1.6 MPa between −0.1 and –1.2 m. θ_e varies between 0 (soil dry) and 1 (at field capacity).

2.4. *Sap flow and wood water content*

Thermal dissipation technique (Granier, 1985, 1987) was used to measure sap flow in trees with 20 mm long radial sap flow meters installed at a height of 1.5 m in the stems. This technique allows at the estimation of sap flux density (F_d, $m^3\,m^{-2}\,s^{-1}$), i.e. the sap flow per unit of sapwood area. In 1996, seven trees were measured continuously; in 1997, 10 trees. In 1996, as most of the trees equipped with sap flow meters were of medium or large circumference ($C_{1.3} > 250$ mm), a complementary sample of five trees of which the circumferences ranged from 130 to 240 mm was measured (from 11 July to 23 September 1996) to assess the dependence of F_d on tree size.

Calculation of sap flow per tree and on a stand basis is based upon sapwood area of the trunk. Unfortunately, in beech, the visual distinction between sapwood and heartwood is impossible. Therefore, additional sap flow experiments were conducted during the 2 years. In three trees, radial variation of F_d was assessed using a set of five 10 mm long sensors inserted at increasing depth (0–50 mm) below the cambium, thus measuring sap flux density within 10 mm wide concentric annulus of sapwood. These measurements were carried out during 1–2 month periods during the vegetation period, resulting in a general relationship between relative sap flux density and depth below the bark. This allowed derivation of a function relating total tree sap flow to the standard measurements of sap flux densities in the first 20 mm of sapwood.

Radial variation of wood water content in the trunk was assessed as an additional source of information on the sapwood extent in the trunk. Cores were taken from the trunks of 20 trees (at 1.3 m height) around the experimental plot among various circumferences, varying in from 240 to 360 mm. Cores were cut in 5 mm long subsamples, on which fresh and dry weight were measured in order to calculate wood moisture content, that was expressed in mass of water per unit of volume.

Trees to be equipped with sap flow meters were selected randomly within sapwood classes, and hence within the basal area classes, having the highest contribution to the stand sap flow (see Fig. 1). For instance, the biggest trees ($C_{1.3} > 500$ mm) were not measured, even if they could exhibit high sap flow rates, because they represented only a small proportion of the stand sapwood area.

Sap flow measurements performed throughout the vegetation period in individual trees were scaled to stand level using sapwood area distribution, as described in Granier et al. (1996a). Stand sap flow (E_T) was calculated as:

$$E_T = S_T \Sigma p_i F_{Di} \quad (2)$$

where S_T is the stand sapwood area per unit of ground area ($m^2\,m^{-2}$), p_i is the proportion of sapwood in the class i, and F_{Di} is the average sap flux density in the class i.

2.5. Eddy covariance

Water vapour and carbon dioxide fluxes were measured at 18 m height, i.e. 5 m above the mean tree height, from a tower installed in the middle of the plot. The three axis components of windspeed were measured with a 3-D sonic anemometer (Solent model R2, Gill, UK). Air was drawn from the top of the tower to a hut through a 30 m long 4 mm diameter PTFE tubing. The inlet, equipped with a 0.2 μm filter, was located at the base of the 3-D anemometer. Air flow rate was $10^{-4}\,m^3\,s^{-1}$. Water vapour and carbon dioxide concentration were measured with a LI-6262 IRGA analyser (Li-Cor, USA). Scanning of windspeed and gas concentration was made at a frequency of 10 Hz. Edisol software (Moncrieff et al., 1997) was used to process on-line sensible heat, carbon dioxide and water fluxes, following the recommendations made by Aubinet et al. (1999). This software calculates the 3-D coordinate rotation and the time lag correction due to the tube length. This time lag was on average equal to 3.8 s for CO_2 and 4.3 s for H_2O. The time constant used for the digital filter was 200 s.

Eddy covariance measurements started on 20 May 1996. On 31 December 1996, 160 days of operation were available, i.e. 70% reliable data. Throughout 1997, 318 days of reliable data were obtained (87%).

The results of the carbon fluxes and carbon balance measurements are published elsewhere (Granier et al., 2000). Spectral and co-spectral analysis were performed periodically to check the quality of fluxes measurements; an average 5% loss of flux was observed between 0.1 and 1.0 Hz frequencies. Energy balance closure, calculated for the 2 years using day and night data, was about 88%, when (1) latent heat was corrected for high frequency losses between 0.5 and 10 Hz, and when (2) heat storage in the vegetation was taken into account. In other words, sum of elementary terms (latent, sensible, soil heat flux, heat storage) was equal to 88% of net radiation.

2.6. Climate

The following instruments were installed above the stand at 17.5 m height: a net radiometer (REBS, Seattle, USA), a global radiometer (Cimel, France), a ventilated psychrometer (INRA, France, with Pt 100 temperature sensors), a raingauge (Campbell ARG 100, UK), and a switching anemometer (Vector Instruments, UK).

Within and below the canopy, global radiation was measured at 1, 8, 10 and 12 m height using 0.33 m long linear pyranometers (INRA, France). Tree pyranometers were installed at 1 m height in order to have a better estimate of the radiation reaching the soil surface. Trunk and branch temperatures were measured at 1.5, 6, 8 and 10 m in one tree with copper–constantan thermocouples, soil heat flux with two heat flux transducers (REBS, Seattle, USA) placed at −5 cm in the soil, soil temperature (with copper–constantan thermocouples) at −10 cm (five replicates) and one vertical profile (−5, −10, −20, −40, −80 cm) in a central plot. Data acquisition was made with a Campbell (UK) CR7 datalogger at 10 s time interval, 30 min averages were calculated and stored.

2.7. Canopy conductance

Canopy conductance for water was calculated by inverting the Penman–Monteith equation in the same way as in Gash et al. (1989). In the present work, we estimated: (1) total canopy conductance (g_{cT}) from water vapour flux, and (2) tree canopy conductance (g_{c}) from scaled sap flow measurements on a ground area basis (see Köstner et al., 1992, Granier and Loustau, 1994, Granier and Bréda, 1996, Granier et al., 1996b). Aerodynamic conductance (g_{a}) was estimated from windspeed using the equation:

$$g_{\mathrm{a}} = \frac{k^2 u}{\ln[(z-d)/z_0]} \tag{3}$$

where z_0 is the surface roughness (=0.1 h), h is the mean tree height (=12.7 m), d is the zero plane displacement (=0.75 h), k is the von Kármán constant, u is the windspeed at height z.

For calculating tree canopy conductance g_{c}, night data and periods of rainfall were eliminated, as well as early morning and late afternoon data when radiation, air vapour pressure deficit and sap flow were close to zero, increasing the relative inaccuracy in canopy conductance calculation. We distinguished between dry and wet canopy conditions for computing g_{cT}.

3. Results

3.1. Throughfall, stemflow, rainfall interception and soil water content

The relationships relating throughfall and stemflow to incident rainfall, shown in Fig. 2, were used to compute rainfall interception. No clear relationship between stemflow and stem diameter was detected (data not shown). Stemflow was observed only when rainfall exceeded the threshold of 2 mm, reflecting the condition when branches and trunks were wet enough to allow water to flow down the bark surface. The quite low scattering of data for throughfall is due to the analysis of individual rain events instead of cumulated rain. For rainfall events of 5, 10 and 15 mm, ratio of intercepted water to incident rainfall reached 30.0, 26.6 and 25.3%, respectively. Over the whole growing season in the Hesse forest, this ratio was 25.3 and 26.8% in 1996 and 1997, respectively, and 23.4% in the Aubure forest. On an average, during the vegetation period, throughfall and stemflow represented 26 and 5% of the incident rainfall, respectively.

During summer 1996, drought developed progressively and water stress lasted from the end of July to the end of October. Water stress was defined when θ_{e} dropped below 0.4 (Black, 1979). The year 1997 was exceptionally wet during spring and in the beginning of summer. Water stress developed from the beginning of September, i.e. 35 days later than in 1996. At the end of the vegetation period, for the 2 years, relative extractable water in the soil decreased to about 0.1. Soil water depletion was analysed from the profiles of volumetric water content at different dates (see Fig. 3). As suspected, when the preliminary soil observations were made, strong differences were observed in the dehydration patterns between the two locations, differing in clay content. The higher the clay content, the lower the maximum depth where water

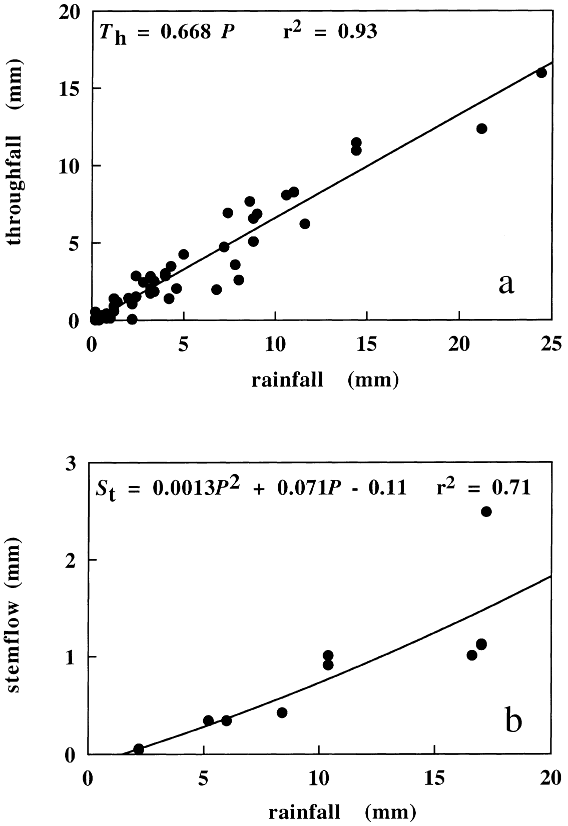

Fig. 2. Top: relationship between stand throughfall, T_h, and gross rainfall, P, each data point corresponding to one rain event ($n = 57$). Data were obtained from two automatic linear collectors previously calibrated against 42 standard raingauges standing on the soil. Bottom: relationship between stand stemflow and gross rainfall, obtained from scaled measurements performed with spiral collectors installed on seven trees of various circumference. Each data point ($n = 12$) is cumulated over 1 week.

extraction occurred was 1.6 m versus 0.8 m, in Zone 1 and Zone 2, respectively. Two phases in dehydration can be observed: first, the decrease in soil water content occurred between soil surface to 1.0 m depth (see curves of 24 May, 18 and 28 June in Fig. 3a), then, as root absorption continued, water was withdrawn in the deeper soil layers, (from 1.0 to 1.6 m in the period from 28 June to 5 September). In Zone 2, water absorption occurred only within the 0–0.8 m soil layer. Maximum extractable water was calculated as the difference between maximum and minimum measured water content. It ranged between 100 and 200 mm and was on average 185 and 130 mm in Zone 1 and Zone 2, respectively. TDR measurements performed in the superficial soil layer (0–0.4 m) confirmed these observations (data not shown).

3.2. Transpiration and sap flow

3.2.1. Radial variation of sap flow in the trunk

Within a given tree, day-to-day radial profiles of sap flux density (F_d) were similar when expressed in percent of the maximum sap flux density (Fig. 4). However, different patterns were observed among the three studied trees: two trees showed maximum rates in the most external measurement layer (0 to −10 mm below cambium), while another tree (tree # P5) showed its maximum rate in the next layer (−10 to −20 mm). For layers deeper than −20 mm, all the trees showed a similar exponential decrease in sap flux density. The proportion of sap flux density circulating in the deeper layers showed a tendency to increase with increasing tree transpiration (data not shown).

Wood water content also varied radially: it was stable between 0 and 30 mm below the cambium (ca. 0.8 g g^{-1}), and decreased subsequently with increasing depth.

The following relationship between F_d (expressed in percent of maximum) and depth (x, in cm) in the trunk was fitted:

$$F_d = 96.14 \times 10^{-0.0121x} \qquad r^2 = 0.86 \tag{4}$$

This function was close to that found by Köstner et al. (1998b) in older beech trees. We used this equation to calculate total sap flow, from F_d as measured in the outside annulus (0 to −20 mm) for all trees, and from tree circumference.

3.2.2. Among tree variation of sap flow

Estimation of stand transpiration requires the analysis of among-tree variation of sap flow (Köstner et al., 1996). During bright days highest F_d rates (above 10^{-4} m s^{-1}) were observed in dominant and codominant trees, while in intermediate and suppressed trees F_d ranged between 0.3×10^{-4} and 0.7×10^{-4} (Fig. 5). The increase in F_d was observed later in the morning and its decrease earlier in the afternoon for the smallest trees than in dominant and codominant trees. This time lag was about 1–1.5 h, depending on the trees. This shorter time course of F_d was probably due

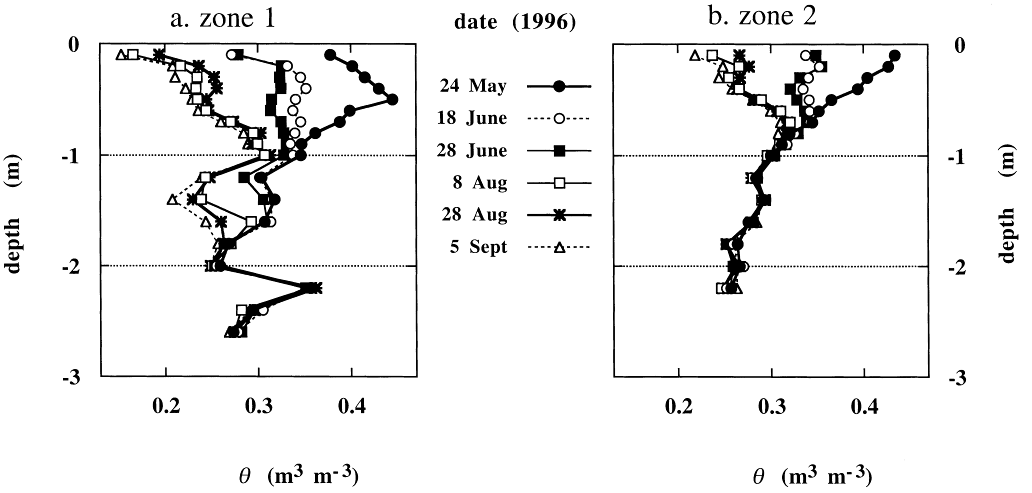

Fig. 3. Vertical profiles of soil water content (θ) on different dates in 1996, at two locations in the experimental plot. Data are averages of five soil water content profiles on the western side (a) and of three soil water content profiles on the eastern side (b) of the experimental plot.

to different crown exposure conditions. Among-tree difference in sap flow varied more than F_d, between 10^{-7} and $6\times10^{-7}\,m^3\,s^{-1}$, because bigger trees had both larger sapwood area and higher F_d.

When all the measured trees (12 in 1996, 10 in 1997) were pooled, a general relationship between F_d and tree basal area was found (Fig. 6). In order to standardise the two data sets for the effects of climate, relative sap flux density in a given tree (averaged over a 10-day period) was calculated as the ratio of actual F_d to the averaged value measured in the largest trees ($C_{1.3} > 330$ mm). Lowest F_d (ca. 20% of the maximum), was observed in smallest trees ($C_{1.3} < 200$ mm). For trees having a circumference

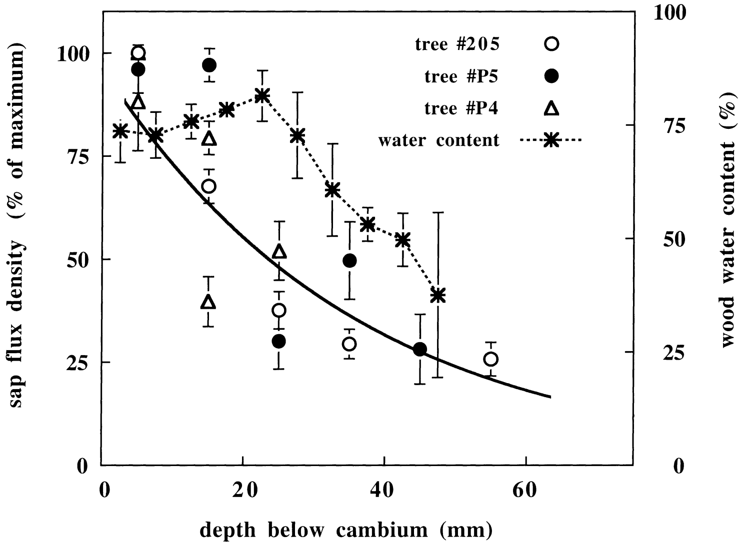

Fig. 4. Radial variation of sap flux density expressed as a percentage of its maximum value, as a function of depth below cambium in three individual *Fagus sylvatica* trees. Data are averaged over 5–10 sunny days. The full line corresponds to the best fit; its Eq. (4) is given in the text. Also shown is the radial variation in water content of fresh wood as measured in 20 cores. Vertical bars indicate standard deviation.

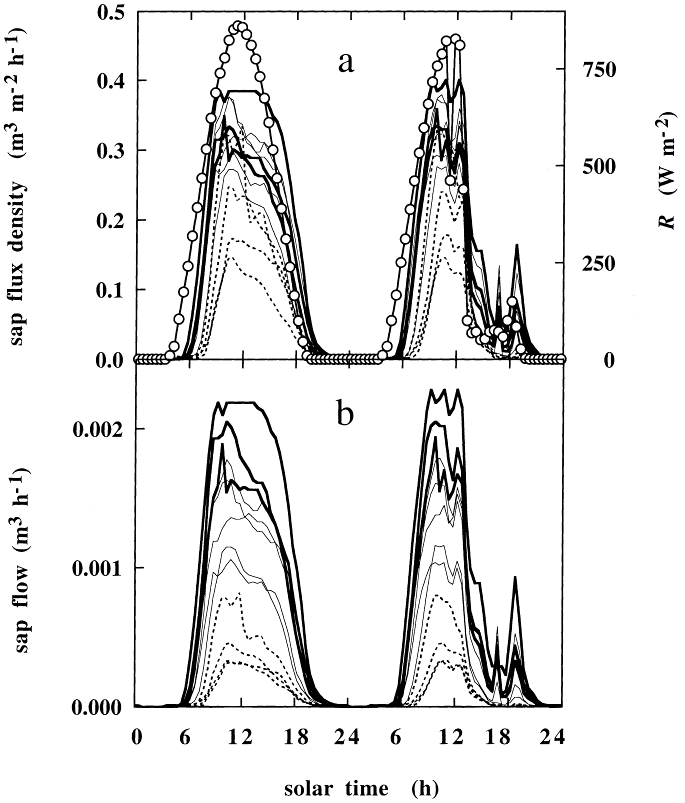

Fig. 5. Sap flux density and global radiation time course (a), and total sap flow per tree (b) in 12 beech trees of various circumferences during two successive days in 1996 (6 and 7 June). Thick solid lines are for dominant, thin solid lines for codominant and dotted lines are intermediate and suppressed trees. Open circles represent global radiation, *R*.

larger than 200 mm (codominant trees), F_d increased linearly with tree circumference.

3.2.3. Stand transpiration and vapour fluxes

Half hourly and daily cumulated stand sap flow (E_T) and vapour fluxes over the stand (E) were compared. The time courses of daily transpiration and total evaporation for the 2 years of measurement are shown in Fig. 7. The increase in SAI, therefore in LAI, and in E_T during spring was fast: it lasted about 25 and 28 days since budbreak for LAI and transpiration, respectively, to reach their maximum values. During summer, a reduction in water fluxes (both E_T and E) was observed, particularly in 1996. This can be linked to the decrease in soil water content (Fig. 7, bottom).

Typical diurnal variation of energy fluxes is shown in Fig. 8. During the daylight hours, the Bowen ratio β was equal to 0.48 under non-limiting soil water and maximum LAI (Fig. 8, top). When soil water decreased (Fig. 8, bottom, September 1997), β increased to 0.79. Soil heat flux and heat storage in the vegetation were much lower than latent and sensible heat fluxes: they did not exceed 5% of the net radiation.

Typical examples of diurnal courses of stand sap flow and of vapour fluxes are shown in Fig. 9a for a bright period and in Fig. 9b for a rainy period. On bright days, during the leafy phase, diurnal patterns of stand sap flow and of vapour fluxes were very close, although sap flow showed smoother short term variations than vapour flux. However, for rainy days, much higher vapour fluxes than sap flow were measured (typically 0.6 mm h^{-1} versus 0.2 mm h^{-1}, respectively). Most of the vapour flux originated in intercepted water evaporation, while sap flow remained very low. Comparison of half hourly fluxes E and E_T is shown in Fig. 10, separately for dry and wet condi-

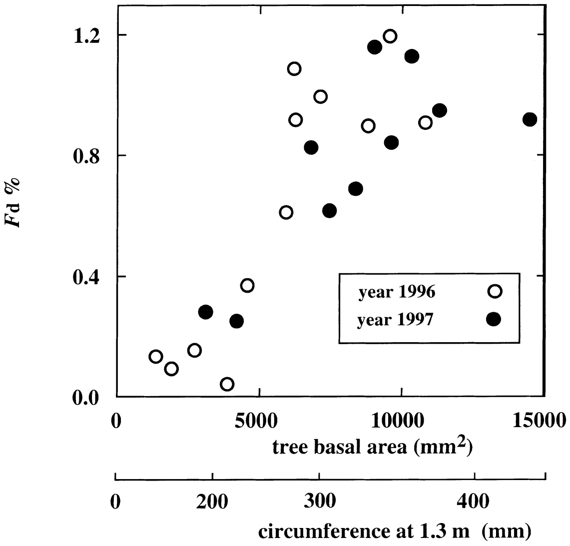

Fig. 6. Sap flux density in beech, F_d, expressed as percentage of maximum value, as a function of tree basal area or tree circumference. Data are standardised as the ratio of actual sap flux density to average sap flux measured in dominant trees (basal area > 7500 mm^2).

tions. During dry conditions, E_T was linearly related to E ($r^2 = 0.85$) with a slope of 0.77. Only a poor relationship ($r^2 = 0.46$) between E and E_T was observed for wet conditions. The quite large scatter of data was due to the rapid variation in E measurements, while E_T variation was more buffered, as shown in Fig. 9. Table 3 gives the cumulated values of rainfall, net interception, transpiration, and of total evapotranspiration for the two vegetation periods. Annual stand transpiration and evapotranspiration were very similar for the 2 years. During 1996, the limited tree transpiration due to water stress was compensated by higher transpiration rates during the first part of the season, due to higher vapour pressure deficit and air temperature than in 1997.

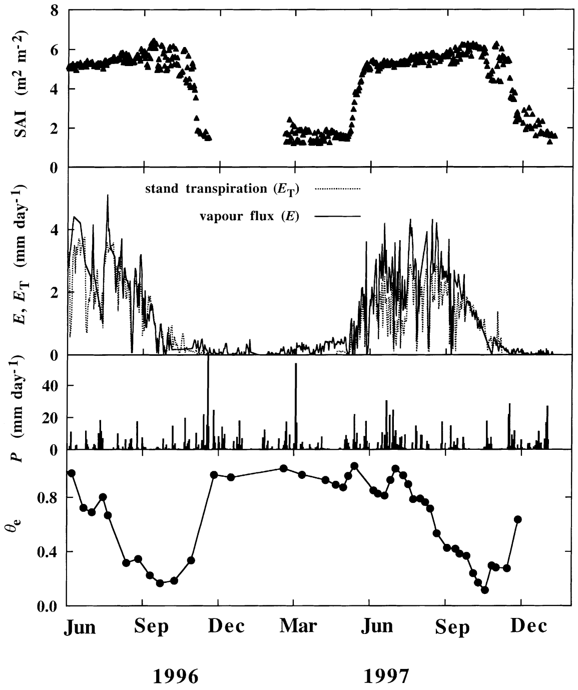

Fig. 7. Variation of 24 h-totals of vapour flux (E) and of stand transpiration (E_T) for the 2 years of experiment (1996–1997) in the Hesse beech forest. Also shown (top) is the variation of leaf + stem area index (SAI), calculated from absorbed global radiation by the canopy (see text). Winter SAI represents trunk and branch area indices. Bottom, the seasonal course of gross rainfall, P, and relative extractable water in the soil (θ_e) obtained from neutron probe and TDR measurements.

3.3. Canopy conductance: modelling and validation

3.3.1. Calibration

Tree and total canopy conductances were derived from climatic data and from either sap flow or eddy covariance measurements, using the Penman–Monteith equation (see Section 2). In this study, we analysed g_c using a multiplicative-type function (Jarvis, 1976;

Table 3
Cumulative values of rainfall (R), net interception (I_n), stemflow (S_t), stand transpiration (E_T) and total evapotranspiration (E)[a]

Year	Site	R (annual)	R (season)	I_n (season)	S_t (season)	E_T (season)	E (season)	E_T/E (season)
1995	Aubure	1255[b]	436	102	–	218	–	–
1996	Hesse	672	458	116	17	256	338	0.76
1997	Hesse	853	466	125	28	253	351	0.72

[a] The season is defined as lasting from budbreak (2 May) to leaf fall (27th October). E_T was computed from scaled sap flow measurements, E was measured over the stand by eddy covariance technique.

[b] Data are expressed in mm.

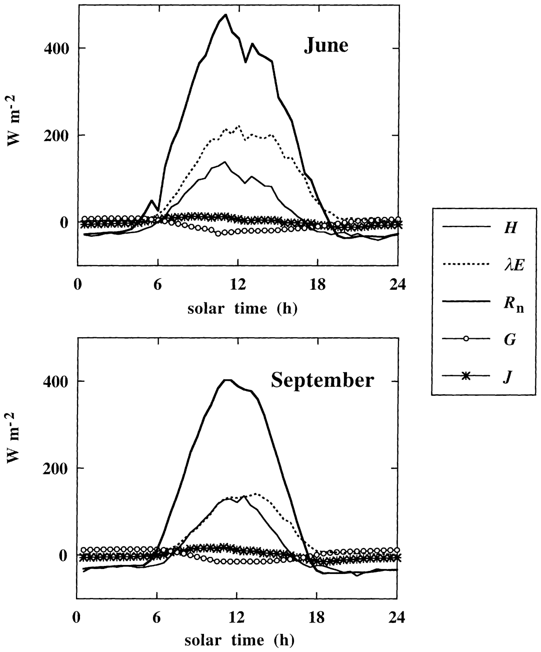

Fig. 8. Monthly average diurnal variation of the energy fluxes in the beech stand: net radiation (R_n), sensible flux (H), latent flux (λE), soil heat flux (G) and heat storage in the vegetation (J). Top: high soil water content (June 1997), bottom: low soil water content (September 1997).

Stewart, 1988), which is defined as follows:

$$g_c = g_{cmax}(R, D) f(T) g(\theta_e) \tag{5}$$

where g_{cmax} (mm s^{-1}) is the canopy conductance, in the absence of limitation due to temperature or to soil water deficit, depending on global radiation (W m^{-2}) and on vapour pressure deficit D (kPa), $f(T)$ and $g(\theta_e)$ are the limiting functions of air temperature and of soil water deficit, respectively.

Maximum tree canopy conductance g_{cmax} was calibrated using measurements performed from 29 May to 18 July 1996 in the Hesse forest. This period corresponds to the time when: (i) LAI had stabilised to its maximum value (as verified from the variation of radiation intercepted by the canopy), and (ii) soil water was not limiting (i.e. relative extractable water was higher than 0.4).

Only data measured on dry foliage conditions when fitting the g_{cmax} function were used, so periods of rainfall and the 2 h following rainfall events were eliminated. Using a two variable non-linear regression (Gauss–Marquart algorithm), equations for g_{cmax} (6) and g_{cT} (9) were fitted. As there could be a time lag between canopy transpiration and sap flow, due to non-conservative water fluxes during the day, the following calculations were performed. We introduced three increasing time lags of 0.5, 1.0 and 1.5 h to these data, the sap flow lagging behind climatic variables. For each set of time-lagged data, we applied the non-linear regression and compared regression coefficients: r^2 was 0.860, 0.768, 0.713 and 0.695 for the increasing time lags from 0 to 1.5 h. As the highest correlation was calculated for zero time lag, we concluded that there was no significant time lag between transpiration and sap flow in beech, at least under high water supply. The absence of time lag was also confirmed by comparing the time courses of E and E_T in Fig. 9.

The relationship relating g_{cmax} to global radiation above the stand (R), and to air vapour pressure deficit (D) are shown in Fig. 11. Then, in order to calculate the effects of the other environmental variables, we plotted the ratio of calculated g_c to modelled g_{cmax} against air temperature (Fig. 12a) and against relative extractable water in the soil (Fig. 12b). We observed a strong limitation of g_c for air temperatures below 15–17°C, and we assumed this decrease to be linear from 17 to 10°C (Eq. (7)). With increasing soil water deficit, g_c/g_{cmax} decreased logarithmically (Fig. 12b, Eq. (8)). We fitted the following functions:

$$g_{cmax} = \left[\frac{R}{R+282}\right]\left[\frac{70.19}{1+3.44D}\right] \qquad r^2 = 0.86 \tag{6}$$

$$f(T) = 1.0 \quad T \geq 17^{\circ}\mathrm{C} \tag{7}$$

$$f(T) = 0.143T - 1.429 \quad 10^{\circ}\mathrm{C} \leq T < 17^{\circ}\mathrm{C}$$

$$f(T) = 0.0 \quad T < 10^{\circ}\mathrm{C}$$

$$g(\theta_e) = 0.723\ \ln(\theta_e) + 1.053 \qquad r^2 = 0.70 \tag{8}$$

where g_{cmax} is expressed in mm s^{-1}, R in W m^{-2}, D in kPa, T in °C.

Slightly lower values of g_{cmax} were found in 1997 than in 1996 (Fig. 12b). This phenomenon could not be explained otherwise than as a consequence of the severe drought occurring in the previous year.

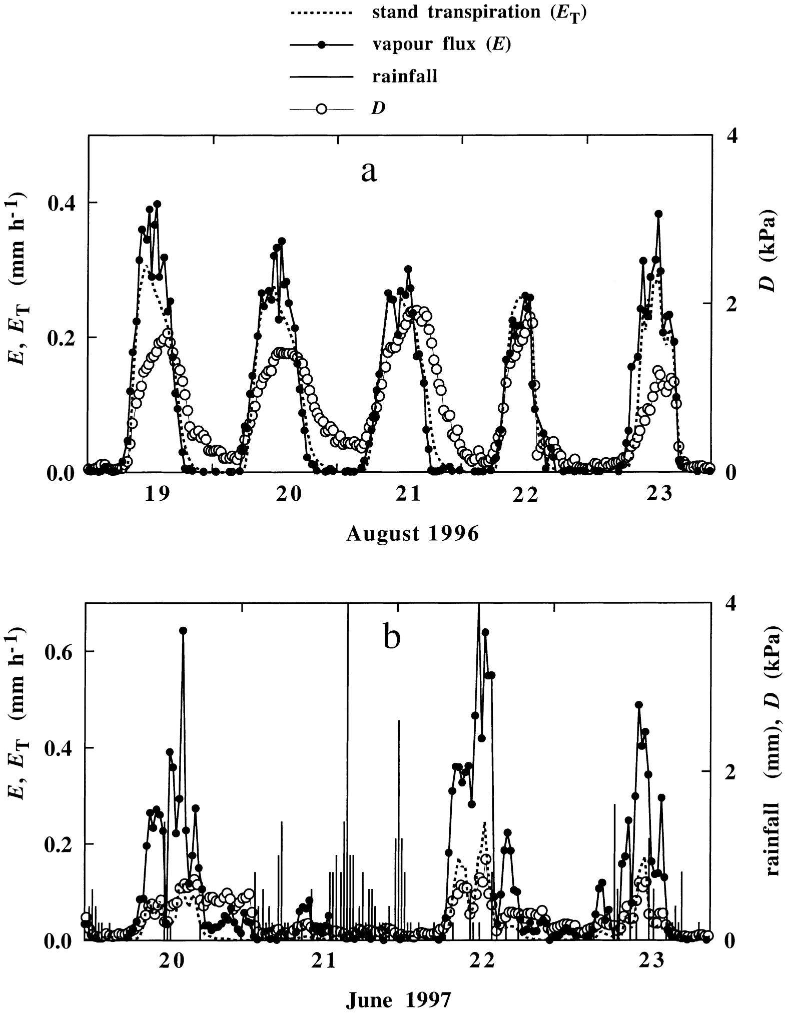

Fig. 9. Diurnal variation of vapour flux (eddy covariance), E, and of stand transpiration (scaled from sap flow measurements), E_T, during successive days under sunny (a) and rainy (b) conditions in the Hesse forest. Air vapour pressure deficit (D) and rainfall are also shown on the second Y-axis.

Total dry canopy conductance g_{cT} followed a similar relationship to R and D :

$$g_{cT} = \left[\frac{R}{R + 550}\right]\left[\frac{46.78}{1 + 0.948D}\right] \qquad (9)$$

Higher values for g_{cT} than for g_c were observed (Fig. 11). The response of g_{cT} to R and D variation was slightly different than for g_c, total conductance showing a less pronounced decrease with increasing D than for g_c.

For wet foliage, the inverted Penman–Monteith equation was used to estimate g_a from the eddy covariance data. Although there was no evident relationship between g_a and windspeed, estimated g_a was in the same range (0.1–0.8 m s^{-1}) than values calculated from the Eq. (3).

We calculated the decoupling coefficient omega (Jarvis and McNaughton, 1986), for non-limiting soil water, from the climatic variables and from calculated g_a and g_c. We found a high degree of coupling (i.e., a low decoupling coefficient) between the beech canopy and the atmosphere, with typical values of omega varying with climatic conditions between 0.05 and 0.20. Windspeed showed a strong influence on

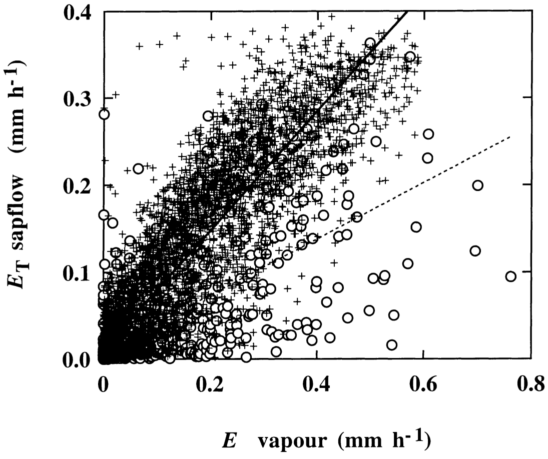

Fig. 10. Relationship between vapour flux measured above the beech stand (eddy covariance), E, and scaled-up tree transpiration measured using sap flow technique, E_T. Half hourly data of 1996 and 1997. Dry (crosses) and wet (circles) canopy conditions are separated. The two lines indicate the best fits for dry (full line) and wet (dotted line) conditions. Equations are $E_T = 0.771\ E$ ($r^2 = 0.85$), and $E_T = 0.425\ E$ ($r^2 = 0.46$) for dry and wet canopy conditions, respectively.

the variation of omega for dry canopy conditions: the lower the windspeed, the higher the decoupling coefficient was. The strong coupling between canopy and the atmosphere was due to a much higher aerodynamic conductance compared to the canopy conductance (typically 10–50 fold).

3.3.2. Validation: modelling of stand transpiration in the Aubure beech forest

After calibrating Eq. (5) on the Hesse forest data set, modelled canopy conductance was introduced in the Penman–Monteith equation for modelling stand transpiration of the beech stand in the Aubure forest. We compared modelled stand transpiration (E_{TM}), using Eq. (6) and (7) with weather data measured close to the experimental plot, to the sap flow measurements performed in the Aubure stand during 1995. Fig. 13 shows the time course of measured and modelled transpiration from mid-June to the beginning of August. For the period of 19–29 June, stand sap flow was slightly lower than E_{TM}, probably because young leaves, even if fully expanded, had not yet reached their physiological maturity. On some days (e.g. 3 and 16 July) transpiration was reduced by rain events due to evaporation of intercepted water. It is also to be noticed (Fig. 13), that on some nights (e.g. 20 and 21 July), sap flow did not completely stop. This observation was also reported by Köstner et al. (1998a) in a Norway spruce stand, but this author could not conclude either in the existence of night transpiration, or in the trunk refilling during the night. We also found at Aubure the same effect of air temperature as at Hesse, that strongly reduced tree canopy conductance approximately below 15–17°C.

Over the period between 18 June and 27 August, E_T and E_{TM} were remarkably close, as can be seen

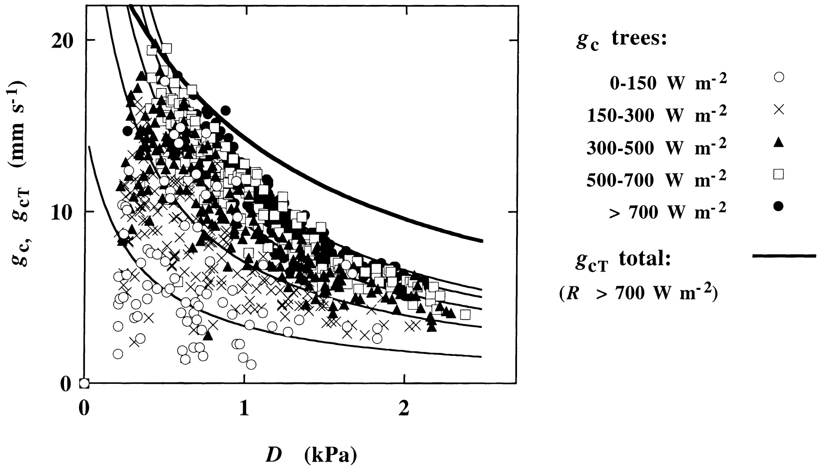

Fig. 11. Calculated tree (g_c) and total (g_{cT}) canopy conductance for water vapour in 1996 as a function of air vapour pressure deficit (D) and of global radiation (half hourly values), for a period when LAI was at its maximum and when both air temperature and soil water content were not limiting.

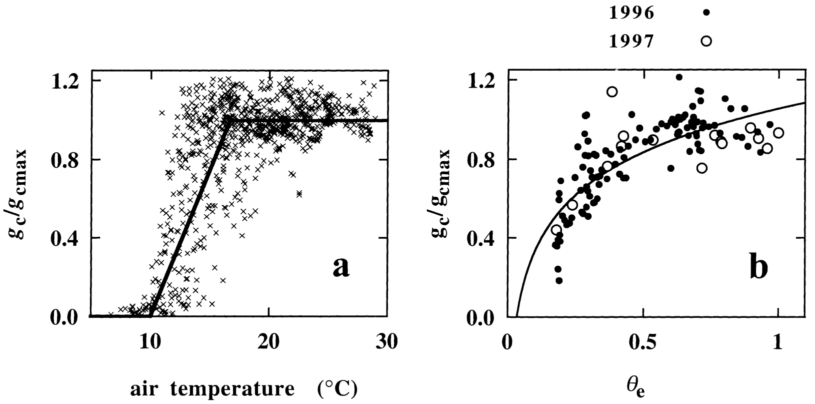

Fig. 12. Ratio of actual to maximum tree canopy conductance g_c/g_{cmax} (see text) as a function of (a) air temperature (6 June–19 July 1997) and (b) relative extractable water in the soil θ_e for periods when LAI was at its maximum. From 20 May to 19 September 1996, θ_e was estimated daily within each week taking into account input (throughfall) and output (stand evapotranspiration) fluxes. From 19 June to 29 September 1997, data points correspond to weekly measurements of θ_e.

in the following equation, calculated from data of Fig. 14 :

$$E_{TM} = 1.055E_T \qquad r^2 = 0.932 \tag{10}$$

in which E_{TM} and E_T are expressed in mm h^{-1}.

4. Discussion

4.1. Water balance and soil water content

Slightly higher values of intercepted rainfall were found in the Hesse forest (25–27%) than in older beech

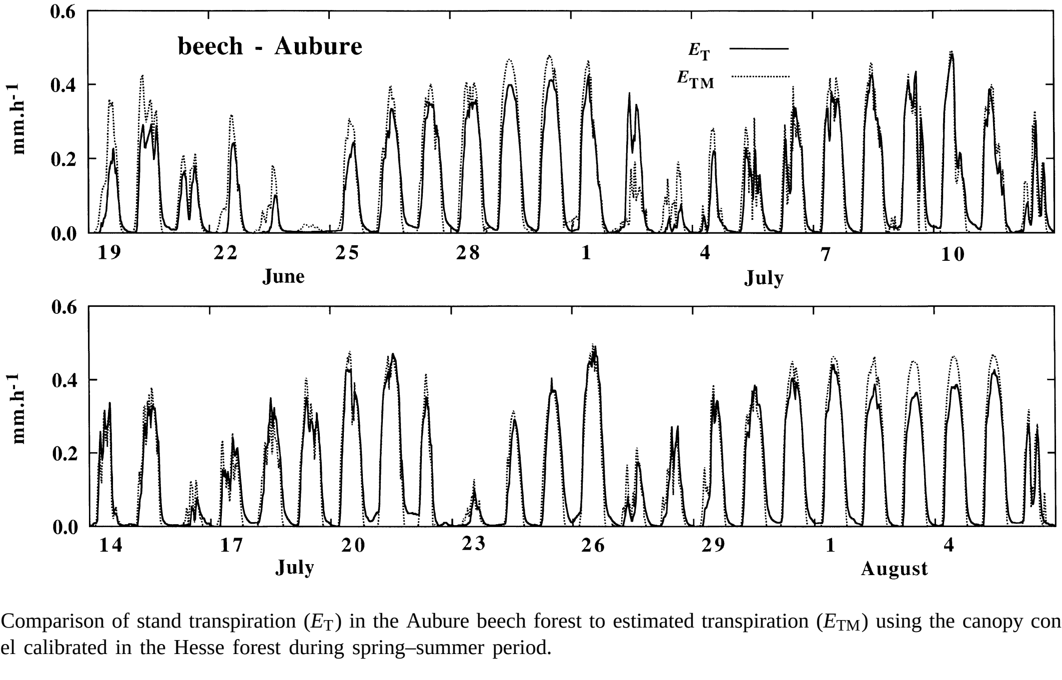

Fig. 13. Comparison of stand transpiration (E_T) in the Aubure beech forest to estimated transpiration (E_{TM}) using the canopy conductance sub-model calibrated in the Hesse forest during spring–summer period.

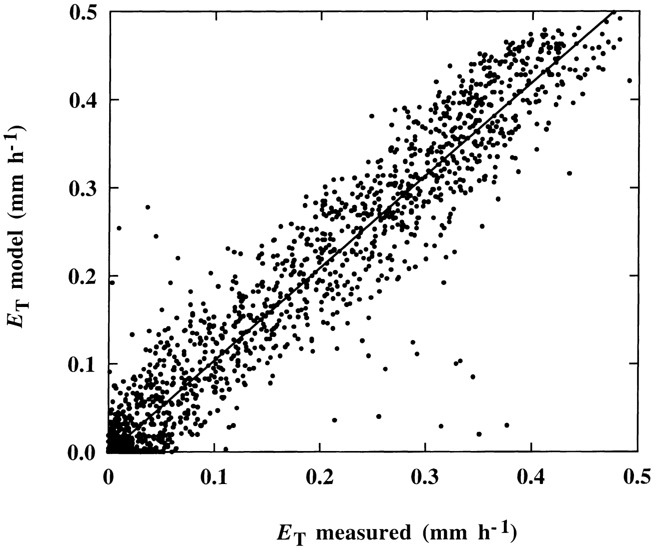

Fig. 14. Comparison of modelled (Penman–Monteith model, parameterised with the canopy conductance function obtained at Hesse) to measured stand transpiration in the Aubure beech forest from 18 June to 27 August, corresponding to full leaf development. The line corresponds to the linear regression: $E_{TM} = 1.055\ E_T$.

stands: 14–16% in Neal et al. (1993), 20.3% in Biron (1994), 23% in Aussenac and Boulangeat (1980). This is probably due to rainfall conditions (intensity and frequency). Cumulated stand transpiration (E_T), interception (I_n) and vapour fluxes (E) were similar for 1996 and 1997 (Table 3). For both years, total vapour flux as measured above the stand was markedly lower than the sum $E+I_n$. The difference amounted to 34 and 27 mm in 1996 and 1997, respectively. This could be attributed to: (i) a loss of vapour fluxes as measured with the eddy covariance technique, or (ii) underestimated measurements during rainfall periods, when the sonic anemometer was wet.

During drought, water absorption by roots from the soil seemed to be strongly dependent on the soil physical properties: we observed that a heavily clayey layer reduced root colonisation and therefore reduced water extraction. When roots could extend below such a layer (as in Zone 1), water absorption was observed in deeper horizons as reported by Bréda et al. (1995) in an oak stand growing on a similar soil type. Nevertheless, we observed a large spatial heterogeneity in maximum extractable soil water in the experimental plot: within a distance of ca. 30 m, maximum extractable water in the soil varied between 130 and 185 mm. This could induce large spatial variations in tree response during severe drought.

4.2. Sap flow

We observed a general pattern of sap flux density relative to the depth below cambium in the beech stems, independent of tree size. This radial profile of sap flux density observed in our study was very similar to that reported on older beech trees (Köstner et al., 1998b; S. Lang, personal communication). The sap flux velocity profile seems to be related to wood water content: the highest F_d rates were observed in the wettest peripheral wood layers, which are probably less embolised and contain more living cells than older and more internal layers. Ladefoged (1960) reported that beech sapwood could extend from 10 to 20 annual rings, corresponding to 20 to 50 mm xylem thickness in our trees. In the present study, no well marked heartwood was found in beech.

No time lag between canopy transpiration and sap flow measured in the trunk was observed in the present work. We concluded therefore that there was no significant water exchange between transpiration and the living tissues during well watered periods. One explanation could be that our measurements were performed in young trees, having probably less exchangeable water than bigger trees. It seems that the capacitance phenomenon has been more often observed in coniferous species (Jarvis, 1975, Schulze et al., 1985, Granier and Loustau, 1994, Loustau et al., 1998) than in broad-leaved trees. In temperate oaks, Granier and Bréda (1996) found a 30 min time lag. Since beech and coniferous species like pines are both characterised by a large sapwood thickness in the trunk, the cause of such difference cannot be attributed to the amount of xylem elements, but probably to the intrinsic capacitance properties of the tissues.

Among-tree variability in sap flow was linked to crown status. Dominant trees, of which the crowns intercept a high proportion of the incident radiation, exhibited higher sap flux densities and therefore much higher total sap flow rates than smaller trees. Because of their ground area distribution, the contribution of dominant trees ($C_{1.3} > 300$ mm) represented about 79% of the stand transpiration.

4.3. Stand transpiration and canopy conductance

Over the 2 years of measurements, a linear relationship was found between stand sap flow and eddy covariance in the Hesse forest, on a hourly as well as on a daily basis. Stand transpiration was equal to 77% of total evapotranspiration when the canopy was dry. The remaining 23% could, at least partly, be due to soil evaporation. Nevertheless, there is a large uncertainty in the difference between E and E_T due to errors of measurements in both terms. On the one hand, total forest evaporation could be underestimated, as suspected when we compared net radiation to the sum of the energy fluxes measured by eddy covariance. The energy balance closure was not met, the difference was 12% of R_n on average. Even if we made an average frequency correction of about 8%, E would still be underestimated. On the other hand, scaling tree transpiration to the stand level includes two types of errors: (i) The measurement error on the average F_d, due to the among-tree variability (see Figs. 5 and 6). It must be emphasised that the accuracy in stand transpiration estimates is very sensitive to the weight given to each sampled tree and to the sample size (see Köstner et al., 1996, 1998b); (ii) The uncertainty in the scaling factor, the stand ground area. Recent forest inventories (data not shown) performed in the surrounding 10 ha, based on 119 local measurements, showed a large spatial variation in the tree ground area, with a coefficient of variation of about 0.18.

In the absence of water stress, Bowen ratio 'β' equalled 0.48 on average, i.e. latent heat flux was almost twice the sensible heat flux. When soil water content decreased during summer, as the result of stomata closure, β increased to 1.25.

As observed here, and reported in other field studies, for non-limiting soil water conditions, tree canopy conductance was shown to vary mainly with radiation and with air vapour pressure deficit. A similar relationship to R and D was found for both estimates of canopy conductance, even if under higher evaporative demand estimated g_{cT} was greater than g_c ($E > E_T$). Under low evaporation demand (i.e., when R and D are low), we could not distinguish between g_c and g_{cT}, probably because of the larger relative errors in E and E_T measurements. The effect of air temperature on g_c has been less studied than the influence of other environmental variables. In beech, we found that air temperature below a threshold of 17°C played an important role, while it was not observed in oak trees (Granier and Bréda, 1996). This rapid decrease in g_c when air temperature fell below 17°C was confirmed by the analysis of the variation of g_{cT} as calculated from vapour flux data for the first half (spring and early summer) of the leafy period. Overdieck and Forstreuter (1994) also showed on young beech plants a significant increase in transpiration at the leaf scale, when air temperature increased in the range of 15–20°C. Nevertheless, this phenomenon was not observed during September and October; then low temperatures did not affect g_c nor g_{cT}.

In the absence of water stress, when comparing low elevation (Hesse) and mountain (Aubure) beech stands, a strong similarity was found in the transpiration rates. This was probably due to very close absolute values of canopy conductances, and to their similar dependence on R and D. Unfortunately, the behaviour of stand transpiration in the Aubure stand could not be analysed during drought conditions, because this area was wet in the year 1995. Therefore, despite important differences in age, stand structure and site conditions, the canopy conductance response of both stands

Table 4
Comparison of modelled canopy conductance in the beech stand to the two models of Herbst (1995), under full leaf expansion, sufficient soil water content, and for different combinations of global radiation (R) and air vapour pressure deficit (D)[a]

R ($\mathrm{W\,m^{-2}}$)	D (kPa)	% differences Model 1	% difference Model 2
200	0.5	14	−19
200	1.0	10	−38
500	1.0	8	14
500	2.0	5	6

[a] Differences in estimates are expressed relative to Herbst model values.

to environmental factors (radiation, vapour pressure deficit, temperature) appeared to be very similar. Furthermore, our canopy conductance function matched also closely with that of Herbst (1995), his g_c-model being calibrated from water vapour measurements performed on a 100-year old beech forest in Germany. He proposed two sub-models of g_c (see Herbst (1995); Eqs. (6) and (7), p. 1013), differing in the effect of global radiation (R): Model 1 used a curvilinear function, whereas Model 2 was linearly related to R. The best estimates were obtained with the linear function of R, while we found that a curvilinear function explained better the observed variation. We compared our estimates of g_c to the two models of Herbst using different combinations of R and D , as shown in Table 4. The relative difference between Herbst's and our g_c estimates ranged from 5 to 14%, and from −38% to 6% when using models 1 and 2, respectively. This would lead to typical differences in stand transpiration of less than 10%. Shuttleworth (1989) and Granier et al. (1996a) previously reported such similarities in the diurnal patterns of g_c when comparing various forest ecosystems. However, when comparing canopy conductance in different forest stands, it seems that LAI plays a more important role than species composition (Granier et al., in prep.). Transpiration rates of our two beech stands were comparable, probably because LAI were very similar.

A strong coupling between the beech canopy and the atmosphere was found here: omega factor remained lower than 0.2, as reported elsewhere for a beech forest by Herbst (1995) and for various other forest stands (Granier and Bréda, 1996, Granier et al., 1996b, c).

5. Conclusions

This work showed that the combination of two methods measuring water vapour fluxes at different spatial scales was possible, however only under some precautions. Nevertheless, we showed that some uncertainties were associated with both methods. Eddy covariance did not give reliable measurements during rainfall, thus rainfall interception could not be measured accurately. For the uncertainties of the energy balance closure, no clear reason was found.

Surprisingly, we did not find significant differences in forest transpiration when comparing beech stands growing under various conditions of age, climate and soil.

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