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Nathalie Jarosz, Yves Brunet, Eric Lamaud, Mark Irvine, J.-M. Bonnefond, et al.. Carbon dioxide and energy flux partitioning between the understorey and the overstorey of a maritime pine forest during a year with reduced soil water availability. *Agricultural and Forest Meteorology*, 2008, 148 (10), pp.1508-1523. 10.1016/j.agrformet.2008.05.001 . hal-00351201

HAL Id: hal-00351201

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Submitted on 8 Jan 2009

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Carbon dioxide and energy flux partitioning between the understorey and the overstorey of a maritime pine forest during a year with reduced soil water availability

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Abstract.

Carbon dioxide, water vapour and energy fluxes were measured above and within a maritime pine forest during an atypical year with long-lasting reduced soil water availability. Energy balance closure was adequately good at both levels. As compared with what is usually observed at this site the ecosystem dissipated less energy via latent heat flux and more via sensible heat flux. The understorey canopy was responsible for a variable, significant component of the whole canopy fluxes of water vapour and carbon dioxide. The annual contribution of the understorey was 38% (154 mm) of the overall evaporation (399 mm) and 32% (89 mm) of the overall sensible heat flux (274 mm). The participation of the understorey reached 45% of the overall evaporation and 30% of the daytime overall assimilation during significant soil water deficit periods in summertime. Even during winter, understorey photosynthesis was consistent as it compensated soil and understorey respiration. The ecosystem behaved as a sink of carbon, with a negative annual carbon budget (-57 gC m^{-2}). However, due to high soil water deficit, the annual ecosystem GPP was 40% less than usually observed at this site. This budget resulted from a sink of -131 gC m^{-2} for the overstorey and a source of $+74 \text{ gC m}^{-2}$ for the understorey. Moreover, on an annual basis the overstorey layer contributed to almost two thirds of the ecosystem respiration. Finally, the effect of long-lasting soil water deficit on the maritime pine forest was found more important than the effect of the heat wave and drought of summer 2003.

Keywords: CO₂, H₂O, eddy covariance, conifer forest, GPP, respiration, WUE

1 INTRODUCTION

Forests extend over large areas and have a major contribution to total energy and mass exchange between the biosphere and the atmosphere. Many studies have been conducted worldwide to evaluate carbon dioxide and water vapour fluxes over various types of forests (Baldocchi et al., 2001; Valentini 2003). However, although forests are greatly variable in structure and composition, they have often been considered as a whole and the respective contributions of the overstorey and the understorey have rarely been quantified. Yet, the fluxes from the bottom layers may constitute a significant part of the overall ecosystem exchanges (Misson et al., 2007).

According to the leaf area index (LAI) of the overstorey, light penetrates more or less deeply in the understorey layer. The LAI of southern pine forests is relatively low and almost constant during the year, owing to the permanent presence of needles. As compared with dense stands, turbulent transport is expected to be more efficient in open stands and the available energy close to the ground surface to be larger (*e.g.* Baldocchi and Vogel, 1996 ; Misson et al., 2007). Additionally, understorey vegetation is usually taller in open stands, thus enhancing evaporation. This implies that mass and energy exchange is expected to be significant at bottom layers in such open environments as temperate pine forests.

In order to understand and quantify the various sources and sinks within the forest canopy, measurements of mass and energy exchange can be performed at various levels. The eddy-covariance (EC) method has been extensively used to estimate energy and mass exchange at the forest scale in programmes such as Euroflux (Aubinet et al., 2000) and FLUXNET (Baldocchi et al., 2001). The feasibility of eddy-flux measurements just above the forest floor has also been considered in various types of forests like temperate broad-leaved, boreal coniferous, coniferous and deciduous forests (*e.g.* Baldocchi and Vogel, 1996; Baldocchi et al., 2000; Blanken et al., 1997; Lamaud et al., 2001; Launiainen et al., 2005; Wilson et al., 2000). Such measurements have two well-known limitations: (i) flux estimates are usually representative of a much smaller area than those performed above the canopy (Baldocchi, 1997; Wilson and Meyers, 2001); (ii) the underlying assumptions of the EC method are not expected to be generally valid in the conditions of highly non-stationary and turbulent flow regime prevailing there (Blanken et al., 1998; Baldocchi et al., 2000). However they have proved to be very useful to determine flux partitioning between the overstorey and the understorey (Misson et al., 2007). But, to our knowledge, none of such measurements

performed just above the forest floor has been used so far to quantify the effect of long lasting reduced soil water availability on mass and energy flux partitioning.

An increasing number of studies deal with either drought or heat effect on ecosystem functioning. They show a reduction of water fluxes, net primary productivity and total ecosystem respiration (*e.g.* Ciais et al., 2005, Granier et al., 2007), usually over short periods of time occurring in summer. However, little is known about possible consequences of longer lasting periods of heat or drought occurring not only in summer but also in winter, whereas such events are expected to be more frequent in the near future (Meehl & Tebaldi, 2004; Giorgi, 2006).

In the present study water vapour (H₂O) and carbon dioxide (CO₂) fluxes were measured with the EC method both above and below a maritime pine forest canopy over a full year characterized by a long lasting period of reduced soil availability. The aim is twofold: (i) to partition above-canopy energy and CO₂ fluxes between the overstorey and understorey components and (ii) to analyse the effect of soil water availability on the fluxes at both levels.

2 MATERIAL AND METHODS

2.1 Site characteristics

The experimental site of Le Bray is located in the Landes forest about 20 km South-West of Bordeaux (latitude 44°43'1.6"N, longitude 0°46'9.5"W, altitude 62 m) in France. The plot is flat and composed of maritime pine (*Pinus pinaster* Ait.) planted in 1970 and covering about 16 ha. Mean annual rainfall over the 1970–1999 period is 972 mm. The trees are distributed in parallel rows along a northeast–southwest axis, with an inter-row spacing of 4 m. In 2002 the canopy crown extended between 12 and 20 m above soil surface and stand density was about 410 trees ha⁻¹. The leaf area index (LAI) of the overstorey evaluated by various optical methods (Demon, LAI 2000) was 2.4 m² m⁻² on average.

The understorey mostly consists of grass, mainly purple moor-grass *Molinia coerulea* L. Moench, that accounts for more than 90% of the LAI when it is well developed (Loustau and Cochard, 1991). In 2002 the understorey LAI, estimated by a destructive method, varied from 0 in winter to 1.6–1.9 m² m⁻² in summer when the purple moor-grass was about 0.7 m high.

The soil is a sandy and hydromorphic podzol, with dark organic matter in the first 0.6 m. It is covered by a litter formed by dead needles, dead grass, dead branches and decayed organic matter. A layer of compact sand, barely penetrable by the roots, is located at a depth of about

0.8 m. Inorganic sand lies below this layer. The water table level reaches the soil surface during most winters, and drops to a depth between 1.2 and 2 m in summer.

A 40 m high instrumented tower is set up in the middle of the stand. The latter is surrounded by similar stands, except in the northwest direction where a clearcut was made at about 200 m from the tower following the December 1999 storm. This sector was excluded from the present analysis.

2.2 Eddy covariance and meteorological measurements

In 2002 turbulent fluxes were measured by two EC systems at 7 and 41 m above ground. The basic instruments and methods have been standardised throughout the Euroflux network (Aubinet et al., 2000). The present EC system is made of a 3D sonic anemometer Solent, R2, above the canopy and R3 below (Gill Instruments, Lymington, Hampshire, UK), coupled with an open path CO₂/H₂O InfraRed Gas Analyzers (IRGA) LI-7500 (LICOR, Lincoln, NE, USA). Instantaneous measurements of the three components of wind velocity, temperature (T) and the molar fractions of H₂O and CO₂ were collected and stored at 20.8 Hz. Turbulent scalar eddy fluxes were then calculated every half hour as the covariance between the vertical wind speed and the scalar variable (CO₂, H₂O, T). The EC system located above the canopy gives fluxes representative of the whole ecosystem, whereas the system located below the canopy gives fluxes from the understory, that includes the soil and the vegetation covering the soil. In what follows, 'overstorey' refers to the difference between the two levels of EC measurements, and therefore corresponds to the pine trees alone.

Net radiation (R_n) was directly measured with a Radiation and Energy Balance Systems model Q7 (REBS, Seattle, USA). Global radiation (R_g) was measured with a CE180 pyranometer (Cimel Electronique, Paris, France). Incident and diffuse photosynthetically active radiation (PAR) was measured above the canopy using a sunshine sensor BF2 (Delta-T Devices, Cambridge, UK). Mean wind speed and direction were measured with a wind vane anemometer (5103 Young, Traverse City, Michigan, USA), and air temperature and relative humidity with a HMP45 (Vaisala, Helsinki, Finland). All these measurements were performed at 41 m above ground. Rainfall was measured at a height of 24 m on a nearby tower, just above the top of the trees, with a rain gauge ARG100 (Campbell Scientific, Logan, USA). Atmospheric pressure was measured at 2 m above ground using a PTB101B Barometric Pressure Transmitter (Vaisala, Helsinki, Finland). Soil heat flux (G) was measured using two flux plates (Campbell Scientific, Shephed, UK) and corrected by an estimation taken from a

two-step version of the null-alignment method using soil temperature, water content and bulk density measurements between the soil surface and 1 m depth (Ogée et al., 2001). Four temperature profiles were set up at depths 1, 2, 4, 8, 16, 32, 64 and 100 cm using 32 homemade thermocouples. Soil water content (SWC) was measured at 0.05, 0.23, 0.34 and 0.8 m depth using a Time-Domain Reflectometry (TDR) Trase (Soil Moisture Equipment Corp., Santa Barbara, CA) sensor at three different locations. Soil bulk density was measured gravimetrically from samples collected at various depths and three locations in the vicinity of the other soil measurements. All signals were sampled every 10 s on CR10X, CR21X and CR23X Campbell data loggers (Campbell Scientific, Logan Utah, USA) and averaged every half hour.

2.3 Methods

2.3.1 Eddy covariance fluxes

The fluxes were computed and corrected for 30 min periods using the EdiRe software (University of Edinburgh, UK) as recommended by Aubinet et al. (2000): after occasional spikes were removed from the raw time series, coordinate axes were rotated so that mean vertical velocity was zero and mean horizontal velocity was aligned with the mean wind direction; water vapour fluxes were corrected for the effect of density fluctuations (Webb et al., 1980). Half-hourly flux values that were missing or did not meet the quality criteria were gap-filled. Above the canopy, the proportion of the missing data was 17% of CO₂, 27% of latent heat and 14% of sensible heat fluxes. As expected, the unsteady nature of turbulence below the canopy caused a greater proportion (40%) of fluxes measured above the forest floor to be rejected. The detailed method applied to fill the gaps in above fluxes can be found in Berbigier et al. (2001). Briefly, gaps were filled on monthly periods using multiple polynomial regressions on the relevant micrometeorological data fitted against the adjacent data, taking care that the weather was similar. As for CO₂ fluxes, gap filling was made with reference to direct and diffuse PAR, air temperature and friction velocity u_* . Daytime and nighttime data were addressed separately. The method of Falge et al. (2001a,b), based on look-up tables, was chosen to fill the gaps in below-canopy fluxes because it appeared more adapted than the polynomial regressions: if all meteorological data were available, the missing value was replaced by the average value under similar meteorological conditions within a time-window of 7 days, and if no similar meteorological conditions were present, the averaging window was increased to 14 days.

2.3.2 Net radiation below the canopy

The net radiation transmitted below the canopy R_{nb} was estimated using a radiation transmission model validated at the same site (Berbigier and Bonnefond, 1995), corrected so that the difference between canopy temperature and litter temperature was taken into account (Ogée et al., 2001):

$$R_{nb} = R_{nb}' + (1-f^2) \sigma \{ T_{a8m}^4 - T_{al}^4 \} \quad (\text{Eq. 2})$$

where R_{nb}' is the net radiation below the canopy, calculated using the model of Berbigier and Bonnefond (1995), $\sigma = 5.674 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ is the Stefan constant, T_{a8m} is the air temperature at 8 m above ground, taken instead of the canopy temperature which was not measured, T_{al} is the litter temperature at the air-litter interface and f is a luminance constant calculated from the LAI:

$$f = \exp(-0.548 \text{ LAI} + 0.0177 \text{ LAI}^2) \quad (\text{Eq. 3})$$

2.3.3 Gross primary productivity and respiration

We splitted the CO_2 fluxes as measured by the EC method into gross primary productivity, GPP, and respiration, R, using the Reichstein et al. (2005) algorithm that we applied separately on the canopy nighttime fluxes measured at the upper and lower levels. Nighttime data ($R_g < 20 \text{ W m}^{-2}$) were selected and splitted among consecutive 15-day periods with a 10-day overlap, giving a total of 78 data sets. The model is as follows:

$$R = R_{\text{ref}} \times \exp(E_0 (1/T_{\text{ref}} - T_0) - 1/(T_a - T_0)) \quad (\text{Eq. 4})$$

where T_0 is a constant temperature at -46.02°C , T_a is the air temperature measured above the canopy, and T_{ref} is a reference temperature taken at 10°C . The model parameters, R_{ref} , the temperature-independent respiration rate, and E_0 , the temperature-dependent activation energy, were calculated for each period. The values obtained were smoothed by sliding averages ($n=3$) and used to estimate half-hourly values of ecosystem respiration for the whole year on the entire data set. No filtering criteria were applied on R_{ref} and E_0 values. Gross primary production was obtained by subtracting the respiration values from the net carbon flux.

2.3.4 Seasonal and weather classes

In order to analyse the full-year data set, the data was separated into 6 classes based on the combination of season, air moisture condition and soil water status (Table 1). 'Summer' refers to the period from early May to late October and 'winter' refers to the rest of the year. The distinction between 'well-watered' and 'water-stressed' summer is based on soil water content: under the threshold value of 65 mm the site experienced a drought and is considered as 'water-

stressed'; otherwise the conditions are referred to as 'well-watered' (Ogée et al., 2003). We also set a threshold value of 5 hPa on mean daily vapour pressure deficit (VPD) in order to separate wet air conditions from dry air conditions. The number of days per class is larger than 30 in five out of six classes (Table 1).

Table 1. Definition of the six classes used in this study: the soil water status is defined as 'well-watered' when soil water content is larger than 65 mm and 'water-stressed' otherwise; the air moisture condition is considered as 'wet' when the vapour pressure deficit is less than 5 hPa and 'dry' otherwise; 'summer' refers to the period between May and October and 'winter' to the rest of the year. The number of days n of each class is also indicated.

Classes	Season	Soil water status	Air moisture condition	n
1	winter	-	wet	129
2	winter	-	dry	41
3	summer	well-watered	wet	32
4	summer	well-watered	dry	85
5	summer	water-stressed	wet	17
6	summer	water-stressed	dry	61

2.3.5 Water use efficiency

Water use efficiency (WUE) represents the ability of the canopy to assimilate carbon while limiting water loss and as such is defined as the ratio between photosynthesis and canopy transpiration. It is computed here as the regression slope between the GPP and water vapour (E) fluxes, at three levels: the entire ecosystem, the understorey and the pine trees. For the latter, GPP and E are estimated from the differences between measurement above and below the canopy.

3 RESULTS AND DISCUSSION

3.1 Meteorological conditions

In 2002, the total annual rainfall was 948 mm, which is close to the mean annual value at this site (Fig. 1). However, it can be seen that rainfall mostly occurred during the last three months of the year (374 mm). Maximum global radiation occurred from the beginning of May to the end of August, coinciding with maximum VPD. Annual net radiation below the canopy was 16% of that above (2613 MJ m^{-2} above and 421 MJ m^{-2} below; table 2). As the overstorey LAI changed by less than 10% during the year, this proportion varied mostly with the solar elevation angle. From the beginning of May to the end of August, net radiation below the canopy was about 30% of that above. Air temperature at the bottom layer tended to be slightly

higher than above the canopy. Mean annual temperature was 13.8°C with a half hourly maximum at 34.1°C in June and a minimum at small negative values on the first days of January. Daily average wind speed above the canopy varied between 1.21 and 6.37 m s⁻¹ whereas at 7 m above ground it was between 0.20 and 1.52 m s⁻¹.

As for soil water availability, year 2002 was atypical. Indeed, soil water content varied from 46 mm in summer to 169 mm in winter, which was particularly low compared to other years. The maximum value generally observed in winter can be twice as large as that observed in 2002. Indeed, the cumulative rainfall during autumn 2001 and the following winter was exceptionally low (289 mm, i.e. 259 mm below the 1950–2000 average). The threshold under which the site is considered as ‘stressed’ correspond to a soil moisture deficit of 25% (Granier and Loustau, 1994). Knowing that wilting point is 45 mm and water holding capacity 85 mm, the threshold value is then 65 mm. However, it is important to note that the soil water content did not fall below this threshold during the considered winter whereas it is the case in summer. The water table level did not reach the soil surface as it usually occurs during most winters. It seems the fact that it remains below the root zone depth was enough to stress the ecosystem.

3.2 Energy balance closure

Fig. 2 shows the relationship between net radiation and the sum of sensible heat flux, H , latent heat flux, LE , and ground heat flux, G , in 2002. Canopy heat storage was not taken into account since it is negligible at the daily time scale. At this scale the energy balance closure above the canopy shows a slope slightly higher than 1 (Fig. 2a), as already observed by Berbigier et al. (2001) at this site. It can be seen that the closure is excellent on clear days when net radiation is large and less on days when net radiation is close to zero. The latter problem may be attributed to a systematic underestimation of the turbulent fluxes in rainy conditions or alternately to problems with net radiation measurements. Indeed, Kohsiek et al. (2007) showed that using REBS radiometers leads to an underestimation of net radiation by about 5% in the daytime and an overestimation by about 20% at night. If we apply these corrections to net radiation, the energy balance closure improves substantially.

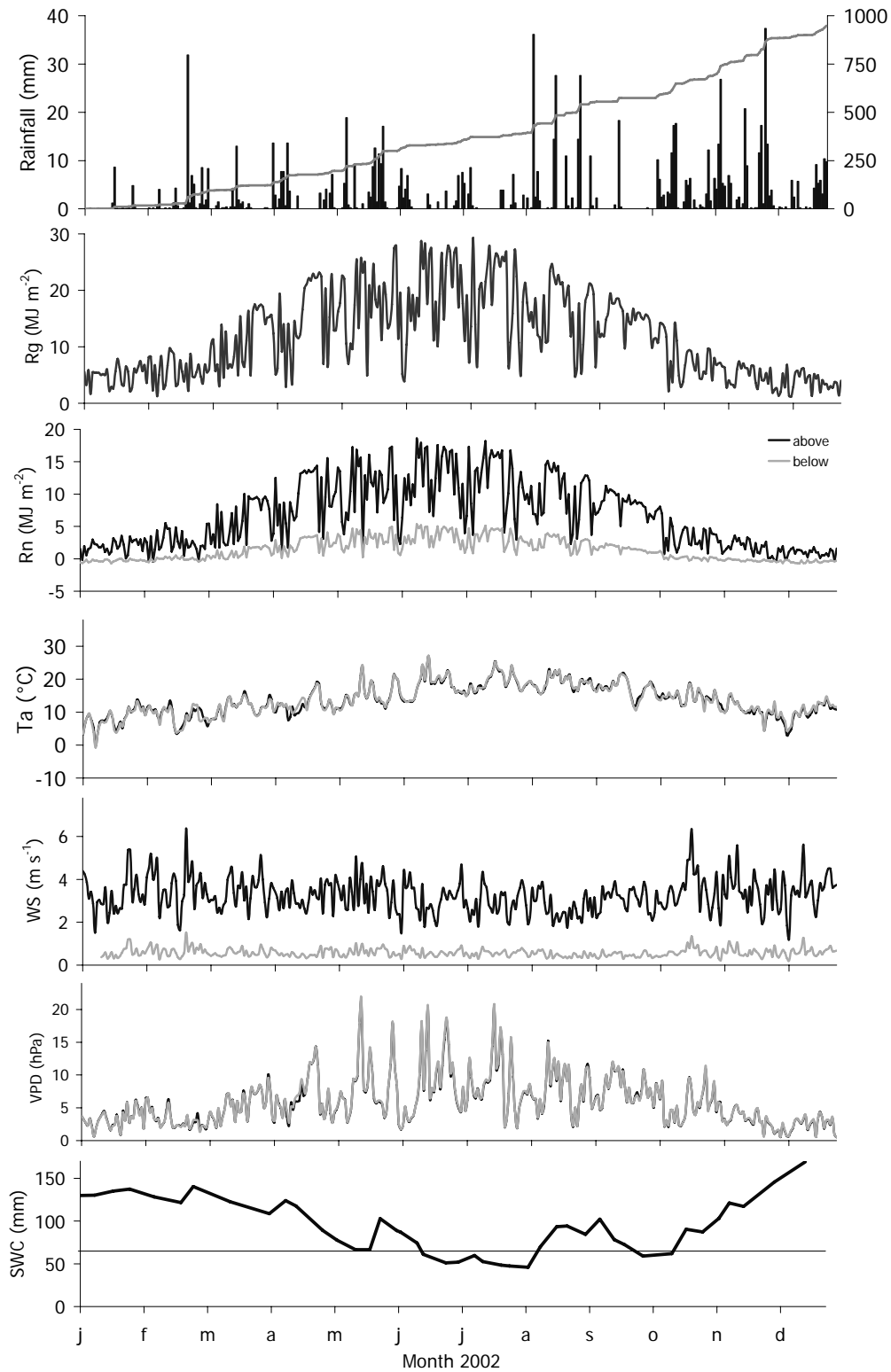


Figure 1. Daily values of rainfall, global radiation (Rg), net radiation (Rn) and soil water content SWC as well as daily means of air temperature (Ta), wind speed (WS), vapour pressure deficit (VPD) in year 2002 at Le Bray site. Rn, Ta, WS and VPD are shown at both levels. Accumulated rainfall is also shown. The horizontal black line marks 65 mm, the threshold value used to delineate well watered from water-stressed periods in summer.

Table 2. Sum of net radiation R_n , sensible and latent heat fluxes, H and LE , respectively, as measured by eddy covariance above (a.) and below (b.) the forest canopy for the six classes defined in table 1. Overstorey fluxes estimated by the difference between the two systems (o.), along with the ratios of understorey flux to total flux (%) are also indicated. Annual fluxes are given at the bottom line. Fluxes are in MJ m⁻². Total transpiration E (mm) above (a.), below (b.) the canopy and of the overstorey (o.) are shown for the six classes as well as evaporative fraction of understorey and overstorey latent heat flux to radiation (LE/R_n).

Class	R_n			H				LE				E			LE/R_n	
	a.	b.	%	a.	b.	o.	%	a.	b.	o.	%	a.	b.	o.	a.	b.
1	289	-18	6	-164	13	-177	7	151	52	99	35	60	21	39	0.52	-2.89
2	345	51	15	103	37	65	36	143	35	108	25	57	14	43	0.41	0.69
3	215	39	18	18	11	6	63	91	37	54	41	37	15	22	0.42	0.95
4	927	177	19	342	73	268	21	341	145	196	42	137	58	79	0.37	0.82
5	83	12	15	1	4	-3	73	42	12	30	29	17	5	12	0.51	1.00
6	754	160	21	385	84	301	22	228	102	126	45	91	41	50	0.30	0.64
Total	2613	421	16	685	222	460	32	997	384	614	38	399	154	245	0.38	0.91

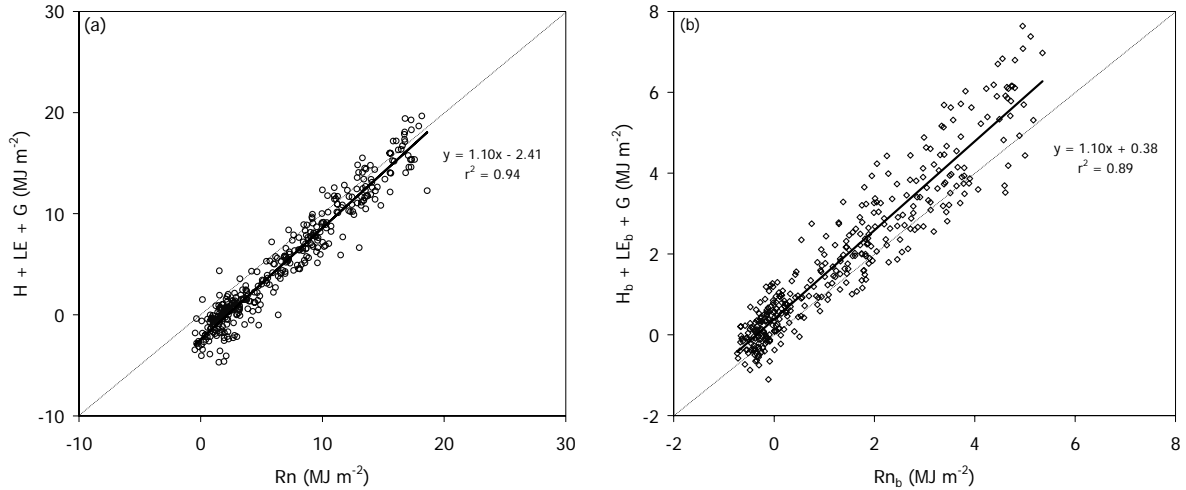


Figure 2. Energy balance closure (a) above the canopy as the relationship between daily values of the sum of sensible and latent heat fluxes, H and LE , respectively and soil heat flux (G) on the one hand and daily values of net radiation (R_n) on the other hand ; (b) below the canopy as the relationship between daily values of the sum of sensible and latent heat fluxes below the canopy, H_b and LE_b , respectively and soil heat flux (G) on the one hand and daily values of net radiation below the canopy (R_{nb}) on the other hand. R_{nb} is estimated using eq. 2 and 3.

The validity of the EC measurements near the forest floor has already been demonstrated in an earlier study at this site (Lamaud et al., 2001). During the present experiment the energy balance closure is also satisfactorily good at the bottom layer of the forest (Fig. 2b): the slope is the same as above (1.10) and the intercept is 0.38 MJ m^{-2} ($r^2 = 0.89$). A slope higher than one indicates that either the turbulent fluxes are overestimated or the available energy is underestimated. Daily and annual sums of energy fluxes from EC measurements are subject to errors when missing or rejected data are gap-filled but such cases occur primarily at night when latent and sensible heat fluxes are expected to be small. The most likely reason is therefore the underestimation of net radiation. The model used to estimate net radiation transmitted below the canopy (Berbigier and Bonnefond, 1995) requires an accurate estimation of LAI (Eq. 3), which is difficult to determine in coniferous forests. Optical methods give the best idea of covering foliage but little is known about the possible errors in the resulting estimation (Guyon et al., 2003). Therefore, in order to investigate the influence of errors in LAI estimation on the energy balance closure, we calculated net radiation with LAI values lower by 5% to 50% than a reference value (set to $2.4 \text{ m}^2 \text{ m}^{-2}$). The regression slope of the energy balance then becomes lower than that found with the reference value by 4% to 39%. As the uncertainty in our LAI measurement is between 10% (i.e. LAI = $2.2 \text{ m}^2 \text{ m}^{-2}$) and 20% (i.e. LAI = $1.9 \text{ m}^2 \text{ m}^{-2}$), the uncertainty in the energy balance closure below the canopy is between 9 and 17%. This may well account for the discrepancy observed in Fig. 2b.

3.3 An overview of fluxes

Throughout the year, the half-hourly values of sensible and latent heat fluxes as well as the CO₂ fluxes show a clear seasonal variation above and below the pine canopy (Fig. 3). They are low in winter and larger the rest of the year at both levels. This seasonal variation corresponds to that of net radiation and the subsequent increase in surface temperature.

The sensible heat flux above the canopy is much larger than the latent heat flux (Fig. 3a, 3b). However, under the canopy the sensible heat flux appears slightly smaller than the latent heat flux. This leads to a lower contribution of the understorey to the overall sensible heat flux (about 10%) than to the overall latent heat flux (about 50%). At the bottom level, H and LE increase as available energy increases and understorey vegetation is growing. It is noticeable that sensible heat flux at the bottom level is rarely negative.

It should be stressed that, due to the low water availability in winter, the pattern of the fluxes was atypical. As expected with a dry soil, maximum values of sensible heat flux tend to be from 22 to 38% higher than what is usually observed at this site (Berbigier et al., 2001). Conversely, maximum values of latent heat flux tend to be lower by 33 to 36%. Since no understorey flux measurements were performed before 2002, it is not possible to quantify these changes in H and LE at the bottom layer and consequently to analyse in depth the respective roles of the understorey and overstorey in the overall fluxes observed in conditions of low water availability.

The annual pattern of carbon dioxide flux F_c above and below the maritime pine forest results from the balance between photosynthesis and respiration processes (Fig. 3c). Negative values stand for canopies acting as a sink of CO₂ and positive values for canopies acting as a source of CO₂. It can be seen that CO₂ uptake increases between mid-April and mid-July at both levels. Again, maximum fluxes observed above the canopy are between 40 to 50% lower than in other years (Berbigier et al., 2001).

3.4 Seasonal variation in energy fluxes

In 2002, wet and dry air conditions prevailed in 'winter' and in 'summer', respectively (Table 1). Sensible heat flux is between 60 and 80% higher in dry air conditions (Fig. 4.2, 4.4 and 4.6) than in wet air conditions (Fig. 4.1, 4.3 and 4.5). In wet air conditions there is virtually no sensible heat flux originating from the understorey and H from the trees does not exceed 50 W m⁻² (Fig. 4.1, 4.3 and 4.5). Peaks occur around midday at both levels. During nighttime in all conditions, H above the canopy is directed downwards ($H = -30 \text{ W m}^{-2}$ on

average) while under the canopy it remains near zero. This is commonly observed above and within forests (Baldocchi et al., 2000; Wilson et al., 2000; Launiainen et al., 2005). The ratios between the standard deviation and the maximum values of H show that the uncertainty is very large in wet air conditions (*i.e.* between 109 and 217%) when the values of H are low. In dry air conditions with higher H, the uncertainty is lower.

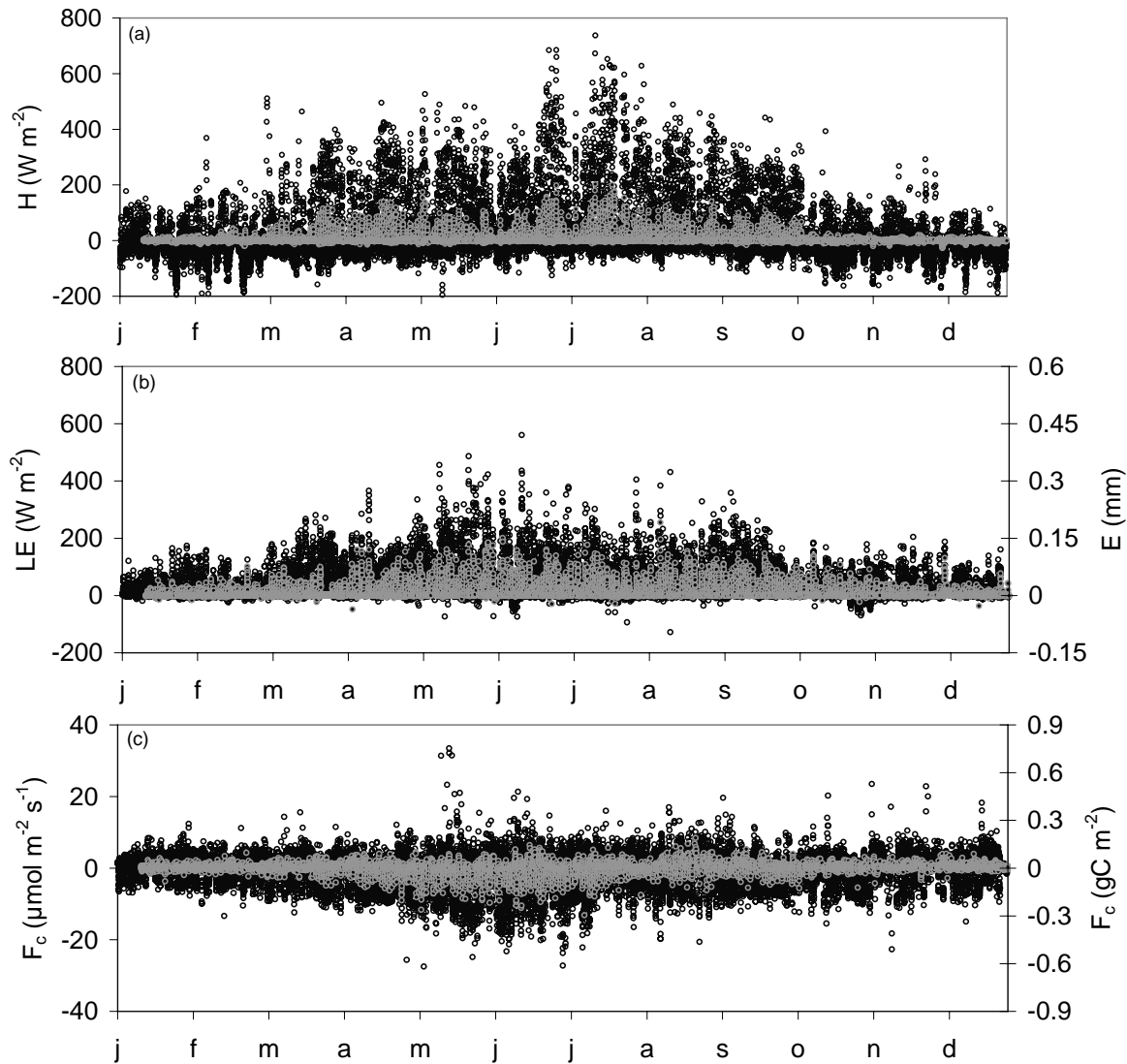


Figure 3. Half-hourly values of (a) sensible heat flux, (b) latent heat flux and (c) carbon dioxide flux, H, LE and F_c , respectively, above the overstorey (open grey symbols) and above the understorey (filled black symbols). Evaporation in mm and F_c in gC m^{-2} are also indicated.

As sensible heat flux, maximum LE generally occurs around midday at both levels, except in water-stressed and wet air conditions where evaporation from the whole forest appears to be low and delayed towards the mid-afternoon (Fig 5.5). This feature is possibly linked with net radiation which was reduced due to passing clouds or overcast conditions that occur more frequently during wet periods. The evaporation from the whole forest as well as from the soil, whether it is covered or not by a photosynthetically active understorey, is generally higher in

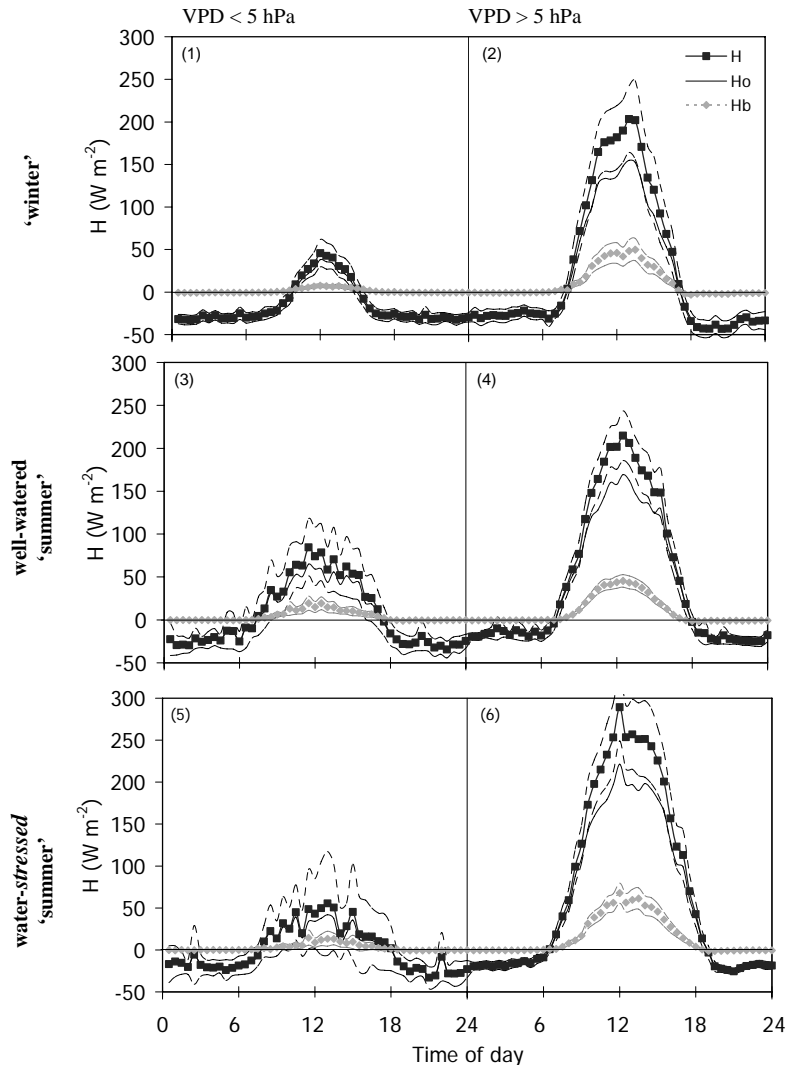


Figure 4. Mean daily course of sensible heat flux above, H , and below, H_b , the canopy averaged over the six classes defined in Table 1. H_0 is the sensible heat flux of the overstorey, deduced from the difference between the two levels. The classes are numbered from top left (1) to bottom right (6). 'Winter' refers to the period between early May to late October and 'summer' to the rest of the year. $VPD < 5$ hPa stands for wet air conditions and $VPD > 5$ hPa for dry air conditions. 95% confidence intervals (lower and upper) for H (black dotted line) and H_b (grey dotted line) are also indicated.

dry (Fig. 5.2, 5.4 and 5.6) than in wet air conditions (Fig. 5.1, 5.3 and 5.5). In water-stressed conditions (Fig. 5.5 and 5.6), the evaporation below the canopy does not vary much, particularly in dry air conditions (Fig. 5.6) although the evaporation measured above the canopy decreases following stomatal closure of the needles. The purple moor-grass composing the understorey does not regulate water loss under significant soil water deficit and dry air conditions (Loustau and Cochard, 1991). At our site evaporation from the understorey represents more than 70% of net radiation in dry air conditions (Table 2), as was already observed over a transpiring vegetative understorey (Blanken et al., 1997). In 'summer' and wet air conditions, these rates can even be closer to 100% whatever the soil water status is, as observed under a Jack pine stand by Baldocchi et al. (2000). The ratio of

the standard deviation to the maximum flux value varies from 50 to 104% above the canopy and from 62 to 110% at the bottom level, with greater accuracy in dry air conditions.

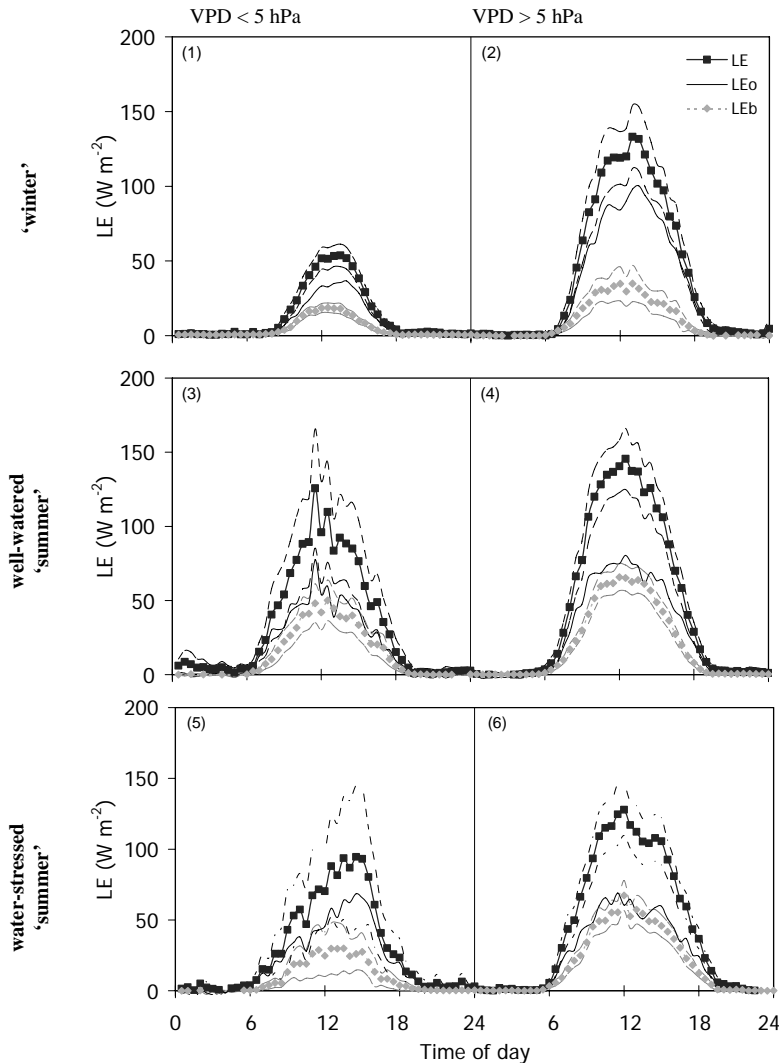


Figure 5. Mean daily course of latent heat fluxes above, LE , and below LE_b , the canopy averaged over the six classes defined in Table 1. LE_o is the latent heat flux of the overstorey, deduced from the difference between the two levels. The classes are numbered from top left (1) to bottom right (6). 'Winter' refers to the period between early May to late October and 'summer' to the rest of the year. $VPD < 5$ hPa stands for wet air conditions and $VPD > 5$ hPa for dry air conditions. 95% confidence intervals (lower and upper) for LE (black dotted line) and LE_b (grey dotted line) are also indicated.

In 'winter', the evaporation from the bottom layer contributes to the overall evaporation by 25% in dry conditions and 35% in wet conditions (Table 2). In 'summer', as the understorey vegetation grows, evaporation from the forest floor contributes up to 45% of the overall evaporation in dry air and water-stressed conditions.

The annual contribution of the understorey is 38% of the overall evaporation and 32% of the overall sensible heat flux (Table 2). Annual evaporation (Fig. 6a) from the understorey is $384 MJ m^{-2}$ (154 mm) and $614 MJ m^{-2}$ (245 mm) from the overstorey. Since the understorey vegetation is photosynthetically active from early spring to late autumn, canopy transpiration

contributes substantially to the total ecosystem evaporation during this period. This contribution appears larger than that observed in other studies performed in pine forests. Berbigier et al. (1996) found that the understorey accounted for only 19% of the total evapotranspiration in a pine forest in Portugal. Even if their stand was similar to the present one in terms of tree density and LAI, the major difference came from the composition of the understorey, which was essentially a bare soil with sparse shrubs. The climate type was also Mediterranean while it is Oceanic in our study. An earlier study performed on the same site as the present study, at a much earlier stage of forest growth (Diawara et al., 1991), shows that understorey contribution was around 25%. A first explanation is that the conditions were not as dry as in our study. Another reason is also that tree density was twice as large as in the present study, and the LAI larger. This reinforces the fact that the understorey takes an important part in the water exchange of more open ecosystems. Indeed, in most open forests, the understorey participation to total evaporation ranges from 20 to 40% in Jack pine stands (Baldocchi and Vogel, 1996; Moore et al., 2000) and a boreal Scots pine forest (Launiainen et al., 2005), from 30 to 50% in temperate pine forests (Baldocchi et al., 2000) to 50% and more in some high-latitude forests (Kelliher et al., 1997), the higher values occurring when the conditions become warmer and dryer. In denser and closer canopies, Black and Kelliher (1989) and Wilson et al. (2000) found that forest floor evaporation is between 3 and 21% of total evapotranspiration.

In wet air conditions the Bowen ratio ($\beta = H/LE$) around midday is less than one above and below the canopy. In dry air conditions $\beta > 1$ above the canopy and $\beta \approx 1$ below, except in well-watered conditions ($\beta < 1$). When water does not limit evaporation, most of the net radiation is dissipated as latent heat fluxes, but as the soil dries out, less water becomes available for understorey transpiration and more energy is dissipated as sensible heat. This is in agreement with Baldocchi et al. (2000), who found a large increase in β as the surface was drying in a ponderosa pine forest. It is also noticeable that in 'winter', the ecosystem behaves as in a water-stressed 'summer', which confirms that the ecosystem is stressed in winter 2002, even if the level of water availability is not as low as during a stressed 'summer'. Indeed, the water table remained below the root zone depth resulting in a winter moisture deficit that may have produced an unusual needle senescence leading to a substantial litterfall, as was observed in February. Such unusual needle mortality was also observed at three other even-aged maritime pine stands in the same region as this study, differing in age, and corresponded to reductions in LAI (Delzon and Loustau, 2005). Roig et al. (2005) have also reported

another peak for litter fall in winter in maritime pines in Spain, which was related to a moisture deficit.

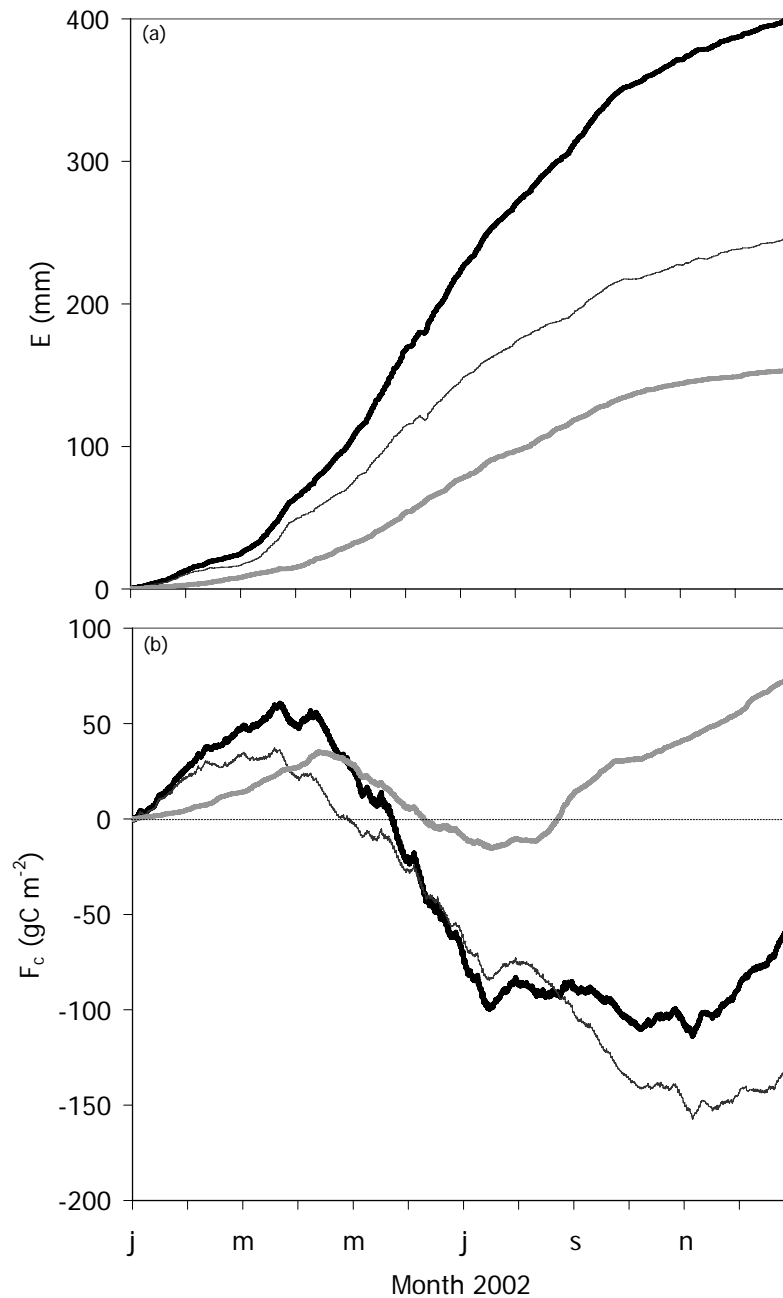


Figure 6. Cumulative (a) transpiration (E) above the forest (black), above the understorey (grey) and of the overstorey (thin black); (b) CO₂ flux (F_c) above the forest (black), above the understorey (grey) and of the overstorey (thin black).

3.5 Seasonal variation in carbon dioxide fluxes

The diurnal variations in F_c averaged over the 6 classes (Fig. 7) show positive values at night and negative values during the day, except in 'winter' at the understorey level where the daytime flux is slightly directed upwards in wet air conditions (Fig. 7.1). This means that

during 'winter', CO₂ is lost from the forest floor at a rate of 0.5 μmol m⁻² s⁻¹ as a result of root and microbial respiration. Nevertheless, there is evidence for photosynthesis by the understorey vegetation: a net daytime uptake from the forest floor is observed at high VPD (Fig. 7.2) and even at low VPD, the small difference between night and day indicates a slight CO₂ uptake (Fig. 7.1). In fact, class 1 is mostly composed of days in the periods from early January to mid-March, and from early November to late December, whereas class 2 (Fig. 7.2) is mostly composed of days from mid-March to the end of April. As in winter the soil is mainly covered by dead pine needles and patches of oat grasses (*Pseudarrhenatherum longifolium*), the small carbon uptake observed in Fig. 7.1 comes from the slight photosynthesis activity of oat grass patches. At higher VPD (Fig. 7.2) corresponding to warmer days of March and April, the higher uptake is obviously due to the presence of purple moor-grass in addition to oat grass. This potential of photosynthesis to offset soil respiration shows the ability of oat grass and purple moor-grass to uptake CO₂ at low radiation levels, as already observed with different understorey species in a boreal forest ecosystem (Whitehead and Gower, 2001).

In 'summer', both forest ecosystem and understorey vegetation photosynthesis are larger than respiration during the day. Under well-watered conditions (Fig. 7.3 and 7.4) and at about midday, the mean rate of CO₂ fluxes reaches -6 μmol m⁻² s⁻¹ and -2 μmol m⁻² s⁻¹ for the overstorey and understorey, respectively. In these conditions, the understorey participates to 20% of daytime overall assimilation. Contrary to what is observed for latent heat fluxes (Fig. 4.3 and 4.4), air dryness does not influence CO₂ assimilation in well-watered conditions. Together, this means that the stomatal conductance of the understorey is relatively constant, so that the latent heat flux increases with VPD while the CO₂ flux does not change. When the soil water deficit becomes larger, the tree carbon uptake is higher at low VPD (Fig. 7.5) and lower at high VPD (Fig. 7.6) while the understorey carbon uptake is lower at low VPD and slightly larger at high VPD. Therefore, in water-stressed conditions the understorey participation raises from 4% to 30 % as the air dries and the overstorey stomata close up. Again, this is well connected with the transpiration of understorey vegetation, which is low in wet air conditions (Fig 4.5) and higher in dry air conditions (Fig. 4.6). The percentage of standard deviation from the maximum values of CO₂ fluxes varies from 51 to 100% above the canopy and 79 and 560% under the canopy. The highest uncertainty occurs in winter with low VPD, when the fluxes are close to 0.

During the night, the ecosystem respiration is larger above (2.1-4 μmol m⁻² s⁻¹) than below (0.6-1.1 μmol m⁻² s⁻¹) the canopy, leading to needle and bole respiration rates from 1.1 to

$3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$. These results should be considered carefully because the estimates below the canopy are usually representative of a much smaller area than the measurements above the canopy (Baldocchi, 1997; Wilson and Meyers, 2001). This often leads to an underestimation of understory CO_2 efflux when compared to chamber measurements (Norman et al., 1997; Kabwe et al., 2005), although some authors (Law et al., 1999) found a good agreement between both methods. However, averaging half-hourly values over several days should decrease the errors caused by the presence of heterogeneities under forest canopies (Baldocchi and Meyers, 1991).

The annual ecosystem carbon budget is negative (-57 gC m^{-2} ; Fig. 6b). During the year, the bottom layer is generally a source of carbon, with an annual budget is $+74 \text{ gC m}^{-2}$, except from mid-June to late August when grass photosynthesis is larger than soil respiration. On a yearly basis, the overstorey behaves as a sink of -131 gC m^{-2} . It is noteworthy that it acts as a source of carbon between January and May, which is unusual at this site. Generally, photosynthesis is higher than respiration rate, resulting either in negative or slightly positive cumulative carbon flux pattern at the beginning of the year. It has to be pointed out that this unusual pattern observed in 2002 results in a very low annual ecosystem carbon uptake compared to other years at this site. Indeed, the annual CO_2 sequestration was between -400 and -500 gC m^{-2} during the 1997 and 1998 studies (Berbigier et al., 2001). Soil water availability in winter is twice as low as usually observed at this site, thus possibly reducing pine photosynthesis and increasing respiration in 2002. The substantial litterfall observed in February may have altered the photosynthesis capacity of the forest crown in winter and subsequent months, during the growing season. Medlyn et al. (2002) showed that the biochemical potential of photosynthesis of maritime pine needles is still high in winter, although it depends on temperature.

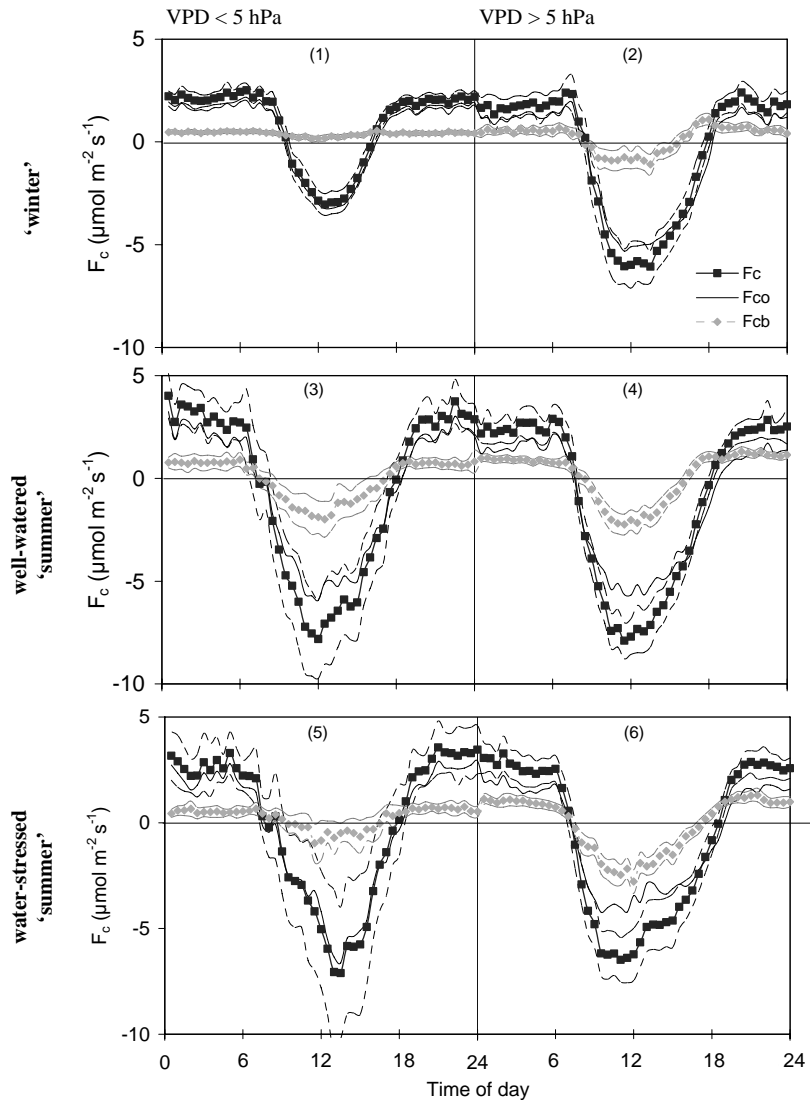


Figure 7. Mean daily course of CO₂ fluxes above, F_c , and below, F_{cb} , the canopy averaged over the six classes defined in Table 1. F_{co} is the CO₂ flux of the overstorey, deduced from the difference between the two levels. The classes are numbered from top left (1) to bottom right (6). 'Winter' refers to the period between early May to late October and 'summer' to the rest of the year. VPD < 5 hPa stands for wet air conditions and VPD > hPa for dry air conditions. 95% confidence intervals (lower and upper) for F_c (black dotted line) and F_{cb} (grey dotted line) are also indicated.

3.6 Seasonal variation in GPP and respiration

Total daily GPP varies from 1 to 4 gC m⁻² during winter and reaches 10 gC m⁻² during summer, with significant depletion in stressed conditions (Fig. 8). Understorey GPP exhibits large variations between winter and summer, following the growth of the main understorey species, *i.e.* the purple moor grass that reaches its maximum LAI in July. However, it did not appear to decrease in the presence of a soil water deficit and varied between 2 and 5 gC m⁻² from early May to late August. It can be seen from F_c fluxes that understorey GPP is not zero during winter, which confirms the existence of a slight photosynthesis activity of the other species composing the understorey at this period. We conclude that understorey GPP plays a

significant role in the annual variations of total ecosystem GPP. Tree GPP, estimated as the difference between the total and understorey GPP, varies between 2 gC m⁻² in winter and 6 gC m⁻² in summer. As noticed for latent heat fluxes, the annual sum of GPP is also low in 2002, about 40% less than for the 1997-1998 period analysed by Berbigier et al (2001) and Medlyn et al (2005). The lag of the understorey GPP behind the pines compared to the overstorey GPP is explained by the respective phenology of the species. Understorey LAI peaks on day 210 which explains the pattern of understorey GPP and R. Also, the understorey species is largely not sensitive to soil drought. Conversely, the pine's GPP decreases at the onset of soil drought on day 170.

The daily respiration of the ecosystem ranges from 2 to 8 gC m⁻² while that of the understorey ranges from 0 in winter to 4 gC m⁻² in summer (Fig. 8). Partitioning respiration among the two canopy layers reveals the large proportion of respiration originating from the overstorey and the relatively low contribution of the understorey (Table 3). On an annual basis the overstorey layer indeed contributes to almost two thirds of the ecosystem respiration. Considering that trees also contribute to the bottom layer respiration through their root system, we conclude that autotrophic respiration largely dominates the respiration flux in 2002. On an annual basis respiration is reduced to a smaller extent than GPP, resulting in a dramatic decline in the annual net ecosystem exchange, that reaches its lowest annual value over the whole period 1997-2006 (unpublished results) and makes the site close to neutral in 2002. It has to be noticed that the discrepancies between measured F_c and values estimated from GPP-R for each canopy layer (Table 3) are rather small and can be attributed to the uncertainty on model parameters.

Table 3. Partitioning of the annual sum of carbon flux components for each ecosystem compartment expressed in gC m⁻² y⁻¹. F_c are values measured by eddy covariance.

	F_c	GPP	R	GPP -R
Total	-57	1167	1088	79
Understorey	74	295	354	-59
Tree layer	-131	872	734	-138

Coinciding with radiation variations, total GPP is almost three times as large in 'summer' as in 'winter' under wet conditions but under dry conditions it shows comparatively little variation (Fig. 9). GPP partitioning between the overstorey and understorey compartments varies according to seasonal and weather classes. Overstorey GPP, *i.e.*, the difference between the two measurement levels, is sensitive to climate and soil water. It peaks in 'summer' at low

VPD (Fig. 9.3 and 9.5), and it is strongly diminished by soil water deficit at high VPD (Fig. 9.6). Understorey GPP is significant only during the growing season of the main species, the purple moor grass. It shows little sensitivity to the levels of vapour deficit under well-watered conditions in ‘summer’. However, it increases with VPD levels in ‘winter’ and decreases with VPD levels in ‘summer’ under water-stressed conditions, in agreement with the behaviour of latent heat flux (Fig. 5). As opposed to the current understanding of the effect of soil water deficit on photosynthesis (Granier et al., 2007), the understorey GPP is even maximum for the class of low soil water and high VPD and it almost equals the pine GPP (Fig. 9.6). Indeed, the understorey layer appears to be well decoupled from the prevailing weather conditions so that gaseous exchanges from the bottom layer are mainly conditioned by its LAI dynamics and the radiation regime (Loustau et al., 1998). We conclude that the annual course of total GPP is actually the result of contrasted behaviour of its two components, with an enhanced contribution of the understorey in mid-summer and predominance of the pine photosynthesis in winter, spring and autumn (Fig. 8). Whether this pattern changes from year to year in relationship with the soil water regime will be further analyzed.

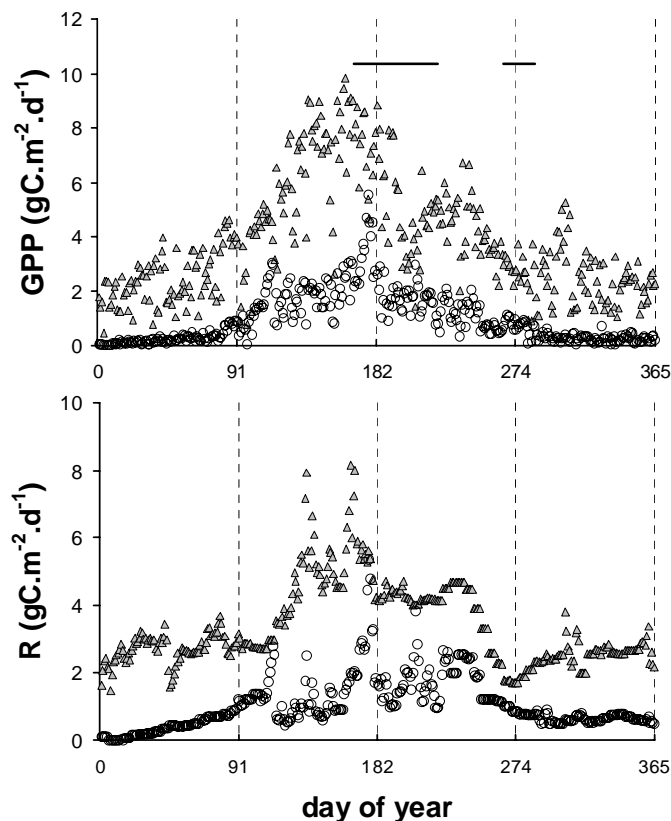


Figure 8. Annual course of daily gross primary productivity, GPP, and respiration, R, for the entire ecosystem (triangles) and the bottom layer (Molinia grass and soil, open circles), as estimated from the CO₂ fluxes at the two levels. Horizontal bars in the top graph delineate the periods where the soil water content was below 65 mm.

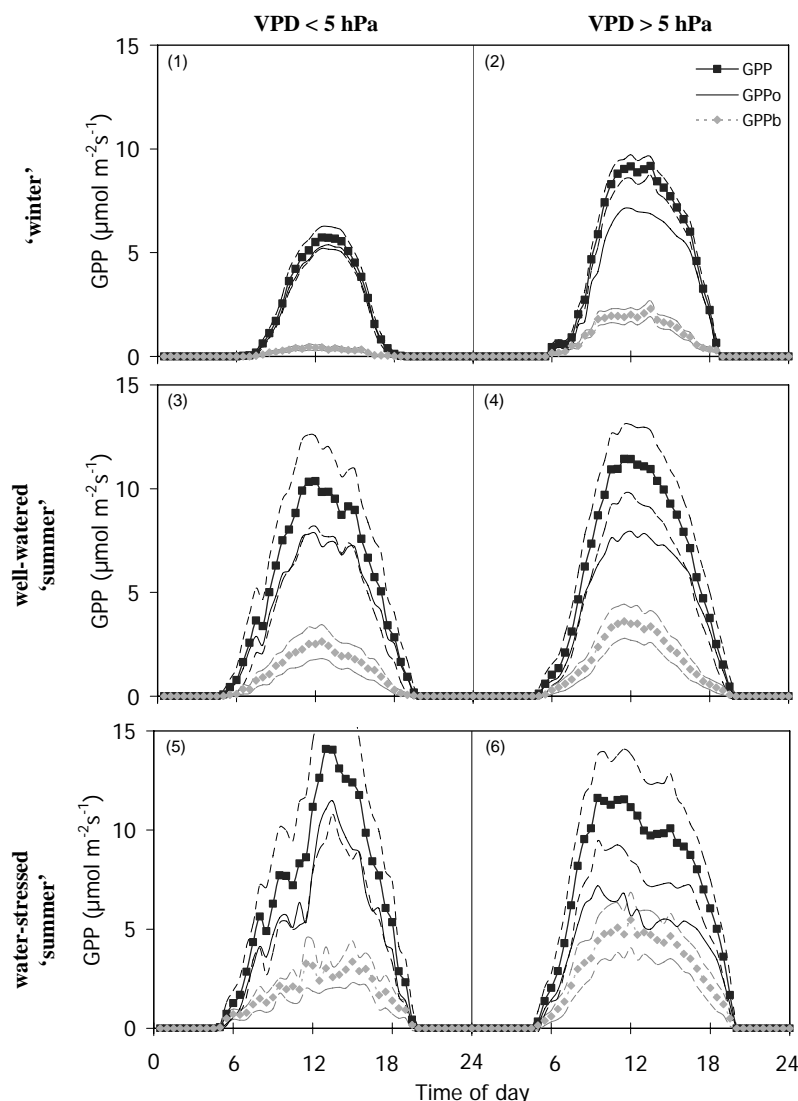


Figure 9. Mean daily course of gross primary productivity, GPP, above the canopy (black symbols), below the canopy (grey symbol) and of the difference between the two levels (broken line) averaged over the six classes defined in Table 1. The classes are numbered from top left (1) to bottom right (6). 'Winter' refers to the period between early May to late October and 'summer' to the rest of the year. VPD < 5 hPa stands for wet air conditions and VPD > hPa for dry air conditions. 95% confidence intervals (lower and upper) for GPP (black dotted line) and GPP_b (grey dotted line) are also indicated.

3.7 Water use efficiency

To further investigate the response of the maritime pine forest ecosystem to drought, we examined the water use efficiency for each weather class (Table 4). As expected, WUE increases in summer with increasing soil water deficit and decreases with increasing VPD. The pine tree canopy uses water more efficiently than the understorey, whose contribution to the overall ecosystem WUE is low. It has to be pointed out that the understorey evaporation includes both water use by the vegetation and soil evaporation, which may account for this difference between the two canopy layers.

Also, the fact that understorey photosynthesis and transpiration shows a reduced sensitivity to climate and soil as well as inefficient stomatal control is consistent with its lower water use efficiency. On the other hand, it contrasts with the pine behaviour which exhibits a drought avoidance strategy with earlier stomatal limitation of water loss under dry conditions (Loustau et al., 1996; Picon et al., 1996).

Table 4. Ecosystem, understorey (index b) and overstorey (index o) water use efficiencies (WUE) expressed in mmol C mol H₂O⁻¹ for the weather classes defined in Table 1. The calculation was made over the whole data set.

	WUE	WUE _b	WUE _o
1	3.6	0.9	3.9
2	2.9	2.2	2.8
3	3.5	2.4	3.4
4	3.2	2.1	3.2
5	4.1	3.6	3.8
6	3.5	3.1	3.2
year	3.3	2.3	3.2

4 SUMMARY AND CONCLUSIONS

CO₂, water and energy exchanges were investigated above and within a maritime pine forest during the year 2002, which displayed a period of unusual reduced soil water availability, lasting from winter 2001/2002 to the beginning of October 2002. The energy balance closure was found adequately good at both levels, to the exception of an underestimation of turbulent fluxes at low radiation levels above the canopy and an underestimation of net radiation at the soil surface. At the bottom level, the underestimation of net radiation was attributed to the difficulty in accurately estimating the leaf area index in a coniferous forest, which is a challenge for future years.

We showed that the annual course of overall fluxes resulted from contrasted dynamics of the overstorey and understorey layers, according to meteorological conditions. In response to the reduced soil water availability, the ecosystem dissipated much less energy via latent heat flux and more as sensible heat flux as compared with what is usually observed at this site. Moreover, because of the openness of the maritime pine forest, the understorey canopy was responsible for a significant and variable component of the total water vapour and carbon dioxide fluxes. The contribution of the understorey might be as large as 45% of the overall evaporation and 30% of the daytime overall assimilation during summer with a significant

soil water deficit. Even in winter, CO₂ fluxes from the forest floor were not negligible. However, due to the noteworthy deficit in soil water during winter, the maritime pine ecosystem behaved as a source of carbon during the first months of the year. This led to a low annual value of ecosystem GPP, 40% less than usually observed at this site, and a high overstorey respiration, almost two thirds of the ecosystem respiration.

During summer drought, the grass species composing the understorey and the maritime pine trees adopted different strategies in response to soil water deficit. Pine trees followed a drought-avoiding strategy while the grasses did not exhibit a clear marked control on the understorey evaporation.

We observe that the short term heat and drought period that occurred during the summer of the following year, 2003 (Ciais et al. 2005), depleted the carbon balance of the site much less than what was induced in 2002 by the long lasting soil water deficit. Indeed in 2003, even though the pines may have released CO₂ during the summer heat and drought, the forest recovered quickly and the annual pattern in 2003 was not as affected as it was in 2002.

This study is being extended to other years in order to draw additional conclusions on the long-term behaviour of this two-layer canopy, and detect the effects of climatic anomalies like heat and drought events experienced in 2003 and 2005. Higher frequency of similar events is expected in the future.

Acknowledgements

This work was partly supported by the CarboEurope-IP project.

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