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The carbon balance of a young Beech forest

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Summary

1. We present measurements of CO_2 fluxes over 2 years above and within a young Beech stand in the east of France. This site is part of the Euroflux network set up to monitor fluxes over representative European forests.

2. The net ecosystem carbon (C) exchange was derived from continuous eddy flux measurements. Major components of the total flux (i.e. soil and above-ground biomass respiration and assimilation of leafy branches) were measured independently using chambers. The main C stocks (i.e. root, stem and branch biomass) were also quantified.

3. Daily minima of CO_2 flux were typically around –20 μmol CO_2 m^{-2} s^{-1} during the period of full leaf expansion, while night-time ecosystem respiration varied between 5 and 15 μmol CO_2 m^{-2} s^{-1}. The seasonal pattern of net ecosystem assimilation was very close to that of net assimilation at the single branch scale. The seasonal variation of net ecosystem exchange was closely related to leaf expansion and soil water content during the dry year of 1996.

4. Measurements of ecosystem respiration (eddy flux) were corrected for CO_2 storage within the stand. This C flux showed a seasonal pattern, the maximum rates (4–7 g C m^{-2} day^{-1}) occurring in spring and summer, and appeared to be correlated with soil temperature. Temporal variation of soil respiration showed the same pattern, and effects of both temperature and soil drying were found. Annual soil respiration was ≈ 70% of ecosystem respiration. Root respiration was 60% of the total below-ground respiration.

5. Annual net C exchange was –218 and –257 g C m^{-2} in 1996 and 1997, respectively, corresponding to net C uptake by the forest. These values are much lower than the annual biomass increment (stems and large roots) of the stand: 427 and 471 g C m^{-2} $year^{-1}$, respectively. The difference may be explained by a release of CO_2 from the decomposition of woody debris.

6. Ecosystem C loss by respiration was 800–1000 g C m^{-2} $year^{-1}$. Gross C gain was 1000–1300 g C m^{-2} $year^{-1}$. Ecosystem respiration therefore played a major role in the annual C balance of this forest.

Key-words: Biomass, eddy covariance, *Fagus sylvatica*, forest ecosystem, respiration

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Introduction

To elucidate the influence of forests on the global carbon (C) cycle and their response to the increase in atmospheric CO_2 concentration ($[CO_2]$), the main CO_2 sinks, sources and stocks of C must be quantified more accurately. CO_2 emissions from fossil fuel burning plus the release of C from deforestation represent ≈ 7·1 Pg C $year^{-1}$ for 1980–89, while the corresponding increase in atmospheric CO_2 is only ≈ 3·2 Pg C $year^{-1}$ (Houghton *et al.* 1996). This imbalance is attributed to C sequestration by oceans and vegetation, although the relative importance of each C sink is unknown. Large variations in the C sequestration capacities of various forest ecosystems have been reported (Nabuurs & Mohren 1995). These variations depend

on climate, species, site productivity and sylvicultural regime. Temperate and boreal forests may sequestrate ≈ 0·7 Pg C year^{-1} (Dixon *et al.* 1994; Jarvis 1995), so reducing the rate of CO_2 release to the atmosphere. Recent estimates show that forest plantations fix ≈ 0·2 Pg C year^{-1} (Winjum & Schroeder 1997). However, the estimates of global fluxes are highly uncertain, and there is a need for direct measurements of these fluxes.

In order to obtain more information on C fluxes over and within forests, the European research programme Euroflux ('long-term carbon dioxide and water vapour fluxes of European forests and interactions with the climate system') was initiated in which a large-scale network of 15 representative forest sites was set up, from western oceanic to continental zones, and from boreal to Mediterranean countries (Baldocchi *et al.* 1996; Tenhunen *et al.* 1998). This programme aims: (1) to characterize and analyse CO_2, energy and water fluxes over representative forest sites in relation to climate, species and stand structure, to provide functions and parameters for global models, and (2) to quantify the sink strength of these forests for CO_2 and its spatial and temporal variation.

This paper presents the results obtained from 2 years of measurements in a young Beech stand. Different methodologies were used to evaluate independently the major components in the forest C balance. C fluxes estimated at different spatial scales (leaf, branch and stand) are compared. A companion paper (Granier, Biron & Lemoine 2000) deals with the water balance of the same forest stand.

Materials and methods

SITE

The experimental plot (Euroflux site FR02) is in the state forest of Hesse, France (48°40′ N, 7°05′ E), in a stand composed mainly (90%) of naturally established Beech (*Fagus sylvatica* L.; see Table 1). Other tree species represented are *Carpinus betulus* L., *Betula pendula Roth*, *Quercus petraea* (Matt.) Liebl., *Larix decidua* Mill., *Prunus avium* L. and *Fraxinus excelsior* L. The stand is on a site of good productivity in the first class of Schober's yield table for Beech which predicts a mean increment of 9 m^3 ha^{-1} year^{-1} at age 100 years (Le Goff 1981). The experimental plot (0·6 ha) was in the central part of a 65-ha zone composed mainly of young Beech. The plot and the surrounding stands were thinned 2 years before C flux measurements began. Most of the root biomass was in the top 40 cm of soil, but roots < 1 mm diameter occurred down to 150 cm.

Three towers were erected. One (18 m high) was used for eddy covariance (EC) and microclimate measurements. The two others (15 m high) were devoted to ecophysiological measurements. Sixty subplots were defined for geostatistical studies of soil and vegetation. Nine of these were used for soil respiration and temperature measurements and 12 others for measurements of tree girth and height.

Table 1. Stand characteristics of the Hesse forest

Stand density (stems ha^{-1})	3480
Stand age in 1996 (years)	30
Mean height of Beech stand (m)	13
Mean girth per tree (cm)	24
Dry weight of trunks (kg ha^{-1})	64500
Dry weight of branches (kg ha^{-1})	11400
Dry weight of leaves (kg ha^{-1})	2400
Dry weight of roots (kg ha^{-1})	15200
Total dry weight (kg ha^{-1})	93500
Understorey vegetation	sparse
Ground area (m^2 ha^{-1})	20·7
Topography	plateau
Slope (%)	<5
Elevation (m above sea level)	300
Soil type	luvisol/stagnic luvisol
Soil clay content (%) 0–0·1 m depth	25–35
Soil clay content (%) > 0·1 m depth	40
Mean annual rainfall (mm)	820
Mean annual temperature (°C)	9·2

CLIMATE AND MICROCLIMATE

The following instruments were installed above the stand, at 18 m: a net radiometer (REBS, Seattle, WA, USA), a solar radiometer (Model CE-180, Cimel, Paris, France), a ventilated psychrometer (manufactured in-house and equipped with Pt 100 temperature sensors), a rain-gauge (Model ARG 100, Campbell Scientific, Logan, UT), and a switching anemometer (Vector Instruments, Rhyl, UK).

Within and below the canopy we measured: global radiation at heights of 12, 10, 8 and 1 m using 33-cm-long linear radiometers (INRA, Versailles, France); trunk and branch temperatures of one tree at four heights (1·5, 6, 8 and 10 m); soil heat flux using two heat flux transducers (REBS) at −5 cm; soil temperature at −10 cm (five replicates) and in one vertical profile (−5, −10, −20, −40 and −80 cm) in a central plot using copper/constantan thermocouples. Each of the five trees on which net C assimilation was measured was fitted with two 30-cm-long linear PAR sensors constructed from 20 amorphous silicon cells each 4 × 10 mm (Solems, Palaiseau, France).

Data were acquired every 10 s and 30-min averages were stored (Model CR7 datalogger, Campbell Scientific, Courtaboeuf, France).

SOIL WATER CONTENT

Soil water content was measured weekly. During 1996 and 1997, volumetric water content (θ) was measured with a neutron probe (NEA, Ballerup, Denmark) in eight aluminium access tubes, six of which were 160 cm long, and two of which were 240 cm long. In 1997, a time-domain reflectometer (TDR; Trase system, Soil Moisture, Santa Barbara, CA) was also

used to measure the soil water content in the upper soil layers. Twelve 40-cm-long stainless steel wave guides were used, two of which were placed in the middle of each of the six plots used for soil respiration and temperature measurements. Relative extractable water in the soil (REW; $m^3\ m^{-3}$) was calculated using the average θ in the 0–160 cm soil layer as: $(\theta - \theta_m)/(\theta_F - \theta_m)$, where θ_m and θ_F are the volumetric minimum water content and the water content at field capacity, respectively. θ_F was taken as the average observed θ during the winter when soil was refilled, and θ_m was estimated from retention curves. REW varies between 0 (soil dry) and 1 (field capacity).

LEAF AREA INDEX

The leaf area index (LAI) was estimated for each of the two years by litter collection in autumn, using 42 square litter traps each covering 0·25 m^2. Litter dry mass was measured weekly during the period of collection (from the beginning of October to the end of December). A subsample of leaves was collected every 2 weeks to estimate leaf area (Delta-T Area meter, Delta–T, Cambridge, UK), in order to convert dry mass into leaf area. Mean LAI was $\approx 5{\cdot}6 \pm 0{\cdot}5\ m^2\ m^{-2}$ averaged over both years. Seasonal variations in LAI were derived from the absorption of global radiation by the canopy (see below) using the Beer–Lambert law and an extinction coefficient of 0·4. LAI was also calculated from direct sampling on 23 representative trees (see below); this method gave a mean LAI of $4{\cdot}9 \pm 0{\cdot}4\ m^2\ m^{-2}$ averaged over both years.

BIOMASS AND BIOMASS INCREMENT

Biomass equations were developed from a sample of 23 representative trees near the experimental stand. Fresh weights of stem, branch and foliage were measured in the field, and dry weights obtained from oven-dried samples. Relative biomass increments of stem and branch sections were obtained from the last 5-year wood increments measured on the samples.

The root systems of a subsample of 16 trees were excavated mechanically. A mechanical digger excavated around the root systems, with trunks being cut at the base of the tree, and then the stump was pulled up carefully and the root system cleaned. Fresh weights of coarse and small roots (diameter 2 mm) were obtained after washing soil from the roots. Biomass and biomass increment of the root systems were obtained from the measurements of the last 5-year wood increments and the dry weights of root samples (Le Goff & Ottorini 2000).

Equations relating tree girth at breast height to biomass data were obtained. Total above-ground and below-ground biomass and the annual biomass increment of the woody parts of the experimental stand were derived from stand girth distributions and from these equations, for 1996 and 1997. Total stand biomass increments (±95% confidence limits) were $10\ 400 \pm 1530\ kg\ ha^{-1}$ and $11\ 300 \pm 1580\ kg\ ha^{-1}$ in 1996 and 1997, respectively.

Biomass data were then converted into C mass, using the following equivalents (Santa Regina *et al.* 1997): 1 kg dry matter = 0·44 kg C in stems, roots and branches and 0·457 kg C in leaves.

Fine root biomass (< 2 mm diameter) was estimated at the stand level from eight soil cores (i.d. 8 cm, depth 12 cm) collected monthly from March to July 1997. Cores were stored in plastic bags at 4 °C until fine roots were washed free of soil, sorted into apparently living and dead fractions and dried at 60 °C for 48 h. Fine root growth into 14 root-free cores was used to estimate annual fine root production from the amount of root that had grown into each core in 1 year (Persson 1983). Soil cores (i.d. 8 cm, depth 12 cm) were taken in March 1997, all roots were carefully removed, and the sifted soil was replaced in the hole. In April 1998, the cores were retrieved and processed as above. These estimations of fine root biomass and annual fine root production were corrected for the spatial and vertical variations of fine root biomass, assuming that fine root biomass in soil cores represented 45% of the total fine root biomass (Epron *et al.* 1999b).

Tree girths were measured manually at breast height every 2 weeks on all trees in the 12 subplots used for growth measurements (541 trees). Five trees were fitted with automatic dendrometer bands, installed at three heights on the stem: breast height, at the base of the living crown, and at the middle of the stem.

ECOSYSTEM GAS EXCHANGE

Water vapour and CO_2 fluxes were measured by EC (Leuning & Moncrieff 1990) at 18 m, i.e. 3 m above the mean tree height, from a tower in the middle of the plot. Air was drawn from the top of the tower via an inlet, which was equipped with a 0·2-μm PTFE filter (Model Spiralcap, Pall-Gelman, Ann Arbor, MI, USA) at the base of a 3D anemometer (Solent, Model R2, Gill Instruments Ltd, Lymington, UK), through a 30-m long PTFE tube (4 mm i.d.). Air was sucked through the tube by two piston pumps in series (Model Rotronic 406G, Reciprotor, Skara, Sweden). The pumps were 180 V AC powered, instead of 220 V, to reduce warming. The flow rate of 6 $dm^3\ min^{-1}$ was monitored by a mass flow controller (Model 5850, Brooks, Veenendaal, Netherlands). Water vapour and CO_2 concentrations were measured with a CO_2/H_2O infra-red gas analyser (IRGA; Model 6262, Li-Cor Inc., Lincoln, NE). Dry, CO_2-free reference air was provided for the IRGA using a diaphragm pump (Model TD3LS, Brailsfort, New York, NY) driving air through two columns of CO_2 absorbant and desiccant, respectively. Calibration was performed periodically: zero was checked weekly and span every 3 months. Drift was 1 μmol mol^{-1}. Wind speed and gas concentration were scanned at

10 Hz. EDISOL software (University of Edinburgh, Edinburgh, UK) was used to calculate on-line sensible heat, CO_2 and water fluxes. The moving average time constant was 200 s. An average 6% loss of CO_2 fluxes was observed between 0·1 and 1 Hz. Raw data were corrected using a relationship between CO_2 flux loss and wind speed.

EC measurements started on 20 May 1996 [day of year (DOY) 141]. By 31 December 1996, 160 out of 226 days (70%) had yielded reliable data. In 1997, we obtained reliable data for 318 days (87%). Some data (1·8% of the total) were excluded if: (1) sensible heat fluxes were abnormally large, corresponding to measurements during rainfall or when the 3D anemometer was wet, or (2) filters were partially blocked, restricting the air flow. We checked that eliminated data were distributed randomly so that no bias was introduced to the C flux estimations. Spectral and cospectral analyses were performed periodically to check the quality of flux measurements. Full energy balance was not achieved even if latent heat flux was corrected (Aubinet *et al*. 1999) for losses at > 0·5 Hz and if heat storage in air and in vegetation was taken into account using the relation $\Phi_L + H + H_s + G = 0{\cdot}88\ R_n$ (where Φ_L, H, H_s, G and R_n are the latent heatflux, sensible heat flux, heat storage in the air and in the vegetation, heat flux in the soil, and net radiation, respectively, in W m^{-2}). Fetch limits were estimated (Gash 1986) as 509 and 77 m from the tower for 90 and 50% of the fluxes, respectively.

CO_2 PROFILES

To quantify the CO_2 stored or released by the forest, [CO_2] was monitored at four additional heights within and below the canopy. Air was sucked through 2-mm i.d. PTFE tubes with 1-μm PTFE filters (Model ACRO 50, Pall-Gelman, Ann Arbour, MI, USA) installed at 0·2, 0·7, 2 and 8 m above ground level. A piston pump (Reciprotor 406 G, Reciprotor, Skara, Sweden) drove air to an IRGA (see above) at a flow rate of 1 $dm^3\ min^{-1}$. Five solenoid valves, driven by a datalogger (see above), allowed sequential measurement of [CO_2] at each height, plus one for zero measurement (air passing through soda lime). The duration of a complete cycle was 15 min. Variation in CO_2 content per unit of ground area within the 0–18 m air layer was calculated every 30 min.

BRANCH GAS EXCHANGE

Three branch bags were used to monitor CO_2/H_2O exchange of branches during the 1997 growing season (25 April to 4 November). Two bags were placed at the top of the canopy (13 m above ground level) and a third was placed at 7 m. Each bag comprised a rigid frame covered with polypropylene film, 0·25 m^3 in volume. Between measurements, air was blown through the bags (at 0·045 $m^3\ s^{-1}$) to minimize overheating. During measurements, bags were closed for 3 min and used as cuvettes operating as a closed system. Bags were scanned sequentially every 30 min and monitored by a datalogger (see above). The CO_2 depletion in the bags was measured using an IRGA (see above) operating in absolute mode, and the H_2O increase was measured using capacitive sensors (Model HMD 30YB, Vaisala OY, Helsinki, Finland). PAR and air temperature were also measured inside the bags. A similar system was described previously by Dufrêne, Pontailler & Saugier (1993) and used in the BOREAS project (Saugier *et al*. 1997).

LEAF NET CO_2 ASSIMILATION

Net C assimilation by leaves was measured throughout the growing season using a portable system IRGA (LI-6200, Li-Cor Inc., Lincoln, NE) on five trees surrounding one of the towers, from different crown classes: two dominant (i.e. tall trees in which most of the crown is sun-exposed), one co-dominant (medium-sized), and two intermediate (small) trees. Those measurements were made under ambient light on all five trees at two heights in the crowns (≈ 1/3 and 2/3 of the crown extent) on 2–4 leaves selected randomly from branches fitted with linear PAR sensors.

Scaling of net C assimilation to the tree and to the stand was carried out as follows: (1) response curves to PAR were derived from leaf measurements for each tree and each height; (2) response curves plus continuous PAR records were used to calculate photosynthesis per unit of leaf area during the season; (3) we assumed that maximum C assimilation per unit leaf area increased linearly for 30 days from budburst to full leaf expansion, and that the reverse occurred during leaf senescence for 30 days; (4) scaling net C assimilation to the stand was carried out from the areas of sun and shade leaves of each crown class, the total leaf area being estimated as 2·6, 1·6 and 1·5 $m^2\ m^{-2}$ for dominant, co-dominant and intermediate/suppressed trees, respectively.

Gross C assimilation was calculated as the difference between net C assimilation and diurnal leaf respiration. The diurnal leaf respiration rate was assumed to be equal to nocturnal leaf respiration. We also assumed that leaf respiration represented half of the respiration by the aerial biomass, and was calculated as $R_{ag} = R_{eco} - R_s$ (see Lebaube *et al*. 1999), where R_{ag} is the above-ground respiration (g C $m^{-2}\ s^{-1}$), R_{eco} is the ecosystem respiration (g C $m^{-2}\ s^{-1}$), and R_s is the soil respiration, including roots and heterotrophic organisms (g C $m^{-2}\ s^{-1}$).

SOIL AND ROOT RESPIRATION

Six subplots each of ≈ 100 m^2 were chosen randomly within the experimental plot for soil CO_2 efflux measurements. Two further 3-m^2 subplots (2 × 1·5 m) containing no trees were established in June 1996 by

Table 2. Characteristics of stem CO_2 efflux measurements at 1·3 m and in the crown

	Characteristics of CO_2 efflux measurements	
	at 1·3 m	in the crown
Chamber	acrylic (5 sizes)	glass (3 sizes)
Stem diameter class (cm)	12–25, 25–32, 32–36, 36–44	0·25–1·3, 1·3–2·5
Measurement period	2–3 days per month (March 1997–February 1998)	continuous (May 1997–November 1997)
Time-step (h)	1·5–2·0	1·5
IRGA system	CIRAS-1, PP-Systems, Stotfold, UK	6262, Li-Cor, Lincoln, NB, USA
Operating mode	manual closed system	automatic open system

digging a trench (1 m deep) around each subplot, lining the trench with a polyethylene film and backfilling the soil. Soil CO_2 efflux was measured with a portable IRGA connected to a chamber (0·854 dm^3 volume; 0·72 dm^2 ground area; Norman, Garcia & Verma 1992). The chamber edge was inserted into the soil to a depth of 1·5 cm. After measuring $[CO_2]$ over the soil surface, $[CO_2]$ within the chamber was reduced by 15 μmol mol^{-1}, and the subsequent increase in $[CO_2]$ recorded for 60 s. Every 2–4 weeks, 12 such measurements were made on each subplot from 0800 to 1600 h local time. Daily means ($n = 72$ for the main plot and 24 for the trenched plots) and confidence intervals ($P = 0·05$) were calculated.

The proportion of soil respiration originating from roots was calculated by subtracting the CO_2 efflux in trenched plots and taking account of the decomposition of roots killed by trenching. Fine root decomposition was estimated by coring and sorting the remaining dead roots in the trenched plots 2 years after trenching. The remaining fine root necromass was compared with initial fine root biomass and necromass in soil cores. Coarse roots (2–10 mm diameter) excavated during trenching were washed free of soil, cut into pieces 4–6 cm long and placed into 10 × 15 cm litter bags (1 mm mesh size). These were then buried in soil at 10–15 cm depth. Fourteen litter bags were collected on each of five occasions during a 20-month period. Roots were carefully washed free of soil and dried at 60 °C for 5 days. Exponential decay functions ($M_t = M_0 e^{-kt}$) were fitted to the data, where M_t and M_0 are, respectively, the remaining and the initial root dry mass, t is time and k is the decay constant. C loss as CO_2 during root decomposition was calculated as $(1 - a)cM_0(1 - e^{-kt})$, where the initial C concentration in roots, c, was assumed to be 44%, a is the fraction of C which is incorporated into soil organic matter (SOM), and $1 - a$ is the fraction lost as CO_2 by microbial respiration during initial decay. a was assumed to be 0·22 (see Epron *et al*. 1999a).

ABOVE-GROUND WOOD RESPIRATION

Respiration from above-ground wood was estimated by measuring stem CO_2 efflux using IRGAs and two-piece cylindrical chambers (see Table 2). Measurements were made at 1·3 m on 15 representative trees of five different diameter classes and also in the crown of a single tree (at three heights). All chambers were covered with aluminium foil to avoid photosynthetic refixation by bark. This simplified the modelling of respiration for estimation of wood CO_2 efflux at the stand scale. The protocols for measurements at 1·3 m and in the crown are given in Table 2. The diurnal temperature variation was related to that of CO_2 efflux (R expressed either as wood volume or wood area) by an exponential equation expressed in terms of Q_{10} (the change in rate for a 10 °C change in temperature):

$$R = R_{15} Q_{10}^{[(T-15)/10]}, \qquad \text{eqn 1}$$

where R_{15} is the respiration at 15 °C (base temperature) and T is the air temperature (°C).

To obtain estimates throughout 1997, we used half-hourly air temperatures and monthly values of Q_{10} and R_{15}. Because global estimates of respiration are often derived from measurements at only one height, we considered two integration methods: (1) the Q_{10} and R_{15} coefficients were taken as the values measured on stems at 1·3 m and applied to both stems and branches, or (2) values measured at 1·3 m were applied to stems and those measured in the crown were applied to branches. Both volume- and area-based estimates were made. To estimate the wood volume and area of the stand, we used tree density, tree diameter at 1·3 m and allometric relationships (Schnock 1983; Bartelink 1997). This gave ratios of branch volume to total volume of 12% and branch area to total area of 70–85% depending on tree diameter.

Results

NET ECOSYSTEM CO_2 EXCHANGE

A typical time-course of net ecosystem exchange is shown in Fig. 1. Maximum CO_2 uptake over the forest was typically *c*. –20 μmol CO_2 m^{-2} s^{-1} during full leaf expansion, but some peaks at –30 μmol CO_2 m^{-2} s^{-1} occurred. (The convention of a negative flux for uptake

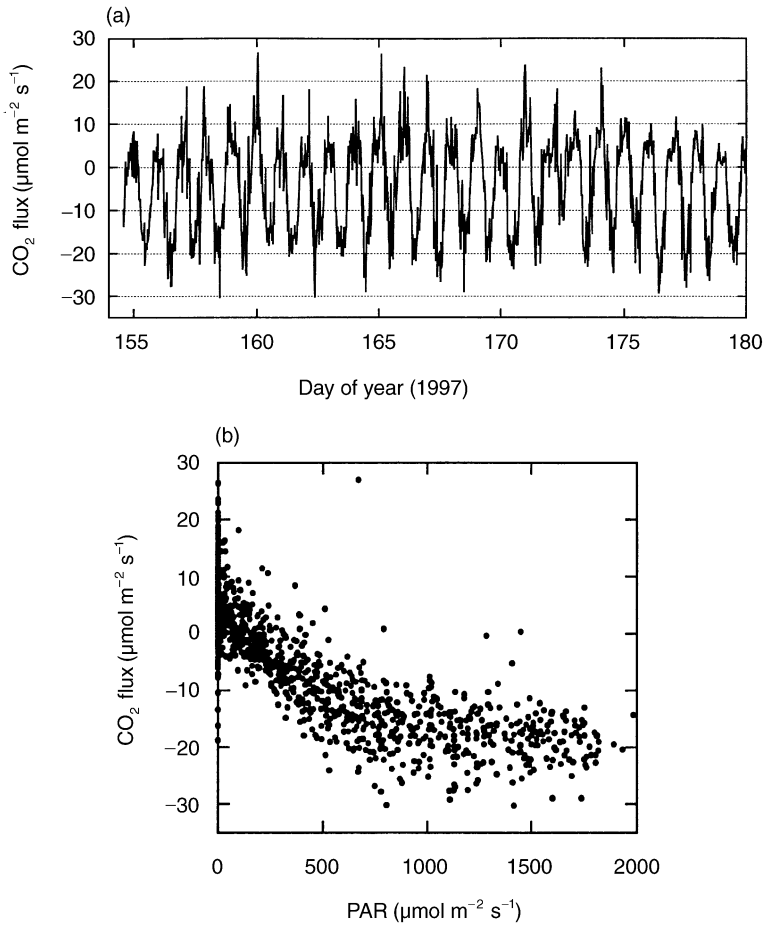

Fig. 1. (a) Time–course of net CO_2 flux above the Beech stand (Euroflux site FR02, Hesse forest, France) from 4 to 28 June 1997. Data were averaged half-hourly and corrected for CO_2 storage in the 0–18 m air layer. (b) Relationship between CO_2 flux and incident PAR for the same period.

and a positive flux for release is used here). We also found a curvilinear relationship between net ecosystem production (NEP, g C m^{-2} s^{-1}) and incident PAR during the day and faster C assimilation under diffuse radiation (e.g. cloudy days) than in direct sunshine. Increases in vapour pressure deficit decreased NEP by closing stomata. During this period, ecosystem respiration was ≈ 5–15 µmol CO_2 m^{-2} s^{-1} at night, but some peaks exceeded 20 µmol CO_2 m^{-2} s^{-1}.

The time-course of daily NEP is shown in Fig. 2. A sharp increase in CO_2 fixation (i.e. NEP more negative) occurred in spring 1997, corresponding to rapid leaf expansion and increased photosynthesis. Within ≈ 33 days, NEP changed from 0 (DOY 122) to *c.* –700 mmol CO_2 m^{-2} day^{-1} (i.e. –8·4 g C m^{-2} day^{-1}). During late summer, ecosystem C fixation decreased slowly (NEP less negative) because of a seasonal decrease in incoming PAR and drying of the soil.

NET CANOPY CO_2 EXCHANGE

Because of technical problems, one of the branch bags at the top of the canopy produced faulty measurements in July and August 1997; otherwise, it provided results similar to those from the other upper bag.

Under saturating light, C assimilation (per unit leaf area) for branches at the top of the canopy was close to that of single leaves, *c.* –9 µmol CO_2 m^{-2} s^{-1}. This rate decreased steadily from the end of May. The maximum C assimilation of the shaded branch was about half that of sunlit branches. Mean daily assimilation of top branches, per unit leaf area, was *c.* –0·3 mol CO_2 m^{-2} day^{-1} from May to July and decreased thereafter (Fig. 3). That of the shaded branch was more stable, *c.* –0·1 mol CO_2 m^{-2} day^{-1}.

Nocturnal respiration of branches decreased from 2·5 to 1 nmol CO_2 gDM^{-1} s^{-1} between May and September (0·8–0·3 µmol CO_2 m^{-2} s^{-1}, per unit leaf area).

From these data, we can estimate the net C assimilation of the canopy (A_n) for the whole growing season (considering leaves and fine branches only). This estimate, which depends on the distribution of sunlit and shaded leaves, was performed over 191 day (from DOY 117 to 307 in 1997) using LAI = 5·6. Assuming that A_n decreased linearly from the top to the bottom of the canopy, we obtain a net C exchange of –1930 g C m^{-2} (ground area). Assuming also that 2/3 of the leaf area was shaded and the rest sunlit, and weighting data from the upper and lower bags accordingly, a smaller estimate of A_n is obtained: –1640 g C m^{-2}. These large values are explained by the photosynthetic rate of the branch in the lower bag being relatively fast despite the small amount of radiation incident on it: 5–10% of incident PAR.

Using these data and respiration rates measured on small branches at the same site, we estimated the respiration of the leaves alone. First, leaf respiration was computed as total bag respiration minus wood respiration for periods of no photosynthesis (0000 to 0530 h local time). Then, Q_{10} and R_{15} values were computed and applied to branch bag data obtained during the day. Over the entire leafed period (from DOY 120 to 305), total leaf respiration was ≈ 240 g C m^{-2} (60 g C m^{-2} at night).

ECOSYSTEM RESPIRATION

We assumed that the respiration of the ecosystem, R_{eco}, could be estimated (as R_E, ecosystem respiration estimated from eddy covariance; g C m^{-2} s^{-1}) by EC over the whole day when trees had no leaves, or at night when leaves were present. A problem is that this measurement is affected by CO_2 storage in the air layer from the soil surface to the height at which EC is measured (18 m). To determine the effect of this, we plotted R_E against friction velocity, u^* (Aubinet *et al.* 2000), for a period when temperature and soil water content were stable, i.e. steady respiration rates were likely. R_E increased with u^* (Fig. 4), indicating that a fraction of CO_2 flux was not

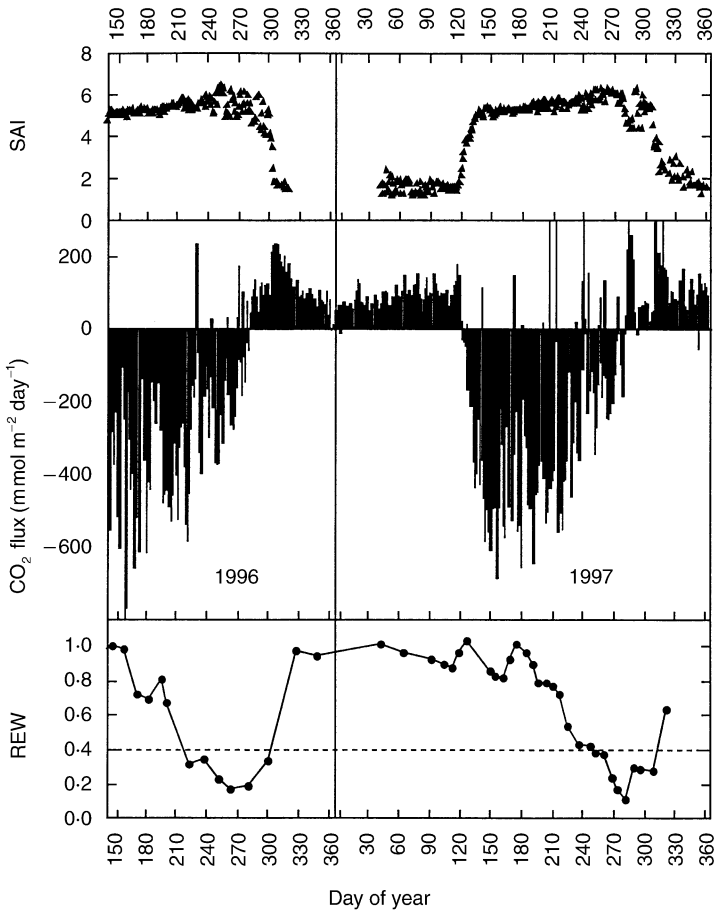

Fig. 2. Top: seasonal course of stem plus leaf area index (SAI), calculated from global radiation intercepted by the canopy. Middle: daily net CO_2 exchange above the Beech stand over 2 years. Gaps caused by missing or unreliable data were filled using functions relating NEP to PAR (for daylight hours during the leafed phase) or to soil temperature (otherwise). Negative values indicate C fixation by the forest ecosystem, and positive values indicate loss of C. Bottom: relative extractable water in the soil (REW) calculated from neutron probe measurements in the 0–60 cm soil layer. REW = 0·4 corresponds to the critical soil water below which stomatal closure occurs.

measured by EC at slow u^*. The CO_2 content of the air between 0 and 18 m, and its temporal variation, were calculated. Figure 5 shows that CO_2 accumulation occurred frequently at night when wind speed was low, while CO_2 release was observed during the day as wind speed increased. When wind speed remained $> 0{\cdot}5\ m\ s^{-1}$ during the night (indicated by an asterisk in Fig. 5), there was little day-to-night variation in CO_2 content. Diurnal variation in CO_2 content was much lower during the unleafed period. This was because the air was cooler than during the spring and summer, leading to slower respiration rates, and there was more ventilation and air mixing within the stand.

Half-hourly CO_2 flux data, for the periods when CO_2 profiles were measured, were corrected (R_E*) by adding the variation in CO_2 content within the 0–18 m air layer to the measured CO_2 flux above the stand. R_E* was not correlated significantly with u^*. For the whole of 1997, failure to account for CO_2 storage/release would have underestimated R_E by ≈ 12%.

R_E* during the leafed period was extrapolated to the whole day by assuming that it depended only on temperature, i.e. we assumed that the relationship between respiration and temperature was the same during the day and the night. This assumption is questionable for leaves because mitochondrial respiration is depressed by 40–90% during the day (Brooks & Farquhar 1985). Multiple sources of C efflux over a stand make it impossible to relate R_E* to a single temperature measurement: soil plus root respiration would depend closely on soil temperature, while aboveground respiration would probably be related to air or trunk temperature. We tested the dependence of R_E* on soil, trunk and air temperatures: the best fit

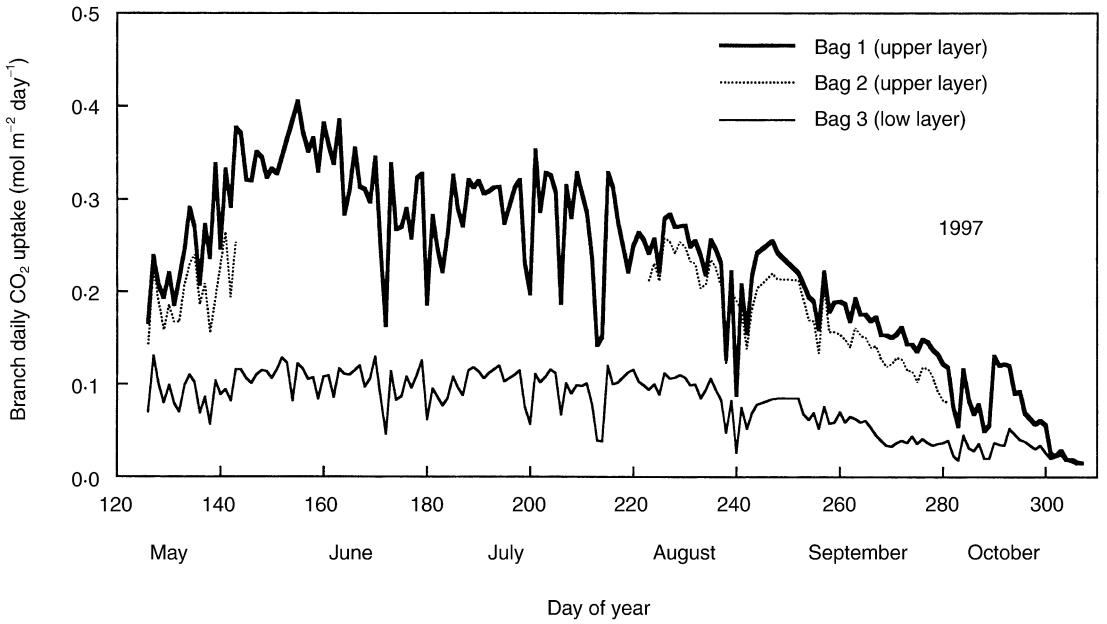

Fig. 3. Daily C balance of three branches over the 1997 growing season. Measurements were made using branch bags. Bags 1 and 2 were at the top of the canopy. Bag 3 was in a low layer. Rates are expressed per unit leaf area.

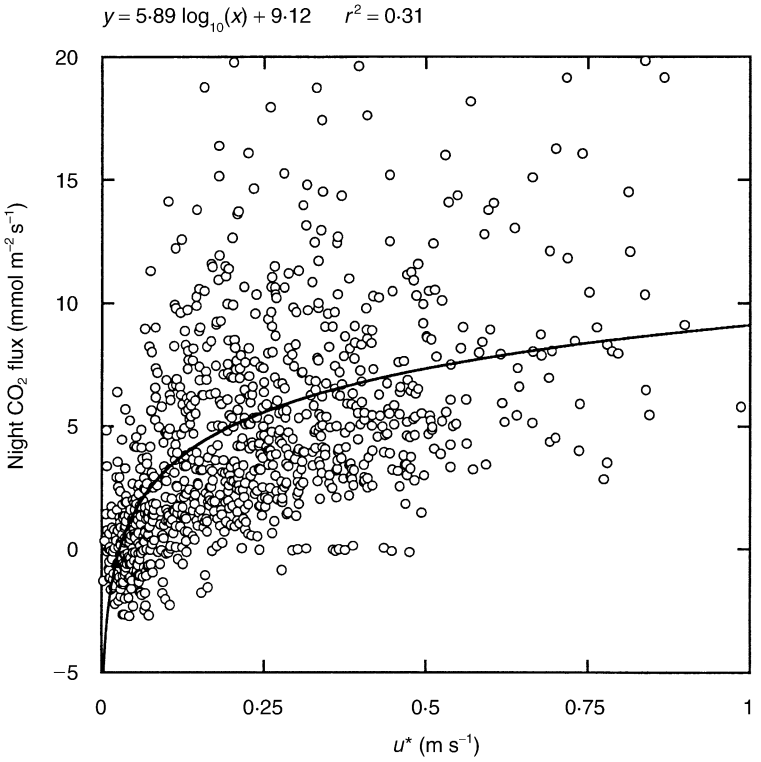

Fig. 4. Nocturnal CO_2 flux above the Beech stand as a function of friction velocity (u^*) during a period of stable temperature (14–17 °C) and soil water content (REW > 0·7). The curve is the fitted function: CO_2 flux = 5·89log(u^*) + 9·12 (r^2 = 0·31).

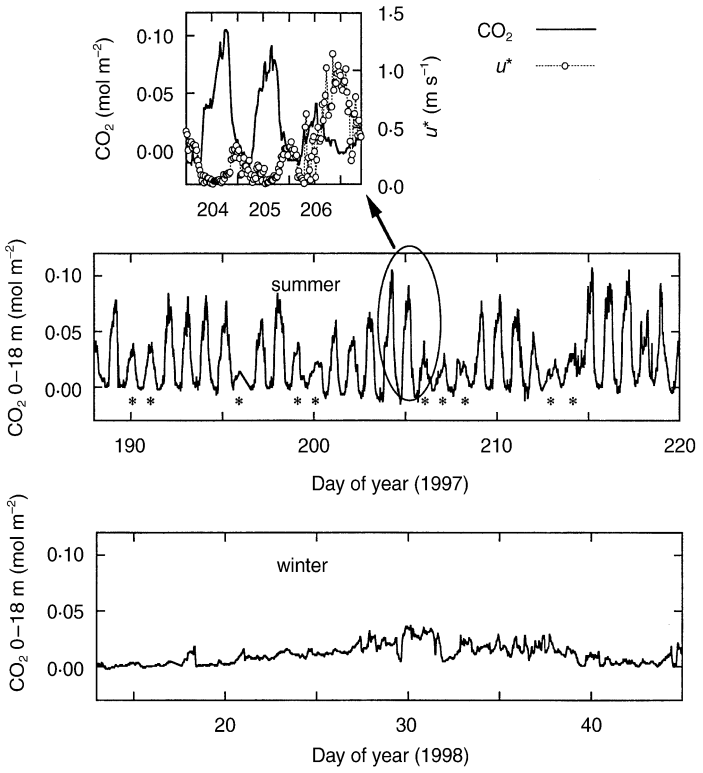

Fig. 5. Time–course of CO_2 storage in the 0–18 m layer in the Beech stand calculated from [CO_2] at five heights (0·2, 0·7, 2·0, 8·0 and 18·0 m) in the stand over 32-day periods in summer and winter. CO_2 storage is the difference between instantaneous CO_2 content minus minimum CO_2 content measured during the period. The enlarged section of the graph shows the simultaneous variation of CO_2 storage and of u^* over a 3-day period. Asterisks correspond to $u^* > 0{\cdot}5$ m s^{-1} at night.

(see Fig. 6) was obtained with soil temperature (°C) at –10 cm (T_{-10}):

$$R_E^* = 0{\cdot}531 \times 10^{0{\cdot}057 T_{-10}} \quad (r^2 = 0{\cdot}57;\ n = 448). \qquad \text{eqn 2}$$

The temporal variation of R_E^* is shown in Fig. 7. To smooth the large day-to-day scattering, which might be due to measurement errors, to the effect of rain showers that often occurred at night, or to an unknown cause, a moving 10-day average was calculated. After budburst (DOY 120), R_E^* increased rapidly (Fig. 7) up to a maximum rate of ≈ 7 g C m^{-2} day^{-1}, at around DOY 170 (19 June 1997), corresponding to the period of maximum tree growth. Thereafter, R_E^* remained between 4 and 7 g C m^{-2} day^{-1} until DOY 250 (7 September 1997). Several periods of slower rates were noted, some linked to a decrease in soil temperature. Soil respiration on different dates and simulated above-ground respiration (R_{ag}) are also presented in Fig. 7. They show roughly the same pattern, and are closely related to soil temperature. There was little respiration during several warm periods, for example on DOY 210–230 and DOY 260–270; this decrease could have been caused by soil drying. Nevertheless, in contrast to the situation for soil respiration (see below), accounting for soil water content did not improve the fit of R_E^* to soil temperature.

SOIL RESPIRATION

The frequency of soil respiration measurements allowed the 95% confidence intervals to be < 10% of the daily means, despite large spatial variability. In August 1997, the minimum was 0·9 μmol m^{-2} s^{-1} while the maximum was 8·6 μmol m^{-2} s^{-1}. Daily means of soil CO_2 efflux ranged from 0·4 μmol m^{-2} s^{-1} in winter to 4·1 μmol m^{-2} s^{-1} in August. This large seasonal variation could be explained only partly by seasonal changes in soil temperature (Fig. 6; r^2 = 0·79). In summer, strong reductions in soil CO_2 efflux were associated with soil drying, as observed in September 1997 (see Fig. 7). Soil respiration was best described with an empirical model including θ_v, the volumetric soil water content, and T_{-10}, the soil temperature (°C), each measured at –10 cm:

$$R_S = 1{\cdot}13 \theta_v e^{0{\cdot}136 T_{-10}} \quad (r^2 = 0{\cdot}86;\ n = 20). \qquad \text{eqn 3}$$

Using this equation, the annual soil respiration was calculated as 575 g C m^{-2} $year^{-1}$ for 1996 and 663 g C m^{-2} $year^{-1}$ for 1997. In 1997, annual soil respiration on the trenched plots was 500 g C m^{-2} $year^{-1}$. Including the decomposition of roots killed by trenching and the difference in soil water content between the main and trenched plots (Epron *et al.* 1999b), the heterotrophic component of soil C efflux was calculated as ≈ 260 g C m^{-2} $year^{-1}$, representing 40% of the total soil C efflux, with root respiration accounting for the rest (i.e. 400 g C m^{-2} $year^{-1}$).

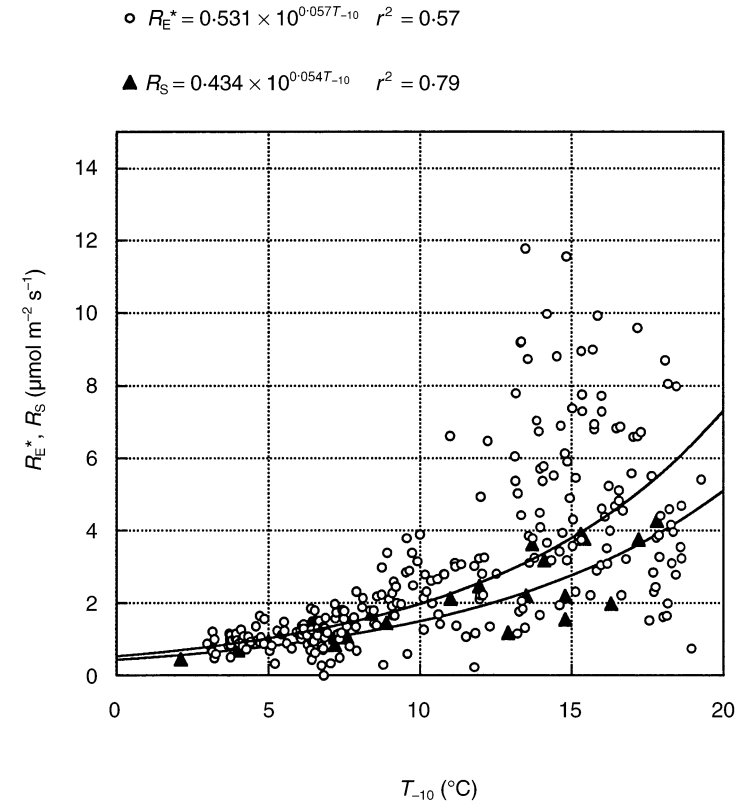

Fig. 6. Relationship of ecosystem respiration (R_E*), corrected for CO_2 storage in the 0–18 m air layer (see text), and soil respiration (R_s) to soil temperature at –10 cm (T_{-10}). R_E* data are averaged over a night during the leafed phase or over a whole day during the unleafed phase.

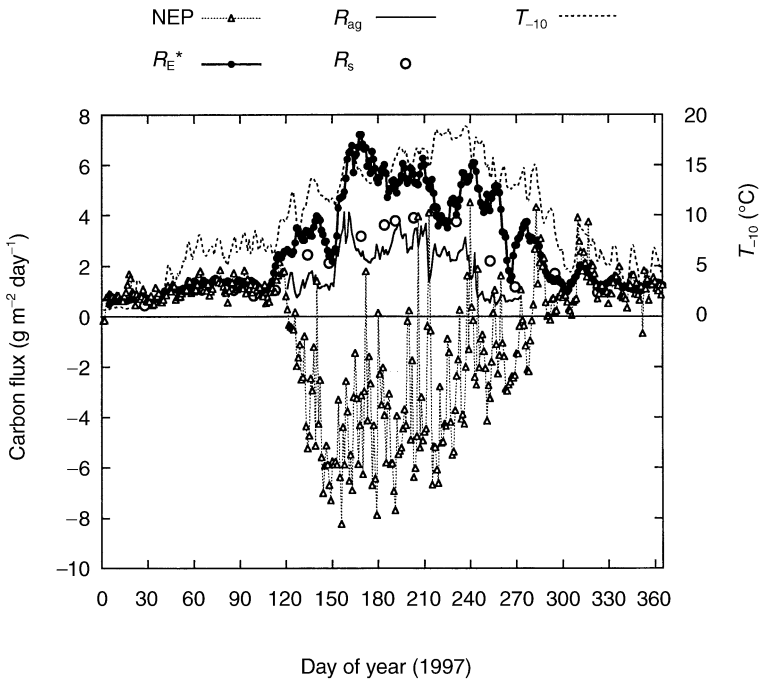

Fig. 7. Time–courses of net ecosystem C exchange (NEP), corrected ecosystem respiration (R_E*, see text), above-ground respiration (R_{ag}) and soil respiration (R_s) during 1997. R_E* is a moving 10-day average. R_{ag} is the simulation of above-ground wood respiration derived using volume-based Q_{10} and R_{15} obtained at 1·3 m (for stems) or in the crown (for branches). Also shown is soil temperature at a depth of –10 cm (T_{-10}).

ABOVE-GROUND WOOD RESPIRATION

For stem CO_2 efflux at 1·3 m, Q_{10} was always stable (data not shown). The annual mean was 1·7 (n = 105, SD = 0·45). Means were usually between 1·6 and 1·8. In contrast to Q_{10}, R_{15} showed large monthly variations. The minimum occurred in February (10·4 μmol CO_2 m^{-3} s^{-1} ≡ 0·2 μmol m^{-2} s^{-1}) and the maximum in July (132 μmol CO_2 m^{-3} s^{-1} ≡ 3 μmol CO_2 m^{-2} s^{-1}). For branch CO_2 efflux, Q_{10} was usually 2–3. Similarly to the results for stems, at 1·3 m branch R_{15} values in summer exceeded those in winter. Maxima (on a volume basis) were measured on the narrowest branches (2400 μmol CO_2 m^{-3} s^{-1}). On an area basis, maximum rates occurred in the thickest branches (3 μmol CO_2 m^{-2} s^{-1}). At the stand level, total annual estimates varied according to the calculation method. The use of volume-based Q_{10} and R_{15} calculated from data measured in the crown led to larger annual estimates than those obtained using only volume-based parameters calculated from data collected at 1·3 m. Annual totals estimated from area-based Q_{10} and R_{15} were much larger than those estimated using volume-based parameters, except when using parameters calculated from data for the smallest diameter of branch (level 3) (Table 3). A seasonal simulation using volume-based parameters (at 1·3 m in the crown at level 2) is shown in Fig. 7.

SYNTHESIS–CARBON BALANCE FROM CO_2 FLUXES *VS* STAND GROWTH

The terms for the annual C balance are shown in Table 4 for the 2 years of observations. In 1996, measurements started at the beginning of May; our estimates are given for the period from 1 May 1996 to 30 April 1997.

Gross primary productivity (GPP = NEP + R_{eco}; g C m^{-2} s^{-1}) calculated from scaled leaf measurements was 1298 g C m^{-2} year^{-1} in 1997, i.e. ≈ 4% more than the GPP obtained from EC, which was 1245 g C m^{-2} year^{-1}. Given the underlying assumptions (especially for respiration estimates) and the different sources of errors (leaf and branch sampling, scaling errors, etc.), these estimates are surprisingly close.

Dendrometric measurements allowed the amount of C stored yearly in aerial and below-ground biomass of trees to be calculated. In 1997, this was 498 g C m^2 year^{-1} for the total stand biomass increment (stems, branches and major roots). From these data, and assuming that the C stock did not vary over the year, we computed another estimate of annual GPP (in 1997) by adding: (1) net annual C gain in wood (= 498 g C m^{-2} year^{-1}); (2) the amount of C corresponding to the annual leaf (C_L) and fine root (C_R) production (= 131 and 57 g C m^{-2} year^{-1}, respectively); (3) respiration losses by aerial plus below-ground biomass. The last term was assumed to equal R_{eco} (= 988 g C m^{-2} year^{-1}) minus C released from

Table 3. Annual totals of respiration by above-ground wood (R_{ag}). Estimates were calculated using monthly volume- or area-based Q_{10} and R_{15}. The Q_{10} and R_{15} used were only those from stems at 1·3 m or from stems in the crown (at three levels: 1, 2, 3, at which stem diameters were 2·5, 1·3 and 0·25 cm, respectively)

		R_{ag} (g C m^{-2} soil)	
Q_{10} + R_{15} derived from	Q_{10} + R_{15} applied to	Volume-based Q_{10} + R_{15}	Area-based Q_{10} + R_{15}
stems at 1·3 m	stems + branches	235	810
stems at 1·3 m	stems	202	202
stems at 1·3 m + level 1	stems + branches	378	1073
stems at 1·3 m + level 2	stems + branches	311	549
stems at 1·3 m + level 3	stems + branches	894	554

Table 4. Annual C fluxes over and within the Beech stand. Values are in g C m^{-2} year^{-1}. Abbreviations are given in the text

		Period of measurement	
Variable	Method	May 1996–April 1997	January 1997–December 1997
NEP	EC	–218	–257
NPP*	NEP-$R_{heterotrophic}$	–448	–522
GPP	EC	–1011	–1245
GPP	Leaf measurements	–1178	–1298
GPP	Sum of C fluxes (see text)		–1409
R_{eco}†	EC	793	988
R_s	Chambers	575	663
$R_{heterotrophic}$	Trenched plots	230	265
R_{roots}	R_s – $R_{heterotrophic}$	345	398
$R_{ag\ (living\ wood)}$	Chambers		311–378
R_{ag}	R_{eco} – R_s		325
Biomass increment‡		456	498

*NPP = net primary productivity (g C m^{-2} s^{-1}).
†In 1996, ecosystem respiration was not corrected for changes in CO_2 content in the 0–18 m air layer.
‡Includes below-ground biomass.

SOM decomposition (40% of 663 g C m^{-2} year^{-1} = 265 g C m^{-2} year^{-1}, i.e. 723 g C m^{-2} year^{-1}). Heterotrophic respiration exceeds the sum of litter production plus fine roots (turnover) = 188 g C m^{-2} year^{-1}, which may indicate that inputs to SOM from coarse woody detritus cannot be ignored (Raich & Nadelhoffer 1989). For 1997, this calculation gave:

$$GPP = C_B + C_L + C_R + R_{eco} - R_{heterotrophic};$$

$$GPP = 471 + 131 + 57 + (988 - 723)$$
$$= 1409 \text{ g C m}^{-2} \text{ year}^{-1}.$$

This estimate of GPP exceeds the 1245 g C m^{-2} year^{-1} derived from EC (Table 4). The former may have been overestimated because we did not take into account C losses from the decomposition of coarse dead wood.

However, there is a large discrepancy between the annual C increment of the stand (498 g C m^{-2} year^{-1}) and NEP (–257 g C m^{-2} year^{-1}). In addition to multiple measurement errors, which are difficult to quantify, at least part of this difference (241 g C m^{-2} year^{-1}) could be attributed to dead wood decomposition. Another possible explanation is litter accumulation in the soil. This was not observed at Hesse: the litter from the previous year had disappeared completely before leaf fall. Nevertheless, some C could progressively accumulate in the upper soil layers, but we did not make any measurements to determine whether this was the case.

Discussion

Peak NEP over our Beech stand was –20 to –30 µmol CO_2 m^{-2} s^{-1}. This is similar to the fluxes measured by EC in various broad-leaved stands over a wide range of latitudes and tree species: –18 to –25 µmol CO_2 m^{-2} s^{-1} in a temperate mixed forest at Harvard (Wofsy *et al.* 1993; Goulden *et al.* 1996), –20 to –30 µmol CO_2 m^{-2} s^{-1} in a mountain Beech forest (Valentini *et al.* 1996), –25 µmol CO_2 m^{-2} s^{-1} in an Aspen (*Populus tremuloides*) forest in the boreal zone (Black *et al.* 1996), –20 µmol CO_2 m^{-2} s^{-1} in a tropical rainforest (Grace *et al.* 1995), and –23 µmol CO_2 m^{-2} s^{-1} in a mixed deciduous forest in Canada (Lee *et al.* 1996).

Nocturnal CO_2 fluxes are more variable among sites. Several authors have reported respiration fluxes similar to those observed at Hesse: 8–10 µmol CO_2 m^{-2} s^{-1}

Table 5. Estimated values of *R*eco (μmol m^{-2} s^{-1}) at three soil temperatures

Reference	Forest type	Soil temperature (°C)		
		10	15	20
Greco & Baldocchi (1996)	Mixed deciduous	2·48	3·16	4·02
Goulden *et al*. (1996)	Mixed deciduous	2·36	3·40	4·90
Black *et al*. (1996)	Aspen boreal	3·41	7·91	18·3
Valentini *et al*. (1996)	Beech	1·65	2·43	3·58
This study	Beech	1·97	3·80	7·33

in the Harvard forest (Goulden *et al*. 1996), 9–11 μmol CO_2 m^{-2} s^{-1} in an Aspen forest (Black *et al*. 1996), and 6–9 μmol CO_2 m^{-2} s^{-1} in a Mediterranean *Quercus ilex* forest (Piñol, Alcaniz & Roda 1995). Others found smaller nocturnal CO_2 fluxes: 2–6 μmol CO_2 m^{-2} s^{-1} in a mountain Beech stand (Valentini *et al*. 1996), 2–7 μmol CO_2 m^{-2} s^{-1} in a *Nothofagus* forest (Hollinger *et al*. 1994), and 4–5 μmol CO_2 m^{-2} s^{-1} in a Brazilian savannah (Miranda *et al*. 1997).

Several authors calibrated a function of soil temperature to their measurements. We applied their functions for simulating R_{eco} at three temperatures: 10, 15 and 20 °C (Table 5). Our estimates of R_{eco} are much larger than those obtained for an Italian Beech stand (Valentini *et al*. 1996), whatever the temperature; above 15 °C, R_{eco} is also larger than that obtained for two North American mixed forests (Goulden *et al*. 1996; Greco & Baldocchi 1996). However, estimates made by Black *et al*. (1996) in a boreal Aspen forest were much larger than ours.

In Table 6, our estimates of annual NEP, GPP and R_{eco} are compared with other estimates (obtained using the same methods). The largest NEP and GPP were found for productive coniferous plantations of Douglas Fir (Vermetten *et al*. 1994) and *Pinus radiata* (Ryan *et al*. 1996). Our estimates of GPP and NEP are similar to those reported for other broad-leaved forests: –1000 to –1300 g C m^{-2} $year^{-1}$ and –100 to –500 g C m^{-2} $year^{-1}$ for GPP and NEP, respectively. Our estimates of R_{eco} are greater than those obtained elsewhere.

Annual NEP varies from one site to another, even between those with similar climates. This variation is explained at least partly by large differences in stand growth and soil respiration. For instance, in temperate ecosystems, annual NEP ranges between –210 g C m^{-2} $year^{-1}$ (Harvard forest, Goulden *et al*. 1996) and –1300 g C m^{-2} $year^{-1}$ (Douglas Fir forest, Vermetten *et al*. 1994). Our site had a comparatively small NEP of –257 g C m^{-2} $year^{-1}$ (even smaller in 1996, a drier year), probably because of its large annual R_{eco} of *c*. 1000 g C m^{-2} $year^{-1}$. Ecosystem respiration is a crucial term in the C balance, varying between 50 and 90% of gross assimilation (80% in our study). In tropical forests, large values of R_{eco} compared with GPP have also been reported (Grace *et al*. 1995); those, too, resulted in a small NEP, of –102 g C m^{-2} $year^{-1}$.

Total soil respiration is often considered an important component of the C balance of an ecosystem. Our estimates of this flux were 600–700 g C m^{-2} $year^{-1}$, similar to other estimates: 800 g C m^{-2} $year^{-1}$ (Hanson *et al*. 1993); 485 g C m^{-2} $year^{-1}$ (Simmons *et al*. 1996); 720 g C m^{-2} $year^{-1}$ (Davidson, Beck & Boone 1998). At Hesse, soil respiration accounted for ≈ 70% of R_{eco} and 55% of GPP. This agrees with data from other sites indicating that soil respiration represents 60–80% of total ecosystem respiration (Wofsy *et al*. 1993; Goulden *et al*. 1996; Davidson, Beck & Boone 1998). R_{eco} reflects the respiration associated with at least three major components: soil (heterotrophic), root, and above-ground biomass. Root and heterotrophic respiration cannot be separated easily, because they

Table 6. Estimates (g C m^{-2} $year^{-1}$) of GPP, NEP and R_{eco} in various forest ecosystems

Reference	Site	Species	LAI	GPP	NEP	R_{eco}
Baldocchi *et al*. (1997)	BOREAS	*Pinus banksiana*	1·9–2·2		–47	
Black *et al*. (1996)	BOREAS	*Populus tremuloides*	5·1*	–1020	–130	890
Cannell *et al*. (1996)	Ireland	*Fagus*, coniferous				740
Frolking *et al*. (1996)	BOREAS	*Picea mariana*			–51	
Goulden *et al*. (1996)	Harvard, USA	Mixed deciduous			–210	
Grace *et al*. (1995)	Amazonia	Tropical rainforest			–102	
Greco & Baldocchi (1996)	Oak Ridge, USA	*Quercus, Acer*	4·9	–1085	–525	560
Ryan *et al*. (1996)	Camberra, Australia	*Pinus radiata*	3–4·6†	–2440 to –3440		
Valentini *et al*. (1996)	Italy	*Fagus sylvatica*	4·7	–1016	–472	544
Vermetten *et al*. (1994)	Netherlands	*Pseudotsuga menziesii*	8–10		–1045 to –1543	
Wofsy *et al*. (1993)	Harvard, USA	Mixed deciduous		–1110	–370	
This study (1996)	Eastern France	*Fagus sylvatica*	5·7	–1011	–218	793
This study (1997)	Eastern France	*Fagus sylvatica*	5·6	–1245	–257	988

*Overstorey + understorey.
†Projected LAI.

are evaluated from chamber measurements and scaled to the stand. We estimated that root respiration was the major component (60%) of soil C efflux at Hesse. A similar estimation was reported by Ewel, Cropper & Gholz (1987) for a *Pinus elliottii* plantation.

As shown in Table 3, there are difficulties in scaling R_{ag} to the stand from chamber measurements. These difficulties concern: (1) choosing the unit that best expresses respiration; (2) properly expressing the percentage of branches relative to stems, and (3) integrating the respiration variability along the stem and between stems and branches. Because our measurements of volume- and area-based stem R_{15} were not constant between breast height and crown level, we estimated R_{ag} using measurements obtained at both levels. One independent estimation of growth respiration was made using stem plus branch growth measured on the site (J.-M. Ottorini & N. Le Goff, data not shown), assuming a growth efficiency [defined as growth/(growth + growth respiration), with terms usually expressed in g C] of 0·65. We obtained R_{ag} = 202 g C m^{-2} year^{-1}. As maintenance respiration generally represents ≈ 40% of total respiration, we assumed a total respiration of 420 g C m^{-2} year^{-1}. Another estimate of R_{ag} calculated as the difference between R_{eco} (EC) and R_s (soil chambers) gave R_{ag} = 325 g C m^{-2} year^{-1}. These two estimates provide a reasonable order of magnitude estimate of R_{ag}. Consequently, our annual total of 235 g C m^{-2} year^{-1} obtained using only volume-based parameters from stems at 1·3 m probably underestimated the true value. Area-based parameters obviously overestimate R_{ag}. Our best estimates were probably those obtained using volume-based parameters from stems at 1·3 m and the two largest branch diameters in the crown (levels 1 and 2). These estimates fall within those found in the literature. Edwards & Hanson (1996) estimated R_{ag} in a mixed Oak and Red Maple stand, growing under warmer and wetter conditions than those in the present study, to be 149–204 g C m^{-2} year^{-1}. For conifers in different climates, Ryan *et al*. (1995) found annual totals of 52–162 g C m^{-2} year^{-1}. Larger values (910 or 1314 g C m^{-2} year^{-1}; Whitmore 1984; Müller & Nielson 1965; cited in Ryan *et al*. 1994) were found in rain forests. Because we did not take bark assimilation into account, we probably overestimated the wood CO_2 efflux. Accurate estimations of this flux are now required.

C sequestration in forest stands can also be estimated from forest inventories. We calculated an annual C immobilization of ≈ 400–500 g C m^{-2} year^{-1} in above- and below-ground biomass. In Ireland, Cannell *et al*. (1996) found a mean immobilization of 190 g C m^{-2} year^{-1} in Beech stands of various ages and at several sites. In a mountain Beech forest, Valentini *et al*. (1996) found that 238 g C m^{-2} year^{-1} was stored in the above-ground biomass.

GPP is related to the amount of solar radiation intercepted by the canopy. Ruimy, Dedieu & Saugier (1996) showed that, as a first approximation, GPP was equal to the product of intercepted PAR and a biological conversion efficiency of 0·02 mol C mol^{-1} photons ≡ 1·1 g C MJ^{-1} PAR. At Hesse, incident global radiation (R_g) from DOY 125 to 300 in 1997 was 2752 MJ m^{-2} ≡ 1376 MJ PAR m^{-2} assuming PAR/R_g = 0·5. If 95% of incoming PAR was absorbed, this gives a GPP of $1376 \times 1{\cdot}1 \times 0{\cdot}95$ = 1438 g C m^{-2} year^{-1}, a larger estimate than that derived from EC (1245 g C m^{-2} year^{-1}) or leaf measurements (1298 g C m^{-2} year^{-1}; Table 4), but smaller than that calculated from branch bag measurements over the growing season (net assimilation of the canopy over 191 days: 1640–1930 g C m^{-2}). Thus, the estimate of GPP remains relatively uncertain.

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