



# Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany

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## Abstract

Unmanaged forests at a late stage of successional development are considered to be insignificant as carbon sinks, since in theory, assimilation is thought to be balanced by respiration. However, little experimental evidence for this hypothesis exists so far for forests at the ecosystem level. Therefore, we performed continuous eddy covariance measurements of carbon dioxide over an unmanaged beech forest in the Hainich National Park in Central Germany as part of the EU project CARBOEUROFLUX. This forest shows typical characteristics of an ‘advanced’ forest with large dead wood pools, a diverse stand structure and a wide tree age class distribution, up to 250 years. This forest was a large carbon sink over 2 years, with 494 g C m<sup>-2</sup> per year in 2000 and 490 g C m<sup>-2</sup> per year in 2001. Daytime summer fluxes were strongly controlled by photosynthetic photon flux density ( $R^2 = 0.7\text{--}0.9$ ), with minor effects of the ratio of diffuse to total downward radiation or the vapor pressure deficit. Nighttime CO<sub>2</sub> fluxes were mainly controlled by soil temperature ( $R^2 = 0.8$ ) and soil moisture. In addition, high nighttime CO<sub>2</sub> fluxes (4–6 μmol m<sup>-2</sup> s<sup>-1</sup>) were found directly before and during bud break in spring as well as just after leaf fall of both years (2000 and 2001), reflecting stand physiology corresponding to phenological changes, independent of soil temperature. Additional wind profile measurements at five heights within the canopy revealed a decoupling of above and below canopy air flow under conditions of low friction velocity ( $u^* < 0.4 \text{ m s}^{-1}$ ), probably indicating down slope drainage. In conclusion, unmanaged forests at a comparatively late stage of successional development can still act as significant carbon sinks with large implications for forest management practice and negotiations about biological sinks within the Kyoto Protocol.

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## 1. Introduction

Understanding processes that control the potential of terrestrial ecosystems to sequester carbon has been of wide interest since the implementation of biological carbon sinks in the Kyoto Protocol. In the negotiations, the focus was set on afforestation, reforestation

and deforestation as well as on management, therefore mainly considering plantations and highly productive stages of forest development. Unmanaged forests at an ‘advanced’ stage of development have been omitted in the Bonn agreement since it is widely assumed that they are insignificant as carbon sinks. In theory, assimilation is thought to be balanced by respiration as a forest stand reaches an ‘advanced’ stage of development (Jarvis, 1989; Melillo et al., 1996). This hypothesis is based on studies showing a decline in net primary productivity with stand age (e.g. Yoder

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et al., 1994; Gower et al., 1996; Ryan et al., 1997). Those experimental findings are mostly derived from even-aged, single-species forests. However, little evidence exists that this hypothesis holds true for net ecosystem exchange of unmanaged forests that cover a wide range of age classes due to natural regeneration and that consist of a highly diverse canopy structure. In contrast, in a recent biomass inventory, net primary production larger than expected was found in multi-species subalpine forest stands, ranging in age from 67 to 458 years (Carey et al., 2001).

Since the mid-1990s, continuous measurements of carbon dioxide exchange have been performed at an increasing number of sites throughout the world, covering a wide range of different ecosystems (e.g. Wofsy et al., 1993; Valentini et al., 1996). Regional flux networks such as CARBOEUROFLUX, AMERIFLUX or ASIAFLUX have created the global network FLUXNET (Baldocchi et al., 2001). However, site selection in the temperate zone has been focused on managed deciduous and coniferous forests at ages between 40 and 150 years (Buchmann and Schulze, 1999). Little emphasis has been put on the early stages of forest development or on natural disturbances of forest ecosystems, although large alterations of ecosystem carbon exchange have been demonstrated (Valentini et al., 2000a; Amiro, 2001; Knohl et al., 2002). In addition, only little information exists about the carbon dioxide exchange of forests at a later stage of forest development (Buchmann and Schulze, 1999). However, data for coniferous forests show, that even when old, some forests can retain their capability to sequester carbon as shown for a 450-year-old Douglas fir/western hemlock site in Washington, USA (Falk et al., 2002), a 250-year-old ponderosa pine site in Oregon, USA (Law et al., 2001) and a 300-year-old *Nothofagus* site in New Zealand (Hollinger et al., 1994).

With our site in the Hainich National Park (Central Germany), an unmanaged, uneven-aged mixed deciduous beech forest is added to the European flux network in the framework of the EU project CARBOEUROFLUX. Among all European flux sites, the forest at the Hainich tower site is the oldest and the stand, least impacted by forest management, showing typical characteristics of a forest at a comparatively late stage of successional development, i.e. occurrence of natural regeneration, a wide tree age distribution, a

diverse canopy structure, and large dead wood pools (Cotrufo, personal communication). Since this forest is not pristine as it was selectively managed in the past by the local village population, we use the expression ‘advanced’ forest as the most appropriate classification term. It is important to note, that it remains unknown how a “true” old growth, pristine deciduous forest in Central Europe would look like, as there are hardly any pristine deciduous forests existing at lower altitudes in Central Europe due to historical land use. Therefore, the Hainich site supplements well measurements at other, managed beech forests within Europe at Hesse (36 years, France: Granier et al., 2000, 2002), Sorø (80 years, Denmark: Pilegaard et al., 2001), Vielsam (94 years, Belgium: Aubinet et al., 2001) and Collelongo (96 years, Italy: Valentini et al., 1996).

For all eddy covariance flux sites, the reliability of nighttime flux measurements is of special interest. Under stable atmospheric conditions, typically at night, turbulence can be suppressed. Therefore, no net flux is measured above the canopy although the biological processes that contribute to respiration still take place. In this case, CO<sub>2</sub> enriched air is accumulated within the canopy. By using profile measurements of CO<sub>2</sub> concentrations within the canopy, this CO<sub>2</sub> storage can be calculated and, in theory, the sum of both fluxes, the turbulent flux plus the storage, should reflect the “true” total flux. However, this only holds true if there is no local advection of air with a different CO<sub>2</sub> concentration, a major problem at measuring sites in complex terrain with a non-horizontal surface. Especially at night, cooling of the air at the surface leads to a higher density and therefore a down slope drainage of cold air. If this CO<sub>2</sub> enriched air is replaced with air from outside the canopy (due to a surface change, from aloft or due to a ridge), the CO<sub>2</sub> storage measured at the site will be lower, leading to an underestimation of the biological flux and therefore an erroneous annual carbon flux.

The objectives of this study were to test the hypothesis that forests at a comparatively late stage of development are insignificant as carbon sinks, and to investigate the driving variables for the carbon dioxide exchange of an unmanaged beech forest. Additionally, we assessed the reliability of our net flux estimates by using within canopy wind profile measurements to detect periods of cold air drainage at the Hainich tower site.

## 2. Materials and methods

### 2.1. Site description

The experimental site is located within the “Hainich National Park”, near the city of Eisenach in Central Germany (51°04′46″N, 10°27′08″E), 440 m a.s.l.). The Hainich National Park was established in 1997 to protect one of the largest beech forests in Central Europe and covers an area of about 7600 ha. Due to a unique history as a military base for more than 60 years prior to 1997, a large part of the forest has been taken out of management and developed basically undisturbed. In the centuries before, the forest at the Hainich tower site was used by the local village population as a coppice with standard-systems (in German *Mittelwald*) and therefore has not been exposed to clearcut. As a consequence, the trees cover a wide range of age classes with a maximum up to 250 years. The forest is dominated by beech (*Fagus sylvatica*, 65%), ash (*Fraxinus excelsior*, 25%) and maple (*Acer pseudoplatanus* and *Acer plantanoides*, 7%), with some European hornbeam (*Carpinus betulus*), elm (*Ulmus glabra*) and other deciduous species interspersed. In the surroundings of the tower, the tree density is about 330 trees ha<sup>-1</sup> (stem diameter >7 cm), resulting in an above-ground stem carbon pool of about 130 tC ha<sup>-1</sup> (Mund, personal communication). Maximum tree height varies between 30 and 35 m with a maximum leaf area index (LAI) of 5.0 m<sup>2</sup> m<sup>-2</sup> and a diverse structured canopy (3.5% gaps, Schmaltsch-

ski, personal communication). Litter production was 2.8 ± 0.2 tC ha<sup>-1</sup> in 2000 and 2.0 ± 0.2 tC ha<sup>-1</sup> in 2001 (Cotrufo et al., 2002). Large amounts of dead wood pools, mainly standing dead wood and coarse woody debris (13.5 tC ha<sup>-1</sup>, Cotrufo et al., 2002), reflect the unmanaged character of this forest.

The Hainich tower site is located in suboceanic/subcontinental climate (long-term annual means: 7.5–8 °C for air temperature, 750–800 mm precipitation) on a gentle north facing slope (2–3° inclination). The forest surrounding the tower site has an extension of more than 3 km in the prevailing wind direction. The closest change in surface land use is a small clearing located about 800 m perpendicular to the prevailing wind, with only 5% contribution to the overall wind distribution. A micrometeorological description of the measuring site is given in Table 1. The typical forest phenology during the year is characterised by a dormant season from November to March, a forest floor covered completely with understory vegetation (*Allium ursinum*, *Mercurialis perennis*, *Anemone nemorosa*) from April to October, and leafed trees from May to October. Bud break of the leaves based on field observations started 2 weeks earlier in 2000 (~25 April) than in 2001 (~8 May). Soils are fertile cambisols on limestone bed rock with a depth of 50–60 cm. The soil is characterised by a large clay content (40%, sand 4%) and a thin litter layer. Soil carbon pools were 5.3 tC ha<sup>-1</sup> in the organic layer and 124 tC ha<sup>-1</sup> in the mineral horizons (Rowland and Mund, personal communication).

Table 1  
Site characteristics of the unmanaged ‘advanced’ beech forest in the Hainich National Park

Measurement height ( $z_g$ ) (m)	43.5
Canopy height ( $h_c$ ) (m)	33
Displacement height ( $d = 0.66 h_c$ ) (m)	22
Aerodynamic height ( $z_{aero} = z_g - d$ ) (m)	21.5
Roughness length ( $z_0$ ) (measured from turbulence data under neutral conditions) (m)	2.5 ± 0.9 (during growing season) 3.3 ± 1.0 (outside growing season)
Prevailing wind direction (°)	200–240
Slope of wind field (prior 2D rotation) (°)	2–3
Average vertical wind speed (prior 2D rotation) (m s <sup>-1</sup> )	0.01 ± 0.11
Average horizontal wind velocity (m s <sup>-1</sup> )	3.6 ± 1.6
Energy balance closure	
For daily sums of net radiation ( $R_n$ ), soil, latent and sensible heat flux ( $G$ , $\lambda E$ , $H$ ) (%)	96 ( $R^2 = 0.94$ )
For 30 min daytime values without storage terms (%)	87 ( $R^2 = 0.93$ )

## 2.2. Instrumentation

Carbon dioxide, water vapor, heat and momentum fluxes were continuously measured at a height of 43.5 m during the years 2000 and 2001 using the eddy covariance technique (Aubinet et al., 2000). The flux system consisted of a triaxial sonic anemometer (Gill Solent R3, Gill Instruments, Lymington, UK) and a fast response CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyser in absolute mode (LiCor 6262–3, LiCor Inc., Lincoln, NE, USA). The sonic anemometer was placed at the top of a 30 cm × 30 cm triangular meteorological tower, while the infrared gas analyser was located at the base of the tower. Air was drawn through Dekabon tubing (50 m length and 3.9 mm inner diameter, Serto Jacob GmbH, Fuldabruck, Germany) and two aerosol filters (one at the tower top, the second in front of the IRGA, ACRO 50 PTFE 1 μm pore-size, Gelman, Ann Arbor, MI, USA) and pumped into the gas analyser through a membrane pump (KNF Neuberger, Freiburg, Germany). The flow rate was controlled at 7 l min<sup>-1</sup>, providing turbulent flow in the tubing. Sampling frequency was 20 Hz for the sonic anemometer. For the infrared gas analyser, we used the linear analyser output (analogue, digitised at the sonic input unit) with an internal resolution of 5 Hz for carbon dioxide and 3 Hz for water vapor. In addition, carbon dioxide and (after April 2001) also water vapor concentrations were measured along a vertical profile at nine heights (0.1, 0.3, 1, 2, 5, 10, 20, 30, and 40 m) using an infrared gas analyser (LiCor 6251, September 1999 to March 2001; LiCor 6262, April to December 2001, LiCor Inc., Lincoln, NE, USA). Both gas analysers were calibrated weekly. From April to October 2001, intensive turbulence measurements inside the canopy were performed. At additional four heights (2, 10, 20, and 33 m), sonic anemometers (Gill Solent R3, Gill Instruments, Lymington, UK) measured the three-dimensional wind field and sonic temperatures at 20 Hz. All data were stored on a laptop using our own acquisition software EddyMeas (O. Kolle) and were regularly stored on CD-ROM.

In addition, the tower was equipped with instruments to measure photosynthetic photon flux density ( $Q_p$ ) (LI-190SA, LiCor Inc., Lincoln, NE, USA), air humidity and air temperature (HMP35D, Vaisala, Helsinki, Finland), air pressure (PTB101B, Vaisala,

Helsinki, Finland), wind velocity (A100R, Vector Instruments, Denbighshire, UK) and wind direction (W200P, Vector Instruments, Denbighshire, UK). Precipitation (RainGauge, Young, Traverse City, MI, USA) was collected inside and outside the forest: at 1 m height about 4 m away from the tower and about 800 m away on a forest clearing at about 3 m height. Net radiation ( $R_n$ , Schulze-Däke LXG055, Dr. Bruno Lange GmbH, Berlin, Germany) and short-wave down and upward radiation (CM14, Kipp & Zonen, Delft, The Netherlands) were measured at the top of the tower. Additionally, diffuse solar radiation was measured on the forest clearing using a pyranometer in combination with a shadow ring (CM11, Kipp & Zonen, Delft, The Netherlands). Five soil heat flux plates (Rimco HFP-CN3, McVan Instruments, Mulgrave, Australia) at 2–3 cm soil depth were used to measure the average soil heat flux ( $G$ ) in the neighborhood of the tower. Since March 2000, soil moisture was measured in one vertical soil profile (5, 15, and 30 cm) and a horizontal pattern with three sensors at 5 cm depth using Theta-probes (ML-2x, DeltaT, Cambridge, UK). Since May 2001, canopy air temperature was measured along a vertical profile at 2, 10, 20, 30, and 40 m height using ventilated thermometers (Frankenberger, Theodor Friedrichs & Co., Schenefeld, Germany). Since June 2001, stem temperature was measured in three different trees (*Fagus*, *Fraxinus* and *Acer*) in three depths within each stem, using PT-100-temperature sensors. All data were collected every 10 s and stored as 10 min average values with a data logger (CR23x and CR10x, Campbell Scientific, Logan, UT, USA). Power was supplied by a solar hybrid system (ASE 50-PWX, ASE GmbH, Alzenau, Germany), consisting of 21 m<sup>2</sup> solar panels, a 800 Ah battery pack (24 V) and a generator (Honda EX 4000S, Honda, Tokyo, Japan), which was located in a forest clearing at a distance of 800 m perpendicular to the mean wind direction. The generator started automatically when sunlight was not sufficient to recharge the batteries of the solar panel system. Matching generator running time and wind direction distribution revealed that exhaust gases did not affect the flux measurements.

Plant area index (PAI) was measured using a Plant Canopy Analyser (Li 2000, LiCor Inc., Lincoln, NE, USA) along a 300 m transect in southwest direction

from the tower during April and November 2001. Three repeated measurements were made every 10 m using a 180° view cap, with a 120° turn after each measurement. Additional measurements were performed along three 200 m transects in the directions northwest, northeast and southeast every 50 m. Leaf area index is calculated as the difference between the measured PAI during summer and winter times.

### 2.3. Flux calculations and corrections

The fluxes were calculated online after each 30 min interval with our own calculation software EddyFlux (O. Kolle) using covariances of detrended high-frequency time series of vertical wind velocity and temperature, carbon dioxide density and water vapor density. Turbulent carbon dioxide and water vapor fluxes ( $F_{C,t}$  and  $F_{H,t}$ ) and sensible heat flux ( $H$ ) were determined as

$$F_x = \overline{\rho w'x'} \quad (1)$$

$$H = \rho c_p \overline{w'T'_{\text{sonic}}} \quad (2)$$

where  $\rho$  is the density of dry air,  $w$  the vertical wind speed,  $x$  the mixing ratio of either CO<sub>2</sub> or H<sub>2</sub>O,  $c_p$  the specific heat capacity of dry air and  $T_{\text{sonic}}$  the sonic temperature. Latent heat flux ( $\lambda E$ ) was calculated from water vapor flux. Overbars denote time averages and primes denote departures therefrom. Air temperature ( $T_a$ ) and sensible heat flux ( $H$ ) were corrected for cross-wind and humidity using the method described by Schotanus et al. (1983). The time lag between measurements of vertical wind velocity and scalar densities due to transport in the tubing was estimated by cross-correlation between both time series and was equal to approximately 5.4 s for carbon dioxide and 6.4 s for water vapor. The time shift was calculated online for each 30 min interval, and data were corrected by shifting the time series by the appropriate time lag. Finnigan et al. (2003) found increasing CO<sub>2</sub> fluxes for averaging periods longer than 30 min. We calculated CO<sub>2</sub> fluxes for July 2001 for intervals of 30, 60, 90, 120, 150, and 180 min, and found only a variation of less than 3% in the cumulative July CO<sub>2</sub> flux. Therefore, we used 30 min intervals for all calculations.

Frequency losses due to damping in the tubing and to slow analyser response were corrected using the

approach by Eugster and Senn (1995). The correction parameter was determined from cospectral analyses of vertical wind speed, sonic temperature, carbon dioxide and water vapor concentration time series. On average, carbon dioxide fluxes were corrected by  $5 \pm 3\%$  and water vapor fluxes by  $14 \pm 9\%$ . Cospectral analysis showed that high-frequency dampening for CO<sub>2</sub> occurred mainly at frequencies higher than 0.5 Hz. At our site, the flux contribution in this frequency range was fairly small (ca. 5% > 0.5 Hz and 0.5% > 2 Hz). Water vapor dilution corrections were made with the internal software of the LiCor 6262; corrections for differences between air pressure in the sampling cell and the atmosphere were calculated automatically with a built-in pressure transducer. As a result, further corrections for density effects (Webb et al., 1980) were not necessary (Leuning and Judd, 1996). A 2D coordinate rotation was applied according to McMillen (1988) to force the average vertical wind speed ( $\bar{w}$ ) to zero and to align the horizontal wind ( $u$ ) to mean wind direction. To investigate the influence of various coordinate rotations we also applied a 3D rotation and a planar-fit rotation (Wilczak et al., 2001). However, differences in the annual carbon flux were small (−0.5% for 3D and +2.5% for planar-fit). To validate the CO<sub>2</sub> measurements with the closed path infrared gas analyser (LiCor 6262–3), we performed a short-term comparison with an open-path infrared gas analyser (LiCor 7500, LiCor Inc., Lincoln, NE, USA) in July 2002. The open-path measurements showed very similar CO<sub>2</sub> fluxes at the half hourly time scale ( $y = 1.018x - 0.25$ ,  $R^2 = 0.98$ ). Over a period of 4 weeks, the open-path sensor measured a slightly higher carbon uptake (7%) than the closed-path sensor.

The CO<sub>2</sub> flux associated with storage of CO<sub>2</sub> below the measuring height of the eddy covariance system ( $F_{C,s}$ ) was determined in two ways: (a) as the time change of an integrated spline function through the CO<sub>2</sub> profile measurements; (b) as the time change of the CO<sub>2</sub> concentration at the top of the tower. As both storage fluxes had similar values, we used (b) for further calculations because it reflects better the same source area as the turbulent flux. Final CO<sub>2</sub> fluxes were calculated as the sum of the turbulent flux and the storage term:

$$F_C = F_{C,t} + F_{C,s} \quad (3)$$



Fluxes into the ecosystem (e.g. assimilation) are noted with a negative sign, while fluxes from the ecosystem to the atmosphere (e.g. respiration) are given with a positive sign.

Available data covered 88% of the measurement time in 2000 and 2001. Small gaps (up to 2 h) due to instrumental errors were filled using interpolation; larger gaps were filled with empirical regressions for respiration and assimilation derived for monthly intervals. Since these empirical regressions should reflect ecosystem processes, only data of high quality were accepted. Non-stationary data (Foken and Wichura, 1996), data with high variance (variance  $[\text{CO}_2] > 5$  and variance  $[\text{H}_2\text{O}] > 1$ ) and nighttime data under low  $u^*$  conditions ( $u^*$  of  $0.4 \text{ m s}^{-1}$  in summer and  $0.5 \text{ m s}^{-1}$  in winter) were excluded from regression analysis. Gaps in daytime data ( $Q_P > 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) were filled by an Michaelis–Menten equation

$$F_C = \frac{a' Q_P F_{P,s}}{F_{P,s} + a' Q_P} + F_{R,d} \quad (4)$$

with  $F_C$  representing the measured net ecosystem exchange,  $a'$  the ecosystem quantum yield,  $F_{P,s}$  reflecting the gross primary productivity at light saturation, and  $F_{R,d}$  the ecosystem respiration during the day (Falge et al., 2001). Gaps in nighttime fluxes (nighttime ecosystem respiration,  $R$ ) were filled using an extended Arrhenius function (Lloyd and Taylor, 1994), which expresses the dependency of  $R$  on soil temperature ( $T_s$ ) as follows:

$$R = R_{10} e^{A(1/(B-C) - 1/(T_s - C))} \quad (5)$$

where  $R_{10}$  denotes ecosystem respiration at  $10^\circ\text{C}$ ;  $A$ ,  $B$  and  $C$  are constants ( $A = 308.56 \text{ K}$ ,  $B = 283.15 \text{ K}$ ,  $C = 227.13 \text{ K}$ ; Lloyd and Taylor, 1994).

An analytical footprint model by Schuepp et al. (1990) was used to estimate source areas for the measured fluxes. Under neutral atmospheric conditions, the source weight function peaked at approximately 80 m distance from the tower, 50% of the integrated source weight function was reached at 200 m, and 80% at 700 m. Throughout the entire text, daytime is defined with  $Q_P > 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , and nighttime with  $Q_P < 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Growing season is defined as the period from the first to the last day with a 24 h net carbon uptake.

### 3. Results

#### 3.1. Local weather and meteorology

The average air temperature at the Hainich tower site was  $8.7^\circ\text{C}$  in 2000, with a absolute minimum of  $-10.7^\circ\text{C}$  in December and maximum temperatures of  $30.6^\circ\text{C}$  in June, while the average temperature in 2001 was  $8.1^\circ\text{C}$ , with a minimum of  $-13.2^\circ\text{C}$  in December and a maximum of  $30.8^\circ\text{C}$  in August. However, both years differed mainly during the summer (Fig. 1). During the summer 2000, June was the month with the highest temperatures and highest vapor pressure deficits, followed by a fairly mild and rainy July. During 2001, a mild June was followed by a hot and dry summer (July and August) with very low soil moisture values over a period of 4 weeks in August. Maximum soil moisture values were reached typically in early spring (45% in April 2000 and 48% in April 2001) and minimum values in late summer (20% in August/September 2001). In total, precipitation was 15% lower in 2001 (770 mm) than in 2000 (911 mm).

Air and soil temperatures in 2 cm depth were closely related with a maximum correlation at a time lag of 2.5 h ( $R = 0.93$ ). However, both temperatures showed profound differences in annual and daily amplitudes (Fig. 2a). Soil temperature reached its maximum in late August 2001 with  $16.8^\circ\text{C}$ . Soil frost was only observed for a few days during winter, with a minimum soil temperature in December 2001 ( $-1.1^\circ\text{C}$ ). Photosynthetic photon flux density ( $Q_P$ ) varied between  $55 \text{ mol m}^{-2}$  per day in summer and  $7 \text{ mol m}^{-2}$  per day in winter. Mid-day albedo values (Fig. 2c) showed a clear annual pattern with low values in winter (5–10%), a sharp transition phase during leaf development and high values during summer (14–18%). During the growing season, there was a continuous decline from about 18–14%, probably indicating increased leaf darkness with senescence. During leaf fall, albedo dropped abruptly to low winter values. Large scatter was observed in winter as an effect of snow reflectance. Plant area index was  $1.4 \text{ m}^2 \text{ m}^{-2}$  in winter and  $6.4 \text{ m}^2 \text{ m}^{-2}$  in late summer, resulting in a maximum LAI of  $5.0 \text{ m}^2 \text{ m}^{-2}$  in September 2001. The annual pattern of PAI matched that of albedo.

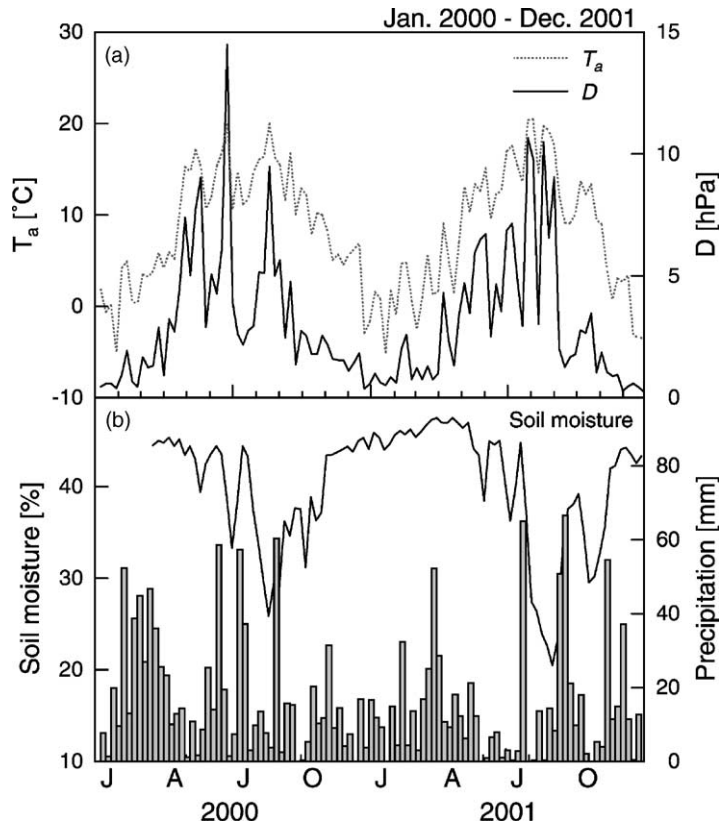


Fig. 1. Weekly averages of (a) air temperature ( $T_a$ ), vapor pressure deficit ( $D$ ); and (b) soil moisture as well as weekly precipitation are shown for the years 2000 and 2001. Measurements of soil moisture started in March 2000 and are averaged for three sensors in 5 cm depth.

### 3.2. Wind profiles within the canopy

Wind direction within (33, 20, 10, and 2 m) and above the canopy (43 m) showed striking relationships (data from May to August 2001, Fig. 3). Wind direction at the canopy top (33 m) showed the expected 1:1 relationship with the wind direction above the canopy (43 m), reflecting close coupling. The deeper is the canopy (20, 10, and 2 m), the more scatter appeared, and the 1:1 line was converted into a pattern with three main axes: (1) the expected 1:1 line; (2) a horizontal line along  $180^\circ$  for the wind within the canopy; and (3) a vertical line along  $225^\circ$  for the wind above the canopy.

We suspected that these three axes might reflect different atmospheric conditions and therefore separated the data set of the wind measurements into nine different classes of friction velocity ( $u^*$ ) measured with

the sonic anemometer above the canopy (2 m versus 43 m, Fig. 4). Now, the three axes can be clearly separated: (a) for conditions with  $u^* < 0.4 \text{ m s}^{-1}$ , when the horizontal axis dominated, mainly during nighttime. This indicated that independent of the wind above the canopy, the wind within the canopy always came from the south ( $180^\circ$ ), following the inclination of the slope; (b) for conditions with  $0.4 \text{ m s}^{-1} < u^* < 0.6 \text{ m s}^{-1}$ , when the diagonal 1:1 axis dominated the pattern, indicating a tight coupling of above and within canopy flow; and (c) for conditions with  $0.6 \text{ m s}^{-1} < u^*$ , when the vertical axis along  $225^\circ$  dominated, which occurred mainly during daytime. Under these high  $u^*$  conditions, a clockwise turn of the wind field with increasing depth in the canopy was observed, possibly indicating the formation of a cavity with reverse surface wind direction due to flow over a hilly landscape (Stull, 1988, p. 601). The effect of friction velocity on

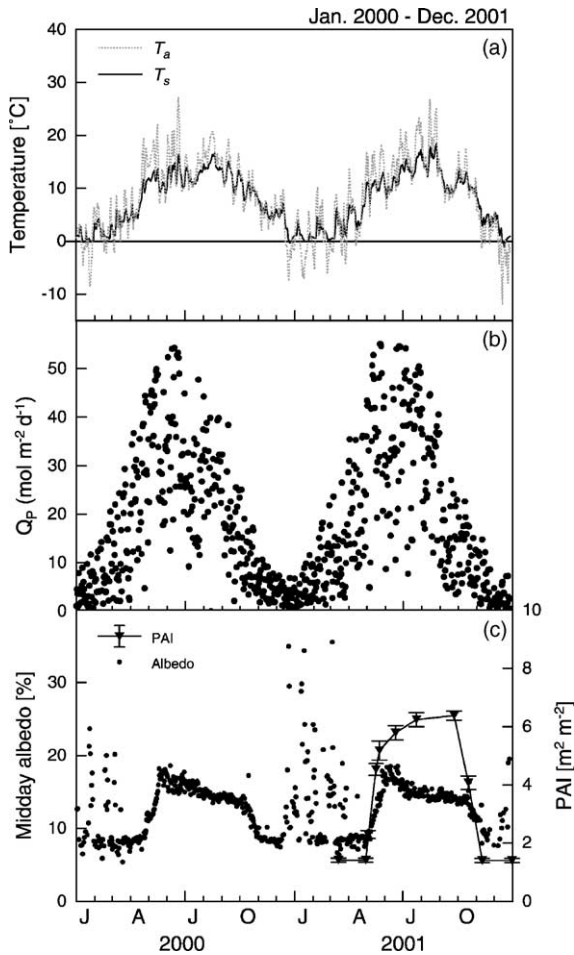


Fig. 2. Daily averages of (a) air temperature ( $T_a$ ), soil temperature in 2 cm depth ( $T_s$ ); (b) photosynthetic photon flux density ( $Q_p$ ); and (c) midday albedo (12:00–14:00 h) and plant area index (PAI) for the Hainich tower site. Bars for PAI represent standard deviation of measurements along a transect.

the wind pattern was also observed for the other measurements heights within the canopy (20 and 10 m), though to a smaller extent (data not shown).

### 3.3. Net $\text{CO}_2$ fluxes

Diurnal courses of net  $\text{CO}_2$  fluxes showed profound changes during both year (example given for year 2000, similar fluxes in 2001, Fig. 5a). In winter (e.g. January),  $\text{CO}_2$  was lost from the ecosystem to the atmosphere at an average rate

of  $1.1\text{--}1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  and showed no fluctuations over a 24 h period. In contrast, during April to October, nighttime  $\text{CO}_2$  fluxes increased to  $3.0\text{--}4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ , with highest nighttime fluxes in May ( $4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ , daily average) followed by a constant decline (Fig. 5b). On average, midday fluxes were about  $-15.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  in May,  $-19.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  in June,  $-16.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  in September and  $-4.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  in October (Fig. 5a). Individual half hourly  $\text{CO}_2$  fluxes could easily exceed  $-40 \mu\text{mol m}^{-2} \text{s}^{-1}$  during midday in July (average  $\text{CO}_2$  flux  $21.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ , data not shown). Although midday fluxes were similar in May and September 2000, differences existed in the number of hours per day with a net carbon uptake (13.5 h per day in May versus 10 h per day in September).

The gross primary productivity at light saturation ( $F_{P,s}$ ), calculated from a Michaelis–Menten regression (Table 2), was higher in May 2000 than in May 2001, probably reflecting the delayed leaf development in 2001.  $F_{P,s}$  was highest in July 2000 ( $-47.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), clearly higher than in July 2001 ( $-39.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). In both years,  $F_{P,s}$  was higher in September than in May, although midday fluxes were approximately the same. Quantum yield in 2000 was higher in the beginning of the summer than later, whereas in 2001 higher quantum yields were reached by the end of the summer. Daytime respiration ( $F_{R,d}$ ) ranged between  $1.5$  and  $5.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , with highest values in June for both years.

From June to September,  $Q_p$  explained about 70–90% of the observed variation in daytime net ecosystem  $\text{CO}_2$  fluxes. The residuals showed a weak, but significant relationship with the ratio of diffuse downward radiation to total downward radiation (larger uptake with increased ratio,  $R^2 = 0.3$ ,  $P \leq 0.001$ ) and with vapor pressure deficit (smaller uptake with increased  $D$ ,  $R^2 = 0.2$ ,  $P \leq 0.001$ ).

Nighttime  $\text{CO}_2$  fluxes, which directly reflect ecosystem respiration at night, were dependent mainly on air (data not shown) and soil temperature (Fig. 6). We used soil temperature as independent variable as it showed a similar temperature range during day and night, necessary to adequately model daytime ecosystem respiration from nighttime flux data. For 2001, a strong relationship between soil temperature and nighttime  $\text{CO}_2$  fluxes was found, when data from spring (1–15 May), a dry period in summer (28



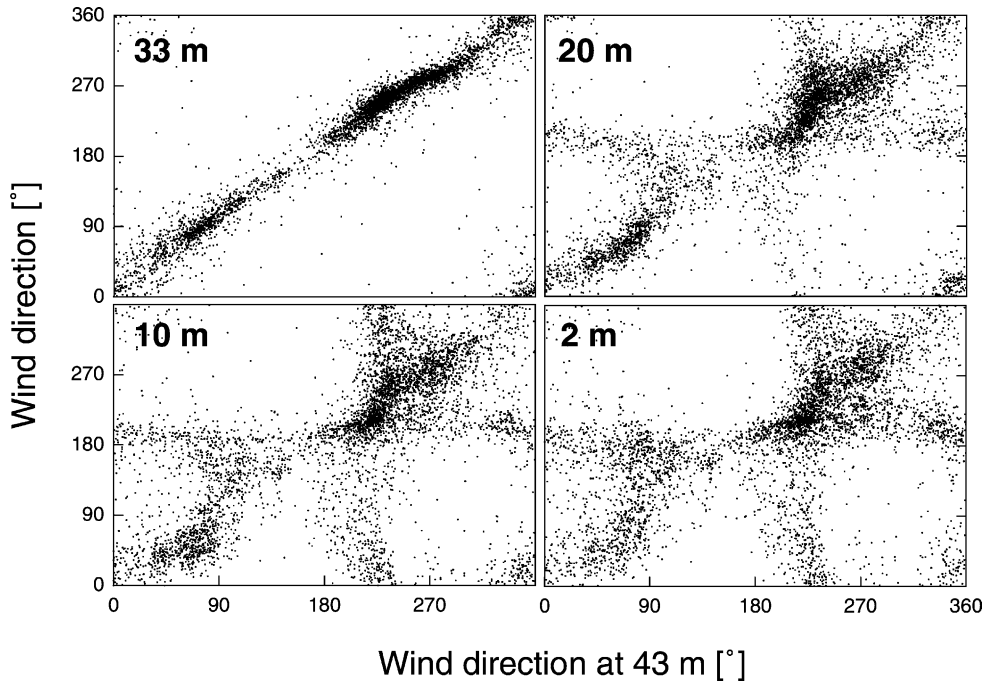


Fig. 3. Comparison of above (43 m) and within canopy (33, 20, 10, and 2 m) wind direction. Half hourly averaged data from May to August 2001.

Table 2  
Parameter for Michaelis–Menten equations (Eq. (4)) to fill daytime data gaps

Year	Month	Quantum yield ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$F_{P,s}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$F_{R,d}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$R_{\text{adj}}^2$
2000	April	-0.023	-6.3	3.3	0.25
	May	-0.085	-23.3	4.9	0.58
	June	-0.094	-30.8	5.0	0.68
	July	-0.073	-47.6	4.2	0.89
	August	-0.061	-38.1	4.1	0.78
	September	-0.085	-28.9	4.3	0.72
	October	-0.040	-19.8	2.4	0.66
	2001	April	-0.009	-3.2	1.5
May		-0.052	-17.7	4.5	0.46
June		-0.072	-36.4	4.4	0.83
July		-0.059	-39.8	4.0	0.78
August		-0.068	-37.9	4.4	0.75
September		-0.071	-39.2	3.4	0.88
October		-0.035 <sup>a</sup>	-30.0 <sup>a</sup>	2.1 <sup>a</sup>	0.57 <sup>a</sup>

Regression parameters are fitted to daytime data for ecosystem quantum yield, gross primary productivity at light saturation ( $F_{P,s}$ ) and ecosystem respiration during daytime ( $F_{R,d}$ ). No assimilation was measured from November to April. In October 2001, calculation of representative parameters was not possible due to missing data (2 weeks).

<sup>a</sup> Gap filling parameters for October 2001 were derived from a mix of late September and late October data.

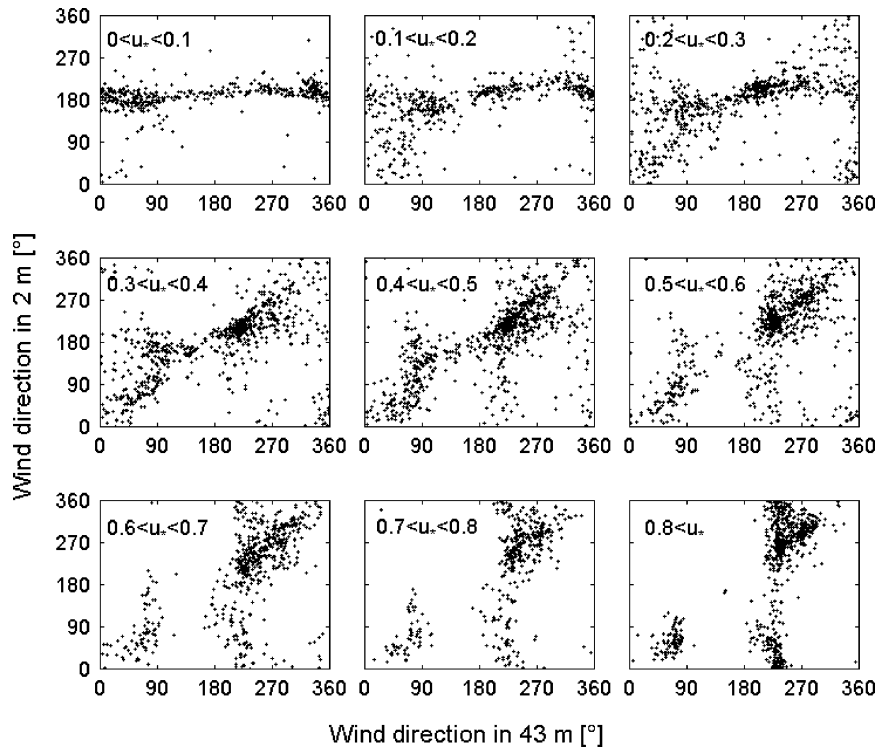


Fig. 4. Comparison of wind direction in 2 m vs. 43 m for nine different classes of friction velocity,  $u^*$ . Half hourly averaged data from May to August 2001.

July to 3 September), and just after leaf fall (10–16 November) were excluded ( $R_{10} = 3.17$ ,  $R^2 = 0.81$ ,  $P < 0.001$ ). Including those periods into the overall regression analysis created substantial scatter ( $R_{10} = 3.14$ ,  $R^2 = 0.64$ ,  $P < 0.001$ ), but changed the regression coefficient  $R_{10}$  by less than  $0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Soil moisture explained 13% of the residual variance. In spring, during bud break, nighttime  $\text{CO}_2$  fluxes were significantly higher than predicted by the regression function ( $P < 0.001$ ), possibly reflecting the increased resource demand of trees for bud break. A similar increase in the flux rates appeared just after leaf fall in November ( $P = 0.003$ ). With a canopy camera, we observed a rapid decline in leaf biomass in two windy nights (9 and 10 November, horizontal wind speed  $>6 \text{ m s}^{-1}$ ). In the three following days, nighttime  $\text{CO}_2$  fluxes increased from an average of  $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $5.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ , decreased over the next 5 days to  $2\text{--}3 \mu\text{mol m}^{-2} \text{s}^{-1}$ , before returning to previous, low values. During

the same time, albedo dropped below 10% (Fig. 2), most likely indicating that increased litter availability for microbial decomposition caused this increase in nighttime  $\text{CO}_2$  fluxes. On the other hand, during a dry period in summer, nighttime  $\text{CO}_2$  fluxes was significantly lower than predicted by the regression line ( $P = 0.03$ , Fig. 6) probably reflecting drought stress. If calculated on a monthly basis from 30 min averages,  $R_{10}$ , the respiration at  $10^\circ\text{C}$  calculated from Eq. (5), varied substantially over the course of the year (Fig. 7a). Maximum  $R_{10}$  values were reached in both years in spring and fall ( $4.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ , triangles) and minimum  $R_{10}$  values in late summer ( $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) resulting in an average  $R_{10}$  of  $3.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  including the high values in spring and fall or  $3.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  excluding the high values in spring and fall. Soil moisture followed a similar pattern with high values in winter and low values in late summer, explaining 43% of the observed variation in  $R_{10}$  at the monthly scale ( $P \leq 0.003$ , linear

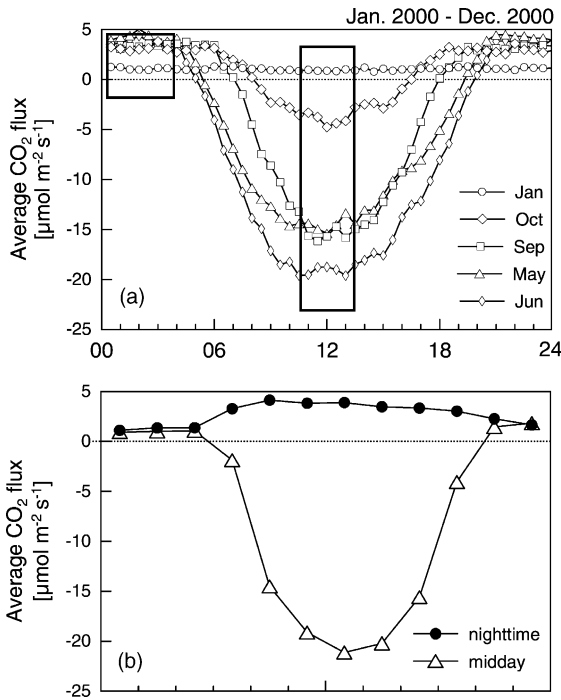


Fig. 5. (a) Average diurnal courses of CO<sub>2</sub> fluxes for the months January, May, June, September and October 2000; (b) annual course of average nighttime and midday flux during the year 2000. The rectangles in (a) indicate the data that were used to calculate average nighttime and midday fluxes in (b).

regression), when the high nighttime CO<sub>2</sub> fluxes in spring and fall were excluded. Respiration during daytime as calculated from nighttime fluxes and temperature regression agreed well with daytime respiration inferred from the Michaelis–Menten regression ( $F_{R,d}$ ) giving confidence in the nighttime measurements.

Daily net ecosystem CO<sub>2</sub> fluxes varied between 3 and -9 g C m<sup>-2</sup> per day during the year (Fig. 8). In both years, large carbon release to the atmosphere was observed just before and during bud break of the dominant beech trees as well as just after leaf fall. In winter, daily carbon fluxes decreased from about 3 g C m<sup>-2</sup> per day (November/December) to 1–2 g C m<sup>-2</sup> per day (January to March). The seasonal course of net ecosystem fluxes showed the delayed start of the growing season in 2001 in comparison to that in 2000 (13 days later) due to lower air temperature in spring. The length of the growing season, defined as the number of days from the first day with 24 h net uptake to the last day with 24 h net uptake, was 177 days in 2000 and 157 days in 2001. Using this definition, the growing season length was much shorter than the time interval with average air temperature higher than 5 °C as typically used in forestry (208 days in 2000, 196 days in 2001). However, in 2000 carbon uptake dropped quite rapidly due to a cold period in early October,

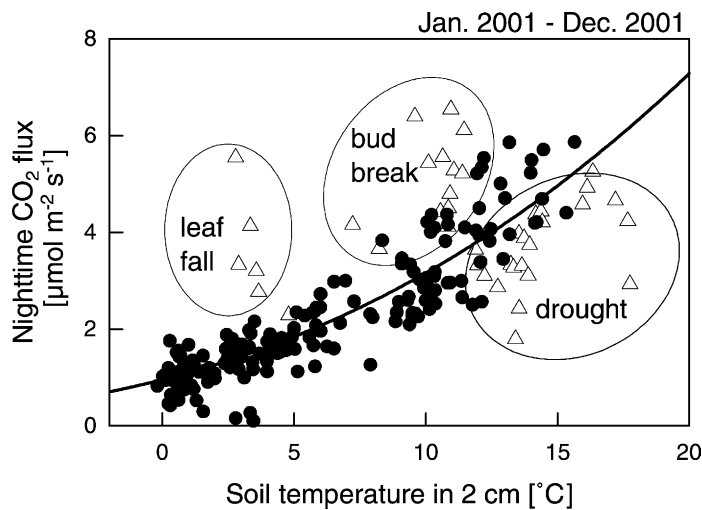


Fig. 6. Dependency of daily averaged nighttime fluxes (friction velocity above threshold, quality checked) on soil temperature in 2001. Data for bud break (27 April to 15 May 2001), for a dry period in summer (drought, 10 August to 5 September 2001) and from just after leaf fall (1 November to 10 November 2001) are circled (open triangles). Regression analyses excluding ( $R^2 = 0.8$ ) and including circled data ( $R^2 = 0.6$ ) resulted in significant relationships ( $P < 0.001$ ).

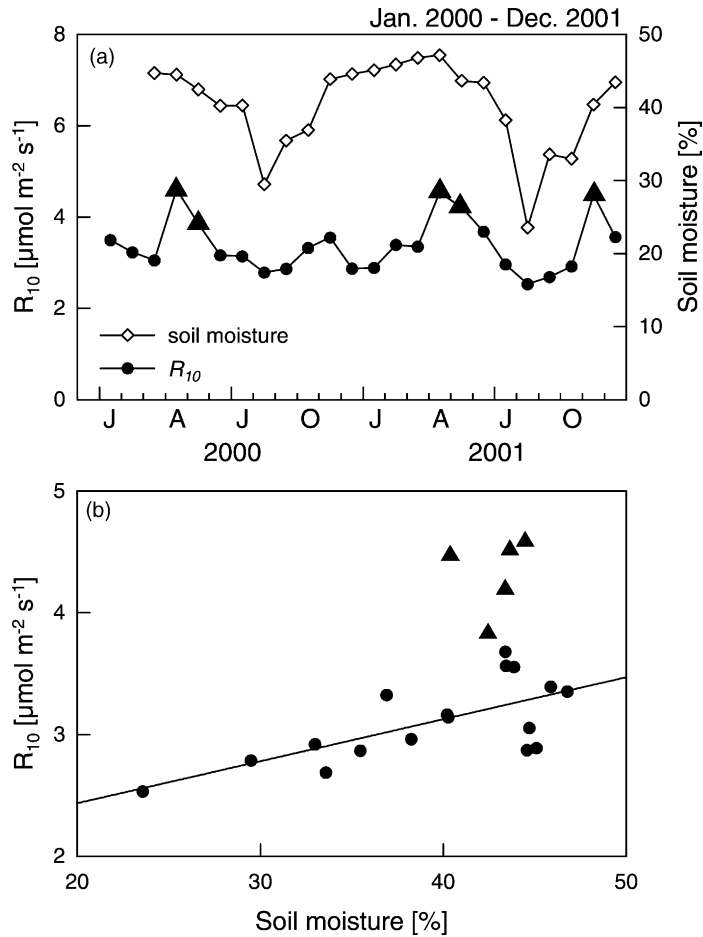


Fig. 7. (a) Temporal variation of nighttime flux temperature regression coefficient  $R_{10}$  and soil moisture in 5 cm depth during the years 2000 and 2001; (b) relationship between soil moisture and  $R_{10}$ ; high  $R_{10}$  values from April and May 2000 and 2001 (solid triangles) were excluded from the regression.

whereas in 2001 a mild October led to a fairly long period with low 24 h net carbon release due to small ongoing uptake during daytime. As a result, cumulative  $\text{CO}_2$  fluxes were quite similar in both years despite the difference in the amount of days with 24 h net uptake. Cumulative  $\text{CO}_2$  fluxes reflected a large carbon uptake:  $494 \text{ g C m}^{-2}$  in 2000 and  $490 \text{ g C m}^{-2}$  in 2001, which was in good agreement with the fairly large observed litter production. Ecosystem respiration, as calculated from measured nighttime fluxes and modelled daytime respiration, reached  $1086 \text{ g C m}^{-2}$  in 2000 and  $1050 \text{ g C m}^{-2}$  in 2001. Total gross assimilation, as the difference of net ecosystem exchange and

ecosystem respiration, was  $-1580 \text{ g C m}^{-2}$  in 2000 and  $-1540 \text{ g C m}^{-2}$  in 2001.

Annual  $\text{CO}_2$  fluxes were corrected for suppressed turbulence under low friction velocity conditions as commonly done within the flux community (e.g. Aubinet et al., 2000). Friction velocity threshold values were calculated for summer ( $0.4 \text{ m s}^{-1}$ ) and winter ( $0.5 \text{ m s}^{-1}$ ) from relationships of total  $\text{CO}_2$  flux (turbulent plus storage fluxes, 30 min values) versus friction velocity (data not shown). Since these threshold values control the fraction of nighttime and winter data that have to be replaced by modelled data (from nighttime flux temperature regression) and

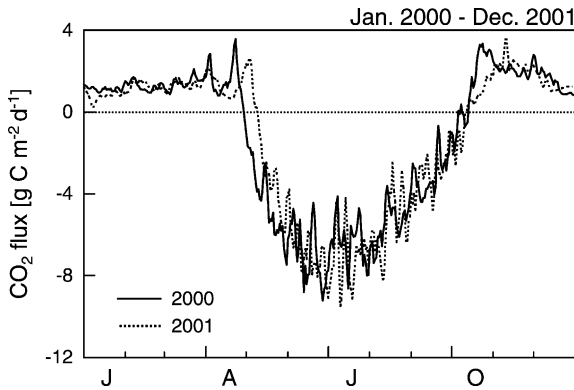


Fig. 8. Daily CO<sub>2</sub> fluxes for the years 2000 ( $-494 \text{ g C m}^{-2} \text{ yr}^{-1}$  per year) and 2001 ( $-490 \text{ g C m}^{-2} \text{ yr}^{-1}$  per year). The period of days with net carbon uptake was 177 days in 2000 and 152 in 2001. Data are friction velocity corrected.

hence have a tremendous influence on the total annual CO<sub>2</sub> flux, a sensitivity test for the year 2000 was performed. With no data being replaced, the net CO<sub>2</sub> flux for the Hainich site reached about  $-600 \text{ g C m}^{-2} \text{ yr}^{-1}$  in 2000 (Fig. 9). With increasing friction velocity threshold the annual carbon uptake decreases. For realistic threshold values ( $0.35\text{--}0.45 \text{ m s}^{-1}$ , dashed box), the total annual CO<sub>2</sub> flux ranges between  $-510$  and  $-480 \text{ g C m}^{-2} \text{ yr}^{-1}$ . For thresholds above  $0.45 \text{ m s}^{-1}$

total carbon uptake remains fairly constant giving confidence in our annual estimate. Additionally, the sensitivity of the total annual CO<sub>2</sub> flux to changes in the respiration coefficient ( $R_{10}$ ) is indicated by the bi-directional error bars for each annual flux estimate. The more data were replaced, the stronger was the influence of a  $\pm 0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  uncertainty in  $R_{10}$  on the total carbon flux. If we conservatively estimate an uncertainty of  $0.3 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in  $R_{10}$ , we obtain a combined uncertainty of less than  $\pm 50 \text{ g C m}^{-2} \text{ yr}^{-1}$  for the annual carbon uptake due to nighttime gap filling. These  $50 \text{ g C m}^{-2} \text{ yr}^{-1}$  represent about 10% of the annual carbon uptake of the Hainich tower site.

#### 4. Discussion

The eddy covariance technique has proved to be a successful tool to study net ecosystem exchange of carbon dioxide for forest ecosystems (Baldocchi et al., 2001). Nevertheless, uncertainties in the annual carbon uptake arise from systematic underestimation of nighttime flux measurements (Goulden et al., 1996). Therefore, it is of critical importance to detect periods when the eddy covariance technique cannot be applied. At our site, the wind profile measurements within the canopy revealed that under conditions of low

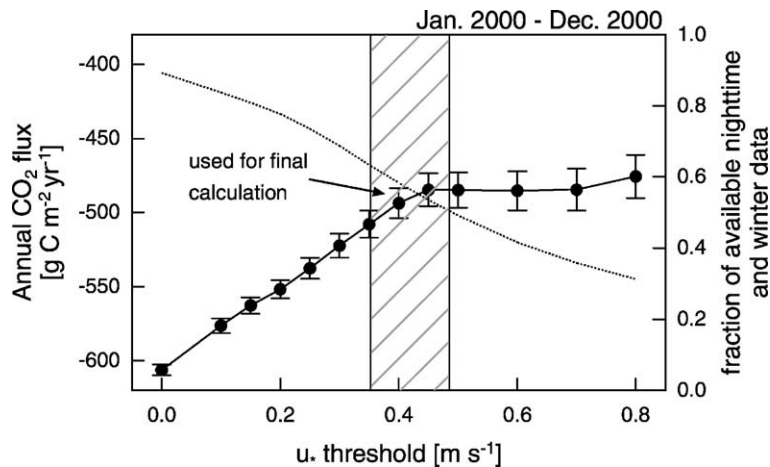


Fig. 9. Sensitivity of annual CO<sub>2</sub> flux in 2000 to different friction velocity thresholds ( $u^*$ ) for nighttime data exclusion. The dashed area indicates the range with realistic threshold values for  $u^*$ . We used  $0.4 \text{ m s}^{-1}$  during the growing season and  $0.5 \text{ m s}^{-1}$  for outside of the growing season (marked by the arrow). Error bars indicate the change in the annual CO<sub>2</sub> flux due to a  $0.1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  change in the respiration coefficient ( $R_{10}$ ). The dotted line represents the fraction of data that were used for calculation.



turbulence (low friction velocity) the within canopy air flow was independent from the above canopy flow, accounting for 30% of the annual nighttime data coverage. The within canopy air flow was always directed from the south and therefore followed the inclination of the slope, although it was only 2–3°. Since these conditions of decoupling can lead to an underestimation of CO<sub>2</sub> storage within the canopy, all data for  $0 \text{ m s}^{-1} < u^* < 0.4 \text{ m s}^{-1}$  were excluded and replaced by a soil temperature regression. For medium  $u^*$  values, above and within canopy flow were closely coupled, indicating appropriate conditions for eddy covariance measurements. Under conditions with high friction velocity, above and within canopy flow were also coupled, but wind direction shifted with decreasing height within the canopy to the right, possibly as a consequence of the formation of a cavity with reverse surface wind direction. This shifting possibly influenced the length of the footprint and its direction, but had no detectable impact on the measured CO<sub>2</sub> fluxes. Thus, the measurement of the within canopy wind field helped to detect periods of potential cold air drainage and showed that friction velocity is a reasonable parameter to determine when to exclude data for long-term carbon balance measurements.

This new approach to determine the  $u^*$  threshold supplements the usual  $u^*$  correction method (Goulden et al., 1996). Since at many flux stations within canopy flux measurements are performed, the comparison of above and within wind direction can be a suitable tool for cold air drainage detection at other sites in complex terrain as well. Using this new technique for the measurements at the Hainich tower site, we could be sure that data affected by cold air drainage were excluded from the annual carbon budget. In combination with the sensitivity test for nighttime gap filling, we estimated that the uncertainty in the annual carbon uptake introduced by problems associated with nighttime measurements was less than  $\pm 50 \text{ g C m}^{-2}$  per year, only about 10% of the total cumulative C flux. These test strengthen the results, that this unmanaged beech forest was a strong carbon sink during the years 2000 and 2001.

$Q_p$  and vapor pressure deficit were major driving variables for ecosystem gross assimilation as typically observed for other deciduous forests as well (e.g. Valentini et al., 1996; Goulden et al., 1996). Furthermore, the ratio of diffuse to total downward radi-

ation affected photosynthesis (Hollinger et al., 1994; Baldocchi, 1997; Gu et al., 1999). Under diffuse conditions, radiation is scattered more strongly, increasing the probability for radiation to penetrate deeply into the canopy. As a consequence, a larger proportion of leaf biomass can actively participate in photosynthesis. Additionally, Gu et al. (1999) pointed out the importance of the interdependencies of air temperature, vapor pressure deficit and radiation, leading to increased photosynthesis under cloudy conditions. Absolute values of gross primary productivity at light saturation ( $F_{p,s}$ ) and quantum yield values observed at the Hainich tower site were slightly higher than those from a beech site in Sorø, Denmark, where  $F_{p,s}$  ranged between  $-20$  and  $-35 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and quantum yield between  $-0.02$  and  $-0.063 \mu\text{mol} \mu\text{mol}^{-1}$  (Pilegaard et al., 2001), possibly reflecting the higher LAI at the Hainich tower site. During the course of both years, we observed higher values for  $F_{p,s}$  in September than in May, although maximum carbon uptake rates were similar. This clearly indicates that leaf growth and physiology controlled ecosystem photosynthetic uptake.

The observed nighttime CO<sub>2</sub> flux rates, i.e. nighttime ecosystem respiration, strongly depended on soil temperature, but varied significantly during three specific periods of the year: during a dry period in summer, during bud break as well as leaf fall. Decreased respiration rates under water stress with high soil temperatures have been reported by several groups, mostly from the Mediterranean region (Matteucci et al., 2000; Reichstein et al., 2002). Nevertheless, our measurements clearly showed that even for a temperate deciduous forest with fairly large annual precipitation sums (800–900 mm), water limitation can occur at the ecosystem level. At our site, soil water availability might be limited during certain times due to a large clay content of the soil. On the other hand, increased nighttime fluxes in spring and fall clearly reflect phenological changes at the ecosystem level. These changes in the flux rates cannot be explained by simple abiotic factors (such as temperature or moisture), but are related to plant physiology during bud break and leaf fall (Schulze, 1970). All these intra-annual variations can lead to a significant underestimation of annual ecosystem respiration, particularly when a single exponential function is applied to model ecosystem respiration at

an annual time scale. In our case, not accounting for the high respiration coefficients in spring would lead to an underestimation of total ecosystem respiration of about  $85 \text{ g C m}^{-2}$  per year and as a consequence, an overestimation of the net annual carbon uptake of about  $15 \text{ g C m}^{-2}$  per year. Thus, accounting for those short-term phenological effects is critical for gap filling methods, which should be based on monthly or bi-weekly data to adequately represent intra-annual variation in net ecosystem exchange.

The annual carbon uptake of the Hainich tower site compared well to other beech forests across Europe, although those other forests are all managed and much younger compared to our site. For a 96-year-old beech stand in northern Italy (Collelongo), a net uptake of  $470 \text{ g C m}^{-2}$  was reported for 1994 and  $660 \text{ g C m}^{-2}$  for 1997 (Valentini et al., 1996, 2000b). A 94-year-old mixed beech/Douglas fir forest in Belgium showed a total net uptake of  $452 \text{ g C m}^{-2}$  in 1996,  $378 \text{ g C m}^{-2}$  in 1997, and  $519 \text{ g C m}^{-2}$  in 1998 (Granier et al., 2003). Lower carbon uptake was found for a 80-year-old beech forest for Sorø, Denmark ( $169 \text{ g C m}^{-2}$  in 1997 and  $124 \text{ g C m}^{-2}$  in 1998) which also had a shorter growing season (Pilegaard et al., 2001); and for a young French beech site (30 years,  $218 \text{ g C m}^{-2}$  in 1996,  $257 \text{ g C m}^{-2}$  in 1997,  $79 \text{ g C m}^{-2}$  in 1998, and  $299 \text{ g C m}^{-2}$  in 1999, Granier et al., 2000, 2003). In a global comparison, Baldocchi et al. (2001) showed that length of the growing season explained 82% of the observed variation in net carbon uptake for a wide range of temperate deciduous forests. Our data from the first 2 years of measurements at the Hainich tower site fit well into this pattern, although our site shows the typical characteristics of an unmanaged 'advanced' forest.

So far, only few measurements of net ecosystem  $\text{CO}_2$  exchange have been carried out in forests at a late stage of development worldwide. A more than 300-year-old *Nothofagus* stand in New Zealand revealed significant carbon uptake during a 15 day measurement campaign (Hollinger et al., 1994). At an annual basis, a 250-year-old ponderosa pine forest showed a net carbon uptake of  $324 \text{ g C m}^{-2}$  in 1996 and  $266 \text{ g C m}^{-2}$  in 1997 (Law et al., 2000). Recent measurements in a 450-year-old Douglas fir/western hemlock site showed carbon uptake of  $150 \text{ g C m}^{-2}$  for 1998/1999 (Falk et al., 2002). Carbon release has also been reported for other 'advanced' coniferous forests

on peaty soils in the boreal zone (Milyukova et al., 2002; Goulden et al., 1998). However, all those carbon budget were much lower than our results from 2 years of continuous measurements of carbon dioxide fluxes from a deciduous temperate forest.

## 5. Conclusions

We found unexpectedly high carbon uptake rates during 2 years for an unmanaged 'advanced' beech forest ( $490\text{--}494 \text{ g C m}^{-2}$  per year), which is in contrast to the widely spread hypothesis that 'advanced' forests are insignificant as carbon sinks. Even if we take methodological uncertainties into account and conservatively estimate an overall error of 20%, a large carbon uptake for the Hainich tower site remains, which is significantly different from 0. Thus, for this forest, assimilation is clearly not balanced by respiration, although this site shows typical characteristics of an 'advanced' forest at a comparatively late stage of development, i.e. a wide tree age class distribution, a diverse canopy structure and dead wood carbon pools. More research is currently going on to understand the carbon dynamics at the Hainich tower site, such as soil respiration, changes in soil carbon stocks, biomass increments and to clarify potential long-lasting effects of historical land use. These aspects will gain further importance because of the issue of biological carbon sinks in the Kyoto Protocol. Although in the negotiations, most attention was given to relatively young and managed forests (Schulze et al., 2002), 'advanced' forests should not be neglected a priori. As a result of our study, we clearly showed that unmanaged forests at a comparatively late stage of stand development have the potential to act as significant carbon sinks.

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## References

- Amiro, B.D., 2001. Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. *Global Change Biol.* 7 (3), 253–268.
- Aubinet, M., Grelle, G., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H., Bernbigier, P., Bernhofer, C., Clement, R., Elbers, J., Grainer, A., Grünwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of European forests: the EUROFLUX methodology. *Adv. Ecol. Res.* 30, 113–175.
- Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., Laitat, E., 2001. Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. *Agric. Forest Meteorol.* 108 (4), 293–315.
- Baldocchi, D., 1997. Measuring and modelling carbon dioxide and water vapour exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant Cell Environ.* 20 (9), 1108–1122.
- Baldocchi, D., Falge, E., Gu, L.H., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X.H., Malhi, Y., Meyers, T., Munger, W., Oechel, W., U, K.T.P., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* 82 (11), 2415–2434.
- Buchmann, N., Schulze, E.-D., 1999. Net CO<sub>2</sub> and H<sub>2</sub>O fluxes of terrestrial ecosystems. *Global Biogeochem. Cycles* 13 (3), 751–760.
- Carey, E.V., Sala, A., Keane, R., Callaway, R.M., 2001. Are old forests underestimated as global carbon sinks. *Global Change Biol.* 7, 339–344.
- Cotrufo, M.F., Matteucci, G., De Pascale, R.A., 2002. Carbon pools in leaf litter and woody debris of European beech forests. In: *Proceedings of the 2nd CarboEurope Meeting*. Budapest, Hungary (Poster).
- Eugster, W., Senn, W., 1995. A cospectral correction model for measurements of turbulent NO<sub>2</sub> flux. *Boundary-Layer Meteorol.* 74, 321–340.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grunwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, H., Moors, E., Munger, J.W., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. Forest Meteorol.* 107 (1), 43–69.
- Falk, M., Paw, U.K.T., Schroeder, M., 2002. Interannual variability of carbon and energy fluxes for an old-growth rainforest. In: *Proceedings of the 25th Conference on Agricultural and Forest Meteorology*, AMS, Norfolk.
- Finnigan, J.J., Clement, R., Malhi, Y., Leuning, R., Cleugh, H.A., 2003. A re-evaluation of long-term flux measurement techniques. Part I. Averaging and coordinate rotation. *Boundary-Layer Meteorol.* 107 (1), 1–48.
- Foken, T., Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. *Agric. Forest Meteorol.* 78, 83–105.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol.* 2, 169–182.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279, 214–217.
- Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. *Trends Ecol. Evol.* 11 (9), 378–382.
- Granier, A., Ceschia, E., Damesin, C., Dufrene, E., Epron, D., Gross, P., Lebaube, S., Le Dantec, V., Le Goff, N., Lemoine, D., Lucot, E., Ottorini, J.M., Pontailler, J.Y., Saugier, B., 2000. The carbon balance of a young Beech forest. *Funct. Ecol.* 14 (3), 312–325.
- Granier, A., Pilegaard, K., Jensen, N.O., 2002. Similar net ecosystem exchange of beech stands located in France and Denmark. *Agric. Forest Meteorol.* 114 (1–2), 75–82.
- Granier, A., Aubinet, M., Epron, D., Falge, E., Umundsson, J., Jensen, N.O., Köstner, B., Matteucci, G., Pilegaard, K., Schmidt, M., Tenhunen, J., 2003. Deciduous forest: carbon and water fluxes, balances and ecophysiological determinants. In: Valentini, R. (Ed.), *Fluxes in Carbon, Water and Energy of European Forests*. Ecological Studies. Springer, Berlin.
- Gu, L., Fuentes, J.D., Shugart, H.H., Staebler, R.M., Black, T.A., 1999. Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: results from two North American deciduous forests. *J. Geophys. Res.* 104 (D24), 31421–31434.
- Hollinger, D.Y., Kelliher, F.M., Byers, J.N., Hunt, J.E., McSeveny, T.M., Weir, P.L., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75 (1), 143–150.
- Jarvis, P.G., 1989. Atmospheric carbon dioxide and forests. *Philos. Trans. R. Soc. London, Ser. B* 324, 369–392.
- Knohl, A., Kolle, O., Minayeva, T.Y., Milyukova, I.M., Vygodskaya, N.N., Foken, T., Schulze, E.-D., 2002. Carbon dioxide exchange of a Russian boreal forest after disturbance by wind throw. *Global Change Biol.* 8 (3), 231–246.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D.D., Unsworth, M.H., 2000. Measuring and modelling seasonal variation of carbon dioxide and water vapour exchange of a *Pinus ponderosa* forest subject to soil water deficit. *Global Change Biol.* 6 (6), 613–630.
- Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., Hultman, N., 2001. Carbon

- dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiol.* 21 (5), 299–308.
- Leuning, R., Judd, M.J., 1996. The relative merits of open- and closed-path analysers for measurements of eddy fluxes. *Global Change Biol.* 2 (3), 241–253.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- Matteucci, G., Dore, S., Stivanello, S., Rebmann, C., Buchmann, N., 2000. Soil respiration in beech and spruce forests in Europe: trends, controlling factors, annual budgets and implications for the ecosystem carbon balance. In: Schulze, E.-D. (Ed.), *Carbon and Nitrogen Cycling in European Forest Ecosystems*. Ecological Studies. Springer, Berlin, p. 500.
- McMillen, R.T., 1988. An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorol.* 43, 231–245.
- Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.-D., Sala, O.E., 1996. Terrestrial biotic responses to environmental change and feedbacks to climate. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., Maskell, K. (Eds.), *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, New York, pp. 444–481.
- Milyukova, I.M., Kolle, O., Varlagin, A.V., Vygodskaya, N.N., Schulze, E.-D., Lloyd, J., 2002. Carbon balance of a southern taiga spruce stand in European Russia. *Tellus Ser. B: Chem. Phys. Meteorol.* 54 (5), 429–442.
- Pilegaard, K., Hummelshøj, P., Jensen, N.O., Chen, Z., 2001. Two years of continuous CO<sub>2</sub> eddy-flux measurements over a Danish beech forest. *Agric. Forest Meteorol.* 107, 29–41.
- Reichstein, M., Tenhunen, J.D., Rouspard, O., Ourcival, J.M., Rambal, S., Dore, S., Valentini, R., 2002. Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics. *Funct. Ecol.* 16 (1), 27–39.
- Ryan, M.G., Binkley, D., Fownes, J.H., 1997. Age-related decline in forest productivity: pattern and process. *Adv. Ecol. Res.* 27, 213–262.
- Schotanus, P., Nieuwstadt, F.T.M., De Bruin, H.A.R., 1983. Temperature measurement with a sonic anemometer and its application to heat and moisture fluxes. *Boundary-Layer Meteorol.* 26, 81–93.
- Schuepp, P.H., Leclerc, M.Y., MacPherson, J.I., 1990. Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. *Boundary-Layer Meteorol.* 50, 355–374.
- Schulze, E.-D., 1970. Der CO<sub>2</sub>-Gaswechsel der Buche (*Fagus sylvatica* L.) in Abhängigkeit von den Klimafaktoren im Freiland. *Flora* 159, 177–232.
- Schulze, E.-D., Valentini, R., Sanz, M.J., 2002. The long way from Kyoto to Marrakesh: implications of the Kyoto Protocol negotiations for global ecology. *Global Change Biol.* 8 (6), 505–518.
- Stull, R.B., 1988. *An Introduction to Boundary Layer Meteorology*. Atmospheric Science Library. Kluwer Academic Publishers, Dordrecht, 670 pp.
- Valentini, R., De Angelis, P., Matteucci, G., Monaco, R., Dore, S., Scarascia Mugnozza, G.E., 1996. Seasonal net carbon dioxide exchange of a beech forest with the atmosphere. *Global Change Biol.* 2, 199–207.
- Valentini, R., Dore, S., Marchi, G., Mollicone, D., Panfyorov, M., Rebmann, C., Kolle, O., Schulze, E.-D., 2000a. Carbon and water exchanges of two contrasting Siberia landscape types: regenerating forest and bog. *Funct. Ecol.* 14 (1), 87–96.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000b. Respiration as the main determinant of carbon balance in European forests. *Nature* 404 (6780), 861–865.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Q. J. R. Meteorol. Soc.* 106, 85–100.
- Wilczak, J.M., Oncley, S.P., Stage, S.A., 2001. Sonic anemometer tilt correction algorithms. *Boundary-Layer Meteorol.* 99 (1), 127–150.
- Wofsy, S.C., Goulden, M.L., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO<sub>2</sub> in a midlatitude forest. *Science* 260 (5112), 1314–1317.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Sci.* 40 (3), 513–527.