

Forest floor CO₂ fluxes estimated by eddy covariance and chamber-based model

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Received 20 August 1999; accepted 17 June 2000

Abstract

An intercomparison study of two methods for estimating forest soil CO₂ efflux was conducted during a 3-week period in summer. An empirical model established from nearly 2 years of chamber measurements predicted that the soil CO₂ efflux ranged from 1.2 to 1.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$. This small range was due to the lack of variability in the model parameters (soil temperature and moisture) during the study period. Eddy covariance measurements showed more variability and diurnal dependence. Turbulent fluxes of CO₂ during the day apparently were influenced by the presence of a moss layer on the forest floor; the combined effects of moss photosynthesis and respiration reduced the turbulent fluxes by an average of 0.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ relative to the modeled soil efflux. At night, the eddy fluxes of CO₂ agreed well with the modeled soil efflux; however, the turbulent fluxes were highly variable (standard deviation exceeding the mean), due to the imperfect sampling conditions associated with the nocturnal boundary layer. These results illustrate the different processes measured by the two methods, and highlight some of the limitations of the eddy covariance technique for estimating soil CO₂ efflux. Finally, they demonstrate the need for more long-term intercomparison studies, covering a broader range in soil temperature and moisture. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Eddy covariance; Empirical model; *Pinus sylvestris*; Scots pine; Soil CO₂ efflux

1. Introduction

The global carbon budget must be better understood if we are to address potential climate changes resulting from anthropogenic activity. Important gaps in our understanding of the global carbon budget include uncertainties about carbon cycling within forest ecosystems

(Vitousek et al., 1997), of which soil CO₂ efflux is an important component (Raich and Schlesinger, 1992). Accurate measurement of soil CO₂ efflux is thus necessary for a thorough understanding of carbon cycling in forests and of below-ground metabolic activity.

Soil CO₂ efflux is the result of two main processes: the production of CO₂ in the soil and its transport from the soil to the atmosphere. Soil respiratory activity releases large amounts of CO₂ into the soil pore space. This leads to high CO₂ concentrations in the soil air, where total storage may equal or exceed the atmospheric CO₂ storage in forests. The transport of CO₂ from the soil into the atmosphere is mainly driven by two mechanisms: diffusion and mass flow (Kimball and Lemon, 1971). Whereas the diffusive

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flux is driven by the concentration gradient between the soil and the atmosphere, the mass flow is the result of air motion. Soil CO₂ efflux can therefore only be accurately measured by a system that does not alter the soil respiratory processes, the concentration gradient and the flow of air across the soil surface.

Chamber-based methods are most frequently used to estimate soil CO₂ efflux due to low cost and ease of use (Edwards, 1982; Norman et al., 1992; Fang and Moncrieff, 1996; Goulden and Crill, 1997; Rayment and Jarvis, 1997; Janssens and Ceulemans, 1998). They are, however, often criticized because they are weak at sampling spatial variability within forests and because they are subject to uncertainties associated with the so-called chamber effects (Mosier, 1990). Chambers may disturb the soil environment and alter CO₂ and pressure gradients, turbulent fluctuations, and air flow. They may thus interfere with both production and transport of CO₂. Modern chamber systems (Norman et al., 1992; Fang and Moncrieff, 1996; Iritz et al., 1997; Rayment and Jarvis, 1997) have eliminated most of these effects, but mass flow across the soil surface, as well as the motion and pressure of air around and within the chamber still remain problems.

Given the uncertainty related to chamber measurements, many alternative techniques have been applied to estimate soil CO₂ efflux. These include the eddy covariance technique, the gradient-flux method, the ²²²Rn method and others (Rosenberg et al., 1983; Baldocchi et al., 1986, 1997; Denmead and Raupach, 1993; Dugas, 1993; Uchida et al., 1997). Unfortunately, these alternative techniques are often more expensive and difficult to apply, and although they are not subjected to “chamber effects”, they involve a wide array of assumptions and prerequisites. Also the eddy covariance technique has a number of limitations that affect its suitability to measure soil CO₂ efflux (see Section 2), but nonetheless appears to be well suited for continuous measurement of soil CO₂ efflux in homogeneous and flat forests without undergrowth. This approach is advantageous in that it does not disturb the soil environment and integrates over a large surface area, and initial investigations have suggested that the method holds some promise for estimation of soil fluxes (Baldocchi and Meyers, 1991; Baldocchi et al., 1997).

Despite the long history of measurements and the development of a large variety of techniques, no method has so far been recognized as the standard or reference technique for measuring soil CO₂ fluxes (Nakayama, 1990; Norman et al., 1992; Rayment and Jarvis, 1997). Uncertainties related to both chamber and eddy covariance flux measurements motivate a comparison of these totally independent methods. As the presence of operators making chamber measurements would affect the eddy fluxes, no direct measurement comparison is possible. Hence, a model based on the chamber measurements is a good alternative. Process-based models may be preferable because they provide insight into underlying root and microbial activity. However, empirical models usually fit the measured chamber data more accurately and are better suited for validation of flux measurements.

The objectives of this study were: (i) to examine the feasibility of measuring soil CO₂ efflux in a Belgian Scots pine forest by eddy covariance, and (ii) to compare the eddy fluxes with the outcome of a simple empirical model based on chamber measurements. This paper describes the chamber and eddy flux measurements, and discusses the model performance and its comparison with the eddy covariance measurements.

2. Materials and methods

2.1. Site description

The study was conducted in an even-aged, 69-year old Scots pine (*Pinus sylvestris* L.) stand in the Belgian Campine region (51°18'33"N, 4°31'14"E), in the context of the European ECOCRAFT and EUROFLUX projects. The 2-ha pine stand was part of a 150-ha mixed coniferous/deciduous plantation — De Inslag — in Brasschaat (de Pury and Ceulemans, 1997; Gond et al., 1999; Janssens et al., 1999a), and is a level-II observation plot of the European program for intensive monitoring of forest ecosystems, managed by the Institute for Forestry and Game Management, Flanders, Belgium.

Mean annual temperature at the site is 9.8°C, with 3 and 18°C as mean temperatures of the coldest and warmest months, respectively. Mean annual precipitation is 767 mm. Climatic conditions during the

Table 1
Daytime (7:30–19:30 h) eddy covariance data for the sample days^a

Sample day	Sample size (No. half hours)	Mean CO ₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	S.D.	Soil temperature (°C)
3/7/98	16	0.77	0.06	15.2
4/7/98	8	0.81	0.31	14.7
9/7/98	6	1.05	0.23	15.0
10/7/98	22	0.74	0.44	15.7
13/7/98	7	1.10	1.04	16.8
14/7/98	13	0.64	0.19	14.5
15/7/98	14	0.77	0.25	15.9
16/7/98	25	0.58	0.36	15.6
17/7/98	23	0.34	0.33	15.3
18/7/98	4	0.03	0.16	14.3
20/7/98	7	0.78	0.48	19.1

^a For each sampling period, total sample size, mean CO₂ flux, standard deviation (S.D.) and mean soil temperature are presented.

experiment (3–20 July 1998) were very homogeneous (Tables 1 and 2), with mainly gray and drizzly weather.

Apart from some shallow drainage ditches, the study site has an almost flat topography, is very gently sloping (0.3%), and is at an elevation of 16 m (Baeyens et al., 1993). In 1995, tree density was 556 trees ha⁻¹, with a mean height of 20.6 m and a mean diameter at breast height (1.3 m) of 0.27 m (Cermak et al., 1998). Tree crowns had a mean depth of 3.7 m, and the canopy had a projected surface area of 65% (Van den Berge et al., 1992) and a leaf area index varying between 1.8 and 2.4 (Gond et al., 1999). All undergrowth was completely removed in 1993, giving way to a dense moss layer dominated by *Hypnum cupressiforme* Hedw., *Dicranium scoparium* Hedw., *Polytrichum commune* L. and *Dicranella heteromalla* (Hedw.) Schimp.

The stand has a moderately wet sandy soil with high hydraulic conductivity and is rarely saturated (Baeyens et al., 1993). However, due to the presence of a clay layer at a depth of 1–2 m, the site is poorly drained and soil moisture generally fluctuates around field capacity (Janssens et al., 1999a). More detailed information

on the soil, vegetation and local climatic conditions can be found in Baeyens et al. (1993), Cermak et al. (1998), Janssens et al. (1999b) and Kowalski et al. (1999).

2.2. Chamber measurements of soil CO₂ efflux

Soil CO₂ efflux was measured with 16 PVC-collars divided over three patches in the stand. The collars had an internal diameter of 20 cm, were 8 cm tall, and were inserted 5 cm in the soil 4 months prior to the onset of the measurements. All live vegetation, including the moss-layer, was removed from inside the collar at the time of insertion. CO₂ release from these 16 collars was measured at 4-week intervals from April 1996 to February 1998 using two different techniques that were selected for their suitability to assess spatial variability. A closed chamber infrared gas analysis (IRGA) system (CIRAS-1 equipped with SRC-1, PP-Systems, UK) was applied in May 1997 and July 1998 to assess the diurnal variation in soil CO₂ efflux. Measurements with the closed chamber system

Table 2
Nighttime (20:00–7:00) eddy covariance data for the sample nights^a

Sample nights	Sample size (No. half hours)	Mean CO ₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	S.D.	Soil temperature (°C)
3/7/98–4/7/98	15	0.77	1.05	13.9
10/7/98–11/7/98	10	−0.06	1.29	15.1
13/7/98–14/7/98	23	1.22	1.14	14.1
15/7/98–16/7/98	18	1.80	1.28	14.4
16/7/98–17/7/98	13	1.65	2.02	13.5
17/7/98–18/7/98	23	1.11	1.31	14.4

^a For each sampling period, total sample size, mean CO₂ flux, standard deviation (S.D.) and mean soil temperature are presented.

systematically allowed a maximum $[\text{CO}_2]$ increase of 50 ppmv inside the chamber headspace, and a maximum duration of 2 min. The soda lime technique (Edwards, 1982) was selected because it produces daily means without requiring the presence of an operator during nighttime. In a laboratory experiment in which both techniques were compared, the soda lime technique was found to underestimate soil CO_2 efflux, especially at higher flux rates (Janssens and Ceulemans, 1998). We therefore corrected the soda lime results for this underestimation at higher flux rates using the calibration function obtained in this laboratory study. After correction, both techniques agreed very well in situ (Janssens et al., 2000).

2.3. Empirical model

Based on the chamber measurements of soil CO_2 efflux, a simple empirical model of the form $Y = f(T) * f(\Psi)$ was developed, where Y is the CO_2 efflux, T the soil temperature (measured at a depth of 5 cm in the mineral soil) and Ψ is the soil moisture (measured by TDRs at a depth of 25 cm in the mineral soil) (Janssens et al., 1999a). The first factor of the equation describes the temperature response and was taken from the BRESP model produced by Schlentner and van Cleve (1985),

$$Y = a + \left(\frac{1}{b + c - ((T-10)/10)} \right)$$

It is a sigmoid function that starts as a regular Q_{10} function (Fig. 1), in which a is the lower limit of soil CO_2 efflux, $a + 1/b$ the maximum flux, and c is the Q_{10} related parameter. T is the soil temperature in $^{\circ}\text{C}$.

The second factor of the equation describes the moisture response (Fig. 1), and consists of two superimposed Gompertz functions (asymmetric sigmoid function with asymptotes at 0 and 1) scaled between 0 and 1 by subtracting 1,

$$Y = \exp\{-e^{(p-q*\Psi)}\} + \exp\{-e^{(r-(s-t*\Psi))}\} - 1$$

where p , q , r , s and t are parameters and Ψ is the volumetric soil moisture content (%). The first Gompertz function is parameterized to describe drought stress. The second part describes water stress near saturation, but was not relevant for the data presented here. Therefore, the model was simplified to:

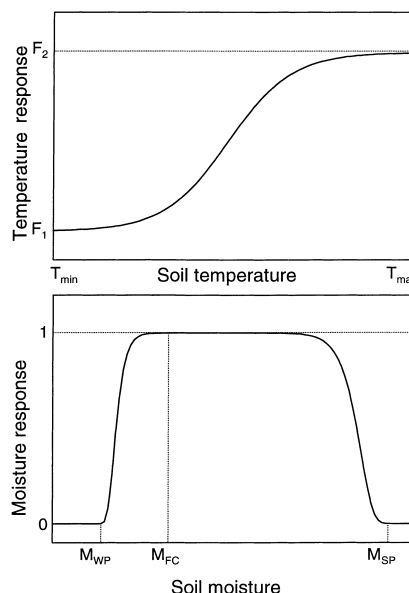


Fig. 1. (Top) The model's response of soil CO_2 fluxes to temperature (see text for discussion). F_1 indicates the lower limit of soil CO_2 efflux reached at T_{\min} . F_2 indicates the upper limit and is reached at T_{\max} . (Bottom) Simulated impact of soil moisture on soil CO_2 efflux (see text for discussion). M_{WP} indicates wilting point, M_{FC} indicates field capacity and M_{SP} indicates saturation point.

$$Y = \exp\{-e^{(p-q*\Psi)}\}$$

All parameters of both the temperature and the moisture functions were fitted to the measurements by means of a nonlinear least-squares fitter (Origin, Microcal Software, USA). Best fit was obtained with the following parameter values: $a = 0.15$, $b = 0.787$, $c = 100.76$, $p = 10$ and $q = 1.2$.

The model was originally developed with data from the entire 2-year period and was meant to simulate daily averages. As such, the model output incorporates the seasonal changes in root and microbial biomass in the temperature response. Simulations on shorter time scales, in which root biomass and microbial populations do not change dramatically, therefore typically overestimate diurnal variation in soil CO_2 efflux (30% of the mean in the model versus 10% in the measurements), although the model output was always in the right order of magnitude. This artifact was overcome by smoothing the model output over time (Fig. 2). The modeled and measured fluxes agreed best after an adjacent-smoothing procedure over a 20 h time period.

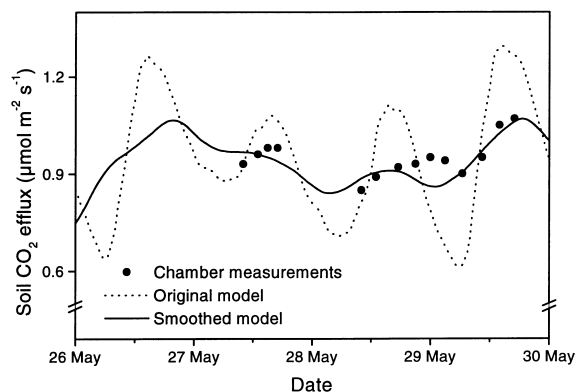


Fig. 2. Comparison of soil chamber measurements and model output from 26 May 1997 to 30 May 1997. Best fit (solid line) was obtained by smoothing the original model (dotted line) over a 20 h period. The chamber measurements ($n = 7$) are closed chamber IRGA results.

2.4. Eddy flux measurements

The eddy covariance instrumentation consisted of a sonic anemometer (Metek USAT-3, Germany) and an IRGA (LI-6262, LI-COR, USA). Data were collected at 10 Hz. The sonic was mounted at a height of 1.65 m above the forest floor; the sample intake for the IRGA was located immediately below the sonic (distance of less than 30 cm). Air was sampled at a rate of 6.21 min^{-1} through a Gelman Acro 50 $1.0 \mu\text{m}$ filter (P/N 4258), into a 4 m Teflon tube of 4.33 mm (inner diameter) and heated to avoid condensation. A subsequent filter (Ballston 300-01961) conditioned the air prior to sampling by the IRGA.

Fluxes were computed based on a 30 min averaging period. Time series of winds were delayed to account for time lag in between wind and gas sampling. Turbulent fluctuations were determined as the difference between the time series and a digital recursive filter approximating a running mean, with a filter time constant of 50 s as described by McMillen (1988). The coordinate system for the fluxes was rotated such that the x -axis is aligned with the mean wind for the averaging period ($\bar{v} = \bar{w} = 0$). The surface-normal flux ($w'c'$) was used as the estimate of surface gas exchange.

Within 25 m around the eddy covariance system, sparse grass and saplings were removed. In contrast with the chamber measurements, however, the moss layer remained untouched. Data were rejected when-

ever the operators were present within 30 m of the sampling system, when the CO_2 concentration was out of the range of the IRGA and whenever the change in CO_2 concentration from one half-hour to the next exceeded 10 ppmv. This effectively screened the data for stationarity and helped to limit the importance of any unmeasured storage term. Total data availability during the experiment was less than expected, due to quality checking as described above, recurring failure of the laptop, and a plumbing problem. Daytime data were available for 11 days, while nighttime data were available for only 6 days (Tables 1 and 2).

The eddy covariance technique is characterized by a number of limitations that affect its suitability to measure soil CO_2 efflux. Some of these are discussed here, but the list is hardly exhaustive. The net flux in the lower atmosphere is a result of exchange between the atmosphere and the underlying surface elements. These elements include not only the soil but also understorey vegetation and those portions of tree boles below the measurement height, all of which respire. Eddy flux measurements should be made in homogeneous turbulence. Under the canopy, a sampling location may be systematically biased. Measurements could be (intermittently) influenced by the wakes of individual boles or surface elements. Local fluxes can also be biased by the presence of thermals associated with the heterogeneous sub-canopy radiation regime. Finally, decreased levels of turbulence below the canopy, especially at night or in weak winds, can lead to artifacts associated with inhomogeneity and/or advection.

3. Results and discussion

3.1. Model performance

Annual variation in soil CO_2 efflux was large and closely linked to the temporal pattern of soil temperature (Janssens et al., 1999a). On this annual time scale, the model fitted the chamber data very well and explained 84% of the temporal variation in soil CO_2 efflux (Fig. 3). Temperature alone explained over 80% of the temporal variation, which relates to the low incidence of severe water stress at the site. The only periods when the model did not correctly simulate the temporal variation in soil CO_2 efflux were January,

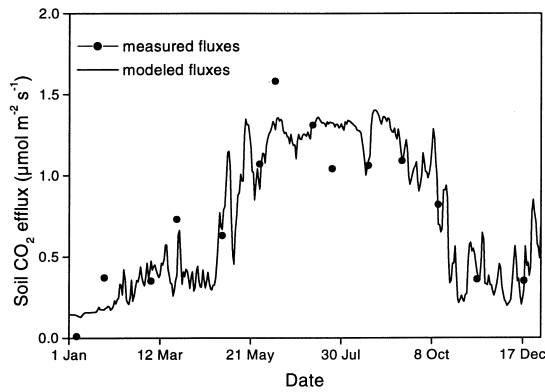


Fig. 3. Comparison of soil chamber measurements and model output for 1997. The solid line represents the unsmoothed model. The chamber measurements ($n = 16$) are corrected soda lime results. Error bars indicate 1 S.D.

when the soil was frozen, and early June, when flux rates peaked (Janssens et al., 1999a).

Soil CO₂ efflux measurements with the closed chamber IRGA system during spring 1997 and during the course of this experiment indicated that the diurnal fluctuations were very small. This observation was consistent with other studies (Kursar, 1989; Janssens et al., 1998), and is probably related to the small changes in soil temperature under forest canopies. Typical ranges for diurnal changes in soil CO₂ efflux at the site were $\pm 10\%$ around the mean. After smoothing, fluxes estimated by the model were always within 5% of the measured flux (Fig. 2).

Due to the homogeneous weather conditions, only small fluctuations in the soil fluxes were observed during the course of the experiment. The mean model output for the entire 3-week period was $1.27 \mu\text{mol m}^{-2} \text{s}^{-1}$, and ranged between 1.15 and $1.39 \mu\text{mol m}^{-2} \text{s}^{-1}$. This mean soil CO₂ efflux was not significantly different from the measured fluxes

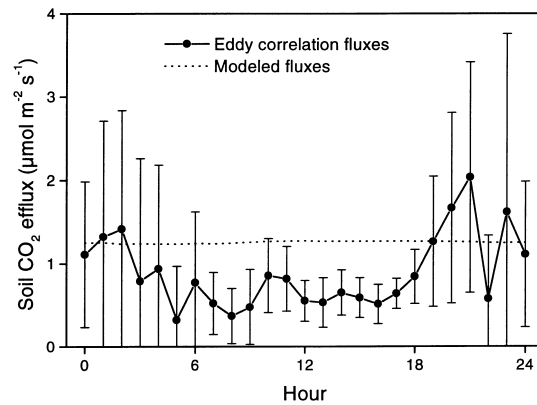


Fig. 4. Diurnal plots of eddy covariance and modeled CO₂ fluxes. Each eddy flux data point is the mean of all measurements obtained during the entire experiment for that time period. Also in the model output, only those time periods with available eddy flux data were incorporated. Error bars indicate 1 S.D. Positive values are upward fluxes.

during the same period in 1996 and 1997 (0.94 and $1.31 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively).

3.2. Eddy covariance measurements

Mean daytime CO₂ flux, averaged over all available half-hourly data between 7:30 and 19:30 h, was $0.66 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 3). This flux was considerably smaller than the nighttime mean of $1.16 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4), but was not statistically different due to the large variability in the nighttime fluxes. Net exchange of CO₂ at the measurement height reflects the sum of moss photosynthesis and bole, moss, and soil respiration. As the CO₂ exchange by the mosses is the only difference between day and night, the observed discrepancy between daytime and nighttime CO₂ fluxes could be related to the

Table 3

Comparison of daytime and nighttime fluxes as estimated by the eddy flux system and the model^a

	Method	Mean CO ₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	S.D.	Range	Sample size (No. half hours)
Daytime	Eddy correlation	0.66	0.43	−0.26–2.84	142
	Modeled	1.27	0.03	1.21–1.34	142
Nighttime	Eddy correlation	1.16	1.41	−2.70–5.70	102
	Modeled	1.25	0.03	1.20–1.29	102

^a Mean CO₂ flux for the entire experiment, standard deviation (S.D.), range of the fluxes and sample size are presented. Negative values indicate downward fluxes.

photosynthetic activity of the dense moss layer at the forest floor. Similar diurnal differences at the moss surface were reported by Goulden and Crill (1997) for a boreal black spruce forest in Canada. They found that in summer, moss photosynthesis represented 20–50% of total forest photosynthesis, and took up most of the CO_2 respired in the soil. As day/night differences in soil temperature were small (Tables 1 and 2), we assumed that total photosynthetic CO_2 uptake by the mosses could be crudely approximated from the day/night difference in gas exchange. The result was a considerable mean uptake of $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 3), which was also consistent with the data reported by Goulden and Crill (1997).

From the available daytime and nighttime eddy flux data (Tables 1 and 2), it is clear that variability was significantly larger at night. Unpredictable fluctuations in the nocturnal flux data are often reported (Greco and Baldocchi, 1996; Valentini et al., 1996) and may be related to incomplete mixing during periods of diminished and/or intermittent turbulence, which are common in canopies. In these conditions, the turbulent flux at the measurement height is not directly related to the soil efflux. When there is no turbulence, there is no turbulent flux, regardless of soil respiratory activity. Other atmospheric processes, not directly detected by an eddy flux system, become important. Storage, advection, and molecular transport may establish heterogeneous and three-dimensional gradients of CO_2 . The observed variability in the measured fluxes may therefore be explained by episodic turbulent mixing across these variable gradients. Application of a threshold in friction velocity did not reduce this variability.

The eddy flux data did not reveal large spatial variability between the different wind directions. This was consistent with chamber measurements of soil CO_2 efflux made around the eddy flux system (data not shown). The flux data were also not correlated with soil temperature, even considering nighttime data only, when moss photosynthesis did not occur.

3.3. Comparison of eddy fluxes and model

Literature data on technique comparisons for measuring soil CO_2 efflux involving eddy covariance are very scarce. Norman et al. (1997) compared the eddy

covariance technique with a closed chamber IRGA system. On one specific day they found a nice agreement between both techniques, but on another day their eddy flux result was only half the flux measured by the closed chamber system. After adjusting their eddy covariance results for the understory photosynthesis both systems agreed better, although the eddy flux result was characterized by a much larger temporal variability than the chamber system (Norman et al., 1997). The latter phenomenon was also observed in this study. Variability in the model output was small ($0.03 \mu\text{mol m}^{-2} \text{s}^{-1}$, Table 3) due to the limited range of soil temperature and moisture over the course of the comparison. The model variability was dominated by the long-term temperature trend over the measurement period and diurnal variations were eliminated largely by the smoothing operation (see Section 2.3). The eddy covariance measurements were far more variable, a result which was consistent with the large fluctuations in eddy fluxes (even for daily averages) observed above a boreal jack pine forest floor (Baldocchi et al., 1997). Variability in such fluxes results from natural geophysical variability in the flow and turbulence (Wesely and Hart, 1985), and appears to be inherent to below-canopy eddy flux measurements.

Whereas the model output was more or less constant throughout the day, the eddy covariance fluxes clearly showed day/night differences (Table 3). The diurnal trend in the eddy fluxes (Fig. 4) indicates that both techniques may be measuring different processes. The model was based upon chamber measurements from which all mosses were removed, and therefore estimates the amount of CO_2 released from the soil. The eddy fluxes on the other hand, included moss photosynthesis and respiration by the boles. The lower daytime fluxes estimated by the eddy covariance system were hence not contradictory to the modeled fluxes. During nighttime, one would expect the eddy fluxes to be higher than the model output, due to moss and bole respiration. However, stem respiration contributes for only a small part to total autotrophic respiration in forests and is usually small compared to root respiration (Ryan et al., 1997). From this relatively small flux, the eddy system only detects bole respiration occurring below the measurement height. Mosses also are characterized by small respiratory fluxes, possibly as a result of the low allocation to respiration in mosses

(Skre and Oechel, 1979; Oechel and van Cleve, 1986). Thus, we did not observe differences in the overall mean nighttime flux estimated by both techniques (Table 3).

4. Conclusions

Soil chambers and eddy covariance are two methods for measuring different aspects of forest carbon cycling, each with advantages and disadvantages. Chamber methods give an estimate of *soil*–atmosphere interactions in specific locations. Eddy fluxes integrate *surface*–atmosphere exchanges over larger spatial areas. The difference between surface and soil can be large, particularly when understorey vegetation is significant.

To avoid interference between the two methods, an empirical model simulated the chamber measurements for comparison against the eddy fluxes. During the intercomparison, the chamber/model approach predicted soil CO₂ effluxes of $1.3 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$. Diurnal variations in the efflux were small relative to changes over the 3-week sampling period. The eddy covariance measurements showed much more variability, and also a diurnal dependence believed to be governed by both biological and atmospheric processes. Daytime turbulent fluxes of CO₂ were lower than the modeled soil efflux by an average of $0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$, probably due to the effects of moss photosynthesis. Nighttime eddy fluxes of CO₂ agreed with the modeled soil efflux, but showed a larger variability that is consistent with the characteristic inhomogeneity and intermittency of nocturnal turbulence.

With the appropriate data analysis and quality checking, the eddy covariance method appears to be well suited to measure below-canopy gas exchange at this site. This intercomparison illustrates the difference between processes measured by this method in comparison with soil chamber measurements. The influence of moss, which did not affect the chamber measurements, appears to have caused the difference between the fluxes measured by the two methods. Although not often modeled or accounted for explicitly, moss may be an important player in carbon cycling for some forests. When eddy covariance is used to estimate soil CO₂ efflux, large uncertainties must be accepted at night. Further intercomparison studies are

needed to illustrate the agreement between the two methods for a wider range of soil temperature and moisture conditions.

Acknowledgements

This work contributes to the GCTE Core project of the IGBP and was funded by the EC Fourth Framework Programme on Environment and Climate Research ‘EUROFLUX’ (Contract No. ENV4-CT95-0078). Special thanks to Andreas Ibrom and Kai Morgenstern (Institut für Bioklimatologie, Universität Göttingen, Germany) for the loan of the sonic anemometer, supporting electronics, and data logging software. The authors acknowledge the input of two anonymous reviewers, whose comments improved the quality of the paper, as well as the Institute for Forestry and Game Management, Flanders, Belgium, for logistic support at the site. Fred Kockelbergh helped to design and construct the plumbing and heating systems. IAJ is a Post-doctoral Fellow of the Fund for Scientific Research Flanders (FWO).

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