Assessing forest soil CO_2 efflux: an *in situ* comparison of four techniques

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Summary   A dynamic, closed-chamber infrared gas analysis (IRGA) system (DC-1: CIRAS-1, PP-Systems, Hitchin, U.K.) was compared with three other systems for measuring soil CO_2 efflux: the soda lime technique (SL), the eddy correlation technique (EC), and another dynamic, closed-chamber IRGA system (DC-2: LI-6250, Li-Cor, Inc., Lincoln, NE). Among the four systems, the DC-1 systematically gave the highest flux rates. Relative to DC-1, SL, EC and DC-2 underestimated fluxes by 10, 36 and 46%, respectively. These large and systematic differences highlight uncertainties in comparing fluxes from different sites obtained with different techniques.

Although the three chamber methods gave different results, the results were well correlated. The SL technique underestimated soil CO_2 fluxes compared with the DC-1 system, but both methods agreed well when the SL data were corrected for the underestimation at higher fluxes, indicating that inter-site comparisons are possible if techniques are properly cross-calibrated. The EC was the only system that was not well correlated with DC-1. Under low light conditions, EC values were similar to DC-1 estimates, but under high light conditions the EC system seriously underestimated soil fluxes. This was probably because of interference by the photosynthetic activity of a moss layer. Although below-canopy EC fluxes are not necessarily well suited for measuring soil CO_2 efflux in natural forest ecosystems, they provide valuable information about understory gas exchange when used in tandem with soil chambers.

Keywords: closed chamber, eddy covariance, infrared gas analysis, soda lime technique.

Introduction

Accurate measurements of soil CO_2 efflux are crucial in ecosystem carbon (C) budgets, but are difficult to obtain (Lund et al. 1999). Soil CO_2 efflux is the result of two processes: soil CO_2 production (mainly root and microbial respiration) and transport of CO_2 to the atmosphere (Fang and Moncrieff 1999). In undisturbed conditions, transport is dominated by gaseous diffusion and mass flow (Kimball and Lemon 1971), although other forms of transport also occur (Thorstenson and Pollock 1989). The diffusive flux is driven by the concentration gradient between the soil and atmosphere, whereas mass flow depends on pumping by atmospheric pressure fluctuations on turbulent scales (Kimball and Lemon 1971, Kimball 1983, Baldocchi and Meyers 1991). Thus, soil CO_2 efflux can be measured accurately only by a system that does not alter either soil respiratory activity, the CO_2 concentration gradient, or the pressure and air motion near the soil surface.

There are many methods for measuring soil CO_2 efflux, with large differences in accuracy, spatial and temporal resolution, and applicability. Hence, the choice of a specific technique is often a trade-off between requirements (accuracy and resolution) and feasibility (applicability and cost). Furthermore, there is no standard or reference to test accuracy (Nakayama 1990, Rayment and Jarvis 1997), and considerable uncertainty characterizes all types of measurements (Lund et al. 1999).

Traditionally, soil CO_2 fluxes were measured with chambers covering small patches of soil. The use of such enclosures is sometimes criticized both because they are not well suited to sample the spatial heterogeneity inherent to soil CO_2 efflux, and because of so-called chamber effects (Mosier, 1990). Chamber effects include: (1) soil disturbance while placing the chamber, causing CO_2 to be released from the compacted soil pores (Matthias et al. 1980); (2) temperature and moisture changes in the soil and air under the chamber, possibly affecting decomposition and root respiration rates; (3) alteration of the CO_2 concentration gradient between the soil and the chamber headspace, influencing diffusion rates (Healy et al. 1996); (4) elimination or alteration of ambient turbulent pressure fluctuations within the chamber, reducing mass flow of CO_2 (Rayment and Jarvis 1997) and affecting the development of the viscous layer near the soil; (5) sensitivity to pressure differences between the chamber headspace and the atmosphere (differences of 1 Pa or less have been found to induce significant mass flow of CO_2 into or out of the soil beneath the chamber, resulting in significant over- or underestimation of the true fluxes (Kanemasu et al. 1974, Fang and Moncrieff 1996, Rayment and Jarvis 1997, Lund et al. 1999); and (6) place-

ment of a soil chamber modifies air motion and generates pressure variations around the chamber that may alter efflux within the chamber, especially in windy sites and on porous soils and litter layers (Matthias et al. 1980, Rochette et al. 1997).

Depending on the presence or absence of air circulation, chamber methods have been categorized as either static or dynamic (Witkamp and Frank 1969). Static chamber techniques are based either on enrichment or absorption. The soda lime method (Lundegårdh 1927, Monteith et al. 1964, Howard 1966, Edwards 1982, Grogan 1998) is frequently used because it is inexpensive, easy to use, and particularly suitable where spatial variability is large (Kleber and Stahr 1995, Keith et al. 1997, Janssens and Ceulemans 1998). However, static techniques tend to overestimate small fluxes and underestimate large fluxes (Nay et al. 1994) and are, therefore, often regarded as inferior to dynamic chamber systems (Norman et al. 1992).

Two approaches have been developed with dynamic chamber systems employing infrared gas analyzers (IRGA). In closed-chamber IRGA systems, air circulates in a loop between the chamber and an external IRGA (Parkinson 1981, Norman et al. 1992, Goulden and Crill 1997, Rochette et al. 1997). Open-chamber systems have a constant airflow through the chamber, and the CO_2 concentrations in the inlet and outlet are continuously monitored. In these systems, air does not circulate but is vented to the atmosphere (Witkamp and Frank 1969, Edwards and Sollins 1973, Kanemasu et al. 1974, Schwartzkopf 1978, Denmead 1979, Fang and Moncrieff 1996, Iritz et al. 1997, Rayment and Jarvis 1997). Open-chamber systems are extremely sensitive to pressure differences between the chamber and the atmosphere (Kanemasu et al. 1974, Fang and Moncrieff 1996, Rayment and Jarvis 1997, Lund et al. 1999). Several approaches have been suggested to minimize these pressure differences, such as simultaneously blowing and drawing air through the chamber (Fang and Moncrieff 1996), and the use of very large air inlet apertures (Rayment and Jarvis 1997). In closed systems, pressure equilibration between the chamber and the atmosphere can be achieved with a properly designed venting tube (Hutchinson and Mosier 1981, Norman et al. 1992) capable of minimizing leakage. Another important chamber-related problem is the elimination of ambient turbulence. In open systems, transfer of atmospheric pressure fluctuations to the chamber headspace may be partly achieved by using large inlets or outlets (Iritz et al. 1997, Rayment and Jarvis 1997).

To avoid chamber-related problems, alternative techniques, such as the soil CO_2 profile method (de Jong and Schappert 1972, Dueñas et al. 1995, Uchida et al. 1997), the mass balance technique (Dabberdt et al. 1993, Denmead and Raupach 1993) and an array of micrometeorological methods (eddy covariance technique, the flux-gradient method, the Bowen ratio/energy balance method, the aerodynamic method and others) have been applied to estimate soil CO_2 efflux (Rosenberg et al. 1983, Baldocchi et al. 1986, 1997, Fowler and Duyzer 1989, Mosier 1990, Baldocchi and Meyers 1991, Dabberdt et al. 1993, Denmead and Raupach 1993, Dugas 1993, Janssens et al. 2000, Kelliher et al. 1999, Law et al. 1999). The basic concept of these micrometeorological methods is that gas transport from the soil surface is accomplished by eddies that displace air parcels from the soil to the measurement height, and that the vertical flux measured at that reference level is identical to the efflux from the soil (Mosier 1990). Micrometeorological techniques have advantages over chamber systems in that they do not modify the microenvironment of the soil surface (Dugas 1993), and can measure soil CO_2 efflux continuously over long time periods. Another advantage is that they integrate larger surface areas (Baldocchi 1997), thereby sampling the spatial heterogeneity (Mosier 1990). Unfortunately, successful application of these techniques is dependent on several conditions. An extensive, homogeneous upwind fetch and atmospheric steady-state conditions are prerequisites (Baldocchi and Meyers 1991). In addition, the presence of vegetation between the soil and the measurement height may alter the measured fluxes (Goulden and Crill 1997, Norman et al. 1997, A.-S. Morén and A. Lindroth, Swedish Univ. Agric. Sci., Uppsala, unpublished results). In view of these strict requirements, it is unlikely that micrometeorological techniques will replace chamber methods as the most common means of measuring soil CO_2 efflux (Norman et al. 1997).

We have measured soil CO_2 effluxes with the eddy correlation technique and with three chamber techniques: the soda lime method and two dynamic closed chamber IRGA systems. The objectives of the study were to determine how the chamber systems compared, and to test the feasibility of using the eddy correlation techniques at the study site. We found large and systematic differences between the different chamber methods. We demonstrated that calibration functions derived in the laboratory are valid for use *in situ*, and that it is possible to calibrate the different chamber techniques to one standard. The eddy correlation system was not suitable for measuring soil CO_2 efflux at our site.

Materials and methods

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′ N, 4°31′ E). The 2-ha Scots pine stand is part of a 150-ha mixed coniferous–deciduous plantation (De Inslag) in Brasschaat (de Pury and Ceulemans 1997, Janssens et al. 1999*b*). The stand is a level-II observation plot of the European program for Intensive Monitoring of Forest Ecosystems (EU and UN/ECE), and is managed by the Institute for Forestry and Game Management, Flanders, Belgium.

Mean annual temperature at the site is 9.8 °C, and mean annual precipitation is 767 mm (Kowalski et al. 1999). Apart from some shallow drainage ditches, the study site has a flat topography, a gentle slope (0.3%), and an elevation of 16 m (Baeyens et al. 1993). In 1995, tree density was 556 trees ha^{-1}, with a mean tree height of 20.6 m and a mean diameter at breast height (1.3 m) of 0.27 m (Čermák et al. 1998). The forest canopy has a mean depth of 3.7 m, a 35% gap fraction (Van den Berge et al. 1992), and a leaf area index varying between 1.9 and 2.4 (Gond et al. 1999). All undergrowth was com-

pletely 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 site has a moderately wet sandy soil with a distinct humus or iron B-horizon, or both (Baeyens et al. 1993). The organic matter content of the soil (up to 1 m) is estimated at 145 Mg ha^{-1}, 19% of which is stored in the Mor-surface litter layer (Janssens et al. 1999*c*). Fine root (diameter < 1 mm) biomass is 3.2 Mg ha^{-1}, and peaks just below the litter layer (Janssens et al. 1999*c*). More detailed information on the soil, vegetation and local climatic conditions can be found elsewhere (Van den Berge et al. 1992, Baeyens et al. 1993, Janssens et al. 1999*c*, Kowalski et al. 1999).

Measurement techniques

Dynamic closed chamber system 1 (DC-1) In this study, DC-1 was the reference system against which the other techniques were compared (Table 1). The DC-1 is a commercially available portable system (PP-Systems, U.K.), and consists of an IRGA (CIRAS-1) and a soil chamber (SRC-1), equipped with a fan. The soil chamber is cylindrical (height = 150 mm; diameter = 100 mm). Pressure differences between the chamber headspace and the atmosphere were below the detection limit of the manometer (0.5 Pa). To mitigate spatial variability, we enlarged the surface area sampled by the chamber (from 78 to 302 cm^2) by attaching a PVC rim to the base of the chamber. The bottom side of the PVC rim had a slot in which a rubber joint provided an airtight seal for the soil collars. These collars were 20 cm in diameter and 8-cm tall, and were inserted in the soil to a depth of 5 cm, one week before the experiment began. All vegetation was removed from inside the collars. Flux rates were calculated from the increase in CO$_2$ over time, the volume of the entire system and the enclosed soil surface area. Each measurement interval was constrained by a maximum increase in CO$_2$ concentration of 50 ppmv and a maximum duration of 120 s.

Dynamic closed chamber system 2 (DC-2) The DC-2 consisted of a homemade chamber (based on the model proposed by Norman et al. 1992) linked to an IRGA (LI-6250 Li-Cor, Inc., Lincoln, NE) and a control console (Li-Cor LI-6200). At a workshop on soil respiration methodology (Uppsala, 1996), the homemade DC-2 chamber was compared with the commercial chamber sold by Li-Cor (LI-6000-09), and both chambers produced similar results.

The chamber (height = 185 mm; diameter = 80 mm) was aluminum with a PTFE coating on the interior. Air enters the DC-2 chamber through an annular manifold just above the forest floor. The manifold generates sufficient air mixing to ensure homogenization within the chamber. A tube, inserted through a 2-mm-diameter hole in the chamber, equilibrates pressure with the outside. A laboratory study indicated that these pressure differences were less than 0.1 Pa (FCO42 differential pressure transducer, Furness Controls Ltd., Bexhill-on-sea, England). Carbon dioxide leakage through the tube was negligible, because the concentration in the chamber is nearly the same as the ambient concentration. The chambers were put on 8-cm collars. Airflow was first scrubbed with soda lime to reduce the CO$_2$ concentration below ambient, and soil efflux rates were then obtained from the rate of increase in CO$_2$ concentration between 15 ppmv below and 15 ppmv above ambient concentration. Measurements on each collar were duplicated (always with less than 10% variation).

Soda lime technique (SL) Soda lime measurements were made with the same 20-cm-diameter soil collars as used for the DC-1 measurements. The chambers were sealed with 3-cm thick PVC lids. The bottom side of the PVC lids had a slot that fitted the soil collars, and a rubber joint provided an airtight seal. For each measurement, 6 g of pre-dried (24 h at 105 °C) soda lime was placed in a 6-cm-diameter tin tray inside the closed chambers for 24 h. Six controls were used to correct for CO$_2$ absorption during transport. Even at peak flux rates, the weight-ratio of absorbed CO$_2$ to exposed soda lime never exceeded 10%, which is well below the value at which saturation reduces absorption efficiency (Edwards 1982). Also, CO$_2$ concentrations in the chamber headspace remained more or less constant and well below ambient concentrations during the entire exposure period, indicating that saturation did not occur. Flux rates were calculated from the mass increase in soda lime (after drying for 24 h at 105 °C) multiplied by 1.69 to correct for the chemical release of water when soda lime reacts with CO$_2$ (Grogan 1998).

Eddy correlation technique (EC) The eddy correlation instrumentation consisted of a sonic anemometer (USAT-3, Metek GmbH, Elmshorn, Germany) and a Li-Cor IRGA (LI-6262). Data were collected at 10 Hz. The anemometer was mounted at a height of 1.65 m above the forest floor, and the sample intake for the IRGA was located immediately below the anemometer. Air was sampled at a rate of 6.2 dm^3 min^{-1} through a 1.0-mm filter (Acro 50, P/N 4258, Pall Gelman Corp., East Hills, NY) into a teflon tube (inner diameter = 4.33 mm; length = 4.4 m) and heated to avoid condensation. A subsequent filter (Balston 300-01961, Balston Inc., Tewksbury,

Table 1. Overview and description of the four techniques used.

System	Abbreviation	Technical Information
Dynamic Closed system 1	DC-1	IRGA: Ciras-1, PP-Systems Chamber: SRC-1, PP-Systems
Dynamic Closed system 2	DC-2	IRGA: Li-6262, Li-Cor Chamber: Norman et al. 1992
Soda Lime Method	SL	See Janssens and Ceulemans 1998
Eddy Correlation System	EC	IRGA: LI-6262, Li-Cor Anemometer: USAT-3, Metek

MA) conditioned the air before sampling by the IRGA. The IRGA ranges of 300–500 ppmv CO_2 and 0–30 pptv H_2O corresponded to analog output signal ranges of 0–5000 mV, which were processed through the A/D converter of the sonic anemometer, digitized and stored in a computer. Fluxes were computed based on a 30-min averaging period. Time series of winds were delayed to account for system lag in the gas sampling system. 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 was aligned with the mean wind for the averaging period ($\bar{v} = \bar{w} = 0$). The surface-normal flux ($\overline{w'c'}$) was used as the estimate of surface gas exchange. Data were rejected whenever the operators were present within 30 m of the sampling system. Some daytime data were also excluded when the CO_2 concentration fell below the lower measurement limit of the IRGA. Finally, whenever the change in CO_2 concentration from one half hour to the next exceeded 10 ppmv, the flux data were rejected; thereby limiting the importance of any unaccounted storage term. Within 25 m around the eddy correlation system, sparse grass and saplings were removed. In contrast with the chamber measurements, however, the moss layer remained untouched.

Comparison experiments

Modified versus original DC-1   In July 1998, we assessed the effect of enlarging the original soil chamber (see description of DC-1). Inside the large, 20-cm-diameter soil collars of the modified chamber, we installed the smaller, 10-cm-diameter collars on which the original soil chamber fitted. All collars were sampled first with one chamber and then with the second, connected to the same IRGA (CIRAS-1). Because the modified chamber measured a larger area than the original chamber, some degree of variability in the results was expected.

DC-1 versus DC-2   On June 25, 1998, we compared the outputs of the DC-1 and DC-2 chamber systems. For this purpose, the smaller DC-2 soil collars were inserted inside the larger collars used for DC-1. Chambers were selected to cover the widest possible range in soil CO_2 efflux.

DC-1 versus SL   Because soda lime measurements take 24 h, *in situ* comparisons involved nighttime DC-1 measurements. The IRGA system provides information on the diurnal changes in soil CO_2 efflux, whereas the soda lime technique only gives the mean flux for the entire period. Because both techniques had to be applied simultaneously, we could not use the same collars. Instead, we installed 52 collars in 10 groups in the forest. Half of the five to six collars in each group were measured with the soda lime technique, and the other half with the DC-1 system. Eight measurements with the DC-1 system were made at frequent intervals during the 24-h period. Mean daily flux for each collar was obtained by linear interpolation between data points and integration over the entire period. For each system, the mean of two to three collars per group was considered as one data point.

A laboratory experiment (Janssens and Ceulemans 1998) showed that, at higher flux rates, SL gave significantly lower results than DC-1 (Figure 1). For this reason, the SL data were corrected:

$$\text{Corrected SL} = -0.137 + 1.071\,\text{SL} + 0.068\,\text{SL}^2 \qquad (1)$$

DC-1 versus EC   The EC system was installed at the forest floor for a three-week period in June–July 1998. Because the EC method integrates larger surface areas than the DC-1 method, we compared the half-hourly averaged eddy fluxes with the mean of 8 to 10 simultaneous DC-1 measurements. To avoid interference due to the operator's respiration, all DC-1 measurements were made downwind of the EC system. For this purpose, we installed 20 soil collars in a regular circular pattern around, and 5 m from, the EC system. Repeated measurements of soil CO_2 efflux from these collars showed significantly different flux rates; however, the footprint of the eddy flux system integrates several collars. When smoothing the measured flux rates with the fluxes from the four adjacent collars, no significant differences between the different wind directions were detected (Figure 2). Therefore, we assumed no differences between the soil CO_2 efflux rates downwind and upwind of the EC system. To avoid problems associated with nighttime eddy flux measurements (Greco and Baldocchi 1996, Valentini et al. 1996), only daytime data were used in this comparison.

Results

Modification of the DC-1 chamber system

Measurements of soil CO_2 efflux obtained with the DC-1 system with the enlarged soil chamber were not significantly different ($P \leq 0.05$) from those made with the DC-1 with the original soil chamber (Figure 3). We observed an almost 1:1
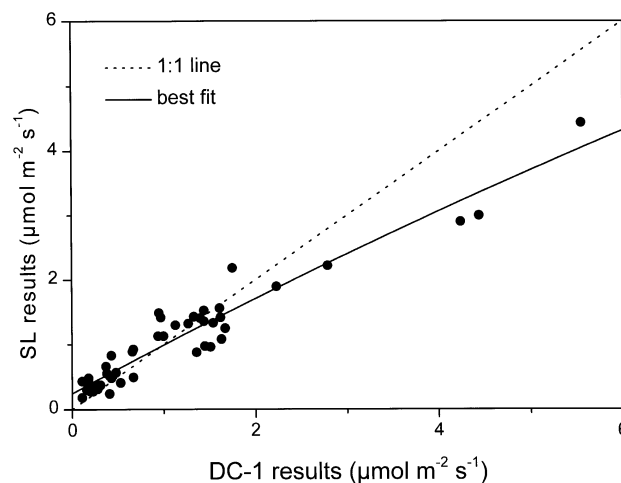

Figure 1. Laboratory comparison of the soda lime (SL) and the dynamic closed chamber (DC-1) techniques (adapted from Janssens and Ceulemans 1998).
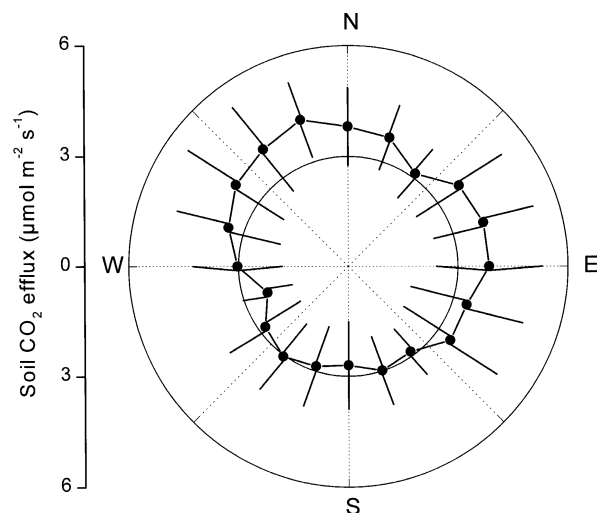
Figure 2. Soil CO_2 efflux rates in different wind directions measured with the DC-1 system at a distance of 5 m from the eddy covariance system. Data from each collar were smoothed with the four adjacent (two at each side) collars. Error bars represent the standard deviation between these five collars.

Figure 4. Comparison of the dynamic closed chamber systems DC-1 and DC-2.

linear relationship ($y = 1.04x$) with good correlation ($R^2 = 0.91$, $n = 19$) between both chambers, despite the use of soil collars of different sizes.

DC-1 versus DC-2

Large differences ($P \leq 0.001$) were detected between the measurements obtained with the two dynamic closed chamber systems, DC-1 and DC-2 (Figure 4). Compared with the results from the DC-1, the DC-2 systematically gave results that were nearly 50% lower (Table 2). Despite the use of different collar sizes, results of both systems were closely correlated ($R^2 = 0.85$, $n = 9$).
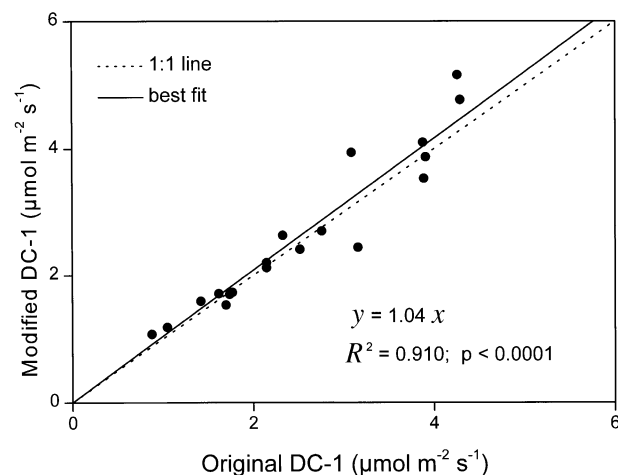
DC-1 versus SL

On average, the SL results were about 10% lower than the DC-1 results (Table 2). Both techniques were well correlated ($R^2 = 0.76$, $n = 10$, Figure 5 top panel), despite the use of different collars, and the fact that the DC-1 result was obtained through linear interpolation of eight data points in the 24-h period. Applying the calibration function to the SL data decreased the difference in absolute values between the two techniques (Figure 5 lower panel).

DC-1 versus EC

Results obtained with the EC system differed significantly ($P \leq 0.001$, $n = 10$) from those obtained with the DC-1 system (Figure 6). On average, the fluxes measured by the EC system were 36% lower than those measured by the DC-1 system (Table 2). However, unlike the chamber systems, the correlation between the DC-1 and EC data was poor (Figure 6 and Table 2). Continuous EC measurements at the site indicated that daytime fluxes were lower than nighttime fluxes, and that variability was much higher during nighttime (Figure 7). Because the lower daytime fluxes measured by the EC system could have been related to moss photosynthesis, we plotted the difference between DC-1 and EC versus PAR (Figure 8).

Figure 3. *In situ* comparison of the original dynamic closed chamber system (DC-1) with the the modified soil chamber.

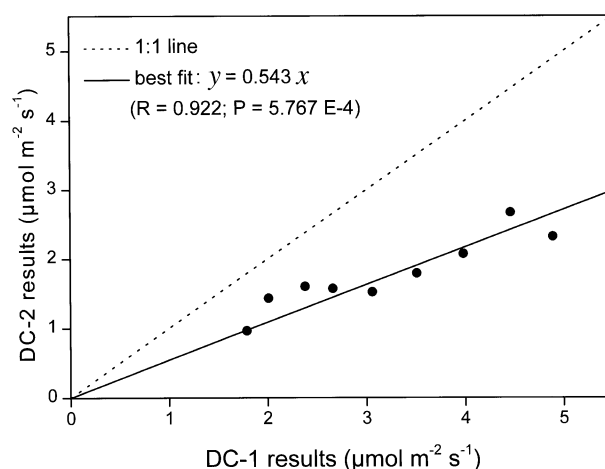Table 2. Relationships and correlations of the soda lime (SL), dynamic closed system 2 (DC-2) and eddy correlation (EC) techniques relative to the dynamic closed system 1 (DC-1).

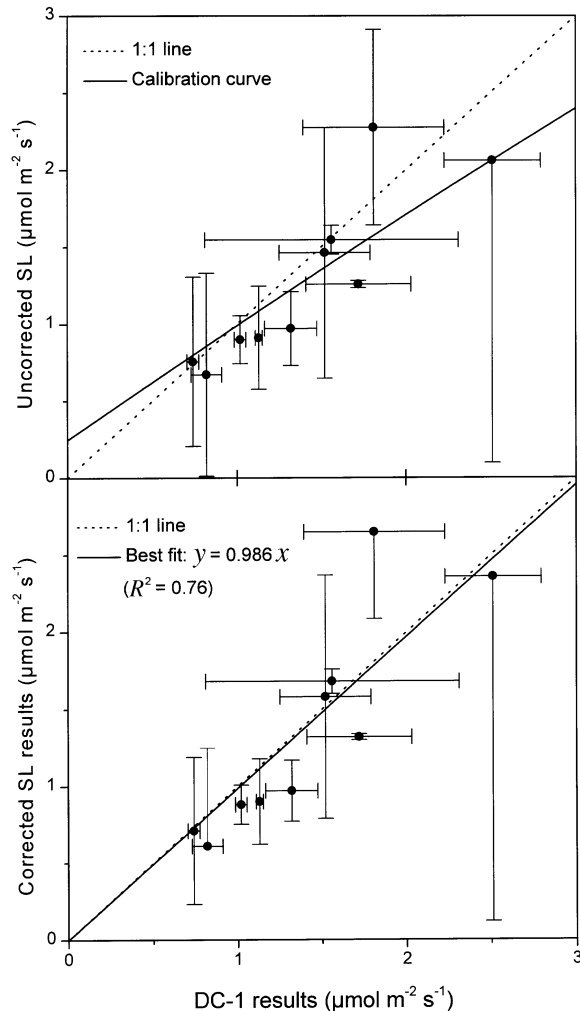| System	Relative to DC-1	R^2
DC-1	1	
SL uncorrected	0.91	0.76
SL corrected	0.99	0.76
DC-2	0.54	0.85
EC	0.64	0.21

Figure 5. Top panel: *In situ* comparison of the soda lime technique (SL) and the dynamic closed chamber system (DC-1). Each data point is the mean of 2–3 soil collars. Error bars represent 1 standard deviation. The calibration function (derived from Figure 1) is also shown. Bottom panel: Corrected SL results (top panel) versus DC-1. For the correction procedure see text and Janssens and Ceulemans (1998). Each data point is the mean of 2–3 soil collars. Error bars represent 1 standard deviation.
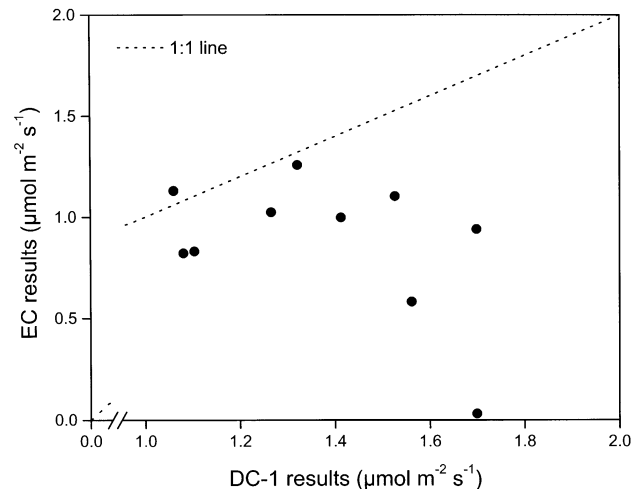

Figure 6. *In situ* comparison of the eddy covariance technique (EC) and the dynamic closed chamber system (DC-1). All DC-1 values are means of 8–10 soil collars that were located downwind to the EC system.
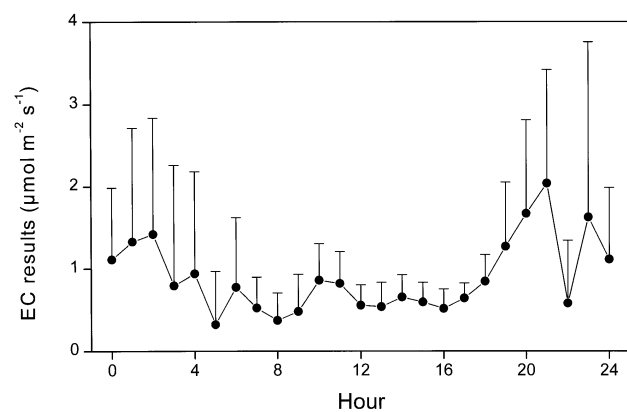

Figure 7. Diurnal trend of CO_2 flux measured by the eddy covariance system (EC). Each data point is the mean of all values monitored at that specific time during a three-week sampling period. Error bars indicate one standard deviation.

Measurements performed at low PAR (left side of Figure 8) were all made under similar soil temperature conditions, whereas measurements made at high PAR were made at different soil temperatures, which could explain the larger scatter at high PAR. There was a positive effect of PAR on the difference between the fluxes measured by DC-1 and EC.

Discussion

Dynamic chambers

Dynamic chamber systems overcome several chamber problems inherent in static chamber systems. Because of the short sampling period required, changes in soil temperature and water content are negligible and buildup of CO_2 in the chamber is limited. Dynamic systems thoroughly mix air in the chamber headspace, preventing the buildup of a thick soil boundary layer.

Inside dynamic chambers, air motion often differs from the prevailing undisturbed conditions. Turbulence influences soil CO_2 efflux directly by the pumping action of the pressure fluctuations, and indirectly by altering the thickness of the viscous boundary layer. In the viscous layer, CO_2 transport occurs slowly by molecular diffusion. An increase in the thickness of the viscous layer will retard diffusion rates, leading to an increased CO_2 concentration in the soil beneath the chamber. Because the soil is porous, CO_2 will diffuse laterally from the soil beneath the chamber to the surrounding area, and chamber flux will be diminished.

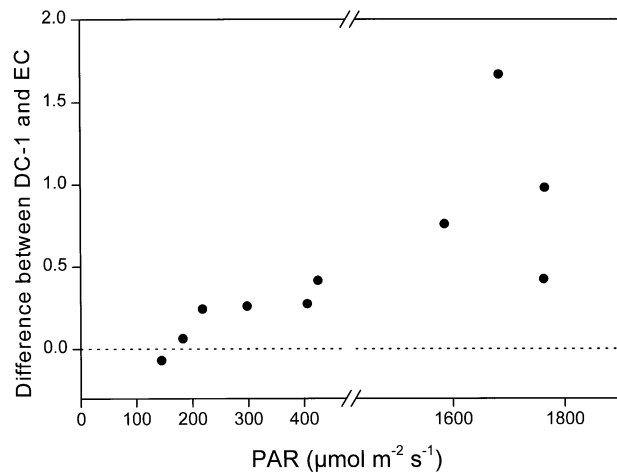Chamber fans may induce unnaturally strong turbulence at

Figure 8. Difference between the dynamic closed chamber system (DC-1) and the eddy covariance technique (EC) as a function of incident photosynthetically active radiation (PAR) above the canopy. (Difference = DC-1 – EC).

the soil surface, enhancing both diffusion (thinner viscous layer) and mass flow (blowing CO$_2$-poor air into the soil, and releasing CO$_2$-rich air from the soil), and thus increase CO$_2$ efflux (Norman et al. 1992, Hanson et al. 1993, Le Dantec et al. 1999). As a result of increased efflux in the chamber, the soil beneath the chamber may be depleted in CO$_2$, which may induce lateral diffusion. This hypothesis is also supported by the studies of Le Dantec et al. (1999). These authors reduced the efflux inside the chamber, by increasing the wind speed outside the chamber to twice that inside the chamber. Le Dantec et al. (1999) concluded that the increased wind speed enhanced soil CO$_2$ efflux outside the chamber, reducing soil CO$_2$ concentrations around the chamber and resulting in lateral diffusion toward the surrounding soil. These studies indicate that, in addition to the sensitivity of chamber measurements to over- or under-pressure, chamber measurements can only be accurate if turbulence inside the chamber resembles ambient conditions. This requirement is almost impossible to fulfill.

The DC-1 and DC-2, dynamic closed chamber IRGA systems, differ with respect to: the ventilation system inside the chambers (DC-1 has a fan); the CO$_2$ concentrations in the chambers during the measurements (DC-2 measures around ambient CO$_2$ concentrations; whereas DC-1 measures above ambient CO$_2$ concentrations); and the pressure equilibration tube in DC-2. Relative to DC-2, the higher CO$_2$ concentrations in the DC-1 chamber would be expected to result in slightly reduced soil fluxes; however, the opposite was observed. The DC-2 systematically gave results nearly 50% lower than the DC-1. In a similar study, Le Dantec et al. (1999) reported 30% lower flux estimates by the DC-2 system compared with the DC-1 system.

Because pressure differences between the chamber headspace and the atmosphere were small in both chambers (below the detection limits of 0.1 and 0.5 Pa), we believe that

the lower fluxes measured by DC-2 were caused by differences in turbulence in the chamber headspace. If this supposition is correct, the higher fluxes measured by DC-1 indicate that fan-induced mass flow in DC-1 is larger than mass flow in DC-2, which is induced by air motion and pressure fluctuations transferred through the pressure equilibration tube.

The ideal chamber system for measuring soil CO$_2$ efflux should mimic ambient conditions perfectly. In a comparison of the DC-1 and DC-2 systems, Le Dantec et al. (1999) found that the average wind speed 1 cm above the soil in the chamber was closer to the prevailing ambient conditions in DC-2 than in DC-1, suggesting that the DC-2 system is more appropriate for measuring soil CO$_2$ efflux in forests. However, because no reference soil CO$_2$ efflux data exist to test the accuracy of either method, it is impossible to say which method is best.

Static chambers

Static techniques for measuring soil CO$_2$ efflux have not evolved much since Lundegårdh's (1927) "respiration bell." Because static chambers have no air motion, molecular diffusion is the dominant process driving soil CO$_2$ efflux (Kimball 1983). In enrichment methods (Crill 1991, Rochette et al. 1992), the buildup of CO$_2$ in the chamber headspace decreases the concentration gradient, and thus the diffusive flux. Enrichment methods therefore tend to underestimate soil CO$_2$ fluxes (Norman et al. 1997).

In contrast to the enrichment methods, absorption techniques such as soda lime (SL) may reduce CO$_2$ concentrations in the chamber headspace (Bekku et al. 1997). Despite the increased concentration gradient between the soil and the chamber air, fluxes are usually underestimated relative to dynamic chamber techniques, especially at high flux rates (Edwards and Sollins 1973, Cropper et al. 1985, Norman et al. 1992, Haynes and Gower 1995, Janssens and Ceulemans 1998). Similarly, we found that the SL results were lower than the DC-1 results.

Depending on efflux rate, soda lime reduced the chamber headspace CO$_2$ concentrations to 40–60 ppmv. These chamber concentrations remained more or less constant throughout the exposure period, indicating that saturation of the soda lime did not occur. Because of the quasi-similar chamber concentrations at all flux rates, the enhancement of the gradient between the soil and chamber was independent of the flux. Therefore, enhancement of molecular diffusion was also similar for all fluxes. Elimination of pumping activity by the chamber, however, had a greater effect on the measured soil CO$_2$ flux when efflux was large than when efflux was small, because mass flow becomes more important when soil CO$_2$ concentrations are high (i.e., at high flux rates).

Thus, the effect of a static chamber with soda lime is to enhance the concentration gradient and to diminish mass flow. The enhanced concentration gradient increases diffusion similarly at all flux rates, whereas the loss of mass flow inside the static chamber becomes more important at higher flux rates. As a result, the SL technique can overestimate small fluxes and underestimate large fluxes (Nay et al. 1994). Alternative

explanations for the underestimation by the soda lime technique, such as a reduction of the concentration gradient or saturation of the absorbent, were not confirmed in this study.

Table 2 suggests that SL overestimated fluxes compared with DC-2, in contrast to previous comparisons (Rochette et al. 1992, Haynes and Gower 1995). Three explanations are considered. First, in all previous comparative studies, fluxes measured by SL were inaccurately corrected for the chemical release of water when soda lime absorbs CO_2. Grogan (1998) has shown that the correction factor should be 1.69 and not 1.4 (the value used in all previous soda lime measurements). Adding 20.7% to the SL results obtained in the other experiments brings the values closer to those obtained with the DC-2. Second, in this study the SL and DC-2 techniques were not directly comparable, because the comparison between DC-1 and SL was done at lower fluxes (0.5–2.5 mmol m^{-2} s^{-1}) than the comparison between DC-1 and DC-2 (2–5 mmol m^{-2} s^{-1}). The SL technique does not underestimate significantly at low fluxes, whereas at high fluxes it does. If the comparison between SL and DC-2 had been done at high flux rates (as were the other comparisons), the SL measurements would probably have been similar to or lower than the DC-2 measurements. Third, different types of soda lime may have been used. The absorption rate of soda lime is related to purity and surface area. Smaller granules are therefore more efficient in absorbing CO_2 and lead to lower CO_2 concentrations in the chamber headspace and increased diffusion rates.

We observed a high correlation between the SL and DC-1 techniques, even though different soil collars were used. The large error bars in Figure 5 were expected, because spatial variability in soil CO_2 efflux is large, and only two to three soil collars were used per data point. After adjusting the SL data with the calibration function, the SL and DC-1 agreed remarkably well, thus validating the SL calibration curve obtained under laboratory conditions (Janssens and Ceulemans, 1998). It also indicates that, when properly used and calibrated against an accurate standard system, the soda lime technique can be a useful tool for measuring soil respiration rates, especially where spatial variability is large.

Large and systematic differences among all kinds of chamber techniques have also been found in other comparative experiments (Cropper et al. 1985, Norman et al. 1997, Le Dantec et al. 1999). Despite large discrepancies between the different chamber systems tested in this study, they were all strongly correlated, indicating that it is possible to calibrate different systems to a reference system. However, because the relationships between the different chamber systems differ on different soil types (Rochette et al. 1992), calibrations should be done *in situ*, or in the laboratory on soil monoliths from the study site.

Eddy covariance

Three weeks of continuous eddy covariance measurements at the site indicated that daytime fluxes were lower than nighttime fluxes. The large variability observed in the nighttime fluxes may be related to incomplete mixing during periods of diminished or sporadic turbulence. During such conditions,

turbulent flux at the measurement height is not necessarily related to soil efflux (Janssens et al. 1999*a*).

In contrast to the findings of Rochette et al. (1997) and Kelliher et al. (1999), we found that the EC system was poorly correlated with DC-1. On average, the EC results were about 40% lower than the DC-1 results. However, underestimation by the EC system was larger during daytime, and increased at high solar irradiances, suggesting that moss photosynthesis contributed significantly to the CO_2 fluxes measured by the EC system. Similar effects of moss or understory plant gas exchange on below-canopy EC measurements have been observed in other studies (Baldocchi et al. 1997, Goulden and Crill 1997, Morén 1999, Norman et al. 1997, Law et al. 1999). Because EC measurements integrate soil respiration as well as understory gas exchange and bole respiration, they are not well suited for estimating soil CO_2 efflux in forest ecosystems with undergrowth. They do, however, provide valuable information on the below-canopy gas exchanges, which are interesting when compared with soil CO_2 efflux and with the above-canopy fluxes.

Conclusions

Large differences in estimated soil CO_2 efflux were found by the four measurement techniques that were tested. There is no means to evaluate which method is most accurate. These different flux estimates imply that inter-site comparisons may be biased if the different measurement systems are not cross-calibrated. However, cross-calibrations should be done *in situ*, because the correction curves are site specific. Despite the large differences in absolute values, the different chamber systems were highly correlated, indicating that it should be possible to calibrate different methodologies against a standard system. After correction, the soda lime results agreed well with the results from the DC-1 closed dynamic chamber system. If sufficient attention is paid to accuracy, the SL method can be a useful technique in heterogeneous forests, where large sample numbers are required. Because the EC system deviated more from the chamber system at high irradiances than at low irradiances, we conclude that photosynthesis by the undergrowth (moss layer) plays an important role. For this reason, micrometeorological techniques are not suited to estimate soil CO_2 efflux in a forest with undergrowth; however, they do provide valuable information on below-canopy gas exchange.

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