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Measuring forest floor CO_2 fluxes in a Douglas-fir forest

G.B. Drewitt [a,*], T.A. Black [a], Z. Nesic [a], E.R. Humphreys [a], E.M. Jork [a], R. Swanson [a], G.J. Ethier [b], T. Griffis [a], K. Morgenstern [a]

[a] *Faculty of Agriculture, University of British Columbia, 2357 Main Mall, Vancouver, BC, Canada V6T 1Z4*
[b] *University of Victoria, Victoria, BC, Canada V6T 1Z4*

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Abstract

CO_2 exchange was measured on the forest floor of a coastal temperate Douglas-fir forest located near Campbell River, British Columbia, Canada. Continuous measurements were obtained at six locations using an automated chamber system between April and December, 2000. Fluxes were measured every half hour by circulating chamber headspace air through a sampling manifold assembly and a closed-path infrared gas analyzer. Maximum CO_2 fluxes measured varied by a factor of almost 3 between the chamber locations, while the highest daily average fluxes observed at two chamber locations occasionally reached values near 15 μmol C m^{-2} s^{-1}. Generally, fluxes ranged between 2 and 10 μmol C m^{-2} s^{-1} during the measurement period. CO_2 flux from the forest floor was strongly related to soil temperature with the highest correlation found with 5 cm depth temperature. A simple temperature dependent exponential model fit to the nighttime fluxes revealed Q_{10} values in the normal range of 2–3 during the warmer parts of the year, but values of 4–5 during cooler periods. Moss photosynthesis was negligible in four of the six chambers, while at the other locations, it reduced daytime half-hourly net CO_2 flux by about 25%. Soil moisture had very little effect on forest floor CO_2 flux. Hysteresis in the annual relationship between chamber fluxes and soil temperatures was observed. Net exchange from the six chambers was estimated to be 1920 ± 530 g C m^{-2} per year, the higher estimates exceeding measurement of ecosystem respiration using year-round eddy correlation above the canopy at this site. This discrepancy is attributed to the inadequate number of chambers to obtain a reliable estimate of the spatial average soil CO_2 flux at the site and uncertainty in the eddy covariance respiration measurements.

Keywords: Soil respiration; Chambers; Coastal temperate Douglas-fir forest; AmeriFlux; Carbon dioxide

1. Introduction

Soils can store and release considerable quantities of carbon through natural processes including litter deposition, decomposition and root respiration (Singh and Gupta, 1977; Raich and Schlesinger, 1992; Sundquist, 1993; Schimel et al., 1994). There has recently been much interest expressed by scientists and policy makers about soil carbon cycling processes. It has been proposed that through careful land use management, it might be possible to increase the quantity of organic matter stored in soils, thereby offsetting a portion of fossil fuel CO_2 emissions. However, there is evidence that the quantity of carbon that can be stored in soils is either quite limited (Schlesinger and Lichter, 2001) or that existing reservoirs of stored soil carbon may act as a net source of CO_2 through increases in respiration rates (Lashof, 1989; Raich and Schlesinger, 1992). While the study of soil carbon dioxide evolution is not new (e.g. Lundegårdh,

* Corresponding author. Tel.: +1-604-822-5654; fax: +1-604-822-8639.
E-mail address: gdrewitt@interchange.ubc.ca (G.B. Drewitt).

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1927; Marsh, 1928), there are still considerable gaps in our understanding of the processes involved. Spatial heterogeneity of local site characteristics and the temporal variability of factors affecting CO_2 production and transport all conspire against any simple descriptions or models (Rayment and Jarvis, 2000). Furthermore, meaningful and reliable field measurements of fluxes from soils are very difficult to obtain (Norman et al., 1997). Researchers have emphasized the importance of improving our understanding of soil processes in order to gain more confidence in projections about future changes in the global carbon cycle (Kirschbaum, 1995; Giardina and Ryan, 2000; Davidson et al., 2000; Cox et al., 2000; Valentini et al., 2000; Grace and Rayment, 2000).

While there are different types of chamber systems to measure gas fluxes from surfaces (for a review, see Livingston and Hutchinson, 1995), there is no standardized approach that is suitable for all situations. One popular method is the flow-through, steady state system with recent examples in Iritz et al. (1997), Morén and Lindroth (2000), Rayment and Jarvis (1998) and Russell et al. (1998). All of these chamber systems measure the gas concentration of air-streams entering and exiting the chamber and compute the flux as being proportional to the product of concentration difference and flow rate through the chamber. This approach has the advantage of being able to transmit natural pressure fluctuations which can contribute to the transport of gas from porous surfaces such as a soil (Kimball and Lemon, 1972; Baldocchi and Meyers, 1991). A disadvantage to this method is the need for the accurate measurement of flow rate and two air-stream concentrations, the latter requiring either two gas analyzers (Russell et al., 1998) or a switching system for alternating sampling of both air-streams (Iritz et al., 1997; Morén and Lindroth, 2000).

A second chamber type that is commonly used is the flow-through, non-steady state type (Livingston and Hutchinson, 1995). With this approach, the rate of increase in gas concentration within the chamber headspace is measured and the flux is assumed to be proportional to the rate of increase. Many research teams have developed and refined various aspects of this method (e.g. see Ambus and Robertson, 1998; Goulden and Crill, 1997; Norman et al., 1992; Norman et al., 1997; Rochette et al., 1997). The main advantage of this method is that a measurement can be obtained relatively quickly so the surface is not enclosed by the chamber for extended periods of time, thereby reducing the amount of soil warming from sunlight when the chamber is closed. Another practical advantage of this method compared to the steady state system is that it requires the measurement of only one CO_2 concentration time series. A limitation is that the increase in CO_2 concentration in the chamber headspace reduces the concentration gradient driving the diffusion of gas from the soil surface (Healy et al., 1996). However, there are methods that can be used to account for this effect (Hutchinson and Mosier, 1981), which will be discussed later.

Problems associated with the use of all types of chambers include the difficulty in capturing spatial variability of fluxes in natural ecosystems (Rayment and Jarvis, 2000) as well as comparing fluxes measured by different chamber systems. Comparison studies between systems at particular sites (e.g. Russell et al., 1998; Norman et al., 1992; Norman et al., 1997; Janssens et al., 2000) have shown that significant differences exist in the fluxes measured by different chambers, but it is very difficult to distinguish between variations caused by chamber differences and those attributed to natural spatial variability. Comparing chamber data with below-canopy eddy correlation measurements can help overcome systematic differences between chamber types and help account for some of the spatial variability. Micrometeorological measurements made within forest understories or in close proximity to a soil surface, however, have their own set of difficulties (Wilson and Meyers, 2001). The use of artificial surfaces with known diffusion coefficients allowing a controlled flux of gas has been shown to be a suitable method of comparing chamber systems (Nay et al., 1994).

This paper has two purposes. The first part describes the design and testing of a chamber system intended to make long-term measurements of forest floor CO_2 fluxes. This chamber system has the advantage of high measurement frequency without disturbing the surface being measured, is suitable for long-term, unattended remote operation and allows the use of multiple chambers that can help account for some of the spatial variability of fluxes from the forest floor. This system was deployed between April and December 2000 in a second growth Douglas-fir forest located on the east coast of Vancouver Island, Canada. The second part

of this paper examines how environmental variables influence the spatial and temporal variability of the forest floor CO_2 flux. Estimates of annual forest floor respiration from this site are derived which will help quantify the role of the soil in the carbon balance of this coastal temperate forest and determine its sensitivity to climate variability. Results from these measurements are compared with other reported fluxes to gain further insight into the role of soil respiration in the carbon budget of this site.

2. Materials and methods

2.1. Site description

The location of this study is on the east side of Vancouver Island, British Columbia, Canada (49°51′N, 125°19′W, 300 m above sea level), 10 km southwest of the city of Campbell River. The terrain slopes towards the Straight of Georgia, approximately 9 km to the east, at an angle of 5–10°. The site naturally regenerated after a forest fire in 1949 with an average tree height during this study of about 33 m, stand density of 1105 stems ha^{-1}, an average DBH of 28.7 cm (95% confidence interval is 26.5–31.9 cm) and a mean annual increment (MAI) of 12 m^3 ha^{-1} per year. The site is in the drier seasonal rainforest of the Pacific Southwest of Canada and belongs to the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar, 1991). The stand is predominantly coastal Douglas-fir (*Pseudotsuga menezeisii* (Mirbel) Franco), while 17% of trees are western red cedar (*Thuja plicata* Donn ex D. Don) and 3% western hemlock (*Tsuga heterophyllla* (Raf.) Sarg.). The base of the canopy is located 15 m above the ground and the overstory canopy projected leaf area index is 6.9 m^2 m^{-2} measured using a LICOR 2000 canopy analyzer (LI-COR, Lincoln, Nebraska, USA) and corrected following the procedure of Chen and Black (1991). The forest understory is quite sparse and low consisting of species such as Oregon grape (*Berberis nervosa* Pursh), Salal (*Gaultheria shallon* Pursh) and Vanilla-leaf deer foot (*Achlys triphylla* (Smith) DC). A 1–5 cm thick discontinuous mat of moss covers both the soil as well as the abundant woody debris and stumps on the forest floor.

The soil is a humo-ferric podzol underlain with a dense compacted till at a depth of 1 m and a surface LFH organic layer, which is between 1 and 10 cm thick (Day et al., 1959). Below the organic layer is gravelly loamy sand grading into gravelly sand below the 40 cm depth with abundant coarse fragments throughout the profile (31% by volume greater than 2 mm in diameter). Mean soil porosity and bulk density between the 10 and 80 cm depths are 49.0 ± 1.1% (±1 S.E.) and 1352 ± 51 kg m^{-3} (±1 S.E.), respectively, with a slightly increasing trend in bulk density with depth. The upper 10 cm of mineral soil has a relatively low and variable density of 971 ± 221 kg m^{-3} (±1 S.E.) (Humphreys, 1999).

2.2. Measurements

As this site is part of the AmeriFlux Monitoring Program, we followed most of the standards set out for measurements in the AmeriFlux science plan (Wofsy and Hollinger, 1998). Details about the main eddy covariance system, measuring above-canopy CO_2 and H_2O turbulent fluxes since August 1997, are available in Jork et al. (1998) and Humphreys et al. (2002). A profile of soil volumetric water content was measured every half hour using four water content reflectometers (Model CS615, Campbell Scientific Inc. (CSI) Logan, UT, USA) at the 2–3, 10–12, 35–48 and 70–100 cm depths. These measurements were adjusted to account for spatial variability in soil water content using manually read time domain reflectometer probes at 11 locations in the vicinity of the flux tower (Humphreys et al., 2002). Climate data, including all components of the radiation budget, profiles of air temperature, atmospheric humidity, soil heat flux and soil temperatures were recorded with dataloggers (Models CR10, 21X, CR7, CSI) connected to a central computer via a multidrop modem network (Model MD-9, CSI). Each night, chamber CO_2 fluxes, eddy fluxes and climate data were sent via cell phone to the University of British Columbia biometeorology laboratory.

2.3. Soil chamber system

The soil chambers used in this investigation were the non-steady state flow-through type (as defined by Livingston and Hutchinson, 1995) constructed from two Plexiglas cylinders 50 cm inner diameter (i.d.) and 15 cm high with walls 3 mm thick. The two cylinders were joined with a hinged aluminum frame and

each cylinder had a 2.5 cm wide flange covered with a 3 mm thick closed-cell foam gasket to provide a seal during measurements. The bottom cylinder was inserted approximately 2–5 cm deep in the soil, cutting as few roots as possible. The upper cylinder (the lid) was covered at the top with a 2 mm thick sheet of Plexiglas. Typical chamber headspace volume when installed in the soil was 65 l, while the chamber covered a soil surface area of 0.19 m^2. A rigid aluminum frame supported a 12 V electric gear motor (Model E-2130, Globe Motor Corporation, Dayton, OH, USA), and pulley assembly, which was attached via flexible nylon cord to the upper cylinder of the chamber. Application of a positive or negative voltage to the motor pulled the lid up or set it down, while two limit switches positioned by the flanges were used to monitor the open/closed status of the lid. When the chamber was closed the weight of the lid caused the two flanges to meet and form an effective seal, while in the open position the lid was positioned vertically allowing precipitation to fall on the soil surface inside the collar. In the event of a fault situation such as a branch falling across the chamber flanges, the lid control program for that particular chamber executed a safety subroutine which left the lid in the open position in order to prevent damage. Faults would then be corrected manually during the next site visit. A 30 cm long 4 mm i.d. vent tube was attached to the collar of each chamber following the procedure in Hutchinson and Mosier (1981) to maintain pressure equilibrium between the inside and outside of the chambers. Measurement timing, control and data acquisition of the chambers and associated signals was done by a 21X datalogger, which in turn operated home-made relay boards. Lid opening and closing was initiated by the 21X, but the specific control tasks (time to open, lid open/closed logic status, fault status) were done by a slave microprocessor (Model Picstic 3, Micromint Corporation, Longwood, FL, USA).

CO_2 concentration in the chambers was measured with an infrared gas analyzer (Model LI-6262, LI-COR Inc., Lincoln, NE, USA) using soda lime and magnesium perchlorate—scrubbed nitrogen as a reference gas. Sampling tubes, 12 m long and 4 mm i.d., (Dekabon Type 1300, Dekaron, Furon Brands, Aurora, OH, USA) linked each chamber to a manifold controlled by AC solenoid valves. Chamber air was pulled through the gas analyzer with an AC linear pump (Model SPP-15EBS-101, Gast Manufacturing, Benton Harbor, MI, USA) and subsequently sent back to the chamber via a second solenoid valve manifold and return line. Flow rate through the 0.3 l volume sampling system was 7 l min^{-1}, resulting in a relatively short residency time (volume/flow rate) of 2.5 s. Tests conducted in the laboratory confirmed the rapid response of the gas sampling loop to step changes in soil chamber gas concentration by exhaling into the vent tube. In order to assure mixing inside the chamber and to avoid any circulation stagnation zones, a small fan was installed in the lid. Measurements with a hand-held hot wire anemometer showed mild turbulence throughout the chamber headspace volume and laboratory measurements showed rapid mixing inside the chamber. The gas analyzer was housed in a thermostated box and automatically calibrated every day. The pump and solenoid manifolds were housed in their own aluminum box, while the rest of the data acquisition and control electronics were enclosed in a third aluminum enclosure.

The control system was designed to allow the operation of six chambers sequentially, each for 5 min of every half hour. This sampling frequency was chosen to match the half hour averaging interval of eddy correlation flux measurements at the field site allowing a more detailed consideration of problems such as temporal variability and partitioning of fluxes from the ecosystem. Closing and opening the chamber required less than 1 min each so that the lid was closed for 3 min of every half hour. Forest floor CO_2 flux (F_{cs}, mol C m^{-2} s^{-1}) was calculated using:

$$F_{cs} = \frac{aPVS_m}{RTA} \quad (1)$$

where V is the volume of the chamber (m^3), A the area (m^2) of soil surface covered by the chamber, S_m the rate of change of CO_2 concentration (mol C mol^{-1} dry air s^{-1}) in the chamber headspace during the measurement, T the chamber air temperature (K) measured in each chamber, P atmospheric pressure (Pa), and R is the universal gas constant, (8.314 J mol^{-1} K^{-1}). The correction factor a, accounts for loss of CO_2 from the chamber headspace during the measurement because of effects such as adsorption on the chamber walls, leaks through the chamber gasket and diffusion through the vent tube. Twice a day, the chambers themselves are calibrated in a procedure first described

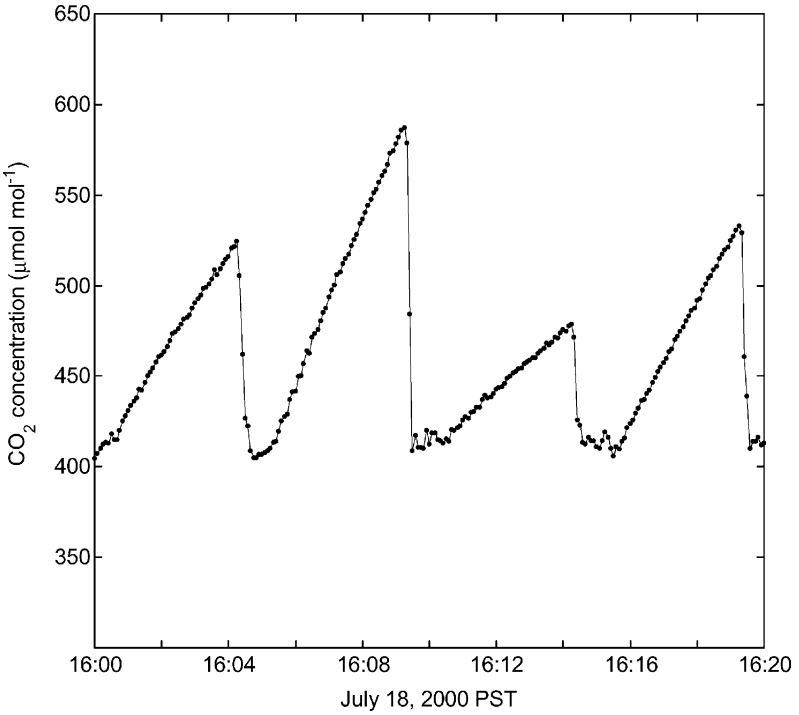

Fig. 1. CO_2 concentration time series for chambers 1 and 2 during measurements and calibration. Chamber 1 begins to close at 16:00 h and the flux is calculated from the rate of CO_2 concentration increase until the lid begins to open at 16:04:20 h. At 16:05 h chamber 1 begins to close again but the mass flow controller delivers a CO_2-in-air mixture which augments the flux from the forest floor surface. This procedure is repeated for chamber 2 beginning at 16:10 h and continues until all six chambers have been calibrated. The calibration procedure is repeated twice daily.

by Goulden and Crill (1997) to calculate a. The product aV is commonly called the effective volume of the chamber. During these chamber calibrations, the usual half hour measurement cycle is extended to 1 h (Fig. 1). Each regular 5 min chamber measurement (lid closing and opening cycle) is immediately followed by a second measurement during which 10 $cm^3\ min^{-1}$ of 10% (by volume) CO_2 in dry air mixture (i.e. 0.1 $mol\ mol^{-1}$) is injected into the chamber return line with a mass flow controller (Model 1179, MKS Instruments, Andover, MA, USA), which corresponds to an injection rate into the chamber of approximately 1 $\mu mol\ C\ s^{-1}$. By rewriting Eq. (1) to account for CO_2 injection and combining the two equations to eliminate F_{cs}, we obtain the following expression for a:

$$a = \frac{IRT}{PV(S_c - S_m)} \quad (2)$$

where S_c ($mol\ C\ mol^{-1}$ dry air s^{-1}) is the rate of CO_2 concentration increase during the calibration period, and I ($mol\ s^{-1}$) is the rate of injection of CO_2 during the calibration period.

Signals from the gas analyzer, flow controller and air temperature thermocouples inside each chamber were sampled at 5 Hz and averaged and recorded every 5 s. This relatively high frequency logging (Fig. 1) allowed the time series of each chamber measurement to be observed in detail and helped with measurement quality control. Forest floor photosynthetic photon flux density was measured at two locations about 10 m from the chambers using quantum sensors (Model LI-190, LI-COR Inc., Lincoln NE, USA). Soil temperatures were measured at each chamber at the 2, 5 and 10 cm depth as well as the chamber headspace air temperature using 20 gauge extension grade chromel–constantan thermocouple wire (Omega Engineering Inc., Stamford, CT, USA). These

climate measurements were sampled at 1 Hz and averaged every minute using a model CR10 datalogger and AM25T thermocouple multiplexer (CSI). All data were written to computer hard disk via the datalogger network every half hour and backed up to optical disk (Iomega Corp, Roy, UT, USA) weekly.

Selecting locations for chamber measurements in a forest is quite difficult because of heterogeneity of the forest floor characteristics, woody debris, roots and rough sloping terrain. The chambers in this study were placed 12–15 m away from the main control boxes on patches of the forest floor surfaces that were subjectively chosen to be representative and showed no sign of disturbance. One obvious, but unavoidable bias was the fact that the chambers did not cover any of the abundant large logs in various states of decomposition strewn throughout the forest floor (relatively high CO_2 fluxes from a log at an advanced stage of decay were measured in 1998 during preliminary experiments). In all cases, the surfaces inside the chambers had a thin (2–5 cm deep) LFH layer and mat of vegetation including mosses and small vascular plants, which were left as undisturbed as possible. All chamber collars were installed in early April 2000, but only chambers 1 and 2 were operated initially until chambers 3–6 were activated in early June. The moss and very small plants inside the chamber collars were not removed in order to keep the forest floor surface as undisturbed as possible. Measurements for a week following chamber installation were discarded to avoid any spurious fluxes caused by recent disturbance to the forest floor surface.

2.4. System testing

The soil chamber system was installed at the field site during August and early September 1999 for preliminary field trials during which 21 days of continuous measurements were obtained. To determine the magnitude of leaks and CO_2 adsorption on the chamber walls, a series of laboratory trials were conducted using the regular chamber calibration procedure with no other CO_2 source in the chamber. CO_2 was injected at a known flow rate and the observed rate of change of concentration in the chamber was subsequently used to calculate the CO_2 flux. Although the injection rate was a volume of gas flowing into the chamber plumbing

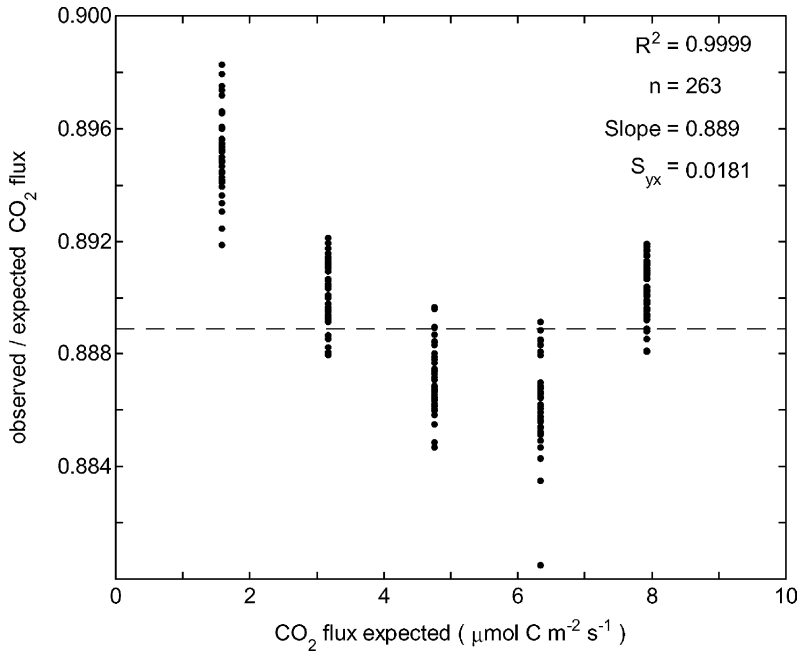

Fig. 2. Ratio of observed to expected CO_2 flux plotted against expected CO_2 flux in the laboratory. The dashed line is the slope of the linear regression of observed flux against expected flux and S_{yx} is the standard error of the regression.

system rather than diffusion from a porous surface, the volume introduced was less than 0.05% the actual chamber volume so the resultant leakage through the pressure equilibration tube and subsequent dilution was negligible. Fig. 2 shows the magnitude of the adsorption and leakage in the laboratory from the addition of CO_2 using five flow rates and calculated from a total of 263 measurements. The effective volume was 11% greater than the geometric volume (i.e. $a = 1.11$) under laboratory conditions (Fig. 2), as measured for one particular chamber. Throughout the field measurements in the year 2000, however, a varied from 1.15 to 1.25 with a range of approximately 0.05 for each chamber. Factors such as needles on the flange, dust accumulation on the chamber walls and slight misalignment of the lid all contribute to the increase in effective volume.

Whether CO_2 accumulation in the chamber headspace caused any decrease in flux by suppressing the concentration gradient was evaluated by examining each concentration rate of change (referred hereafter as "slope") constituting a chamber measurement during the field measurement period. Measurements obtained between 0 and 1 min after the start of lid closure were disregarded to allow for the lid to close and seat properly (requiring 40 s). Slopes were calculated for the three intervals, 1–2, 2–3 and 3–4 min with the 4–5 min interval reserved for lid opening (i.e. the lid started to open 4 min after the start of lid closure). The average slope between 1 and 4 min was also calculated for comparison purposes. Nighttime fluxes calculated from 1 to 4 min interval led to a 10% underestimate when compared to fluxes calculated from 1 to 2 min interval (Fig. 3). This suggests that even with the chamber closed for a relatively short time (3 min duration), accumulation of CO_2 in the chamber headspace will measurably inhibit diffusion from the soil surface. This effect was observed consistently

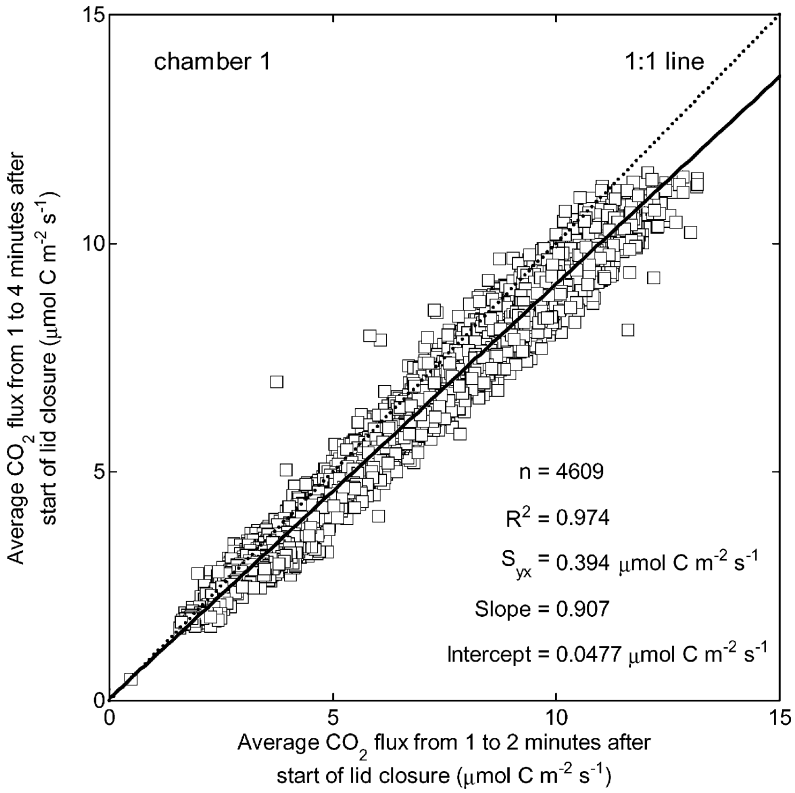

Fig. 3. Nighttime forest floor CO_2 fluxes calculated from the CO_2 concentration rate of change in chamber 1 during 1–4 min (after lid closure initiation) vs. the fluxes calculated from the change during 1–2 min. The solid line is the linear least squares best fit and the dotted line is the 1:1 relationship.

throughout the measurement period between April and December 2000.

A second method to calculate fluxes, reported by Hutchinson and Mosier (1981) corrects for the effect of increasing CO_2 concentration in the chamber headspace. They derived the following equation for the initial flux (f_0) at the instant when the chamber is closed assuming: (1) that chamber headspace concentration is equal to the gas concentration at the soil surface, (2) there is a depth in the soil at which the CO_2 concentration is unaffected by the chamber placed over the soil surface, and (3) gas concentration is a linear function of depth between the surface and this zone of constant concentration:

$$f_0 = \frac{aV(C_1 - C_0)^2}{A\,\Delta t(2C_1 - C_2 - C_0)} \ln\left[\frac{C_1 - C_0}{C_2 - C_1}\right] \quad (3)$$

where C_0, C_1, C_2 are the headspace gas concentrations measured at equally spaced time intervals, Δt. While their analysis focused on measurements of N_2O fluxes measured with sampling syringes, this method can be applied to other gases and measurement techniques providing the assumptions are reasonably met. This method of calculating the initial flux (f_0) was compared with that using the slope of the CO_2 concentration for the 1–2 min interval. C_0, C_1 and C_2 were measured 90 s apart (i.e. at $t = 0$, 90 and 180 s after lid closure) to get three equally spaced measurements in time spanning the period when the lid was closed. Fig. 4 shows that calculating CO_2 flux from the slope during 1–2 min will result in a further underestimation of the flux by approximately 6–8% compared to f_0 obtained from Eq. (3).

When considering the use of Eq. (3) in the calculation of flux for this particular chamber system, care must be taken to evaluate the influence of factors such as the chamber headspace volume and gas sampling flow rate. Obtaining an average CO_2 concentration

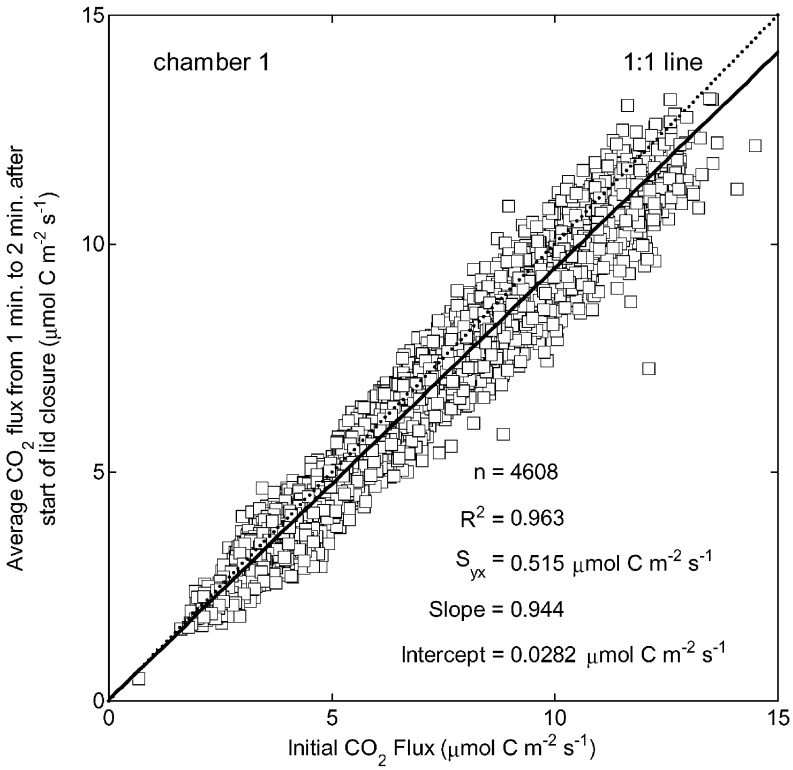

Fig. 4. Nighttime forest floor CO_2 fluxes calculated from the CO_2 concentration rate of change in chamber 1 during 1–2 min (after lid closure initiation) vs. the initial flux calculated using Eq. (4). The solid line is the linear least squares best fit and the dotted line is the 1:1 relationship.

from a continuous time series at equally spaced times must take into account the variability or noise in the CO_2 concentration signal (see Fig. 1). This variability makes the calculation of initial CO_2 flux sensitive to the method chosen to obtain an average C_0, C_1 and C_2. Obtaining a single "batch" sample to arrive at a concentration (for example, by the use of a syringe or an appropriate sampling volume) might reduce some of this variability although this was not tested during these measurements. In all fluxes reported in this study, both factors to account for leaks and adsorption (typically, 15–25% increase during field measurements) as well as the non-linearity of the slope as a result of the suppressed concentration gradient (typically, 6–8% increase during field measurements) were applied.

Without an independent means to generate or measure a known flux of CO_2 from a surface such as that used by Nay et al. (1994), it is difficult to provide an accurate estimate of the absolute error associated with the use of these chambers in the field. It is encouraging to note that the direction and magnitude of the two correction factors applied were physically reasonable and corresponded to our field experience with the mechanical tolerances of the individual chambers. Although the chamber sealing mechanisms were designed to be forgiving with regards to the manufacturing tolerances and installation procedure, some of the chambers did work slightly better than others and the occasional small problems required attention during site visits (loose hinges, twigs on gaskets, insects, etc.). There was never any inexplicable change in chamber performance, which indicates that they were stable and suitable for continuous measurements throughout the year.

3. Results and discussion

3.1. Temporal and spatial variability of CO_2 fluxes

Fig. 5 illustrates CO_2 fluxes measured by chamber 2 between 26 September and 10 October 2000, a period when soil moisture and the deep soil temperatures were relatively steady. Diurnal flux variations were clearly associated with variations of the 5-cm depth soil temperature. Daily amplitudes of

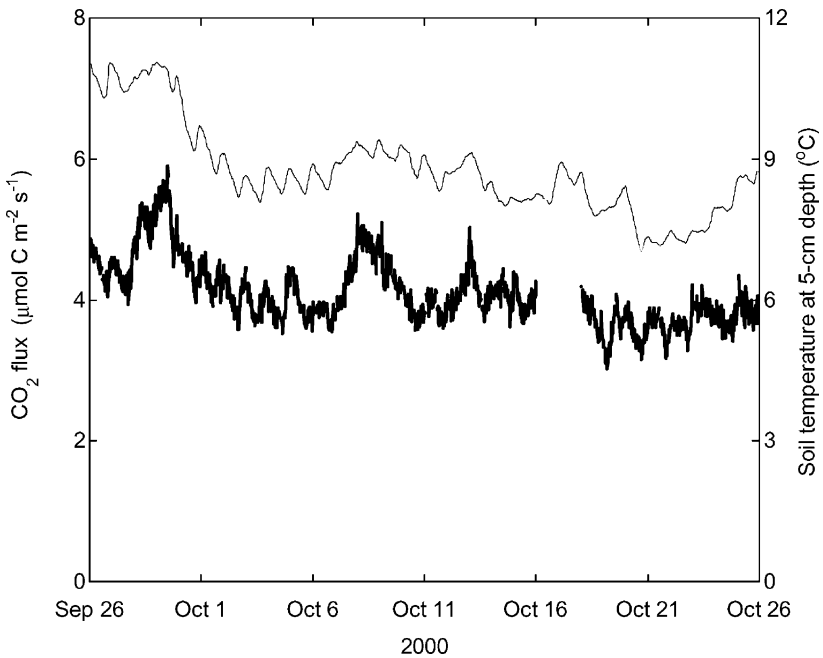

Fig. 5. Time series of chamber 2 forest floor CO_2 fluxes (thick line) and 5 cm depth soil temperature measured adjacent to the chamber (thin line) between 26 September and 26 October 2000.

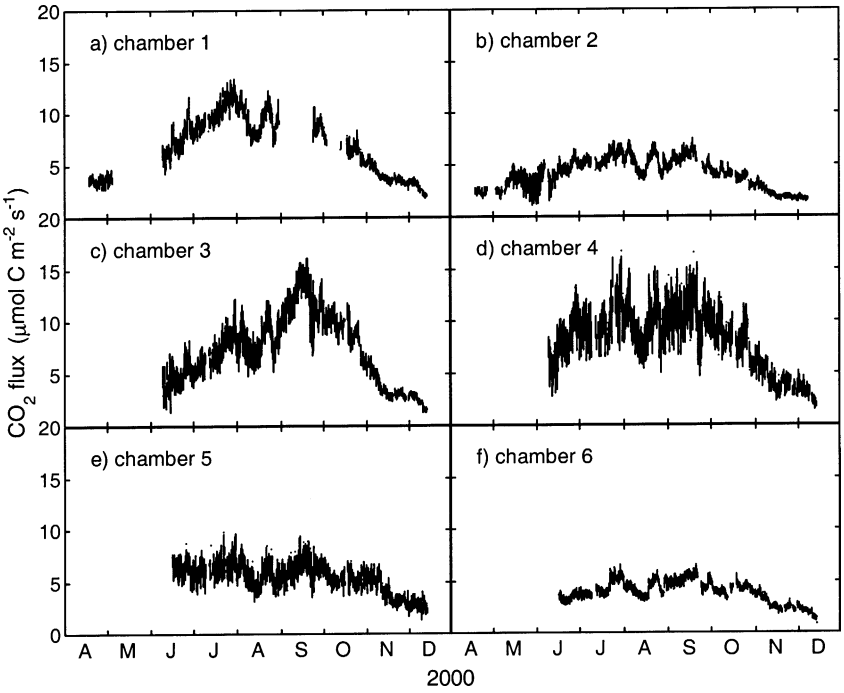

Fig. 6. Half hourly forest floor CO_2 flux measured at six locations between April and December 2000.

the fluxes were between 0.5 and 1.5 μmol C m^{-2} s^{-1} and were generally the lowest observed for all six chambers (Fig. 6). Chamber 4 had an extremely high daily amplitude during the warmest time of the year with the difference between daily maximum and minimum approaching 8 μmol C m^{-2} s^{-1} (Fig. 6d). In warm weather, the daily flux amplitudes for all chambers were usually between these two extreme values. In early winter, daily amplitudes were considerably lower ranging between approximately 0.5 and 2 μmol C m^{-2} s^{-1}. The highest daily flux usually occurred in the mid to late afternoon local time coinciding with the maximum daily soil temperatures at the 2 and 5 cm soil depths. The effect of temperature will be considered in more detail in Section 3.2.

In addition to the effect of diurnal temperature variations, there was also the marked seasonal effect of the soil warming in spring and summer, and cooling in the autumn and winter. Fig. 6 shows that fluxes from all six chambers had a seasonal trend with peak values occurring in summer and early autumn when soil temperatures were the highest. Maximum daily average fluxes in summertime varied widely between chamber locations (6–14 μmol C m^{-2} s^{-1}). Chambers 2 and 6 had the lowest summertime fluxes with maximum daily average values generally less than 7 μmol C m^{-2} s^{-1}, while chambers 1 and 5 were between 7 and 10 μmol C m^{-2} s^{-1}, and chambers 3 and 4 had the highest summertime values, near 15 μmol C m^{-2} s^{-1}. Conversely, the cold winter weather caused a considerable reduction in fluxes (with the exception of chamber 5) to less than 3 μmol C m^{-2} s^{-1} (Fig. 6.)

There were strong similarities in the responses of the measured chamber fluxes during the year even though there was notable difference in magnitude of flux between chambers. This is likely due to changes in environmental variables affecting all chambers simultaneously. Chamber fluxes were highly correlated with each other with values of the correlation coefficients (R) exceeding 0.72 (Table 1). This indicates that all the chambers responded similarly to the factors controlling soil CO_2 production and transport at this site. While the flux magnitudes varied by a factor

Table 1
Correlation coefficients (R) computed between all half-hourly forest floor CO_2 flux measurements in 2000 for all six chambers

Chamber	1	2	3	4	5	6
1	1	–	–	–	–	–
2	0.968	1	–	–	–	–
3	0.808	0.761	1	–	–	–
4	0.934	0.923	0.809	1	–	–
5	0.844	0.858	0.723	0.826	1	–
6	0.871	0.856	0.906	0.878	0.823	1

of 2–3 between the chambers, it is impossible to determine quantitatively how fluxes vary with distance over the forest floor surface without a sampling program explicitly designed for such a purpose. Other researchers have observed considerable spatial variability in forest floor CO_2 fluxes even over relatively small distances (Rayment and Jarvis, 2000; Norman et al., 1997). Soil samples were obtained from the inside of each chamber collar at the end of the measurement season for analysis of carbon and nitrogen contents. There were visible differences in the quantity and quality of organic matter present in the soil samples obtained from the different chambers. Much of the spatial variability in fluxes is likely caused by the uneven distribution of organic substrate.

3.2. Temperature responses of forest floor CO_2 flux

Forest floor CO_2 flux was generally well described by an exponential function of soil temperature (T) at the 5 cm depth:

$$F_{cs} = R_{ref} Q_{10}^{(T-T_{ref})/10} \quad (4)$$

The Q_{10} coefficient is the relative increase in respiration rate for a 10 °C change in temperature, while R_{ref} is the respiration rate at an arbitrary reference temperature, T_{ref} (in this case, 10 °C). While Eq. (4) is useful in determining the sensitivity of fluxes to temperature and can be instructive for data quality assurance and rough comparisons between and within study sites and field campaigns, it does not always provide an unbiased estimate of respiration rates (Lloyd and Taylor, 1994; Howard and Howard, 1979). In certain cases, an Arrhenius-type equation, which accounts for changes in activation energy at different temperatures, can better describe the relation of respiration with temperature (Lloyd and Taylor, 1994). In this study, however, it was consistently found that a single parameter mechanistic equation (e.g. Eq. (11) in Lloyd and Taylor, 1994) did not fit the observations as well as the simple empirical model of Eq. (4).

Fig. 7 shows the nightly average forest floor CO_2 flux measurements obtained at each chamber location plotted against nighttime average 5 cm depth soil temperature between 15 April and 15 December. Rejecting data below a volumetric water content threshold showed a slight reduction in flux when the soil was the driest (near 0.09 $m^3 m^{-3}$). However, this did not account for the multiple, distinct, flux temperature-relationships observed for some of the chambers. These relationships were found to have a relatively strong dependence on date when fluxes were measured, so fluxes from each chamber were separated into two subsets. Generally, at any given temperature, fluxes measured in the spring and early summer (prior to 7 August) were lower than fluxes measured in the fall (after 27 August). During the transition period between 7 August and 27 August, the considerable variation in the flux (Fig. 7c) appeared to be unrelated to both soil temperature or water content. Table 2 shows the model parameters computed for the early season (before 7 August) and late season (after 27 August) as well as the overall best fit line to all observations (all data, including the period between 7 August and 27 August). These results show that separating the data into subsets often yielded higher R^2 values, but there was a very large range in the computed Q_{10} and R_{10} parameters between the chamber locations. The overall effect of this seasonal dependence of respiration was an annual hysteresis loop that was more evident in some chambers than others. Seasonal hysteresis-type behavior in soil CO_2 flux measured in the field has been observed by other researchers (Morén and Lindroth, 2000; Goulden et al., 1998).

It is possible that the late summer increase in flux was the result of an increase in fine root respiration. Grier et al. (1981) observed that both young and mature sub-alpine Douglas-fir ecosystems showed increased root growth in the latter part of the growing season which could partially account for the high fluxes observed at these times. A second factor, that can contribute to variability in the flux–temperature relationship is that details of the soil temperature

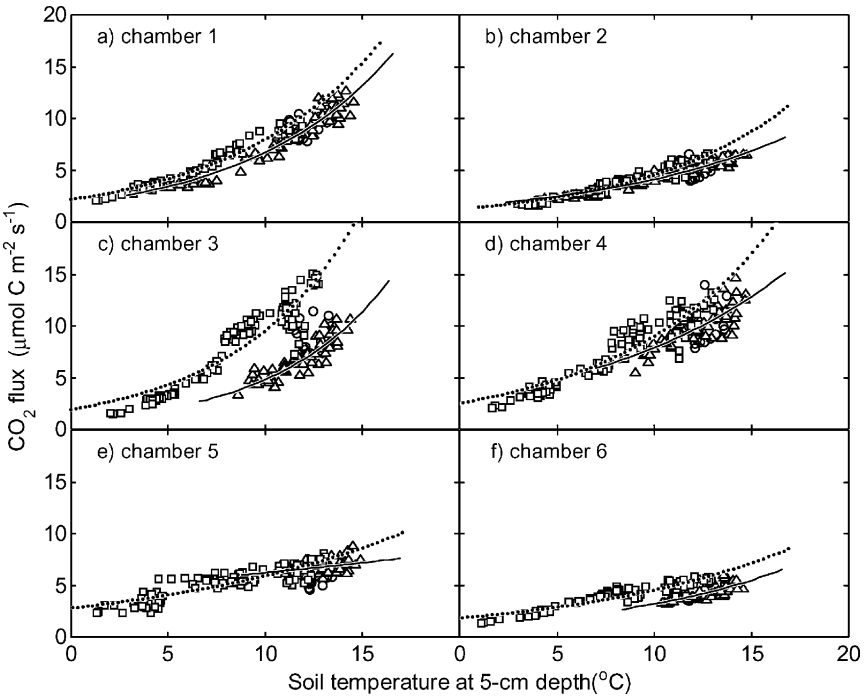

Fig. 7. Relationship between nighttime average CO_2 flux and 5 cm depth soil temperature prior to 7 August 2000 (triangles, solid line) and after 27 August 2000 (squares and dashed line). Data between these two dates are plotted as circles. Lines are least squares best fit using Eq. (4).

profile throughout the year are not captured by a measurement at a single shallow depth. While it is convenient to develop flux–temperature relationships using a single-depth soil temperature, the value of a Q_{10} should strictly be reported when all other confounding factors such as microbial populations, root density and soil temperatures at other depths are constant. Q_{10} values that describe the temperature sensitivity of CO_2 flux from the forest floor surface, but not the actual respiration processes in the soil are referred to as the "effective" Q_{10} by Morén and Lindroth (2000). It is likely that the hysteresis in the annual surface CO_2 flux–temperature response is affected by the interactions between root phenology, microbial population density and soil temperature at deeper depths, as well as other physical and chemical factors such as

Table 2
Model parameters obtained from fitting Eq. (5) to all measured nighttime forest floor CO_2 fluxes in 2000 ($n = 236$)[a]

Chamber	R^2			Q_{10}			R_{10}		
	All	Early	Late	All	Early	Late	All	Early	Late
1	0.920	0.928	0.948	3.22	3.84	3.72	7.15	6.70	7.93
2	0.870	0.915	0.942	2.87	2.77	3.71	4.20	4.12	4.52
3	0.425	0.793	0.895	2.56	5.58	4.96	7.49	4.81	9.52
4	0.780	0.649	0.893	2.66	2.64	3.55	8.29	7.90	8.99
5	0.685	0.134	0.772	1.82	1.33	2.13	5.63	6.22	5.89
6	0.581	0.531	0.881	1.84	2.94	2.49	3.99	3.20	4.51

[a] Also shown are parameters for fluxes before 7 August (early, $n = 126$) and after 27 August (late, $n = 196$).

gas diffusivities and nutrient status (Schlentner and Van Cleve, 1985; Bouma et al., 1997; Flanagan and Van Cleve, 1983). Multilayered approaches, such as those proposed by Fang and Moncrieff (1999) and Swanson and Flanagan (2001), could account for some of the effects of changes in soil temperature and soil properties with depth.

3.3. Light response of forest floor CO_2 flux

During late May and early June, when the system was unattended for a long time, a considerable amount of Vanilla-leaf deerfoot sprouted inside the collar of chamber 2 (maximum leaf area index of approximately $0.25\,m^2\,m^{-2}$). This vegetation was subsequently clipped at the base of the stems to return the surface to the original dominant moss cover. Before the stems were cut, daytime CO_2 net fluxes were noticeably lower than nighttime values because of photosynthetic uptake of CO_2. Fig. 8 compares the daytime and nighttime net CO_2 fluxes in chamber 2 before and after clipping on 15 June. For soil temperatures between 11 and 13 °C, daytime fluxes increased by roughly $2\,\mu mol\,C\,m^{-2}\,s^{-1}$ after removal of the vegetation (Fig. 8b). The well defined nighttime flux–temperature relationship before and after removal of the plants (Fig. 8a) suggests that nighttime respiration of live vegetation and the respiration from decomposing roots after clipping are similar in magnitude. However, since this chamber had very little variability in fluxes during the entire measurement campaign, it is also possible that the vegetation respiration and decomposition of the remaining roots were low and did not cause a significant overestimate of forest floor CO_2 flux from this location. Comparing the daytime and nighttime fluxes after clipping the vegetation (Fig. 8a and b) shows that in chamber 2 the moss alone had a very low net rate of carbon assimilation. To avoid confounding photosynthesis with other environmental variables, all daytime respiration measurements were flagged for caution to ensure there were no correlations of low fluxes with periods of bright sunlight. A decrease in CO_2 flux caused by photosynthesis was almost negligible at most times of

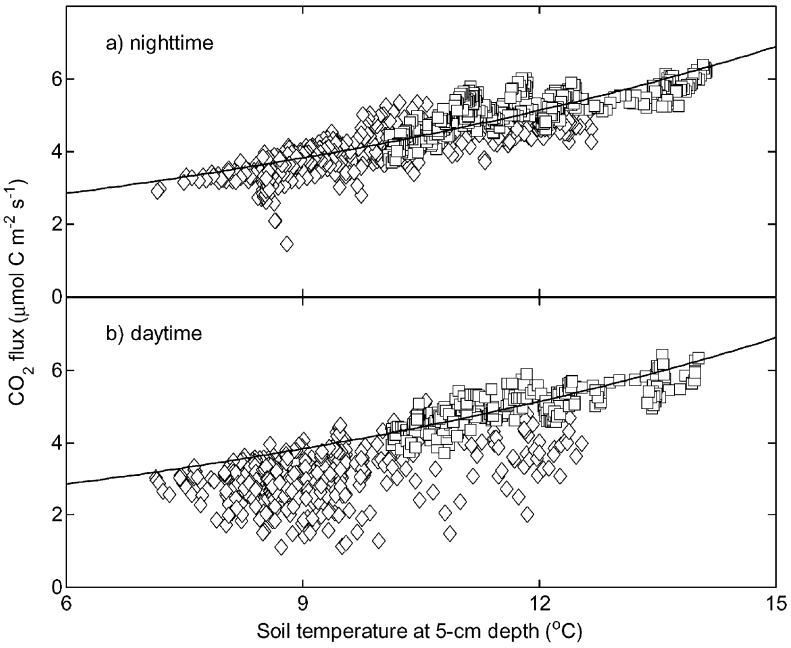

Fig. 8. Comparison of chamber 2 nighttime and daytime (PPFD $> 3\,\mu mol\,m^{-2}\,s^{-1}$) half hourly net forest floor CO_2 fluxes during period of 21 May to 12 June (diamonds, before clipping the vegetation in the chamber on 15 June) and 20 June to 8 July (squares, only moss remaining in the chamber). The equation of the line in both (a) and (b), which was fit by non-linear least squares using nighttime data from both periods, is $F_{cs} = 4.220 \times 2.664^{(T-10)/10}$.

the year in most chambers except for chambers 4 and 5, which had measurable differences in their daytime and nighttime flux–temperature relationship even in December when air temperatures often fell below 0 °C. Photosynthetic uptake by moss at cold temperatures was also observed by Goulden et al. (1998) on a boreal black spruce forest floor. In this study, negative fluxes (i.e. when forest floor respiration is less than photosynthesis) were not observed during almost 8 months of measurements at the six different chamber locations. This relatively low photosynthetic rate is in contrast to results of others (e.g. Goulden and Crill, 1997; Morén and Lindroth, 2000; Swanson and Flanagan, 2001) and is likely due to the sparse nature of the moss layer at our site and the very low light levels at the forest floor.

3.4. Responses of CO_2 fluxes to soil water content

The site examined in this study receives considerable precipitation, but it is not unusual for summertime tree water stress to occur (soil water potential less than −1 MPa). Observations in the field and laboratory show that too much or too little water can inhibit respiration in soil micro-organisms (Bunnell et al., 1977), although establishing the exact nature of this relationship has been very difficult because of other factors such as nutrient availability (Schlentner and Van Cleve, 1985). Fig. 9 is a time series plot of chamber 6 forest floor respiration during the entire measurement period plotted with the shallowest volumetric water content measured (2–3 cm depth). There is an apparent correlation between soil moisture and surface CO_2 fluxes especially during the warmer season between late June to mid October. However, there was also a relatively strong negative relationship between temperature and moisture (correlation coefficient $R = -0.763$) so that separating the relative role of these two variables was difficult. This increases the uncertainty in the role of high soil water contents on forest floor CO_2 fluxes.

Bunnell et al. (1977) proposed an empirical model to explain the role of soil moisture and temperature on soil CO_2 flux by combining Eq. (4) with a soil moisture function as follows:

$$F_{cs}(\theta, T) = \frac{\theta}{a_1 + \theta} \frac{a_2}{a_2 + \theta} a_3 Q_{10}^{(T - T_{ref})/10} \quad (5)$$

where θ is the soil volumetric water content ($m^3\ m^{-3}$), and a_1, a_2, a_3 as well as Q_{10} are fitted parameters, in

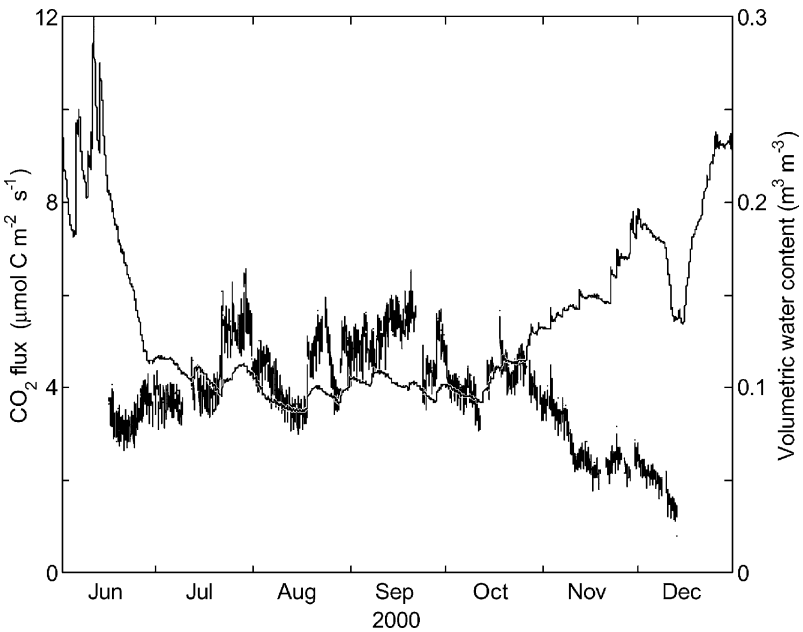

Fig. 9. Time series of chamber 6 forest floor CO_2 fluxes (thick line) and volumetric water content at the 2–3 cm depth (thin line) from June to December 2000.

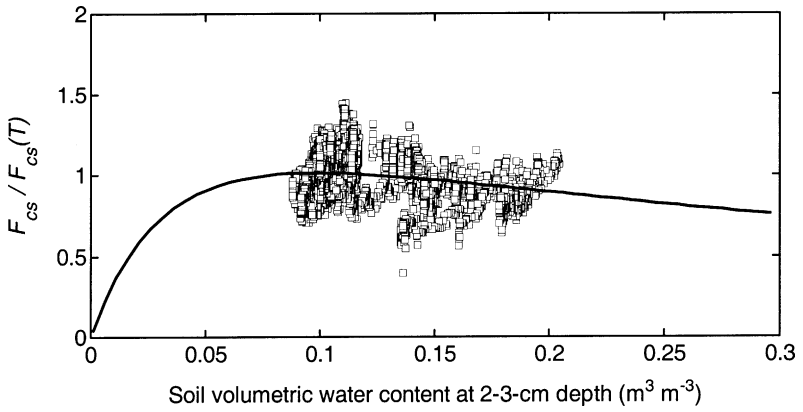

Fig. 10. Chamber 6 half-hourly nighttime forest floor CO_2 fluxes normalized by the best fit line of Eq. (4) vs. 2–3 cm depth soil volumetric water content. The solid line is the non-linear least squares best fit of the θ-terms of Eq. (5).

this case, obtained using a constrained non-linear least squares parameter searching procedure (Nelder–Mead simplex method, Matlab, The Mathworks Inc.).

Fluxes from chamber 6 (shown in Fig. 9) were normalized by the best fit values of $F_{cs}(T) = a_3 Q_{10}^{(T-T_{ref})/10}$ in Eq. (5) and plotted against the observed volumetric water content (Fig. 10). These "temperature normalized" fluxes are compared with the product of the first and second terms of Eq. (5), which shows the shape of the flux-water content response curve developed by Bunnell et al. (1977). This demonstrates the relatively poor agreement of the observations to the modeled CO_2 flux response to θ given in Eq. (5). Table 3 shows the R^2 values comparing the least squares best fit equations to observed fluxes using Eq. (4), the water content effects of Eq. (5) (terms 1 and 2) and both temperature and water content effects of Eq. (5) (all terms). Clearly, water content explained little of the variance in soil CO_2 fluxes from most chambers (chamber 3 being the notable exception). It should be noted that fitting this equation ignores the hysterisis previously described in Section 3.2. It is possible that careful consideration of the temperature—flux relationship for different seasons would reduce the scatter in Fig. 10 although it would reduce the general applicability of Eq. (5) and likely not improve our ability to predict fluxes. Fig. 10 also indicates the possible appearance of a soil water content threshold just below 0.09 m^3 m^{-3}, where data in this range show a reasonably distinct break with observed fluxes dropping off considerably at lower water contents. Plotting the normalized flux data against soil water potential derived from soil water retention curves developed in the laboratory from intact soil cores (Humphreys, 1999) showed considerable scatter and no clear relationship. It would have been useful to obtain measurements in the early spring when the soil is near saturation in order to reduce the uncertainty of fluxes at very high water contents. Future observations could include artificial irrigation as well as setting up a simple shelter above one or more chambers to allow soil to become very dry.

Table 3
R^2 coefficients obtained from fitting the temperature-dependent model (Eq. (4)) as well as the soil temperature and water content-dependent model (Eq. (5)) to observed nighttime fluxes for six chambers

Chamber	Temperature	Water content	Temperature and water content
1	0.905	0.502	0.914
2	0.833	0.350	0.846
3	0.366	0.517	0.540
4	0.673	0.417	0.700
5	0.562	0.239	0.582
6	0.547	0.450	0.610

3.5. Estimating net annual forest floor respiration

Using Eq. (5), an estimate of the annual net forest floor CO_2 flux was calculated for the six chambers using the measured temperature and soil water content

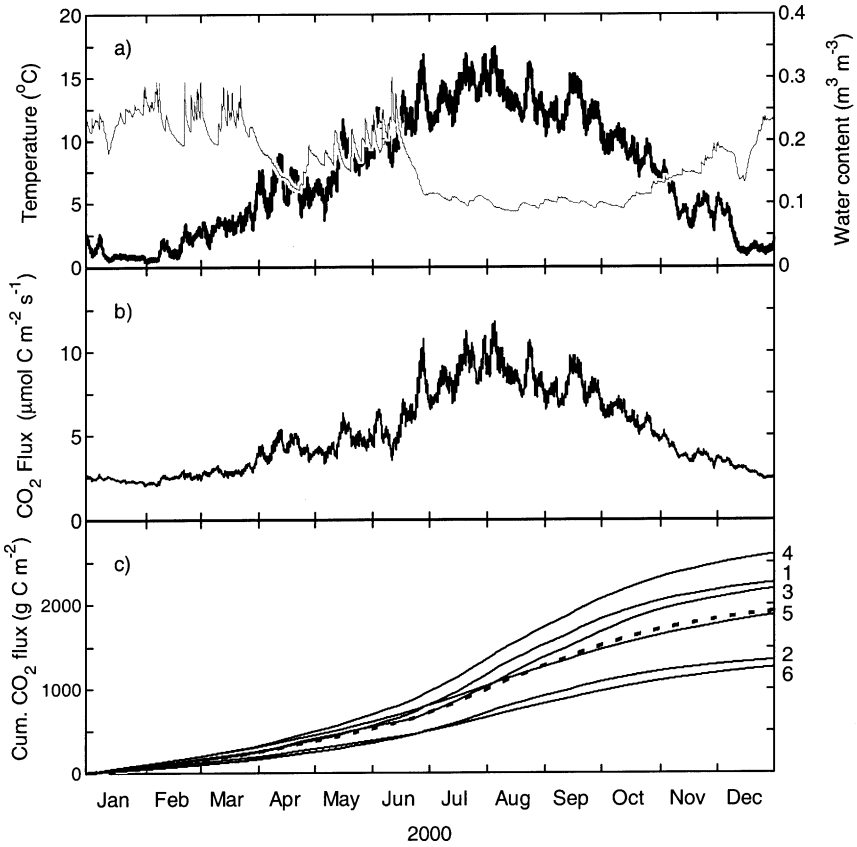

Fig. 11. (a) Soil temperature at the 5 cm depth (thick line) and volumetric water content at the 2 cm depth (thin line). (b) Calculated average forest floor CO_2 flux obtained from the average of six chambers using best fit models of Eq. (5) for the six chambers and using temperature and water content observations from (a). (c) Calculated cumulative flux from each of the six chambers (labeled on right vertical axis). The dashed line is the average cumulative flux.

data. Fig. 11a is a plot of the soil temperature at the 5 cm depth and the 2–3 cm depth soil volumetric water content measured continuously during 2000 at the research site used to calculate half hourly values of CO_2 flux. Fig. 11b is the corresponding plot of the average of each half hourly flux estimate obtained using Eq. (5) derived for each of the six chambers. It is worthwhile noting that Eq. (5) was fitted to the entire nighttime observation dataset for each chamber and there was no stratification done on the basis of date. This is reasonably justified since there is insufficient data to accurately model the date-dependent change in fluxes caused by biological effects and until we can better understand these processes, it would only cause unrealistic discontinuities in the calculated time series of half hourly CO_2 flux. Since temperature was found to be a dominant influence in the fluxes observed, it is not surprising that the temperature trace of Fig. 11a and the modeled flux trace of Fig. 11b show remarkable similarity in their shape. The annual cumulative average of the flux from all chambers range between 1260 and 2600 g C m^{-2} with an average of 1920 $\pm$ 530 g C m^{-2} (standard deviation of the six chambers). This represents a very high average flux of carbon out of these locations and is much higher than the total ecosystem respiration of 1640 $\pm$ 300 g C m^{-2} estimated by the above-canopy eddy correlation system using a simple soil temperature dependent exponential model fitted to nighttime fluxes measured at a friction velocity greater than 0.3 m s^{-1} (Black et al.,

1996). The discrepancy is possibly caused by the fact that chambers are unable to provide an accurate spatial average flux as well as difficulties in estimating nighttime ecosystem fluxes in stable conditions using above-canopy eddy correlation measurements in well mixed conditions (Lavigne et al., 1997).

Flux measurements obtained under very cool and wet conditions (for example, January to April) would be useful in reducing the uncertainty of the net forest floor respiration at these times. Factors such as heterogeneous distribution of large organic debris and underground root location could also account for some of the spatial variability of fluxes observed during this study. It would be of great benefit to augment these long-term measurements of CO_2 flux from fixed locations with portable chamber measurements to capture more of the spatial variability at this site.

Estimates of net annual CO_2 exchange provided here are higher than the yearly soil fluxes reported in Raich and Schlesinger (1992) as well as those fluxes measured by Janssens et al. (2000) and reviewed in Janssens et al. (2001) from European forests. However, Morén and Lindroth (2000) estimated a relatively high annual forest floor flux of over $1000\,g\,C\,m^{-2}$ per year from a boreal spruce and pine forest floor and Rayment and Jarvis (2000) estimated annual flux between 786 and $1026\,g\,C\,m^{-2}$ per year from the BOREAS Southern Old Black Spruce site. Moncrieff and Fang (1999) determined a value of $1400\,g\,C\,m^{-2}$ per year from a Florida slash pine plantation which has a much warmer climate. It has recently been reported in Janssens et al. (2001), that soil respiration is generally related to annual net ecosystem productivity at many different European forests. Since the west coast Douglas-fir forest in this study is very productive (Kurz et al., 1996), it might be expected that annual cumulative carbon losses from the forest floor should be large.

4. Conclusions

This study presents the results of soil chamber measurements obtained from the forest floor of a second growth managed coastal temperate Douglas-fir forest. Correction factors were applied to account for adsorption and leaks of the chamber as well as suppression of CO_2 gradients from increasing concentration in the chamber headspace. After accounting for these factors, the maximum observed fluxes were $16\,\mu mol\,C\,m^{-2}\,s^{-1}$ at two chamber locations for a short period during the warmest part of the growing season. In general, the fluxes from the chambers were lower than this and usually on the order of $4–10\,\mu mol\,C\,m^{-2}\,s^{-1}$ decreasing to $2–4\,\mu mol\,C\,m^{-2}\,s^{-1}$ in the early winter at the onset of freezing in the uppermost soil layers. Forest floor CO_2 flux was well described by a relatively simple exponential function with the 5 cm depth soil temperature, consistent with many other chamber-derived CO_2 flux measurements reported in the literature. However, the flux–temperature relationship varied considerably among and between the chamber locations in this study suggesting a strong dependence on micro-site characteristics. These measurements also indicate the possibility of seasonal changes in microbial activity or root respiration causing an apparent hysterisis in the production of CO_2. The relationship of CO_2 flux to soil moisture was much more difficult to describe in any satisfactory manner. A relatively simple model proposed by Bunnell et al. (1977) helped to explain some of the variations in forest floor flux although there remained considerable variability that could not be attributed to moisture or temperature.

Estimates of net annual CO_2 flux ranged between 1260 and $2600\,g\,C\,m^{-2}$ per year at the six chamber locations with an average of $1920\,g\,C\,m^{-2}$ per year. The similarity of this value and the estimate of ecosystem respiration derived from nighttime eddy correlation measurements indicates that soil respiration likely dominates ecosystem respiration at this site. The rate of soil respiration in this Douglas-fir stand is higher than most values reported in the literature and is likely due to the presence of large quantities of forest floor organic matter and the relatively high productivity of the site.

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