

Seasonal contribution of CO₂ fluxes in the annual C budget of a northern bog

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[1] Peatlands are sinks for carbon dioxide (CO₂) because net primary production exceeds decomposition. The contribution of non-growing-season fluxes to the annual C budget of a peatland is, to date, little studied. We therefore measured the changes in the pattern of carbon exchange with seasons in a bog located in the cool temperate climate region. The growing season CO₂-C uptake was of -113 g m^{-2} . During the non-growing season, 36 g C m^{-2} was lost to the atmosphere, resulting in an estimated net ecosystem production of -76 g C m^{-2} . Despite the non-growing-season loss equaling 33 to 40% of the summer uptake, the net annual accumulation of was 3 times the long-term average net accumulation rate usually cited in the literature. The high rate of non-growing-season efflux could be supported directly by temporal concurrent respiration and the release of stored CO₂ from prior production. These results indicate the need to revise current models to address peat thermal properties inducing CO₂ production at lower temperature ranges. *INDEX TERMS*: 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1610 Global Change: Atmosphere (0315, 0325); 1890 Hydrology: Wetlands; *KEYWORDS*: carbon dioxide, winter, seasonality, net ecosystem exchange, carbon budget

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1. Introduction

[2] Peatlands comprise 95% of northern wetlands [Matthews and Fung, 1987] and contain 30% of the world's soil carbon [Gorham, 1991]. Long-term average accumulation rates of $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ are typical for peatland ecosystems [Gorham, 1995]. This accumulation is equivalent to 10% of the annual net primary production (NPP) of peatland plants [Gorham, 1995]. NPP in peatlands is particularly sensitive to both hydrology and temperature [Billings *et al.*, 1982; Kim and Verma, 1992; Moore and Knowles, 1989; Silvola *et al.*, 1996] and, therefore, should be responsive to changes in climate. While NPP is difficult to measure, there are several examples of direct measurements of net ecosystem exchange (NEE: NPP minus soil respiration), though only for part of the year [Carroll and Crill, 1997; Klinger *et al.*, 1994; Neumann *et al.*, 1994; Shurpali *et al.*, 1995; Szumigalski and Bayley, 1997]. The exchange of CO₂ in winter is usually ignored, as it is assumed to be small. Our objective was to determine the magnitude and, hence, the significance of the winter exchange of CO₂ to the annual net ecosystem production (NEP) in a mid continental bog. Few researchers have addressed the role of

the non-growing-season CO₂ flux in peatlands [Mast *et al.*, 1998; Panikov and Dedysh, 2000], and even fewer compare the winter flux with the growing season exchange of the same year [Alm *et al.*, 1999; Lafleur *et al.*, 2001]. The non-growing-season exchange has been shown to offset between 5 and 40% of the net growing season C uptake [Alm *et al.*, 1999; Panikov and Dedysh, 2000]. Moreover, the winter-summer comparisons have been done mostly on more nutrient rich peatlands (e.g., fens, appa mires, etc.) located in climate regions not representative of the large mid continental peatland regions of North America and Russia.

[3] Typical growing season daily mean NEE varies between 0.18 and $0.57 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ [Frolking *et al.*, 1998; Bubier *et al.*, 1998] and is strongly correlated with photosynthetically active radiation (PAR), biomass, and to a less extent, temperature and moisture. CO₂ efflux may occur during the non-growing season due to the release of stored CO₂ by diffusion and sustained heterotrophic respiration. Snow insulation, the low thermal conductivity of the unsaturated moss and near-surface peat and the large heat capacity of the moist peat below the surface [Roulet and Mortsch, 1997] maintain peat temperatures relatively near or above freezing during most of the winter. Meanwhile, microbial activity can occur down to temperatures of -6.5°C [Coxson and Parkinson, 1987; Zimov *et al.*, 1993]. Zimov *et al.* [1993] attributed winter CO₂ production

and efflux to the high mineralization by soil biota in the aerobic layer, resulting in a retardation of soil freezing and thus a prolongation of biological activity. In the case of methane (CH₄), flux/storage ratios suggest that winter fluxes could result from production of CH₄ and the release of the temporary storage of gases produced during the growing season [Dise, 1992], and a steady loss of older gases from the deeper peat layers [Clymo, 1984]. Schimel and Clein [1996] hypothesized that low non-growing-season microbial respiration rates are of importance in the annual carbon budget of northern peatlands due to the length of the snow-covered season. Current estimates of the non-growing-season CO₂ contribution to the annual C budget, based on nonconcurrent measurements of summer and winter exchange, are 21% in a Finnish mixed mire [Alm *et al.*, 1999], 25% in an Alaskan forest [Sommerfeld *et al.*, 1996], 17% in an alpine wetland [Mast *et al.*, 1998], and 37% in boreal mineral soils [Pajari, 1995].

[4] Owing to the large temporal variability of fluxes in peatlands, it is important to determine the seasonal contribution of CO₂ from the same year of study. The present study determines the contribution of non-growing-season CO₂ fluxes to the annual carbon budget of a peatland in Québec, Canada. Particular attention is paid to the seasonal dynamics of the fluxes to identify the principal controls (e.g., temperature, moisture and snowpack characteristics) on the annual C fluxes.

2. Methods and Materials

2.1. Site Description

[5] The Mirabel peatland complex is situated 45 km north of Montréal, Québec, Canada (45°42'N, 73°55'W). The region lies in the cool temperate zone, where the local climate is characterized by a mean annual temperature of 6.1°C and a mean annual precipitation of 940 mm, 23% of which falls as snow (normals for 1941 to 1990, Canada Climate Normals: Environment Canada). The snow-covered period extends from late November to mid-April.

[6] The peatland complex is a raised, open ombrotrophic bog more typical of the boreal zone than the temperate zone. Covering an area of 1.2 km², the site is flanked to the north by a 0.4 km² poor fen located in a slight depression. The peat depths range from over 4 m at the deepest point to 1 m at the margins [Muller, 2001]. The mean soil pH values are 3.3 and 3.6 for the bog and fen, respectively. The mean annual water table depth at the central bog site is -0.29 m. Hummocks and hollows occur throughout the peatland with an average hummock/hollow vertical difference of approximately 0.15 m. A mixture *Picea mariana* and *Larix laricina* borders the bog. In the center of the bog, the hummocks are dominated by *Sphagnum fuscum*, *Sphagnum russowii* and *Lycopodium* mosses and ericaceous shrubs of *Chamaedaphne calyculata* and *Ledum groenlandicum*. In the hollows, *Sphagnum magellanicum* predominates and ericaceous shrubs are less abundant.

2.2. Non-Growing-Season Carbon Dioxide Measurements

[7] NEE was measured weekly using insulated polyethylene plastic chambers (volume ≈ 8 L; surface area =

0.052 m² [Moore and Roulet, 1991]) that were permanently set in collars inserted 5 cm into the peat at the soil/snow interface for the snow covered period (measurements were taken from February 1997 to mid-April 1997). The insulation was to attempt to mimic the insulating properties at the base of the snow cover. The chambers were placed both on hollow and hummock sites, in order to represent an integrated view of a spatially heterogeneous microtopography and vegetation. The vegetation consisted of two chambers of just mosses and two with a combination of mosses and vascular plants per microstructure. The chambers became completely snow covered after the first or second snowfall. The head space of the chambers was accessed by sampling tubes and the chambers were flushed for 2 min with ambient air to reduce the CO₂ concentrations that had built up between sample dates. After sealing, i.e., closing the sample loop through the chamber, five 20-ml-headspace gas samples were extracted over a period of 20 min. Chamber measurements were also made at the snowpack surface in order to compare the magnitude of the flux across the snow-air interface to those at the snow-soil interface. Snowpack density was determined using snow depth, porosity and snow-water equivalent data. Snow air CO₂ concentrations were taken within each layer of snow separated by ice lenses, by horizontally inserting a steel rod, with a crimped 0.1 m perforated tip, 0.5 m into the snowpack face. All non-growing-season gas samples were analyzed within 12 hours of collection, on a Shimadzu Mini2 gas chromatograph with a MTN-1 methanizer. The methanizer used Ni-reduced shimalite to reduce CO₂ to CH₄ at a detector block temperature of 375°C and He and H₂ were the carrier gases (flow rate of 40 cm³ min⁻¹). Gas standards of 345, 1986, and 10,000 ppm CO₂ were used.

2.3. Growing Season Carbon Dioxide Measurements

[8] At the onset of snowmelt all environmentally controlled clear Plexiglas chamber replaced the static chambers. This chamber transmits 87% of incident photo-synthetically active radiation (PAR) and had a cooling system that kept the temperature and humidity within 10% of ambient [Waddington and Roulet, 1996]. Incident PAR and chamber temperatures were measured concurrently with the CO₂ samples. The chambers were inserted on pre-installed collars, and half-light and dark runs were undertaken immediately following each full light run after the headspace concentrations in the chamber had returned to ambient levels. The dark runs were used to define the efflux of CO₂ due to respiration and CO₂ emitted due to changes in stored CO₂ in the soil, while the half light runs were used alongside the full light runs for the development of a NEE-PAR curve. CO₂ exchanges were measured in the field using a LICOR-6252© differential nondispersive infrared gas analyzer (NDIR). The LICOR was calibrated daily prior to use with N₂-CO₂ free standard for the zero span and a 355 ppm CO₂ standard for the ambient span.

2.4. Stored CO₂ and Environmental Variables

[9] Air in the soil pores was sampled weekly for CO₂ during the non-growing season at depths of 0.05, 0.15,

0.25, 0.35, 0.65 and 1.00 m. Silicone membrane tubing permeable to gas and impermeable to water was used (3 mm width i.d. & 38.88 cm³ volume per depth) [Jacinthe and Dick, 1996]. The depth of frost penetration was seldom greater than 5 to 10 cm and the surface layers of the peat had between 20 and 40% air filled porosity. No corrections were made for the temperature dependency of the gas permeability of the sampler membrane, but the minimum interval between samples was 3 days, allowing adequate time for equilibrium between concentration in the soil and samplers. The membrane samplers were installed in the peat at the beginning of the study and the same sampler was repeatedly sampled. Dissolved gases from growing season measurements of pore water taken from depths of 0.1, 0.2, 0.3, 0.4 and 0.6 m were made when the water table was within these depths. Air samples were analyzed on the Shimadzu GC. Dissolved CO₂ was determined after equilibration with an equal volume of nitrogen in the syringe headspace by shaking the samples vigorously for 2 min. Thermocouples were inserted at the same depth as the non-growing-season pore air samplers and readings were made every 60 s and averaged every half hour. PAR, wind speed, relative humidity and ambient temperature were measured every minute and averaged every half hour from the end of April 1997 to the completion of the study.

2.5. Analysis

[10] A NEE-PAR relationship, defined by a rectangular hyperbola [Waddington and Roulet, 1996], was developed to quantify the seasonal fluxes using continuous measurements of PAR. A linear relationship was derived between 5-cm peat temperatures and dark fluxes, as the relationship between other temperature depths and dark CO₂ efflux was poorer. The continuous record of temperature was then used to produce an estimate of total dark efflux. Due to a poorer relationship between WT and dark fluxes and the small improvement observed in the multiple linear regression (including 5-cm peat temperatures), WT was not used as a variable for the linear regression model (see section 3). It was also assumed that due to the microtopographic diversity of the sites, picked specifically to cover the whole range of vegetation and topographic differences, the variation in the WT over the seasons would not be a representative environmental variable for the whole site. A positive sign was adopted to indicate a release of CO₂; hence, a negative sign indicates CO₂ uptake.

[11] The diffusion of CO₂ through the snowpack was determined by Fick's one-dimensional diffusion equation,

$$J = -\tau\phi D \times dc/dz, \quad (1)$$

where ϕ is porosity of the layer, τ is tortuosity of the layer, D is the diffusion coefficient for CO₂ in air, and dc/dz is the concentration gradient across a uniform layer. Tortuosity was assumed to be within the range of 0.75 to 0.92 [Sommerfeld *et al.*, 1996] and was taken as the equivalent of $\phi^{1/3}$.

[12] Statistical analysis of the data was undertaken using SYSTAT. The NEE-PAR curves and linear correlations for

the dark fluxes were fit using Table Curve version 2D (Jandel Scientific).

3. Results

[13] Instantaneous measurements of NEE taken from February 1997 to December 1997 displayed a characteristic pattern of growing season net uptake and non-growing-season release of CO₂ (Figure 1b). Based on the general trend of fluxes through time, the growing season was broken into spring, summer and fall seasons as follows: spring from April 11 to June 5; summer from June 6 to September 15; and fall from September 16 to November 21 (Figure 1a). These seasonal differentiations correspond to the periods of increasing photosynthesis (green up), the period of maximum CO₂ uptake and senescence, respectively. The non-growing season was assumed to begin as soon as the ground was covered with permanent snow. The transition from mean daily net release to net daily uptake during the spring period was between April 2 (0.053 ± 0.045 mg CO₂ m⁻² s⁻¹; mean \pm standard error) and the last day of snowmelt, April 10 (-0.039 ± 0.014 mg CO₂ m⁻² s⁻¹). From July 21 to August 7, the mean uptake (-0.018 ± 0.001 mg CO₂ m⁻² s⁻¹) was unusually small compared to the average mean summer uptake (-0.051 ± 0.010 mg CO₂ m⁻² s⁻¹). From August 25 to December 7 the mean net daily uptake slowly decreased from -0.107 ± 0.023 to 0.006 ± 0.004 mg CO₂ m⁻² s⁻¹.

3.1. Non-Growing Season

[14] Measurements of non-growing-season NEE were taken at the soil-snow interface between the beginning of February and the end of snowmelt on April 11. The mean seasonal release was of 0.012 ± 0.003 mg CO₂ m⁻² s⁻¹. Variations through the season range from a mean daily release of 0.074 ± 0.044 mg CO₂ m⁻² s⁻¹ on March 2, to a mean uptake of -0.039 ± 0.014 mg CO₂ m⁻² s⁻¹ on April 10. Mean daily flux was positively but not significantly correlated to 5-cm peat temperatures ($r^2 = 0.60$, $p < 0.5$). Temperature-flux relationships for greater depths produced worse relationships. Fluxes measured at the snow surface were highly variable and generally slightly negative and showed no temporal trend or relationship to other environmental variables such as temperature. Because we suspect the snow surface measurements are erroneous due to ventilation, only the soil fluxes were used in the determination of the annual carbon budget.

[15] CO₂ concentrations in the snowpack increased with depth (Figure 2). Although higher CO₂ concentrations were observed below thicker ice lenses, the concentrations were not notably affected by ice lenses with the exception of March 28. Estimates of snow surface effluxes by Fickian diffusion based on the observed concentration gradients were an order of magnitude higher than those measured with snow surface chambers on two out of the three occasions (Table 1). The model estimates fall within the range observed by Sommerfeld *et al.* [1996]. Pore air concentrations of peat CO₂ were temporally variable but generally increased with depth (Figure 3), with the exception of March 7 and 28 and April 8. The concentration

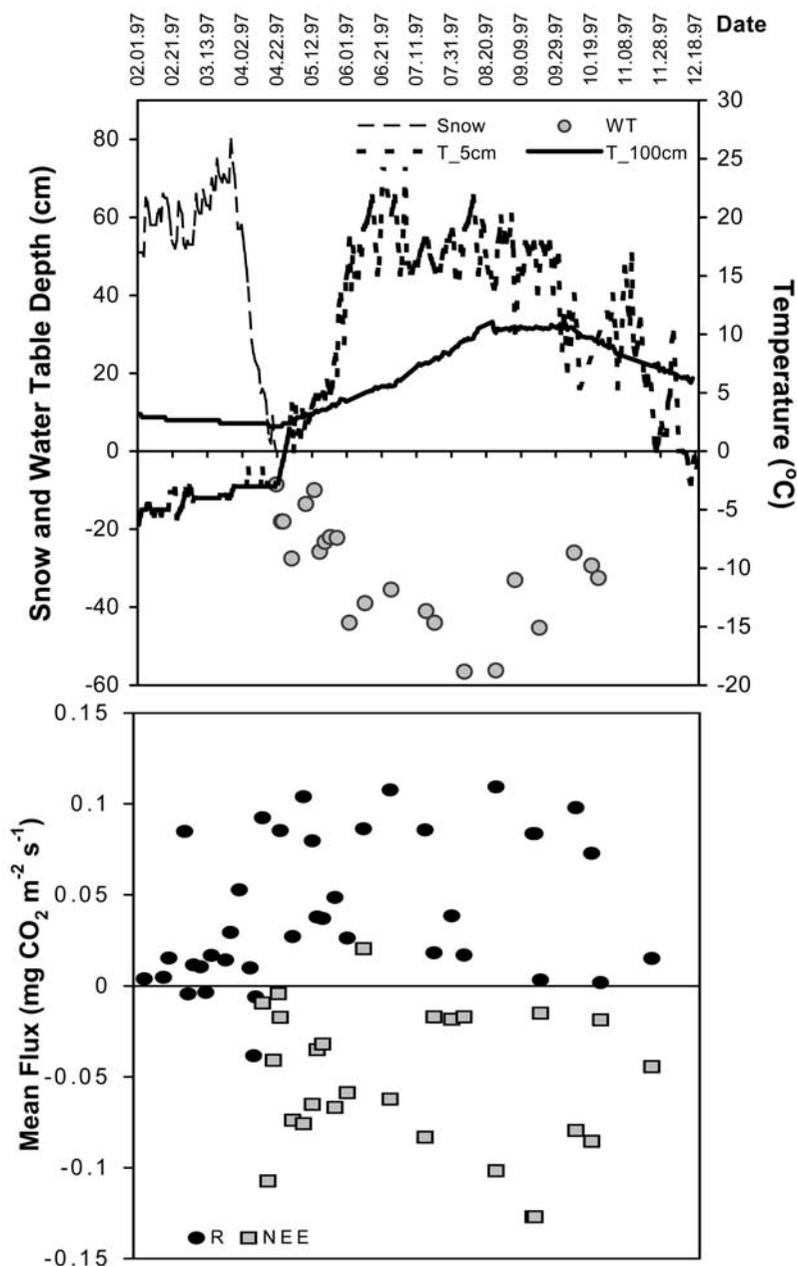


Figure 1. (top) Annual snow cover, water table and 5-cm and 100-cm peat temperatures. (bottom) Instantaneous CO₂ net ecosystem exchange (February through December 1997).

measured on March 7 was unexplainably lower and may be an artifact of disturbance or due to spatial variation in snow cover properties (i.e., cracking of ice lenses).

3.2. Growing Season

[16] Growing season NEE measurements were from April 11 to November 21. Five-centimeter peat temperatures ranged from 1.2° to 22.3°C in the spring and summer and dropped to 0.5°C during the fall period. Five-centimeter peat temperatures showed the best correlation to CO₂ fluxes and, hence, were used for the regression analysis. Mean photon flux density (PPFD) peaked in June at 2,152 $\mu\text{mol m}^{-2} \text{s}^{-1}$. PPFD steadily decreased to an average 93 μmol

$\text{m}^{-2} \text{s}^{-1}$ by November 21. On several days, PPFD was very low as a result of cloud cover, particularly later in the summer and the fall. In the early spring, there was an inverse relationship between 5-cm peat temperatures and CO₂ flux (Figure 4). However, if the regression is confined to fluxes and temperatures after May 16, then the expected positive relationship emerges ($r^2 = 0.57$, $p < 0.1$).

[17] Spring NEE and PPFD rectangular hyperbola had an average r^2 of 0.67 ($p < 0.001$) and with a departure from linearity of 0.130 (Table 2; Figure 5). A multiple stepwise regression of NEE against water table depth and 5-cm peat temperature yielded an r^2 of 0.90 ($p < 0.05$). Water table depth and 5-cm peat temperatures were positively but not

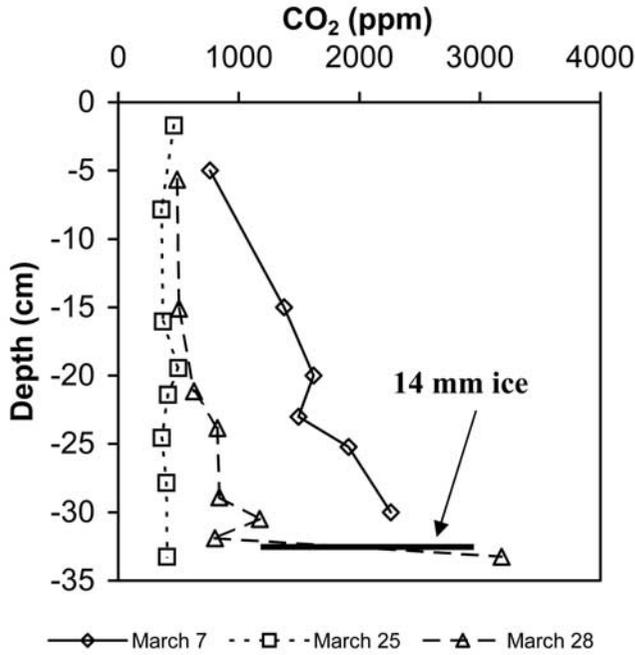


Figure 2. Snowpack CO₂ concentration gradients for March 7, March 25 and March 28.

significantly correlated with each other ($r^2 = 0.64$, $p < 0.5$) but water table by itself was not correlated with NEE ($r^2 = 0.09$).

[18] Midsummer fluxes ranged between a mean daily release of 0.021 ± 0.019 mg CO₂ m⁻² s⁻¹ on June 11 and a maximum mean daily uptake of -0.127 ± 0.020 mg CO₂ m⁻² s⁻¹ on September 15. Mean dark CO₂ efflux was well correlated with the 5-cm peat temperatures ($r^2 = 0.80$, $p < 0.01$). Multiple regressions including water table did not significantly improve the relationship ($r^2 = 0.84$). The summer relationship between NEE and PPFD ($r^2 = 0.54$) was significant ($p < 0.001$) but not as strong as it was in the spring period (Table 2). The modeled departure from linearity was only 0.01 with a maximum gross photosynthetic capacity of -0.330 ± 0.27 mg CO₂ m⁻² s⁻¹. At PPFD < 1000 $\mu\text{mol}/\text{m}^2/\text{s}$, there was a net CO₂ efflux and relatively low variability, while at PPFD > 1000 $\mu\text{mol}/\text{m}^2/\text{s}$, variability increased. Water table, 5-cm peat temperature and air temperature were not well correlated with NEE ($r^2 = 0.4$).

Table 1. Comparison of Measured and Estimated Fluxes of CO₂ From the Soil-Snow and Snow-Air Interfaces^a

Date	F _{soil-snow} , mg CO ₂ /m ² /s	F _{s-s/calc} , mg CO ₂ /m ² /s	F _{snow-air} , mg CO ₂ /m ² /s	F _{s-a/calc} , mg CO ₂ /m ² /s
March 7	-0.0025	-0.0064	0.0010	0.0465
March 25	0.0143	0.0003	0.0019	0.0012
March 28	0.0294	-0.0006	-0.0012	0.0437

^aThe estimated fluxes are based on the Fickian diffusion model presented in equation (1). F_{soil-snow}, flux at soil-snow interface measured with chambers; F_{s-s/calc}, calculated flux at soil-snow interface using equation (1); F_{snow-air}, flux at snow-air interface measured with chambers; F_{s-a/calc}, calculated flux at snow-air interface using equation (1).

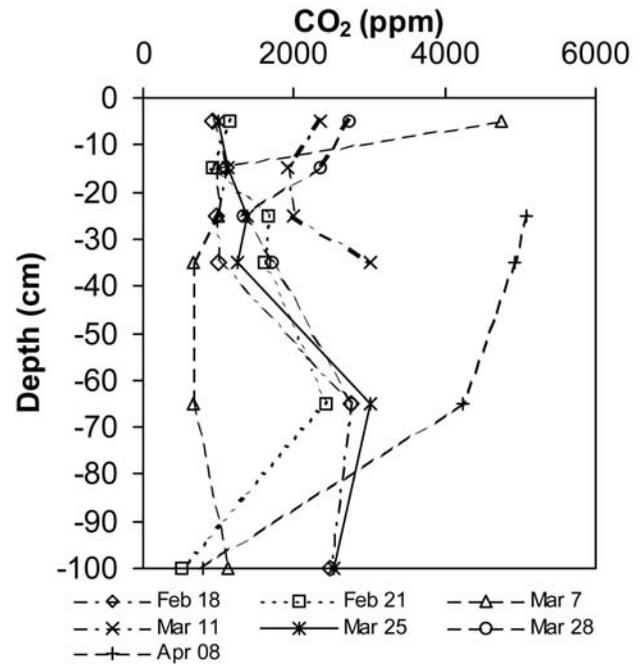


Figure 3. Peat pore air CO₂ concentrations.

[19] Fall mean daily dark CO₂ efflux and 5-cm peat temperature were positively correlated ($r^2 = 0.38$, $p < 0.01$), but water table position was not correlated with either temperature or dark CO₂ flux. NEE versus PPFD had an r^2 of 0.49 ($p < 0.001$), but the departure from linearity is 0.071 (Table 2). The maximum gross photosynthetic capacity was still quite high, -0.102 mg CO₂ m⁻² s⁻¹, but the mean NEE was lower than that of the summer season due to a shift to a higher light compensation point. Dark CO₂ efflux

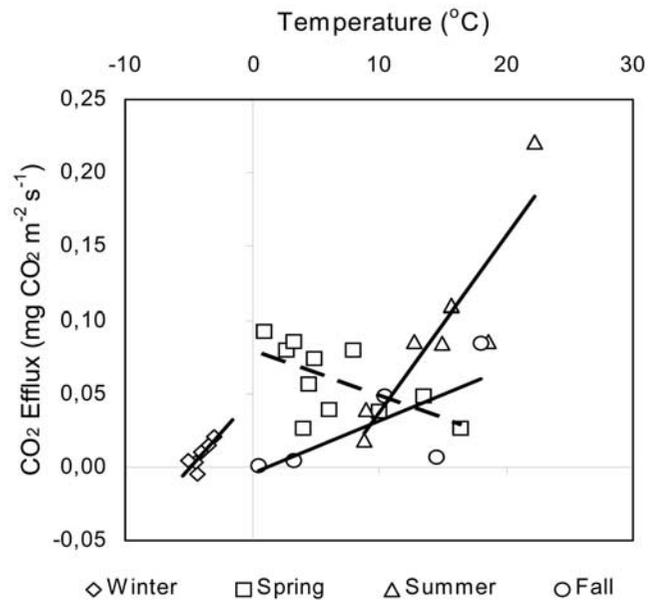


Figure 4. Seasonal relationships between CO₂ effluxes and 5-cm peat temperatures.

Table 2. Parameters Derived From Linear and Rectangular Hyperbola Curve Fits for Net Ecosystem Exchange and Respiration

Period	n	α	P_{\max}/β	R	NEE _{cap} ^a	r^2	D ^b
Winter	6	0.0096 (0.0039)	0.0471 (0.016)	0.0120 ^c	n/a	0.60	n/a
Spring	58	-0.0005 (0.0004)	-0.1263 (0.030)	0.0578 ^d	0.1841	0.69	0.1300
Summer	82	-0.0001 (0.0001)	-0.3296 (0.270)	0.0788 ^d	0.4084	0.54	0.0100
Fall	45	-0.0004 (0.0004)	-0.1022 (0.030)	0.0344 ^d	-0.1366	0.49	0.0710

^aNEE_{cap} at PPFD = 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Rect. Hyp.

^bDeparture from linearity = r^2 of rectangular hyperbola minus r^2 of linear fit.

^cMean adjusted respiration regressed against ground temperature ($\text{mg CO}_2 \text{m}^{-2} \text{s}^{-1}$).

^dRespiration ($\text{mg CO}_2 \text{m}^{-2} \text{s}^{-1}$) at PPFD = 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Rect. Hyp.

decreased dramatically from 0.084 to 0.001 $\text{mg CO}_2 \text{m}^{-2} \text{s}^{-1}$ toward the end of the season as the 5-cm peat temperatures approached 0°C and the plants senesced.

3.3. Winter Efflux Contribution to Annual C Budget

[20] Table 3 shows the calculated seasonal C contribution to the annual carbon budget, based on extrapolations of the measured fluxes using the NEE-PPFD relationship to estimate gross production and the linear dark CO₂ flux-temperature relationship to estimate ecosystem respiration. The

non-growing-season dark efflux (36.8 to 49.7 g C m^{-2}) comprised 20 to 28% of the annual respiration and 15 to 20% of the gross production. The springtime acted as a transitional time period, where the system was in between a net source and net sink of C. The annual budget indicated the system was a sink of approximately $-76 \text{g C m}^{-2} \text{yr}^{-1}$, which is 33 to 40% smaller than what would have been estimated based solely on growing season measurements. This is not a complete C budget as the loss of carbon via CH₄ or water-borne export as DOC and/or DIC was not

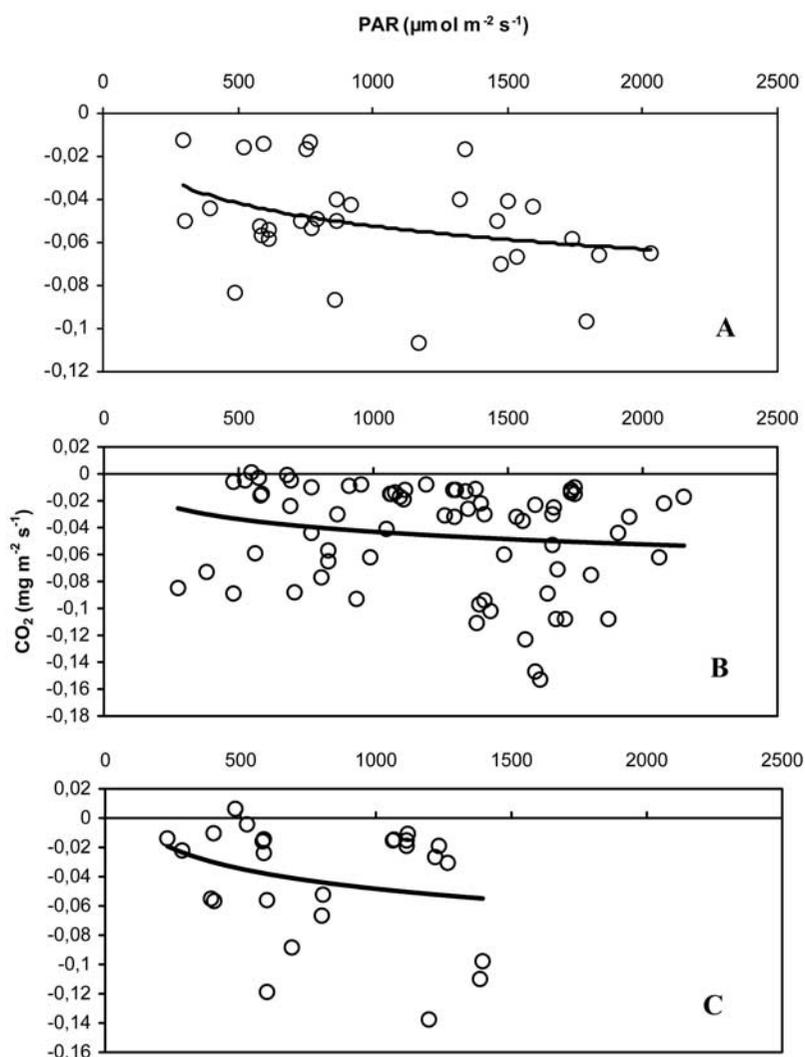


Figure 5. NEE-PPFD curves for the (a) spring, (b) summer and (c) fall seasons.

Table 3. Seasonal Contributions to the Peatland C Budget (g C m⁻²)^a

Season	Scenario 1			Scenario 2		
	GP	R	NEE	GP	R	NEE
Winter	0.0	49.7	49.7	0.0	36.8	36.8
Spring	-35.5	22.5	-12.9	-35.5	35.0	-0.5
Summer	-173.6	80.3	-93.2	-173.6	80.3	-93.2
Fall	-45.0	25.7	-19.3	-45.0	25.7	-19.3
Total	-254.0	178.2	-75.7	-254.0	177.8	-76.2

^aScenario 1 assumes spring respiration and Scenario 2 assumes spring degassing. GP = Gross Production (g C m⁻² yr⁻¹) derived as NEE-R; R = Dark CO₂ Efflux (g C m⁻² yr⁻¹); NEE = Net Ecosystem Exchange (g C m⁻² yr⁻¹). Positive exchange indicates a net uptake of carbon in the peatland.

considered. The CH₄ was measured and found to be insignificant (C. Roehm, unpublished data, 1997). This is not surprising since the water table ranged between -20 and -40 cm which would allow for substantial oxidation of produced CH₄. DOC and DIC loss was not measured. However, *Fraser et al.* [2001] measured a water-borne loss of C of between 8 and 10 g C m⁻² yr⁻¹ for the structurally and botanically similar peatland Mer Bleue, located near the Mirabel peatland.

4. Discussion

4.1. Non-Growing Season

[21] Our findings show that carbon sequestration can be overestimated if the non-growing season fluxes are not included in budget calculations. While winter CO₂ effluxes were correlated to 5-cm peat temperatures on a daily basis, there was no correlation between instantaneous CO₂ efflux and peat temperature. In addition, the gas transfer from deeper in the peat profile to the soil/snow interface and then through the snow cover can impose significant temporal separation between CO₂ production and efflux. It was observed that following a period when air temperature exceeded 0°C, the effluxes at the soil-snow interface dropped dramatically. It is possible that water from melting snow reduced gas diffusion at this time. An appropriate test for this hypothesis would be to have concurrent measurements of the flux and moisture.

[22] The 5-cm peat temperatures did not fall below the threshold value (-5°C) for microbial production. The increasing concentrations of CO₂ with depth in the peat profile, where the temperatures remain above freezing, may contribute to some of the variation observed in the soil-snow effluxes. The positive CO₂ concentration gradients in the surface layers of the peat indicate an efflux to the atmosphere throughout most of the season. Increases in concentration near the surface of the peat result from diffusional limitations due to the frozen upper peat layers and snowpack basal concentrations. On March 7 and 28, it was observed that the high concentrations found in the upper layers of the peat profile coincided with the steepest gradients of CO₂ concentration in the snowpack. These two dates show distinctly different flux behavior, with a slight uptake on March 7 and a large release on March 28. The data also indicate a sink for CO₂ in both the atmosphere and the deeper peat layers. At the soil-snow interface, the

difference in concentration between the bottom of the snowpack and the peat surface would indicate a release on March 7 and an uptake on March 28, opposite to the observed fluxes. It is unclear how production and diffusion combine to contribute to the non-growing-season CO₂ efflux. If it were assumed that the difference between the change in CO₂ storage and diffusion is equivalent to the CO₂ production, then the winter production would account for a little less than 50% of the observed fluxes.

[23] The temporal changes in snow CO₂ concentrations correspond to changes in the snow water equivalent (Table 4), a finding similar to that of *Sommerfeld et al.* [1996]. Ice lenses, that result from thawing and refreezing or from freezing rain, physically constrain CO₂ diffusion [*Albert and Hardy, 1995; Melloh and Crill, 1996; Mast et al., 1998*], but in the present study, ice lenses exerted only a minor influence on the observed concentrations, with the exception on March 28.

[24] Snow porosity and tortuosity control diffusion mechanism [*Albert and Hardy, 1995; Mast et al., 1998*] and ventilation. Ventilation is believed to be the main transport mechanism and seems to be important at the Mirabel bog, where wind prevails most of the winter. The diffusion model consistently produced higher fluxes to the atmosphere than those observed from the snow surface chamber measurements. Since a sink for CO₂ in the snow cover is unlikely, we believe our snow-air flux measurements are low because of measurement artifacts. The closed-flow snow surface chambers are affected by boundary layer conditions at the snow surface [*Winston et al., 1997*], and by the lack of a good seal in the snow [*Mast et al., 1998*].

4.2. Growing Season

[25] This study placed more emphasis on the non-growing season fluxes, but growing season fluxes were obtained to be able to place the winter exchange in context. The summer fluxes were similar to those of other studies [e.g., *Bubier et al., 1995*]. The results of the present study, however, indicate a problem allocating the seasonal source of CO₂. This problem is particularly acute for the transition from winter release to spring uptake. At this time, there was an increase in CO₂ loss from around 0.010 mg CO₂ m⁻² s⁻¹ during the last days of snowmelt on April 10 and 11 to around 0.089 mg CO₂ m⁻² s⁻¹ on April 24 and 27. The relationship between surface fluxes and 5-cm peat temperatures also inverted.

[26] This spring anomaly can be ascribed to two processes: degassing as the peat surface thaws and/or increased respiration stimulated by the appearance of easily metabolized substrates when photosynthetic uptake begins or due to increased C compounds resulting from wintertime microbial cell lysis. The first process has been identified as being

Table 4. Changes in Mean CO₂ Concentrations and Snow Water Equivalents in the Basal Snow Layer

Date	Concentration, ppm	SWE, cm ³
07/03/97	2204.10	6.70
25/03/97	423.12	5.00
28/03/97	3172.70	7.90

significant in a subarctic mire in Sweden [Friborg *et al.*, 1997]. Bubier *et al.* [1998] reported that the ericaceous shrubs and mosses found on bog ecosystems are able to start fixing carbon earlier in the spring when PAR levels are seasonally high and the snow cover is nearly zero, suggesting that the influence of root exudates may be present at this time and, hence, highly spatially variable. The latter process may be more important in peatlands of the low boreal and temperate regions, which experience only shallow frost and often do not freeze at all compared with peatlands of the subarctic and arctic regions [Roulet and Mortsch, 1997].

4.3. Annual Contribution of Winter C Fluxes

[27] The winter CO₂ fluxes observed in our study are higher than in previous studies [Alm *et al.*, 1999; Pajari, 1995]. The deeper peatland may contribute to steady and continuous production and diffusion of gases from depth where the temperatures remain above freezing. High concentrations of CO₂ were observed continuously throughout the winter at depths of 65 to 100 cm, producing a gradient to sustain gas diffusion. The fluxes may also reflect a release of carbon stored from the previous season, which may have been constrained by diffusional limitations.

[28] The spring poses a problem for allocation of carbon. If the high efflux rates in the springtime are a result of degassing and, therefore, are assumed to be part of the winter CO₂ production/diffusion and not a result of contemporaneous respiration, then the annual contribution of the non-growing-season release of C is equivalent to approximately 20% of the gross production and accounts for 28% of the annual ecosystem respiration (Scenario 1, Table 3). However, if the springtime efflux is the result of contemporaneous respiration, then the winter release of carbon is equivalent to approximately 15% of the gross production and 21% of ecosystem respiration (Scenario 2). Other studies [e.g., Schimel and Clein, 1996] have shown that freezing and thawing can stimulate heterotrophic respiration, which could also enhance the spring CO₂ flux.

[29] Regardless of which scenario is a better representation of the source of the winter flux of C, these results indicate the winter period constitutes a substantive component of the annual exchange of CO₂. Assuming the winter to be zero, the annual carbon accumulation would have been estimated to be between -113 and -125 g C m⁻² yr⁻¹ rather than -76 g C m⁻² yr⁻¹. It is interesting to note that the magnitude of overestimation observed in this study ($25-30$ g C yr⁻¹), is roughly equivalent to the magnitude of the long-term rate of carbon accumulation in peatlands, estimated by Gorham [1991, 1995], therefore, an error of the magnitude has serious implications in assessing the importance of peatlands in global carbon budgets. The first complete annual record of CO₂ exchange for a peatland confirms the importance of winter release and produces a similar result as that found in this study [Lafleur *et al.*, 2001].

5. Conclusion

[30] This study has demonstrated that peatland ecosystems continue to emit CO₂ through the winter and that the amount of CO₂ released represents a significant offset to the

magnitude of uptake during the growing season. By inference, the results indicate that a large proportion of the CO₂ released over the winter has to be produced during the winter and is not simply the release of CO₂ stored from the growing season.

[31] These findings have three important implications. First, it is common that studies of net carbon exchange of ecosystems are conducted for only part of the year. However, extrapolating the results of these studies to estimate the annual exchange of CO₂ is problematic. There is a significant offset from winter release, so growing season uptake will over estimate the role of a peatland as carbon sink. This study also shows the difficulty in relating CO₂ release to processes. This has no implication for the net annual carbon budget, but it does have implications for the relationship between environmental variables and exchange rates. The final important implication of this study is in the modeling of winter processes. Our results indicate that terrestrial biogeochemical models should either continue to allow for some respiration at temperatures between 0 and -5°C and/or incorporate a function to represent the leakage of stored CO₂. Whatever the process, the study clearly shows release of CO₂ at temperatures below 0°C.

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