Net Ecosystem CO_2 Exchange Measured by Autochambers During the Snow-Covered Season at a Temperate Peatland

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ABSTRACT

Net ecosystem exchange of carbon dioxide (CO_2) was measured at a temperate peatland in southeastern New Hampshire. Classified as a mineral-poor fen owing to deep, water-logged peats that are influenced to a limited extent by groundwater, the ecosystem is dominated by plants such as sedges (*Carex* spp.) and evergreen shrubs. Ten automatic chambers measured fluxes every three hours by sampling changes in headspace concentration of CO_2 from November 2000 through March 2001. The fen was covered in snow for most of this period and CO_2 was emitted from the snow pack throughout the winter. The largest fluxes were associated with ground temperatures of 0^oC and with declining atmospheric pressure. Effluxes up to 3 µmol CO_2 m^{-2} s^{-1} were recorded when the ground temperature reached the thaw point. Fluxes were lower when the ground temperature rose above 0^oC, however, suggesting that the large fluxes were associated with a build up and release of stored CO_2 degassing as soon as the ground thawed, or enhanced microbial activity associated with freeze-thaw dynamics. The large number of thaw events coupled with frequent short-term releases of CO_2 suggest that degassing occurred on a regular basis with changes in atmospheric pressure and/or microbial decomposition occurred beneath the snowpack. The extent of soil freezing prior to thaw was also an important factor, with colder soils yielding smaller CO_2 emissions upon thaw. Although most of the observed CO_2 flux was efflux from the ecosystem, occasional uptake by the ecosystem of up to 1 µmol CO_2 m^{-2} s^{-1} was also observed, indicating small rates of photosynthesis even during winter. Photosynthesis occurred only when the ground temperature was $> 0 \ ^oC$. The implications for a warmer climate are unclear. If warmer winter temperatures yield less snow in the temperate region, then soils could freeze more deeply and result in lower CO_2 emissions. However, if less snow results in a higher frequency of freeze-thaw events, then winter CO_2 emissions could be larger with a warmer climate.

Key Words: CO_2 flux, net ecosystem CO_2 exchange, peatland, winter, snow, autochamber

INTRODUCTION

Winter measurements of net ecosystem CO_2 exchange (NEE) are rare. Yet, over half of northern and high elevation ecosystems are snow-covered most of the year (Sommerfeld *et al.*, 1993). The few studies that have quantified dark CO_2 flux (respiration) during the cold and snow-covered season have shown that that winter fluxes are a significant component of the annual carbon

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balance. Winston *et al.*, (1997) reported that 40-55 g CO_2-C m^{-2} was emitted during the winter from the snow pack, an amount totally 20% of the annual respiration in a black spruce forest in boreal Canada. Winter emissions of 3-50% of the annual respiratory loss of CO_2 have been reported in northern wetlands, subalpine ecosystems, and arctic tundra (Lafleur *et al.* 2001; Wickland *et al.*, 2001; Hobbie *et al.*, 2000; Panikov and Dedysh, 2000; Alm *et al.*, 1999; Fahnestock *et al.*, 1999; Mast *et al.*, 1998; Oechel *et al.*, 1997), depending on moisture status, length of the non-growing season, snow cover, and temperature.

The factors contributing to winter release of CO_2 and CH_4 include both biological and physical mechanisms. Changing snow and ice characteristics contribute to physical factors, such as the release of gas during the phase change from soil water to ice (Coyne and Kelley, 1971), melt channeling in the snow by plant stems (Winston *et al.*, 1997), formation of ice lenses in the snow pack which trap gases, then release after thawing (Melloh and Crill, 1995), and wind and pressure changes, which may enhance or inhibit diffusion through the snow pack (Jones *et al.* 1999a; Massman *et al.*, 1997; Sommerfeld *et al.*, 1996). Biological processes are uncertain, but studies have shown that microbial decomposition of organic matter can occur below the freezing point, as low as –16°C (Panikov and Dedysh, 2000; Clein and Schimel, 1995). Root respiration may also contribute to the CO_2 flux in winter (Grogan *et al.*, 2001). In addition to production of recently fixed carbon, winter respiration may include the decomposition of older pools of soil organic matter (Goulden *et al.*, 1998; Winston *et al.*, 1997; Trumbore and Harden, 1997).

Snow is an important mediator of biological and physical processes, influencing biogeochemical cycling of carbon and nitrogen. Snow effectively insulates the soils from extreme freezing temperatures (Hardy *et al.*, 2001), thus controlling the temperature regime in the soil. The timing, duration and depth of snow are all important factors affecting winter CO_2 fluxes. Several studies have shown that winters with deeper snow packs yield larger CO_2 and CH_4 emissions than those with less snowfall (Welker *et al.*, 2000; Melloh and Crill, 1996; Brooks *et al.*, 1997; Mariko *et al.*, 1994). The timing of snow accumulation and snowmelt are also important to the seasonal flux. Early snowfall with warm temperatures enhanced CO_2 flux in some studies (Welker *et al.*, 2000), while a deep freeze before the onset of snow was important in others (Brooks *et al.*, 1997). Large pulses of CO_2 and CH_4 are often seen in late winter as the snow and ice thaws, releasing trapped gas (Jones *et al.*, 1999b; Mast *et al.*, 1998; Friborg *et al.* 1997; Bubier *et al.*, 1995; Zimov *et al.*, 1993; Windsor *et al.*, 1992; Dise, 1992).

Freeze-thaw events have been the subject of recent study with intriguing evidence that the freeze-thaw cycle stimulates pulses of microbial decomposition. Microbes that are killed by freezing may provide substrate for surviving microbes upon thawing (Schimel and Clein, 1996). This stimulates mineralization of C and N (Prieme and Christensen, 2001; Panikov and Dedysh, 2000; Groffman *et al.*, 2001; Hobbie and Chapin, 1996), resulting in losses of CO_2 and N_2O to the atmosphere. Although freeze-thaw dynamics have been studied in the laboratory, few studies have examined this process in the field over short-time scales.

Climate change research has intensified interest in snow as a regulator of biogeochemical processes, since warming temperatures will likely affect snow cover in northern latitudes. A recent snow manipulation experiment in northern New Hampshire reported the paradoxical result that colder soils may result from a warmer climate (Groffman *et al.*, 2001). Removing snow eliminated the insulation necessary to keep soils from deep freezing (Hardy *et al.*, 2001), caused fine root death, and altered mineralization rates of C and N (Groffman *et al.*, 2001). Climate warming may also increase the number of freeze-thaw events. This may be particularly important in northern peatlands, which store up to one-third the global pool of soil carbon (Gorham, 1991). If decomposition rates were to increase in winter, this could contribute to a positive feedback to climate change.

In this study, we present automatic chamber measurements of NEE at a peatland in southeastern New Hampshire during one of the snowiest winters on record in New England. Our objectives were to examine CO_2 fluxes at high temporal frequency and to explore the relationships among NEE, photosynthesis and respiration with a suite of environmental variables, including soil and air temperature, snow depth, photosynthetically active radiation, and atmospheric pressure. Fluxes were measured every 3 hours over the 24-hour daily cycle from late November 2000 through

March 2001, permitting a closer examination of soil temperature and CO_2 interactions before and after the snow pack developed, as well as the effect of numerous freeze-thaw events on CO_2 flux. Most field studies sample every few days and cannot assess the hourly and daily changes in biogeochemical processes. Several micrometeorological studies have made continuous measurements of winter NEE, demonstrating that that cold season fluxes are important to the annual C balance (e.g (Aurela *et al.*, 2001; Lafleur *et al.*, 2001; Goulden *et al.*, 1998). While towers have the advantage of integrating fluxes over larger spatial scales, autochambers can assess the small-scale interactions between soil climate and NEE. The uniqueness of this dataset is that the frequent freeze-thaw events were sampled throughout the winter showing dynamics of CO_2 exchange under temperature regimes that vary by hour, day and month.

METHODS

Site description

Sallies Fen is a mineral poor, *Sphagnum*-dominated peatland located in southeastern New Hampshire in Barrington (43° 12.5' N, 71° 03.5 W). Gas exchange studies at this 1.7 ha fen have been ongoing since 1989 focusing on growing season exchange of CH_4 and CO_2 (e.g. Carroll and Crill, 1997; Frolking and Crill, 1994; Bubier *et al*. 2002) and winter fluxes of CH_4 (Melloh and Crill, 1995; Melloh and Crill, 1996). The fen surface is dominated primarily by *Sphagnum* mosses (e.g. *Sphagnum fallax* and *S. magellanicum*). The overall fen complex has a nutrient and hydraulic gradient of minerotrophic wet edges to an oligotrophic central area with pH ranging from 4.2 to 5.7 and peat depth ranging from 2 to 4.5 meters (Melloh and Crill, 1996). The sedge *Carex rostrata* dominates the plant communities in the wetter portions of the fen, while ericaceous shrubs, such as leatherleaf (*Chamaedaphne calyculata*) and cranberry (*Vaccinium oxycoccus*) dominate the drier areas. Red maple (*Acer rubrum*) is common along the margins of the fen, while speckled alder (*Alnus rugosa*) and highbush blueberry (*Vaccinium corymbosum*) are interspersed throughout the fen. Chambers were placed along plant community gradients to sample all dominant species, ranges of plant biomass, and soil thermal and moisture regimes.

NEE measurements

In May 2000 ten automatic chambers and an associated control system were installed approximately 10 m from the lagg entrance to the fen, and has been operational since June 2000. Chambers are 45.7 x 45.7 cm in diameter and either 34 or 68 cm tall depending on the height of the vegetation. Each chamber was anchored at 5 points to wood strapping that was driven into the silt or sand below the peat surface. The chambers are attached to the control box sampling manifold (Action Automation, North Attleboro, Massachusetts) with high density polyethylene (Read Plastics, Rockville, Maryland) tubing (Fig. 1). Chambers represent the multiple vegetation types observed throughout the fen and are within a 20 m radius of the control box, in order to minimize the length of tubing attached to each chamber.

The chambers were constructed out of 2.54 cm aluminum channel and angle, and 0.31 cm thick polycarbonate lexan at the University of New Hampshire Space Science Machine shop. The lexan lid is 15.3 cm x 45.7 cm x 45.7 cm and is motivated by a 20.3 cm stroke double acting pneumatic cylinder (Clippard Minimatic, Cincinnati, OH). A 2.54 cm x 46 cm x 46 cm trough built into the chamber framework receives the lid during a sampling run to ensure an adequate seal. The lexan chamber walls or skirts are 40.6 x 15.3 cm each and fastened below the trough framework; two skirts can be used on top of each other doubling the total chamber height above the peat surface (Fig. 1).
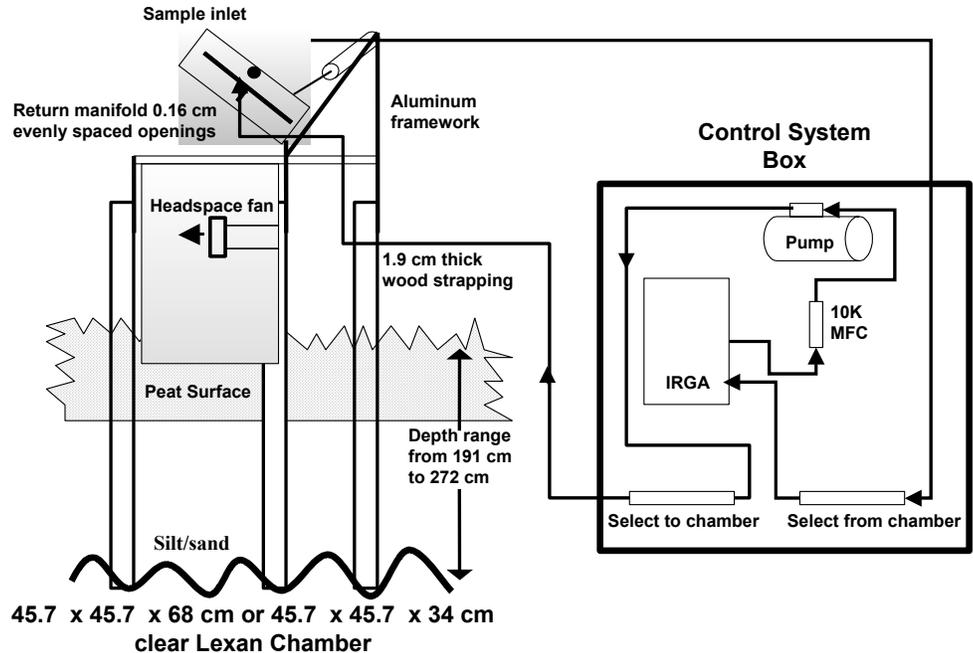
Figure 1. Chamber design and control system diagram.

The automatic CO_2 exchange system at Sallies Fen is similar in design to one used by Goulden and Crill (1997) at a black spruce forest in central Manitoba, although the chambers in this study are much larger to enclose a taller canopy. Line power is provided from a near by residential house and the total consumption for the system is ~ 1.150 KW at 115 VAC. The air supply for the pneumatics is provided by a small air compressor (GAST Manufacturing Inc., Bridgnam MI). Air from each chamber is pulled continuously by a diaphram pump (KNF Neuberger, Inc., Trenton, New Jersey) through a CO_2 infrared gas analyzer in absolute mode (IRGA, Model 6252, LiCor, Inc., Lincoln NE). The flow through the system is controlled by a mass flow controller (MKS Instruments, Andover MA) at 5 l m^{-1} (Fig. 1). Inflow and outflow rates were balanced in the chambers and internal pressure dynamics were examined with a micromanometer. Chamber closure produced a transitory spike of less than 10 Pa that decayed within 2 seconds to a condition of no detectable pressure differential between the outside and inside of the chambers. The pressure within the sample cell of the IRGA is a good indicator of tubing blockage. Large internal diameter tubing (0.64 cm) is used to minimize water entrainment into the air stream as well as to allow for uniform airflow back to detector (Goulden and Crill, 1997). A 12V brushless muffin fan (NMB, Minebea Co. LTD., Thailand) with a flow rate of 708 – 1301 L min^{-1} is used to mix the chamber head space during lid closure and to induce transverse winds that may be prevented by the high chamber walls. There were no noticeable temperature increases in the chamber after lid closure due to the internal 12V fans. However, the blowing action of the fans sometimes created a small channel in the snow, but not to the peat surface. This may have altered diffusion gradients to some extent, but ensured that air within the chamber was well-mixed.

A weather tight box containing three control boards opens and closes each of the 10 chambers every 3 hours. An individual chamber is selected every 18 minutes. The first 9 minutes flushes the tubing, clearing the sample line of previous air artifacts. At 10 minutes the lid closes, CO_2 concentration is sampled every 3 seconds and averaged every 30 seconds. Since CO_2 within the chamber can become saturated, the initial five points (2.5 minutes) of this trace are used to calculate an r^2 and a slope of the increase or decrease in CO_2 concentration over the sampling period.

Data analyses

Data acquisition and mechanical control were performed by a CR10X datalogger (Campbell Scientific, Logan UT). Data were transferred to a SM4M storage module (Campbell Scientific, Logan UT), which was then downloaded to a computer every 4 – 7 days for processing. The sign convention for chamber fluxes of CO_2 in $\mu mol\ m^{-2}\ s^{-1}$ in this study uses positive values to represent net uptake by the ecosystem and negative values to indicate CO_2 efflux from the chamber to the atmosphere. Ecosystem respiration is the total of heterotrophic (microbial) and autotrophic (plant) respiratory processes.

When calculating fluxes using the r^2 and slope of the increase or decrease in CO_2 concentration in the chamber over time, fluxes with $r^2 < 0.80$ were eliminated. Low r^2 occurred frequently in early morning when frost build-up reduced light transmission and occasionally prevented a good lid seal. Other reasons for filtering data included pneumatic line seizure and ice blockage, and intermittent power outages. Approximately 36% of the measured data were not included in the final filtered dataset after quality checking fluxes. However, the rejected fluxes were normally distributed around zero indicating no systematic bias, and 90% of these fluxes were less than the minimal detectable flux of $0.09\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$ based on the analytical uncertainty of the IRGA.

Statistical tests were performed on the data using the software JMP-IN (version 4.0.3 SAS Institute, 2001) to examine the relationships between CO_2 flux and various environmental variables.

Environmental variables

Peat temperature and internal chamber air temperature were measured at each chamber with type-T thermocouples (Omega Engineering, Stamford, CT). Photon flux density was measured with gallium arsenide phosphide photodiode (Hammamatsu, Bridgwater, NJ) at three locations representing the range of light conditions. In addition, two quantum sensors (LiCor, Inc., Lincoln NE) measured photosynthetically active radiation (PAR), one associated with the permanent meteorological station in the center of the fen, and the other near the automatic chamber control system. The ancillary chamber temperatures, flows and photon fluxes were sampled every 3 seconds and recorded every 9 minutes. The meteorological station sampled air and peat temperature at several depths (10, 30, 90 cm below the peat surface), water table position, relative humidity, barometric pressure, PAR, and precipitation every minute and hourly averages and total precipitation were recorded every hour.

Snow precipitation and snow depth were measured at a meteorological station in Epping, New Hampshire, approximately 16 km south of Sallie's Fen, but the same distance from the coast as the fen (Barry Keim, New Hampshire State Climatologist). Sallie's Fen experienced the same snow events, although snow depth was generally larger at the fen compared with the Epping data, perhaps due to slightly colder temperatures at the fen (Tables 1,2). There was no difference between snow depth inside and outside the chambers. The changes in snow depth and porosity may have altered diffusion gradients, but the system is designed to sample air throughout the chamber by placing the intake tube in the middle of the chamber headspace. The volume of the chamber may have been reduced by at most 10% during the two major snow events, which would result in a slight underestimate of the CO_2 flux during those periods.

Climate

New England experienced one of the largest snowfalls on record in the winter of 2000-2001 with 225 cm of snow from December through March in Epping, NH, compared with the 30-year mean of 145 cm for the same period (Table 1). The months of December, January and February did not vary from the long-term mean as significantly as the month of March, which had 97 cm of snow compared with the normal of 25 cm. Total precipitation was 39 cm for the 4-month period, only 3 cm greater than normal, but March had over twice the normal precipitation. Precipitation for December through February was slightly lower than normal. Mean air temperature was $-3.2^{\circ}C$, $0.4^{\circ}C$ colder than normal. However, December and March were the only months that were colder than normal, while January and February were slightly warmer.

Table 1. Air temperature (^{o}C), total precipitation and snowfall (cm) data for Epping, New Hampshire (16 km south of Sallie's fen in Barrington, NH). Monthly mean with 30-year normal for each month listed in row below. Departure from normal is the difference between the monthly mean and the 30-year normal, which is defined as 1971-2000 mean for temperature and total melted precipitation; and as 1961–1990 mean for total snowfall (Barry Keim, NH State Climatologist, pers. comm. 2002).

	mean max T	mean min T	mean T	Dep from normal	total precip	total snowfall
Dec 2000	0.94	-8.61	-3.78	-0.50	9.53	40.64
normal	2.33	-8.06	-3.28		10.49	37.08
Jan 2001	0.39	-11.11	-5.33	0.11	4.29	38.10
normal	0.44	-11.39	-5.44		8.20	42.42
Feb. 2001	1.94	-8.33	-3.17	0.67	5.66	49.53
normal	2.22	-9.89	-3.83		8.33	40.13
Mar 2001	3.94	-4.78	-0.39	-1.72	19.56	96.52
normal	7.28	-4.61	1.33		8.74	25.40
4 month mean	1.81	-8.21	-3.17	-0.36	39.04	224.79
4 month normal	3.07	-8.49	-2.81		35.76	145.03

RESULTS AND DISCUSSION

Seasonal patterns of NEE, temperature and snowfall.

The magnitude of NEE ranged from 1 to –3 µmol CO_2 m^{-2} s^{-1} from end of November 2000 until the end of March 2001 (Fig. 2a; Table 2). The ranges and daily averages of CO_2 emission were similar to those reported during the winter at other temperate and boreal/subarctic peatlands (Aurela *et al.*, 2001; Lafleur *et al.*, 2001; Panikov and Dedysh, 2000; Alm *et al.*, 1999). CO_2 was emitted throughout the winter period, not just during the warmest part of the season. Although most of the fluxes were negative, small positive fluxes persisted during the daytime suggesting that photosynthesis was occurring at a very low level at times.

The patterns of soil temperature and snow depth show that the soil temperature varied widely from 6 to –11°C before the snow pack developed (Fig. 2b). The first major snowfall of the season occurred on Dec. 30-31, 2000 (day 364-365) resulting in a snow depth of 15 cm. Snow continued to accumulate from the end of December through March with no periods of bare ground. From the first snowfall until the end of winter, the fluctuations in peat temperature were reduced dramatically compared to the pre-snow period, ranging from only 2 to –6°C. The insulating quality of snow is evident in the synchronous timing of temperature modulations with snow pack development. The ability of snow to moderate extreme ranges in temperature has been documented in many other studies. Most recently, a snow manipulation experiment showed that snow removal permitted frost to penetrate down to 25 cm below the soil surface in a hardwood forest, while the plots with snow cover only experienced frost to a depth of 5 cm (Hardy *et al.*, 2001).

The largest fluxes of CO_2 occurred when the temperature reached 0°C (Figs. 2a, 4). In addition, large emissions of CO_2 were associated with snowstorms (e.g. day 402, Fig. 2). The reasons for the timing of CO_2 release with snow events could be associated with lowering of atmospheric pressure, which would allow a greater rate of diffusion to the atmosphere (Massman *et al.*, 1997) (Sommerfeld *et al.*, 1996). CO_2 emissions increased as atmospheric pressure fell on several occasions (e.g. days 400-425; Fig. 3). The largest decline in atmospheric pressure during this February time period was on day 402 during one of the largest snow events of the winter (Figs. 2, 3). Maximum CO_2 emissions were usually associated with the lowest pressure readings. The lack of synchronous timing of maximum flux with lowest pressure resulted in a non-significant statistical correlation between pressure and flux. However, the highest effluxes were always

observed during the period of falling atmospheric pressure and effluxes were suppressed as pressure was rising. This suggests that the releases of stored CO_2 in the peat may be triggered by increased rates of diffusion as atmospheric pressure declines. Roulet et al. (1997) also found that changes in atmospheric pressure were important in predicting fluxes of CO_2 from the surface of a boreal beaver pond.
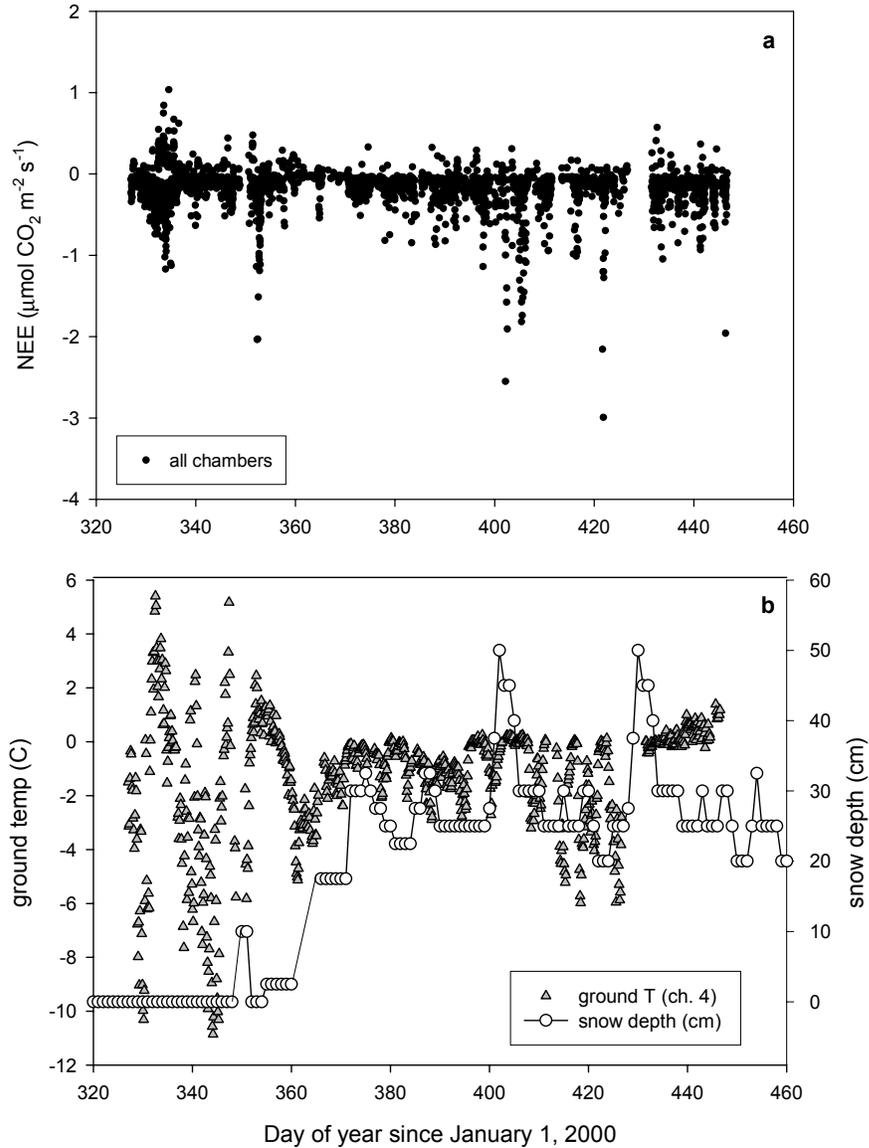

Figure 2. a) NEE for all chambers and b) Epping, NH snow depth and chamber 4 ground temperature (November 22, 2000 – March 22, 2001). Day of year (DOY) begins with January 1, 2000 and January 1, 2001 is DOY 366.
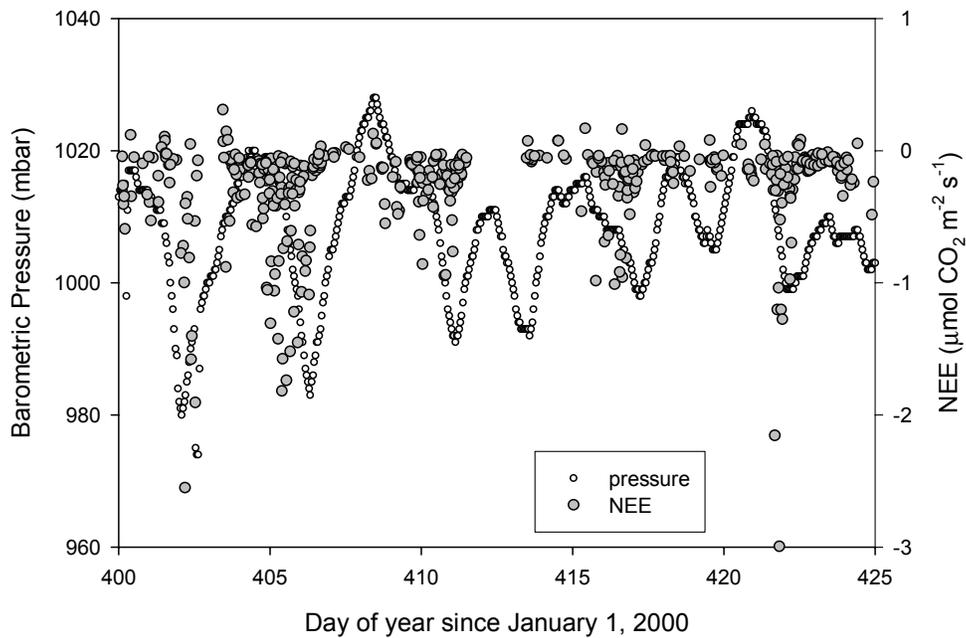
Figure 3. Atmospheric pressure and NEE during February 2001 (days 400-425) showing increases in CO_2 emission as barometric pressure declines.
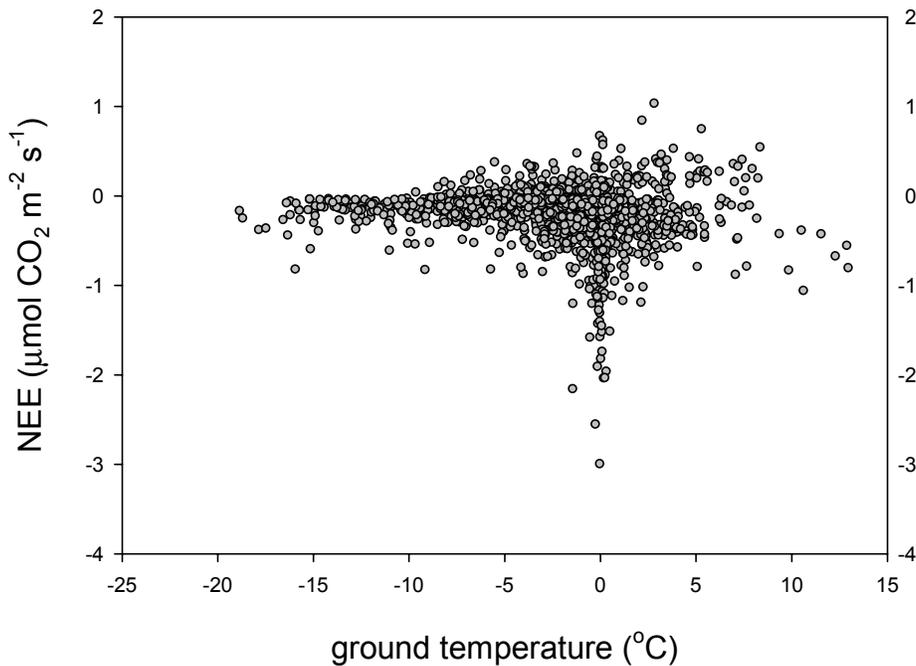

Figure 4. Relationship between NEE and ground temperature at 5 cm depth. Largest respiration rates occur at $T = 0^o$C. This pattern is seen in all chambers.

Freeze-thaw dynamics

The relationship between NEE and peat temperature is shown in Fig. 4. Most of the positive values (CO_2 uptake) occurred at $T > 0^o$C, but negative values (CO_2 emission) were more complex. Unlike the temperature vs. respiration relationship in summer where respiration increases with

higher temperatures (e.g. Raich and Schlesinger, 1992), the winter pattern is not as simple. The largest CO_2 emissions occurred at $T = 0^o$C and were smaller at both lower and higher temperatures, suggesting a release of stored CO_2 during thaw events or an enhancement of microbial activity from freeze-thaw dynamics. We found no significant correlation between dark CO_2 flux and temperature. Several studies of winter CO_2 emissions have reported that there was either no correlation or a weak relationship between soil temperature and CO_2 flux (Jones *et al.*, 1999b), or that the relationship was different depending on whether soils were warming or cooling (Winston *et al.*, 1997). The pattern in this study agrees with the lack of a simple relationship. The advantage of high frequency measurements is that the thaw events were sampled with enough regularity that a pattern emerged in the CO_2 vs. temperature relationship, even though that pattern was not a predictable increase or decrease in CO_2 flux across the range of ground temperatures.

The temporal pattern of NEE and surface peat temperature is shown in Figs. 2 and 5. In the early season, the largest fluxes of CO_2 occurred when the ground temperature rose above freezing (e.g. late November - early December, Fig. 2). The ground temperature steadily declined after that brief warming period and did not rise above 0^oC until January 2001. There was very little CO_2 flux throughout this cold period (e.g. days 360-380, Fig. 2). After the snow began to accumulate and ground temperatures were more moderate (Fig. 2), several thaw events occurred throughout the winter. The largest emissions of CO_2 occurred during these events. Taking a closer look at a three-week period in February, for example (Fig. 5, days 400-425), CO_2 emissions occurred after the ground was frozen and as soon as the temperature reached 0^oC. These emissions were observed at every thaw event, not just during the first one, suggesting that the CO_2 flux may be a result of recent CO_2 production over a period of hours and days. The frequent emissions may also indicate surface degassing of stored CO_2, then recharge from the large reservoir of CO_2 in the underlying peat. The latter mechanism is supported by the synchronous timing of increasing CO_2 emission with declining atmospheric pressure (Fig. 3).

The importance of the timing and magnitude of freezing before a thaw event is illustrated in Fig. 5, which show that chambers that experienced colder temperatures (as low as -3^oC) before a thaw (Fig. 5b) had smaller CO_2 emissions than those with less extreme freezing temperatures (-1°C) before each thaw event (Fig. 5a). Therefore, the extent of soil freezing preceding a thaw event may be as important as the thaw itself in determining the magnitude of CO_2 flux. Panikov and Dedysh (2000) studied production of CO_2 under freezing temperatures as well as under thawing conditions. They found that microbes were active down to -16^oC in laboratory incubations. Upon thawing, a hump-shaped pattern in CO_2 flux was observed where respiratory activity was raised sharply immediately after thaw reaching a maximum after 50-60 hours, then declining to a steady state level. The highest stimulation in microbial activity was observed in the surface soil layers (5-10 cm) where CO_2 production was 3 times higher than the rate prior to thawing. Prieme and Christensen (2001) reported a 5-fold increase in CO_2 emission following thawing of intact organic soil cores, but this rate decreased during successive freeze-thaw cycles. Our field study shows that thawing results in fluxes 2-3 times greater than pre-thaw rates, and that high rates occur within a few hours of thaw. However, the extent of prior freezing is related to the rate of release after thaw. Surface soils that were only frozen to -1^oC yielded higher CO_2 emissions after thaw than those that froze to a deeper level (Fig. 5). This suggests that the more severe freezing may kill more of the microbial population so that there are fewer survivors when the soil thaws. The actual state of frozen versus unfrozen soil is unknown in this study. We are basing our analyses on soil temperature alone. It is also possible that the increased emissions after thaw are due to water, supersaturated with CO_2, releasing gaseous CO_2 upon melt.
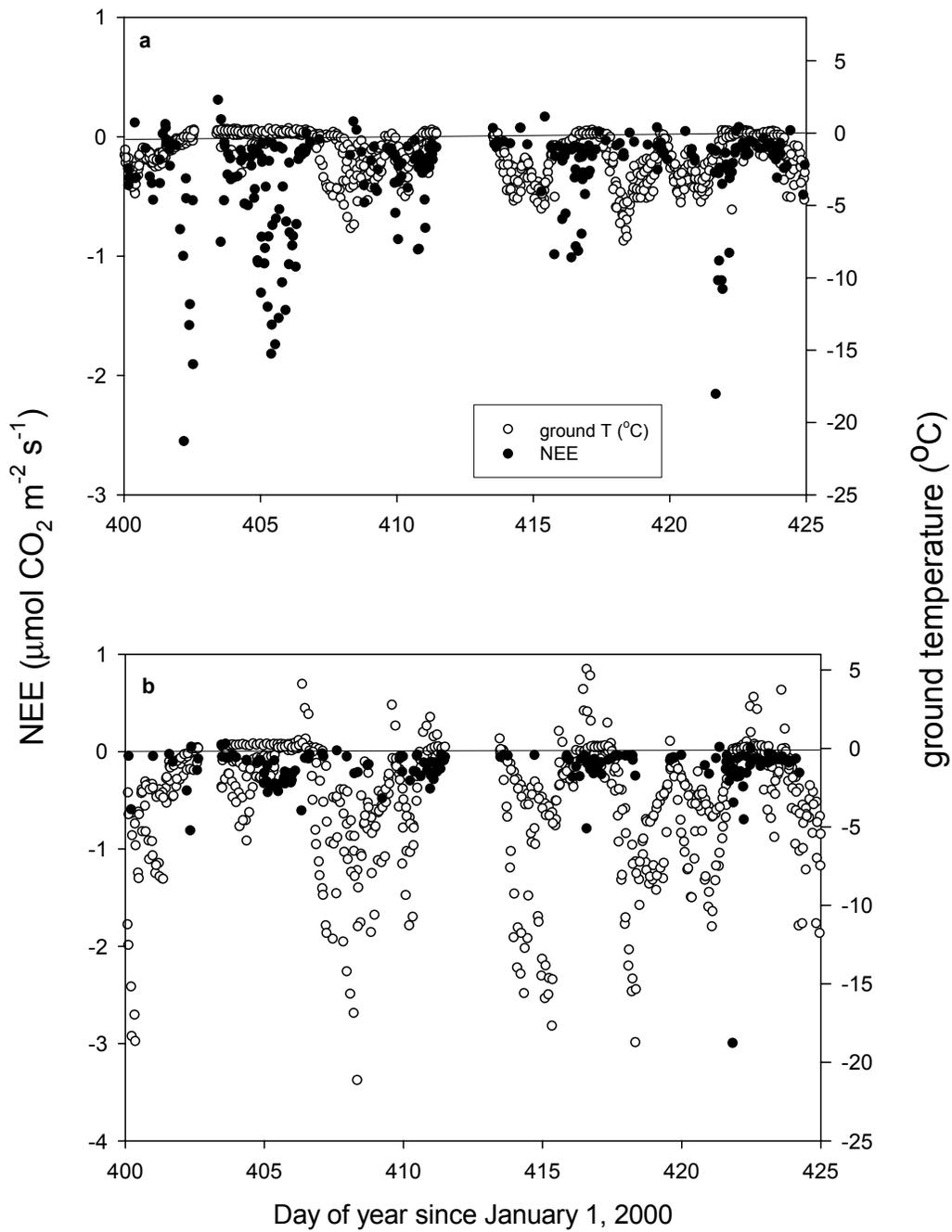
Figure 5. Relationship between NEE and ground temperature (5 cm depth) in February 2001 (days 400-425) showing emissions of CO_2 when ground T reaches $0^{\circ}C$. This occurs several times, not just one release. Note larger releases of CO_2 in (a) warmer chambers vs. (b) chambers with more severe freezing before each thaw event.

Relationships among NEE, temperature, and plant processes. The relationship between NEE and hour of day (Fig. 6) shows that most of the largest positive and negative fluxes occurred during daylight hours. The observation that CO_2 uptake occurred only during daytime supports the hypothesis that photosynthesis is persistent, albeit at very low levels, throughout the winter

months. The relationship between photosynthetically active radiation and NEE was weak, perhaps due to the fact that when the snow depth was greatest in late winter, much of the photosynthetic tissue was buried by snow as PAR was increasing. Earlier in the winter, however, when PAR was lower, the snow was less deep exposing more photosynthetic tissue. The uptake rates were highest before the snow began to accumulate in November and December, but small amounts were observed even in mid-winter (Fig. 2). The highest positive fluxes were observed at ground $T > 0^{\circ}C$ (Fig. 4) and during the day (Fig. 6), however, indicating that photosynthesis is only occurring when plant tissues are above freezing, and when there is sufficient light for photosynthesis. Most of the chambers contained leatherleaf (*Chamaedaphne calyculata*), an evergreen shrub that retains photosynthetic tissue throughout the winter. Although studies have shown that evergreens have lower rates of photosynthesis than deciduous shrubs during the growing season, they maintain a competitive advantage in low-nutrient ecosystems by using nutrients more efficiently (Aerts, 1995). They can also continue to fix CO_2 through the cold-season period after deciduous species have lost their leaves (Goulden *et al.* 1997).
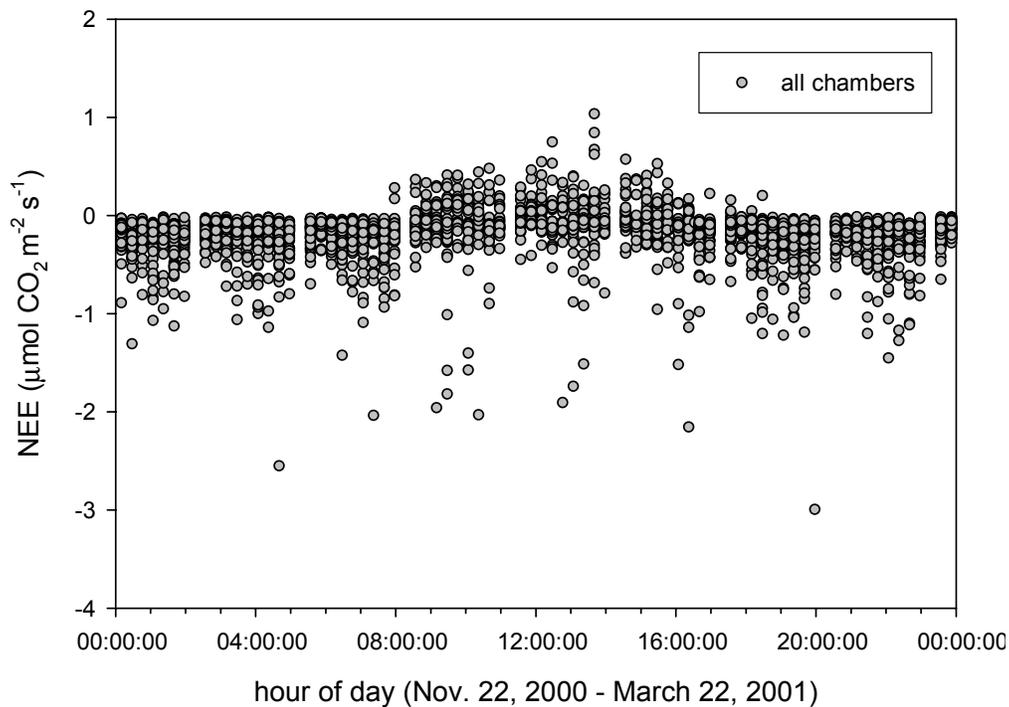

Figure 6. NEE for all chambers from Nov. 22, 2000 through March 22, 2001 by hour of day. Note that all positive fluxes (uptake by ecosystem) occur during daylight, which suggests that photosynthesis is occurring. Highest negative fluxes (efflux to atmosphere) also occur during daylight hours. This corresponds with higher temperatures during daytime.

Since individual chambers varied in magnitude of NEE during the winter (Table 2), and chambers varied in their species composition and biomass, relationships between NEE and ground temperature, water table position and biomass were examined (Fig. 7). There is a strong relationship between winter seasonal mean ground temperature and NEE ($r^2 = 0.61$; $p < 0.01$; Fig. 7a). This supports the hourly and daily associations between thaw events and CO_2 emission (Fig. 5) and shows that on a seasonal basis, warmer soils yield higher CO_2 emissions. There was no relationship between late summer water table position and CO_2 emission (Fig. 7b), although the water table was within 20 cm of the peat surface for all chambers.
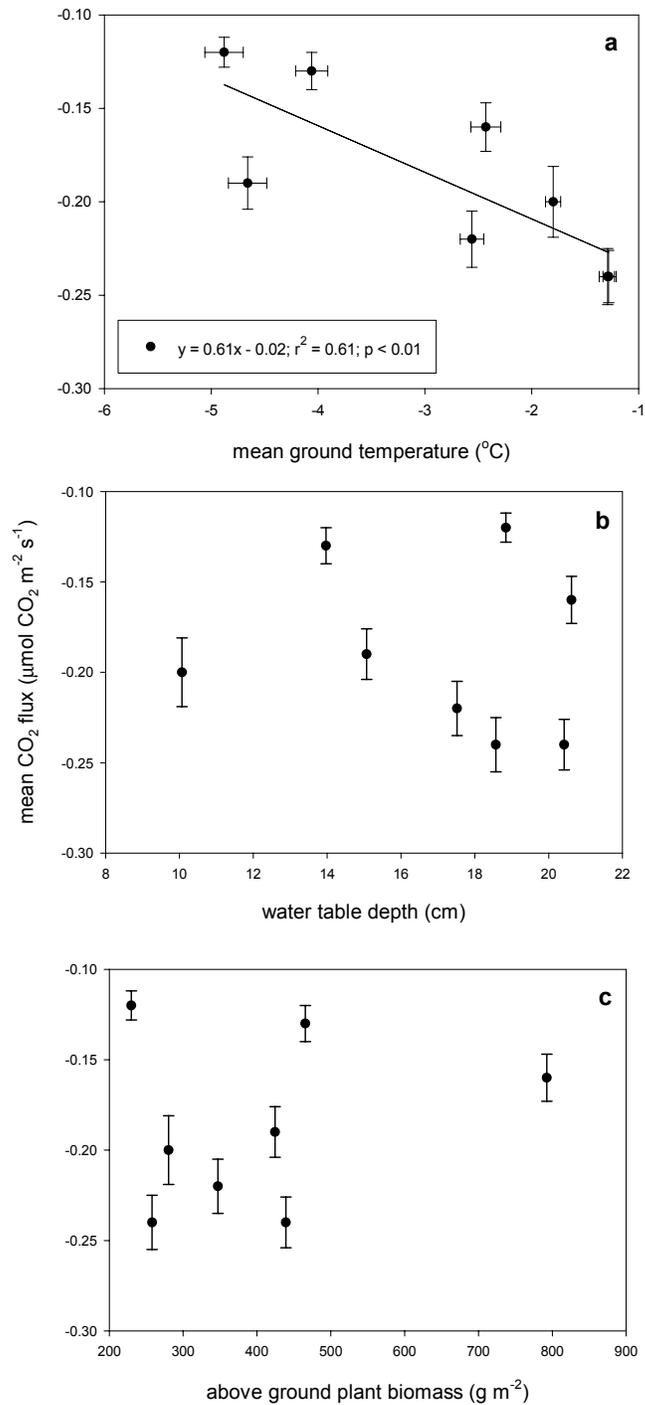
Figure 7. Relationship between mean winter dark CO_2 flux by chamber and (a) mean winter ground temperature, (b) late summer water table position, and (c) above ground plant biomass. Note that ground temperature is the only variable that has a significant correlation with CO_2 flux.

There was no relationship between CO_2 flux and above ground plant biomass (Fig. 7c), suggesting that plant respiration may not play an important role in explaining differences among chambers. Although we did not measure below ground biomass for these chambers, our data show a fairly consistent ratio between above and below ground biomass across sites at this fen (Bubier, unpubl. data). In a field experiment where plants were clipped prior to winter, Grogan *et al.* (2001) concluded that recently-fixed plant carbon was the dominant source of winter respiratory CO_2 flux in arctic soils because control plots had larger CO_2 emissions than clipped plots. In this study, the strong relationship between soil temperature and CO_2 emission, and repeated emissions of CO_2 during thaw events, imply that microbial processes dominate ecosystem respiration in winter; although microbial decomposition of the previous growing season's leaf and root litter may be an important component of the total microbial activity. In addition, the association of CO_2 releases with declining atmospheric pressure suggests that the some of the emitted CO_2 may be derived from degassing of stored CO_2. Using ^{14}C measurements in a black spruce forest, Winston *et al.*, (1997) reported that a larger fraction of the CO_2 flux in winter, compared to summer, originated from decomposition of older carbon stored at depth in the soil rather than from recently produced carbon from root respiration.

Table 2. Winter CO_2 flux (μmol CO_2 m^{-2} s^{-1}), ground and air temperature (^{o}C), above ground plant biomass (g m^{-2}), and water table position (cm below peat surface in late August 2001) for each autochamber, and mean value (standard error) for all chambers. Winter flux is based on filling missing values in the 3-hour sampling regime with the mean winter value and interpolating over 120 days from December 2000 through March 2001. Negative values indicate CO_2 efflux; positive values indicate yet ecosystem CO_2 uptake.

	all chambers	ch. 1	ch. 2	ch. 3	ch. 4	ch. 5	ch. 6	ch. 7	ch. 9	ch. 10
mean CO_2 flux	-0.18	-0.13	-0.22	-0.16	-0.24	-0.2	-0.24	-0.19	-0.12	-0.18
s.e.	0.0044	0.01	0.015	0.013	0.015	0.019	0.014	0.014	0.008	0.007
n	2976	329	350	293	344	292	382	291	365	328
max CO_2	1.04	0.55	0.75	0.41	0.40	0.44	1.04	0.36	0.57	0.46
min CO_2	-2.99	-1.96	-1.82	-1.91	-1.74	-2.16	-2.56	-2.99	-0.8	-0.42
winter flux (120 days) (g CO_2-C m^{-2})	-21.06	-15.47	-26.18	-19.04	-28.56	-23.32	-28.32	-22.61	-14.28	-9.88
mean ground T	-2.63	-4.06	-2.56	-2.43	-1.29	-1.8	-1.28	-4.66	-4.88	-1.76
s.e.	0.04	0.15	0.11	0.14	0.08	0.07	0.054	0.18	0.18	0.07
max	12.94	8.33	9.83	10.6	5.4	3.88	2.8	12.87	12.94	4.19
min	-21.22	-18.97	-15.51	-16.15	-10.85	-7.8	-6.93	-21.12	-21.22	-8.86
median	-1.61	-3.47	-1.66	-1.36	-0.69	-1.56	-0.81	-4.15	-4.01	-1.5
mean air T	-4.21	-4.04	-4.61	-3.92	-4.43	-4.36	-3.93	-4.49	-3.75	-4.43
s.e.	0.06	0.17	0.19	0.16	0.21	0.18	0.22	0.2	0.16	0.17
max	15.53	13.28	12.45	12.88	13.58	12.38	15.3	12.95	12.24	11.98
min	-21.32	-18.32	-20.11	-18.32	-20.45	-19.86	-20.91	-21.32	-17.62	-18.6
median	-3.71	-3.41	-4.16	-3.77	-4.08	-3.92	-3.47	-4.13	-2.92	-3.97
biomass	377.29	465.50	347.18	792.62	258.3	280.31	439.23	424.53	229.94	158.24
water table	15.30	13.97	17.52	20.62	18.57	10.07	20.42	15.07	18.845	13.27

Contribution of snow-covered season to annual respiratory CO_2 flux. The contribution of winter CO_2 emission to the annual CO_2 loss by the ecosystem was calculated by filling in missing values in the 3-hour sampling regime with the mean winter flux and integrating over the 4-month time period from December through March (120 days)(Table 2). Using the gross mean value of the fluxes of –0.18 µmol CO_2 m^{-2} s^{-1}, the winter flux is –21.6 g CO_2-C m^{-2}, ranging from –9.98 to –28.32 g CO_2-C m^{-2} across the suite of chamber locations. This range in chamber fluxes is smaller than found in a study by Alm et al. (1999), where species composition and microsite CO_2 fluxes were more variable.

Most studies use measurements taken every few days or weeks. These are not continuous and therefore do not capture the full range of CO_2 emissions. Large pulses may be missed or overemphasized in the winter calculation. When calculating the contribution of winter to the annual flux, the same problem exists. Most studies use only daytime summer measurements of respiration, not the full diurnal cycle. Our summer measurements of dark CO_2 during night (with autochambers) and during the day (with shrouded manual chambers) show that the average rate of ecosystem respiration during the four month growing season (June through September 2001) was –5.80 µmol CO_2 m^{-2} s^{-1} during the day, and –3.90 µmol CO_2 m^{-2} s^{-1} for nighttime. Using a mean value of –0.18 µmol CO_2 m^{-2} s^{-1} for winter (120 days), the average of day and nighttime respiration of –4.88 µmol CO_2 m^{-2} s^{-1} for summer (120 days), -1.27 µmol CO_2 m^{-2} s^{-1} for April and May, and –2.30 µmol CO_2 m^{-2} s^{-1} for October and November, 120 days of winter would account for 3% of the annual gross respiratory flux.

Not accounting for the months of transition in the spring and fall underestimates the non-growing season contribution to the annual flux. Depending on the definition of the non-growing season, the contribution of shoulder seasons to the annual budget could vary considerably. In Sallie's Fen, four months of spring (April, May) and fall (October, November) contribute an additional 25% to the annual respiratory CO_2 loss, with four months of summer accounting for the remaining 72%. Using three months of winter (December through February), Melloh and Crill (1996) found that winter methane emissions from the same fen accounted for 4.3% of annual emissions to the atmosphere over a 5-year period. Our conservative estimate of 3% using the 4-month snow-covered season in 2000-01 indicates a comparable winter contribution to the annual respiratory CO_2 flux. When considering the entire CO_2 budget, respiration only accounts for the loss of CO_2 to the atmosphere, not the uptake by plants. Depending on the balance between photosynthesis and respiration, which varies annually because of temperature and precipitation fluctuations, winter NEE may assume larger importance in years when growing season NEE is low.

CONCLUSIONS

CO_2 fluxes were continuous throughout the snow-covered season from December through March. Snow insulated the ground from extreme fluctuations in temperature and prevented deep soil freezing. The largest emissions of CO_2 occurred when the ground temperature reached 0°C and during periods of declining atmospheric pressure. CO_2 emissions occurred repeatedly with freeze-thaw events suggesting ongoing microbial decomposition activated by freeze-thaw dynamics and/or frequent releases of stored CO_2 facilitated by changes in atmospheric pressure, which increased rates of diffusion. The extent of soil freezing prior to thaw influenced the magnitude of CO_2 flux with colder pre-thaw soils yielding lower emissions during thaw events. Although there was not a simple relationship between CO_2 emission and temperature over the full range of ground temperatures, there was a significant correlation between mean winter ground temperature and mean NEE across the range of chamber locations. The weak relationship between NEE and above ground plant biomass implies that plant activity was less important than microbial decomposition in explaining the range of CO_2 emissions among the different plant communities at the fen. The implications for a warmer climate are unclear. If warmer winter temperatures yield less snow in the temperate region, then soils could freeze more deeply and result in lower CO_2

emissions. However, if less snow results in a higher frequency of freeze-thaw events, then winter CO_2 emissions could be larger with a warmer climate. Photosynthetic rates might also increase with a warmer climate, but the measured magnitude of respiratory losses in this study were far greater than plant uptake during thaw events.

ACKNOWLEDGEMENTS

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