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Jill L. Bubier

Patrick M. Crill
Stockholm University

Tim R. Moore

Kathleen Savage

Ruth K. Varner
University of New Hampshire, Durham, ruth.varner@unh.edu

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Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex

Jill L. Bubier¹ and Patrick M. Crill

Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space
University of New Hampshire, Durham

Tim R. Moore and Kathleen Savage

Geography Department, McGill University, Montreal, Quebec, Canada

Ruth K. Varner

Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space
University of New Hampshire, Durham

Abstract. We measured seasonal patterns of net ecosystem exchange (NEE) of CO₂ in a diverse peatland complex underlain by discontinuous permafrost in northern Manitoba, Canada, as part of the Boreal Ecosystems Atmosphere Study (BOREAS). Study sites spanned the full range of peatland trophic and moisture gradients found in boreal environments from bog (pH 3.9) to rich fen (pH 7.2). During midseason (July–August, 1996), highest rates of NEE and respiration followed the trophic sequence of bog (5.4 to -3.9 μmol CO₂ m⁻² s⁻¹) < poor fen (6.3 to -6.5 μmol CO₂ m⁻² s⁻¹) < intermediate fen (10.5 to -7.8 μmol CO₂ m⁻² s⁻¹) < rich fen (14.9 to -8.7 μmol CO₂ m⁻² s⁻¹). The sequence changed during spring (May–June) and fall (September–October) when ericaceous shrub (e.g., *Chamaedaphne calyculata*) bogs and sedge (*Carex* spp.) communities in poor to intermediate fens had higher maximum CO₂ fixation rates than deciduous shrub-dominated (*Salix* spp. and *Betula* spp.) rich fens. Timing of snowmelt and differential rates of peat surface thaw in microtopographic hummocks and hollows controlled the onset of carbon uptake in spring. Maximum photosynthesis and respiration were closely correlated throughout the growing season with a ratio of approximately 1/3 ecosystem respiration to maximum carbon uptake at all sites across the trophic gradient. Soil temperatures above the water table and timing of surface thaw and freeze-up in the spring and fall were more important to net CO₂ exchange than deep soil warming. This close coupling of maximum CO₂ uptake and respiration to easily measurable variables, such as trophic status, peat temperature, and water table, will improve models of wetland carbon exchange. Although trophic status, aboveground net primary productivity, and surface temperatures were more important than water level in predicting respiration on a daily basis, the mean position of the water table was a good predictor ($r^2 = 0.63$) of mean respiration rates across the range of plant community and moisture gradients. Q₁₀ values ranged from 3.0 to 4.1 from bog to rich fen, but when normalized by above ground vascular plant biomass, the Q₁₀ for all sites was 3.3.

1. Introduction

Recent studies have shown that northern ecosystems may already be experiencing changes in carbon cycling because of climate warming. Arctic tundra soils in some areas are now losing CO₂ to the atmosphere, presumably because of increases in soil drying and warming [Oechel *et al.*, 1995]. Peatlands are significant components of the boreal biome because they contain 25–33% of the global pool of soil carbon [Gorham, 1991; Schlesinger, 1996].

Partially decomposed plant material (peat) accumulates when production exceeds slower decomposition in cold, water-logged soils. Although peatlands have significantly lower carbon fixation potential than upland ecosystems [Frolking *et al.*, 1998], they have been net sinks of CO₂ since deglaciation [Harden *et al.*, 1992]. Decay resistant plant types, such as *Sphagnum* mosses and evergreen shrubs [Johnson and Damman, 1993; Chapin *et al.*, 1997], in addition to anaerobic soils and infrequent disturbance [Trumbore and Harden, 1997], contribute to slow rates of decomposition.

Short-term (1–2 seasons) studies of carbon exchange in peatlands have suggested that lower water tables will enhance decomposition over plant production and may convert peatlands from a net sink to a source of CO₂ to the atmosphere [Shurpali *et al.*, 1995; Waddington and Roulet, 1996; Carroll and Crill, 1997; Bellisario *et al.*, 1998]. Studies of peatlands that have been drained for 30 years or more are equivocal. Some peatlands sequester more carbon after water table lowering because plant production (especially tree,

¹Now at Environmental Studies Program, Mount Holyoke College, South Hadley, Massachusetts.

fine root, and litter production) exceeds decomposition over longer time periods [Laine *et al.*, 1996]. However, the change in carbon balance may depend on trophic status of the peatland owing to different rates of fine root production, mineralization potential [Updegraff *et al.*, 1995], bulk density of the peat, and changes in the carbon storage in biomass (trees and shrubs) [Minkkinen and Laine, 1996].

Most studies of net CO₂ exchange have focused on the midgrowing season, yet a modeling study of a boreal black spruce ecosystem showed that the timing of spring was one of the most important factors explaining interannual variability in the carbon balance [Frolking *et al.*, 1996]. Fall periods may also be significant because soil respiration continues past the decline in plant photosynthesis in some boreal ecosystems as a result of a lag in the warming of deep soils relative to surface temperatures [Goulden *et al.*, 1998].

The purposes of this study were to 1) measure rates of net ecosystem exchange (NEE) of CO₂ from the period of snowmelt through the growing season until fall freeze-up to assess the differences among seasons; 2) compare the seasonal patterns and ranges of NEE and respiration in peatlands with different trophic, plant community, thermal, and moisture regimes; and 3) develop predictive relationships among photosynthesis, respiration, and the environmental controls on these processes to improve our understanding and modeling of wetland carbon exchanges.

2. Study Site

The peatland complex in this study was chosen for its diverse representation of plant communities, thermal and hydrochemical gradients, and the presence of peat plateaus, palsas, and collapse scars. The field experiment was located in the Northern Study Area of Boreal Ecosystems Atmosphere Study (BOREAS) [Sellers *et al.*, 1995], near Thompson, Manitoba (55.91° N, 98.42° W). The average annual temperature and precipitation for the region are -3.9° C and 542 mm (40% as snow; 60% as rain). The sampling year 1996 was normal, within 1 standard deviation of 30 year precipitation and temperature means. The underlying substrates supporting the wetlands are Glacial Lake Agassiz sediments overlying the regional bedrock of Canadian Shield Precambrian gneissic granite. Soils are derived predominantly from Glacial Lake Agassiz sediments and consist mostly of clays and organics. Wetlands are common in the region owing to poor drainage across the flat terrain. The wetlands include a wide range of types found in northern peatlands from rich fen to bog (pH 7.2-3.9) [Zoltai, 1988]. Plant associations in rich fens are diverse, dominated by brown mosses (e.g., *Drepanocladus* spp., *Scorpidium* spp.) and deciduous shrubs (e.g., *Salix* spp., *Betula* spp.) Sedges (particularly *Carex* spp.) are common in poor and intermediate fens with water tables close to the surface. Permafrost underlies many of the peatlands; frozen palsas and peat plateaus are dry and wooded with upland plant communities such as black spruce (*Picea mariana*), feather mosses (e.g., *Pleurozium schreberi*), and ericaceous shrubs (e.g., *Ledum groenlandicum*). Areas of permafrost degradation are found interspersed in the frozen features. These collapse scars become bogs (species poor, *Sphagnum*-dominated communities) if they collapse completely internal to a peat plateau, isolated from groundwater, or may develop into fens if they collapse on the edge of a peat plateau where groundwater intrudes [Vitt *et al.*, 1994; Zoltai, 1993].

Four sites were chosen within the larger peatland complex: rich fen, intermediate fen, poor fen, and bog according to classifications by Chee and Vitt [1989] (Table 1). The bog and poor fen were collapse scars adjacent to permanently frozen peat plateaus. Within each site, collars were placed along moisture, thermal, plant community, and chemical gradients to capture the full range of environmental conditions. Plant community descriptions for each site are found in Table 1.

3. Materials and Methods

3.1. CO₂ Measurements

Net ecosystem CO₂ exchange (NEE), photosynthetically active radiation (PAR), relative humidity (RH), and chamber temperature were measured with a LI-COR 6200 portable photosynthesis system, which includes a LI-6250 infrared gas analyzer, thermistor, hygrometer, quantum sensor, and data logger. Whole ecosystem measurements were made with clear, climate-controlled chambers, modeled after a chamber described by Whiting *et al.* [1991] and Carroll and Crill [1997], designed and constructed at the University of New Hampshire. The chamber walls were constructed of clear lexan and teflon film with a removable top to allow equilibration of plant communities to ambient conditions between sampling runs. The climate-control system consisted of a heat exchanger (Dodge Motors transmission cooler) and a cooler to store cold water that was pumped through the heat exchanger. Fans mounted on the inside of the chamber circulated air across the heat exchanger, maintaining the enclosed air to within 1°C of outside air temperature. The area of the base of the chambers was 3660 cm² to fit a collar with the same area. Chamber heights were either 45 cm or 90 cm to accommodate the varying heights of the vegetation at the different sites. Aluminum collars with a groove for chamber placement were inserted into the peat in the fall of 1995 so that measurements could begin during the thaw period of 1996 with minimal peat disturbance. The groove was filled with water before each sampling run to ensure an airtight seal. In order to establish relationships between NEE and PAR on each sampling day, shrouds with different mesh sizes were used to reduce the light entering the chamber to 1/2 and 1/4 full light. Morning and afternoon sampling runs at equivalent PAR showed similar CO₂ response (D. Joiner, personal communication, tower data, 1998). An opaque shroud was placed over the chamber to eliminate all light for measuring ecosystem respiration (autotrophic and heterotrophic). Four 2.5 min sampling runs at different light levels were conducted at each collar location on a weekly basis from April 15 to October 23, 1996.

3.2. Environmental Variables

Water table positions relative to the peat surface and peat temperature at 5, 10, 20, and 50 cm depth were measured continuously at each collar location with CR10 and CR7 data loggers (Campbell Scientific, Inc.). Water table measurements were made with a float and counterweight attached to a wheel and potentiometer [Roulet *et al.*, 1991] mounted on a platform that was anchored by a wooden post driven into the clay below the peat (peat thickness varied from 2 to 5 m). Wells were constructed of PVC tubing, and the height of the peat surface in each collar was measured with a tube level referenced to the nearest well. Peat temperatures were measured with thermocouples attached at four levels to wooden stakes and inserted into the peat in October 1995.

Table 1. Characteristics of NEE Sampling Sites by Wetland Class and Microtopographic Category

Site	Class	Hummock	Hollow	Carpet	pH	ANPP	WT		Number
							hk	hw	
CB1	OgB			<i>Sphagnum riparium</i> <i>Chamaedaphne calyculata</i> <i>Carex paupercula</i> <i>Vaccinium oxycoccus</i>	3.9 (0.1)	59.28 (8.36)		-6.73 (3.65)	14
CB2	OlsB	<i>Sphagnum fuscum</i> <i>Chamaedaphne calyculata</i> <i>Smilacina trifolia</i>	<i>Sphagnum angustifolium</i> <i>Cladopodiella fluitans</i> <i>Vaccinium oxycoccus</i>		4.1 (0.1)	48.36 (4.76)	-19.66 (2.11)	-10.30 (1.08)	10
CB3	OlsB	<i>Sphagnum fuscum</i> <i>Chamaedaphne calyculata</i> <i>Smilacina trifolia</i>			4.1 (0.1)	46.08 (0.64)	-16.06 (1.76)		10
PF1	OgPF			<i>Sphagnum riparium</i> <i>Carex aquatilis</i> <i>Carex limosa</i>	4.3 (0.0)	69.96 (2.92)		-7.69 (4.98)	9
PF2	OgPF			<i>Sphagnum riparium</i> <i>Carex paupercula</i> <i>Carex aquatilis</i>	4.4 (0.2)	88.47 (5.68)		-6.76 (1.14)	10
PF3	TlsPF	<i>Sphagnum fuscum</i> <i>Kalmia polifolia</i> <i>Larix laricina</i>	<i>Cladopodiella fluitans</i> <i>Sphagnum angustifolium</i> <i>Vaccinium oxycoccus</i>		4.7 (0.1)	85.60 (7.76)	-31.22 (5.12)		21
PF4	OgPF			<i>Warnstorfia exannulata</i> <i>Carex limosa</i> <i>Carex aquatilis</i>	5.9 (0.2)	143.60 (26.16)		0.44 (2.58)	20
IF1	TlsIF	<i>Sphagnum fuscum</i> <i>Ledum groenlandicum</i> <i>Picea mariana</i> <i>Rubus chamaemorus</i>			5.9 (0.2)	58.00 (16.56)	-37.83 (7.12)		12
IF2	OlsIF	<i>Tomenthypnum nitens</i> <i>Sphagnum warnstorffii</i> <i>Salix pedicellaris</i>	<i>Limprichtia revolvens</i> <i>Meesia triquetra</i> <i>Carex tenuiflora</i> <i>Menyanthes trifoliata</i>		6.2 (0.2)	126.60 (9.36)	-21.54 (6.55)	-7.69 (6.51)	32
IF3	OglF	<i>Sphagnum warnstorffii</i> <i>Salix pedicellaris</i> <i>Carex rostrata</i>		<i>Sphagnum riparium</i> <i>Warnstorfia exannulata</i> <i>Carex rostrata</i> <i>Potentilla palustris</i>	5.8 (0.1)	129.08 (21.80)	-17.37 (3.34)	-3.56 (3.12)	27
RF1	TtsRF	<i>Larix laricina</i> <i>Sphagnum warnstorffii</i> <i>Tomenthypnum nitens</i> <i>Salix pedicellaris</i>			6.7 (0.1)	161.80 (116.44)	-10.06 (5.04)		34
RF2	TtsRF	<i>Larix laricina</i> <i>Sphagnum warnstorffii</i> <i>Tomenthypnum nitens</i> <i>Salix pedicellaris</i>	<i>Limprichtia revolvens</i> <i>Menyanthes trifoliata</i> <i>Salix pedicellaris</i> <i>Calliergon giganteum</i>		6.9 (0.2)	212.44 (17.56)	-23.53 (5.32)	-9.83 (5.14)	47

Table 1. (continued)

Site	Class	Hummock	Hollow	Carpet	pH	ANPP	WT		Number
							hk	hw	
RF3	OlsRF	<i>Sphagnum warnstorffii</i> <i>Betula pumila</i> var. <i>glandulifera</i> <i>Salix pedicellaris</i>		<i>Scorpidium scorpioides</i> <i>Menyanthes trifoliata</i> <i>Andromeda glaucophylla</i>	7.1 (0.2)	163.84 (6.64)	-13.74 (4.66)	-6.64 (5.26)	45
RF4	OlsRF	<i>Sphagnum warnstorffii</i> <i>Betula pumila</i> var. <i>glandulifera</i> <i>Salix pedicellaris</i>		<i>Scorpidium scorpioides</i> <i>Menyanthes trifoliata</i> <i>Andromeda glaucophylla</i>	7.2 (0.1)	157.84 (15.16)	-10.97 (4.52)	2.09 (6.00)	44

Site codes are CB (collapse bog), PF (poor fen), IF (intermediate fen), and RF (rich fen). Classes are O, open; T, treed; ts, tall shrub; ls, low shrub; g, graminoid; B, bog; IF, intermediate fen; PF, poor fen; RF, rich fen. Major bryophyte and vascular plant species are listed for each microtopographic category within the site. Mean values (standard deviations) for pH, WT (mean water table position in centimeters below peat surface for hummock (hk) and hollow (hw)), ANPP (above ground net primary productivity for vascular plants) in g dry biomass m⁻² are listed with total number of species per site. For each pH and ANPP measurement, n=6; WT for each site is the average of continuous measurements averaged every hour from May through October. Site names correspond to the following sites in Bubier et al. [1995] and Bellisario et al. [1998]: CB, BC (bog collapse scar); PF, FC (fen collapse scar); IF, ZF (Zoltai fen); and RF, TF (tower fen). Also, see Bubier et al. [1995, Table 3] for CH₄ fluxes and cation concentrations.

The acidity of surface water was measured at monthly intervals from May to October 1996 at each site with a portable pH meter. Calcium, magnesium, and electrical conductivity were measured at each site in 1994 and are reported by Bubier et al. [1995].

3.3. Vegetation Sampling

Plant species composition was recorded in each collar by percent cover of vascular plant and bryophyte species [Daubenmire, 1968]. Nomenclature follows Anderson et al. [1990] for true mosses, Anderson [1990] for *Sphagnum* moss species, Stotler and Crandell-Stotler [1977] for liverworts, and Fernald [1950] for vascular plant species. Sites were classified after a modification of the Canadian peatland classification system [Zoltai, 1988; Riley, 1987] that uses vegetation physiognomy (tree, shrub, graminoid) and water chemistry (pH, calcium, magnesium) [Chee and Vitt, 1989] as the treed sites had 10-30% tree cover; the pH was as follows: bogs, 3.8-4.7; poor fens, 4.5-5.1; intermediate fens, 5.1-6.2; and rich fens, 6.2-7.0. In order to describe microtopographic differences in surface elevation, each collar was given a microtopographic designation of hummock, hollow, carpet, or pool as an indirect measure of water table position. Carpets, relatively flat areas where the water table was near the surface, consisted of loosely consolidated and often floating peat. Hummocks and hollows were smaller features (<1-2 m²) in more undulating terrain.

Aboveground net primary productivity (ANPP) was measured for the vascular plant and bryophyte component of each sampling site. Productivity for vascular plants was measured by clipping aboveground vegetation at the end of August before the plants senesced. Since NEE measurements were made through the period of plant senescence and fall freeze-up, three replicate plots were chosen within the vicinity of each collar. Clipped vascular plants were sorted into three categories: (1) woody leaf and stem, (2) graminoid, and (3) other herbaceous plant material. The biomass samples were dried at 60°C for 24-48 hours and weighed. Bryophyte productivity was measured by a cranked wire technique [Rocheffort et al., 1990] for *Sphagnum* mosses and other mosses

with a vertical growth pattern and by velcro markers for prostrate growth forms, such as "brown" mosses (e.g., *Scorpidium scorpioides*) and feather mosses (e.g., *Pleurozium schreberi*). For each technique, linear increments in growth were measured and converted into mass per unit area using the average bulk density of three replicate 10³ cm samples for each species.

3.4. Data Analyses

The relationship between NEE and PAR (photosynthetically active radiation) was described by a rectangular hyperbola using a curve fitting technique [Thornley and Johnson, 1990]:

$$NEE = \frac{GP_{max} \times \alpha \times PAR}{\alpha \times PAR + GP_{max}} + R$$

where alpha α is the initial slope of the rectangular hyperbola (also called the apparent quantum yield), GPmax \pm R is the NEE asymptote, and R is the y axis intercept (or dark respiration value, R < 0). Since different plant communities saturate at different light levels, and GPmax assumes an infinite upper limit for PAR, we calculated the average rate of photosynthesis for each site for PAR > 1000 μ mol CO₂ m⁻² s⁻¹ in order to more realistically compare the maximum rates of photosynthesis for each site. We adopted the sign convention of CO₂ uptake by the ecosystem as positive and CO₂ emission from respiration as negative. The dark chambers measured ecosystem respiration (total of enclosed plants, roots, and soil microbes). Since light and dark measurements were made within a few minutes of each other, the difference between NEE at full or fractional light and NEE with a dark chamber (respiration) was considered to represent the gross photosynthesis at that light level for the vegetation within the chamber. Multiple stepwise regression (SYSTAT package, Wilkinson [1990]) was used to develop empirical models for NEE, photosynthesis, and respiration with the measured environmental variables.

4. Results

4.1. Seasonal Patterns of CO₂ Exchange

Measurements of net ecosystem CO₂ exchange from April through October 1996 show a similar pattern of CO₂ uptake and release but a difference in magnitude from bog to rich fen (Figure 1). In all four sites, the timing of maximum positive CO₂ uptake and the timing of dark respiration are tightly coupled to one another; as the season progresses, the increase and decrease in both uptake and release follow similar patterns. In the early summer when the plants first emerge from the snow and ice (late May), light levels are near maximum for the season, which allows the system to "turn on" very rapidly and reach maximum NEE levels within a shorter period of time than it takes for the system to senesce in the late summer. The magnitude of the fluxes varies, however, during peak periods, with the bog showing the smallest range in NEE and the rich fen having the largest. Maximum NEE and respiration values are as follows: bog, 5.4 and -3.9; poor fen, 6.3 and -6.5; intermediate fen, 10.5 and -7.8; and rich fen, 14.9 and -8.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

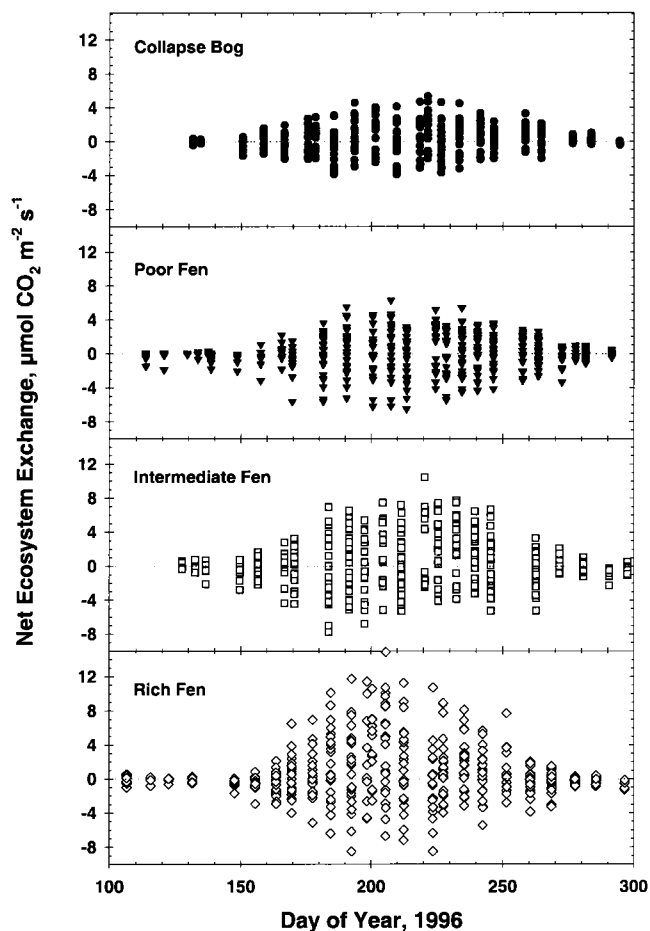


Figure 1. Net ecosystem exchange (NEE) of CO₂ and dark CO₂ fluxes from respiration in a bog, poor fen, intermediate fen, and rich fen, from mid-April through October 1996 (see Table 1 for site descriptions and Table 2 for NEE-PAR parameters). Different values of NEE on the same date represent measurements taken under different light conditions ranging from full light to dark. Positive values indicate CO₂ uptake by the ecosystem; negative indicates net release of CO₂ from respiration.

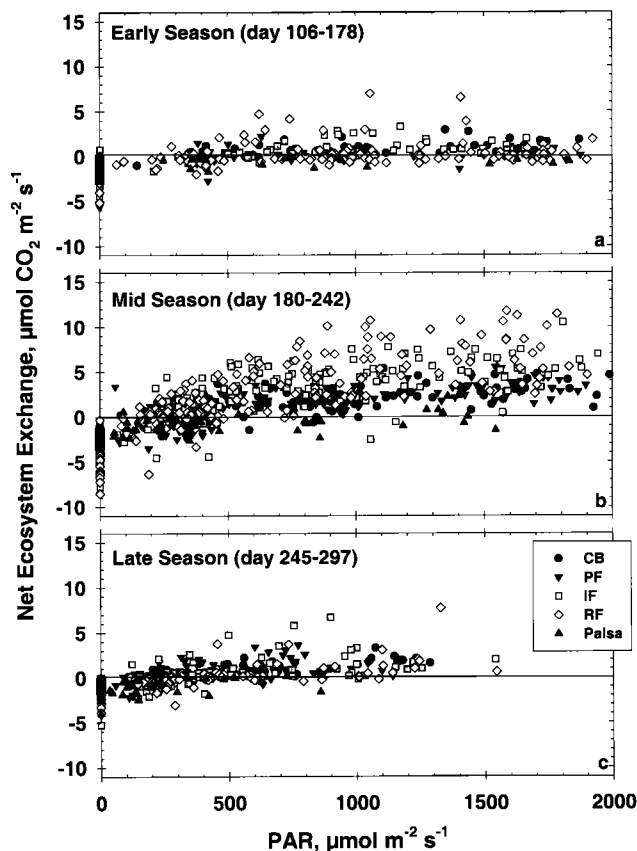


Figure 2. Relationships between NEE and photosynthetically active radiation (PAR) for (a) early season (April-June), (b) midseason (July-August), and (c) late season (September-October) for whole ecosystem bog (CB), poor fen (PF), intermediate fen (IF), and rich fen (RF) sites. NEE for palsa does not include the tree canopy. See Table 2 for NEE-PAR parameters.

The growing season was divided into three components in order to compare the relationships between NEE and seasonal light responses for the four sites (Figure 2). Midseason was defined as JD 180 - 240 (June 28 to August 28), the approximate period of maximum NEE at full light levels. For most sites, the beginning of the midseason was marked by net CO₂ uptake at PAR levels over 500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, although some sites were still showing net release at those light levels owing to differential timing of snowmelt and surface thaw.

Early season (May 10 to June 26) included the period of snowmelt, thaw, and early plant growth (Figure 2a). While snow was still on the ground, all sites had a net release of CO₂ at maximum light levels. CO₂ flux during this period ranged from -0.1 to 5.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The fluxes varied according to microtopography and characteristics of the snow pack. Drier hummock sites with no ice layers had the highest emissions, while the flooded, ice-covered hollows had little or no CO₂ flux until the thaw began. Ice lenses in the snowpack also corresponded with lower fluxes [J. Bubier and B. Davis, unpublished data, 1996].

During the transition from snow cover to plant emergence, the sites did not melt and thaw at the same time. Some sites began fixing CO₂ while others with remaining snow and ice were still net sources of CO₂ to the atmosphere at high light levels (Figure 2a).

Over 40% of the fluxes at high light (PAR > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were negative during the early season, compared with less than 5% in the midseason. Drier sites emerged first from the snow and began to fix CO₂ as soon as the moss layer was exposed (Figures 2a and 3a). Wetter sites thawed days to weeks later. A hummock-hollow pair within 2 m of each other, for example (Figure 3a), had a 20 day lag in the onset of net CO₂ uptake from day 135 in the hummock to day 155 in the hollow. The lag in CO₂ fixation corresponded with a similar lag (15 days) in the warming of the peat above freezing at 5 cm depth in the hummock and hollow (Figure 3b). As soon as the 5 cm peat temperature rose above 0°C, photosynthesis in the moss layer began; the peat was still frozen below 5 cm (Figure 4).

The diurnal surface temperature variation in the hummock and hollow corresponded to the position of the water table over the course of the season (Figure 3b). Unlike the hummock, surface temperatures in the flooded hollow were relatively uniform on a daily basis in the early season (owing to the heat capacity of water) until the water table dropped to 5-10 cm below the peat surface around day 190-200. The hollow then showed a strong diurnal fluctuation in the surface temperatures until the water table rose again in the fall (day 255) to 5-10 cm below the peat surface.

Although there was a lot of intrasite variability in the spring owing to hummock-hollow microtopography, some differences between sites were also apparent. The rich fen had the greatest range in NEE at maximum light from 6.9 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ into the

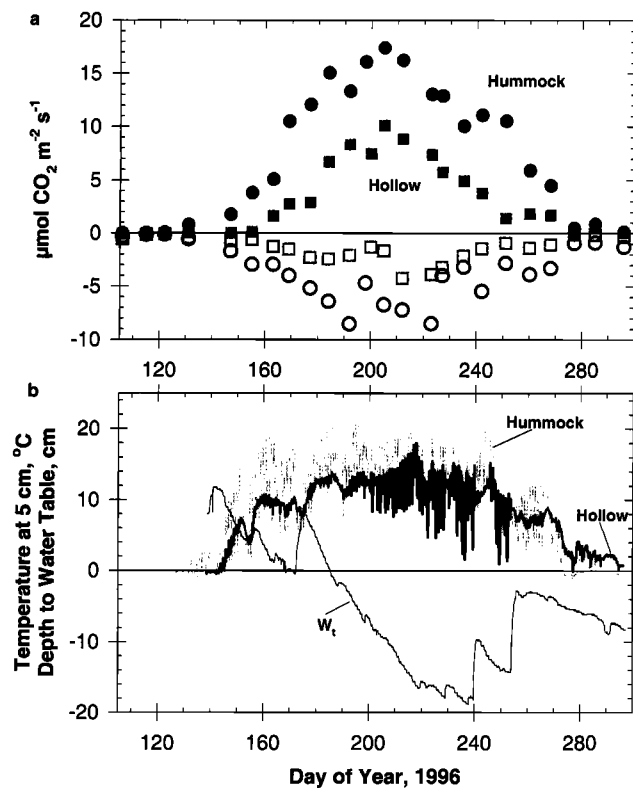


Figure 3. (a) Photosynthesis at PAR values > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and respiration for a hummock-hollow pair in the rich fen; (b) temperatures at 5 cm peat depth for the same hummock-hollow pair. The water table relative to the hollow peat surface is shown along with peat temperature.

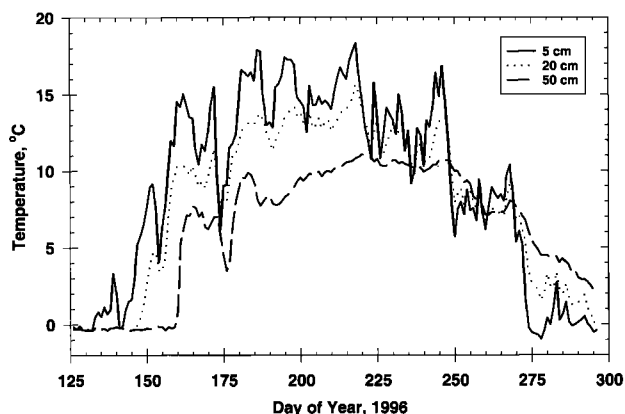


Figure 4. Peat profile of daily average temperatures (May-October 1996) at 5, 20, and 50 cm below the peat surface for rich fen hummock shown in Figure 3.

hummocks to -2.6 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ from the wetter depressions, while the bog had much less variation. The spatial variation in average depth to water table was also less pronounced in the bog compared with the rich fen (Table 1). However, when combining all collars within each site, the bog had higher maximum photosynthesis (PSN_{max}) (2.44 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; SE 0.24) during the early season than the rich fen (1.63 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; SE 0.37)(Table 2). The bog also had a lower average water table than the rich fen (Table 1). The bog and intermediate fen had the highest PSN_{max} during this period and the poor fen had the lowest (1.03 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$; SE 0.36). The intermediate and poor fen sites also had the highest and lowest respiration values (R values of -1.54 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.19) to -0.94 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.17), respectively).

Midseason (July-August) NEE-PAR relationships (Figure 2b; Table 2) show the largest differences among sites. The palsa was the only site that still had net CO₂ release at high light levels, although it was the only site that did not include the entire plant canopy. Because it was well-drained, the trees were too large to enclose in the chambers, but the tree roots were included. All other sites had net CO₂ uptake at PAR levels above 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The range in magnitude varied, however, from PSN_{max} in the rich fen of 10.49 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.59) to 5.06 (SE 0.22) in the bog. The poor and intermediate fens had midrange PSN_{max} values of 6.39 (SE 0.92) and 8.40 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.27), respectively. Mean respiration values ranged from -2.44 (SE 0.16) in the bog to -3.45 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.29) in the rich fen. Mean respiration was similar midseason for the poor and intermediate fens at -3.20 (SE 0.18) and -3.16 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ (SE 0.25), respectively.

Late season (September - October) NEE-PAR curves (Figure 2c) show that maximum light levels were much lower at 1400-1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ than during the early and midseason (2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Most sites still showed positive NEE at PAR > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, but the relative dominance in maximum uptake among sites shifted from midseason to late season. In summer, the rich fen had the highest photosynthetic capacity, but by late season, the sedge (*Carex* spp.)-dominated intermediate fen and the evergreen, ericaceous shrub bog had higher CO₂ uptake than the rich fen, which was dominated by the deciduous shrub *Betula glandulosa*.

Table 2. Nonlinear NEE-PAR Rectangular Hyperbola Curve Fit Parameters for Early Season, Midseason and Late Season Periods

Site	n	GP _{max}	PSN _{max}	α	R	r ²
<i>Early Season (May 10 to June 26; JD 125-178, 1996)</i>						
CB	105	3.04 (0.56)	2.44 (0.24)	0.005 (0.020)	-1.38 (0.15)	0.73-0.85
PF	82	0.94 (0.37)	1.03 (0.36)	0.010 (0.029)	-0.94 (0.17)	0.65-0.77
IF	98	3.22 (0.69)	2.24 (0.41)	0.007 (0.004)	-1.54 (0.19)	0.68-0.84
RF	152	2.19 (0.49)	1.63 (0.37)	0.007 (0.004)	-1.22 (0.20)	0.69-0.78
<i>Midseason (June 28 to Aug. 28; JD 180-240, 1996)</i>						
CB	226	6.29 (0.56)	5.06 (0.22)	0.011 (0.002)	-2.44 (0.16)	0.73-0.84
PF	202	8.44 (0.56)	6.39 (0.92)	0.017 (0.002)	-3.20 (0.18)	0.73-0.83
IF	192	11.52 (0.83)	8.40 (0.27)	0.022 (0.003)	-3.16 (0.25)	0.72-0.83
RF	206	17.33 (1.78)	10.49 (0.59)	0.017 (0.002)	-3.45 (0.29)	0.73-0.88
<i>Late Season (Aug. 28 to Oct. 23; JD 240-297, 1996)</i>						
CB	124	6.27 (2.53)	3.39 (0.22)	0.004 (0.001)	-1.09 (0.12)	0.65-0.91
PF	129	3.88 (0.67)	2.99 (0.44)	0.010 (0.003)	-1.24 (0.15)	0.69-0.83
IF	106	5.32 (1.53)	3.49 (0.58)	0.008 (0.003)	-1.47 (0.23)	0.66-0.85
RF	118	3.90 (1.31)	3.14 (0.81)	0.004 (0.001)	-1.08 (0.14)	0.67-0.86

Site codes: CB, collapse bog; PF, poor fen; IF, intermediate fen; RF, rich fen. GP_{max} +/- R = asymptote for NEE; PSN_{max} = maximum photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for PAR > 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$; alpha α = initial slope of the curve; R = respiration (y intercept) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); standard error in parentheses. See equation for NEE parameters in section 3.4. Ranges of r² are applicable for all parameters except PSN_{max}, which is calculated as the mean and SE for all psn values for PAR > 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$.

4.2. Environmental Controls on Photosynthesis and Respiration

The relationship between respiration and photosynthesis at maximum light levels (PAR > 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$) shows a positive correlation at all sites during all seasons (Figure 5; $r^2 = 0.66$). Although the range varies with the bog having the lowest rates of photosynthesis and respiration to rich fen with the highest, the relationship is similar across sites. The slope of the regression line is -0.34 for the combined data set, indicating that the ratio of combined autotrophic and heterotrophic respiration to maximum CO₂ uptake at high light is approximately 1/3. At low levels of photosynthesis and respiration (< 5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), the relationship is even stronger ($r^2 = 0.70$). These low levels occur in the early and late season, suggesting that even though the two processes are controlled by different factors, they are closely coupled and there is no offset in the timing of carbon uptake and release during the thaw and freeze-up periods. The greatest intersite variability in the relationship occurs at the mid-high range of photosynthesis and respiration in midseason, when these two processes are affected differently by various factors, including light levels, water table positions, temperatures, and differences in plant phenology.

Ecosystem respiration is closely tied to changes in near-surface peat temperatures at 5 cm depth at all sites. The correlation with 5 cm is the best from the depths measured, but may be even stronger with 1-2 cm surface temperatures. Temperatures at 50 cm depth lag behind the surface temperatures by several weeks (Figure 4), but the pattern of respiration increase and decline is more closely associated with the surface temperatures. At a hummock site at the rich fen, for example, surface temperatures rose above freezing around JD 132, a few days before respiration began to increase. The temperature at 50 cm did not rise above 0 until JD 158, 26 days later. At the end of the season, the temperature profile inverted around JD 273, with the warmest temperatures at 50 cm and the

coldest near the surface, reflecting the sharp decline in average daily air temperatures at that time. The 50 cm temperature was still above 0 through the end of the measurement period at the end of October, while the 5 cm temperature fell below 0 at JD 273 and did not rise above 3°. In conjunction with the drop in surface temperatures, CO₂ flux from respiration fell sharply to near zero around JD 275 (Figure 3a).

The correlation between respiration and 5 cm peat temperature is strong within sites (r^2 ranging from 0.57 to 0.88), but the slope and intercept of the regressions vary significantly between sites. However, the relationship becomes more similar across sites when adjusted for aboveground vascular plant productivity and biomass (Figure 6). Aboveground net vascular plant productivity (ANPP)

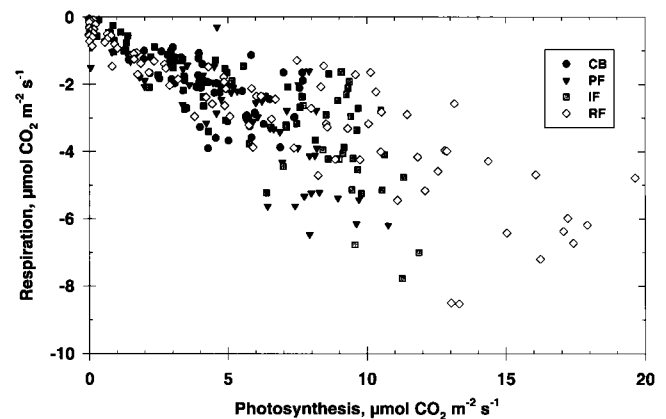


Figure 5. The relationship between respiration and photosynthesis at PAR > 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (max psn) for bog (CB), poor fen (PF), intermediate fen (IF), and rich fen (RF) from April through October 1996. Respiration = -0.34 max psn + 0.56 ($r^2 = 0.66$; $p < 0.05$ for correlation coefficient; $n = 287$).

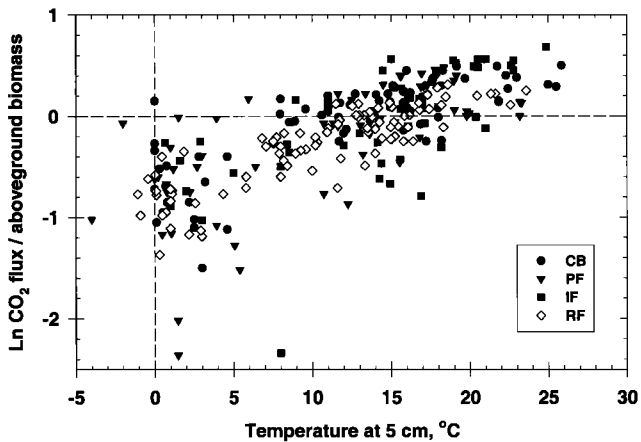


Figure 6. The relationship between respiration and temperature at 5 cm peat depth, normalized for aboveground vascular plant biomass, which is strongly correlated with aboveground vascular plant net primary productivity (ANPP). See Table 1 for ANPP values for each site. Respiration rates were changed to positive values to calculate the log values. Log CO₂ fluxes for each collar were divided by the aboveground biomass of vascular plants. Log CO₂ flux/aboveground biomass = $0.052 T_{5\text{cm}} - 0.784$ ($r^2 = 0.57$; $p < 0.01$ for correlation coefficient; $n = 566$).

for the 1996 growing season ranged from collar means of 46.08–59.28 g dry biomass m⁻² in the bog to 161.80–212.44 g dry biomass m⁻² in the rich fen (Table 1). The poor and intermediate fens had ranges of 69.96–143.60 and 58.00–129.08 g dry biomass m⁻², respectively. Each CO₂ flux was divided by the above ground biomass (strongly correlated with ANPP) for that collar to normalize the respiration-temperature relationship by site. The combined temperature-biomass versus CO₂ flux regression is significant ($r^2 = 0.57$) with a slope of 0.052 and intercept of -0.784. The Q_{10} value is approximately 3.31 in the range 5°–15°C, when normalized by dry biomass.

We developed empirical models for photosynthesis and respiration using stepwise multiple regression, combining the environmental variables and ranking them by order of importance (Table 3). Separate models were developed for each site, but the controlling variables are similar in each, with slightly different rankings. Generally, temperature at 5 cm explains 43–74% of the variability in respiration (see partial r^2 values), with water table explaining an additional 5–20%. The coefficients of determination (r^2) for the multiple regressions range from 0.65 to 0.80. At the collapse bog and collapse poor fen sites, temperature at 50 cm depth is an additional explanatory factor but of minor importance. The coefficient for the 5 cm temperature variable increases in the order bog < poor fen < intermediate fen < rich fen, which indicates increasing rates of respiration for each increment in temperature along the bog-fen gradient. The Q_{10} values (without normalizing for ANPP) for each site range from 3.0 to 4.1 for this trophic gradient.

Although water table position is less important than temperature in explaining respiration on a daily basis, the average seasonal dark CO₂ flux is correlated strongly with average water table position for each collar location (Figure 7). The water table generally has an inverse relationship with surface temperatures during the season (Figure 3b), which may explain the weak relationship between daily

respiration and water table position. However, the seasonal average water table position is an indication of the depth of the aerobic zone in the peat profile, which explains between-site differences better than average peat temperature.

The models for photosynthesis (Table 3) show that PAR is the most important factor, explaining 39–58% of the variation (see partial r^2), while temperature at 5 cm and daily average air temperature are the second most important, explaining an additional 8–16%. Daily average temperature and peat temperature at 5 cm are strongly correlated at all sites ($r^2 = 0.60$). Adding water table position as the third most important variable resulted in r^2 values of 0.60–0.73. The collapse bog site is the only one with a slightly different order of importance. At that site, after PAR explains 58% of the variation in photosynthesis, temperature at 10 cm explains more of the additional variability than either daily average temperature or peat temperature at 5 cm depth. Water table position does not make an additional contribution. The collapse bog site had the least water table variation spatially (Table 1) and temporally because the peat surface was floating and adjusted to the falling water table (see *Bubier et al.* [1995] for data on peat surface adjustments).

5. Discussion

The ranges of maximum NEE and respiration follow the general progression bog < poor fen < intermediate fen < rich fen. This progression fits within the general understanding of peatland ecology where bogs are more nutrient limited than fens because of their hydrology and position on the landscape. Bogs are isolated from groundwater and receive nutrients primarily from precipitation. They have lower species diversity [*Malmer, 1986; Glaser et al., 1990*], pH [*Vitt and Bayley, 1984*], fewer mineral nutrients [*Malmer, 1993*], less net primary production [*Thormann and Bayley, 1997; Bartsch and Moore, 1985*], and slower decomposition rates [*Szumigalski and Bayley, 1995; Johnson and Damman, 1993*] than fens. Fens, which receive nutrients from groundwater input, have a wide range of variability from mineral poor to mineral rich with corresponding ranges in water chemistry,

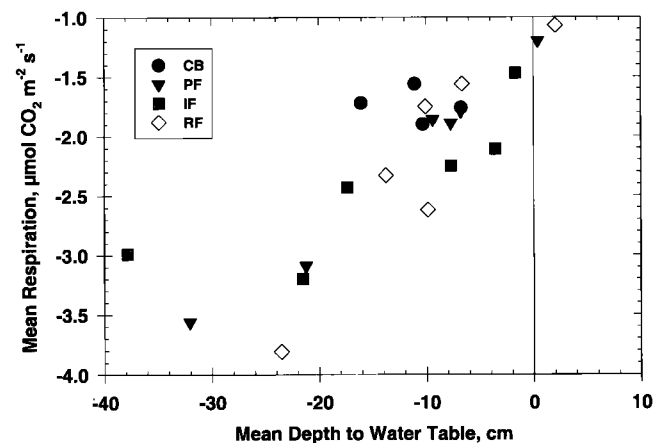


Figure 7. The relationship between seasonal mean respiration (MR) and mean water table (MWT) position for all collar locations (MR = $0.06 \text{ MWT} - 1.42$; $r^2 = 0.63$; $p < 0.001$ for correlation coefficient; $n = 24$).

Table 3. Stepwise Multiple Regression for Daily Measurements of Photosynthesis and Respiration April-October 1996

Site	n	Constant	w	x	y	z	r ²
<i>Photosynthesis = constant + w(PAR) + x(T5cm or Tdavg) + y(WL) + z(T10cm)</i>							
CB	278	-0.804	0.003 (0.58)			0.268 (0.73)	0.73
PF	393	-1.614	0.003 (0.41)	0.179 (0.63)	-0.051 (0.68)		0.68
IF	368	-4.857	0.004 (0.43)	0.153 (0.51)	-0.033 (0.60)		0.60
RF	436	-1.812	0.004 (0.39)	0.162 (0.55)	-0.142 (0.60)		0.60
<i>Respiration = constant + x(T5cm) + y(WL) + z(T50cm)</i>							
CB	223	-0.041		-0.176 (0.74)	0.015 (0.78)	0.071 (0.80)	0.80
PF	127	0.060		-0.185 (0.43)	0.080 (0.62)	0.140 (0.68)	0.68
IF	147	1.385		-0.219 (0.60)	0.058 (0.71)		0.71
RF	306	0.219		-0.322 (0.58)	0.093 (0.65)		0.65

Sites: collapse bog (CB), poor fen (PF), intermediate fen (IF) and rich fen (RF). Variables are listed by order of importance in the regression models. T5m, T10cm, T50cm = temperature at 5, 10, and 50 cm peat depth; Tdavg, daily average air temperature; WL, water level below peat surface. T5cm and Tdavg were strongly correlated ($r^2 = 0.60$) and are considered as the same variable in the photosynthesis model. Partial cumulative r^2 are in parentheses. All parameters are significant at $p < 0.01$.

production, and decomposition rates, and species composition [Chee and Vitt, 1989; Slack et al., 1980]. These differences in biogeochemical characteristics between bog and fen have implications for long-term carbon accumulation rates [Damman, 1996; Tolonen et al., 1994] and exchanges of CO₂ and methane (CH₄) with the atmosphere [e.g., Martikainen et al., 1995].

In this study, the maximum NEE values in bog sites are 3 times lower than in rich fens and half that of intermediate fens (Figure 1). Respiration rates are also lower in the bog sites than in fens with a maximum of $-3.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, compared with $-8.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for rich fens. NEE-PAR relationships (Table 2) show that midsummer maximum gross production (PSN_{max}) for the bog is only $5.06 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, compared with $10.49 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for rich fen sites. The midseason values for PSN_{max}, alpha (see equation in section 3.4), and respiration are similar to those reported in bogs and fens elsewhere in North America and Europe [Frolking et al., 1998; Alm et al., 1997]. Average PSN_{max} for rich fens is 11.20 ($n = 1665$) [Frolking et al., 1998], compared with 10.49 for rich fen collars in this study; average PSN_{max} for bogs is 4.70 ($n = 2789$) for northern peatlands, compared with 5.06 in this study. Midsummer average respiration rates for rich fens and bogs in the combined data set [Frolking et al., 1998] are -2.56 (0.09) and -1.99 (0.05), respectively, compared with -3.45 (0.29) and -2.44 (1.61) in this study. The low photosynthesis and respiration rates in the bog site dominated by *Sphagnum fuscum* and ericaceous shrubs were comparable to exchange rates in *S. fuscum* moss sites at black spruce upland forest during the same period [Goulden and Crill, 1997].

The greatest variation occurs in the poor fen class, which includes a wider range of vegetation and chemical gradients than

either the bog or rich fen class. Midsummer PSN_{max} and respiration values for North American and European poor fens are 9.90 ($n = 1043$) and $-2.57 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ [Frolking et al., 1998], compared with 6.39 and -3.20 for the poor fen and 8.40 and -3.16 for the intermediate fen in this study.

Rich fens, which have the largest exchange rates of all peatland types, are still significantly lower than upland ecosystems [Frolking et al., 1998; Ruimy et al., 1996]. GP_{max} ranges from 35.3 to 82.9 for forest, grassland, and cropland, compared with 12.1 for rich fens. The rich fen midsummer GP_{max} in this study was 17.3, higher than the rich fen average, but much lower than upland systems. Midsummer respiration is correspondingly lower in peatlands compared with uplands (average of -2.44 versus -4.29), although some upland boreal ecosystems show similarly small rates [e.g., Raich and Shlesinger, 1992; Pajari, 1995].

Few studies have measured NEE outside the midsummer growing season to assess the impact of spring and fall on the annual carbon balance [e.g., Alm et al., 1997; Ball, 1996; Bhardwaj, 1997]. In a modeling study of a boreal black spruce forest, Frolking et al. [1996] found that the timing of spring was one of the most important factors explaining interannual variability. By the time the snow melts in northern latitudes, light levels are already near their annual maximum. Carbon uptake for evergreens reaches its maximum soon after the soil thaws.

Although differences in trophic status were more important than microtopography in explaining the range of NEE and respiration rates across sites midseason, microtopography was important within sites, particularly in the spring. In this study, emissions of CO₂ occurred through the snow in early spring and varied according to the presence or absence of ice lenses in the peat and within the

snowpack. Differential rates of snowmelt and thaw across the peatland controlled the onset of net carbon uptake. Moss photosynthesis began on the drier hummocks as soon as the surface 5 cm was thawed (Figure 3). Saturated hollows continued to be a net source of CO₂ until the ice thawed, as much as 3 weeks later than the drier areas. This staggered timing of carbon uptake may be important for the carbon balance, especially in peatlands with significant microtopography [Ball, 1996; Waddington and Roulet, 1996]. In this study, the NEE-PAR curves for this early transition period (Table 2; Figure 2) show that a greater percentage of sites were net sources of CO₂ to the atmosphere compared with midseason, owing to differential rates of snowmelt and thaw. The rich fen had the greatest range of NEE at maximum light levels with some of the drier hummock sites showing uptake rates of up to 6.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while the saturated sites were still net sources of CO₂ (-0.5 to -2.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to the atmosphere at high light levels.

NEE-PAR curve parameters (Table 2) show that the bog and intermediate fen had higher GP_{max} and PSN_{max} values than the rich fen in the early season, the reverse of the summer order. The same order of maximum production occurred in the late season period as well, suggesting that the different plant types in these sites may have different lengths of growing season. Rich fen plant communities that have higher photosynthetic capacity in summer may have a shorter growing season. The bog was dominated by ericaceous shrubs, which have evergreen leaves, permitting them to photosynthesize earlier and later in the season than the dominant deciduous shrubs in the rich fen (e.g., *Betula glandulosa*). Sedge-dominated communities in the intermediate fen also appear to have longer growing seasons. Late season maximum production values were highest for the intermediate fen (Figure 2), especially sites that were dominated by the sedge *Carex. Bellisario et al.* [1997] and *Alm et al.* [1997] found that sites dominated by *Carex rostrata* had higher net annual carbon accumulation than wet sites dominated by other species. The higher photosynthetic capacity of *Carex* in spring and fall observed in this study may explain the higher net carbon uptake on an annual basis, even though rich fen communities have higher maximum production potential midsummer.

The strong correlation between photosynthesis at maximum light and respiration (Figure 5), suggests that the two processes are tightly coupled even though different factors are controlling uptake and release of carbon. PAR is the primary control on photosynthesis, but increasing light levels are correlated with increases in soil temperature, which is a dominant control on respiration. Although it is difficult to sort out the components of ecosystem respiration, there may be a strong physiological link between photosynthesis, plant metabolism, and respiration. Even though these processes occur on different timescales, the ratio of combined autotrophic and heterotrophic respiration to maximum CO₂ uptake at high light is consistently 1/3. Other studies have found that 30-70% of total respiration in bogs is due to root respiration or root-derived microbial respiration [Bhardwaj, 1997; Silvola et al., 1996b]. The close relationship between surface temperatures and respiration suggests that root-associated processes may be responsible for a substantial portion of total respiration.

Research in boreal upland sites shows a lag between photosynthesis and respiration, with higher respiration rates continuing well past plant senescence into the fall [Goulden et al., 1998]. This offset is attributed to deep soil warming, which lags

behind the surface temperatures and dominates the late season CO₂ flux. Although the 50 cm soil temperatures lagged behind the surface temperatures in all the peatland sites in this study (Figure 4), respiration was not correlated with deep temperatures. Instead, there was a strong correlation between respiration and 5 cm temperatures at all sites (Figures 5 and 6; Table 3). Peatlands may be different from uplands in this respect because of the presence of a near-surface water table, which restricts the aerobic zone to within 10-30 cm of the peat surface, on average. Since decomposition rates are faster above the water table [Moore and Dalva, 1993], the influence of deep soil warming on total respiration is less important than near-surface processes. Most of the plant roots, especially from woody species, also occur in the oxygenated zone above the water table [Wallen, 1992]. This study did not measure respiration during the late fall and winter, which may be a significant part of the annual budget [Alm et al., 1997] and may not be correlated as strongly with surface temperatures.

The temperature coefficients (Q₁₀) along the bog to rich fen trophic gradient range from 3.0 to 4.1. When normalized by aboveground vascular plant biomass, the Q₁₀ for all sites becomes 3.3 (Figure 6). These values are generally higher than for mineral soils; in a review by Raich and Schlesinger [1992], the range for all soils is 1.3-3.3 (median 2.4). The higher Q₁₀ values in this study correspond with high values found in wet, organic soils and lower temperatures [Kirschbaum, 1995; Silvola et al., 1996a,b]. Chapman and Thurlow [1996] propose that an increased temperature sensitivity may be characteristic of acidic, organic soils, which may make these soils more sensitive to climate change.

Water table is an important control on respiration, although its significance is greater on an average seasonal basis than on a daily one. In the empirical model for respiration (Table 3), water table was the third most important factor explaining daily respiration rates at each site; but when averaged over the season, the relationship with average respiration was much stronger (Figure 7). Lower water tables have been shown to enhance CO₂ production in a number of studies that have included laboratory experiments [Moore and Dalva, 1993], drained peatlands [Silvola et al., 1996a,b], natural spatial variability in water table position [Alm et al., 1997; Kim and Verma, 1992] and drier than average years [Carroll and Crill, 1997; Bellisario et al., 1998].

Although there have been few studies on interannual variability of NEE, evidence suggests that there can be large differences in carbon exchange from year to year. In some years, peatlands change from a sink to a source of CO₂. Shurpali et al. [1995] reported a gain of 32 g CO₂-C m⁻² in a wet summer and a 71 g CO₂-C m⁻² loss of CO₂ from the same peatland in a dry summer. Suyker et al. [1997] reported a gain of 88 g CO₂-C m⁻² in a rich fen in Saskatchewan during a year with above average summer precipitation, while Lafleur et al. [1997] reported a net loss of 30 g CO₂-C m⁻² in a rich fen during the same year that was unusually dry in northern Manitoba. In some cases, drier years can turn certain portions of a peatland into a source while others remain a sink in peatlands with significant microtopography [Waddington and Roulet, 1996].

Comparing results from this study with NEE measurements made at some of the same sites in 1994 shows that interannual differences in water table and temperature had an effect in the rich fen but were less significant in the other sites [Bellisario et al., 1998]. In the warmer and drier 1994 season, respiration rates were significantly higher in late summer when the water table dropped.

Average respiration rates were over 6.24 g CO₂-C m⁻² d⁻¹, compared with 3.45 g CO₂-C m⁻² d⁻¹ during the same period in 1996. Other sites showed an increase in respiration during the same dry period in 1994, but the difference between 1994 and 1996 was not as pronounced as at the rich fen site. One possible explanation is that most of the other sites measured in 1994 had floating peat surfaces and adjusted to the falling water table, minimizing the increased depth of the aerobic zone. Another possibility is that lowering the water table in rich fen sites has a larger impact on CO₂ production than in sites that are more nutrient-limited. In Finland, sites with higher minerotrophic status had a larger increase in dark CO₂ flux after drainage than poor sites [Martikainen et al., 1995]. In our study sites, the lower water table in 1994 resulted in a net ecosystem loss of CO₂ during the dry period in late summer; although maximum plant productivity (GP_{max} and PSN_{max}) increased, the plants senesced earlier in 1994 than in 1996, resulting in a shorter growing season.

Although peatlands have been a net sink of carbon for thousands of years, the balance between CO₂ uptake and release may be so close that a small change in water table, temperature, or timing of thaw and senescence could favor decomposition over plant production. Silvola et al. [1996a,b] predict that an increase of 2–4°C in the boreal region (an estimate from global climate models) would cause a 30–60% increase in CO₂ emissions from peatlands. This calculation was based on average Q₁₀ values, which were lower than in this study, suggesting that a comparable increase in temperature would result in even higher CO₂ fluxes in our study sites. Silvola et al. [1996a,b] also estimate that lowering the water table by 14–22 cm, as predicted by Roulet et al. [1992], would increase CO₂ emissions by 50–100%. However, Laine et al. [1996] have also shown that lower water tables are correlated with increased CO₂ fixation and plant production in some peatlands after long-term drainage.

Changes in surface temperatures and water table are more important in peatland environments than in deep soil warming, which may be a significant factor in altering the carbon balance in upland boreal ecosystems [e.g. Goulden et al., 1998]. The strong relationship between photosynthesis at maximum light and respiration in this study suggests that these processes are closely coupled during the growing season and are correlated with easily measured variables such as surface temperatures, water level, and trophic status (bog versus fen; ANPP). Although we need to improve our understanding of the physiological and microbial processes, these predictive relationships may improve our ability to model wetland CO₂ exchanges and to predict the effect of a changing climate on peatland carbon balances.

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J. Bubier, Environmental Studies Program, Mount Holyoke College, 50 College Street, South Hadley, MA 01075-6418. (e-mail: jrbubier@mtholyoke.edu)

P. M. Crill and R. K. Varner, Complex Systems Research Center, Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824. (e-mail: patrick.crill@unh.edu; ruth.varner@unh.edu)

T. R. Moore and K. Savage, Geography Department, 805 Sherbrooke Street West, McGill University, Montreal, Quebec, Canada H3A 2K6.

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