

Microtopographical and canopy cover controls on moss carbon dioxide exchange in a western Boreal Plain peatland

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ABSTRACT

Climate change may have profound impacts on the maintenance of peatlands and surface water systems in the sub-humid western Boreal Plain (WBP) of Northwestern Canada. Wetlands in the WBP, whereas significant carbon stocks are sensitive to changes in climate, because in most years potential evapotranspiration (ET) exceeds precipitation. In this study, a dynamic closed chamber technique was used to examine the relative midday (10:00–16:00 h) growing season (April–October) contributions of heterotrophic and autotrophic respiration (R_{tot}) and moss photosynthesis (gross ecosystem production, GEP) to net ecosystem exchange (NEE) of CO_2 at the soil surface of different degrees of spruce forest canopy cover and microtopography (lawn and depression) in two peatland–pond complexes in the WBP, north–central Alberta, Canada. Results demonstrate that *Sphagnum* lawns showed the greatest amount of uptake, and dominant surface cover plant communities (*Sphagnum* and feather mosses) were associated more with canopy cover and incident radiation (photosynthetically active radiation, PAR) than microclimate and hydrology. Although microclimate and hydrology varied spatially, no major changes in plant communities were observed across microtopographic gradients (lawns and depression). Differences in NEE with hydrology and microclimate were observed between microtopographic units (depression and lawns), but this was not consistent with surface cover plant community types, which makes generalized fluxes in this landscape particularly challenging. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS peatland; CO_2 ; microtopography; *Sphagnum*; feather moss

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INTRODUCTION

There have been many studies on CO_2 exchange from northern peatlands over the past decade because of their importance in climate change scenarios (Gorham, 1991; Waddington *et al.*, 1998; Moren and Lindroth, 2000). Boreal peatlands especially have been implicated as important sources or sinks of carbon. However, the Boreal zone spans large geologic and climatic ranges, from the more humid Eastern Boreal Shield with low soil storage to the sub-humid western Boreal Plain (WBP) with much larger soil storage (Devito *et al.*, 2005; Tarnocai *et al.*, 2009). Although there is currently a paucity of information in the WBP, the sub-humid climate indicates that peatland systems may be more sensitive to any climatic variability due to the dominance of evapotranspiration (ET) in summer hydrologic budgets. Furthermore, due to the large areas covered by these peatlands, there is a need for generalizing and extrapolating the carbon functioning of these landscape units. However, due to the complexity of regions like the WBP, it is essential to develop key relationships with net ecosystem

CO_2 exchange [net ecosystem exchange (NEE) (gross ecosystem production, GEP and R_{tot})] and metrics that can be easily mapped, such as vegetation or other environmental controls and physical processes (Black *et al.*, 1996; Joabsson *et al.*, 1999; Hobbie *et al.*, 2000; Amiro, 2001; Petrone *et al.*, 2003).

As observed in many ecosystems, measurements of NEE show large spatial variability within and among northern peatlands (Waddington and Roulet, 1996; Bubier *et al.*, 1998; Heijmans *et al.*, 2001). This is largely due to the fact that the carbon budgets of these ecosystems are controlled by the balance between carbon uptake during photosynthesis (GEP) by plants and carbon losses during autotrophic and heterotrophic respiration (R_{tot}) (Potter *et al.*, 2001; Bubier *et al.*, 2003), which are controlled by differing interactions between physical, biogeochemical and ecological processes that vary within and across peatlands. Vegetation communities can represent distinct ecological processes while integrating a range of environmental controls that influence spatial variability in the carbon exchange processes within peatland ecosystems (Waddington and Roulet, 1996; Swanson and Flanagan, 2001; Bubier *et al.*, 2003). Although vegetation community and microform (microtopographical) approaches have both been used to explain and predict the spatial variability in CO_2 exchange and the controlling

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factors within peatlands, most studies have addressed these interrelationships (between vegetation, hydrology and microtopography) independently and have largely focused on hydrologic and microtopographical controls (Waddington and Roulet, 1996; Camill and Clark, 1998; Yavitt *et al.*, 2000; Potter *et al.*, 2001; Bubier *et al.*, 2003; Biasi *et al.*, 2005). More studies incorporating the combined roles of vegetation cover and microtopography are needed to better understand carbon dynamics in peatlands.

The surface vegetation cover in a peatland has been shown to be important, largely through its control on GEP (Bubier *et al.*, 1998). This is particularly important in the black spruce (*Picea mariana*) dominated peatlands in the WBP, where the excurrent profile and low density overstories with *Sphagnum* species and feather mosses (e.g. *Pleurozium schreberi* and *Hylocomium splendens*) allow for a substantial portion of solar energy to reach the moss-covered floor (Heijmans *et al.*, 2001). These bryophyte surface covers can contribute significantly to ecosystem CO₂ exchange due to their large aboveground biomass (Goulden *et al.*, 1997; Waddington *et al.*, 1998). Moreover, the live biomass (over- and understory) of a system not only influences GEP directly, but also greatly influences the net function of the ecosystem by affecting the hydrology, microclimate (especially photosynthetically active radiation, PAR) and nutrient availability that also controls GEP (Oechel and Van Cleve, 1986; Bisbee *et al.*, 2001; Heijmans *et al.*, 2001). For example, dominant peatland surface cover communities such as *Sphagnum* mosses also insulate the soil, intercept atmospheric nutrients and decompose very slowly, thereby reducing the soil temperatures and rates of nutrient supply for GEP (Oechel and Van Cleve, 1986). Thus, the approach of using vegetation patterns to explain the spatial variability in CO₂ exchange requires the assumption that vegetation is the primary control on local-scale hydrologic conditions and therefore CO₂ exchange compared with other factors such as surficial geology, microtopography and climate. However, due to interactive and confounding effects, it is often difficult to distinguish hydrological from vegetation controls. Thus, overstory and peat surface vegetation structure, as they influence PAR and GEP, may be significant.

An alternative approach to characterize carbon exchange in peatlands makes the assumption that microtopography drives hydrological gradients, which in turn control both vegetation patterns and soil respiration, and consequently CO₂ exchange (Waddington and Roulet, 1996; Bubier *et al.*, 1998). For example, microtopographic highs (e.g. hummocks, lawns and moss cushions) are generally drier than adjacent microtopographic lows (e.g. hollows, depressions) (Waddington and Roulet, 1996; Petrone *et al.*, 2005) and consequently have different vegetation distributions and subsequent CO₂ exchange rates than topographic lows (Strack *et al.*, 2006).

In sub-humid regions, such as Canada's WBP, where peatlands and surface water systems persist in much

drier conditions (Devito *et al.*, 2005), the correlation between CO₂ exchange and patterns in vegetation and microtopography may differ from studies conducted elsewhere (Waddington and Roulet, 1996; Petrone *et al.*, 2004). In more humid climates, depressions often experience saturated conditions or standing water. The drier climate and large soil moisture storage in the WBP may produce a relationship between microtopography and vegetation patterns, which is highly variable and dissimilar to other systems, with required moisture thresholds (differences) between microtopographical highs and lows, which may not be the same as those that are needed to drive vegetation differences relative to CO₂ differences. Therefore, a difference in CO₂ exchange may be observed between lawns and depressions, but not a difference in relative ground cover vegetation distributions, which in the WBP largely comprised bryophytes (Solondz *et al.*, 2008). Furthermore, because bryophytes form such a large contribution to the boreal carbon cycling, a better understanding of the factors influencing bryophyte distribution, such as interactions with canopy cover (i.e. PAR interception) and microtopography, and their resulting NEE is needed to quantify the boreal forest carbon cycle (Frolking *et al.*, 1998; Bisbee *et al.*, 2001; Gower *et al.*, 2001).

Therefore, the objectives of this study are to measure the rates of NEE, GEP and R_{tot} for different types of moss cover through the growing season to determine (1) whether there is a relationship between NEE and dominant moss species as related to differences in canopy cover and (2) whether patterns in CO₂ exchange between microtopographical units differ with dominant moss species. This information will determine whether microtopography or canopy closure is more important in determining patterns of surface cover CO₂ exchange and whether these controls complicate the use of understory vegetation patterns as a proxy for patterns in CO₂ exchange.

MATERIALS AND METHODS

Site description

The two forested peatland complexes (ponds 40 and 43) in this study are situated on a disintegration moraine (Redding *et al.*, 2005), located in the Utikuma Region Study Area (URSA) near Utikuma Lake, northern Alberta (56°20'N, 115°30'W) within the WBP ecozone (Figure 1) (Devito *et al.*, 2005). The climate is characterized by warm summers and long and cold winters. The average 30-year climate normals in annual temperature, precipitation and potential ET for the region are 1.7 °C, 485 and 515 mm, respectively (Environment Canada, 2007). The average temperature and precipitation for 2005 and 2006 were 2.8 and 2.9 °C and 374 and 396.5 mm, respectively, making them slightly warmer and drier than the 30-year normal.

In most years, PET exceeds precipitation in this region, making it a sub-humid climate. Up to 84% of the area

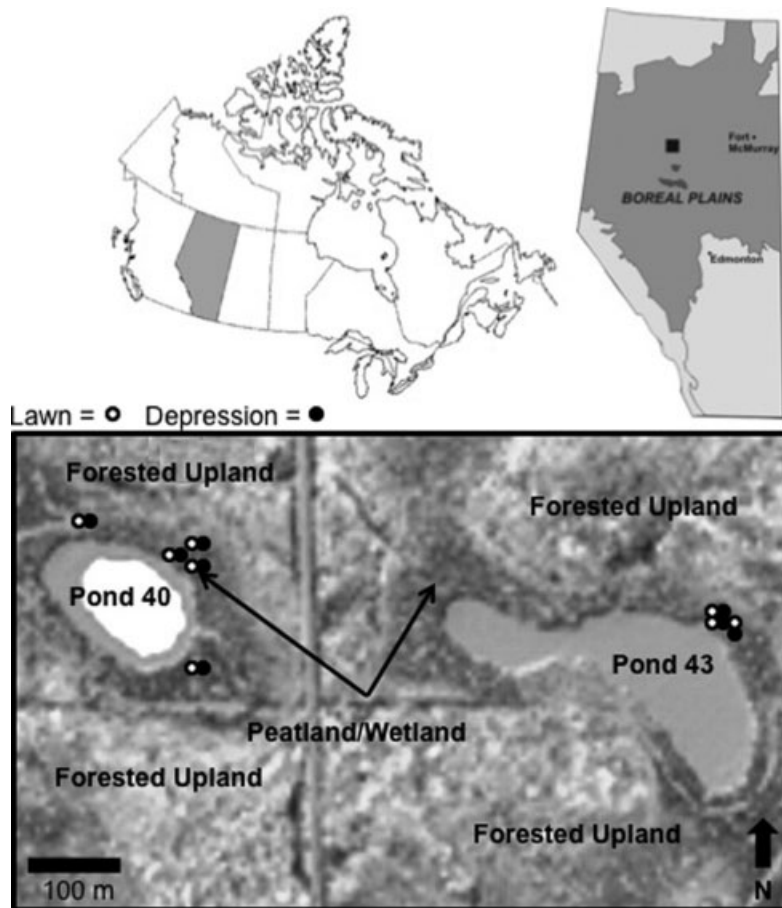


Figure 1. Study site (ponds 40 and 43) located within the WBP ecozone, URSA, Alberta, Canada. Circles represent site locations, with solid and open circles representing bare soil and vegetated collars, respectively.

in this ecozone is covered in conifer and deciduous forests (Johnson *et al.*, 1995). Typical vegetation of the uplands includes trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) in sandy areas, whereas balsam poplar (*Populus balsamifera*) and black spruce (*P. mariana*) dominate in the lowland and peat-dominated areas (Johnson *et al.*, 1995). The arborescent layer of peatlands in the area is dominated by *P. mariana* and larch (*Larix laricina*) with occasional *Salix* species found mostly along the pond edges.

The two adjacent study peatlands each circumvent a shallow pond (<<<1 m depth) with a riparian treed poor fen and bog grading from open water to thicket swamp at the base of aspen-dominated uplands as described by Ferone and Devito (2004). The peatland–pond complexes are located on a topographical high glacial till moraine adjacent to an upland forested hill slope reaching a height of 7 m above the pond surface. The pond and peatlands are located in a recharge zone, and water tables typically grade away from the peatland into the adjacent hillslope (Ferone and Devito, 2004; Redding and Devito, 2008). There is some disturbance associated with access roads for oil drilling located outside the study peatland–pond complex, and seismic lines (where strips of vegetation are removed) occur through upland and peatland landscape units. Seismic lines were avoided for this study.

At a larger scale, peatland areas tend to be composed of regions of low density black spruce cover and regions of old burns. The shrub layer of the peatlands are mostly composed of *Ledum groenlandicum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*. The ground cover of these peatlands is comprised mainly of bryophyte and lichen species that are characteristic of poor fen communities. Lawns are classified as topographically high mounds, whereas depressions are low lying. The dominant lawn species were *Sphagnum fuscum*, *S. capillifolium*, and feather mosses such as *P. schreberi* and *H. splendens*, and the lichens *Cladina mitis* and *Cladina stellaris*. Other bryophyte species found on lawns included *Dicranum undulatum* and *Polytrichum strictum*. The dominant depression species were *Sphagnum angustifolium* and *Plagiomnium cuspidatum*, although most of the species listed for the lawns could frequently be found in the depressions. The feather moss *Tomenthypnum nitens* can also occasionally be found in depressions. A general survey of surface vegetation reveals that bryophyte communities composed of two dominant types: (1) *Sphagnum*-dominated areas that generally had canopy closures of 35% or lower and topographic relief of about 70 cm between lawns and depressions, and (2) feather moss communities that occurred in areas generally greater than 35% canopy closure and had maximum relief of 35–40 cm (Table I).

Table I. Vegetation as per cent coverage in vegetated collar for each lawn and depression site and above canopy closure. Bare collars are not shown as no live material was present.

Canopy closure (%)	Lawn (L)		Depression (D)		
	Vegetation	%	Canopy closure (%)	Vegetation	%
4.5	<i>E. nigrum</i>	10	2	<i>T. nitens</i>	4
	<i>L. groenlandicum</i>	25		<i>L. groenlandicum</i>	5
	<i>O. microcarpus</i>	30		<i>O. microcarpus</i>	3
	<i>S. fuscum</i>	90		<i>S. fuscum</i>	85
	<i>V. vitis-idaea</i>	10		<i>V. vitis-idaea</i>	15
8	<i>C. mitis</i>	15	5	<i>C. mitis</i>	90
	<i>E. nigrum</i>	30		<i>V. vitis-idaea</i>	30
	<i>L. groenlandicum</i>	25		<i>O. microcarpus</i>	5
	<i>O. microcarpus</i>	10		<i>S. fuscum</i>	100
	<i>S. fuscum</i>	100			
10	<i>V. vitis-idaea</i>	3	8		
	<i>C. mitis</i>	12		<i>S. fuscum</i>	90
	<i>E. nigrum</i>	25		<i>V. vitis-idaea</i>	20
	<i>L. groenlandicum</i>	20		<i>C. mitis</i>	30
	<i>O. microcarpus</i>	10		<i>O. microcarpus</i>	9
11	<i>S. fuscum</i>	100	16		
	<i>L. groenlandicum</i>	21		<i>C. mitis</i>	65
	<i>E. nigrum</i>	12		<i>V. vitis-idaea</i>	15
	<i>S. fuscum</i>	60		<i>O. microcarpus</i>	4
	<i>S. trifolia</i>	9		<i>S. fuscum</i>	84
40	<i>C. mitis</i>	15	40		
	<i>T. nitens</i>	40		<i>H. splendens</i>	20
	<i>L. groenlandicum</i>	30		<i>T. nitens</i>	55
	<i>S. trifolia</i>	1			
	<i>V. vitis-idaea</i>	25			
64	<i>T. nitens</i>	40	62	<i>T. nitens</i>	95
	<i>V. renifolia</i>	10		<i>V. vitis-idaea</i>	30
66	<i>H. splendens</i>	25	86	<i>H. splendens</i>	55
	<i>L. groenlandicum</i>	9		<i>L. groenlandicum</i>	10
	<i>V. vitis-idaea</i>	20		<i>P. schreberi</i>	40
	<i>T. nitens</i>	43		<i>T. nitens</i>	40
				<i>V. vitis-idaea</i>	15
69	<i>T. nitens</i>	95	84	<i>T. nitens</i>	20
	<i>L. groenlandicum</i>	15		<i>L. groenlandicum</i>	10
	<i>P. schreberi</i>	90		<i>P. schreberi</i>	95
	<i>V. vitis-idaea</i>	15		<i>V. vitis-idaea</i>	30
				<i>H. splendens</i>	20

Over 100% coverage is observed at some collars as moss mats were present with vascular vegetation growing through. Canopy closure at all sites was composed of black spruce (*P. mariana*). URSA, Alberta, Canada.

Therefore, collars were placed throughout the peatlands to capture the range of microtopography and the different vegetation communities: lawn ($n = 8$) (*Sphagnum* lawn $n = 4$ and feather moss lawn $n = 4$) and depression ($n = 8$) (*Sphagnum* depression $n = 4$; feather moss depression $n = 4$). Nomenclature follows Johnson *et al.* (1995) for all species. Peat depths ranged from 1.5 to 4 m in both peatlands.

CO₂ measurements

CO₂ exchange between the surface and atmosphere was measured using a dynamic closed chamber system with an EGM-4 Infrared Gas Analyzer (IRGA) (P.P. Systems, MD, USA). Net ecosystem CO₂ exchange (NEE) was measured using clear lexan chambers, whereas total respiration (R_{tot}) was measured using an opaque neoprene shroud over the lexan similar to that used by Waddington and Roulet (1996, 2000). Measurements were conducted

from 30 April (DOY 120) to 7 September (DOY 250) 2005 and 26 April (DOY 116) to 3 October (DOY 276) 2006. Polyvinylchloride collars (radius = 13.2 cm), with a groove for chamber placement, were inserted approximately 10 cm into the soil 1 week prior to initial measurements. The groove was filled with water and remained throughout the measurements to insure an airtight seal when the chamber was inserted during the flux measurements. A climate-controlled system in each chamber consisted of a cooler with cold water pumped through a coolant tube to maintain chamber conditions within approximately 4% and 1.5 °C of ambient relative humidity (RH) and T_{air} , respectively, and a fan mounted on the inside of the chamber to minimize concentration build-up influencing the gradient without ventilating the surface (Welles *et al.*, 2001). Five 1-min CO₂ concentrations were sampled at each collar location midday (0900–1600 h), twice a week. The rate of

CO₂ concentration increase within the 5 min interval and was then used to determine the average flux (Lund *et al.*, 1999). The concentration of CO₂ was measured in ppm and then converted into mg CO₂ m⁻² s⁻¹ using

$$F = \frac{\Delta \cdot M}{N} \cdot \frac{V}{A} \cdot CF \quad (1)$$

where F is the gas flux (mg CO₂ m² s⁻¹), Δ is the linear change in CO₂ concentration with time (μmol mol⁻¹), M is the molar mass of CO₂ (44 010 mg mol⁻¹), N is the molar volume of a gas (0.224 m³ mol⁻¹) at standard temperature and pressure (STP), V is the temperature corrected volume within the chamber (m³), A is the chamber area (m²) and CF is the conversion factor from ppm to mol (1 ppm = 10⁻⁶ mol). Sampling times at each site were irregularly selected throughout each sampling day to reduce confounding effects of the different light, temperature and moisture regimes that occur throughout the day and to ensure sampling over a wide range in environmental conditions.

GEP was estimated by subtracting the gross respiration (R_{tot} = autotrophic and heterotrophic) from NEE, which is the combined above and below ground respiration and photosynthesis:

$$\text{GEP} = \text{NEE} - R_{\text{tot}} \quad (2)$$

The sign convention of CO₂ uptake by the ecosystem as positive and CO₂ emissions from respiration as negative was adopted here. The measurement period includes all the snow-free seasons at this boreal location, which for comparative purposes was divided into different time periods [early green (EG), green (G), late green (LG) and senescence (S)]. The periods fluctuated slightly between the years as they were based on precipitation, temperature and vegetation growth. Early green in 2005 (2006) extended from DOY 120 (116) to 161 (157). During this time, vascular species emerge but are immature. Green extended from DOY 161 (157) to 218 (212). During this time, vascular species are maturing. Late green extended from DOY 218 (212) to 250 (244). During this time, the vascular species have reached maturity and maximum leaf area index (LAI). The senescence period was only monitored in 2006 and extended from DOY 244 to 276, during which time the onset of dormancy occurred.

The relationship between GEP and PAR was fitted empirically using an equation for a rectangular hyperbola regression (Whiting, 1994; Waddington and Roulet, 1996):

$$\text{GEP} = \frac{(\alpha \times \text{PAR} \times \text{GP}_{\text{max}})}{[\alpha \times \text{PAR} + (\text{GP}_{\text{max}})]} \quad (3)$$

where PAR is the measured PAR (in μmol m⁻² s⁻¹), GP_{max} is the empirically derived gross photosynthetic exchange of CO₂, and α is the initial slope of GEP versus PAR.

Environmental variables

RH, air temperature (T_{air}) and PAR were all measured at each site during each 5 min chamber sample period, both

inside and outside of the chamber (1.5 m above the forest floor) using an EGM-4 atmospheric probe (P.P. Systems, Maryland, USA). In the regression analysis that follows, data from inside the chambers are used in an attempt to most accurately characterize the RH, T_{air} and PAR, especially by the vegetation being measured. Peat and soil temperatures were recorded at the same temporal and spatial scale as the CO₂ fluxes using a digital thermocouple at 2, 5 and 10 cm in the soil. Volumetric moisture content (VMC) was measured using a soil moisture probe (HydroSense Probe, Campbell Scientific Inc., UT, USA) inserted into the top 20 cm of the soil substrate beside each collar during each measurement. The soil moisture probe was calibrated in the lab by extracting representative, intact samples (including moss and peat) from the field and then allowing them to dry to different moistures (Solondz, 2007). Depth to ground frost was recorded in triplicate at each site by probing through peat to the ice surface with a 1 cm in diameter welding rod, and depth of frost was determined when resistance to pounding with a hammer suddenly increased. This method was checked periodically by drilling holes and measuring ice thickness and comparing with thermistor temperatures at each site (at depths of 5, 10, 25 and 50 cm).

Vegetation and soil sampling

Plant species composition was recorded in each collar by per cent cover of vascular plant and bryophyte species. Canopy closure was determined using digital photographs. The camera (Kodak DC-120) with a fixed 39–114 mm $f/2.5$ – 3.8 lens and 1280 × 960 pixel image resolution was levelled above each collar and manual photos were taken (Guevara-Escobar *et al.*, 2005). Photos from all sites were taken midday on clear days to avoid large variations in brightness across the pictures. Images were analysed using Adobe Photoshop CS (Adobe Systems incorporated). The threshold to classify pixels into 'sky' and 'canopy' was determined on the first image and then applied to the rest of the images in that set. Classified images were then analysed to calculate canopy area. The ratio of the canopy area to frame area of the image was expressed as a percentage and used to estimate canopy cover (Guevara-Escobar *et al.*, 2005).

To determine aboveground biomass (Table II), two representative plots per collar were harvested to a depth of 12–17 cm (bottom of collar), and were separated into aboveground vascular plants (clipped from above the moss surface), moss, belowground vascular plant parts (fine roots, rhizomes, belowground stem parts), and soil organic matter (SOM) (the remainder) (Heijmans *et al.*, 2001). The aboveground vascular plant parts were sorted into three categories: (1) herbaceous plant material, (2) graminoids and (3) woody leaf and stem (evergreen) (Thormann and Bayley, 1997; Bubier *et al.*, 1998). The moss fraction was 4–6 cm thick and only green moss was included; clearly decomposed and compacted moss was included in the SOM fraction (Heijmans *et al.*, 2001).

Table II. Mean (SE) measured total AGB, moss above ground biomass (M-AGB), below ground biomass (living roots) (BGB), SOM, carbon : nitrogen ratio (C:N), bulk density (ρ_b), VMC (θ), soil porosity (ϕ) and soil specific yield (Sy) for lawn and depression microtopographical units dominated by *Sphagnum* and feather moss species, pond 40, URSA, Alberta, Canada. Negative values indicate a release of carbon to the atmosphere 2005 and 2006.

Site	AGB	M-AGB	BGB	SOM	C:N	ρ_b	θ	ϕ	Sy
<i>Sphagnum</i> lawn	1698 (224)	1494 (197)	131 (45)	4368 (325)	72.4 (30.9)	0.023 (0.01)	17.6 (0.81)	0.94 (0.01)	0.12 (0.01)
<i>Sphagnum</i> depression	1654 (853)	1489 (768)	212 (55)	5279 (348)	42.1 (7.6)	0.055 (0.01)	16.3 (0.98)	0.94 (0.01)	0.07 (0.02)
Feather moss lawn	2089 (766)	1274 (587)	318 (42)	4062 (402)	31.9 (11.2)	0.057 (0.04)	32.0 (1.45)	0.89 (0.02)	0.11 (0.02)
Feather moss depression	1393 (94)	989 (67)	291 (31)	5371 (640)	37.1 (6.7)	0.052 (0.01)	72.4 (1.22)	0.88 (0.02)	0.07 (0.02)

AGB, M-AGB, BGB and SOM (g dry mass m⁻²), C:N (%), ρ_b (g cm⁻³), θ (%), ϕ (%), Sy (%).

The lichens were separated from the mosses, and mosses were separated into *Sphagnum* and feather mosses (*P. schreberi*, *H. blandowii*, *H. splendens*). All plants were oven dried at 60 °C for 2 days, whereas the large SOM fraction was dried for a week and then all samples were weighed.

The belowground biomass was determined by taking two 20 cm representative cores for each site. Roots were removed and separated into living and dead, and live roots were oven dried at 60 °C for 2 days. Soil cores were also taken in duplicate from each collar site in August 2005 and were analysed for bulk density (ρ_b), porosity (ϕ), SOM, specific yield (Sy) and C:N ratios (Table II).

Statistical analysis

Literature that examines chamber flux measurements generally uses standard deviation (McNeil and Waddington, 2003; Botting and Fredeen, 2006; Strack *et al.*, 2006) or standard error (Tufekcioglu *et al.*, 2001; Heijmans *et al.*, 2001) to assess the daily uncertainty between and within sites. For this study, standard error was used as it better describes the confidence of the reported mean, rather than the natural variability (Ambus *et al.*, 2001). For each parameter, analyses of variance (ANOVAs) were run using year, moss cover and microtopography as factors. Where appropriate, two-way ANOVAs were also run. If the assumption for a general linear model was not met, data were log transformed to meet the assumptions prior to the statistical analyses. Data for GEP were not normally distributed following log transformation. Consequently, non-parametric statistics (Kruskal–Wallis) tests were used. Differences were deemed to be statistically significant if they met a significant level of 0.001.

When modelling temperature dependence with total respiration (R_{tot}), in some circumstances, linear (Fang *et al.*, 1998; Heijmans *et al.*, 2001) or quadratic (Maestre and Cortina, 2003) relationships fit well. However, most studies represent temperature and R_{tot} using exponential relationships (Fang and Moncreiff, 2001). This exponential relationship suggests that microbial activity increases at an accelerated, non-linear rate as temperature rises, and thus exponential relationships were used to model temperature and R_{tot} .

A linear model can suitably explain variability in R_{tot} with volumetric moisture content (VMC) if small seasonal ranges of VMC occur, or majority of measurements occur in conditions that are either separately in 'wet' or 'dry' ends of the spectrum (Simek *et al.*, 2004). However, when a range of 'wet' and 'dry' conditions occurs, a quadratic relationship is more representative (Davidson *et al.*, 1998). Therefore, within this study, a quadratic model was used to represent the relationships between R_{tot} and soil moisture, as a range of VMC were observed over the study period.

RESULTS

Vegetation distribution and soil properties

In general, areas of low canopy cover were dominated by *Sphagnum*, whereas those of high cover were dominated by feather moss species regardless of topographic position (Table I). Bryophyte sites did not differ in their aboveground biomass (AGB) (Table II) although it should be noted that estimates do not include the spruce canopy. Belowground vascular plant biomass (BGB) was the highest within the feather moss plots, which may be associated with the quantity of evergreen shrubs with deep roots and/or spruce canopy on these plots (Table II). The SOM was similar across all plots, ranging from 4062 to 5371 g dry mass m⁻² in feather moss lawn and depressions, respectively. The *Sphagnum* lawns had the lowest bulk densities and the largest C:N ratios (Table II). However, specific yield (Sy) and porosity was similar between the lawn and depression microtopographical units within the two moss covers, whereas specific yield was larger for lawns and microtopographical values were similar for both mosses (Table II).

Variability in hydrometeorology conditions

The seasonal changes in rainfall, surface soil moisture and depth to ice with microtopographic position and bryophyte type are illustrated in Figure 2. Although the snow-free seasons in both years experienced similar amounts of rainfall (374 and 370 mm in 2005 and 2006, respectively), the distribution of events throughout the season differed. In 2005, with the exception of one

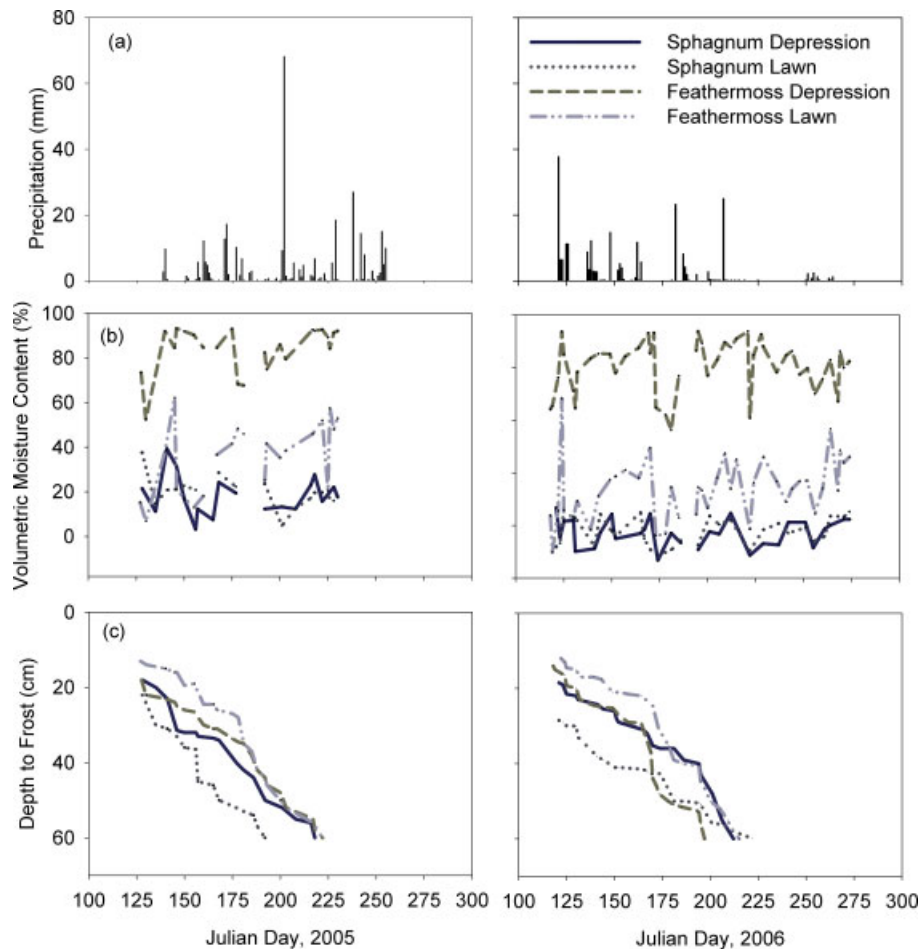


Figure 2. Total daily (a) precipitation and daily averages of (b) soil moisture (θ) at 7 cm below surface, and (c) depth to frost, for the study peatland-pond complexes, 2005 and 2006, URSA, Alberta, Canada.

large 70 mm event on JD 203, events were more evenly distributed over the season. This contrasts 2006, where events tended to be more concentrated earlier in the season with no appreciable rain event after JD 200 (Figure 2a). VMC differed among sites [$F(3, 532) = 472.18$; $p \lll 0.001$] but not between years [$F(1, 532) = 0.019$; $p = 0.891$] (Figure 2b). *Post hoc* (least significant difference, LSD) tests revealed no difference between *Sphagnum* hummocks and hollows ($p = 0.856$) but showed that hollows were wetter than hummocks at feather moss sites ($p \lll 0.001$), and that feather moss sites were wetter than *Sphagnum* sites ($p \lll 0.001$).

In both years, the depth to frost at the beginning of the season was similar (~ 10 cm below surface) at all sites except the *Sphagnum* lawns, which started at a depth of approximately 28 cm (Figure 2c). Ice depth was shallower than 40 cm, and within the rooting zone until JD 175 and 180 in 2005 and 2006, respectively. Complete loss of ground frost occurs late into the growing season, between JD 200 and 225 (Figure 2c).

Microclimatological variables were examined at the same temporal scale as the CO₂ fluxes to determine whether there was variation between the microtopographical and moss covers (Figure 3). No significant differences were observed between 2005 and 2006 for air temperature (T_a) [$F(1, 94) = 0.070$;

$p = 0.791$], soil temperature at 5 cm (T_{soil}) [$F(1, 94) = 0.713$; $p = 0.401$], and PAR [$F(1, 94) = 0.507$; $p = 0.478$], although 2006 was more humid than 2005 [$F(1, 91) = 53.84$; $p \lll 0.001$]. Carbon dynamics also did not differ between years for NEE [$F(1, 585) = 3.33$; $p = 0.068$] or R_{tot} [$F(1, 585) = 2.83$; $p = 0.093$] or GEP [$\chi^2(1) = 9.107$; $p = 0.003$]. Consequently, data were grouped for both years to better examine the influences of microtopography and canopy cover on CO₂ exchange from dominant bryophyte communities (Figure 3). An ANOVA found significant differences in PAR among all sites [$F(3, 547) = 61.31$; $p \lll 0.001$]; however, *post hoc* tests (LSD) found this to be caused by differences in PAR between the *Sphagnum* sites and feather moss sites ($p \lll 0.001$) rather than differences within bryophyte sites (Figure 3a). Indeed, there was little difference between lawns and depression at each dominant bryophyte or canopy cover type at the start of the season, followed by small declines throughout the summer, with the exception of *Sphagnum* lawn sites, which had slightly higher PAR than depressions in the LG and S periods (Figure 3a). This is likely attributed to the on average higher per cent canopy closure in the depressions, and the differential shading by the canopy when the sun was lower in the sky.

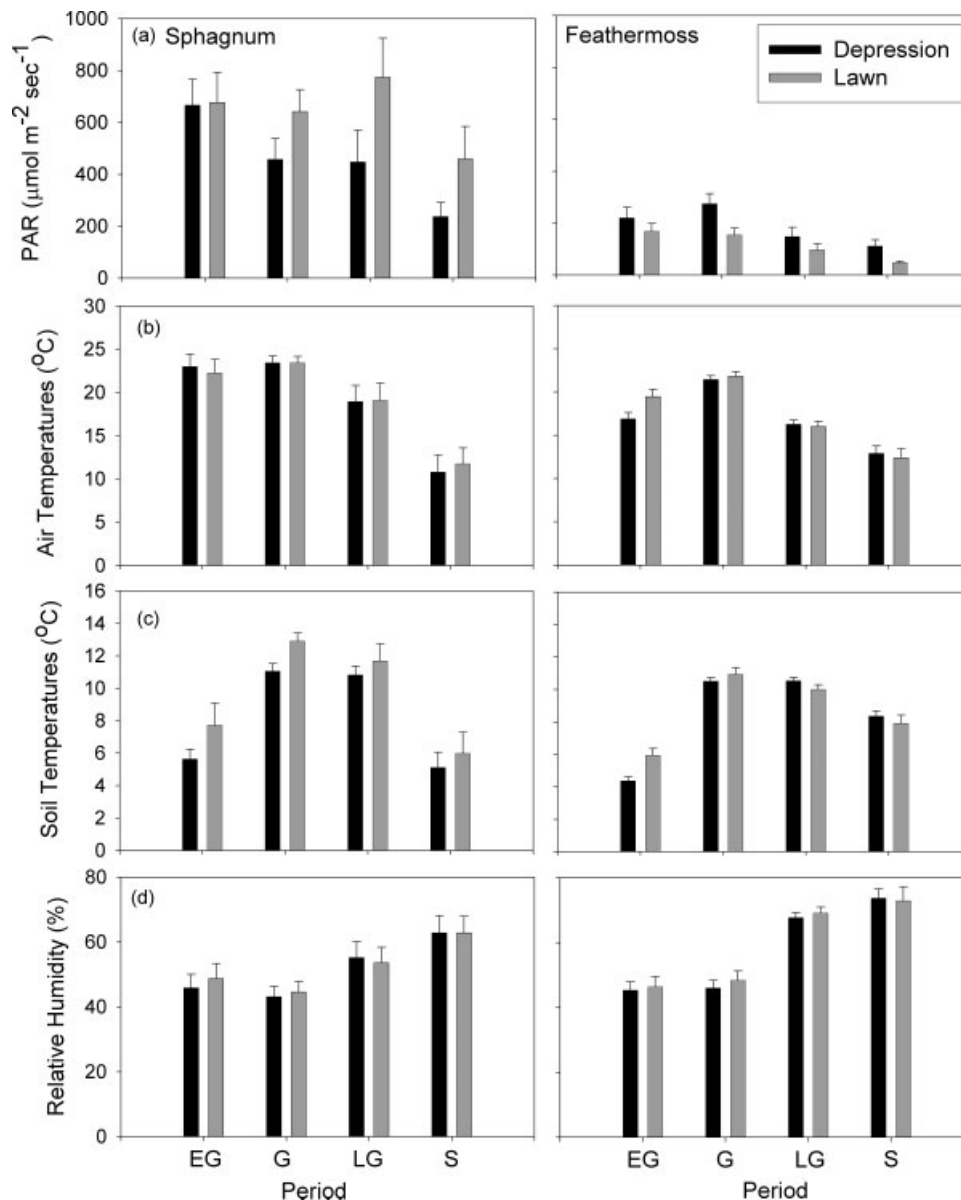


Figure 3. Average seasonal (a) PAR, (b) soil temperature (T_{soil}), (c) air temperature (T_a) and (d) RH at each microtopographical (lawn and depression) unit of each vegetation cover, for ponds 40 and 43, 2005 and 2006 (error bars are standard error), URSA, Alberta, Canada.

A comparison of T_a and T_{soil} across all sites demonstrated similar temporal trends (Figure 3b) and showed that the maximum T_{soil} was reached during the green (G) period when maximum T_a values were also observed (Figure 3c). Differences in T_a [$F(3, 563) = 11.316$; $p \lll 0.001$] and T_{soil} [$F(3, 563) = 10.62$; $p \lll 0.001$] were observed across sites. *Post hoc* (LSD) tests showed that differences in T_a were between *Sphagnum* and feathermoss sites ($p \lll 0.001$) but not within bryophyte cover types. In contrast, differences in T_{soil} were due to differences in microtopography, showing significant differences between the *Sphagnum* lawn and *Sphagnum* depression ($p = 0.001$) and feather moss depression ($p \lll 0.001$), likely a result of dominant patterns in canopy closure, but not between the *Sphagnum* lawn and feather moss lawn ($p = 0.142$). Depressions were cooler than lawns at the feather moss sites but were not significantly different ($p = 0.002$).

RH increased slightly through the study seasons, but did not vary between microtopographical units [$F(1, 515) = 0.439$; $p = 0.508$] and bryophyte cover type [$F(1, 515) = 6.26$; $p = 0.013$] (Figure 3d).

Spatiotemporal variability in CO₂ exchange

Note that the fluxes in this study represent short duration (5-min samples) period midday fluxes, which cannot be extrapolated to daily or seasonal carbon gain or loss (Heijmans *et al.*, 2001). The 2-year average daily NEE differed across all sites [$F(3, 545) = 165.19$; $p \lll 0.001$] (Figure 4a). NEE was less negative in depressions relative to lawns at the feather moss sites [$F(1, 397) = 109.45$; $p \lll 0.001$] and at the *Sphagnum* sites the lawns were actually positive [$F(1, 148) = 247.53$; $p \lll 0.001$]. The magnitude and net uptake of CO₂ also varied with bryophyte cover

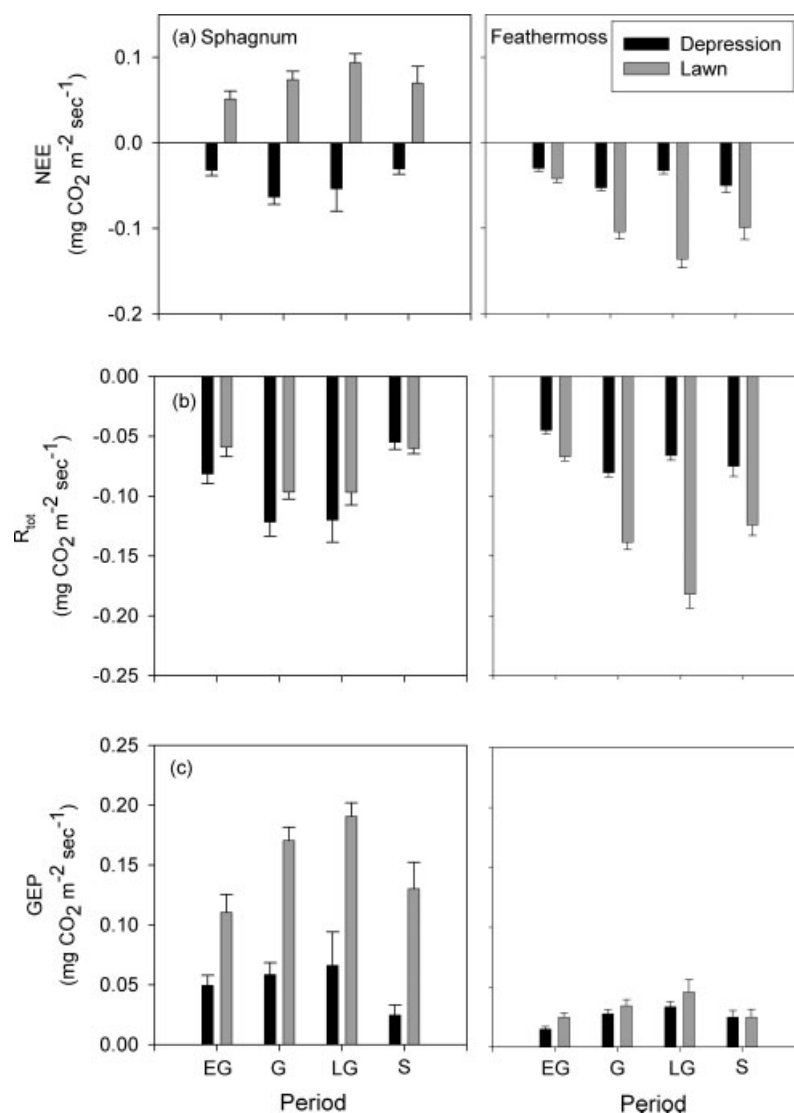


Figure 4. Average midday (a) NEE, (b) total respiration (R_{tot}) and (c) GEP from microtopographical lawn and depression units, URSA, Alberta, Canada combined for 2005 and 2006. Negative values indicate CO₂ release from respiration; positive values represent uptake by the ecosystem (error bars are standard error).

[$F(1, 547) = 59.86$; $p \lll 0.001$], which showed differences in PAR (canopy closure) (discussed previously).

R_{tot} did not differ between bryophyte communities [$F(1, 547) = 7.59$; $p = 0.006$] (Figure 4b). However, a comparison within sites showed that R_{tot} from *Sphagnum* lawns was not statistically different from depression [$F(1, 148) = 0.138$; $p = 0.710$] (Figure 4b), whereas feather moss lawns and depressions were statistically different [$F(1, 397) = 111.93$; $p \lll 0.001$]. Furthermore, R_{tot} was the greatest from the feather moss lawns, which coincides with lower C:N ratios (Table II) at these sites.

Figure 4c shows the difference in GEP among the four sites. GEP from *Sphagnum* lawns was significantly larger than the other sites [$\chi^2(1) = 156.01$; $p \lll 0.001$]. Although the feather moss lawns and depressions did not differ significantly [$\chi^2(1) = 0.115$; $p = 0.734$] in their GEP, there was a significant difference between the *Sphagnum* and feather moss sites (when microtopographic units are combined) [$\chi^2(1) = 91.62$; $p \lll 0.001$] (Figure 4c).

There were also temporal trends apparent in mid-day CO₂ exchange from April through October among the microtopographical vegetation units (Figure 4). The *Sphagnum* lawns showed an average net CO₂ uptake during all seasonal periods, whereas all other sites showed an average loss of CO₂ to the atmosphere for the entire study season, with the lowest rates in the feather moss depressions (Figure 4a). The timing of maximum GEP occurred earlier than maximum R_{tot} for all sites (Figure 4b and c), with the timing differing between microtopographical units. All sites showed a general trend with R_{tot} at a minimum during EG, with shallow depth to ice and cooler soil temperatures (Figures 2 and 3). However, although low, GEP is proportionally greater and similar to R_{tot} , resulting in low NEE.

The lowest R_{tot} and GEP averages and minimums were observed in the EG when the soils were still cold and had a shallow frost depth (Figure 4). However during the G period, lawn sites with higher temperatures and deeper frost exhibited higher average R_{tot} and GEP for

this seasonal period. The open *Sphagnum* sites had peaks in R_{tot} similar to GEP, resulting in relatively constant NEE throughout the snow-free season. However, the closed canopy feather moss cover sites showed low GEP, with peaks during G and LG, but an R_{tot} that continued to increase, producing peaks in NEE loss in S (or fall period).

Environmental relationships

All lawn sites experienced larger ranges in soil temperature, and the feather moss depressions experienced a larger range in VMC (Figure 5). However, the feather moss depression sites responded with lower R_{tot} to similar temperatures and VMCs observed in the lawn sites. A strong exponential relationship between temperature and R_{tot} is observed at all four sites (Figure 5a), with the temperature range being slightly greater in lawns of both cover types. Thus, the highest R_{tot} during the study were observed at lawn sites. Furthermore, a comparison of this relationship at different microtopography and dominant cover sites indicates that the shallowest slope was observed in feather moss depressions, which also has the greatest range in soil moisture content (Figure 5). The slopes of feather moss lawn and *Sphagnum* lawn and depression sites are similar, and averages in R_{tot} for 2005 and 2006 were therefore also similar.

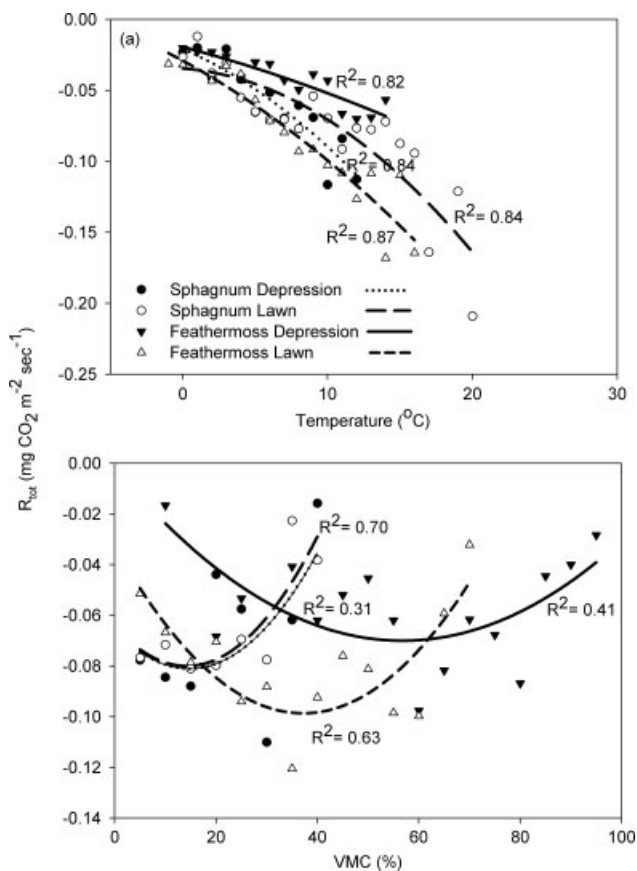


Figure 5. Variations in total respiration (R_{tot}) with (a) soil temperatures at 5 cm below the surface and (b) VMC. URSA, Alberta, Canada, 2005 and 2006. Independent variables were rounded up to the nearest whole temperature or moisture content, with R_{tot} averaged for each.

These microtopographical and cover variations showed an apparent average soil moisture threshold in R_{tot} . R_{tot} ranged from 0.07 to 0.17 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ over the growing season in the drier *Sphagnum*-dominated lawns and depressions and drier feather moss lawns, and was half (0.04–0.07) in the cooler and wetter feather moss depressions (Figure 4), which was great enough to produce a quadratic relationship with R_{tot} (Figure 5b). Little difference was observed between lawn and depression sites in open areas with *Sphagnum*, with peak R_{tot} occurring at soil moisture values of 15%. However, the soil moisture conditions observed during the study were mostly below peak rates and may have resulted in reducing the temperature— R_{tot} slope. VMC conditions showed a much greater range in closed canopy sites, where feather moss dominated the surface cover. Feather moss lawns had R_{tot} peaks near 40%, whereas the R_{tot} peak was slightly lower in the feather moss depressions, occurring near VMCs of 60% (Figure 5b). Thus, the interaction of increased rates with temperature and reduced rates with soil moisture in *Sphagnum* sites resulted in similar R_{tot} rates across the peatland, with the exception of the feather moss depression sites.

More scatter is observed for GEP and PAR when all lawn and all depression sites are grouped (Figure 6a). When partitioned among *Sphagnum* and feather moss lawns and depressions clearer distinctions between microtopographical and bryophyte units are observed (Figure 6b and c). Maximum GEP at similar PAR levels are more than double for *Sphagnum* lawns (0.22 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than depressions (0.08 $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Figure 6b). However, no significant increase in GEP is observed between the feather moss lawn and depression sites (Figure 6c). That is, feather moss lawns are associated with much lower PAR values. This difference in GEP observed between microtopography and vegetation cover sites shows that maximum GEP in this landscape is occurring on *Sphagnum* lawns, which also show the strongest correlation between PAR and GEP ($r^2 = 0.61$) and that the apparently poor correlation on feather moss lawns ($r^2 = 0.12$) is apparently a result of the much narrower range in PAR (Figure 6c).

DISCUSSION

The average range in summer daytime NEE for the 2 years was -0.12 to $0.05 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which lies within the range reported by other studies (Waddington and Roulet, 1996; Bubier *et al.*, 1998; Lafleur, 1999), although these studies were conducted in areas where soil moisture and temperatures differed from the current study region. Furthermore, studies that have examined inter-annual NEE variability have observed that there can be large differences in carbon exchange from year to year (Shurpali *et al.*, 1995; Lafleur *et al.*, 1997; Griffis *et al.*, 2000), although large differences were not observed among years in this study.

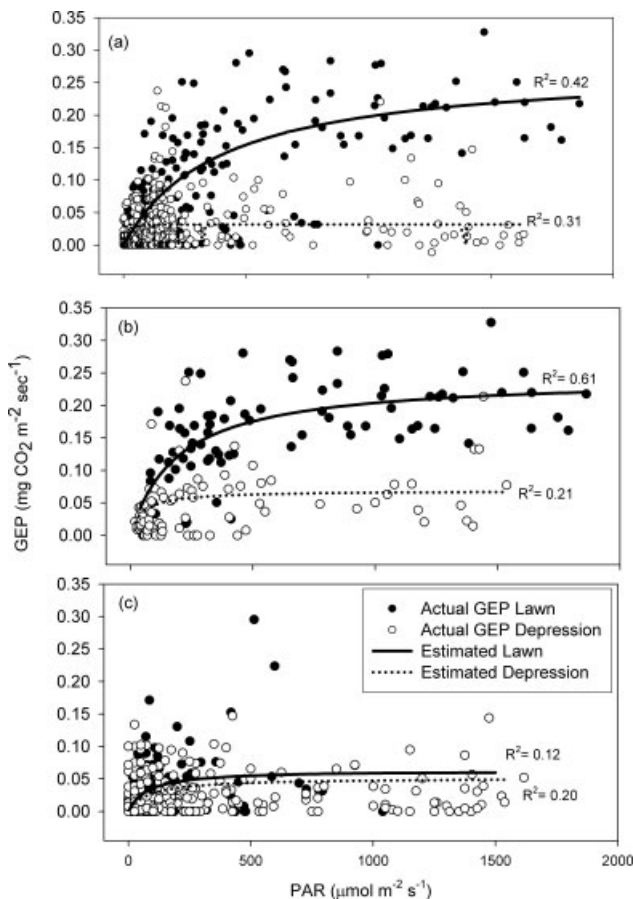


Figure 6. Relationships between average GEP and PAR for combined data of 2005 and 2006 data for (a) all lawns and depressions, (b) *Sphagnum* (lawns and depressions) and (c) feather moss (lawns and depressions). Curve fits for GEP versus PAR were calculated with a rectangular hyperbola model from Equation (3), URSA, Alberta, Canada.

Microtopographic and vegetation controls on carbon dynamics

Studies in more humid climates such as those found in Sweden, eastern Canada (Quebec), and northern USA (Minnesota) have shown significant differences between lawn (hummock) and depression (hollow) CO₂ exchange (Kim and Verma, 1992; Waddington and Roulet, 1996; Strack *et al.*, 2006) and have attributed this to differences in water table position and near surface temperatures (Kim and Verma, 1992; Waddington and Roulet, 1996), whereas others have also linked this variability to different vegetation communities between microtopographic units (Strack *et al.*, 2006). Although microtopographic units are present within peatlands in the WBP, differences between these units are less pronounced than has been shown in more humid peatlands.

In more humid regions, strong hydrologic gradients have been observed between dry, aerobic topographic highs and saturated, anoxic topographic lows. For example, the depressions in a Swedish peatland described in Waddington and Roulet (1996) were generally saturated. In contrast, in this study, the depressions had an average VMC of 65% and were rarely saturated. In addition, depression sites in this study had higher bulk densities and therefore higher water holding capacities.

In the *Sphagnum*-dominated sites, this may reflect the need for a tighter growth form (smaller pore space) to maintain hydrologic connectivity around non-*Sphagnum* shoots (Luken and Billings, 1985; Bauer *et al.*, 2007). This suggests that higher bulk densities in depressions here are a result of an increased need to maintain hydrological connectivity that resembles the lawn sites due to their distance from the water table, whereas in more humid peatlands, the bulk densities of the lawns tend to be larger as the depressions are located closer to the water table.

The topographically driven hydrologic gradients in humid peatlands with larger moisture gradients tend to also drive distinct vegetation differences (Moore, 1989; Vitt, 1990; Strack *et al.*, 2006), which have been documented to subsequently alter CO₂ dynamics (Botting and Fredeen, 2006; Strack *et al.*, 2006). Although small differences in moisture and temperature were observed between lawn and depression microtopographic units in the WBP peatlands, there was little to no variation in the vegetation patterns in the lawns and depressions. It is likely that the small hydrologic gradients present are not great enough to lead to change in vegetation communities.

Spatial variability in carbon dynamics across a peatland have previously been related to microtopography (Waddington and Roulet, 1996; Moore, 1989; Strack and Waddington, 2007), variation in vegetation (Heijmans *et al.*, 2001; Botting and Fredeen, 2006) and canopy coverage (Swanson and Flanagan, 2001). The variability of CO₂ exchange observed within this riparian peatland is not uncommon for northern forested wetland complexes. However, CO₂ exchange for sites with microtopographical differences but little variation in the composition of the vegetation, as observed here, has not been well documented.

The reduced hydrologic gradients and lack of difference in vegetation cover between microtopographic units has produced more complex CO₂ exchange relationships in peatlands in the WBP. Differences in NEE (0.08 to -0.05 mg CO₂ m⁻² s⁻¹) among microtopographical units (lawns and depressions), although statistically significant, were small relative to differences observed in many other studies, although Bubier *et al.* (2003) observed similar NEE for lawns and depressions at a site in Ottawa, Canada. Overall, GEP was lower and R_{tot} was larger in magnitude at this sub-humid site than has been observed in more humid regions (Kim and Verma, 1992; Waddington and Roulet, 1996; Strack *et al.*, 2006). Differences were observed in R_{tot} between microtopographic units but not between different types of vegetation cover. In contrast, differences in GEP were observed between vegetation types and between microtopography within the *Sphagnum* site, but differences were not observed between microtopographic units at the feather moss sites. Because NEE is a function of GEP and R_{tot} , both vegetation type and microtopography were found to be important for NEE in peatlands in the WBP. Thus, although spatial differences within this landscape

are less pronounced than has been observed between microtopographic units or vegetation types in other landscapes, neither of these variables can be used as a proxy to delineate spatial patterns in carbon exchange processes due to the complexity of the landscape and the small hydrologic gradients within the sub-humid peatlands in the WBP.

Microclimate and canopy cover

Previous studies have also shown that temporal variability in GEP is strongly related to PAR and that R_{tot} is coupled to soil and air temperatures (Waddington and Roulet, 1996; Bubier *et al.*, 1998; Law *et al.*, 2002; Botting and Fredeen, 2006). The scatter in the GEP-PAR model for this study is typical of that found in other studies (Bubier *et al.*, 1998; Lafleur, 1999), which is often attributed to limiting environmental conditions (e.g. high temperature or vapour deficit) (Lafleur, 1999) and differential timing of snowmelt and thaw (Bubier *et al.*, 1998). The fluxes here appeared to vary according to microtopography (Figure 6b) with larger maximum fluxes from the lawns. However, partitioning these data into the dominant ground cover vegetation communities shows that *Sphagnum* lawns (Figure 6a) had three times higher A_{max} than *Sphagnum* depressions and both feather moss groups. This suggests that *Sphagnum* are better suited for more moderate moisture conditions (Figure 6b) and usually grows in less dense portions of black spruce forests (i.e. lower degrees of canopy closure), whereas feather mosses do not show a strong dependence on moisture and are in higher abundance areas where tree density is higher (i.e. higher degree of canopy closure) (Gignac, 1992; Brisbee *et al.*, 2001). Therefore, higher PAR (Table II) in *Sphagnum*-dominated areas also favours enhanced GEP.

The lowest R_{tot} was observed in the feather moss depressions, where the Bulk Density and VMC were the largest (Table II), suggesting that a high water holding capacity of the feather moss at this site may be causing anoxic conditions to occur. However, the feather moss lawns had similar BD but the highest R_{tot} for both feather moss and *Sphagnum* microtopographical units (Table II, Figure 4). This suggests that while the topographically high feather moss lawns had the potential to hold water they were unable to draw water up, likely permitting the lawns to maintain an optimal VMC for decomposition, in addition to have warmer temperatures than the depressions. However, as PAR values were similar, there was little difference observed in GEP between feather moss lawns and depressions. In addition, PAR values were similar between *Sphagnum* sites. This suggests that the difference in temperature related to the degree of canopy closure between *Sphagnum* microtopographical units drove the differences GEP.

Seasonal interactions between ecohydrological controls and CO₂ exchange

Although this study examined point CO₂ measurements, it has been observed that CO₂ fluxes vary diurnally and longer (e.g. with precipitation events) (Kim and

Verma, 1992; Suyker *et al.*, 1997; Xu *et al.*, 2004). Given that this study focused on midday CO₂ exchange, the importance of GEP may be over estimated. For example, it has been observed that GEP exhibits a midmorning maximum (Shurpali *et al.*, 1995; Suyker *et al.*, 1997) and can be highly variable on diurnal timescales (Griffis *et al.*, 2000), whereas, total respiration generally peaks midday and the ecosystem continues to respire throughout the night (Jarvis *et al.*, 1997). Therefore, it is likely that total respiration in this peatland–pond complex is higher when examining the exchange for the entire day, and GEP may be over estimated if extrapolated for the entire day.

The NEE from lawns and depressions exhibited marked seasonal variations (Figure 4). When the study began, there was no snow present but the peatland still had a shallow frost depth. Thus, sites were only slowly fixing CO₂ from the beginning of this study, whereas cool soil temperatures resulted in the lower GEP and R_{tot} measured during the EG. This is similar to Bubier *et al.* (1998), who found a peatland in northern Manitoba fixed CO₂ as soon as the top 5 cm of peat warmed above 0°C. During the middle of the growing season, maximum R_{tot} and GEP values were observed in both lawns and depressions, when deepening of the active soil layer from higher air temperatures was likely increasing decomposition, resulting in higher R_{tot} . In addition, during this period, light levels were high, soil conditions were warm and moist, and LAI was large, all of which favoured GEP. The CO₂ flux then declined with decreasing temperatures at the end of the growing season as soils cooled and plants began to senesce.

Implications for climate or land use change

The WBP is a region where these wetlands already exist in a moisture deficit. Thus, these systems are already at a hydrological risk, which has implications for the C sink status. It is well documented that soil respiration rates correlate significantly with mean annual air temperatures and precipitation (Raich and Schlesinger, 1992; Xu *et al.*, 2004) and as such soil T, θ and water table (Alm *et al.*, 1999; Smith *et al.*, 2004; Dunn *et al.*, 2007). Thus, in any region, small changes to the climate or the landscape (e.g. removal of canopy cover) may increase the rates of soil respiration (Davidson and Janssens, 2006). Consequently, as it is anticipated that climate change is going to be most pronounced in areas, a further increase in temperature and decrease in precipitation may drive the study site to be a larger source of CO₂ to the atmosphere.

Industrial pressures will play a significant role in altering the CO₂ biogeochemical cycles within these areas. Corridor creation to access prime regions for the extraction of timber and oil and gas exploration may cause enhanced aerobic soil respiration due to the lowering of water tables and higher peat temperatures due to canopy removal (Devito *et al.*, 2005; Petrone *et al.*, 2005) causing a release in stored carbon to the atmosphere. As a result of their hydrological connections, alterations to the upland and riparian areas (e.g. forest harvesting)

may also impact the peatlands. Thus, drying peatlands to below 20% VMC or wetting above 60% VMC may decrease R_{tot} as both the bryophyte communities optimally respire in this VMC range (Figure 5) (Alm *et al.*, 1999; Smith *et al.*, 2004). In addition, increased warming could influence the depth to frozen soil, decrease the water table and extend thawed conditions therefore exposing larger amounts of organic carbon to microbial activity for longer periods of time (Goulden *et al.*, 1997; Schuur *et al.*, 2008). Currently, however, it is difficult to conclude with confidence how these climate changes will immediately affect the NEE of CO₂ exchange at high latitudes due to the uncertainty surrounding changes in evaporation rates, active layer deepening, water balance, water table elevation and soil moisture content (Griffis *et al.*, 2000). Furthermore, there is still some debate as to the deviation of enhanced decomposition rates in these systems, which it is suggested will be a strong function of soil nutrient status and variations in higher quality organic material in the peat profile (Christensen *et al.*, 1999; Pendall *et al.*, 2004; Davidson and Janssens, 2006; Bardgett *et al.*, 2008; Bronson and Gower, 2010). Therefore, studies such as this are important as they allow for the development of predictive relationships among photosynthesis, respiration and the environmental controls on these processes, which help to improve the understanding and modelling of peatland–pond complex CO₂ exchange in a range of boreal wetland systems that span all the climatic zones of the boreal region.

CONCLUSION

Midday growing season ecosystem CO₂ exchange, hydrology and microclimate data suggest that in a sub-humid environment like the WBP, moisture differences (gradients) between microtopographical highs and lows are reduced compared with other environments wetter conditions and larger gradients (i.e. saturated conditions or standing water in depressions). This results in moisture gradients with microtopography that are not significant enough to result in differences in vegetation distribution, but are large enough to cause differences in the level of productivity within a species when incorporated with changes in microclimate (especially radiation receipt) as a result of canopy closure. Thus, the variability observed in CO₂ exchange between microtopography and similar vegetation communities demonstrates that vegetation communities or microtopographic units alone cannot be used as a proxy for CO₂ exchange and that the two must be considered together.

In addition, the water holding capacities in depressions of the WBP are different than those observed in more humid peatlands, suggesting that these peatlands may not react the same to climatic and environmental changes and that peatlands located in a moisture deficit ecozone with considerable microtopography and different vegetation communities should not be lumped together as one component of a boreal forest ecosystem.

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