Summer carbon dioxide and water vapor fluxes across a range of northern peatlands

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[1]   Northern peatlands are a diverse group of ecosystems varying along a continuum of hydrological, chemical, and vegetation gradients. These ecosystems contain about one third of the global soil carbon pool, but it is uncertain how carbon and water cycling processes and response to climate change differ among peatland types. This study examines midsummer CO_2 and H_2O fluxes measured using the eddy covariance technique above seven northern peatlands including a low-shrub bog, two open poor fens, two wooded moderately rich fens, and two open extreme-rich fens. Gross ecosystem production and ecosystem respiration correlated positively with vegetation indices and with each other. Consequently, 24-hour net ecosystem CO_2 exchange was similar among most of the sites (an average net carbon sink of 1.5 ± 0.2 g C m^{-2} d^{-1}) despite large differences in water table depth, water chemistry, and plant communities. Evapotranspiration was primarily radiatively driven at all sites but a decline in surface conductance with increasing water vapor deficit indicated physiological restrictions to transpiration, particularly at the peatlands with woody vegetation and less at the peatlands with 100% *Sphagnum* cover. Despite these differences, midday evapotranspiration ranged only from 0.21 to 0.34 mm h^{-1} owing to compensation among the factors controlling evapotranspiration. Water use efficiency varied among sites primarily as a result of differences in productivity and plant functional type. Although peatland classification includes a great variety of ecosystem characteristics, peatland type may not be an effective way to predict the magnitude and characteristics of midsummer CO_2 and water vapor exchanges.

1.   Introduction

[2]   Peatlands are a diverse set of wetland ecosystems that have accumulated at least 30–40 cm of partially decomposed organic material over the past millennia [*Zoltai and Vitt*, 1995]. Northern peatlands occupy only 3% of the land surface but contain 250–455 Pg carbon (C), about one third of the total global soil C pool [*Gorham*, 1991]. Classification of peatlands is generally made along hydrological and chemical gradients, resulting in a continuum of peatland types, varying from ombrotrophic bogs to poor fens to nutrient rich fens [*Zoltai and Vitt*, 1995]. Considerable variations in vegetation structure and species composition exist among and within each peatland type ranging from acidic *Sphagnum*-dominated bogs to alkaline brown moss-dominated fens with sedge, shrub, tree, or no vascular overstory [*Vitt*, 2000]. These differences in moisture, chemistry, and vegetation across peatland types are potentially important for ecosystem function, such as the net ecosystem exchange of CO_2 (NEE) and evapotranspiration (ET), and their response to climate.

[3]   Despite the low productivity of peatlands, historically peat has accumulated at a rate of 20–30 g C m^{-2} yr^{-1} [*Gorham*, 1991] as a result of the slow decomposition of decay-resistant plant material in cool, saturated conditions. Bryophytes make up the major component of accumulated peat and although the composition and structure of peatland vegetation may vary widely, peatlands generally have a ground layer of moss species covering 90–100% of the surface [*Vitt*, 2000]. This moss layer is often the most productive plant type within a peatland and its growth tends to vary more between years as a result of variations in climate than it does among different peatland types [*Szumigalski and Bayley*, 1997; *Thormann and Bayley*, 1997]. A survey of continental peatlands in western Canada also found that bogs and fens did not have significant differences in peat depth [*Vitt*, 2000]. *Vitt* [2000] suggested that the moss layer effectively controls nutrient movement

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and total plant production thereby minimizing differences in the long-term C accumulation among peatland types. In contrast, however, *Thormann et al.* [1999] found peat depth along a bog-fen-marsh gradient in southern boreal Alberta to increase with deeper water tables, lower pH, and greater moss and woody shrub production. Studies of annual aboveground net primary production (NPP) of peatlands of western Canada give conflicting results including no observed difference in NPP of bogs and fens [*Thormann and Bayley*, 1997; *Campbell et al.*, 2000] and greater NPP at a fen than at a bog [*Szumigalski and Bayley*, 1997; *Thormann and Bayley*, 1997].

[4] Variations in atmosphere-peatland CO_2 exchange among peatland types or within peatland complexes have been investigated primarily by chamber techniques. Soil CO_2 emissions in Finnish mires varied significantly among peatlands of different trophic status and among drained and undrained sites [*Silvola et al.*, 1996]. NEE has been found to vary among the various plant communities within peatland complexes [e.g., *Waddington and Roulet*, 1996; *Bubier et al.*, 1999, 2003] and among peatland types along a trophic gradient [*Bubier et al.*, 1998]. Controlled studies that varied the environmental and nutrient conditions within a peatland type have also had mixed results. Fertilization occasionally results in shifts in the species composition and enhanced aboveground NPP [*Chapin et al.*, 2004], but does not necessarily affect CO_2 fluxes [*Keller et al.*, 2005]. Experimentally drained peatlands and wet sedge tundra became C sources while control plots remained C sinks [*Silvola et al.*, 1996; *Oechel et al.*, 1998]. While such studies are useful for examining C exchange processes, they are difficult to extrapolate to the whole peatland (or ecosystem) scale.

[5] Micrometeorological techniques, such as eddy covariance, provide measurements of whole ecosystem CO_2 exchange and are most often used to examine variations in NEE at a single peatland within a growing season or between years. Previous studies using these methods have shown the importance of light, temperature, and water table depth on NEE [e.g., *Shurpali et al.*, 1995; *Lafleur et al.*, 1997, 2001; *Arneth et al.*, 2002; *Aurela et al.*, 2002; *Lafleur et al.*, 2003; *Aurela et al.*, 2004]. In two subarctic fen studies, the timing of spring thaw and growing season length were important factors influencing the annual C sink strength of these peatlands [*Griffis et al.*, 2000; *Aurela et al.*, 2004]. Most studies show that during the growing season peatlands are net sinks for CO_2. The exception being that warm and dry growing seasons greatly reduce the peatland sink strength and in some cases lead to net CO_2 losses [*Bubier et al.*, 2003; *Lafleur et al.*, 2003]. While no previous micrometeorological studies were designed to directly compare CO_2 exchange across a range of peatland types, *Frolking et al.* [1998] showed that the light response curve for NEE differed between bogs and fens, and that all peatlands as a group could be differentiated from forests, grasslands, and crops. However, it is anticipated that the large variability in hydrological characteristics, water chemistry, and species composition among peatlands should lead to significant differences in whole ecosystem CO_2 exchange.

[6] The studies noted above often emphasized a strong link between peatland hydrology and NEE. The position of the water table determines the layer of peat available for aerobic respiration, the soil thermal regime, the water available for capillary uptake by moss and transpiration imposed by vascular vegetation, and consequently rates of photosynthesis. Climate models predict increased ET with climate warming leading to lower water tables at many northern latitudes [*Intergovernmental Panel on Climate Change*, 2001]. Despite an abundance of water and non-vascular vegetation, ET in peatlands is generally less than open water ET as a result of physiological limitations to transpiration by the vascular vegetation [*Lafleur et al.*, 1997; *Kellner*, 2001]. Moss surface conductance to water vapor transfer has also been found to vary with moss water content [*Williams and Flanagan*, 1996]. In addition, the plant canopy and litter above the moss layer restricts energy exchange and turbulent transfer of water vapor between the moist peat and the air above, further inhibiting evaporation in many peatlands [*Campbell and Williamson*, 1997]. In peatlands with an abundance of vascular plants, there is evidence that ET is strongly controlled by surface (stomatal) conductance. By contrast, ET is more strongly controlled by the amount of solar radiation in moss-dominated peatlands [*Kurbatova et al.*, 2002]. However, the response of ET and water use efficiency to varying environmental conditions across peatland types with different water table depths is still not clear.

[7] To assess how CO_2 and water vapor exchange processes differ among northern peatlands, fluxes of CO_2 and water vapor were measured at seven peatlands in Canada: two from the Great Lakes–St. Lawrence forest region in eastern Ontario, two from the boreal forest region in Saskatchewan, and three from the boreal forest region in Alberta. These sites are part of the Fluxnet Canada Research Network. All the peatlands in this study have vascular plant canopies with a moss/water substrate and peat soils from 1 to 5 m in depth. Using a common classification based largely on hydrology, chemistry, and dominant vegetation and moss species [*Vitt*, 2000], the range of peatlands included an ombrotrophic, low-shrub bog, two open poor fens, two wooded moderately rich fens, and two open extreme-rich fens. At each site, the eddy covariance method was used to provide in situ measurements of NEE that have the potential to be continuous in time and represent a relatively large area (typically 1000 to 10,000 m²). Ecosystem respiration (ER) and gross primary production (GEP) were derived from the eddy covariance data and allowed us to explore the major flows of C between the atmosphere and ecosystem. The analysis period was limited to July and August 2004 in order to minimize the effects of climate and growing season length on C and water exchange processes. The objectives of this study were to (1) quantify midsummer CO_2 and water vapor fluxes in the seven different peatlands, (2) identify and compare the environmental and physiological factors that influence these fluxes, and (3) explore the link between these two important mass exchanges.

2. Methods

2.1. Site Descriptions

[8] The locations and general characteristics of the seven peatlands in this study are described in Tables 1 and 2. The most southerly peatlands are the ombrotrophic low-shrub

Table 1. Peatland Characteristics

	ON-B	ON-PF	AB-PF	AB-WF	SK-WF	AB-RF	SK-RF
Peatland classification	low-shrub bog	open poor fen	open poor fen	wooded moderately-rich fen	wooded moderately-rich fen	open extreme-rich fen	open extreme-rich fen
Location and nearest community	45°25'N, 75°31'W Ottawa, ON	45°25'N, 75°31'W Ottawa, ON	55°54'N, 112°33'W Lac La Biche, AB	54°57'N, 112°28'W Lac La Biche, AB	53°57'N, 105°57'W Prince Albert, SK	54°47' N, 113°32'W Athabasca, AB	53°57'N, 105°57'W Prince Albert, SK
Elevation, m	70	70	730	540	525	670	525
Average annual temperature,[a] °C	5.8	5.8	2.1	2.1	0.4	2.1	0.4
Average annual precipitation,[a] mm	910	910	504	504	467	504	467
Measured (30-year average) July–Aug air temperature,[a] °C	18.4 (20.2)	18.4 (20.2)	13.3 (15.7)	14.5 (15.7)	14.4 (15.5)	14.8 (15.7)	14.3 (15.5)
Measured (30-year average) July–Aug precipitation,[a] mm	222 (178)	222 (178)	205 (167)	182 (167)	231 (140)	229 (167)	270 (140)
Measured mean (min, max) July–Aug water table depth, cm	−37(−46, −32)	−16(−28, −7)	−29(−36, −24)	−29(−36, −22)	−3(−9, +6)	−18(−28, −11)	+4(−4, +16)
Depth of peat, m	5	1.5	>3	2	3	2	2
pH	3.9[b]	4.5[b]	4.0	6.2	7.5[c]	6.5	8.1[d]
NH$_4$ in pore water, µg L^{-1} (in peat, µg/g)	310[e] (2.1)[f]	n/a	48 (n/a)	48 (n/a)	n/a (705)[c]	423 (n/a)	n/a (963)[c]
NO$_3$ in pore water, µg L^{-1} (in peat, µg/g)	30[e] (3.6)[f]	n/a	5 (n/a)	5 (n/a)	n/a (50)[c]	30 (n/a)	n/a (89)[c]
Total P in pore water, µg L^{-1} (in peat, µg/g)	n/a (0.7)[f]	n/a	19 (n/a)	630 (n/a)	n/a (234)[c]	488 (n/a)	n/a (430)[c]

[a]Thirty-year climate normals published for nearest Environment Canada weather stations (Ottawa Macdonald-Cartier International Airport, ON, Waskesiu Lake, SK, and Athabasca, AB).
[b]*Bubier et al.* [2003].
[c]I. Bauer and R. Errington (unpublished data, 2005).
[d]Surface pH for BOREAS TE-1 SSA-Fen from the BOREAS CD-ROM Set, March 2000.
[e]J. Rattle (unpublished data, 2005).
[f]*Basiliko et al.* [2006].

Table 2. Characteristics of Peatland Vegetation

	Aboveground Live Biomass, g dry weight m^{-2}	LAI (Vascular Plants)	Approx. Average Height of Overstory Species, m	Tree Density, trees/ha	Percent Moss Cover	Typical Vegetation				
						Trees	Shrubs	Herbs	Sedges	Moss
ON-B	587[a]	2.36[b]	0.3	negligible	100	negligible	Chamaedaphne calyculata, Kalmia angustifolia, Ledum groenlandicum, Vaccinium myrtilloides, Vaccinium oxycoccos	Maianthemum trifolium	Eriophorum vaginatum	Sphagnum spp.
ON-PF	317[a]	1.84[b]	0.3	negligible	100	negligible	Chamaedaphne calyculata, Kalmia angustifolia, Andromeda glaucophylla	negligible	Carex oligosperma	Sphagnum spp.
AB-PF[c]	320	0.52	0.3	0	100	none	Andromeda polifolia Betula pumila	Maianthemum trifolium	Carex limosa	Sphagnum spp.
AB-WF[d]	863	1.76	3.4	1500	85	Picea mariana, Larix laricina		Menyanthese trifoliata, Maianthemum trifolium, Potentilla palustris, Oxycoccus microcarpus	Carex spp.	Sphagnum spp., Drepanocladus spp., Calliergon spp., Aulacomnium palustre, Pleurozium schreberi
SK-WF[e]	842	n/a	4.8	2000	50	Picea mariana, Larix. laricina	Betula pumila, Salix spp., Andromeda polifolia	negligible	Carex spp.	Aulacomnium palustre, Campylium stellatum, Hematocaulis vernicosus
AB-RF[c]	140	0.43	0.3	0	66	none	Salix spp.	negligible	Carex lasiocarpa	Drepanocladus spp.
SK-RF[f]	275[e]	n/a	n/a	negligible	50	negligible	Salix spp. Betula pumila	Menyanthese trifoliata	Carex spp., Eriophorum spp.	Drepanocladus spp., Calliergon spp.

[a] Moore et al. [2002].
[b] Measured using 250 vertical point intercepts July 2005.
[c] Glenn et al. [2006].
[d] Syed et al. [2006].
[e] All information approximated using FEN transect locations 4 and 6 described by Bhatti et al. [2006].
[f] All information from Suyker and Verma [1997] unless otherwise noted.

Table 3. Characteristics of the Eddy Covariance Flux Measurement Systems and Analysis

	ON-B	ON-PF	AB-PF	AB-WF	SK-WF	AB-RF	SK-RF
EC height, m	3	3	3	10	12	3	2
Sonic anemometer and IRGA	Gill R3, LI7000 (closed-path)	Gill R3, LI6262 (closed-path)	Roving CSAT3, LI7500 (open-path)	Gill R3, LI7000 (closed-path)	CSAT3, LI7500 (open-path)	Roving CSAT3, LI7500 (open-path)	CSAT3, LI7500 (open-path)
Measurement frequency, Hz	20	8	10	20	10	10	20
Threshold friction velocity, m s^{-1}	0.09	0. 09	0. 09	0.16	0.17	0. 09	0.09
Number of Observations[a]	2079 (98%, 28%)	612 (28% 9%)	926 (48%, 13%)	1924 (90%, 23%)	1764 (80%,20%)	550 (25%,7%)	815 (37%,12%)

[a]Number of observations indicates the number of half hours with flux data for 1 July to 31 Aug 2004 meeting quality control criteria with the % of total possible daytime and nighttime half hours in parentheses.

bog (ON-B) and an open poor fen dominated by sedges and low shrubs (ON-PF), both part of a 2800 ha peatland complex in eastern Ontario. Measurements at ON-B began in June 1998 and have resulted in a number of studies on hydrology and C exchange processes [e.g., *Fraser et al.*, 2001; *Bubier et al.*, 2003; *Lafleur et al.*, 2003].

[9] In central Saskatchewan, measurements were made in an open extreme-rich fen dominated by sedge and birch shrubs (SK-RF) and a wooded moderately rich fen (SK-WF), both part of a larger patterned fen complex surrounded by boreal black spruce and jack pine forests. Previous CO$_2$ flux measurements in the open part of the fen were carried out as part of the BOREAS project in 1994 [*Suyker and Verma*, 1997].

[10] Three fens in Alberta were selected to represent the most common peatland types in western Canada including an open moss-dominated poor fen (AB-PF), a wooded moderately rich fen (AB-WF), and an open sedge-dominated extreme-rich fen (AB-RF). Micrometeorological measurements were recently established in 2003 and 2004. Recent studies at these sites include those by *Syed et al.* [2006] and *Glenn et al.* [2006].

2.2. Eddy Covariance Measurements

[11] The eddy covariance (EC) technique was used to measure 30-min fluxes of CO$_2$ (F_c, μmol m^{-2} s^{-1}), latent heat (λE, W m^{-2}), and sensible heat (H, W m^{-2}). The eddy covariance instrumentation at each peatland included a sonic anemometer-thermometer and infrared gas analyzer (IRGA) (Table 3). The sonic anemometer-thermometers measured high frequency wind velocity in three coordinates (u, v, and w) and temperature (T_{sonic}). High-frequency air temperature was derived from T_{sonic} following *Aubinet et al.* [2000]. Closed-path IRGAs were used at ON-B and AB-WF and measured high frequency fluctuations of CO$_2$ and H$_2$O mole fractions. The other sites were outfitted with open-path IRGAs that measured CO$_2$ and H$_2$O molar densities (ρ_c and ρ_v, mmol m^{-3}, respectively). Three-axis coordinate rotations were used to align the streamlines with the surface of each peatland resulting in zero mean w, v and covariance of v and w [*Tanner and Thurtell*, 1969]. Fluxes were computed using the 30-min covariance of vertical wind speed (w) and the appropriate scalar entity as described by *Chen* [1999]. The effects of fluctuations in air density on F_c and λE were accounted for by converting mole fractions to mole mixing ratios (s_c, μmol mol^{-1} dry air and s_v, mmol mol^{-1} dry air) in

the covariance calculations when closed-path IRGAs were used. When open-path IRGAs were used, the WPL procedure was applied to F_c and λE [*Webb et al.*, 1980]. Evapotranspiration (ET, mm) was derived from λE. NEE was calculated as the sum of F_c and the change in CO$_2$ stored beneath the height of the EC instrumentation. Positive NEE indicates a loss of CO$_2$ from the peatland surface.

[12] Measurements of NEE and ET were made continuously for the 2-month study period at only ON-B, AB-WF, and SK-WF. A single set of sensors was moved every 2 weeks between AB-PF and AB-RF to measure fluxes of CO$_2$ and water vapor. Flux measurements at ON-PF and SK-RF were also intermittent owing to power and instrumentation problems. Nighttime measurements of NEE were discarded at all sites when values were less than zero (indicating net CO$_2$ uptake) or during calm conditions. Friction velocity (u_*, m s^{-1}) was derived from sonic anemometer measurements and used to designate calm versus turbulent conditions with respect to a threshold u_* value. Thresholds were identified as the value above which nighttime NEE no longer changed with increasing u_*. Using only the July and August data, a clear threshold value of 0.16 m s^{-1} was found for AB-WF and 0.17 m s^{-1} for SK-WF, the two aerodynamically rough sites dominated by trees. A distinct threshold value of 0.09 m s^{-1} was also found for ON-B. Partly owing to having fewer measurements (Table 3), results for the remaining sites were ambiguous so threshold values were also assumed to be 0.09 m s^{-1}. This is reasonable given that all these sites are dominated by short vegetation and are relatively smooth aerodynamically. The remaining nighttime measurements of NEE were kept if they fell within 3 standard deviations of the mean nighttime NEE. Daytime NEE outliers were also removed using these criteria, although standard deviations were computed for a 5-day running mean. Outliers in daytime and nighttime λE were determined using a similar procedure on a 30-day time period. In addition, λE were also rejected for half hours without valid NEE measurements. Table 3 indicates the total number of half hours with high-quality flux measurements available for analysis. The sites with roving towers and/or less reliable power systems had only 25 to 50% of the data coverage of the permanent installations with AC power. As with most eddy covariance studies [*Baldocchi*, 2003], there was approximately 3 to 4 times more good quality daytime NEE than nighttime NEE

measurements (Table 3). The impact of these differences in data coverage will be discussed.

2.3. Supporting Measurements

[13] Weather and other energy budget terms were measured continuously at each site every 2 to 10 s and averaged for 30-min intervals. Radiation variables included net radiation, component radiation fluxes (shortwave up and down, longwave up and down), and photosynthetically active radiation, PAR. Air temperature (T_{air}) and relative humidity were measured above the canopies near the height of the EC instrumentation and used to compute vapor pressure deficit (D). The temperature of the peat (T_{soil}) was measured 5 cm below the surface at a hummock and hollow location at all but the SK-WF and ON-PF sites where there was only a single 5-cm T_{soil} measurement. For those sites with two measurements, an average 5 cm T_{soil} was computed. In addition, the percent coverage of hummocks (70%) and hollows (30%) [*Lafleur et al.*, 2001] was used to weight the two T_{soil} measurements at ON-B. Depth of the water table (WTD) with respect to the average peat hummock was measured within wells using either a float and counterweight system attached to a potentiometer (ON and AB sites) or by means of sensitive vibrating- wire pressure transducers referenced to the peat surface (SK sites). The average height difference of microtopographical features was 25 cm at ON-B [*Lafleur et al.*, 2001], 6 cm at SK-WF and SK-RF [*Suyker and Verma*, 1997], and visually estimated from photographs to be 10 cm or less for the remaining sites.

2.4. Analysis

[14] NEE is the difference between CO$_2$ uptake through photosynthesis (gross ecosystem production, GEP) and CO$_2$ loss through respiration and decomposition (ecosystem respiration, ER). Variations in half-hour NEE can largely be described using the following function:

$$\text{NEE} = -\frac{\alpha \cdot \text{PAR} \cdot A_{\max}}{\alpha \cdot \text{PAR} + A_{\max}} + R_{10} \cdot Q_{10}^{(T-T_{\text{ref}})/10} \quad (1)$$

The first term on the right hand side of equation (1) describes the rectangular hyperbolic relationship between GEP and PAR where negative GEP indicates CO$_2$ uptake by the ecosystem and the second term describes the exponential relationship between ER and temperature (T) where positive ER indicates CO$_2$ loss by the ecosystem. $A_{\max}$ is the maximum photosynthetic uptake of CO$_2$ for unlimiting PAR while α is the effective quantum yield. R_{10} is ER at a reference temperature of 10°C (T_{ref}) and Q_{10} is the relative increase in ER for a 10°C increase in temperature. We used T_{air} in equation (1) so that the differences in source areas of respired CO$_2$ and in understory microclimate might be identified among these peatlands. The first three parameters of this nonlinear regression function were determined using least squares estimation by way of the Gauss-Newton algorithm with Levenberg-Marquardt modifications for global convergence [*MathWorks Inc.*, 2004]. Owing to the limited variations in nighttime T_{air} over a 2-month period, equation (1) was fit with only daytime measurements of NEE and Q_{10} values constrained to ±35% of 2.0. The chosen Q_{10} value was associated with the highest coefficient

of determination, R^2. The 95% confidence intervals for the estimates of $A_{\max}$, α, and R_{10} were used to determine significant differences among sites.

[15] Daytime estimates of ER were derived using the second term of equation (1) for periods when NEE was available. GEP was then computed as the difference between NEE and ER. To estimate daily NEE, GEP, ER, and ET for the 2-month period, available measurements were grouped by hour of the day, averaged, and then summed. The uncertainty in these daily estimates (e.g., $\Delta\text{NEE}_{\text{daily}}$) was computed by propagation of errors using the standard error of the mean for each hour (ΔNEE_i). For example,

$$\Delta\text{NEE}_{\text{daily}} = \sqrt{\sum_i^{24} \Delta\text{NEE}_i^2}.$$ Differences among sites were

significant when the 95% confidence limits (e.g., $\text{NEE}_{\text{daily}} \pm 1.96\Delta\text{NEE}_{\text{daily}}$) did not overlap.

[16] As expected, greater data coverage tended to improve the precision of a number of variables and model parameters resulting in smaller confidence intervals (CI) and standard errors (SE). The influence of data coverage on daily estimates of NEE was further investigated using a resampling exercise where a proportion of the largest data set (2079 half hours at ON-B) was randomly selected without replacement 1000 times, keeping the relative proportion of nighttime to daytime data constant, and used to recompute 1000 average daily NEE values and associated 95% CI. The average of these 1000 estimates of daily NEE did not change while the precision of the estimate decreased (CI increased) as data was removed. Daily average NEE for the full ON-B data set was −1.14 g C m^{-2} d^{-1} with a 95% CI of −1.03 to −1.25 g C m^{-2} d^{-1}. None of the 1000 resampled estimates of NEE were significantly different from this estimate until 20% or less of the original data was available. A similar analysis for AB-WF (1924 half hours) only found significant differences between the resampled estimates and the full data set estimate when 30% or less of the original data was available. On this basis, the smaller amount of data for AB-RF and ON-PF (between 26% and 32% of the data coverage obtained for ON-B and AB-WF) does not significantly bias estimates of average daily NEE although the precision of these values is less. In terms of determining significant differences in NEE between sites, the probability of falsely accepting or falsely rejecting the null hypothesis decreases with increasing sample size and precision. The difference in daily NEE was 0.6 g C m^{-2} d^{-1} between ON-B and AB-WF (see Figure 3 in section 3.2). Using the resampling method above, average daily NEE remained significantly different between ON-B and AB-WF until there was 50% or less measurements available for both sites. Conversely, estimates of average daily NEE were within 0.1 or 0.2 g C m^{-2} d^{-1} for ON-B, ON-PF, AB-PF and AB-RF indicating that NEE was not different among these sites (see Figure 3 in section 3.2). Since these estimates of average NEE did not change with a reduction in sample size, an improvement in precision with greater data coverage would not reasonably affect this conclusion.

[17] In contrast, the practice of rejecting nighttime measurements on the basis of a measure of atmospheric turbulence when the theoretical requirements for the eddy covariance technique are not met introduces a bias to the data set. In particular, this has the potential to bias nighttime
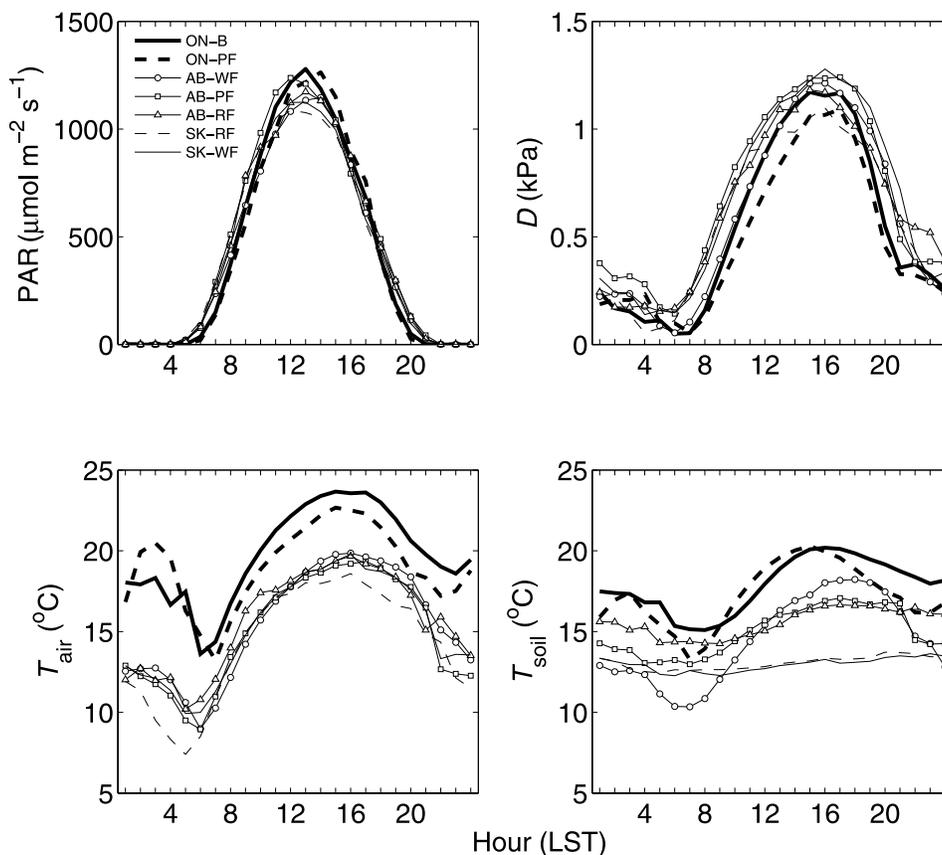
Figure 1. Average diurnal variations in micrometeorological conditions at each peatland site. Downwelling photosynthetically active radiation (PAR), vapor pressure deficit (D) and air temperature (T_{air}) were measured at the height of the eddy covariance instrumentation (Table 3). Soil temperature (T_{soil}) was measured 5 cm below the surface of the peat. Measurements were sorted by hour of day, adjusted to local solar time (LST), and then averaged. Measurements correspond to times when NEE and λE measurements were available in July and August 2004 (see Table 3 for data availability).

data to environmental conditions associated with turbulence. Although there is no physiological or mechanistic link between ER and wind, T_{air} and T_{soil} tend to be warmer under turbulent conditions (see Figure 1). Owing to the exponential relationship between ER and temperature, the effect would be expected to overestimate nighttime ER to some degree at all the sites. The alternative would be to model nighttime ER using equation (1) parameters derived from daytime data and the weather data for the missing nighttime periods. However, owing to down-regulation of leaf respiration during the daytime, the assumption that daytime ER is equivalent to nighttime ER may not be valid. Although nighttime ER may be slightly overestimated as described above, this would have happened at all the sites where the relative proportion of daytime and nighttime data were similar and does not present a serious problem to this comparison study. Furthermore, since variations in nighttime ER tend to be less than variations in NEE during the day (see Figure 2), this would diminish the impact of missing data.

[18] The surface conductance (g_c) to latent heat transfer between the atmosphere and the peatland surface including plant stomates and wet surfaces such as open water, moss and vascular plant surfaces, was calculated using a rearrangement of the Penman-Monteith equation [*Monteith and Unsworth*, 1990],

$$\frac{1}{g_c} = \left(\frac{s}{\gamma} \left(\frac{R_a}{\lambda E} - 1 \right) - 1 \right) r_a + \frac{\rho c_p D}{\gamma \lambda E} \quad (2)$$

where available energy, R_a, was approximated using the sum of H and λE, s is the change in saturation vapor pressure with temperature, γ is the psychrometric constant, and ρ and c_p are the density and specific heat of air, respectively. The aerodynamic conductance, g_a, was computed from the inverse of the aerodynamic resistance to momentum transfer including an approximation of the excess resistance to heat and water vapor transport [*Verma*, 1989],

$$g_a = \left(\frac{2}{k u_*} \left(\frac{d_h}{d_v} \right)^{2/3} + \frac{U}{u_*^2} \right)^{-1} \quad (3)$$

where $k = 0.4$ is von Karman's constant, U is the mean cup wind speed. The value of 2 is an estimate of the logarithmic
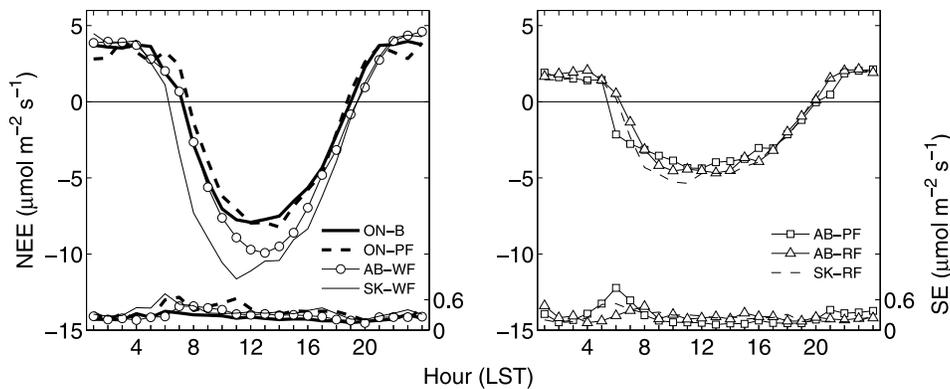
Figure 2. Average diurnal variations in net ecosystem CO$_2$ exchange (NEE) at each peatland site. Available measurements were sorted by hour of day, adjusted to local solar time (LST), and then averaged. Standard errors of the mean hourly NEE ranged from 0.1 to 0.9 μmol m^{-2} s^{-1}.

ratio of the roughness lengths for momentum to mass or sensible heat (kB^{-1} value) for these vegetated sites multiplied by a fraction of the ratio of thermal diffusivity (d_h) to molecular diffusivity of water vapor (d_v), where d_h/d_v is 0.89 at 20°C.

[19] The Priestley-Taylor coefficient ($\alpha_{P\text{-}T}$), the ratio of observed latent heat flux to equilibrium latent heat flux was calculated as, $\alpha_{P\text{-}T} = \lambda E/(sR_a/(s + \gamma))$ [*Priestley and Taylor*, 1972]. Potential ET (ET$_o$), or open water ET, was computed from the Penman-Monteith equation with $g_c^{-1} = 0$.

[20] Correlations among variables were considered significant when the *p*-value was less than 0.05. All analyses were carried out using MATLAB 7.0.1 [*MathWorks Inc.*, 2004].

3. Results and Discussion
3.1. Weather Conditions

[21] The weather during July and August 2004 was cooler and wetter than normal at all sites (Table 1). Despite over 200 mm of rainfall in July and August at almost all sites, the average water table depth (WTD) varied greatly among sites (Table 1). WTD was farthest from the hummock surface at ON-B; however, this WTD of 37 cm is relatively high compared to drier years when WTD drops over 60 cm below the average hummock surface [*Lafleur et al.*, 2003]. WTD was near or above the average hummock surface at the two SK sites where rainfall was over 65% greater than the 30-year normal. The average WTD was 16 to 18 cm below the surface at AB-RF and ON-PF and 29 cm below the surface at AB-WF and AB-PF.

[22] Average weather conditions associated with the periods when flux measurements were made during July and August are shown in Figure 1. Differences in data coverage (Table 3) as well as site location and general climate resulted in differences in PAR among the sites with midday PAR lowest at SK-RF and highest at the ON sites. T_{air} was very similar among the AB and SK sites but about 4°C cooler than the more southerly ON sites. Since EC fluxes are rejected at night during calm periods, the relatively high T_{air} and T_{soil} at night at ON-B and ON-PF in Figure 1 likely reflected the warmer weather associated with turbulent conditions rather than the average diurnal trend. Average

midday D was similar among all sites with slightly lower values at ON-PF and SK-RF. The inundated SK-WF and SK-RF had the most damped and lagged diurnal variations in T_{soil} measured 5 cm below the peat surface.

3.2. Net Ecosystem CO$_2$ Exchange

[23] The average diurnal variations in NEE indicated a net uptake of CO$_2$ by all the peatlands during daytime and a net loss of CO$_2$ at night (Figure 2). The magnitude of hourly NEE (night and day) was lower at the three western open fens (AB-RF, AB-PF, and SK-RF). In contrast, the two wooded fens (AB-WF and SK-WF) and the ON-B and ON-PF had similarly high nighttime NEE fluxes, near 4 μmol m^{-2} s^{-1}, and larger maximum daytime fluxes ranging from −11.5 μmol m^{-2} s^{-1} at SK-WF to −8 μmol m^{-2} s^{-1} at ON-B.

[24] These average differences in hourly NEE among sites led to some variation in the average daily fluxes (Figure 3). Statistically, the peatland NEE fell into three groups. The two ON sites and AB-RF were similar and had the lowest daily net C uptake (−1.0 to −1.2 g C m^{-2} d^{-1}). AB-PF, AB-WF and SK-RF fell into an intermediate group that had some commonality with the low NEE group and some differences. Daily NEE for this group ranged from −1.3 g C m^{-2} d^{-1} at AB-PF to −1.8 g C m^{-2} d^{-1} at AB-WF. SK-WF had distinctly higher net C uptake than all other peatlands, with mean daily NEE value of −2.8 g C m^{-2} d^{-1}. Despite these statistical differences, we believe that in practical terms it is likely the case that all of the peatlands had similar daily NEE except for the greater net uptake at SK-WF. These midsummer NEE indicated slightly greater C uptake than has been found in a number of previous studies of northern, subarctic and arctic wetland C exchange reviewed by *Griffis et al.* [2000, Table 1], ranging from +0.3 to −1.0 g C m^{-2} d^{-1}. The results of this study were similar to those for *Sphagnum* bogs in eastern Europe and Siberia (−0.7 and −1.2 g C m^{-2} d^{-1}) [*Schulze et al.*, 1999] and in a subarctic fen ($\sim$ −1 g C m^{-2} d^{-1}) [*Aurela et al.*, 2004]. Slightly greater net uptake of C in July−August was found for earlier work at SK-RF ($\sim$ −2 g C m^{-2} d^{-1}) [*Suyker and Verma*, 1997] while slightly less net uptake of C was found at ON-B (−0.4 to
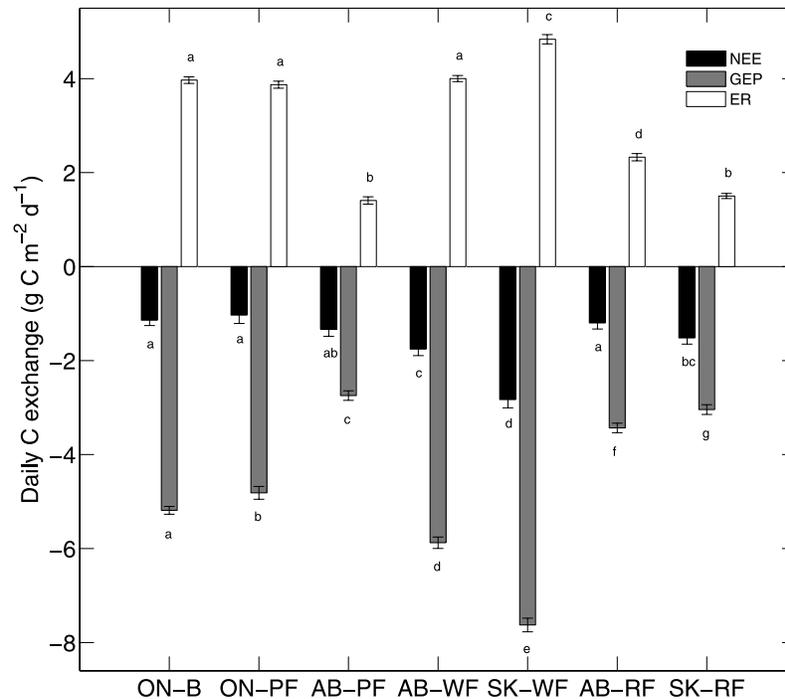
Figure 3. Average daily net ecosystem exchange of CO$_2$ (NEE), gross ecosystem production (GEP) and ecosystem respiration (ER). Error bars are ±95% CI. Bars of a common shading with different letters are significantly different (p < 0.05).

−0.8 g C m^{-2} d^{-1}) [*Lafleur et al.*, 2003]. The midsummer peatland NEE in this study exceeded that of mature boreal coniferous forests (∼−0.4 g C m^{-2} d^{-1} [*Griffis et al.*, 2003], 0 to −0.5 g C m^{-2} d^{-1} [*Litvak et al.*, 2003]) but was less than that of younger boreal coniferous forests [e.g., *Litvak et al.*, 2003], boreal aspen [e.g., *Griffis et al.*, 2003] and other temperate broadleaf forests [e.g., *Anthoni et al.*, 2004] as well as crops [e.g., *Anthoni et al.*, 2004] and grasslands [e.g., *Flanagan et al.*, 2002].

[25] Estimates of daily GEP and ER were more variable than NEE, with several statistically distinct sites (Figure 3). In general, the three western open fens were similar and had the lowest magnitudes of GEP and ER. The two wooded fens (AB-WF and SK-WF) had the highest magnitudes of GEP and ER and ON-B and ON-PF were intermediate. This pattern was proportional to differences in aboveground vascular biomass (Table 2). Peatland GEP was highly correlated to ER (r = −0.95, p = 0.001), as well, mean daytime and nighttime NEE were strongly correlated (r = −0.79, p = 0.03). This suggests that there is a strong link between ecosystem production and respiration processes across these peatland types. The mean ratio of daily |ER/GEP| was 0.65 and varied from 0.49 (SK-RF) to 0.80 (ON-PF). However, it is unknown how decomposition rates differ among sites and how much of the ER at each peatland is attributable to autotrophic or heterotrophic respiration.

[26] By expressing NEE as a function of downwelling PAR and T_{air} (equation (1)), C exchange processes could be compared among sites without the confounding effects of local weather conditions (Table 4). Similar patterns as discussed above arise. The three western open fens with

lowest biomass had significantly lower A_{max} and lower R_{10} than the other sites. The two wooded fens with greatest biomass had the highest A_{max} and R_{10}, with significantly higher A_{max} at AB-WF (25.5 μmol m^{-2} s^{-1}) than at SK-WF (22.5 μmol m^{-2} s^{-1}). The ON-PF and ON-B had intermediate values. There was no significant difference in R_{10} at the two wooded sites. Values of the effective quantum yield were less distinct, with the highest value at SK-WF and all other sites varying within ±0.01 of the mean for these sites, 0.025 mol CO$_2$/mol PAR. The model parameters (α, A_{max}, and R_{10}) derived from our study fall within the range given by *Frolking et al.* [1998].

[27] The influence of moisture status on variations in NEE at a given site was investigated by multiplying the respiration term of equation (1) by the relative water table depth (value between 1 and 0 where 1 indicates the driest observed conditions). The increase in R^2 was only 4% at AB-RF and 6% at SK-RF and less than 2% for the remaining sites. This suggests that variations in ER at a given site were not significantly related to moisture status likely due to the relatively small range in water table depth at all the sites within the short two-month time period (Table 1).

[28] A_{max} was strongly correlated with measures of vascular vegetation including aboveground biomass (r = 0.86, p = 0.014, n = 7) and to a lesser extent, LAI (r = 0.73, p = 0.16, n = 5). Similarly, R_{10} correlated well with LAI (r = 0.89, p = 0.045, n = 5) and aboveground biomass (r = 0.78, p = 0.04, n = 7). Consistent with the findings for GEP and ER noted above, there was also a strong positive correlation between A_{max} and R_{10} parameters (r = 0.95, p = 0.001). Data

Table 4. Parameters for Equation (1) Derived From July and August Daytime NEE, PAR, and T_{air}[a]

Site	A_{max}, μmol m^{-2} s^{-1}	α, mol CO_2/mol PAR	R_{10}, μmol m^{-2} s^{-1}	Q_{10}	R^2	n	Mean Daytime PAR, μmol m^{-2} s^{-1}	Mean T_{air}, °C
ON-B	16.6a (16.1, 17.2)	0.036a (0.032, 0.040)	2.7a (2.5, 2.9)	1.4	0.74	1766	721 (13)	20.8 (0.1)
ON-PF	18.1a (16.8, 19.4)	0.028ab (0.022, 0.034)	2.9a (2.4, 3.4)	1.3	0.76	505	718 (25)	19.8 (0.2)
AB-PF	7.0b (6.3, 7.6)	0.021bc (0.015, 0.026)	0.9b (0.5, 1.2)	1.5	0.39	805	747 (17)	17.0 (0.2)
AB-WF	25.5c (23.9, 27.1)	0.026b (0.023, 0.029)	3.1a (2.8, 3.5)	1.3	0.72	1736	663 (12)	16.8 (0.1)
SK-WF	22.5d (21.5, 23.5)	0.054d (0.048, 0.060)	3.2a (2.9, 3.6)	1.8	0.62	1511	671 (13)	16.9 (0.1)
AB-RF	10.7e (9.9, 11.6)	0.021bc (0.017, 0.026)	1.4b (1.17, 1.71)	2.0	0.65	476	695 (21)	17.3 (0.2)
SK-RF	10.4e (9.4, 11.4)	0.017c (0.012, 0.022)	1.1b (0.65, 1.62)	1.3	0.54	694	699 (18)	16.3 (0.2)

[a]Values in parentheses for the first three columns are the 95% CI, for the last two columns are SE of the mean. Parameter estimates with different letters are significantly different (p < 0.05).

from *Frolking et al.* [1998, Table 2] also show this strong association ($r = 0.85$, $p = 0.0002$, $n = 13$). Others have documented the positive correlation between GEP and ER for a variety of ecosystems [*Janssens et al.*, 2001; *Law et al.*, 2002] which is attributed to the dependence of autotrophic respiration on photosynthesis as well as a link between decomposition and litter inputs. For the peatland ecosystems in this study, the close correlation emphasizes that the similarity in daily NEE among most sites (Figure 3) arises from compensation between GEP and ER. The one exception was SK-WF where the high water table and damped T_{soil} appears to have resulted in relatively unvarying ER compared to GEP. This resulted in significantly greater daily net uptake of C despite the similarity in average PAR and T_{air} (Figure 1) to the other western sites.

3.3. Evapotranspiration

[29] Average diurnal patterns of λE were similar at all sites, with maximum λE occurring between 12 and 15 h local time (Figure 4), corresponding to maximum PAR rather than maximum D (Figure 1). Both average daily ET, derived by integrating under the curves in Figure 4, and average midday ET (Table 5) were remarkably similar among a number of the peatlands and did not appear to be related to peatland type. Average daily ET fell into three groups: SK-RF = 1.7 mm d^{-1}, AB-RF, AB-WF, SK-WF and ON-PF $\sim$ 2.0 mm d^{-1} and ON-B and AB-PF $\sim$ 2.5 mm d^{-1}. The ET rates for our peatlands are within,

but tend toward the lower end of the range of peatland ET rates from past studies (see literature surveys by *Lafleur et al.* [2005, Table 2] and *Campbell and Williamson* [1997, Table 1]). We will make the case that the differences that exist in daily or midday ET among these peatlands are a function of how the specific functional plant community responds to environmental controls rather than a simple effect of peatland type or WTD.

[30] There was no correspondence between daily or midday ET rates and average WTD, as the site with the lowest ET (SK-RF) had the highest average WTD (4 cm above the peat surface) and the sites with the highest ET (ON-B and AB-PF) had the lowest average WTD (37 cm and 29 cm below the peat surface, respectively). This is consistent with recent findings by *Lafleur et al.* [2005], who suggested that there is limited response of ET to WTD in a peatland with both moss and vascular vegetation until the WTD drops below a critical depth (65 cm for ON-B). At this critical depth, roots of vascular vegetation may lose contact with the water table and the supply of water via capillary uptake by mosses in the hollows is restricted. For WTD between this critical depth and a shallower depth (30 cm at ON-B), hummock moss ET may be restricted and result in locally warmer and drier conditions that could enhance ET from the vascular vegetation and the moss located in the hollows.

[31] Although soil water may not have been limiting at these peatlands, evaporation parameters α_{P-T} and ET/ET$_o$,

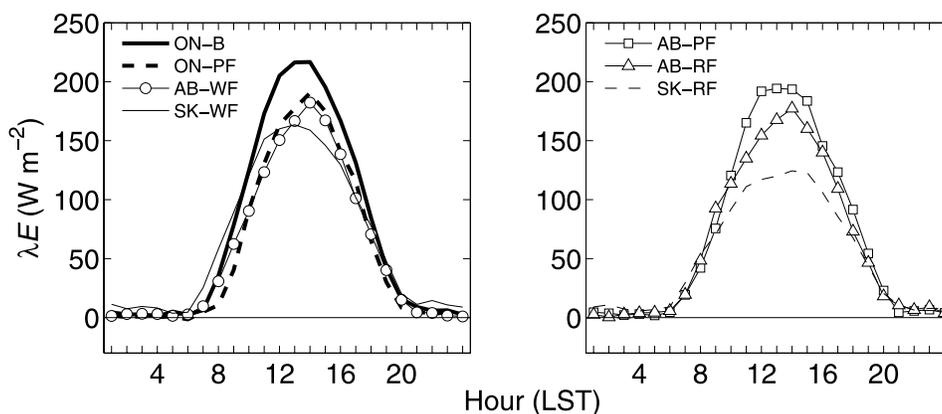**Figure 4.** Average diurnal variations in latent heat flux (λE) at each peatland site. Measurements were sorted by hour of day and then averaged. Standard errors of the mean hourly λE (not shown) ranged from 0.3 to 15.9 W m^{-2}.

Table 5. Summary of Midday Evapotranspiration, Priestley-Taylor Coefficient, and the Ratio of Actual to Potential ET for All Peatlands in July and August 2004[a]

Site	ET, mm h^{-1}	α_{P-T}	ET/ET$_o$	n
ON-B	0.34 (0.004)a	0.88 (0.003)a	0.59 (0.003)a	585
ON-PF	0.29 (0.006)bc	0.91 (0.006)b	0.56 (0.007)b	171
AB-PF	0.31 (0.006)b	1.05 (0.004)c	0.64 (0.006)c	283
AB-WF	0.29 (0.004)c	0.82 (0.005)d	0.41 (0.005)d	517
SK-WF	0.26 (0.003)d	0.84 (0.006)e	0.38 (0.006)e	477
AB-RF	0.26 (0.005)d	0.88 (0.008)ab	0.55 (0.010)b	157
SK-RF	0.21 (0.004)e	0.88 (0.006)a	0.43 (0.006)d	223

[a]Abbreviations: midday evapotranspiration, ET; Priestley-Taylor coefficient, α_{P-T}; potential ET, ET$_o$. All data correspond to periods when ET measurements were available for rain-free periods between 10 and 16 h, inclusive when PAR > 800 μmol m^{-2} s^{-1} (n indicates sample size). Values in parentheses are SE of the mean. Values with different letters are significantly different (p < 0.05).

indicate that ET was not at its maximum potential (Table 5). α_{P-T} at all sites was less than 1.0 for all but AB-PF and considerably less than 1.26, which is characteristic of extensive well-watered land surfaces such as agricultural crops [*Priestley and Taylor*, 1972]. The ET/ET$_o$ ratio was also much less than 1.0 at all sites (Table 5). These results suggest that physiological limitations to ET were present at all sites.

[32] The average diurnal variations of surface conductance (g_c) to latent heat transfer, and aerodynamic conductance (g_a) are shown in Figure 5. Aerodynamic conductance was highest at the two wooded fens owing to enhanced momentum absorption by the tall vegetation. High wind speeds at SK-RF resulted in larger midday g_a than at the other open peatlands. Mean midday (10–14 h, inclusive) g_c was slightly lower at the wooded fens (7.3 mm s^{-1} at SK-WF and 8.2 mm s^{-1} at AB-WF) than at the open peatlands (9.3 mm s^{-1} at ON-B and ON-PF, 9.4 mm s^{-1} at AB-RF, and 10.7 mm s^{-1} at AB-PF) except for SK-RF where g_c was 6.4 mm s^{-1}. Canopy conductance tended to decline through the day from either early morning or midday peak values (Figure 5). Such patterns have been observed in other wetland environments (bog [*Price*, 1991]; fens [*Lafleur and Rouse*, 1988]; wooded swamp [*Munro*, 1987]) where it has been attributed to stomatal sensitivity to D. This explanation would be consistent with results from our peatlands, as D peaked in late afternoon at all sites (Figure 1).

[33] We explore the relationship between g_c and D at high light levels using the following function:

$$g_c = g_{cmax} \frac{1}{1 + bD} \qquad (4)$$

where g_{cmax} is an estimate of the maximum conductance and b is a slope coefficient (Figure 6). Although all sites showed g_c decreasing with increasing D, two patterns of
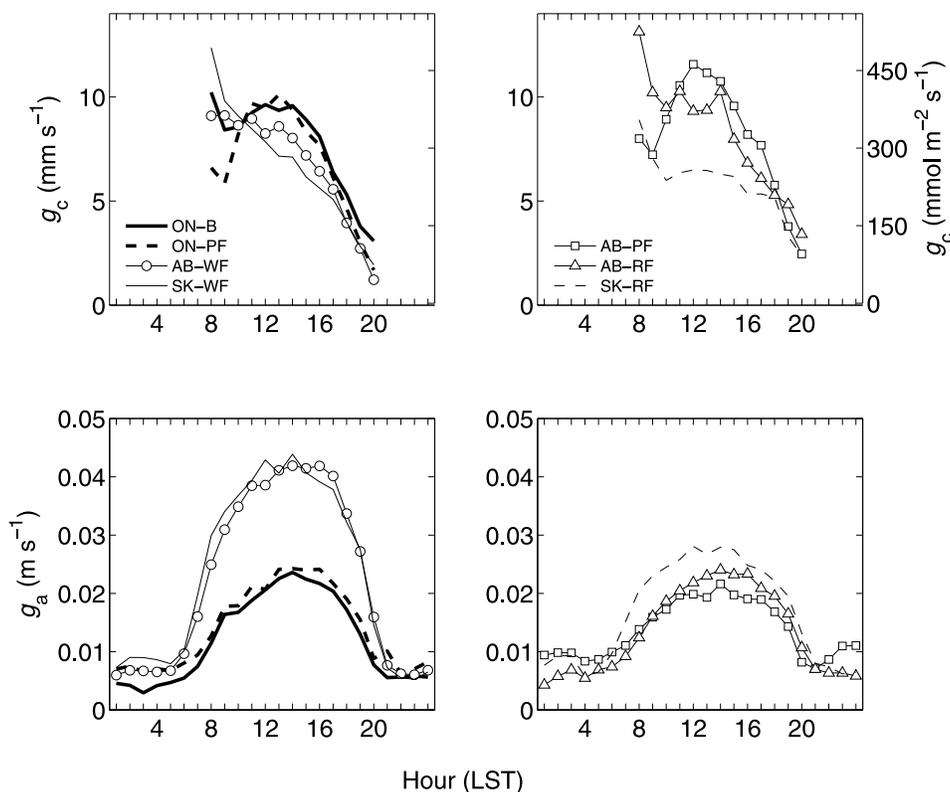

Figure 5. Diurnal patterns of surface conductance (g_c) in units of mm s^{-1} or mmol m^{-2} s^{-1} and aerodynamic conductance (g_a) for each peatland (data points are mean values for periods at least 6 hours after rainfall).
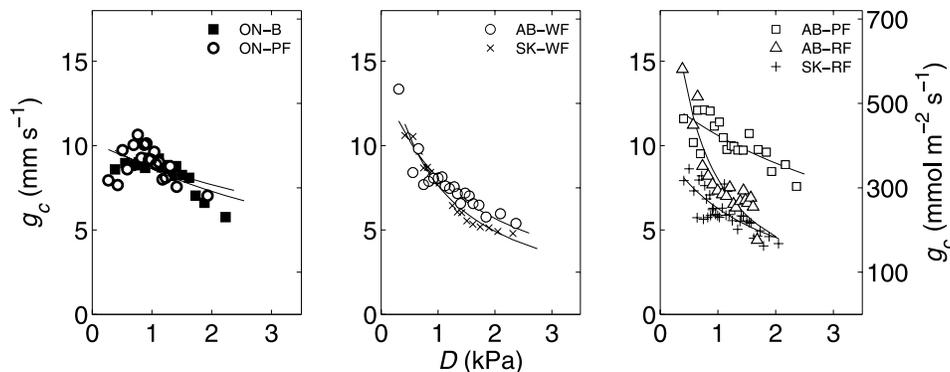
Figure 6. Surface conductance (g_c) versus vapor pressure deficit (D). Data points are the average g_c after sorting by D for periods at least 6 hours after rainfall and PAR > 800 μmol m^{-2} s^{-1} where the number of samples per data point is 5% of total number of available samples ($n = 7-32$). On average, standard errors of the mean g_c were 0.9 mm s^{-1}. Solid lines show the parameterization of equation (4).

response emerged among the sites. The two wooded fens and AB-RF exhibited strong responses, with large g_{cmax} values and slope coefficients exceeding 1.0 (b = 1.1, 2.6, and 3.7 kPa^{-1} at AB-WF, SK-WF, AB-RF, respectively). At AB-PF, SK-RF, ON-PF and ON-B g_{cmax} was lower and b was less than 1.0 ($\sim$0.3 kPa^{-1}) suggesting a relatively weak response by g_c to D. The strong response by g_c to D at the wooded sites would be expected because of their large g_a [*Jarvis and McNaughton*, 1986]. The g_c response to D at the open sites presents an interesting puzzle: Why did only the AB-RF exhibit a strong response? The limitations of the present data set do not permit a full analysis of this quandary, yet a line of reasonable speculation is possible. Since g_c is computed using above canopy micrometeorological measurements, it represents a "bulk" evaporating surface and includes the effects of contrasting sources of moisture. Others have shown that the ground surface can contribute a considerable proportion of the total ET at wetland sites [*Lafleur*, 1992; *Burba et al.*, 1999]. Thus the behavior of g_c is determined by the type and amount of vascular vegetation present and the evaporating characteristics of the ground surface. One of the important differences among these sites is that AB-RF has low biomass and LAI and a surface cover of brown mosses, whereas ON-B and the two poor fens have a 100% ground cover of *Sphagnum* mosses with an overstory canopy of evergreen shrubs or sedges. These two types of mosses display quite different water relations. *Sphagnum* mosses are highly effective at drawing water from deeper in the peat profile [*Hayward and Clymo*, 1982], and thus will stay adequately supplied with water over a large range of WTD. Conductance to water vapor of *Sphagnum* has been shown to be relatively invariant over a wide range of moisture contents and only decreases at very low moisture content [*Williams and Flanagan*, 1996]. Therefore, at the *Sphagnum* dominated sites (ON-PF, ON-B, and AB-PF), WTD was never deep enough to limit moisture supply to the mosses and affect their g_c such that the bulk g_c for these sites is only a function of the vascular vegetation canopy. In contrast, brown mosses are less tolerant of changing WTD [*Janssens et al.*, 1992] and presumably their g_c is sensitive over a wide range of moisture contents. Combined with the fairly strong

stomatal control of transpiration by the dominant *Carex* spp. [e.g., *Lafleur*, 1988] at AB-RF, the net effect is a greater sensitivity of bulk site g_c to D. SK-RF likely behaves much like the *Sphagnum* dominated sites, because standing water was present throughout much of the study period, effectively giving the ground surface no resistance to ET ($g_c^{-1} = 0$). This would then dampen the bulk g_c response for the site. Clearly, more detailed studies separating canopy and ground surface ET components would help elucidate this issue.

[34] Midday and daily rates of ET correlated well with mean midday g_c ($r = 0.75$, $p = 0.053$, and $r = 0.72$, $p = 0.055$, respectively, $n = 7$). Maximum g_c (maximum data point in Figure 6) and mean midday g_c did not correlate with biomass ($p = 0.92$ and 0.48, respectively $n = 7$). Maximum and midday g_c correlated more, but negatively to LAI ($r = -0.74$, $p = 0.157$, $n = 5$ and $r = -0.56$, $p = 0.32$, $n = 5$). This again suggests that the conductance to water vapor of moss and open water contributes significantly to the overall peatland g_c and total ET. The more conservative water use of woody shrubs and trees relative to the water use of sedges and herbs may also contribute to the negative correlation between peatland g_c and LAI. The g_c values in this study are similar to values for other wetland ecosystems reviewed by *Campbell and Williamson* [1997, Table 3]. The average maximum g_c for the seven peatlands in this study (11 mm s^{-1}) was slightly lower than grasslands (17 mm s^{-1}), deciduous and coniferous forests ($\sim$21 mm s^{-1}) and much lower than agricultural crops ($\sim$32 mm s^{-1}) [*Kelliher et al.*, 1995, Table 1] despite having similar LAI in some cases. Both maximum stomatal and canopy conductance have been related to leaf N content and net assimilation [*Schulze et al.*, 1994]. In this study, there was little evidence to relate g_c to nutrient status. For example, maximum daytime g_c was similarly low at SK-RF (8.6 mm s^{-1}) and ON-B (9.3 mm s^{-1}) and similarly high at AB-RF (14.5 mm s^{-1}) and AB-WF (13.3 mm s^{-1}) despite differences in peat or pore water chemistry (Table 1). Again, the parallel conductance associated with moss evaporation complicates this relationship but the low nutrient status of most peatland vegetation likely plays a role in the low g_c

Table 6. Water Use Efficiency Statistics[a]

Site	Mean daytime WUE (mmol CO$_2$/mol H$_2$O)[b]	Mean WUE (in mmol CO$_2$/mol H$_2$O) for $D > 1.5$ kPa and PAR > 800 μmol m^{-2} s^{-1}
ON-B	4.5 (1.1)	1.9 (0.04)
ON-PF	5.9 (1.6)	1.9 (0.07)
AB-PF	2.8 (0.6)	1.0 (0.02)
AB-WF	6.5 (1.0)	2.9 (0.04)
SK-WF	6.3 (0.6)	3.8 (0.07)
AB-RF	3.0 (0.4)	1.9 (0.12)
SK-RF	2.8 (0.3)	1.8 (0.05)

[a]WUE is water use efficiency. Values in parentheses are the SE of the mean.
[b]Data were first sorted by hour (6 to 21 h inclusive) and then averaged for every hour prior to deriving these statistics.

and low productivity for a given g_c when compared to other vegetated ecosystems.

[35] In summary, midday and daily ET were remarkably similar among a number of the peatlands. The similarities in ET could be largely attributed to similarities in g_c that arose from a complex set of factors related to the plant community structure of each site that did not correspond simply to peatland type or vascular vegetation characteristics.

3.4. Water Use Efficiency

[36] The exchange of CO$_2$ and H$_2$O between vascular vegetation and the atmosphere occurs through molecular diffusion through the stomata. Water use efficiency (WUE) has been traditionally used to link these two important mass exchanges in a variety of applications including agriculture and landscape modeling. WUE is defined here as the molar ratio of CO$_2$ uptake (GEP) by the whole ecosystem to H$_2$O loss through transpiration and evaporation from the surface (ET). Average daytime WUE varied by about a factor of 2 among the most water use efficient sites (WUE $\sim$ 6 mmol CO$_2$/mol H$_2$O – SK-WF and AB-WF) and the least efficient sites (WUE $\sim$ 3 mmol CO$_2$/mol H$_2$O – AB-RF, SK-RF, and AB-PF) (Table 6). The average WUE for the wooded fens, ON-B and ON-PF was similar or only slightly greater than for a boreal aspen forest (5.4 mmol CO$_2$/mol

H$_2$O) while WUE at the open fens was similar to that of a prairie grassland (2.6 mmol CO$_2$/mol H$_2$O) [*Ponton et al.*, 2006].

[37] At the scale of a vascular leaf, stomatal closure occurs with increasing D and generally leads to higher WUE as transpiration is inhibited more than photosynthesis [*Farquhar and Sharkey*, 1982]. At the ecosystem level, WUE tends to decrease with increasing D [*Law et al.*, 2002; *Scanlon and Albertson*, 2004; *Ponton et al.*, 2006]. A decline in WUE with increasing D was also observed at all seven peatlands in this study (Figure 7). As D increases, ecosystem ET increases in response to enhanced evaporative demand while g_c and GEP decline (Figures 6 and 8). For a given D, the sites with greater biomass and LAI and GEP have highest WUE (ON-B, ON-PF, AB-WF, and SK-WF) but are also the most sensitive to D. The difference in WUE among peatlands diminishes as D exceeds 1.5 kPa (Table 6 and Figure 7).

[38] Since differences among sites were relatively greater for GEP than ET, it followed that average daytime WUE increased with increasing biomass and LAI associated with a greater presence of woody shrubs and coniferous trees. At all sites, the nonvascular ground cover likely reduced the WUE of the total ecosystem as C assimilation and most importantly, evaporation from the moss surfaces are not
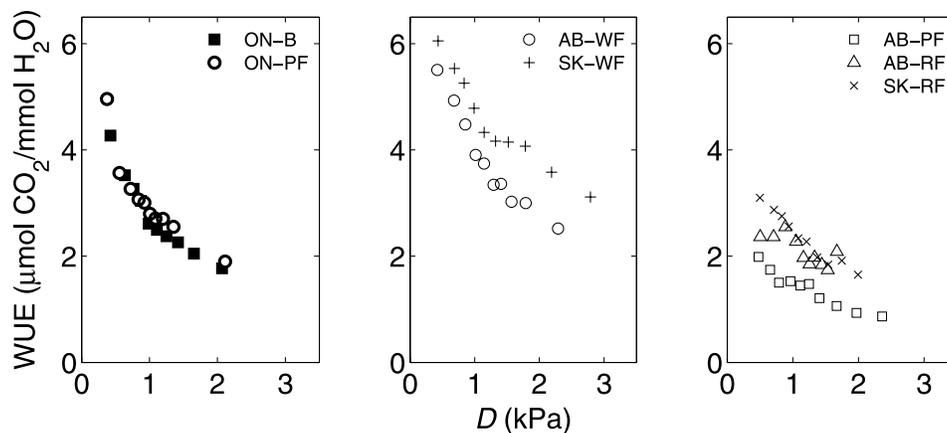

Figure 7. Water use efficiency (WUE = GEP/ET) versus vapor pressure deficit (D) for periods without rain, $\lambda E > 50$ W m^{-2}, and PAR > 800 μmol m^{-2} s^{-1} (approaching saturating light levels). Data points are the average WUE after sorting by D where the number of samples per bin is 5% of total number of available samples ($n = 20-72$).
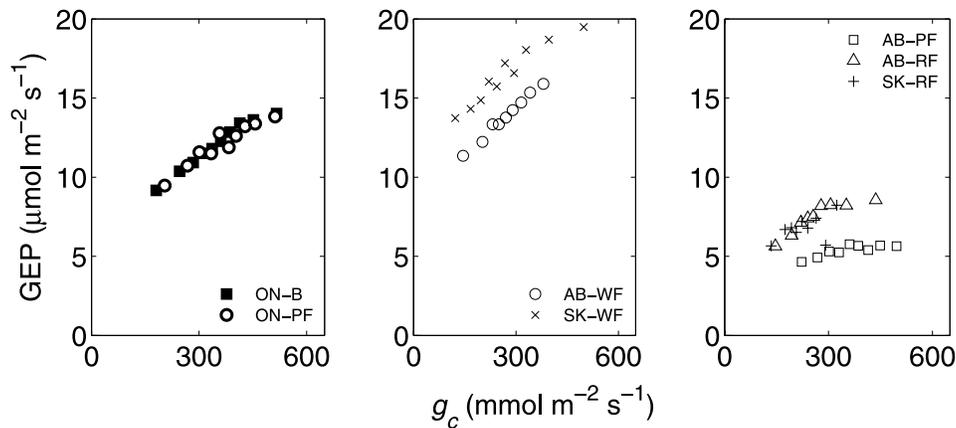
Figure 8. Gross ecosystem production (GEP) versus surface conductance (g_c) for periods without rain, $\lambda E > 50$ W m^{-2}, and PAR > 800 μmol m^{-2} s^{-1} (approaching saturating light levels). Data points are the average GEP after sorting by g_c where the number of samples per data point is 10% of total number of available samples ($n = 18-70$).

limited by stomatal control but by water availability primarily as a function of WTD. However, it is interesting to note that mean daytime WUE (Table 6) did not correlate with WTD ($p = 0.88$, $n = 7$). For example, average WTD was only 3 cm below the surface at SK-WF while it was 29 cm below the surface at AB-WF yet these two sites had similarly high WUE due in combination to greater production and greater physiological resistance to water loss (Table 5). In contrast, it is uncertain if low WUE at the sites with low production and low biomass simply reflect greater water loss from nonvascular sources rather than dramatically less efficient use of transpired water by vascular vegetation. Vascular peatland vegetation generally consists of slow growing, water conservative species constrained by the cool temperatures and limited available nutrients. The different plant functional groups found within this study, including conifer trees, evergreen and deciduous shrubs, herbs and forbs, tend to have different ratios of stomatal conductance to photosynthetic capacity that lead to different ratios of intercellular to atmospheric CO₂ concentrations (leaf c_i/c_a) [*Brooks et al.*, 1997] and different WUE. Lower leaf c_i/c_a corresponds to higher WUE and is associated more with coniferous than deciduous species and more with forbs than herbs. Although peatland WUE would be influenced by nontranspired sources of evaporation to varying degrees, these results agree with these general trends.

4. Summary and Conclusions

[39] This study has identified some of the compensating factors that under well-watered conditions, resulted in similar midsummer CO₂ and water vapor fluxes in seven northern peatlands with dramatic differences in plant species composition, water chemistry, and hydrological characteristics. The main findings of this comparison study are as follows.

[40] 1. GEP and ER varied among peatlands but correlated well with vegetation indices and with each other.

Consequently, midsummer 24-hour NEE was similar among most of the peatlands.

[41] 2. ET was similar among a number of the sites and was not a simple function of water table depth, biomass, or leaf area. Although ET was largely radiatively driven at all sites, rates of midday ET were below potential rates indicating physiological limitations to ET at all sites.

[42] 3. Surface conductance did not differ greatly among most of the peatlands despite differences in amount and type of vascular vegetation suggesting that the conductance to water vapor of moss and open water contributed substantially to the overall peatland g_c. Surface conductance did display varying sensitivity to atmospheric vapor deficit as a function of both the vascular vegetation canopy and the ground cover characteristics.

[43] 4. Differences in WUE among peatlands related to peatland productivity and plant functional type. WUE declined with increasing atmospheric vapor deficit to some extent at all peatlands due to both a decline in GEP with decreasing g_c and an increase in ET assumed to be supported in part by evaporation from the non-vascular vegetation.

[44] Overall, we have found that peatland classification along a bog–poor fen–rich fen gradient based on hydrology, chemistry, and dominant vegetation and moss species was not a prime driver of the magnitude and characteristics of midsummer CO₂ and water vapor exchanges of peatlands across Canada. Instead, vegetation characteristics such as vascular plant biomass, LAI, and moss cover played a much larger role in these atmospheric exchanges.

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