Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown

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[1]   Northern peatlands are significant stocks of terrestrial soil carbon, and it has been predicted that warmer temperatures and lower water tables resulting from climate change will convert these ecosystems into sources for atmospheric carbon dioxide (CO_2). However, these predictions do not consider the potential for hydrologically induced ecological succession or the spatial variability of carbon accumulation rates between different microforms in peatlands. To address these issues, the vegetation community was described, and the rates of gross ecosystem photosynthesis (GEP), ecosystem respiration (R_{tot}) and net ecosystem CO_2 exchange were determined along poor fen microtopographic gradients at a control site and at a site which experienced a water table drawdown of ~20 cm 8 years prior to the study (drained). Sampling plots within these sites were classified as microforms of hummocks, lawns, or hollows. The coverage of *Sphagnum* moss declined on drained hummocks, drained lawns were invaded by sedges, and hollows shifted from open water plots at the control site to *Sphagnum*-dominated plots with sparse vascular plant cover at the drained site. As a result, R_{tot} was significantly greater at the drained site at all microforms while maximum rates of GEP declined at drained hummocks and were enhanced at drained lawns and hollows compared to similar control microforms. These results suggest that predictions about the response of northern peatland carbon exchange to climate change must consider the interaction between ecology and hydrology and the differential responses of microforms related to their initial ecohydrological conditions.

1. Introduction

[2]   Northern peatlands are important reservoirs of terrestrial carbon, storing an estimated 455×10^{15} g C [*Gorham*, 1991]. It is important to understand the fate of this carbon in response to global climate change since its release to the atmosphere could act as a positive climatic feedback. Carbon accumulation depends on the differences between carbon uptake by photosynthesis and its release through decomposition, and carbon accumulation in peatlands is primarily the result of slow decomposition rates under saturated conditions [*Clymo*, 1984]. Carbon dioxide (CO_2) emissions from peat soils, resulting from respiration, are positively related to temperature [*Billings et al.*, 1982; *Moore and Dalva*, 1993; *Updegraff et al.*, 1998] and depth to the water table [*Billings et al.*, 1982; *Moore and Knowles*, 1989; *Freeman et al.*, 1993; *Moore and Dalva*, 1993], and

both of these are likely to be affected by climate change. For example, on the basis of a $2 \times CO_2$ scenario [*Mitchell*, 1989], *Roulet et al.* [1992] predicted that peat temperatures at 10 cm depth in subarctic fens would increase 0.8°C and that water table position would be lowered by 14 to 22 cm. Thus it has often been hypothesized that climate change will result in enhanced rates of CO_2 emissions from northern peat soils [*Billings et al.*, 1982; *Freeman et al.*, 1993; *Moore*, 1998; *Dalva et al.*, 2001].

[3]   These relationships between peatland CO_2 emissions, temperature, and water table position may vary spatially between different microtopographic zones, or microforms, within peatland ecosystems (microform term in the sense of *Charman* [2002, p. 27] and equivalent to the term of nanotope of *Joosten and Clarke* [2002, p. 90]). For example, *Waddington et al.* [1998] report steeper slopes for temperature-respiration relationships at lawns and small hummocks than at large hummocks and hollows. Also, significant increases in respiration have been observed to occur during a dry summer at bog hollows while hummock respiration rates were not significantly affected [*Bubier et al.*, 2003]. Moreover, microtopographic low areas of peatlands, such as hollows and pools, have been observed to have low productivity [*Rochefort et al.*, 1990; *Vitt*, 1990] and may act as sources of CO_2 to the atmosphere [*Moore*,

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Table 1. Climatic Data for an Environment Canada Weather Station at Québec City (30 km From St. Charles-de-Bellechasse) During the Period of Water Table Drawdown at the Drained Site and During the Study Seasons 2001 and 2002

	May	June	July	August	September	Seasonal
1993–2000						
Precipitation, mm	94.3	121.2	130.4	101.8	112.8	560.4
Temperature, °C	11.6	17.2	19.4	16.2	13.1	15.5
2001						
Precipitation, mm	58.4	103.1	72.2	105.7	93.8	433.2
Temperature, °C	13.5	17.6	17.7	18.8	14.0	16.3
2002						
Precipitation, mm	107.6	67.7	63.4	11.8	107.7	358.2
Temperature, °C	9.5	14.9	19.8	19.4	15.6	15.8
Normal						
Precipitation, mm	105.5	114.2	127.8	116.7	125.5	589.7
Temperature, °C	11.2	16.5	19.2	17.9	12.5	15.5

1989; *Waddington and Roulet*, 1996; *Waddington et al.*, 1998]. Thus it has been hypothesized that ecological succession in response to altered hydrology resulting from climate change will enhance productivity at currently wet locations, leading to increased carbon accumulation at these sites [*Waddington et al.*, 1998].

[4] Natural draining of pools by pipes in patterned peatlands leads to the conversion of mud bottom habitats to *Sphagnum* carpets [*Foster et al.*, 1988] and peatland drainage in Finland has enhanced carbon accumulation in peat at several sites [*Minkkinen et al.*, 2002; *Laiho et al.*, 2003]. To date, studies linking shifts in vegetation community and carbon exchange with climate and hydrological conditions have been primarily based on paleoecology [e.g., *Blackford*, 2000]. Also, while the importance of ecological succession in determining peatland carbon accumulation rates under lower water table positions has been identified by *Belyea and Malmer* [2004], the differential response of the vegetation community and CO₂ exchange at various peatland microforms has not been examined. Moreover, while *Belyea and Clymo* [2001] note the importance of including a feedback between carbon accumulation and hydrology for the description of microform dynamics, we are unaware of any studies that have carried out a field-scale investigation of the response of CO₂ exchange at various peatland microforms following a water table drawdown. Consequently, the objectives of this study were to (1) compare a natural peatland microtopographic gradient to an adjacent gradient which had experienced a 20 cm water table drawdown, (2) determine the vegetation changes along the microtopographic gradient in response to a water table drawdown, and (3) determine the shift in CO₂ fluxes along this gradient in response to shifts in the water table position and vegetation community.

2. Materials and Methods

2.1. Study Site

[5] The study was carried out in a poor fen (46°40′N 71°10′W) near St. Charles-de-Bellechasse (SCB), Québec, Canada. Within the fen are several pool-ridge complexes, one of which had the water table lowered approximately

20 cm with a ditch connecting the pool to a larger drainage network 8 years prior to the study (drained). This drained site was compared to another sector of the same poor fen with a natural (control) pool-ridge complex. Peat depth at the control site is approximately 120 cm, while at the drained site it is 80 cm. Nine sampling plots were arranged along the microtopographic gradient at each site. These locations represented a moisture gradient, with three sites at each of hummock, lawn, and hollow microforms. Measurements were conducted from July 2001 to October 2002. Average growing season (May–September) water table positions relative to the moss surface during this period were −32.0, −16.5, and −7.7 cm (at the drained site) and −17.5, −10.3, and 9.8 cm (at the control site) at hummocks, lawns, and hollows, respectively. Despite a reduction of the water table in pool/hollow by 20 cm, peat subsidence across the drained site has mediated water table decline particularly at lawns.

[6] The two study seasons were drier than average with 2001 and 2002 receiving 433 and 358 mm of precipitation between May and September, respectively. The 30-year normal precipitation for the same time period is 590 mm (climate data available from Environment Canada at http://www.climate.weatheroffice.ec.gc.ca). Despite the dry conditions during the study period, the 8 years during which the drained site had been exposed to water table manipulation were similar to the long-term average in terms of precipitation and average temperature (Table 1). This suggests that any shifts in the vegetation community at this location have occurred under relatively normal climatic conditions.

2.2. Environmental Variables

[7] Water table position was measured continuously at a central meteorological station within the SCB experimental fen in 2001 and at each site (drained and control) in 2002 using pulleys on potentiometers. Air temperature and soil temperature at 2, 5, 10, and 20 cm below the peat surface were measured continuously with thermocouples at the SCB fen meteorological station. At this location photosynthetically active radiation (PAR) was also recorded continuously using a quantum sensor (LI-190, LI-COR, Nevada, United States). Water level recorders, thermocouples, and quantum sensor were connected to a data logger, measured each minute, and averaged at 20 min intervals (CR10X, Campbell Scientific, Alberta, Canada). In 2001, instrumental problems resulted in large data gaps for soil temperature. Air temperature measurements from Québec City (30 km from the site) were well correlated ($R^2 = 0.87$) to available air temperature data from the site, and these temperatures were used for modeling seasonal CO₂ flux (discussed in section 2.4). Weekly, at each of the CO₂ sampling plots, water table was measured manually in wells constructed from 1.9 cm PVC pipe, and soil temperature was manually measured with a thermocouple thermometer at 2, 5, 10, 15, and 20 cm below the peat surface.

2.3. Vegetation Survey

[8] In August 2001, three vegetation transects encompassing the entire microtopographic gradient were sampled at each site (drained and control). At each meter along transects the percentage cover of vascular species was determined within a 50 × 50 cm quadrat, and the cover

of understory species such as mosses and hepatics was determined in a 20 cm diameter round sampling ring. Each quadrat was classified as a microform (hummock, lawn, hollow), and the average surface cover of each species at each of these microforms was computed for each site. Average surface cover of vegetation functional groups was also computed. The functional groups considered were *Sphagnum* mosses, Ericaceous shrubs, terrestrial herbs (mainly composed of *Carex oligosperma*, *Eriophorum virginicum*, and *Rhynchospora alba*), and aquatic herbs (mainly composed of *Carex limosa*, *Nuphar spp.*, *Scheuchzeria palustris*, *Scirpus subterminalis*, and *Utricularia cornuta*). The percentage cover of each functional group was also determined in August 2001 and 2002 at sampling plots where CO$_2$ flux measurements were conducted. Nomenclature follows *Marie-Victorin* [1964] for vascular plants and *Anderson et al.* [1990] for bryophytes.

[9] Leaf area index (LAI) was determined by counting all vascular plant leaves within five 7.5 × 7.5 cm subplots systematically distributed throughout each CO$_2$ sampling plot each month. Total leaf numbers within the CO$_2$ sampling plot were extrapolated from these subplots. Individuals of the dominant plant species were selected outside of the CO$_2$ sampling plots at each site and their leaves measured biweekly. An average biweekly surface area of leaves was computed and multiplied by leaf numbers to determine LAI.

2.4. Net Ecosystem Exchange and Respiration

[10] Carbon dioxide exchange was measured weekly during the growing season (July to mid-October 2001 and May to September 2002) and monthly between November 2001 and April 2002. Net ecosystem exchange (NEE) was measured using a clear Plexiglas chamber placed on water-filled 60 × 60 cm aluminum collars installed into the peat at each of the sampling plots. Carbon dioxide concentration inside the chamber was determined every 30 s for 2–3 min using a PP systems EGM portable infrared gas analyzer (Massachusetts, United States). The temperature inside the chamber was maintained within 5°C of ambient temperatures using a radiator cooling system. These measurements were carried out at several levels of PAR created using shades. It has been reported that using shades to reduce light levels during midday manual chamber measurement can result in an underestimation of apparent quantum efficiency for the light response curve [*Burrows et al.*, 2005]. Since the experimental design allows for a comparison between CO$_2$ fluxes at the control and drained sites any underestimation will occur at both sites and not affect the conclusions of the study. Ecosystem respiration (R_{tot}) was determined by obscuring the chamber with an opaque shroud. Gross ecosystem photosynthesis (GEP) was calculated as the difference between NEE and R_{tot}. We have chosen the convention that positive values of CO$_2$ exchange indicate uptake by the ecosystem while negative values represent a release of CO$_2$ to the atmosphere. Maximum rates of GEP and NEE were determined by considering values determined when PAR was greater than 1000 μmol m^{-2} s^{-1} [*Bubier et al.*, 2003]. Differences in maximum GEP, maximum NEE, and R_{tot} between sites and microforms were tested at the 95% confidence level using two-way analysis of variance, with factors of drainage treatment and micro-

form, using Minitab release 14 statistical software (Minitab Inc., PA, United States). A seasonal average value of maximum GEP, maximum NEE, and R_{tot} was computed for each sampling plot resulting in three replications at each microform. The overall design was pseudoreplicated (one control site and one drained site [*Hurlbert*, 1984]) but as it was not materially feasible to replicate this at the ecosystem level, precaution was taken in the interpretation of the data.

[11] Values for GEP were divided into different time periods (mid and late season in 2001 and early, mid, and late season in 2002) and fitted to PAR values with a nonrectangular hyperbola using Photosyn Assistant 1.1 software (Dundee Scientific, United Kingdom) according to the equation,

$$ \text{GEP} = \frac{\phi Q + \text{GP}_{max} - \sqrt{(\phi Q + \text{GP}_{max})^2 - 4\phi Q k \text{GP}_{max}}}{2k}, $$

where Q is the level of PAR, Φ is the apparent quantum efficiency, GP_{max} is the light saturated maximum rate of GEP, and k is the convexity which describes the progressive rate of bending of the hyperbola. Residuals around this relationship were regressed with additional environmental variables (water table, air temperature, LAI) to determine if the variability was related to these parameters. The relationships were then combined with continuously measured PAR, water table, temperature, and calculated LAI in order to estimate seasonal CO$_2$ uptake at each sampling plot. Respiration was regressed against air temperature measured 30 km from the site at an Environment Canada weather station in Québec City in 2001, peat temperature at 5 cm depth in 2002, and water table position. In most cases the inclusion of water table did not improve the regression; however, for a few plots it explained the majority of the variability in R_{tot}. These regressions were combined with the continuously measured temperature and/or water table data to estimate seasonal R_{tot} at each plot. Seasonal values of GEP and R_{tot} were combined to compute cumulative NEE during the growing season.

3. Results

3.1. Vegetation Community

[12] The vegetation community differed between microforms and sites (Table 2). On the basis of a general linear model (Minitab 14), the coverage of *Sphagnum* and terrestrial herbs was influenced by a significant interaction between drainage and microform type. *Sphagnum* cover was higher at control hummocks and lawns than the same drained microforms, whereas control hollows had less *Sphagnum* cover than drained hollows. For terrestrial herbs, there was a significant increase in coverage at drained lawns and hollows relative to these control microforms while no change occurred at hummocks between the two sites.

[13] At the control site, hollows were primarily open water zones dominated by aquatic herbs such as *Scirpus subterminalis*. Lawns had surface covers of *Sphagnum* moss or hepatics (*Cladopodiella fluitans* and *Gymnocolea inflata*) and vascular vegetation dominated by sedges such as *Carex limosa*, *Carex oligosperma* and *Rhyncospora alba*. Most hummocks had nearly complete moss cover dominated by

Table 2. Vegetation Cover (%) at Control and Drained Sites for Each Microform as Determined From Vegetation Transects and CO_2 Sampling Plots in August 2001[a]

% Cover Mean (Standard Error)	Sphagnum[b]	Terrestrial Herbs[c]	Aquatic Herbs[d]	Ericaceous Shrubs[e]
Hummock				
Control	86 (13)(c)	3 (6)(ab)	0(a)	11 (10)(ab)
Drained	26 (32)(ab)	12 (19)(ab)	0(a)	17 (30)(b)
Lawn				
Control	65 (38)(bc)	5 (8)(ab)	4 (7)(a)	2 (4)(a)
Drained	38 (34)(b)	32 (24)(c)	0 (1)(a)	7 (14)(ab)
Hollow				
Control	3 (10)(a)	2 (5)(a)	9 (13)(a)	0(a)
Drained	25 (31)(b)	14 (16)(b)	8 (17)(a)	1 (2)(a)

[a]Species included in each functional group are given in the text. Differences in the extent of the cover of each functional group between locations were assessed with one-way analysis of variance, and results are given as mean percentage cover (standard error). Significant differences ($p < 0.05$) are present for a functional group between locations when no letters are in common. No comparisons were made between functional groups, and thus letters should only be used to assess significant difference within a column.

[b]$F_{(5, 95)} = 15.36$, $p < 0.001$.
[c]$F_{(5, 95)} = 8.93$, $p < 0.001$.
[d]$F_{(5, 95)} = 2.63$, $p = 0.028$.
[e]$F_{(5, 95)} = 4.28$, $p = 0.001$.

Sphagnum magellanicum, Sphagnum rubellum, and *Polytrichum strictum* with an overstory of sedges such as *Carex oligosperma* and Ericaceous shrubs including *Chamaedaphne calyculata* and *Vaccinium oxycoccus.* In contrast, hollows at the drained site had *Sphagnum* (primarily *Sphagnum majus*) and hepatic cover with sparse *Carex oligosperma* and *Rhyncospora alba.* Drained lawns had a substantial sedge layer dominated by *Carex oligosperma* with an understory of *Sphagnum papillosum* and *S. magellanicum.* Drained hummocks had a more limited moss cover of *Polytrichum strictum, S. rubellum,* and *S. magellanicum* than hummocks in the control site, but the overstory of *Carex oligosperma, Andromeda polifolia var. glaucophylla* and *Chamaedaphne calyculata* increased.

3.2. Carbon Dioxide Exchange

[14] Emissions of CO_2 during winter (November–April) were not significantly different between the control and drained sites. Estimated CO_2 loss during this period was 82, 53, and 157 g CO_2 m^{-2} at control hummocks, lawns, and hollows and 59, 86, and 52 g CO_2 m^{-2} at drained hummocks, lawns, and hollows. This resulted in values of NEE over the study period (July 2001 to September 2002) of −445, 164, and −118 g CO_2 at hummocks, lawns, and hollows at the control site and −1321, −228 and 38 g CO_2 at drained hummocks, lawns, and hollows. Negative values indicate a release of CO_2 to the atmosphere, and standard deviations for all values were between 100 and 250 g CO_2.

[15] During the 2002 growing season at the control site, lawns and hollows were generally net sinks of CO_2 during the day, with hummocks shifting between acting as sinks and sources. At the drained site, lawns and hollows were also net CO_2 sinks, but hummocks were sources of CO_2 on most sampling dates. The rates of GEP and R_{tot} varied over the measurement period (Figure 1) corresponding to shifts in available PAR, LAI, water table, and temperature between sampling dates. Rates of GEP and R_{tot} were generally greater in 2002 than 2001 (Figure 2). Despite this interannual variability, differences between sites were consistent in both growing seasons. The two-way analysis of variance revealed a significant interaction between drainage and microform type for both maximum GEP and NEE. This interaction was present because while drainage resulted in higher productivity at lawns and hollows, hummocks became less productive and larger sources of atmospheric CO_2. No significant interaction existed for R_{tot} but there were significant differences between microforms and sites with hummocks and lawns having greater rates of R_{tot} than hollows and the drained site having greater rates of R_{tot} than the control site (Figure 2b).
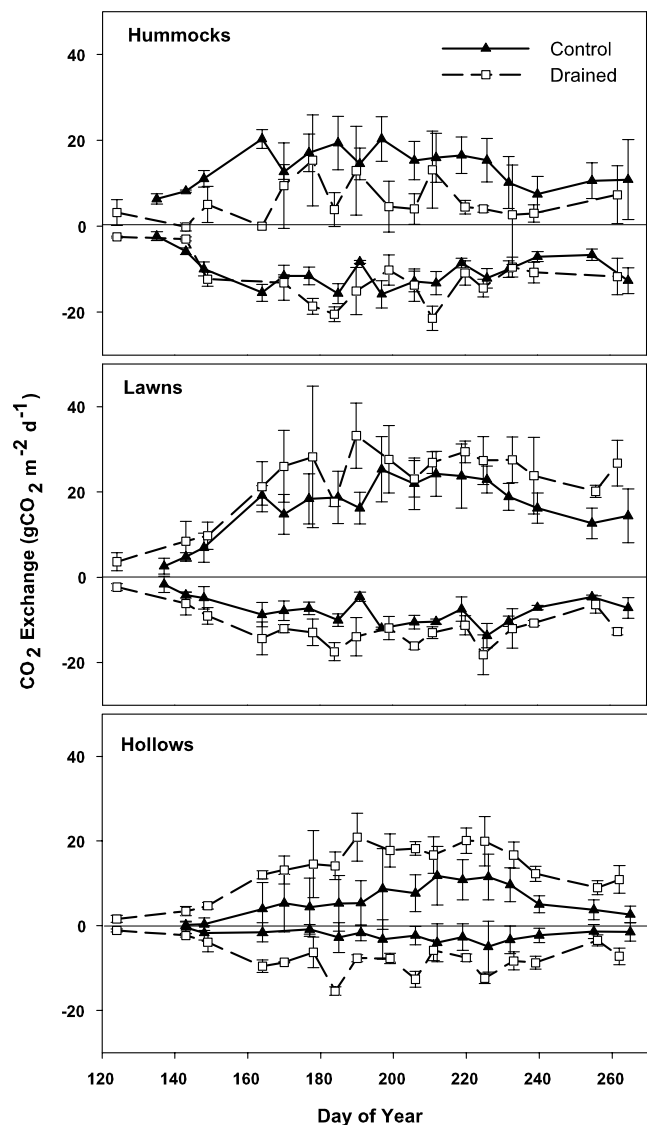

Figure 1. GEP (positive values) at ambient PAR and (negative values) R_{tot} through time at (solid line, solid triangles) the control and (dashed line, open squares) drained sites in 2002. Error bars indicate one standard deviation.
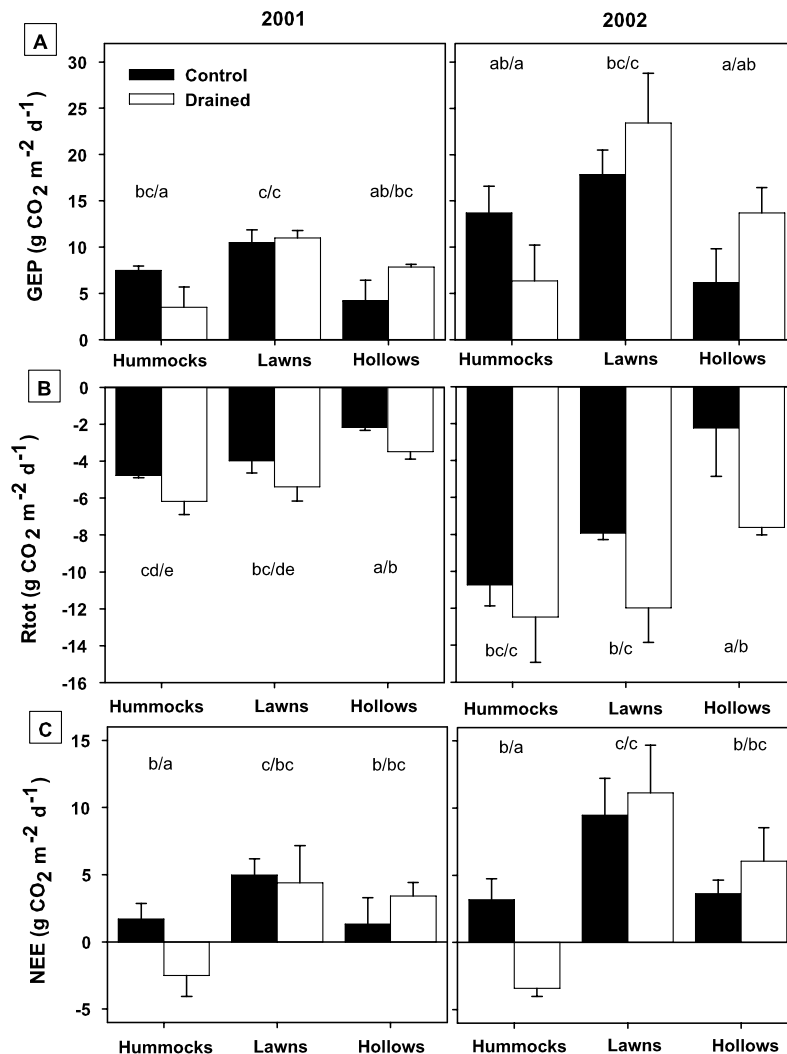
Figure 2. (a) Maximum GEP, (b) R_{tot}, and (c) maximum NEE for all microforms at (solid rectangles) control and (open rectangles) drained sites during the growing season in 2001 and 2002. Error bars indicate one standard deviation. Results from one-way analysis of variance completed separately for each year are indicated by letters above each bar. Differences were assessed between groups of study plots grouped according to microform and drainage. Sites are significantly different at $p < 0.05$ if they have no letters in common (letters should be compared only within one plot; 2001: GEP, $F(5, 12) = 13.64$, $p < 0.001$; R_{tot}, $F(5, 12) = 21.03$, $p < 0.001$; NEE, $F(5, 12) = 12.36$, $p < 0.001$; 2002: GEP, $F(5, 12) = 9.99$, $p = 0.001$; R_{tot}, $F(5, 12) = 14.58$, $p < 0.001$; NEE, $F(5, 12) = 16.07$, $p < 0.001$). Negative values correspond to a flux of CO$_2$ toward the atmosphere.

[16] Control hummocks had greater rates of maximum GEP than drained hummocks while drained hummocks had significantly higher rates of R_{tot} in 2001 but not 2002 (Figures 2a and 2b). This resulted in greater CO$_2$ uptake as maximum NEE at control hummocks with drained hummocks often acting at net sources for atmospheric CO$_2$ (Figure 2c). At lawns, despite the fact that drained lawns had significantly greater rates of R_{tot} than control lawns, larger rates of maximum GEP at the drained site (Figure 2a) resulted in no difference in maximum NEE between the two locations. The hollows at the drained site had higher rates of maximum GEP and maximum NEE (CO$_2$ uptake) and significantly higher rates of R_{tot} than the control site hollow plots (Figure 2).

[17] Large within-microform variability in rates of CO$_2$ exchange was observed and is partially due to the fact that sampling plots were arranged along the microtopographic gradient to encompass the extent of the water table variability at each site in order to gain insight into the differential response of the vegetation community and CO$_2$ fluxes along this gradient. Therefore GEP-PAR and R_{tot}-peat temperature relationships were determined for each individual sampling plot, and examples of these relationships in August 2001 and 2002 for one representative plot within each microform are shown in Figures 3 and 4. Photosynthetically active radiation explained most of the variability in GEP at all sampling plots except for hollows at the control site and hummocks at the drained site. Early in the
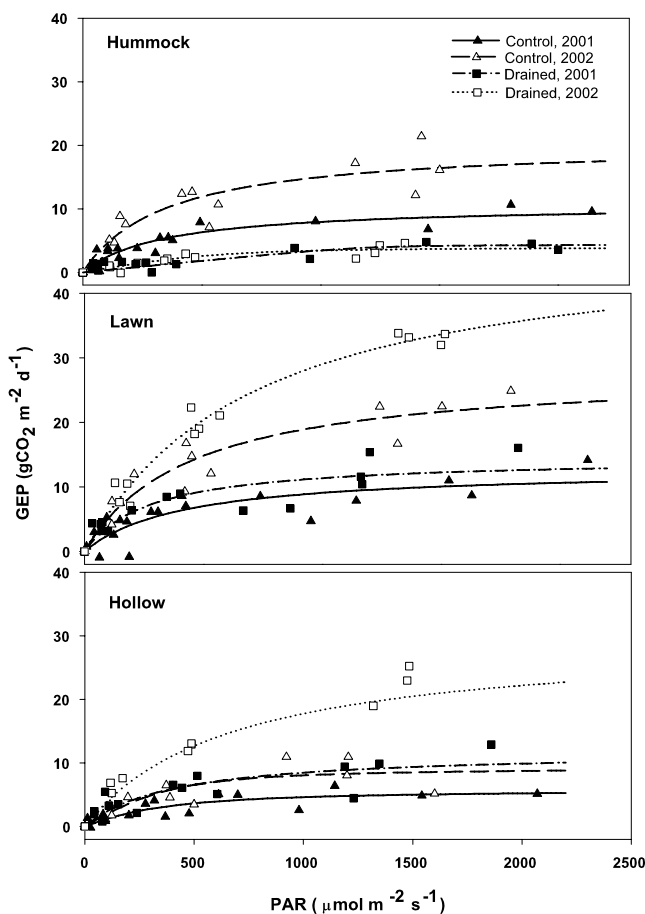
Figure 3. Relationships between GEP and PAR during August at one representative hummock, lawn, and hollow. (solid triangles) Control site, 2001; (open triangles) Control site, 2002; (solid squares) Drained site, 2001; (open squares) Drained site, 2002. Solid and dashed lines give the GEP-PAR curves at the control site in 2001 and 2002, and the dash-dotted and dotted lines show the 2001 and 2002 curves at the drained site.

season, up to 10% more of the variability in GEP could be explained at control and drained lawns and drained hollows by shifting GP$_{max}$ in relation to LAI, and thus this was included for modeling GEP in 2002. Similarly, much of the variability in R_{tot} was related to peat temperature (R^2 = 0.42 to 0.88) except at control hollows where R^2 was often below 0.4. The variability described by these relationships is similar to that in other studies [*Waddington et al.*, 1998; *Dalva et al.*, 2001; *Bubier et al.*, 2003]. In 2002, at the control hollow with an intermediate water table there was no significant relationship between air temperature and R_{tot}; however, a significant negative relationship (R^2 = 0.50, p = 0.007) was present between water table and R_{tot}, and this was used to predict seasonal R_{tot} at this site. In most cases, temperature was related exponentially to R_{tot}; however, if more of the variability in R_{tot} could be explained with a linear relationship, this was used to improve the modeling of R_{tot}.

[18] Using relationships between GEP and PAR and R_{tot} and air/peat temperature with continuously measured PAR and temperature data, seasonal NEE was determined for

each sampling plot for the sampling period (July–October 2001 and May–September 2002; Table 3). Winter flux measurements were weighted for the number of days between measurements and averaged to determine a value for winter NEE. In both years drained hummocks and lawns have become larger sources of CO$_2$ to the atmosphere relative to the control site while seasonal NEE at drained hollows has remained unchanged or shifted to a slightly larger CO$_2$ sink. Because of the low R^2 of some of the relationships used to compute seasonal NEE, particularly at the control hollows and drained hummocks, there is large uncertainty in these estimates, and thus seasonal NEE may not be significantly different between microforms at each site. However, since these modeled values are consistent with the results of the statistical comparisons of maximum GEP, R_{tot}, and maximum NEE, we are confident that they accurately represent the shift in seasonal CO$_2$ exchange that has occurred at the drained site.

4. Discussion

[19] Northern peatlands are expected to become drier under climate change scenarios [e.g., *Roulet et al.*, 1992],
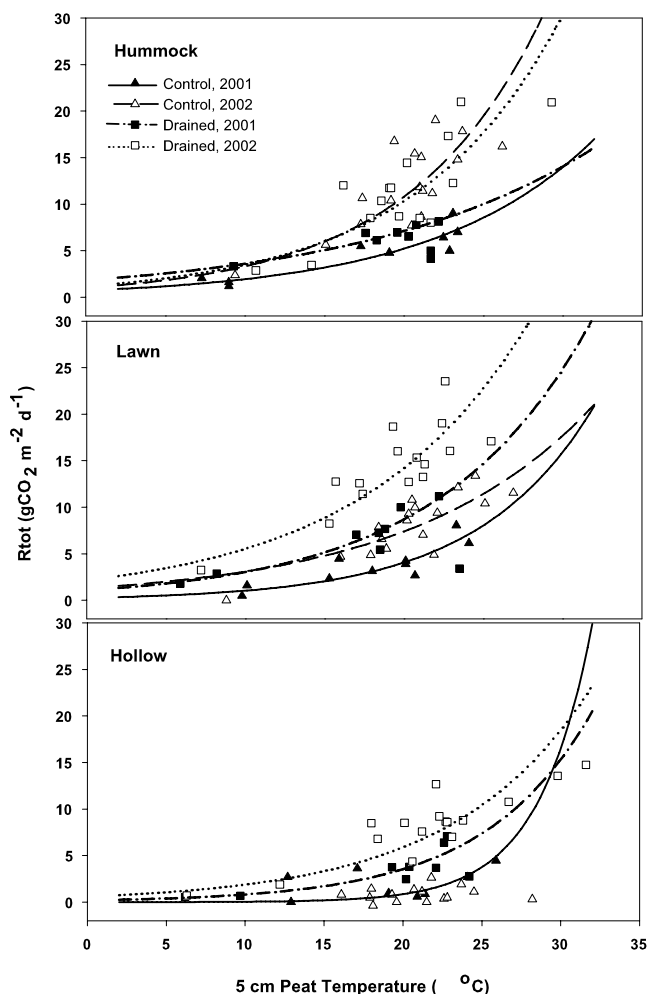

Figure 4. Relationships between R_{tot} and peat temperature at 5 cm depth at hummocks, lawns, and hollows. Symbols and lines are the same as those used in Figure 3.

Table 3. Seasonal GEP, R_{tot}, and NEE for the Sampling Periods July to October 2001 (Day 184 to 292) and May to September 2002 (Day 132 to 267) at Hummocks, Lawns, and Hollows at the Control and Drained Sites[a]

	Growing Season 2001 (July–October)				Growing Season 2002 (May–September)			
	GEP[b]	R_{tot}	NEE	R^2	GEP	R_{tot}	NEE	R^2
				Hummock				
Control	280 (26)	−403 (9)	−123 (35)	0.39−0.66	753 (97)	−993 (105)	−240 (25)	0.52−0.70
Drained	215 (42)	−541 (90)	−326 (63)	−0.20−0.66	361 (113)	−1297 (138)	−936 (25)	0.12−0.40
				Lawn				
Control	368 (22)	−307 (37)	61 (59)	0.30−0.65	958 (88)	−802 (13)	156 (76)	0.72−0.86
Drained	393 (13)	−424 (44)	−32 (31)	0.43−0.73	1215 (151)	−1325 (156)	−110 (19)	0.81−0.85
				Hollow				
Control	129 (42)	−171 (44)	−42 (82)	−0.20−0.22	326 (142)	−245 (156)	81 (23)	0.64−0.80
Drained	311 (7)	−241 (3)	70 (7)	0.48−0.63	698 (79)	−668 (25)	30 (59)	0.54−0.84

[a]Values given are mean (standard error) of the modeled CO$_2$ of three sampling plots for each microform. R^2 was computed for each sampling plot as $1 − $ SST/SSE where SSE was the sum of squares of the difference between modeled and measured NEE, and the range of R^2 at each microform is given. Negative values correspond to a flux of CO$_2$ toward the atmosphere.
[b]GEP, R_{tot}, and NEE are given in g CO$_2$ m^{-2}.

and recently several studies have investigated differences in net ecosystem CO$_2$ change between wet and dry years in order to predict the response of peatland carbon cycling to this potential drying. In most cases, these studies have concluded that under drier conditions, peatland carbon uptake will be reduced or that peatlands will become sources of atmospheric CO$_2$ because of enhanced respiration [*Moore and Dalva*, 1993; *Bellisario et al.*, 1998; *Christensen et al.*, 1998; *Bubier et al.*, 2003] and reduced rates of photosynthesis [*Alm et al.*, 1999; *Griffis et al.*, 2000]. In this study, 2002 was a drier year than 2001, receiving 358 and 433 mm of precipitation, respectively, between May and September (30 year average is 590 mm) resulting in higher rates of R_{tot} and GEP supporting the hypothesis that reduced rates of NEE during drought result from enhanced respiration.

[20] At a raised bog (Mer Bleue) in the same climatic zone, *Lafleur et al.* [2003] observed enhanced respiration rates and reduced rates of photosynthesis during a dry 2001 growing season compared to the previous three wet to average years. Thus the dry conditions during the study period of the present study may have enhanced respiration rates at the drained site and increased moisture stress for vegetation, particularly at drained hummocks. However, since the drained site experienced average climatic conditions during the period between initial water table drawdown and the study seasons (Table 1), the vegetation communities present during the study represent those able to develop under the normal climate at this site. Also, since the CO$_2$ fluxes at the drained site were compared to those from the control site, which likely also experienced enhanced respiration rates, moisture stress at hummocks, and reduced flooding at the hollows during the dry study seasons, the observed differences between the sites should be valid under a range of climatic conditions.

[21] While the comparison of NEE in wet and dry years provides some insight into the response of peatland ecosys-

tems to drought, it represents only a short-term perturbation. In contrast, lower water tables in response to climate change will likely be persistent, allowing time for ecological succession to occur resulting in widespread shifts in the vegetation community. This in turn may lead to very different rates of carbon exchange than those observed when the existing community undergoes stress. Evidence from naturally pipe drained peatland pools and peatlands drained for forestry or research has revealed that persistently lowered water tables will result in ecological succession [*Foster et al.*, 1988; *Minkkinen et al.*, 2002; *Laiho et al.*, 2003; *Weltzin et al.*, 2003] leading to subsequent shifts in carbon accumulation [*Minkkinen et al.*, 2002]. In the present study, changes in the vegetation community were observed at all microforms following 8 years of persistent water table drawdown. The relative vegetation cover (the ratio of total moss and vascular cover to the maximum moss and vascular cover observed in the study plots) was significantly correlated to estimated growing season GEP in both study seasons (2001: $p = 0.001$, $R^2 = 0.49$; 2002: $p = 0.06$, $R^2 = 0.21$). Similarly, *Bubier et al.* [2003] report significant relationships between foliar biomass at sampling plots in a bog with measurements of CO$_2$ exchange. This link between this changing vegetation and observed shifts in CO$_2$ exchange highlights the importance of considering ecological succession when predicting changes in peatland carbon accumulation rates under climate change scenarios.

[22] Despite the fact that the vegetation community was altered at all sampling plots, the resulting community and subsequent rate of NEE varied between microforms. Water table drawdown results in peat compression [*Price and Schlotzhauer*, 1999; *Kellner and Halldin*, 2002] and oxidation [*Schothorst*, 1977] in the larger aerobic zone, leading to a dense peat which experiences large water table fluctuations [*Price*, 2003], particularly at hummocks. At drained hummocks, the availability of surface moisture was reduced since the average water table was 32 cm below the surface.

The survival of *Sphagnum* moss is limited when soil moisture content is low [*Clymo and Hayward*, 1982; *McNeil and Waddington*, 2003; *Price and Whitehead*, 2004], and *Sphagnum* cover at the drained hummocks was reduced compared to the control site (Table 2). Although some *Sphagnum* species (e.g., *Sphagnum fuscum*) may be able to maintain productivity under these conditions, those dominant at control hummocks at SCB (*Sphagnum rubellum* and *S. magellanicum*) have been reduced in surface cover following water table drawdown. Despite a small increase in vascular plant cover, the large reduction in the presence of mosses resulted in reduced GEP at the drained hummocks. Because the water table drawdown also enhanced the size of the aerobic zone, respiration rates increased at drained hummocks. The reduced rates of GEP and enhanced R_{tot} both contributed to the creation of the larger source of atmospheric CO_2 at the drained hummocks. At lawns, peat subsidence in response to the water table drawdown allowed the water table to remain close enough to the surface that *Sphagnum* could thrive, while the slightly drier conditions enabled an invasion by sedges, particularly *Carex oligosperma*. This increase in sedge LAI was primarily responsible for the higher rates of GEP at drained lawns compared to control lawns. However, this increased biomass and the larger aerobic zone in the peat profile increased R_{tot} rates to more than compensate for the enhanced GEP. Thus despite ecological succession, drained lawns were net sources of atmospheric CO_2 differentiating them from the control lawns which acted as CO_2 sinks. At the hollow plots, the water table drawdown primarily resulted in the removal of open water revealing a moist, unvegetated peat surface. The elimination of long periods of flooding allowed the colonization of these sites by *Sphagnum* and vascular plants which resulted in increased rates of GEP. Respiration rates were also enhanced at these locations; however, since the water table remained near the surface of the peat, this increase was limited. Thus rates of NEE at drained hollows were unchanged or CO_2 uptake slightly enhanced relative to the control site following the water table drawdown. This suggests that in some years the drained hollows may act as larger sinks for atmospheric CO_2 than those at the control site.

[23] The changes in hydrology and vegetation community following water table drawdown may be important for peat mineralization and nutrient cycling which may feedback to further shifts in the vegetation community. Since *Sphagnum* mosses decompose very slowly [e.g., *Hobbie*, 1996] the reduction in *Sphagnum* cover at drained hummocks and lawns may result in enhanced rates of peat decomposition at these locations regardless of the change in water table position. This, combined with the potential for enhanced nutrient mineralization in the expanded aerobic zone at these microforms, has the potential to improve nutrient availability. *Chapin et al.* [1995] have shown that shrub growth in arctic ecosystems is increased when rates of nutrient cycling are enhanced, and thus the shifting vegetation community is likely driven not only by direct changes in soil moisture and water table but also the corresponding shifts in nutrient cycling which occur following water table drawdown.

[24] The results of this study are consistent with the relationships between peat formation and water table depth
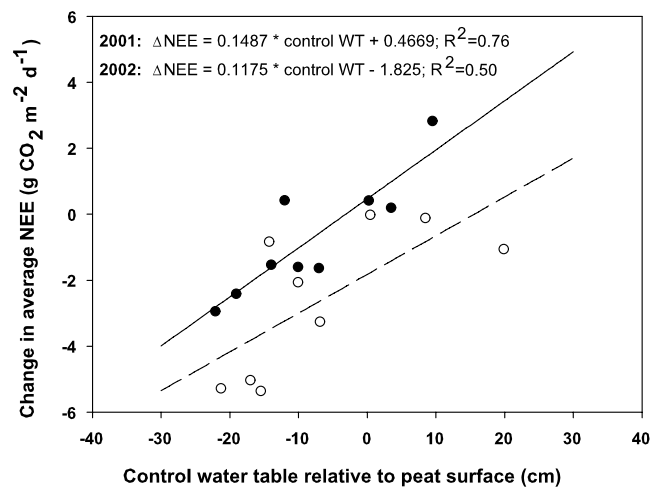

Figure 5. Shifts in seasonal NEE in response to the water table drawdown in relation to initial (control) average water table position. Solid symbols/lines and open symbols/dashed lines correspond to 2001 and 2002, respectively.

determined by *Belyea and Clymo* [2001]. In their investigation of peat microforms they observed a unimodal relationship between productivity and water table, increasing rates of decay with deeper water tables, and a unimodal relationship between the rate of peat formation and water table depth with maximum rates when water table was 10 cm below the surface. Similar relationships were observed in the present study with the highest GEP and NEE observed at intermediate water table depths at control lawns and drained lawns and hollows, while respiration increased at all microforms following water table drawdown. Incorporating these results in a model linking changes in peat accumulation and water storage, *Belyea and Clymo* [2001] suggest that on short timescales, individual microforms may vertically expand and contract in response to changes in water storage while on a longer timescale the rate of peat accumulation and dominant microform type may be altered. Our results support this hypothesis as the increased release of CO_2 from hummocks and net CO_2 uptake at hollows suggests that the surface of the peatland is becoming flatter, limiting the area of hollows and pools and resulting in a system with more uniform CO_2 exchange rates similar to control lawns and hummocks.

[25] Since different microforms have differential responses to water table drawdown it is essential that the initial distribution of microforms be considered when predicting peatland NEE under climate change scenarios. As hypothesized by *Waddington et al.* [1998], we have observed that the shift in NEE resulting from a hydrologic change is dependent on the initial water table position (Figure 5). We suggest that a peatland with an average water table that is currently 20 cm below the surface is expected to become a large source of atmospheric CO_2, whereas sites where the water table is 5–10 cm above the surface will maintain their current rate of CO_2 exchange. While a linear relationship between initial water table position and change in NEE is given in Figure 5, we expect that the true relationship is not this simple. In this study, sampling plots with initial water table of 25 cm below the

surface to 20 cm above the surface are considered; however, sites with water tables beyond this range will likely behave differently. For example, lowering the water table 20 cm at a flooded site with over 50 cm of standing water will probably not enhance GEP or R_{tot} since the site will remain flooded. Similarly, at very dry sites, further drying may not significantly affect the productivity of the vegetation community or the rate of respiration. Thus we hypothesize that the relationship given in Figure 5 may be S shaped if the range of water tables considered is expanded. Further investigation is required to test this prediction.

[26] Ecological succession induced by lowered water tables will also influence other aspects of the peatland carbon cycle. The development of a dense sedge community at drained lawns and hollows and the corresponding enhancement of GEP at these microforms may enrich the pool of labile carbon available for methane (CH$_4$) production and provide a pathway for CH$_4$ release from the anoxic zone via vascular plant aerenchyma [e.g., *Whiting and Chanton*, 1993]. At the drained site the presence of sedges at lawns enhances CH$_4$ emissions during wet conditions [*Strack et al.*, 2006]. Similarly, CH$_4$ emissions from drained and control hollows are similar and are well related to seasonal GEP at the sampling plot [*Strack et al.*, 2004]. The shift in the vegetation community may also be important for altering the quantity and nature of the organic carbon produced and flushed from peatlands [*Kalbitz et al.*, 2000; *Laiho et al.*, 2003]. Consequently, the magnitude of carbon fluxes from peatlands under climate change scenarios cannot be simply predicted from contemporary relationships between these fluxes and environmental variables such as temperature and water table. Instead an approach considering the interactions between peatland hydrology and ecology and the spatial variability of these interactions is required in order to achieve a more accurate understanding of peatland response.

5. Conclusions

[27] In response to a persistent water table drawdown of approximately 20 cm, changes in the vegetation community and rates of NEE within a poor fen differed between peatland microforms. Drained hummocks exhibited dry surface conditions resulting in a reduction in *Sphagnum* cover and GEP and an increase in R_{tot}. Thus hummocks at the drained site were larger sources of atmospheric CO$_2$ than those at the control site. The vegetation community at drained lawns consisted of a *Sphagnum* cover similar to control lawns along with a dense overstory of sedges. While the increased sedge cover was linked to higher rates of GEP, the enhancement of R_{tot} in response to ecohydrological changes resulted in conversion of drained lawns to net CO$_2$ sources over the growing season while control lawns acted as net sinks. Drained hollows were transformed from sparsely vegetated open water habitats at the control site to low-lying moist *Sphagnum* carpets at the drained site. This resulted in higher rates of GEP and R_{tot} and may result in enhanced CO$_2$ uptake in some years. The response of the vegetation community to a persistently lower water table was integral in controlling the shifts in carbon exchange. Therefore the prediction of future carbon accumulation rates in northern peatlands should consider the effects of ecolog-

ical succession in addition to contemporary water table-temperature-NEE relationships. Furthermore, since the response of microforms to drying was different, it is important to consider the antecedent moisture conditions and the distribution of microforms within a peatland when predicting rates of ecosystem carbon accumulation under future climate scenarios.

References

Alm, J., L. Schulman, J. Walden, H. Nykanen, P. J. Martikainen, and J. Silvola (1999), Carbon balance of a boreal bog during a year with an exceptionally dry summer, *Ecology*, *80*, 161–174.

Anderson, L. E., H. A. Crum, and W. R. Buck (1990), List of the mosses of North America north of Mexico, *Bryologist*, *93*, 448–499.

Bellisario, L. M., T. R. Moore, and J. L. Bubier (1998), Net ecosystem CO$_2$ exchange in a boreal peatland, northern Manitoba, *Ecoscience*, *5*, 534–541.

Belyea, L. R., and R. S. Clymo (2001), Feedback control of the rate of peat formation, *Proc. R. Soc., Ser. B*, *268*, 1315–1321.

Belyea, L. R., and N. Malmer (2004), Carbon sequestration in peatland: Patterns and mechanisms of response to climate change, *Global Change Biol.*, *10*, 1043–1052.

Billings, W. D., J. O. Lukens, D. A. Mortensen, and K. M. Peterson (1982), Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment?, *Oecologia*, *53*, 7–11.

Blackford, J. (2000), Palaeoclimatic records from peat bogs, *Trends Ecol. Evol.*, *15*, 193–198.

Bubier, J. L., G. Bhatia, T. R. Moore, N. T. Roulet, and P. M. Lafleur (2003), Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada, *Ecosystems*, *6*, 353–367.

Burrows, E., J. Bubier, A. Mosedale, G. Cobb, and P. Crill (2005), Net ecosystem exchange of carbon dioxide in a temperate poor fen: A comparison of automated and manual chamber techniques, *Biogeochemistry*, *76*, 21–56, doi:10.1007/s10533-004-6334-6.

Chapin, F. S., III, G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre (1995), Responses of arctic tundra to experimental and observed changes in climate, *Ecology*, *76*, 694–711.

Charman, D. (2002), *Peatlands and Environmental Change*, John Wiley, Hoboken, N. J.

Christensen, T. R., S. Jonasson, A. Michelsen, T. V. Callaghan, and M. Havstrom (1998), Environmental controls on soil respiration in the Eurasian and Greenlandic Arctic, *J. Geophys. Res.*, *103*, 15–29.

Clymo, R. S. (1984), The limits to peat bog growth, *Philos. Trans. R. Soc., Ser. B*, *303*, 605–654.

Clymo, R. S., and P. M. Hayward (1982), The ecology of *Sphagnum*, in *Bryophyte Ecology*, edited by A. J. E. Smith, pp. 229–289, CRC Press, Boca Raton, Fla.

Dalva, M., T. R. Moore, P. Arp, and T. A. Clair (2001), Methane and soil and plant community respiration from wetlands, Kejimkujik National Park, Nova Scotia: Measurement, predictions, and climatic change, *J. Geophys. Res.*, *106*, 2962–2995.

Foster, D. R., H. E. Wright Jr., M. Thelaus, and G. A. King (1988), Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada, *J. Ecol.*, *76*, 1164–1185.

Freeman, C., M. A. Lock, and B. Reynolds (1993), Fluxes of CO$_2$, CH$_4$ and N$_2$O from a Welsh peatland following simulation of water table drawdown: Potential feedback to climatic change, *Biogeochemistry*, *19*, 51–60.

Gorham, E. (1991), Northern peatlands: Role in the carbon cycle and probable responses to climatic warming, *Ecol. Appl.*, *1*, 182–195.

Griffis, T. J., W. R. Rouse, and J. M. Waddington (2000), Interannual variability of net ecosystem CO$_2$ exchange at a subarctic fen, *Global Biogeochem. Cycles*, *14*, 1109–1121.

Hobbie, S. E. (1996), Temperature and plant species control over litter decomposition in Alaskan tundra, *Ecol. Monogr.*, *66*, 503–522.

Hurlbert, S. H. (1984), Pseudoreplication and the design of ecological field experiments, *Ecol. Monogr.*, *54*, 187–211.

Joosten, H., and D. Clarke (2002), *Wise Use of Mires and Peatlands—Background and Principles Including a Framework for Decision-Making*, Int. Mire Conserv. Group and Int. Peat Soc., Saarijärvi, Finland.

Kalbitz, K., S. Solinger, J. H. Park, B. Michalzik, and E. Matzner (2000), Controls on the dynamics of dissolved organic matter in soils: A review, *Soil Sci.*, *165*, 277–304.

Kellner, E., and S. Halldin (2002), Water budget and surface-layer water storage in a *Sphagnum* bog in central Sweden, *Hydrol. Processes*, *16*, 87–103.

Lafleur, P. M., N. T. Roulet, J. L. Bubier, S. Frolking, and T. R. Moore (2003), Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochem. Cycles*, *17*(2), 1036, doi:10.1029/2002GB001983.

Laiho, R., H. Vasander, T. Penttilä, and J. Laine (2003), Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands, *Global Biogeochem. Cycles*, *17*(2), 1053, doi:10.1029/2002GB002015.

Marie-Victorin, F. (1964), *Flore Laurentienne. Deuxième Édition*, Les Presses de l'Univ. de Montréal, Montréal, Que., Can.

McNeil, P., and J. M. Waddington (2003), Moisture controls on *Sphagnum* growth and CO$_2$ exchange on a cutover bog, *J. Appl. Ecol.*, *40*, 354–367.

Minkkinen, K., R. Korhonen, I. Savolainen, and J. Laine (2002), Carbon balance and radiative forcing of Finnish peatlands 1900–2100: The impact of forestry drainage, *Global Change Biol.*, *8*, 785–799.

Mitchell, F. B. J. (1989), The "greenhouse" effect and climatic change, *Rev. Geophys.*, *27*, 115–139.

Moore, P. D. (1998), The future of cool temperate bogs, *Environ. Conserv.*, *29*, 3–20.

Moore, T. R. (1989), Plant production, decomposition, and carbon efflux in a subarctic patterned fen, *Arct. Alp. Res.*, *21*, 156–162.

Moore, T. R., and M. Dalva (1993), The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils, *J. Soil Sci.*, *44*, 651–661.

Moore, T. R., and R. Knowles (1989), The influence of water table levels on methane and carbon dioxide emissions from peatland soils, *Can. J. Soil Sci.*, *69*, 33–38.

Price, J. S. (2003), Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands, *Water Resour. Res.*, *39*(9), 1241, doi:10.1029/2002WR001302.

Price, J. S., and S. M. Schlotzhauer (1999), Importance of shrinkage and compression in determining water storage changes in peat: The case of a mined peatland, *Hydrol. Processes*, *13*, 2591–2601.

Price, J. S., and G. S. Whitehead (2004), The influence of past and present hydrological conditions on *Sphagnum* recolonization and succession in a block-cut bog, Quebec, *Hydrol. Processes*, *18*, 315–328.

Rochefort, L., D. H. Vitt, and S. E. Bayley (1990), Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions, *Ecology*, *71*, 1986–2000.

Roulet, N., T. Moore, J. Bubier, and P. Lafleur (1992), Northern fens: Methane flux and climatic change, *Tellus, Ser. B*, *44*, 100–105.

Schothorst, C. J. (1977), Subsidence of low moor peat soil in the western Netherlands, *Geoderma*, *17*, 265–291.

Strack, M., J. M. Waddington, and E.-S. Tuittila (2004), Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change, *Global Biogeochem. Cycles*, *18*, GB4003, doi:10.1029/2003GB002209.

Strack, M., M. F. Waller, and J. M. Waddington (2006), Sedge succession and peatland methane dynamics: A potential feedback to climate change, *Ecosystems*, *9*, 278–287, doi:10.1007/s10021-005-0070-1.

Updegraff, K., S. D. Bridgham, J. Pastor, and P. Weishampel (1998), Hysteresis in the temperature response of carbon dioxide and methane production in peat soils, *Biogeochemistry*, *43*, 253–272.

Vitt, D. H. (1990), Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients, *Bot. J. Linn. Soc.*, *104*, 35–59.

Waddington, J. M., and N. T. Roulet (1996), Atmosphere-wetland carbon exchanges: Scale dependency of CO$_2$ and CH$_4$ exchange on the developmental topography of a peatland, *Global Biogeochem. Cycles*, *10*, 233–245.

Waddington, J. M., T. J. Griffis, and W. R. Rouse (1998), Northern Canadian wetlands: Net ecosystem CO$_2$ exchange and climatic change, *Clim. Change*, *40*, 267–275.

Weltzin, J. F., S. D. Bridgham, J. Pastor, J. Chen, and C. Harth (2003), Potential effects of warming and drying on peatland plant community composition, *Global Change Biol.*, *9*, 141–151.

Whiting, G. J., and J. P. Chanton (1993), Primary production control of methane emission from wetlands, *Nature*, *364*, 794–795.

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