Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO_2 Fluxes in an Alaskan Rich Fen

M. R. Chivers,[1] M. R. Turetsky,[2]* J. M. Waddington,[3] J. W. Harden,[4] and A. D. McGuire[5]

[1]Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824, USA; [2]Department of Integrative Biology, University of Guelph, Guelph, Ontario N1G 1G2, Canada; [3]School of Geography and Earth Sciences, McMaster University, Hamilton, Ontario L8S 4L8, Canada; [4]U.S. Geological Survey, Menlo Park, California 94025, USA; [5]U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA

ABSTRACT

Peatlands store 30% of the world's terrestrial soil carbon (C) and those located at northern latitudes are expected to experience rapid climate warming. We monitored growing season carbon dioxide (CO_2) fluxes across a factorial design of in situ water table (control, drought, and flooded plots) and soil warming (control vs. warming via open top chambers) treatments for 2 years in a rich fen located just outside the Bonanza Creek Experimental Forest in interior Alaska. The drought (lowered water table position) treatment was a weak sink or small source of atmospheric CO_2 compared to the moderate atmospheric CO_2 sink at our control. This change in net ecosystem exchange was due to lower gross primary production and light-saturated photosynthesis rather than increased ecosystem respiration. The flooded (raised water table position) treatment was a greater CO_2 sink in 2006 due largely to increased early season gross primary production and higher light-saturated photosynthesis. Although flooding did not have substantial effects on rates of ecosystem respiration, this water table treatment had lower maximum respiration rates and a higher temperature sensitivity of ecosystem respiration than the control plot. Surface soil warming increased both ecosystem respiration and gross primary production by approximately 16% compared to control (ambient temperature) plots, with no net effect on net ecosystem exchange. Results from this rich fen manipulation suggest that fast responses to drought will include reduced ecosystem C storage driven by plant stress, whereas inundation will increase ecosystem C storage by stimulating plant growth.

Key words: peatland; boreal; wetlands; Alaska; carbon; carbon dioxide; climate change; drought; flooding; warming.

INTRODUCTION

Wetlands store about 50% of the total carbon (C) stock in northern North America, and the majority of this C is stored in peatlands (Pacala and others 2007; Bridgham and others 2006). Peatlands globally store an estimated 397–455 Pg C, equivalent to about 30% of the world's terrestrial soil C (Gorham

1991; Zoltai and Martikainen 1996; Moore and others 1998), though recent soil carbon inventories suggest that deeper soil carbon underneath permafrost-regulated ecosystems, including some northern peatlands, may be underestimated (Schuur and others 2008). Globally, peatlands currently are thought to function as a net sink for atmospheric carbon dioxide (CO_2), sequestering approximately 76 Tg (10^{12} g) C y^{-1} (Zoltai and Martikainen 1996), and as a net source of atmospheric methane (CH_4). In general, peat accumulates where C fixation through net primary production (NPP) at the surface exceeds losses from decomposition, leaching export, and/or disturbance throughout the entire peat column (Clymo 1983). As climate change alters hydrologic and soil thermal regimes in peatlands, changes in C inputs to soils by vegetation, decomposition rates, and C export could all potentially alter C fluxes and peat accumulation rates.

Alaskan wetlands are estimated to store approximately 42 ± 20 Pg C, or over 10% of the global wetland C pool (Bridgham and others 2006). Over the past several decades, interior Alaska has experienced rapid climate change that has resulted in soil warming, permafrost degradation, decreased snow pack thickness, and increased growing season length (Keyser and others 2000; Serreze and others 2000; Goetz and others 2005; Osterkamp and Romanovsky 1999; Hinzman and others 2005). Throughout much of interior Alaska, there has been a recent decline in the surface area of open water bodies, often accompanied by the encroachment of drier terrestrial vegetation (Riordan and others 2006). Wetland contraction likely is associated with increased summer water deficits due to increased evapotranspiration, or drainage associated with permafrost thaw (Oechel and others 2000; Hinzman and others 2005). However, in some other Alaskan regions such as the Tanana Flats, wetlands are becoming more saturated due to permafrost thaw and increased upwelling of melt water (Jorgenson and Osterkamp 2005). Thus, while some wetlands in Alaska are drying, others currently are becoming wetter, suggesting that future changes in wetland hydrology could include either drying or inundation depending on landscape position and response to increased runoff, permafrost thaw, changes in precipitation, and increased evapotranspiration.

Water table drawdown in peatlands can have either negative (Laine and others 1996; Minkkinen and Laine 1998; Weltzin and others 2000) or positive (Moore and Dalva 1993; Waddington and others 2001; Freeman and others 1996, 1997; Updegraff and others 2001) feedbacks to greenhouse

gas emissions depending on site and vegetation characteristics. Although lower water tables generally are expected to increase decomposition rates in the short-term (that is, fast ecosystem responses), several longer-term studies have shown that drainage of Finnish peatlands ultimately increased soil C storage through altered soil C inputs (Minkinnen and others 2002; Laiho and others 2003). There are few studies investigating the consequences of flooding on fast or slow peatland C responses, although more inundated conditions following permafrost thaw in general has led, at least initially, to both increased gross primary production and CH_4 fluxes (Turetsky and others 2002; Wickland and others 2006).

Warmer air and soil temperatures will affect evapotranspiration rates, and also will have direct effects on autotrophic and heterotrophic CO_2 fluxes. Previous studies have shown that warmer soil temperatures generally stimulate microbial activity, resulting in increased ecosystem respiration (Moore and Dalva 1993; Frolking and Crill 1994; Silvola and others 1996; Christensen and others 1999). Soil warming also may increase vegetation productivity in northern ecosystems due to greater nutrient availability (Hobbie and Chapin 1998).

Although many studies have investigated climatic controls on C cycling processes using peat microcosms in the laboratory, few studies have used in situ experimental approaches to study peatland C cycling processes at ecosystem scales. The majority of field experiments have been limited to water-table drawdown studies in *Sphagnum*-dominated bogs and poor fens (for example, Strack and Waddington 2007). In general, these experiments have shown that changes in the vegetation community plays an important role in CO_2 exchange, highlighting the importance of larger-scale experimental manipulations. Rich fens represent the most common peatland type in western North America (Vitt 2006). We recently initiated one of the first ecosystem-scale experiments to test hydrologic and warming controls on C cycling responses in a rich fen. In this experiment, we manipulated water table position (three treatments including a control, a lowered, and a raised water table treatment) and surface soil temperature (two treatments including an ambient temperature control treatment and a surface soil warming treatment via open top chambers) in a factorial design. At least in the short-term, we predicted that ecosystem CO_2 fluxes would be driven by variation in ecosystem respiration, and that greater soil respiration rates in the warming and lowered water

table treatments would result in net losses of eco-system C to the atmosphere.

METHODS

Experimental Design

The Alaska Peatland Experiment (APEX) sites are located outside the boundaries of the Bonanza Creek Experimental Forest and within the Tanana River floodplain, approximately 35 km southeast of Fairbanks, Alaska, USA (64.82 °N, 147.87 °W). The APEX site used for this study is a moderate rich fen (surface water pH 5.2–5.4). The mean annual temperature of the area is $-2.9°C$ with mean annual precipitation of 269 mm (Hinzman and others 2006). This site lacks trees and is dominated by brown moss, *Sphagnum*, and emergent vascular species (*Equisetum, Carex,* and *Potentilla*). There is little microtopography across the site and the peat depth exceeds 1 m at the center of the site. Seasonal ice is present until late August and there is no surface permafrost (that is, in the top 40 cm of organic soil) at the APEX fen.

During early spring of 2005, we established a factorial design of water table position (control, raised water table, and lowered water table) and soil warming (control or ambient temperature versus passive soil warming) treatments. We created three 120 m^2 plots and assigned each to one of three water table treatments (raised or flooded, lowered or drought, and control or no change) based on water flow. In March 2005, while soils were still frozen, we used a small excavator to dig drainage channels to divert water from the lowered water table plot to a small holding trench down slope. In May and June 2005, solar powered bilge pumps were installed to pump water into the raised water table treatment from a surface well located about 20 m down slope of the treatment. Water was added to the raised water table treatment at a rate of approximately 10 cm of water/day. The chemistry of water additions was similar to ambient pore water in the raised water table treatment (no significant differences in pH, electrical conductivity, DOC, anion, cation, or organic acid concentrations; Turetsky and others 2008).

The goal of the experiment was to maintain lowered (drought) and raised (flooded) water table positions relative to the control without minimizing the considerable ambient variability in water table position at this site. A Campbell Scientific datalogger communication system (Logan, Utah) facilitated the maintenance of natural fluctuations in water table levels in the experimental treatments

by turning pumps on and off based on fluctuations in the control plot. In general, water levels in the raised and lowered water table treatments tracked control treatment water table changes in response to precipitation and seasonal drying trends (Figure 1).

Within each water table treatment, we established six 3 m^2 subplots, which were randomly assigned to one of two warming treatments; including ambient temperature (control) and seasonal warming. Warming treatments were thus replicated in triplicate within each water table treatment. We manipulated air and surface soil temperatures within the warming treatment subplots using open top chambers (OTCs) during the snow-free period following Walker and others (2006). The OTCs were constructed of 0.16 cm thick Lexan, with base dimensions of 0.8 m^2. Throughout the growing season of 2005 and 2006, OTCs passively warmed surface soil (2 cm beneath moss) and air temperatures by 0.5 and 0.7°C, respectively. There was no effect of OTCs on deeper soil temperatures. Although the OTCs in our study system created a subtle warming treatment, we note that permafrost in this region is vulnerable to thawing with such small temperature increases, as permafrost temperatures in interior Alaska are already near 0°C (Osterkamp and Romanovsky 1999; Osterkamp 2007).

Environmental Variables

Beginning in June 2005, mean hourly water table level, photosynthetically active radiation (PAR), and air and soil temperature were recorded continuously with Campbell Scientific dataloggers in each warming subplot over two growing seasons. Air temperature and a depth array of soil temperatures (above moss surface and 2, 10, 25, and 50 cm beneath moss surface) were measured within each subplot using thermistors (Yoshikawa and Hinzman 2003; 6 arrays per water table treatment, 18 total). Water table levels were measured using a pressure transducer (Campbell Scientific, Logan, Utah) installed at the bottom of 5 cm diameter, 1 m long PVC wells in each water table treatment (1 per water table treatment, 3 total). The spatial variability in water table position inside each water table treatment was determined with weekly manual measurements of water table position collected from shallow wells within each subplot during the 2005 and 2006 growing seasons.

In 2006 we experienced datalogger malfunction, which impacted the lowered and control treatment water table data. Weekly manual water table
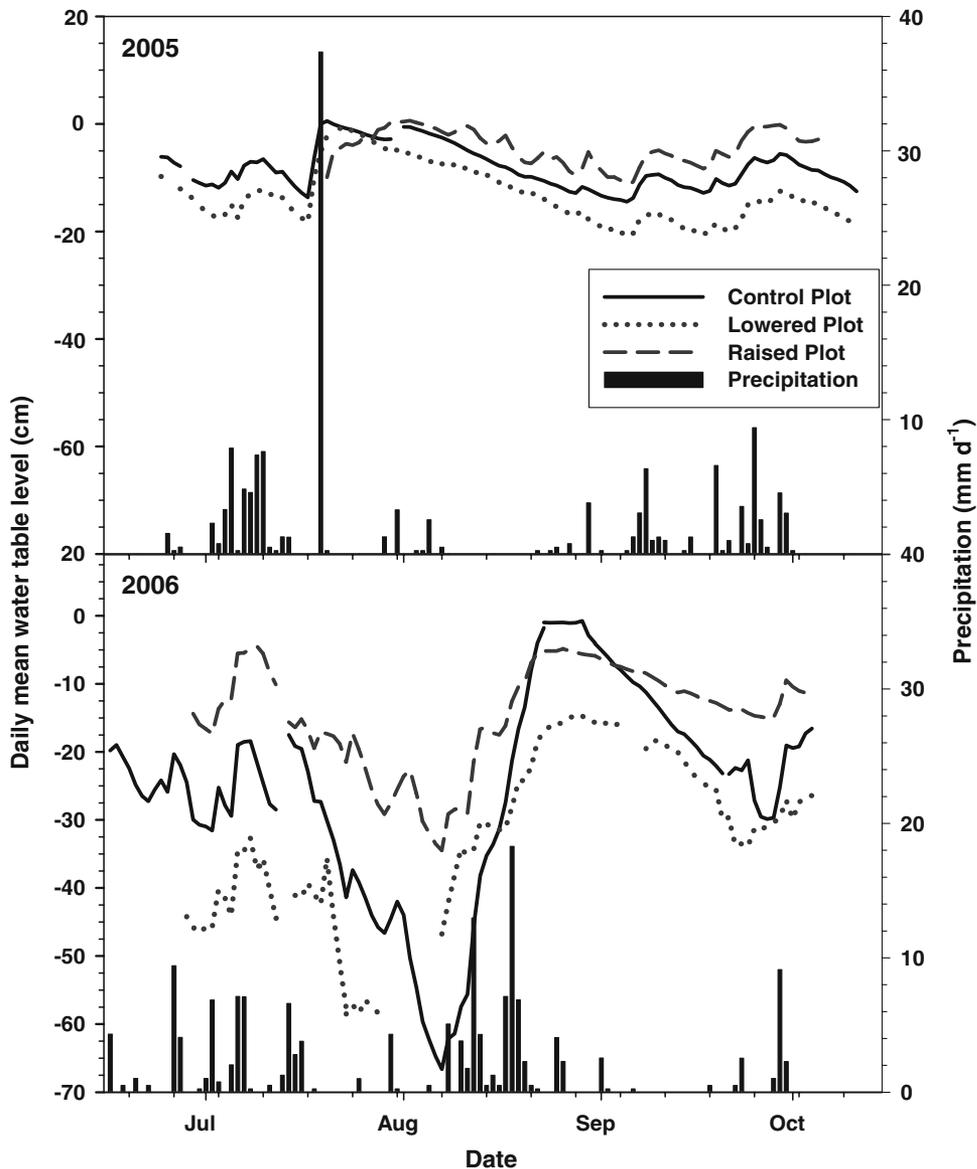
Figure 1. Water table levels and precipitation at the Alaska Peatland Experiment manipulation treatments in 2005 and 2006. Positive values denote water table position above the peat surface (*inundated*). Bars represent precipitation events. Cumulative annual precipitation was not significantly different between the two study years ($F = 1.61$, df = 1, $P = 0.21$).

measurements, the continuous raised water table treatment data, and water storage properties of the peat were used to model continuous water table position in the lowered (July 23–September 20, 2006) and control (July 14–September 20, 2006) water table treatments.

Photosynthetically active radiation (PAR) was measured at each gas flux collar using a Li-COR (Lincoln, Nebraska) quantum light sensor (μmol m^2 s^{-1}). These variables were logged every 5 s and hourly averages were recorded at each water table treatment using Campbell Scientific CR10X dataloggers (Logan, Utah). Hourly averaged tipping bucket precipitation was measured at a meteorological station located within the Tanana River Floodplain.

Vegetation Surveys

Qualitative plant species surveys were performed in 2004 prior to manipulation and showed that species composition did not vary across the plots at the start of experimentation. The percent cover of vascular and bryophyte species was visually estimated within each subplot in July and August 2007. Dominant vascular species included *Carex atherodes*, *Carex canescens*, *Potentilla palustris*, and *Equisetum fluviatile*. Dominant bryophyte species at the site include *Sphagnum* (*Sphagnum obtusum*, *Sphagnum platyphyllum*) and brown moss (*Hamatocaulis vernicosus*, *Drepanocladus aduncus*) species.

In 2007, vascular green (photosynthetic) area (VGA) was measured by counting all vascular plant

leaves within five 8×8 cm subplots systematically distributed in each gas flux collar (see below) each month (Wilson and others 2007); these data were used to extrapolate an estimate of total leaf numbers within each 1 m^2 flux collar. We measured the leaf area of individual plants of each species outside of the flux collars biweekly using a caliper. Species VGA was calculated by multiplying average biweekly surface area of leaves by total leaf numbers within each gas flux collar, and these values were summed for all species present within a flux collar to estimate total VGA. We modeled daily VGA data for each water table treatment × warming treatment as:

$$\text{Daily VGA} = \text{VGA}_{\max} \, e^{\left(-0.5\left(\frac{\text{julian} - x_{\max}}{b}\right)^2\right)} \quad (1)$$

where $\text{VGA}_{\max}$ is the maximum VGA during the season, julian is julian day, $x_{\max}$ is the julian day when maximum VGA occurs, and b denotes the shape of the curve (Wilson and others 2007). This approach assumes that seasonal development of VGA is unimodal and normally distributed, which was supported by our data.

Quantifying and Modeling Ecosystem CO$_2$ Fluxes

Net ecosystem CO$_2$ exchange (NEE) was measured using conventional static chamber techniques following Carroll and Crill (1997). Immediately following snowmelt in 2005, we installed permanent clear Lexan chamber bases, or gas flux collars, in all 18 subplots. The gas flux collars were inserted approximately 10 cm into the soil, taking care not to damage roots, and allowed to equilibrate for one week prior to taking the first flux measurement. A clear plexiglass chamber constructed out of 0.3 cm thick Lexan (area = 0.362 m^2 and volume = 0.227 m^3) was placed and sealed over the collars using foam tape around the chamber base during each flux campaign. An internal fan was used to try to maintain ambient temperature and humidity conditions within the chamber; within-chamber air temperature increased consistently by about 0.3°C over the flux period.

Carbon dioxide (CO$_2$) exchange measurements were conducted weekly throughout the growing season from late May through early October during 2005 and 2006. Carbon dioxide concentration inside the chamber was determined every 1.6 s for 2–3 min using a PP Systems EGM-4 portable infrared gas analyzer (IRGA; Amesbury, Massachusetts).

The IRGA was calibrated before each gas flux campaign using external CO$_2$ standards. In 2006, temperature, relative humidity, and PAR were logged continuously within the chamber during each flux measurement with a PP Systems TRP-1 sensor attached to the inside of the chamber. We attempted to randomize time of day and weather conditions among all measurements to capture full variations of light and temperature for each collar. The CO$_2$ flux rate (μmol CO$_2$ m^{-2} s^{-1}) was calculated as the slope of the linear relationship between headspace CO$_2$ concentration and time. We excluded any slopes with r^2 less than 0.8, which represented less than 3% of flux rates. Immediately following the NEE measurements, the area above the gas flux collars was vented by opening the chamber for approximately one minute. Immediately after this venting, we measured ecosystem respiration (ER) using a dark shroud that blocked all PAR from entering the gas flux chambers. We also used a series of opaque shrouds placed over the chamber to quantify NEE as a function of light intensity (Bubier and others 1998). This included a shroud made of 1.2 mm^2 polyester mesh netting that blocked approximately 50% of PAR, as well as a shroud made of 0.5 mm^2 polyester mesh netting that blocked about 75% of incoming PAR. Gross primary production (GPP) was determined as the difference between NEE and ER from each gas flux collar during the same sampling period. We represent net CO$_2$ uptake from the atmosphere as negative flux rates and net CO$_2$ sources to the atmosphere as positive flux rates.

We analyzed CO$_2$ fluxes using a repeated measures analysis of variance (ANOVA) and Tukey's post hoc comparison of means (SAS Proc Mixed; Littell and others 2006) to determine the effects of water table treatment, soil warming treatment, year, and all interactions among these fixed effects on all three CO$_2$ flux components (NEE, ER, and GPP).

Our water table treatment was not replicated and thus location is confounded with water table plot. We note, however, that the effects of the water table treatment were tested with a small number of degrees of freedom (Table 1). Thus, although some caution is warranted due to the lack of true replicates, we believe that differences in our data are most parsimoniously interpreted as differences in water table depth. Moreover, our baseline data suggested no differences in water table position, vegetation structure, or gas fluxes among water table plots prior to our manipulations. The warming treatment is replicated in our crossed design, as every warming treatment is found within each water table treatment.

We modeled the dependence of photosynthetic activity on variations in PAR and water table position across each water table × soil temperature treatment as:

$$GPP = P_{MAX(PPFD,WT)} \cdot \frac{PPFD}{k + PPFD} \cdot \\ \times \exp\left[-0.5 \cdot \frac{(WT - uP)^2}{tP^2}\right] \quad (2)$$

where PPFD is photon flux density, $P_{max\ (PPFD,WT)}$ is the rate of maximum photosynthesis under light-saturated conditions when water table position (WT) is optimal for photosynthetic activity, uP is the optimal water table for photosynthesis, and tP is a measure of the width of water table amplitude following Tuitilla and others (2004).

We modeled the unimodal dependence of ecosystem respiration, including both autotrophic and heterotrophic respiration rates, on water table position for each experimental treatment as:

$$ER = R_{MAX} \cdot \exp\left[-0.5 \cdot \frac{(WT - uR)^2}{tR^2}\right] \quad (3)$$

where R_{max} is the maximum rate of ecosystem respiration when water table position (WT) is optimal for plant and heterotrophic respiration, uR is the optimal water table for respiration, and tR is a measure of the width of water table amplitude following Tuitilla and others (2004). We also modeled the temperature dependence of ecosystem respiration as:

$$ER = A \times Q_{10}^{\left(\frac{T}{10}\right)} \quad (4)$$

where A is the rate of ecosystem respiration at 0°C, Q_{10} is the temperature dependence of ecosystem respiration, and T is soil temperature at 2 cm beneath the moss surface. We used Proc NLIN in SAS and data from each water table × temperature treatment to model GPP and ER.

Table 1. Results of a Repeated Measures Analysis of Variance Analyzing Weekly Measurements of Net Ecosystem Exchange (NEE), Ecosystem Respiration (ER), and Gross Primary Production (GPP) Across the Experimental Treatments

	df (numerator, denominator)	F	P
Net Ecosystem Exchange (NEE)			
Water table treatment	2, 8	44.73	**<0.0001**
Warming treatment	1, 5	0.11	0.76
Year	1, 5	4.07	0.10
Water table treatment × warming treatment	2, 8	1.70	0.24
Water table treatment × year	2, 8	44.77	**<0.0001**
Warming treatment × year	1, 5	3.98	0.10
Water table treatment × warming treatment × year	2, 8	0.76	0.50
Ecosystem Respiration (ER)			
Water table treatment	2, 8	0.41	0.68
Warming treatment	1, 5	14.18	**0.01**
Year	1, 5	0.71	0.44
Water table treatment × warming treatment	2, 8	1.59	0.26
Water table treatment × year	2, 8	8.85	**0.01**
Warming treatment × year	1, 5	0.67	0.45
Water table treatment × warming treatment × year	2, 8	0.71	0.52
Gross Primary Production (GPP)			
Water table treatment	2, 8	28.64	**0.0002**
Warming treatment	1, 5	12.65	**0.02**
Year	1, 5	17.48	**0.01**
Water table treatment × warming treatment	2, 8	0.53	0.61
Water table treatment × year	2, 8	60.75	**<0.0001**
Warming treatment × year	1, 5	1.54	0.27
Water table treatment × warming treatment × year	2, 8	2.05	0.19

Significant higher-level predictors are marked in bold (P < 0.05).

RESULTS

Soil Climate and Vegetation

Our site experienced warmer and wetter conditions in 2005 than in 2006. Daily air temperatures averaged from May 1 to September 30 were warmer in 2005 ($13.4 \pm 0.1°C$) than in 2006 ($12.3 \pm 0.1°C$; $F_{1,7337} = 53.06$, $P < 0.0001$). The site received more snowfall in 2005 than 2006 (snow water equivalent = 120 mm in 2005; 73 mm in 2006), whereas mean annual growing season precipitation did not vary between years ($F_{1,304} = 1.61$, $P > 0.10$) (Turetsky and others 2008). The raised (flooded) water table treatment had average depths of 9 and 11 cm above that of the control plot in 2005 and 2006, respectively. The lowered (drought) treatment had average water table levels 5 and 8 cm beneath the control plot in 2005 and 2006, respectively (Figure 1). All plots experienced lower water table positions in 2006 than the previous year. The OTCs passively warmed surface soil (2 cm beneath moss) on average by 0.7, 0.9, and 0.6°C in the control, lowered, and raised treatments, respectively. Depths below 2 cm were not affected by the OTCs.

The 2007 vegetation surveys showed that the lowered water table plot had higher cover of dead moss and litter, reduced cover of *Sphagnum* (20% less), and reduced cover of brown moss (50% less) relative to the control plot. Vegetation communities in the raised and control water table plots were similar, although the raised plot had less *Potentilla palustris* cover (~20% less) than the control plot (data not included).

Maximum total vascular green area (VGA) ranged from 0.3 to 0.7 m^2 m^{-2} and was highest on average in the control treatment and lowest in the drought (lowered water table) treatment (Table 2). There was a positive correlation between maximum total VGA and percent moss cover across our treatments (Figure 2; Pearson correlation coefficient 0.87, $P = 0.02$, $n = 6$). The timing of maximum VGA (X_{max}) tended to occur 2–3 days later with warming across all water table treatments (Table 2).

Carbon Dioxide Fluxes

Fluxes of NEE, ER, and GPP varied by a water table treatment (control, lowered, raised) × year interaction (Table 1, Figure 3). During our flux measurements, the control water table treatment had negative NEE values (net sink of CO_2) in both 2005 and 2006. Although the lowered and raised water table treatments both served as small sinks of CO_2

Table 2. Estimated Parameter Values for the Vascular Green Area (VGA, Equation 1) and Gross Primary Production (GPP, Equation 2) Models for Each Water Table × Soil Warming Treatment

	VGA parameters			GPP parameters (PAR, WT)				GPP parameters (PAR)	
	VGA_{max} (m² m⁻²)	X_{max} (julian day)	b (dimensionless)	$P_{max(PAR, WT)}$ (μmol CO₂ m⁻² s⁻¹)	k (μmol m⁻² s⁻¹)	uP (cm)	tP (cm)	$P_{max(PAR, WT)}$ (μmol CO₂ m⁻² s⁻¹)	k (μmol m⁻² s⁻¹)
Control ambient temp.	0.59 ± 0.09	208 ± 5	24.5 ± 5.0	12.7 ± 3.0	729.7 ± 372.9	−17.5 ± 1.6	9.9 ± 11.9	8.4 ± 1.9	469.1 ± 290.1
Control warming	0.70 ± 0.10	210 ± 4	22.3 ± 3.4	16.6 ± 3.4	1112.3 ± 408.8	−15.1 ± 1.4	11.3 ± 2.9	9.6 ± 2.1	604.6 ± 316.3
Lowered ambient temp.	0.30 ± 0.04	204 ± 9	41.6 ± 15.7	–	–	–	–	6.3 ± 4.0	1053.5 ± 869.7
Lowered warming	0.31 ± 0.03	207 ± 3	30.4 ± 4.6	–	–	–	–	6.2 ± 1.3	265.0 ± 195.3
Raised ambient temp.	0.53 ± 0.12	215 ± 9	34.1 ± 15.6	29.2 ± 10.8	1864.5 ± 1117.6	−19.3 ± 1.8	12.5 ± 1.6	23.0 ± 15.1	2711.3 ± 2485.0
Raised warming	0.36 ± 0.06	218 ± 10	38.7 ± 15.5	37.3 ± 15.6	2712 (1602.9)	−15.9 ± 1.5	13.0 ± 1.9	61.3 ± 74.75	265.0 ± 195.3

All modeled parameters were significant at the P = 0.05 level. The model following equation (2) failed to converge in the lowered water table treatment because GPP did not exhibit a unimodal response to water table position (Figure 6). Thus, here we also estimated $P_{max(PAR)}$ and k across the experimental treatments based on light dependence of GPP alone. Reported parameters are means ± approximated one standard error.
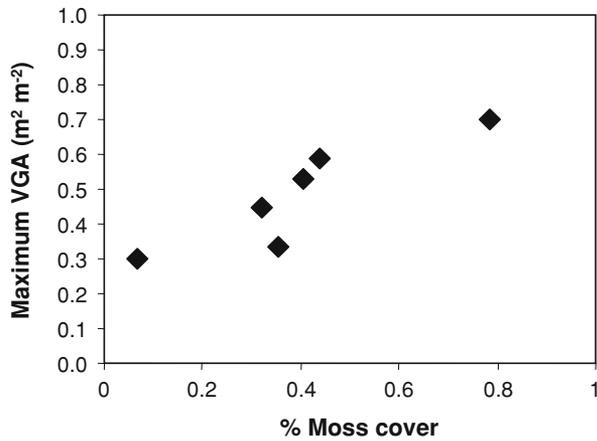
Figure 2. Relationship between total vascular green area (VGA) and percent moss cover averaged for each water table × warming treatment.

in 2005, the following year the lowered water table treatment had positive rates of NEE (net CO_2 source) whereas the raised water table treatment had more negative NEE (stronger net CO_2 sink). Rates of gross primary production (GPP) were lower in 2006 than in 2005 for the control and lowered water table treatments whereas the raised treatment showed the opposite trend among years. There were few differences in ER across experimental treatments and study years, although the raised water table treatment had higher rates of ER in 2006 relative to the other treatments (Figure 3).

Fluxes of ER and GPP varied by a warming effect, with no other significant interactions among main effects (Table 1). Ecosystem respiration averaged 3.99 ± 0.13 and 3.46 ± 0.12 µmol CO_2 m^{-2} s^{-1} within the warmed and ambient temperature subplots, respectively. Fluxes of GPP averaged -4.31 ± 0.13 and -5.08 ± 0.13 µmol CO_2 m^{-2} s^{-1} within the warmed and ambient temperature subplots, respectively.

To explore CO_2 fluxes during different periods of the growing season, we plotted ER versus GPP for early (JD 140–200) versus late (JD 200–277) season periods (Figure 4). In 2005, flux measurements across each water table treatment generally clustered together near the 1:1 line, whereas in the subsequent year there was more variability in CO_2 fluxes across each water table treatment, likely due to the drier conditions that occurred in 2006. Early season GPP was approximately three times greater in 2006 than in 2005, whereas a moderate increase in late season GPP between 2005 and 2006 was accompanied by a large increase in ER.

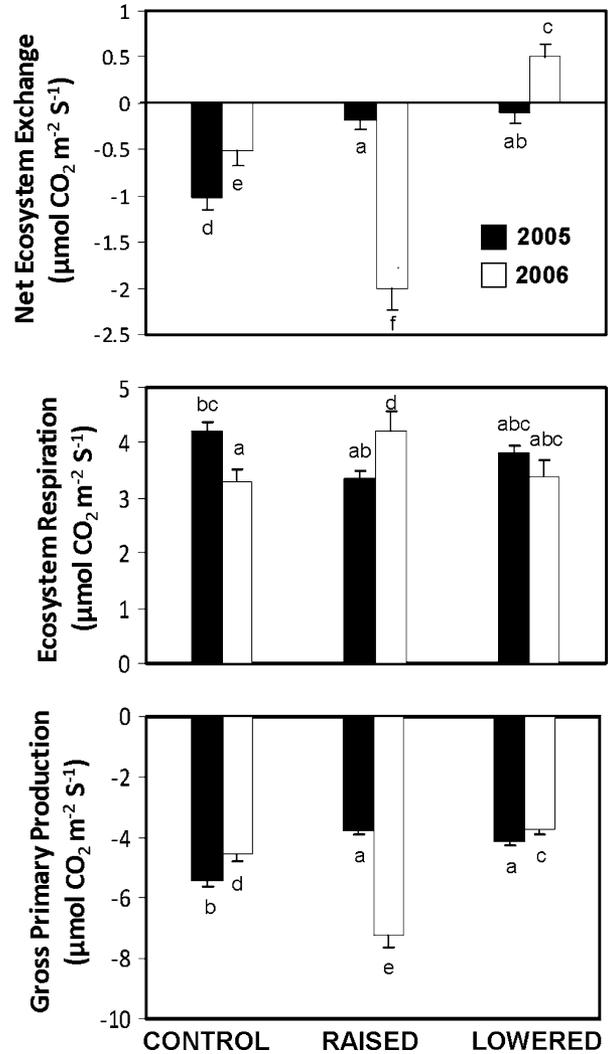In the control water table treatment, the response of GPP to PAR exhibited typical patterns,

Figure 3. Results of a repeated measures analysis of variance model analyzing weekly CO_2 flux measurements of net ecosystem exchange, ecosystem respiration, and gross primary production across water table treatments and years. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from *post hoc* comparison of means tests.

with greater GPP as PAR increased from 0 to approximately 1000 µmol m^{-2} s^{-1} (Appendix 1). GPP responses to water table also exhibited the expected unimodal pattern in the control treatment, with GPP peaking at a water table position of -15 to -16 cm beneath the moss surface. Across experimental treatments, P_{max} tended to be highest in the raised treatment and lowest in the lowered water table treatment (Table 2). The warming treatments had no effect on P_{max} in the lowered water table treatment, but did result in increased P_{max} in the other water table treatments, particularly
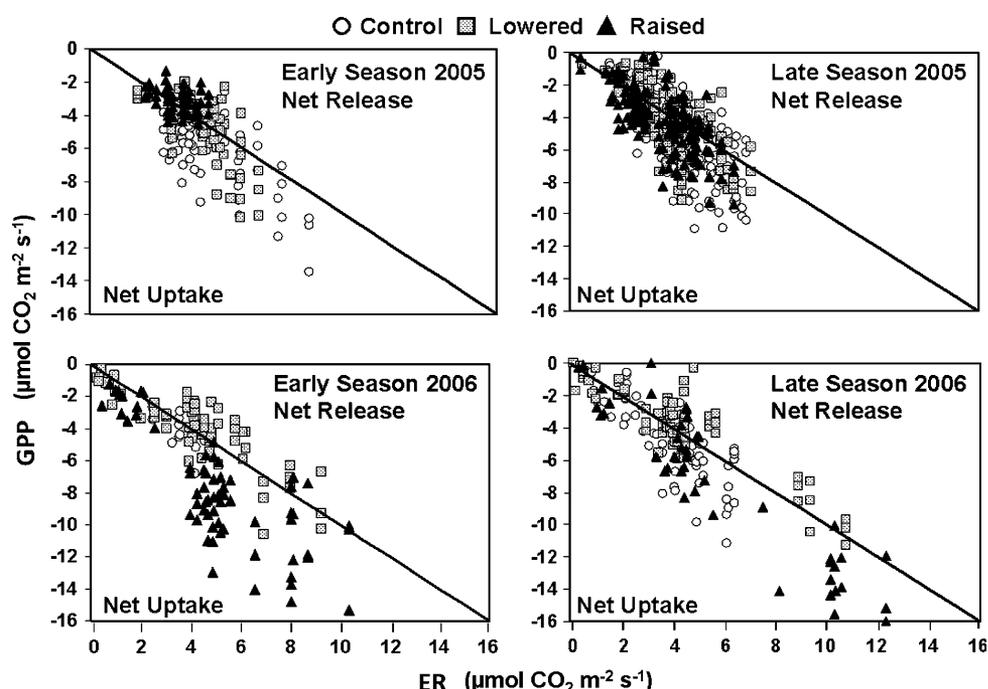
Figure 4. Relationships between ecosystem respiration and gross primary production for early (julian day 140–200) and late (julian day 201–277) season fluxes in 2005 and 2006. Individual data points represent a single measurement of CO_2 flux collected from a gas flux collar.

the raised plot. There were no relationships between P_{max} and species % cover, however, P_{max} was positively correlated with the timing of maximum vascular photosynthesis (x_{max}; Figure 5). Estimates of k were variable across experimental treatments, but were higher in the raised water table treatment (Table 2).

GPP exhibited a typical unimodal response to water table position in the control and raised water table treatments, with maximum GPP occurring at water table positions ranging from approximately -15 to -19 cm (Table 2). However, GPP did not exhibit a unimodal response to water table position in the lowered water table treatment (Figure 6). Rather, GPP in the lowered treatment showed a peak in GPP between -5 to -10 cm as well as a second increase in GPP at water table positions deeper than about -35 cm.

Similar to GPP responses in the control and raised plots, responses of ecosystem respiration to water table position across the experimental treatments followed a unimodal pattern (Table 3). R_{max} (equation 3) averaged 4.4 μmol CO_2 m^{-2} s^{-1} but tended to be lower in the raised water table treatment than in the control or lowered plots. R_{max} also increased from 0.52 to 1.06 μmol CO_2 m^{-2} s^{-1} with warming across all water table treatments. In the control water table treatment, maximum respiration rates tended to occur at a water table position around -6 to -7 cm beneath the moss surface (that is, uR), whereas maximum respiration

occurred at about -8 cm and -4 cm in the lowered and raised treatments, respectively (Table 3).

The temperature dependence of ecosystem respiration followed an Arrhenius relationship across all of our experimental treatments (Table 3). Mean rates of ecosystem respiration at 0°C (A) ranged from 0.76 to 2.77 μmol CO_2 m^{-2} s^{-1}, and in general were lower in the raised water table treatment. The temperature dependence of ecosystem respiration to temperature (Q_{10}) averaged 1.6 across experimental treatments, and was higher in the raised treatment than in the control or lowered water table treatments (Table 3). In the control water table plot, warming increased Q_{10}, though this pattern was not observed in the raised or lowered plots (Table 3).

DISCUSSION

Responses of Ecosystem C Fluxes to Water Table Position

Several studies have documented reduced GPP in peatlands during drought due to the effects of moisture stress on plant productivity (Alm and others 1999; Griffis and others 2000; Weltzin and others 2000). However, other studies have found that lowered water table levels can stimulate GPP by promoting woody vegetation productivity and/or stimulating nutrient availability for plant uptake (Gorham 1991; Thormann and Bayley 1997;
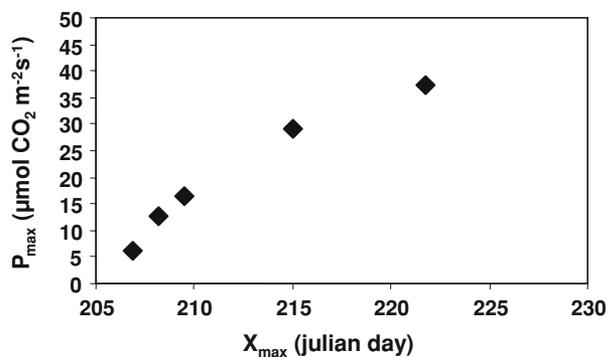
Figure 5. Relationship between $P_{\max}$ (µmol CO_2 m^{-2} s^{-1}) and $X_{\max}$ (julian day).
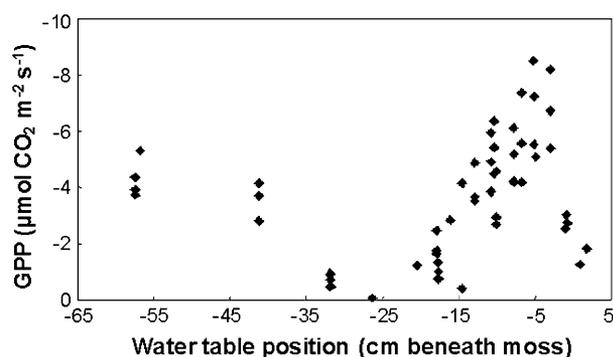

Figure 6. Relationship between gross primary production and water table position in the lowered water table treatment.

Weltzin and others 2000). Drier conditions and lower water table positions in northern peatlands also are expected to affect NEE by increasing oxygen diffusion into soils, stimulating aerobic decomposition, and increasing ER (Moore and Knowles 1989; Nykanen and others 1995; Silvola and others 1996). In our rich fen, GPP on average was generally

reduced in the drought (lowered water table) treatment relative to the control, whereas there were no differences in ER among these treatments (Figure 3). These results suggest that our drought treatment affected NEE, leading to a net source of atmospheric CO_2 in 2006, primarily by reducing plant C uptake rather than by increasing ecosystem respiration. Given that autotrophic respiration often scales with plant growth (compare Hobbie and Chapin 1998; Bubier and others 1998), it is possible that drought led to a simultaneous decrease in autotrophic respiration and increase in heterotrophic respiration, with no substantial net changes in ecosystem respiration. Future work to partition the components of ecosystem respiration and their individual responses to changes in moisture availability will test this hypothesis.

Water table drawdown studies in peatlands have shown that decreasing bryophyte cover (including Sphagnum and brown mosses) leads to an overall decline in photosynthetic capacity (Moore 1989; Tuba and others 1996; Alm and others 1999; McNeil and Waddington 2003; Strack and Waddington 2007). Across the ambient temperature subplots, the lowered water table treatment had the lowest values of maximum photosynthesis and total vascular green area (VGA) (Table 2). The lowered treatment also had the lowest percent cover of mosses (including both Sphagnum and brown mosses; data not shown). Percent moss cover was positively correlated to maximum VGA across our experimental treatments (Figure 2). Together, this suggests that drought led to reduced photosynthetic material of both vascular and nonvascular species. The lowered water table treatment also corresponded to an earlier occurrence of maximum VGA (that is, $x_{\max}$) relative to the other experimental treatments. The correlation between maximum photosynthesis and $x_{\max}$ (Figure 5) suggests that VGA peaking earlier in the growing season is related

Table 3. Estimated Parameter Values for the Two Ecosystem Respiration Models (equations 3 and 4) for Each Water Table × Soil Warming Treatment

	$R_{\max}$ (µmol CO_2 m^{-2} s^{-1})	uR (cm)	tR (cm)	A (µmol CO_2 m^{-2} s^{-1})	Q_{10}
Control ambient	4.13 ± 0.27	−7.1 ± 0.9	7.6 ± 1.4	2.77 ± 0.33	1.17 ± 0.07
Control warmed	5.19 ± 0.33	−6.0 ± 0.7	6.4 ± 1.0	1.62 ± 0.31	1.54 ± 0.13
Lowered ambient	4.44 ± 0.32	−8.3 ± 0.5	5.8 ± 0.6	1.21 ± 0.31	1.58 ± 0.18
Lowered warmed	5.35 ± 0.32	−8.0 ± 0.4	5.8 ± 0.6	1.49 ± 0.26	1.55 ± 0.12
Raised ambient	3.38 ± 0.29	−3.9 ± 1.1	5.7 ± 1.6	0.78 ± 0.25	1.99 ± 0.25
Raised warmed	3.90 ± 0.32	−4.0 ± 1.9	8.0 ± 3.5	0.67 ± 0.21	1.99 ± 0.20

All modeled parameters were significant at the P = 0.05 level. Reported parameters are means ± one approximated standard error.

to reduced photosynthetic capacity at the plot-scale, which might be related to functional changes induced by shifts in the abundance of dominant species or functional groups.

On a decadal scale, we expect that succession in our experimental drought treatment will likely increase the abundance of local woody species such as *Betula nana* and *Picea mariana* or drought-resistant species, leading to increases in GPP and changes in the response of GPP to resources such as light and moisture. Increases in the abundance of woody vegetation would increase soil lignin content, likely leading to greater substrate quality limitations on soil decomposition rates (compare Updegraff and others 1995), which also could contribute to decreased NEE and increased C storage.

Few experiments have examined the effects of raised water table positions on ecosystem CO_2 fluxes in the field. The saturation of surface soils limits the diffusion of oxygen into the peat, thereby limiting microbial activity and decomposition rates, and generally is expected to decrease CO_2 emissions to the atmosphere. Chimner and Cooper (2003) elevated water table position by approximately 5 cm and measured a 42% decrease in ER in a subalpine fen. However, Updegraff and others (2001) found no effect of flooding on ER in bog or fen mesocosms. Research in both Alaskan and Canadian peatlands showed that flooding due to permafrost thaw and thermokarst increased ER and CH_4 emissions, but also increased GPP (Turetsky and others 2002, 2007; Myers-Smith and others 2007). Thus, flooding can reduce ER by minimizing acrotelm thickness, or can increase GPP and possibly ER through changes in plant community composition and substrate quality.

In this study, the raised water table treatment increased GPP in 2006, increased P_{max}, and increased k relative to the other water table treatments (Figure 3, Table 2). In 2006, changes in GPP appeared to be driven by large increases in early season GPP in the raised treatment (Figure 4). Given that mosses are able to photosynthesize earlier in the spring than vascular plants; this result could highlight the importance of mosses in driving the increases in GPP with flooding. Although the raised water table treatment did not reduce fluxes of ER as expected, R_{max} and A tended to be lower in the raised treatment relative to the control. Also, ER in the raised treatment was more sensitive to temperature (higher Q_{10}) (Table 3). There were no relationships between either R_{max} or Q_{10} and any of our percent vegetation cover data.

Responses of Ecosystem C Fluxes to Warming

Temperature is often shown to be a major control on boreal ecosystem CO_2 fluxes, as warmer air and soil temperatures can stimulate biological activity resulting in increased ER (Crill and others 1988; Frolking and Crill 1994; Silvola and others 1996) and/or GPP (Hobbie and Chapin 1998; Arft and others 1999). Hobbie and Chapin (1998) attributed increases in GPP with soil warming primarily to greater N availability in their arctic tundra sites. Our results suggest that, averaged across water table treatments and study years, warming increased both ER and GPP by approximately 16%. Because warming led to increases in both GPP and ER rates of similar magnitude, there was no significant effect of warming on NEE. These results are similar to other temperature manipulations in arctic tundra sites and peatland mesocosms that also showed little net effect of warming on NEE (Hobbie and Chapin 1998; Arft and others 1999; Updegraff and others 2001). This effect, however, is consistent with an acceleration of C cycling under warmer climatic conditions, where growing season-warming stimulates several processes controlling near-surface C cycling (including both plant C fixation and respiration processes) (for example, Kimball and others 2007).

Warming did not appear to have consistent effects on the responses of GPP to PAR or water table position (Table 2). The warming treatment did affect the response of ER to water table position by increasing R_{max} slightly across water table treatments (Table 3). Additionally, in the control water table treatment only, warming increased the temperature dependency of ER (Q_{10}), though this pattern did not hold for the two experimental water table treatments. Consequently, our results demonstrate a complex response of ecosystem CO_2 fluxes to warming due to different responses of GPP and ER, and interactions with water table position.

Conclusions

In the first 2.5 years of manipulating water table position and surface temperature in a rich fen, we documented significant changes to ecosystem CO_2 fluxes. Experimental drought, via lowered water table positions, changed the ecosystem from a net sink to a net source of atmospheric CO_2, primarily by reducing plant productivity. Experimental flooding caused the ecosystem to serve as a stronger net CO_2 sink (second year of study only), which we attribute to greater plant productivity and

light-saturated photosynthesis as well as lower maximum respiration rates and reduced sensitivity of respiration to temperature. Soil warming affected ecosystem CO_2 fluxes across all water table treatments, but resulted in no net effect on net ecosystem exchange. Light availability, water table position, soil temperature, and the timing and amount of vegetation biomass were important controls on the responses of gross primary productivity and ecosystem respiration across our experimental design. Thus far, our work has characterized rapid ecosystem responses in CO_2 fluxes to changing soil hydroclimate. Longer-term successional responses to these soil climate manipulations could alter plant productivity and C uptake, but also will likely influence microbial metabolism by influencing shading, physical peat properties, and litter quality entering the soil system.

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