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ORIGINAL PAPER

Long-term water table manipulations alter peatland gaseous carbon fluxes in Northern Michigan

Drew M. Ballantyne · John A. Hribljan · Thomas G. Pypker · Rodney A. Chimner

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Abstract Northern peatland water table position is tightly coupled to carbon (C) cycling dynamics and is predicted to change from shifts in temperature and precipitation patterns associated with global climate change. However, it is uncertain how long-term water table alterations will alter C dynamics in northern peatlands because most studies have focused on short-term water table manipulations. The goal of our study was to quantify the effect of long-term water table changes (~80 years) on gaseous C fluxes in a peatland in the Upper Peninsula of Michigan. Chamber methods were utilized to measure ecosystem respiration (ER), gross primary production (GPP), net ecosystem exchange (NEE), and methane (CH_4) fluxes in a peatland experiencing levee induced long-term water table drawdown and impoundment in relation to an unaltered site. Inundation raised water table levels by approximately ~10 cm and resulted in a decrease in ER and GPP, but an increase of CH_4 emissions. Conversely, the drained sites, with water table levels ~15 cm lower, resulted in a significant increase in ER and GPP, but a decrease in CH_4 emissions. However, NEE was not significantly different between the water table treatments. In summary, our data indicates that long-term water table drawdown and inundation was still altering peatland gaseous C fluxes, even after 80 years. In addition, many of the patterns we found were of similar magnitude to those measured in short-term studies, which indicates that short-term studies might be useful for predicting the direction and magnitude of future C changes in peatlands.

Keywords CO_2 · Climate change · Methane · Drainage · Flooding

D. M. Ballantyne · J. A. Hribljan · T. G. Pypker · R. A. Chimner (✉)
School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA
e-mail: rchimner@mtu.edu

Introduction

Peatlands are important ecosystems because their vast peat deposits store substantial amounts of carbon (C), particularly in tropical and boreal regions (Wieder et al. 2006). Peat accumulates when long-term net primary productivity exceeds decay and other losses, resulting in the accumulation of incompletely decomposed organic matter, or peat. While peatlands cover only 3–5 % of the global land area, they store between 20 and 30 % of the global soil C pool (270–455 Pg) (Gorham 1991). The total peatland area in North America is 1,735,000 km^2 of which 3.5 %, or 60,000 km^2, is located in the Great Lakes region (Boelter and Verry 1977). The large pools of C sequestered in peat soils are potentially susceptible to changes in climate, especially peatlands in the Great Lakes region because they reside at the southern limit of northern peatlands (Vasander and Kettunen 2006).

The exchange of carbon dioxide (CO_2) between peatlands and the atmosphere is the result of two major fluxes; C fixation associated with photosynthesis, hereafter referred to as gross primary production (GPP), and ecosystem respiration (ER) that is the summation of heterotrophic and autotrophic respiration. The rate of heterotrophic respiration is primarily controlled by soil temperature and pH, oxic peat layer volume, nutrient availability, and the quality and quantity of decomposable material. In contrast, autotrophic respiration can be influenced by photosynthesis, temperature, moisture, and nutrient availability (Chapman and Thurlow 1998).

The response of peatland ER to climate warming and precipitation changes are a concern, because C efflux to the atmosphere is a major positive feedback associated with climate change (Bond-Lamberty and Thomson 2010). Peatlands also emit methane (CH_4), which has a global warming potential approximately 25 times greater than CO_2 over a time horizon of 100 years (Intergovernmental Panel on Climate Change (IPCC) 2007).

Carbon cycling in peatlands is expected to be modified by future anthropogenically induced changes to global temperatures and precipitation that can affect rates of peat production and decomposition (Updegraff et al. 2001; Chimner and Cooper 2003). The IPCC is predicting an increase in precipitation for the Great Lakes region, especially in winter (IPCC 2007). Furthermore, the IPCC predicts warmer temperatures for high latitude regions in the northern hemisphere, which may cause additional alterations in peatland hydrologic budgets by increasing evapotranspiration, altering seasonal rain patterns, and changing the form of precipitation from snow to rain. Previous peatland climate change research focusing on C dynamics has primarily investigated temperature effects on peatland C fluxes (Chen et al. 2008; White et al. 2008); however, current research indicates that changes in water table position may be more influential than temperature in regulating C cycling (Dinsmore et al. 2009; Strakova et al. 2010).

Peatland studies investigating the effects of long-term altered hydrology on peatland C cycling in the southern boreal forest regions of the northern hemisphere are scarce, and the majority of these studies occurred in vitro incorporating peat monoliths in mesocosm experiments (Updegraff et al. 2001; Chen et al. 2008; White et al. 2008). Additionally, water table manipulation studies have included in situ short-term drainage manipulations conducted in boreal regions (Strack et al. 2006a; Turetsky et al. 2008) and long-term Finnish peatland drainage investigations associated with higher water table drawdown (>30 cm) (Laine et al. 1995). However, a concern with short-term water manipulations is that plant communities and peat chemistry have not had sufficient time to change to reflect the new hydrologic conditions (Couwenberg et al. 2011). Therefore, long-term changes in hydrological conditions may show different responses of gas fluxes than short-term drainage. Furthermore, most long-term drawdown investigations have been with a water table drawdown that might not be commensurate with the more modest water table changes that could occur with climate change. The objective of this study was to investigate how long-term ($\sim$80 years) changes in water table position has affected ecosystem CO_2 and CH_4 fluxes in a Northern Michigan peatland. We hypothesized CO_2 and CH_4 fluxes would still be altered after 80 years of hydrologic alterations, but the magnitude would be less than short-term water manipulation studies.

Methods

Study site

We established a field experiment in the Seney National Wildlife Refuge (SNWR) located in the east-central region of Michigan's Upper Peninsula, USA approximately halfway between Lake Michigan and Lake Superior (46° 19′N and 86° 03′W). The SNWR is situated in the Manistique River watershed, which drains approximately 3,885 km^2 before discharging into the northeast corner of Lake Michigan. The watershed is within the southernmost area of widespread continental peatlands. The SNWR includes approximately 38,000 hectares of which 2/3 is covered with peat often exceeding 1 m in depth (Kowalski and Wilcox 2003). Annual precipitation averages 810–860 mm and the mean average temperature is 5.1 °C (USFWS 2009; Wilcox et al. 2006). The combination of snowpack melt in April and May and above average precipitation in June, often results in an early-season peak of water table levels.

In the late 1800s, the greater Seney area was heavily logged, burned, ditched, and drained. Around 1908 the

Western Land Surety Company purchased the land comprising the future SNWR with the intention of draining the vast wetlands for farm land. However, the farming attempt failed and the land reverted back to the State of Michigan and eventually was acquired by the Federal Government to form the SNWR in 1935. With the aid of The Civil Conservation Corps, a complex system of levees, water control structures, ditches, and roads were built after the refuge was established to convert existing wetlands into open water impoundments for waterfowl habitat (Kowalski and Wilcox 2003).

Experimental design

We established a field experiment in three adjacent peatlands to investigate peatland C cycling responses to long-term altered water table levels. Historical aerial imagery indicates the fens were originally an interconnected large peatland complex (Fig. 1a). However, road and levee construction during the 1930s utilized existing eskers also crossed sections of the peatland, fragmenting the greater peatland complex. In these locations, eskers were connected by filling the peatland with mineral soil to create a continuous levee. The constructed levee blocked surface flow across the peatland complex, causing flooding on the north side of the levee (raised treatment) and partially draining the south side (lowered treatment) (Fig. 1b).

Two sites (A and B) were positioned in an area of the peatland complex that was not drained and relatively unaltered (intermediate treatment) by the levee and road construction (Fig. 1a, b). Examination of aerial photography in this area revealed no apparent changes of surface flow hydrology or vegetation between the 1930s and present. Within the intermediate treatment, we selected one location with a light cover of *Picea mariana* (site A) and a second site with no tree cover (site B).

We established the lowered water table treatment sites (E and F) on the southern leeward side of the levee that was constructed in the early 1940s. Site F was disconnected from the prominent northwest to southeast surface sheet flow by the levee construction (Fig. 1b) that resulted in water table drawdown and significant tree encroachment of tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*) that started in the 1950s (Hribljan 2012). Site E was not located directly adjacent to a major surface flow channel; however, ground truthing indicated that a small isthmus filled in

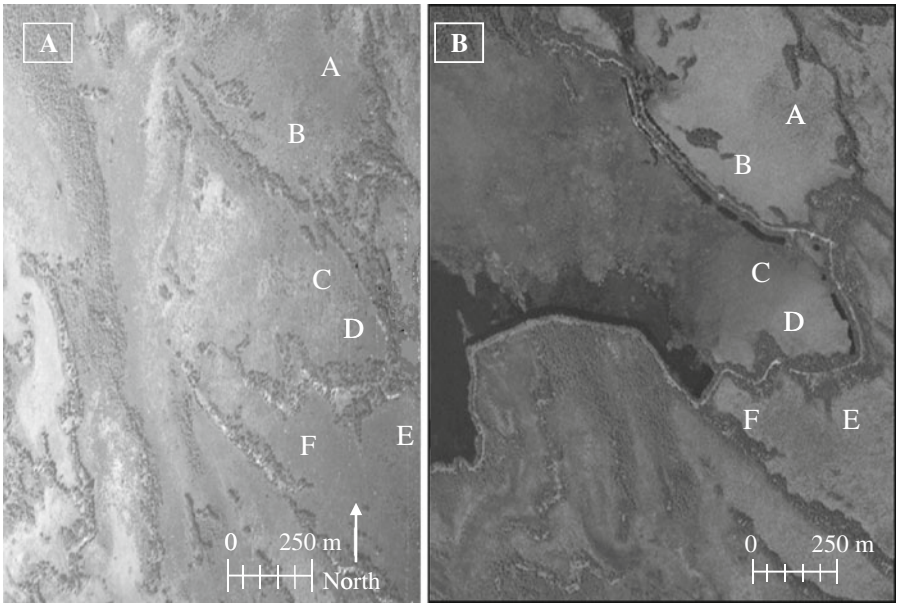

Fig. 1 **a** Aerial photo from 1930 of the peatland before road and levee were constructed in the 1940s and **b** Photo of study site in 2010 illustrating location of levee. *Letters* indicate site locations within each water table treatment (*C* and *D* raised treatment, *A* and *B* intermediate, and *E* and *F* lowered)

by the levee construction connected the peatland by site E to the southern end of site D on the northern side of the levee (Fig. 1a, b). Site E did not have tree encroachment.

The two sites (C and D) comprising the raised water table treatment were established north of the levee. Site C had the highest water table position and site D was located in a slightly drier area (Fig. 1b). Site C did not support trees and site D contained very sparse tree cover that was mostly reserved to the outer edges of the peatland.

Average peat depth measured from lawn microforms was 115.9 ± 5.6 cm (mean ± 1 SE) in the lowered water table treatment, 114.4 ± 9.4 cm in the intermediate treatment, and 131.5 ± 5.1 in the raised treatment. Peat bulk density (B_d) was similar across the water table treatments in the hummock microforms: intermediate, 0.02 ± 0.003; raised, 0.03 ± 0.002; and lowered 0.02 ± 0.001(mean ± 1 SE of 10 cm increments from a 0–50 cm horizon). Lawn peat B_d was lower in the intermediate treatment (0.04 ± 0.002) than the raised (0.06 ± 0.003) and lowered (0.05 ± 0.003) treatments (Hribljan 2012).

All sites (A–F) supported similar vegetation structure that was representative of poor fens in the Great Lakes region. Dominant vegetation species included *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Vaccinium oxycoccos, Eriophorum vaginatum, Larix laricina, Picea mariana, Kalmia polifolia*, *Sphagnum* spp. (*angustifolium, capillifolium, magellanicum*), and *Carex oligosperma* (Hribljan 2012) (Table 1).

Chamber based CO_2 and CH_4 fluxes

All sites (sites A–F) contained a 400 m^2 sampling area stratified into four equal quadrats each containing two randomly chosen plots split between a hummock and lawn for a total of 48 plots across the water table treatments. Each plot consisted of a 60 cm by 60 cm galvanized steel collar permanently installed 10 cm into the peat for chamber based gas flux measurements. A series of boardwalks were constructed to minimize disturbance while sampling.

Seasonal CO_2 and CH_4 fluxes were measured approximately biweekly during the snow free seasons (April–Oct) of years 2009 and 2010. All 48 plots were measured within 4 days between 10:00 and 17:00 h (EST) during each sampling period to insure photosynthetic photon flux density (PPFD) remained similar (typically >1,000 umol m^{-2} s^{-1}). We used static chamber methods to measure CO_2 exchange (Carroll and Crill 1997). A custom made clear plexiglass chamber (60 × 60 × 60 cm) vented to minimize pressure effects and connected to an infrared gas analyzer (PP-Systems, EGM-4, Amesbury, Massachusetts, USA) was used to quantify net ecosystem exchange (NEE), ER, and GPP. The chamber was equipped with two small fans to ensure mixing of air, a hinged lid for venting between measurements, and weather stripping to provide a gas-tight fit on the collar.

Carbon dioxide fluxes were calculated by measuring the change in CO_2 concentrations (adjusted for chamber volume and area) during the sampling period

Table 1 Water chemistry, topographic mean, water table position below topographic mean, and vegetation percent cover across the water table treatments (intermediate, raised, and lowered)

Water table treatment	Intermediate	Raised	Lowered
pH	3.78 (0.02)	3.96 (0.04)	3.70 (0.01)
Sp. Cond (μS cm^{-1})	63.0 (1.7)	49.4 (1.7)	75.7 (2.4)
Topographic mean (cm)	22.6 (1.0)	17.0 (0.9)	22.6 (1.0)
Water table (cm)[a]			
2008	33.4 (1.0)	15.8 (0.7)	50.8 (0.9)
2009	28.5 (0.9)	20.1 (1.0)	43.7 (0.6)
2010	20.1 (0.5)	11.2 (0.6)	38.2 (0.5)
2011	23.0 (0.8)	13.0 (0.9)	35.3 (1.1)
Average	26.2 (0.8)	15.0 (0.8)	42.0 (0.8)
Vegetation percent cover			
Graminoid	7 (4)	41 (7)	40 (9)
Moss	100 (4)	73 (7)	107 (4)
Shrub	105 (11)	99 (7)	99 (7)
Tree (<1 m height)	7 (2)	>1	3 (1)

[a] Water table levels below topographic mean refers to the distance below the average microtopography height from a 50 m transect at each site. Values in parentheses indicate one standard error

using the built in quadratic line equation. Chamber measurements were initiated after a steady mixing of air was established, determined when CO_2 concentration increased or decreased at a constant rate (typically 20–30 s). Chamber NEE was measured for two minutes (short measurement period minimized temperature and water vapor increases inside the chamber; Vourlitis et al. 1993), the chamber was then vented for 20–30 s and subsequently fitted with an opaque reflective white cloth to arrest photosynthesis. Lastly, ER was measured for 2 min. Calculation of GPP was performed by subtracting ER from NEE. In this manuscript, GPP is defined as negative, ER is presented as positive, and NEE is defined as ER + GPP, so negative values of NEE indicate ecosystem uptake of CO_2. In conjunction with CO_2 concentrations, we measured relative humidity, photosynthetically active radiation (PAR), and air and soil temperature inside the chamber using EGM-4 standard probes.

Methane fluxes were also measured using a static chamber technique. Chambers constructed of opaque white polyvinyl chloride (PVC) (60 × 60 × 30 cm) were equipped with a pressure vent and contained a fan for mixing chamber air. Chambers were placed on the collars and gas samples were collected during a 40 min sampling period at 10 min intervals (0,10, 20, 30, 40 min) using a plastic syringe and injected into pre-evacuated 1.5 ml glass vials (Tuittila et al. 2000). The highly reflective white surface on the chamber reduced temperature effects during the sampling period and foam weather stripping insured a gas-tight fit on the collars. Gas samples were analyzed within 10 days using gas chromatography (Varian 3800 CP1177 injector, CarboPlot P7 column, 13.6 mL/min flow rate, 35–63 °C temperature range). Methane fluxes (mg m^{-2} h^{-1}) were calculated from the slope of the regression line between the concentration of CH_4 and time (Moore and Dalva 1993) and were adjusted for chamber volume and area. Artificial ebullition events that occurred when placing the chamber on the collars within the first 10 min of sampling were not included in the analysis. Approximately 15 % of the samples were adjusted due to ebullition.

Environmental and vegetation parameters

Water table levels were monitored hourly at each site with non-vented pressure transducers (Levellogger Junior Model 3001; Solinst, Canada) set in slotted wells inserted to the mineral soil. A barologger (Baralogger Gold Model 3001; Solinst, Canada) provided barometric compensation for all pressure transducers. Water table elevations are in relation to the mean microtopography of each site. Microtopography was measured at each site with a transit level at 0.5 m increments along a 50 m transect centered at the monitoring well. Well elevations were surveyed relative to each other and referenced to a common datum. The seasonal water table average by year (2008–2011) from April 12th to October 12th are shown in Table 1. Precipitation was measured using a TE525 tipping bucket rain gauge (Texas Electronics, Dallas, TX, USA) mounted 0.7 m above the peat surface.

Soil temperature was recorded in each plot at three depths (5, 22.7, and 40.1 cm) using thermocouples (I-Button model DS9108-150, Maxim Integrated Products, Sunnyvale, CA, USA) every hour during the snow free season of 2009 and 2010 and every 3 h from November 2009 to April 2010.

Statistical analysis

We treated the different water table levels created by the hydrologic alterations (intermediate, raised, and lowered) as a natural experiment, with water table levels used as treatments. A two-way, repeated measures analysis of variance (ANOVA) was conducted using PROC MIXED to test for water table treatment and topographic (hummock and lawn) effects on ecosystem CO_2 and CH_4 efflux (SAS 2009). Our intent was to detect differences in spatial variation between the water table treatments, since individual water table treatments were not replicated to the landscape scale. Each plot was analyzed as an experimental unit. Individual sites within each water table treatment were used as replications, water table treatments were treated as whole plots, and microtopography was treated as subplots. Water table treatment and microtopography interactions were treated as fixed effects, plots were treated as random effects, and sample years were treated as repeated measures. We used variance components symmetry covariance structure for repeated measures analysis and the Kenward and Roger's correction for degrees of freedom (Littell et al. 2006). Descriptive statistics were determined with Sigmastat software and

comparisons between all treatments were conducted using Tukey's post hoc test with differences at $p < 0.05$ considered significant.

Results

Water table treatments

The expected differences in mean seasonal (April–October) water table position across the water table treatments were confirmed for 2008–2011 relative to mean microtopography of each site. The lowered water table treatment leeward of the levee experienced the greatest water table draw-down with a 4 years seasonal mean water table of 42.0 ± 0.8 cm (mean ± 1 SE below mean topography) (Table 1). The raised water table treatment displayed the highest water table (15.0 ± 0.8 cm) while the intermediate treatment (26.2 ± 0.8 cm) was in-between the raised and lowered water table treatments.

CO_2 and CH_4 fluxes

Annual precipitation amounts were similar during 2009, and 2010, averaging 1.55 and 1.93 mm day^{-1}, respectively. May and June was the wettest period in 2009, with a more even distribution in 2010. This affected the gas fluxes as they peaked later in the summer in 2009 compared to 2010 (Fig. 2).

Ecosystem CO_2 fluxes responded to both changes in water table level and temperature. Mid-day ER and GPP both increased with declining water table levels, but little change is seen with NEE (Fig. 3). ER, GPP and NEE all increased with increasing soil temperature (Fig. 3).

Seasonal mean ER fluxes were significantly greater at the lowered water table treatment (3.0 ± 0.1 umol CO_2 m^{-2} s^{-1}) ($p < 0.001$) than at the intermediate (2.4 ± 0.1) and the raised treatments (2.1 ± 0.1). Seasonal mean GPP fluxes were also significantly greater at the lowered water table treatment (−5.1 ± 0.1 umol CO_2 m^{-2} s^{-1}) ($p = 0.001$) than at the intermediate (−4.5 ± 0.2) and raised treatments (−4.3 ± 0.2). Seasonal mean NEE displayed no significant differences across the raised (−2.3 ± 0.1 umol CO_2 m^{-2} s^{-1}), intermediate (−2.1 ± 0.1), and lowered water table treatments (−2.1 ± 0.1) (Table 2; Fig. 4). We also detected no significant differences in CO_2 flux across microtopography for ER, GPP, and NEE (Table 2).

Seasonal mean CH_4 fluxes were significantly greater ($p = 0.03$) at the raised water table treatment (0.61 ± 0.12 mg CH_4 m^{-2} h^{-1}) than at the lowered treatment (0.12 ± 0.12) (Table 2; Fig. 4). The seasonal mean CH_4 fluxes at the intermediate water table treatment were 0.26 ± 0.12 mg CH_4 m^{-2} h^{-1}. Emissions of CH_4 were significantly different between microforms (Table 2: $p = < 0.001$ and Fig. 5), with lawns (0.524 mg CH_4 m^{-2} h^{-1}) displaying greater CH_4 fluxes than hummocks (0.254 mg CH_4 m^{-2} h^{-1}).

Discussion

Water table effects on ER

Our study measured significantly greater GPP and ER emissions associated with long-term water table drawdown. These results suggest that ecosystem CO_2 release is not just a short-term response to drawdown, but has sustained long-term ramifications for peatland C cycling. Water table drawdown increases the diffusion of oxygen into the peatland, thereby stimulating microbial processing of peat that facilitates gaseous C emissions (Moore and Knowles 1989; Nykanen et al. 1995; Silvola et al. 1996; Chimner and Cooper 2003). Strack et al. (2006a) reported that ER was 54 % greater in a drained site that experienced a persistent water table drawdown of ~20 cm for 8 years compared to a site unaltered by drainage. Short-term studies in Finland have reported a 10–50 % increase of ER with a lowered water table (Riutta et al. 2007; Makiranta et al. 2009). Additionally, 1 year drought studies utilizing climate induced water table drawdown have measured similar increases of ER to water table manipulation studies (Schreader et al. 1998; Cai et al. 2010). These results are comparable to our long-term drained water table treatment that displayed ER fluxes 25 % greater than an unaltered intermediate treatment.

We found that long-term inundation lowered peatland ER fluxes relative to the drawdown treatment. Sulman et al. (2010) reported that wetter conditions were correlated with lower ER at fens, whereas bogs displayed higher ER associated with an increase in water table position. However, research conducted in Alaskan and Canadian peatlands displayed contrasting

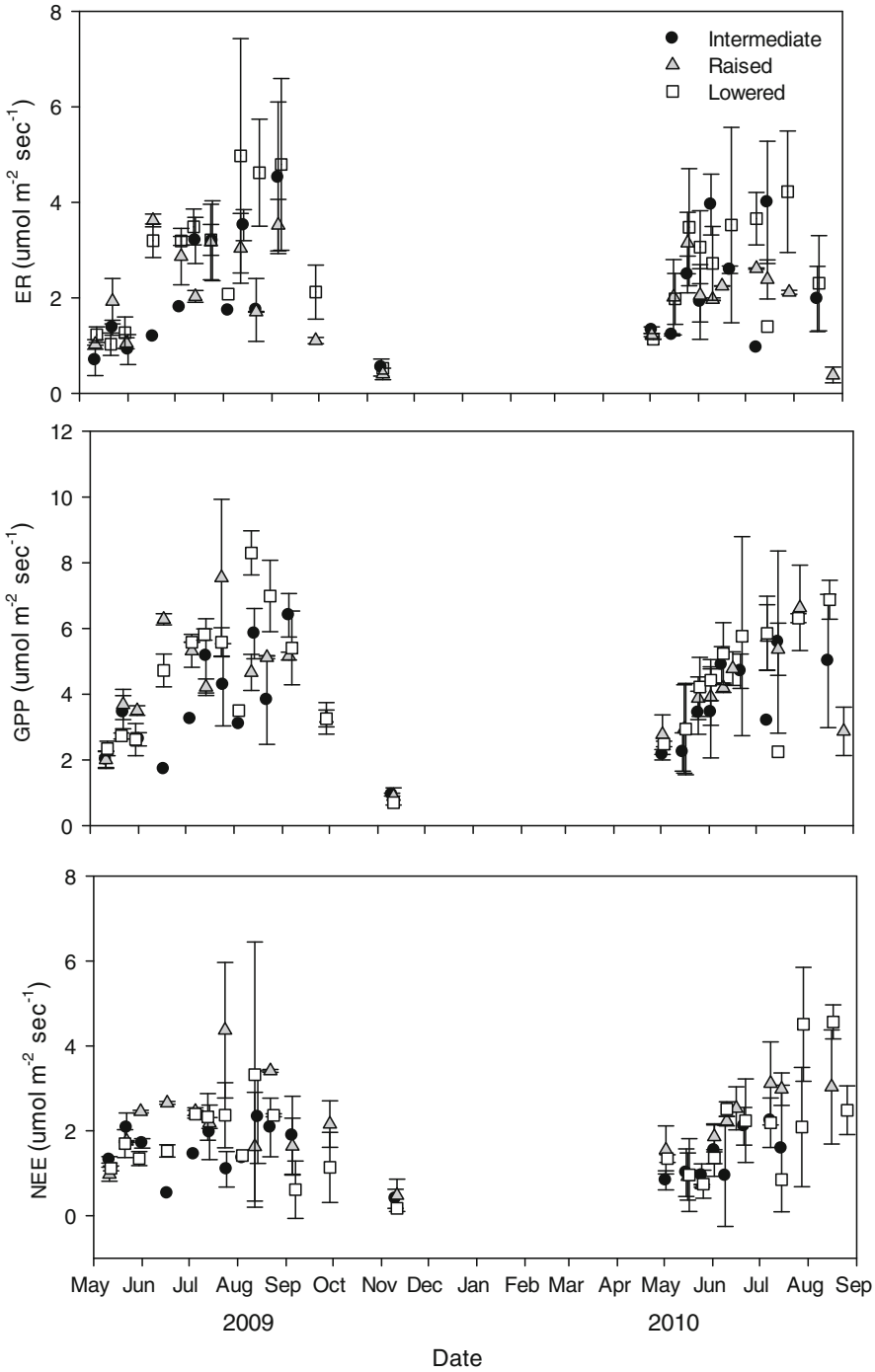

Fig. 2 Treatment means of NEE, ER and GPP (umol CO_2 m^{-2} s^{-1}) by date over 2 years. *Error bars* indicate one standard error

results to our findings with increased ER associated with inundation (Turestky et al. 2002, 2007; Myers-Smith et al. 2007). In these studies, the elevated CO_2 emissions were associated with permafrost thaw, which can release a highly labile C source that can stimulate microbial activity (Schuur et al. 2008). Therefore, variation in oxygen availability, vegetation structure, peat quality, and permafrost conditions can have multidimensional and synergistic effects on peatland ER. We propose that the decreased ER

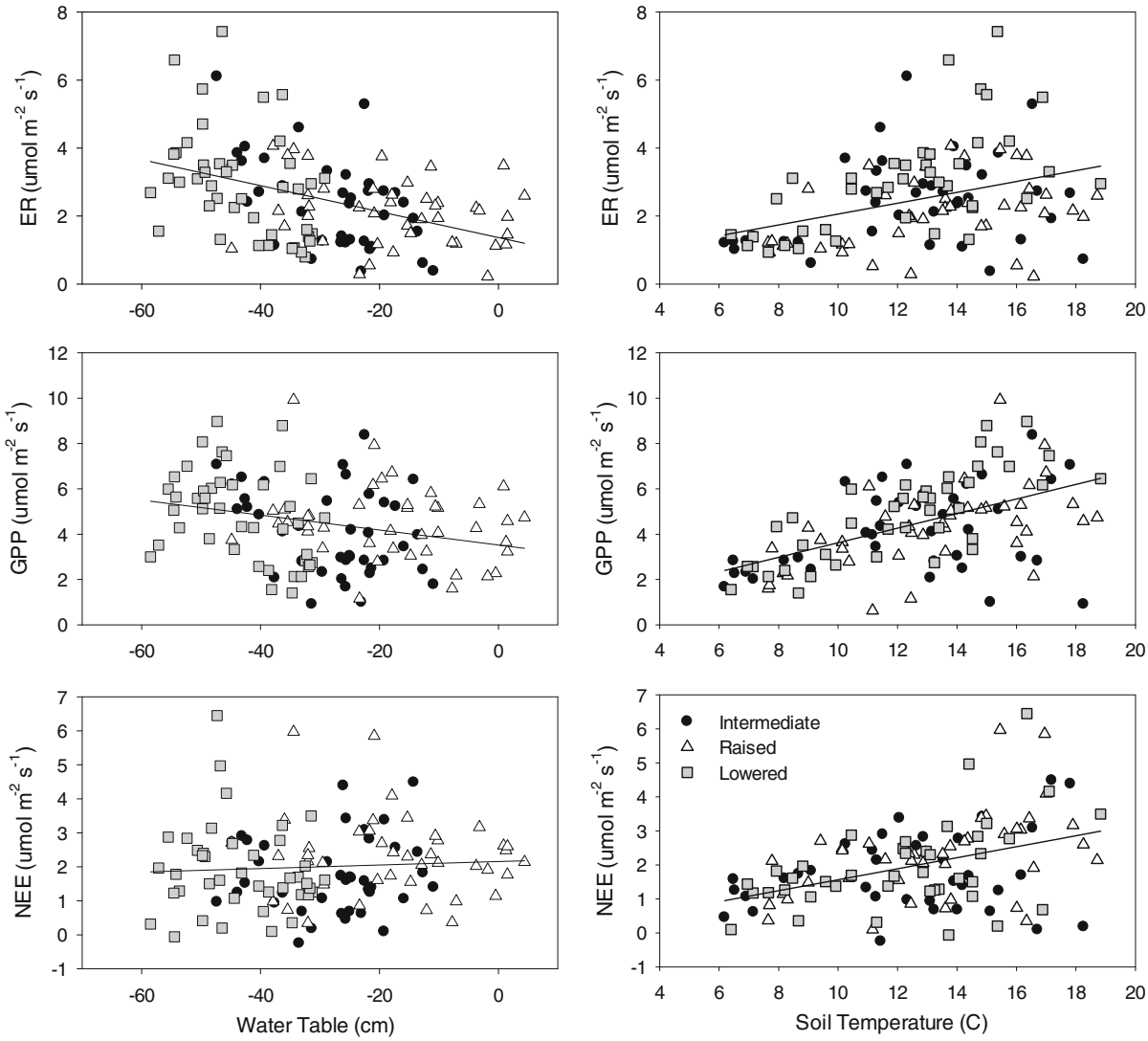

Fig. 3 Correlations between depth of water table (negative numbers indication water table below surface), soil temperature (5 cm) and ecosystem CO_2 fluxes

measured in the raised water table treatment is primarily from the highly anaerobic conditions limiting microbial activity.

Water table effects on CH_4 emissions

Previous studies have consistently demonstrated that CH_4 emissions decline following short- and long-term water table drawdown (Laiho 2006; Turetsky et al. 2008). Drawdown increases the diffusion of oxygen into the peatland, decreasing CH_4 production due to aerobic conditions and enhanced CH_4 oxidation (Strack and Waddington 2007). Short-term water table drawdown experiments have displayed decreased CH_4 emissions ranging from 17 to 150 % depending on the extent of water table drawdown and vegetation community structure (Dise et al. 1993; Blodau et al. 2004; Funk et al. 1994, Aerts and Ludwig 1997; Strack and Waddington 2007; Turetsky et al. 2008). Yrjala et al. (2011), in a long-term water table study, measured a 70 % and a 96 % decrease of CH_4 emissions associated with a 6 and 11 cm respectively drawdown in a boreal fen. Similar results are reported from long-term (>30 years) drained forested mire

Table 2 Results of a repeated measures ANOVA designed to test the singular and interactive effect of water table treatment (intermediate, raised, and lowered) and microtopography (hummock and lawn) on chamber based ecosystem C fluxes

	Df (numerator, denominator)	F	*P*
Net ecosystem exchange (NEE)			
Water table treatment	2, 18	1.07	0.34
Microtopography	1, 18	0.49	0.73
Water table treatment x microtopography	2, 18	10.08	<0.001
Ecosystem respiration (ER)			
Water table treatment	2, 18	24.65	<0.001
Microtopography	1, 18	0.25	0.62
Water table treatment x microtopography	2, 18	0.05	0.95
Gross primary production (GPP)			
Water table treatment	2, 18	9.86	<0.001
Microtopography	1, 18	0.09	0.77
Water table treatment x microtopography	2, 18	6.65	<0.001
Methane flux (CH_4)			
Water table treatment	2, 18	7.04	0.001
Microtopography	1, 18	13.57	<0.001
Water table treatment × microtopography	2, 18	0.85	0.45

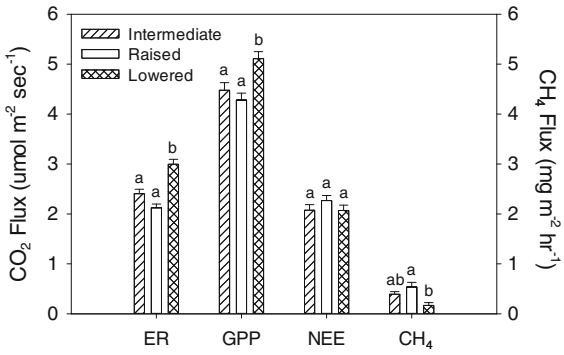

Fig. 4 Two years mean NEE, ER, GPP (umol CO_2 m^{-2} s^{-1}) and CH_4 (mg CH_4 m^{-2} $h-^{1}$) emissions by water table treatment (intermediate, raised, and lowered). *Error bars* indicate one standard error (ANOVA, $\alpha = 0.05$). *Letters* indicate significant differences between water table treatments ($p < 0.05$)

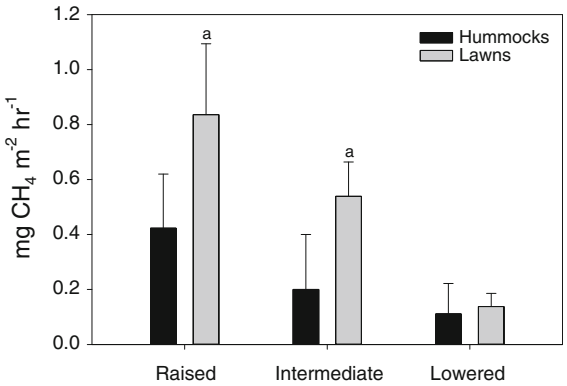

Fig. 5 Two years mean of CH_4 emissions from the hummocks and lawns across the water table treatments (intermediate, raised, and lowered). *Error bars* indicate one standard error. *Letters* indicate significant differences between microtopography types within a treatment ($p < 0.05$)

studies in Finland. Nykanen et al. (1998) found a 70 % reduction in CH_4 emissions from a peatland when the water table was lowered by 10 cm. Commensurate with these short- and long-term water table drawdown studies, we measured CH_4 emissions in our long-term water table drawdown treatment that were 67 % less than the unaltered intermediate water table treatment.

However, it should be noted that short-term water table manipulation studies under drier conditions have also found increases in CH_4 emissions (Weltzin et al. 2000). Increased belowground root growth of emergent plants can stimulate methanogenic activity from the amplified production of labile root exudates and improve CH_4 transport through plant aerenchyma (Strack et al. 2006b). Our lowered water table treatment did not display an increase in CH_4 emissions. Decreased CH_4 in our lowered water table treatment is associated primarily with reduced anaerobic conditions in the upper peat layer. Furthermore, increased root exudate production following drawdown could stabilize in decadal water table alterations and not create a significant long-term influence on

methanogens. We found that total belowground productivity was not significantly different between the water table treatments (Hribljan 2012).

Inundation can also reduce peatland CH_4 emissions (Bellisario et al. 1999); however, studies typically display an increase of CH_4 release with an elevated water table (Chivers et al. 2009; Myers-Smith et al. 2007). Turetsky et al. (2008) measured greater CH_4 emissions in a raised water table treatment relative to an intermediate treatment from a short-term manipulation experiment in a boreal fen. Our results displayed similar CH_4 release with mean emissions 65 % higher in the raised water table treatment compared to the intermediate treatment.

Elevated water table levels usually increase CH_4 emissions (Dise et al. 1993; Weltzin et al. 2000) by increasing methanogenesis in saturated soils and graminoid abundance (Yavitt et al. 2000; Treat et al. 2007). Graminoids are very efficient at facilitating CH_4 transport to the atmosphere through aerenchymous tissue and can stimulate methanogens with highly labile root exudates (Chanton et al. 2008; Bellisario et al. 1999). In our study, sites B and D from the intermediate and raised water table treatments displayed similar seasonal mean water table levels. Surprisingly, site B had significantly greater CH_4 emissions than site D (0.61 ± 0.12 and 0.37 ± 0.10 mg m^{-2} h^{-1} respectively; $p = 0.089$). We believe that the discrepancy in CH_4 emissions is from differences in sedge cover between sites B and D (47 and 19 % respectively; data not shown).

Variable response of GPP to water table position

While short- and long-term water table manipulations in peatlands display relatively predictable results with respect to ER and CH_4, GPP is more unpredictable and is particularly sensitive to changes in vegetation dynamics. In this study, mean GPP was elevated 15 % in the lowered water table treatment compared to the intermediate treatment. Our results support other studies reporting that water table drawdown can stimulate higher rates of C fixation (Gorham 1991; Thormann and Bayley 1997; Weltzin et al. 2000). Water table drawdown typically facilitates greater nutrient and oxygen availability to plant roots, contributing to a higher photosynthetic capacity (Laiho 2006). However, severe moisture stress from a drastic reduction in the water table has also been shown to reduce plant GPP (Alm et al. 1999; Griffis et al. 2000; Weltzin et al. 2000). Schreader et al. (1998) reported that seasonal drought stress in a subarctic fen sedge community decreased vegetation GPP except during a short midseason period of high photosynthetic activity. Furthermore, Chivers et al. (2009) measured reduced GPP in a boreal peatland water table manipulation experiment during a dry year for a lowered water table treatment, while a raised treatment displayed contrasting results with a higher GPP.

These data suggest that plants exposed to short-term water table changes may experience physiological stress altering their photosynthetic potential. However, long-term water table alterations are further complicated by vegetation successional trajectories and peat chemical and physical transformations influencing GPP dynamics (Foster and Wright 1988; Minkkinen et al. 2002; Laiho et al. 2003; Weltzin et al. 2003). Moreover, because the relationship between GPP and water table position is widely cited as unimodal (Tuittila et al. 2000; Chivers et al. 2009; Pelletier et al. 2011), it is not surprising that the absolute water table position is critically important in controlling GPP. Depending where the peatland is located along the GPP/water table curve, a change in water table position can have very different effects on vegetation GPP dynamics.

Implications for long-term carbon storage

In addition to water table levels directly influencing C fluxes, indirect changes from persistent long-term altered water tables can change peat properties and drive ecological succession contributing to shifts in decadal carbon accumulation (Minkkinen et al. 2002). Past studies have found that long-term drainage reduces carbon storage primarily through increased heterotrophic respiration (Strack and Waddington 2007) and increased fire frequency and severity (Turetsky et al. 2011). In addition, water table drawdown can support significant increases in woody biomass counteracting increased ER and increasing peatland C storage (Hargreaves et al. 2003; Laiho 2006). However, increased tree growth and biomass may not result in increased long-term C storage as peat. In contrast, impoundments typically increase peatland C storage from greater anoxic conditions reducing peat loss through heterotrophic respiration despite typically higher CH_4 emissions.

Despite the measured difference in ER and GPP with long-term water table changes, we measured little differences in NEE. Our data indicate that the wet sites had slightly greater NEE, but not significantly so. However, a companion study, which was conducted at the same sites, used a series of three eddy flux towers to measure CO_2. The eddy flux data showed the same trend as the chambers for ER, but showed that NEE in the dry side was lower, and NEE in the wet side greater, then the intermediate side (Pypker unpublished data). We attribute the differences in NEE between chambers and eddy flux to be likely caused by two chamber methodological issues. Firstly, chambers were only measured in the middle of the day (which may or may not reflect diel patterns), and only every 2 weeks (which may or may not reflect weekly patterns). Secondly, chambers cannot contain large trees, which are not a problem in the treeless wet site, but there are many trees in both the drained and intermediate sites.

In summary, our data indicates that long-term water table drawdown and inundation was still altering peatland gaseous C fluxes, even after 80 years. In addition, many of the patterns we found were of similar magnitude to those measured in short-term studies, which indicates that short-term studies might be useful for predicting the direction and magnitude of future C changes in peatlands.

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