A decade of boreal rich fen greenhouse gas fluxes in response to natural and experimental water table variability

DAVID OLEFELDT1,2, EUGÈNIE S. EUSKIRCHEN3, JENNIFER HARDEN4, EVAN KANE5, A. DAVID MCGUIRE6, MARK P. WALDROP4 and MERRITT R. TURETSKY1

1Department of Integrative Biology, University of Guelph, Science Complex, Guelph, ON N1G 2W1, Canada, 2Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada, 3Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA, 4U.S. Geological Survey, Menlo Park, CA 94025, USA, 5School of Forest Resources and Environmental Sciences, and USDA Forest Service, Michigan Tech University, Northern Research Station, Houghton, MI 49931, USA, 6U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

Abstract

Rich fens are common boreal ecosystems with distinct hydrology, biogeochemistry and ecology that influence their carbon (C) balance. We present growing season soil chamber methane emission ($F_{CH4}$), ecosystem respiration (ER), net ecosystem exchange (NEE) and gross primary production (GPP) fluxes from a 9-years water table manipulation experiment in an Alaskan rich fen. The study included major flood and drought years, where wetting and drying treatments further modified the severity of droughts. Results support previous findings from peatlands that drought causes reduced magnitude of growing season $F_{CH4}$, GPP and NEE, thus reducing or reversing their C sink function. Experimentally exacerbated droughts further reduced the capacity for the fen to act as a C sink by causing shifts in vegetation and thus reducing magnitude of maximum growing season GPP in subsequent flood years by ~15% compared to control plots. Conversely, water table position had only a weak influence on ER, but dominant contribution to ER switched from autotrophic respiration in wet years to heterotrophic in dry years. Droughts did not cause interannual lag effects on ER in this rich fen, as has been observed in several nutrient-poor peatlands. While ER was dependent on soil temperatures at 2 cm depth, $F_{CH4}$ was linked to soil temperatures at 25 cm. Inter-annual variability of deep soil temperatures was in turn dependent on wetness rather than air temperature, and higher $F_{CH4}$ in flooded years was thus equally due to increased methane production at depth and decreased methane oxidation near the surface. Short-term fluctuations in wetness caused significant lag effects on $F_{CH4}$, but droughts caused no inter-annual lag effects on $F_{CH4}$. Our results show that frequency and severity of droughts and floods can have characteristic effects on the exchange of greenhouse gases, and emphasize the need to project future hydrological regimes in rich fens.

Keywords: carbon dioxide, climate change, ecosystem respiration, methane, peatland, soil temperature, water table, wetland

Received 7 April 2016; revised version received 6 November 2016 and accepted 7 December 2016

Introduction

Northern peatlands cover ~3% of the global land cover and are dominant ecosystems in many boreal regions. As the end of the last glaciation, peatlands have accumulated ~500 Tg carbon (C) in the form of peat (Yu, 2012). This represents ~15–30% of the total current global soil C pool (Batjes, 1996). Accumulation of soil C in northern peatlands is primarily a result of restricted rates of decomposition under cool and often anaerobic soil conditions (Clymo et al., 1998; Roulet et al., 2007; Yu, 2012). However, anaerobic conditions also promote the production and release of methane ($CH4$), and northern peatlands are responsible for ~20% of all natural $CH4$ sources to the atmosphere (Bergamschi et al., 2007). Although $CH4$ is a more potent greenhouse gas than $CO2$, it has a much shorter half-life in the atmosphere (Hartmann et al., 2013). The net effect of sustained $CO2$ uptake and $CH4$ release from northern peatlands over the Holocene has overall resulted in a net cooling effect on the global climate system (Frolking & Roulet, 2007). The future greenhouse gas exchange of northern peatlands is uncertain, but will likely be strongly influenced by interactions between peatland type and climate change impacts on hydrological regimes.

Recent climate change at high latitudes has been occurring at rates faster than the global average. Interior
Alaska has over the last few decades experienced both increasing air temperatures and an amplification of the hydrological cycle that includes increases in precipitation, potential evapotranspiration and river discharge (Hinzman et al., 2005; Serreze & Francis, 2006; Wendler & Shulski, 2009; Rawlins et al., 2010). An amplified hydrological cycle is likely to redistribute soil moisture at the landscape scale and is expected to cause reduced summer soil moisture conditions in ecosystems that are largely dependent on precipitation inputs (Rouse, 1998; Lafleur et al., 2005; Berg et al., 2009). Rich fens, which receive substantial water inputs from their surrounding landscapes, could, however, experience a differential response due to potentially coinciding greater surface water and groundwater runoff (Walvoord & Striegl, 2007; Olefeldt & Roulet, 2012; Tardif et al. 2015).

The position of the water table in a peatland often has strong influences on the greenhouse gas exchange. A higher water table is generally associated with higher net methane emissions ($F_{CH4}$), as the balance between anaerobic methane production and aerobic oxidation is shifted, but vegetation composition can modify this relationship significantly (Segers, 1998; Limpens et al., 2008; Olefeldt et al., 2013; Turetsky et al., 2014). Different peatland ecosystems have also shown positive, negative and no relationships between ecosystem respiration (ER) and water table position (Chinner & Cooper, 2003; Lafleur et al., 2005; Ballantyne et al., 2014; Juszczyk et al., 2013; McConnell et al., 2013). This is potentially due to independent responses of constituent autotrophic and heterotrophic respiration. Peat mineralization, i.e., heterotrophic respiration, increases substantially under aerobic conditions (Moore & Knowles, 1989; Silvola et al., 1996). However, droughts can also influence gross primary productivity (GPP) of wetland plant species (Sulman et al., 2009; Adkinson et al., 2011; Lund et al., 2012) and thus affect rates of autotrophic respiration (Crow & Wieder, 2005; Han et al., 2014). Vegetation composition further influences the location of optimal water table position for maximum GPP and net ecosystem exchange (NEE) (Yurova et al., 2007; Adkinson et al., 2011). Altered frequencies or severities of droughts and floods are thus likely to affect the C sink function of peatlands, but responses are also likely to depend on peatland type.

Droughts and floods can further impact peatland C balance through lag effects over various timescales. Water table fluctuations can cause short-term lag effects on $F_{CH4}$ through transient soil conditions, including the regeneration or depletion of terminal electron acceptors and re-establishment of microbial communities (Dowrick et al., 2006; Knorr & Blodau, 2009; Deppe et al., 2010; Sun et al., 2012). In nutrient-poor peatlands, the degradation of phenolic compounds during severe droughts has been shown to enable drastically increased rates of anaerobic heterotrophic respiration in subsequent wet years (Fenner & Freeman, 2011). Over longer timescales, it is likely that the most important effects of altered drought and flood characteristics are due to induced shifts in vegetation composition, as individual vegetation communities have specific relationships between C fluxes and abiotic variables such as water table position, soil temperatures and light conditions (Laiho, 2006; Lindroth et al., 2007; Olefeldt et al., 2013; Ward et al., 2013).

The Alaska Peatland Experiment (APEX) was initiated in a rich fen in 2005 as a long-term ecosystem-scale experiment designed to study potential effects of climate change on peatland greenhouse gas exchange. One goal at APEX was to create a lowered and a raised water table regime through water table manipulations, yet without altering the natural inter- and intra-annual water table variability that characterizes these ecosystems. In this study, our objective is to investigate the influences of water table position and variability on rich fen C fluxes, including long-term influences arising due to experimentally altered drought severity.

Materials and methods

Study site and experimental design

The Alaska Peatland Experiment is located adjacent to the Bonanza Creek Long-Term Ecological Research forest, ~35 km southwest of Fairbanks, Alaska, USA (64.82°N, 147.87 W). Mean annual temperature (1917–2000) is 3.1 °C, and mean annual precipitation is 287 mm (Hinzman et al., 2006). The site is positioned within the Tanana River floodplain and is characterized as a rich fen (surface water pH 5.2–5.4), with vegetation dominated by marsh cinquefoil (Potentilla palustris), wheat sedge (Carex atherodes), water horsetail (Equisetum fluviatile) and a ground cover mostly comprised of brown mosses (Drepanoclados aduncus and Hamatocaulis vernicosus) and sparse Sphagnum spp. (Churchill et al., 2015). Biomass harvest indicates an aboveground net primary productivity of vascular plants of ~300 g m$^{-2}$ yr$^{-1}$. A maximum vascular green area of ~2.5 m$^2$ m$^{-2}$ is attained between late June and mid-August (Churchill et al., 2015). Peat depth is ~1 m, the site lacks permafrost, and it has no distinct microtopography.

In the spring of 2005, three 120-m$^2$ plots were randomly assigned to a control, raised and lowered water table treatment. Drainage channels were dug around the lowered water table plot to divert water ~20 m downslope to a surface well, from which solar-powered bilge pumps added up to 100 mm day$^{-1}$ to the raised plot during the thawed seasons (for further information, see Turetsky et al., 2008). No significant difference in water table position or vegetation composition among plots was observed prior to treatment initiation. Within each plot, six subplots were established for greenhouse gas flux measurements.
Water table and temperature records

Data loggers (CR10x, Campbell Scientific, Logan, UT) recorded hourly air temperature at 1.5 m height, hourly water table positions in 1-m-long 5-cm-diameter PVC wells in each treatment plot and hourly soil temperatures at 2 and 25 cm depths in all 18 subplots and at 50 cm depth in six subplots. Daily data records were compiled using the hourly data. There were several gaps in the continuous temperature and water table records due to sensor or logger malfunctions during the 9-year study period. Soil temperature records had 75% data coverage on average, ranging between 23 and 90% coverage for individual sensors. Variation in soil temperature among subplots was not associated with water table treatments, or an intended warming treatment (see supplementary information; Fig. S1). Hence, we compiled single site common soil temperature records for each depth by using the average of daily soil temperatures across subplots (Fig. 1a). Weekly manual measurements of water table position within each plot were used to linearly gap-fill the continuous records during parts of 2006 (lowered and control plots) and for all of 2007 (all plots) (Fig. 1b).

Measuring greenhouse gas fluxes

Greenhouse gas flux measurements were taken using static chamber techniques (Carrol & Crill, 1997). Collars (0.36 m²) were inserted to 10 cm depth at all 18 subplots in 2005. A clear chamber (0.23 m³) was constructed out of 0.6-cm-thick Lexan, and an airtight seal was created between base and chamber using foam tape applied during each measurement campaign. Two internal fans were used to mix the air within the chamber during measurements.

Fluxes of CO₂ were measured under ambient light conditions (measuring NEE) followed by dark conditions using a dark shroud (ER measurement). The difference between NEE and ER equals our GPP estimate. Chambers were closed for 2–3 min, and CO₂ concentrations were determined every 1.6 s using a PP Systems EGM-4 portable infrared gas analyzer (IRGA; Amesbury, MA, USA). The IRGA was calibrated before each measurement campaign, using external CO₂ standards. From 2006 and onward, a PP Systems TRP-1 measured temperature and photosynthetic photon flux density (PPFD, μmol m⁻² s⁻¹) within the chamber. Chamber measurements of CH₄ were typically taken on days immediately following CO₂ measurements due to time constraints. Chambers were closed for 30–40 min, and four 20 mL gas samples were taken, using plastic syringes with three-way stop cocks. Samples were analyzed within 24 h, using a Varian 3800 gas chromatograph with a FID detector with a Haysep N column (Varian Analytical Inc., Palo Alto, California). We report net CO₂ (reported in μmol CO₂ m⁻² s⁻¹) and net CH₄ (reported in mg CH₄ m⁻² day⁻¹) fluxes to the atmosphere as positive and net uptake as negative.

Sampling was initiated between May 20 and June 15 each year except during 2012 and 2013 when the site was flooded and measurements could not start until July 1 and August 5, respectively. Weekly sampling was carried out in 2005–2007 and 2010–2013, while 2008 and 2009 had biweekly sampling. Last samplings were carried out between September 1 and October 1 except in 2008 and 2009 when they were completed in mid-July. A total of 1380 paired NEE and ER flux measurements and 918 F₃CH₄ measurements were accepted after data quality check (see supplementary information). Maximum and minimum measurements per year were 259 and 46 for 2005 and 2013, respectively, for CO₂ and 219 and 31 in 2006 and 2013, respectively, for F₃CH₄.

We define fluxes measured between day-of-year (DOY) 165 and 235 (June 13 to August 22 in non-leap years) as peak growing season fluxes (NEEPeak, GPPPeak, ERPeak, F₃CH₄Peak).

Fig. 1 Peak growing season (June 13–August 22) data from 2005 to 2013, including (a) site common air and soil temperatures at 2, 25 and 50 cm and (b) water table position for each treatment plot (positive values indicate water table above peat surface).
Peak growing season was defined to include the period of maximum vascular green area (Churchill et al., 2015). As sampling periods varied substantially among years, using peak growing season data allows for a better comparison of abiotic controls on C fluxes among years and treatments as it reduces confounding influences that arise due to seasonally developing phenology (Peichl et al., 2015). Peak growing seasons included 65% of CO2 flux measurements and 74% of CH4 measurements (Figs S2 and S3). Whether all data or only peak growing season data are used is explicitly stated for each analysis.

Data modeling and statistical analysis
We used both linear and nonlinear analyses to assess abiotic controls on FCH4, ER, NEE and GPP. All statistical analyses were conducted in MatLab R2014a, with the Statistics Toolbox and the Curve Fitting Toolbox (v 3.4.1) (MathWorks, Natick, Massachusetts). The linear mixed effects models (function: fitlme) included a categorical variable for water table treatment (control, raised, lowered) and continuous abiotic variables as fixed effects. Collar ID was included as a random effect nested within treatment plots to account for the lack of independence of repeated measurements. Abiotic variables included water table position (WT), soil temperatures at 2 and 25 cm depth (T2 and T25) and PPFD (only included for NEE and GPP analysis). Interactions between water table treatments and all abiotic variables were also included as fixed effects. The analysis was carried out on log10-transformed FCH4 fluxes [log10(FCH4)], due to a non-normal distribution. Logarithmic transformation excluded negative FCH4 fluxes, representing 8% of FCH4 measurements. Analysis of variance (ANOVA) was performed on the marginal effects, and yielded F and P values for each fixed effect, including interactions. Significant variables, as indicated by the linear mixed effects model, were subsequently included in a forward stepwise multiple linear regression (function: stepwise) to estimate parameter coefficients for each variable.

We used residuals from the stepwise linear model to assess potential time lags in relationships between water table position and ER and FCH4. Coefficients of determination were determined for linear correlations between model residuals and the net shift in water table position over a time period preceding a flux measurement. Time periods for lag effects ranging from 1 to 50 days were considered. Inter-annual time-lag effects, i.e., the effect of the wetness of the preceding year on the current year fluxes, were assessed by linear correlations between the current year average model residual within each plot and its average water table position during the preceding year.

A nonlinear model was used to assess temperature sensitivity:

\[ \text{Flux} = A \times Q_{10}^T \]  

where Flux is either FCH4 or ER, A is Flux at 0°C, Q_{10} is the temperature dependence of Flux and T is soil temperature at either 2 or 25 cm below the surface. The analysis was carried out for parsed datasets to assess differences in temperature dependence under four water table ranges; <-25 cm, -25 to -10 cm, -10 to 0 cm and >0 cm (positive values indicate water table above the surface).

Nonlinear dependence of GPP on variation in PPFD was modeled using:

\[ \text{GPP} = \frac{\text{GPP}_{\text{max}} \times \text{PPFD}}{k + \text{PPFD}} \]  

where GPP_{max} is the maximum rate of GPP under light saturation and k is the PPFD level where half of GPP_{max} is attained. Our analysis estimated parameters using only peak growing season GPP data, for six groups based on water table treatment and annual wetness (dry years vs. wet years; see below).

Optimal water table position and the range over which maximum fluxes occur were estimated as:

\[ \text{Flux} = F_{\text{base}} + F_{\text{opt}} \times \exp \left[ -0.5 \times \left( \frac{\text{WT} - \text{WT}_{\text{opt}}}{\text{WT}_{\text{rng}}} \right) \right] \]  

where Flux is either log10(FCH4Peak), ERPeak, GPPPeak or NEEPeak. F_{base} is Flux outside the range of optimal water table position, F_{opt} is the addition to F_{base} at the optimal water table position (i.e., F_{base} + F_{opt} = maximum Flux), WT is the water table position at the time of flux measurement, WT_{opt} is the water table position where maximal Flux occurs and WT_{rng} is the distance of the water table range around WT_{opt} where increased Flux occurs. Unit of F_{base} and F_{opt} is the same as for Flux, while the unit for WT, WT_{opt} and WT_{rng} is in cm. Equation 2 is a modified version of an equation used by Tuitilla et al. (2004) and Chivers et al. (2009), but it assumes that fluxes can be 0 outside the water table range for optimal fluxes. For NEE and GPP, we used only data measured when PPFD > 400 μmol m^{-2} s^{-1}, i.e., when light limitation was minimal (see Results). Data from all water treatment plots were pooled for this analysis, as data from each treatment separately did not yield significant model parameters.

Results
Climate and abiotic variables
During our measurement period, mean annual air temperatures ranged from -1.7 °C (2005) to -4.9 °C (2012), while peak growing season average air temperatures varied between 14.4 °C (2008) to 17.0 °C (2013) (Fig. 1a). Average peak growing season soil temperatures were more variable than air temperatures, and inter-annual variability increased with soil depth (Fig. 1a). The standard deviation of average growing season temperatures over the nine study years was 0.9 °C for air temperature, 1.1 °C for soil temperature at 2 cm, 2.0 °C at 25 cm and 2.8 °C at 50 cm. Average peak growing season soil temperature at 2 cm was significantly correlated with average peak growing season air temperatures, while soil temperature at 25 cm was significantly correlated with average peak growing air temperatures.
season growing season temperature at 25 cm depth was ~8 and ~12 °C in dry and wet years (see below), respectively (Fig. 1a, b).

Water table position varied greatly between years, with average peak growing season water table positions in the control plot varying between −32 cm (2006) and +21 cm (2013) (Fig. 1b). In subsequent analysis, we define years when the control plot had average growing season water table position below −20 cm as dry years (2006, 2010 and 2011) and other years as wet years. The water table treatments had no effect on water table position among treatments in wet years, but in dry years the lowered plot had an average water table position that was 9 cm lower than the control and the raised plot had an average water table position 11 cm higher than the control plot (Fig. 1b).

Methane fluxes

The linear model found measured log-transformed \( F_{\text{CH}_4} \) fluxes \( [\log_{10}(F_{\text{CH}_4})] \) to be strongly related to WT and T\(_{25}\), with minor, but significant, influences from both T\(_2\) and the interaction between water table treatment and WT (Table S1; overall \( R^2_{\text{adj}} = 0.63 \)). The non-linear model showed that variability of T\(_{25}\) explained between 28 and 33% of the variability in \( F_{\text{CH}_4} \), except for during the driest periods (WT < −25 cm) when only 10% of variability was explained (Fig. 2a, Table S2). Variability in T\(_2\) only explained between 4% and 9% of \( F_{\text{CH}_4} \) (Table S2). The seasonal trend in \( F_{\text{CH}_4} \) during wet years thus followed the seasonal trend of T\(_{25}\), leading to a late peak emissions period between mid-August and late September (Fig. S2). Higher water table led to higher \( F_{\text{CH}_4} \) (Fig. 2a), and maximum \( \log_{10}(F_{\text{CH}_4}) \) was modeled (Eqn 3) to occur when the water table was well above the peat surface (WT\(_{\text{opt}} = 8.0 \pm 3.4 \) cm) (Table 1). As a result of the influences of wetness and T\(_{25}\), wet years with associated warmer T\(_{25}\) (see above) had 4–20 times greater average \( F_{\text{CH}_4}\text{Peak} \) than dry years associated with colder T\(_{25}\) (Fig. 3a).

Significant short-term lags were present in the relationship between \( F_{\text{CH}_4} \) and water table position. The residuals from the linear model were significantly correlated with the net shift in water table position that occurred 3–7 days prior to \( F_{\text{CH}_4} \) measurements (maximum \( R^2 = 0.08, P < 0.01 \), Fig. 4). For example, this lag effect indicated that measured \( F_{\text{CH}_4} \) was ~25% higher than predicted by the linear model when the water table had been dropping by 5 cm over the last 5 days, and equally lower than predicted when the water table had been rising. We found no evidence of inter-annual lag effects, as residuals in average annual \( F_{\text{CH}_4} \) were not significantly related to the average water table position of the preceding year in any plot.

Ecosystem respiration

The linear mixed effects model indicated significant influences on measured ER fluxes from T\(_2\), T\(_{25}\), WT and the interaction between T\(_2\) and treatment, but the model explained only 20% of the variation in ER (Table S1). The most important predictor of higher ER was increasing T\(_2\) (Fig. 2b). The general dependency of

![Fig. 2](image-url) Influence of water table position and soil temperature on a) measured methane fluxes and b) measured ecosystem respiration. Data from both outside and within peak growing season are included. Bars represent median fluxes measured within specified water table and soil temperature intervals. Positive water table position indicates water table above the peat surface. Error bars represent first and third quartiles of the data. Note that soil temperatures at 25 and at 2 cm were used for methane fluxes and ecosystem respiration, respectively, as data at these depths had the greatest explanatory power (see Table S2).
ER on T2 led to a seasonal pattern with a period of maximum fluxes between June 20 and August 10 (Fig. S2), i.e., a longer and earlier peak period than for maximum FCH4 (see above). Nonlinear analysis showed that T2 was a better predictor than T25 for ER, except under the driest conditions when the water table was below -25 cm (Table S2). The interactive effect of the water table treatment and T2 on ER suggested that the lowered water table treatment plot had lower temperature sensitivity of ER than the other plots – although this effect may be an indirect consequence of treatment effect on NEE/GPP through autotrophic respiration.
In any plot, water table fluctuations were found to cause neither NEE Peak nor inter-annual lag effects on ecosystem productivity among subplots was associated with higher GPP Peak during wet years of the study (Fig. 7). Light response curves for each plot similarly showed that magnitude of GPP Peak and NEE Peak both among treatments and between wet and dry years, with the ratio starting to drop once the average peak growing season water table position was below –20 cm (Fig. 5b).

**Gross primary production and net ecosystem exchange**

Abiotic variables explained 36% and 33% of variation in measured GPP and NEE fluxes in the linear mixed effects model, respectively (Table S3). Both GPP and NEE were related to WT, T$_2$ and PPFD and had significant Treatment x PPFD interactions. The interaction term indicated that the lowered treatment had lower sensitivity to increasing light levels (Table S3). The nonlinear model showed that both GPP Peak and NEE Peak had their greatest magnitude (i.e., greatest productivity and net C uptake) when the water table was level with the peat surface (Table 1 and Fig. 6a, b). Water table position also had a significant influence on maximum GPP Peak and NEE Peak both among treatments and between wet and dry years (Fig. 3c, d). However, reduced magnitude of NEE Peak and GPP Peak in the lowered water table plot during wet years (Fig. 3c, d) was not due to water table position, as there were no differences among plots in water table position during wet years (Fig. 1). This treatment effect on NEE Peak in the lowered water table plot occurred in both early (2007–2009) and late (2012–2013) wet years of the study (Fig. 7). Light response curves for each plot similarly showed that magnitude of GPP$_{max}$ was reduced under drier conditions, but that the lowered water table treatment further had reduced magnitude of GPP$_{max}$ compared to the other plots also during wet years despite no difference in water table position (Fig. 8).
Discussion

Rich fens are a common peatland type in the boreal biome (Vitt et al., 2000; Whitcomb et al., 2009), but tend to be understudied compared to boreal poor fens and bogs because of the complexity of these systems and the difficulty of making measurements in systems that flood and dry regularly (Lund et al., 2009; Turetsky et al., 2014). The experimental design and nine-year duration of the study allowed the exploration of long- and short-term effects of water table fluctuations. Results discussed below further show that the studied rich fen has both similarities and differences to the likely impacts of altered hydrological regimes of other boreal peatland types. Understanding impacts of altered hydrological regimes, and potential differences among peatland types, is critical for making predictions about the future greenhouse gas balance of boreal peatlands under future climates.

Long-term effects of experimentally modified drought severity

The effects of our wetting and drying treatment on vegetation composition were assessed in 2010, six years after the establishment of the water table manipulations (Churchill et al., 2015). In brief, the study found that water table treatment led to no significant changes in total biomass or vascular net primary productivity, but that the raised water table plot had slightly increased abundance of sedges, while the lowered plot had reduced brown moss cover and increased total vascular

![Graph showing the relationship between ecosystem respiration and net ecosystem exchange and water table position.](image)

Fig. 5 Relationships between (a) average measured peak growing season (13 June–22 August) ecosystem respiration and net ecosystem exchange fluxes and (b) the average ratio of measured peak growing season net ecosystem exchange to ecosystem respiration magnitude and water table position. Each symbol represents an individual subplot, and error bars represent ±1 standard error. Only fluxes measured under high light conditions (PPFD > 400 μmol m⁻² s⁻¹) were included in analysis. Positive water table position indicates water table above the peat surface. Fitted line shows a significant linear relationship between subplot NEEPeak and ERPek during wet years across all treatments. Dry years were 2006, 2010 and 2011, and wet years were 2005, 2007, 2008, 2009, 2012 and 2013.

![Graph showing the relationship between peak growing season net ecosystem exchange and water table position.](image)

Fig. 6 Relationship between peak growing season (13 June–22 August) net ecosystem exchange and water table position. Only measurements taken under high light conditions (PPFD > 400 μmol m⁻² s⁻¹) are included. The dashed line represents a nonlinear regression based on data from all subplots using Eqn (2), which is described in Table 1. Positive water table position indicates water table above the peat surface.
have led to lower rates of autotrophic respiration (Han et al., 2014) and thus caused the observed reduction in ER. The net effect was reduced magnitude of NEE, indicating reduced capacity for C uptake during summers. These treatment effects on the lowered water table plot were evident in the lowered plot after just 2 years of water table manipulation (Chivers et al., 2009; Churchill et al., 2015), and this study shows that these effects have been maintained over the 9 years of the experiment.

**Water table variability and CO2 fluxes**

Our chamber flux measurements corroborate results from an eddy covariance study carried out at the site (Euskirchen et al., 2014), showing that both NEE and GPP peak (i.e., have maximum rates of photosynthesis and C uptake) when the water table is approximately level with the peat surface. The optimal water table position at the APEX fen for NEE (~2 to +5 cm) is wetter than has been observed in a boreal poor fen (~10 to ~20 cm) (Yurova et al., 2007), likely due to differences in vegetation composition and rooting depths, where the APEX fen has relatively more emergent vascular plants and less Sphagnum mosses than the poor fen. Reduced photosynthetic uptake of mosses is likely when the water table is above the peat surface. Conversely, reduced uptake during drier periods could be due to plant moisture stress – particularly for bryophytes (Turetsky, 2003) and dwarf shrubs (Lindroth et al., 2007).

Relative to relationships with NEE and GPP, the influence of water table position on ER was weaker but indicated two optima: when the water table was just under the peat surface and again once the water table dropped below ~40 cm. Previous peatland studies have found conflicting relationships (including positive, negative and no relationships) between ER and water table position (Chimner & Cooper, 2003; Lafleur et al., 2005; Juszczak et al., 2013; McConnell et al., 2013; Ballantyne et al., 2014). These conflicting results may partially be due to previous studies not being able, as in this study, to determine the influence of water table position over a wide water table range under comparable soil temperatures. The influence of water table position on ER is also likely obscured by the fact that ER is the sum of autotrophic and heterotrophic respiration that each is affected independently by water table position. Peat mineralization rates (heterotrophic respiration) are expected to decrease with wetter conditions as incubation experiments show rates reduced by on average by 80% under anaerobic conditions compared to aerobic conditions (Schuur et al., 2015). However, photosynthetically driven respiration, including both strict

---

**Fig. 7** Average peak growing season (13 June–22 August) net ecosystem exchange fluxes among treatments measured under high light conditions (PPFD > 400 μmol m−2 s−1) during early (2007–2009) and late (2012–2013) wet years in the study. Error bars represent ±2 standard errors. Two-way ANOVA followed by a multiple comparison using a Bonferroni correction indicated that the lowered treatment had lower magnitude fluxes during both periods (P < 0.1). In wet years, there was no difference in water table position among treatments (control, lowered and raised) (see Fig. 1). Lower magnitude fluxes during the late wet years are primarily due to measurements being taken later in the season on average, with average dates July 3 and August 7 for early and late wet years, respectively (see Fig. S3 for seasonality of NEE).

---

The abundance of drought-tolerant shrub species did not increase in the lowered water table treatment, which has been observed in long-term water table manipulations in nutrient-poor peatlands (Laine et al., 1996; Weltzin et al., 2000). This is likely due to how our measurement period included years when the water table remained above the peat surface throughout the growing season even in the lowered water table plot. Hence, in the lowered water table plot, exacerbated drought conditions during dry years caused the loss of drought-sensitive brown mosses but wet years still likely prevented the establishment of drought-tolerant but flood-sensitive shrubs. This highlights how natural hydrological variability of rich fens influences stability of vegetation communities, which in turn has implications for impacts of hydrological variability on C cycling.

The lowered water table treatment exhibited altered relationships between CO2 fluxes and abiotic variables relative to the other treatment plots, likely linked to shifts in vegetation composition. Under conditions optimal for maximum GPPpeak and ERpeak i.e., measurements taken under full sunlight when the water table was near the peat surface, the lowered treatment plot had GPP and ER fluxes that were reduced in magnitude by ~15% compared with control and raised water table plots. Reduced GPP is likely to
autotrophic respiration (foliage, stems and roots) and rhizospheric respiration of root exudates, often dominates wetland ER (Frolking et al., 2002; Crow & Wieder, 2005) and can be highly responsive to short-term variation in GPP (Han et al., 2014). The observed relationship in this study between NEE and ER among subplots under high light conditions in wet years suggested that photosynthetically driven respiration represented 35±14% of GPP under such conditions. This implies that photosynthetically driven respiration represented ~70±28% of ER during such periods (GPP_{peak} × 0.35 ± 0.14/ER_{peak}). If photosynthetically driven respiration as a fraction of GPP can be assumed similar during dry years, it follows that photosynthetically driven respiration as a fraction of ER under similar light conditions in dry years drops to 63 ± 25, 50 ± 20 and 41 ± 16%, respectively, in the raised, control and lowered treatment subplots, with concurrent increases in heterotrophic contribution.

Increased importance of heterotrophic respiration during drier periods was further supported by the increasing predictive capability of soil temperatures at 25 cm depth for ER during the driest periods. A potentially interesting influence on heterotrophic respiration is thus that deep soil temperatures in dry years are substantially colder than in wet years, thus suppressing rates of peat mineralization despite aerobic conditions (c.f. Ise et al., 2008).

Lag effects on ER following droughts have been observed in nutrient-poor peatlands due to temporary reductions of biogeochemical constraints on anaerobic microbial activity. In nutrient-poor peatlands, droughts initiate a biogeochemical cascade where increased aerobic microbial activity causes a release of nutrients and increased pH, which in turn significantly increases anaerobic rates of peat mineralization following rewetting when compared to before the drought (Fenner & Freeman, 2011). In this study, we found neither short-term (1–50 days) nor inter-annual lag effects on ER linked to shifts in water table position. Furthermore, a peat incubation experiment using soil organic matter from the APEX treatments showed only a minor difference between aerobic and anaerobic rates of peat mineralization (Kane et al., 2013), with much higher rates of anaerobic CO2 production than expected. These results support the interpretation that biogeochemical constraints on anaerobic microbial activity are less strict in more nutrient rich peatlands with higher pH (Ye et al., 2012) and that ER in rich fens thus is less likely to exhibit inter-annual lag effects following drought.

Methane emissions and water table variability

It is well established in the literature, and corroborated in our results, that the balance between anaerobic CH4 production below the water table and oxidation above...
it leads to rapidly increasing CH$_4$ fluxes with a higher water table position (Bridgham et al., 2013). Our results further showed short-term lag effects on CH$_4$ emissions due to water table fluctuation. This lag effect was ecologically significant as our linear model over- and underestimated CH$_4$ emissions by $\sim$25% when the water table had raised or dropped by 5 cm over the preceding 5 days, respectively. These short-term lag effects may arise due to physical processes such as changes in hydrostatic pressure, due to suppression of methanogens until alternate electron acceptors are depleted (Knorr and Blodau, 2009; Deppe et al., 2010) or due to differential growth rates between methanogens and methanotrophs (Segers, 1998). Given that water table position generally drops over the season, our results suggest that short-term lag effects are required to be taken into account when modeling methane emissions from northern peatlands.

Methane emissions were strongly associated with soil temperatures at 25 cm depth. Average peak growing season soil temperature at 25 cm over the 9 years was uncorrelated with air temperatures, but was on average $\sim$3.5 °C warmer in wet than in dry years. Higher deep soil temperatures in wet years are likely due to increased soil thermal conductivity of flooded soils. Our empirical models indicate that a 3.5 °C increase at 25 cm soil depth when the water table is level with the peat surface leads to 85% to 120% increases in methane emissions. As such, higher methane emissions in wet years are indicated to be equally due to increased rates of methanogenesis in warmer anaerobic peat layers as it due to reduced capacity for methanotrophy in a thinner aerobic layer. A coupled hydrological and biogeochemical model of wetland greenhouse gases has accordingly shown that wet years can lead to increased soil temperatures, which in turn raise CH$_4$ emissions (Grant, 2015). This connection between water table position and deep soil temperatures is thus important to consider not to underestimate future methane emissions in wetlands that occasionally flood.

Climate change implications for boreal rich fens

Studies of water table and soil temperature influences on methane emissions and the balance between GPP and ER for the overall C balance of northern peatlands have shown that different peatland types can be expected to respond differently (Bubier et al., 1998; Sulman et al., 2010; Turetsky et al., 2014). Our results show that altered frequency and severity of droughts and floods will have a strong influence on the overall C balance of rich fens like APEX. Eddy covariance measurements have found the site to be a significant C sink (~80 g C m$^{-2}$ yr$^{-1}$) during wet years (2012 and 2013), but the record does not yet include a dry year for comparison (Euskirchen et al., 2014). Our results show that dry years lead to reduced capacity for C uptake as a result of inhibited GPP, while ER magnitude is sustained by a shift in dominance from autotrophic to heterotrophic respiration. Similar negative influence of dry years on photosynthetic capacity has been suggested based on eddy covariance measurements for a boreal rich fen in Finland (Aurela et al., 2009). However, we further observed reduced rates of peak growing season GPP and NEE in the lowered treatment during subsequent wet years despite there being no difference in water table position among treatments in wet years. This indicates that extreme droughts have long-term, inter-annual, effects on C uptake in rich fens, likely due to reduced photosynthetic capacity of an altered vegetation community.

It is not certain that climate change will lead to increased frequency or severity of summer droughts in rich fens as is expected for boreal nutrient-poor peatlands (Wu & Roulet, 2014). Given the amplification of the hydrological cycle, wetness of rich fens may not respond to climate like the overall landscape given the importance surface water and groundwater inflows (Walvoord & Striegl, 2007; Olefeldt & Roulet, 2012). For example, the APEX rich fen is located on a floodplain and remained flooded throughout the 2013 growing season despite less than average seasonal precipitation. There is currently a limited understanding of how climate change may affect regional hydrology and thus hydrological regimes of rich fens. Projecting future hydrological regimes of rich fens thus represents a key uncertainty future greenhouse gas exchange of northern peatlands overall.

Acknowledgements

This APEX has been supported by National Science Foundation grants (DEB-0425328, DEB-0724514 and DEB-0830997) to M.R.T, A.D.M, J.H., E.E. and E.S.K., the Bonanza Creek Long-Term Ecological Research program (funded jointly by NSF Grant DEB-0620579, an USDA Forest Service Pacific Northwest Research Grant PNNW01-JV1261952-231) and U.S. Geological Survey Climate and Land Use Change Program and Climate Science Center grant funds to J.H., A.D.M., M.W. and E.E. During manuscript compilation and writing, D.O. was supported by a Campus Alberta Innovates Program grant. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank all collaborators and students who have contributed over the years to the APEX project, namely Bill Cable, Colin Edgar, Michael Waddington, Jamie Hollingsworth, Teresa Hollingsworth, Rebecca Finger, Amy Churchill, Nicole McConnell and Molly Chivers. The authors claim no conflicts of interest.
References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Relationships between (a) average daily soil temperature at 25 cm depth and soil temperatures at 25 cm in the raised and lowered water table treatment, and (b) average daily soil temperature in subplots without open top chambers (OTC) and subplots with OTC.

Figure S2. Median measured daytime fluxes of methane fluxes and ecosystem respiration throughout the season.

Figure S3. Median measured fluxes under high light conditions (PPFD > 400 mmol m⁻² s⁻¹) throughout the season of (a) NEE and (b) GPP. Dry years were 2006, 2010 and 2011, while wet years were 2005, 2007, 2008, 2009, 2012, and 2013.

Figure S4. Average peak growing season (DOY 165-234) soil temperatures (2005–2013) at 2 and 25 cm peat depths plotted against (a) average peak growing season air temperatures, and (b) average peak growing season water table position in the control plot.

Table S1. Results from linear mixed effects model analyzing controls on measured daytime ER and Log10 transformed CH₄ fluxes across three water table treatments: ANOVA of the marginal effects of the parameters and the final regression model with estimates of significant fixed effects coefficients.

Table S2. Estimated parameters for models examining the non-linear temperature dependencies of methane fluxes and ecosystem respiration (Eq. 1: Flux = A × Q¹⁰⁻¹⁰). 

Table S3. Results from linear mixed effects model analyzing controls on measured GPP and NEE fluxes across three water table treatments: ANOVA of the marginal effects of the parameters and the final regression model with estimates of significant fixed effects coefficients.