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# Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland

M. R. Turetsky,[1,2] C. C. Treat,[1] M. P. Waldrop,[3] J. M. Waddington,[4] J. W. Harden,[3] and A. D. McGuire[5]

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[1] Growing season $CH_4$ fluxes were monitored over a two year period following the start of ecosystem-scale manipulations of water table position and surface soil temperatures in a moderate rich fen in interior Alaska. The largest $CH_4$ fluxes occurred in plots that received both flooding (raised water table position) and soil warming, while the lowest fluxes occurred in unwarmed plots in the lowered water table treatment. A combination of treatment and soil hydroclimate variables explained more than 70% of the variation in ln-transformed $CH_4$ fluxes, with mean daily water table position representing the strongest predictor. We used quantitative PCR of the $\alpha$-subunit of mcr operon to explore the influence of soil climate manipulations on methanogen abundances. Methanogen abundances were greatest in warmed plots, and showed a positive relationship with mean daily $CH_4$ fluxes. Our results show that water table manipulations that led to soil inundation (flooding) had a stronger effect on $CH_4$ fluxes than water table drawdown. Seasonal $CH_4$ fluxes increased by 80–300% under the combined wetter and warmer soil climate treatments. Thus, while warming is expected to increase $CH_4$ emissions from Alaskan wetlands, higher water table positions caused by increases in precipitation or disturbances such as permafrost thaw that lead to thermokarst and flooding in wetlands will stimulate $CH_4$ emissions beyond the effects of soil warming alone. Consequently, we argue that modeling the effects of climate change on Alaskan wetland $CH_4$ emissions needs to consider the interactive effects of soil warming and water table position on $CH_4$ production and transport.

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## 1. Introduction

[2] Boreal ecosystems cover 14% of the earth's vegetated surface (14–18.5 million km$^2$) [*Bolin et al.*, 2000; *McGuire et al.*, 1995] and store between 25 and 30% of the world's soil carbon (C) stocks [*Gorham*, 1991; *McGuire et al.*, 1995, 1997] largely in poorly drained peatlands and permafrost forests. Peatlands cover 24% of the circumboreal land area or 3.3–3.5 million km$^2$ [*Vitt*, 2006; *Wieder et al.*, 2006], and are distributed extensively throughout Siberia, Canada, Alaska, and Scandinavia [*Gorham*, 1991; *Kuhry and Turunen*, 2006; *Vitt*, 2006]. Generally, peat accumulation is thought to be controlled more by slow rates of decomposition under cold, saturated soil conditions than by net primary productivity [e.g., *Clymo et al.*, 1998; *Turetsky et al.*, 2005]. Recent estimates suggest that peatlands contain between 270–370 Pg C [*Turunen et al.*, 2002; *Vasander and Kettunen*, 2006], a substantial portion of boreal forest C stocks.

[3] Owing to thousands of years of C fixation and peat accumulation, peatlands have had a global net radiative cooling effect [*Frolking et al.*, 2006]. However, northern wetlands also are important sources of atmospheric methane ($CH_4$), releasing an estimated 30 to 50 Tg $CH_4$ yr$^{-1}$ [*Chen and Prinn*, 2006; *Zhuang et al.*, 2004, 2006], approximately 20% of the estimated 190 Tg $CH_4$ yr$^{-1}$ emitted from wetlands globally [*Bergamaschi et al.*, 2007]. Given that $CH_4$ has a net radiative capacity 23 times greater than $CO_2$ on a 100-year timescale [*Houghton et al.*, 2001], large-scale changes in $CH_4$ emissions from boreal peatlands due to changes in soil hydroclimate conditions may impact the radiative forcing of the global climate system.

[4] Climate change has the potential to influence $CH_4$ emissions through complex controls on $CH_4$ production, oxidation, and plant mediated transport. Methane emissions

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


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are the net result of $CH_4$ production (methanogenesis) through anaerobic microbial respiration and $CH_4$ oxidation (methanotrophy) in aerobic soil layers. Water table position often serves as the dominant control on $CH_4$ emissions in northern wetlands [cf. *Bubier et al.*, 1995; *Moore and Roulet*, 1993] by influencing the zonation of methanogenesis and methanotrophy. Lower water tables and increasing acrotelm thickness with drought or drainage in peatlands generally increase $CO_2$ emissions and reduce atmospheric $CH_4$ fluxes, and can cause individual peatlands to switch from net C sinks to sources [e.g., *Alm et al.*, 1999; *Moore and Roulet*, 1993; *Shurpali et al.*, 1995]. However, other studies have shown that increases in the belowground productivity of emergent plants under drier conditions [*Weltzin et al.*, 2000] can stimulate $CH_4$ emissions in wetlands by increasing the availability of labile substrates in soil via root exudation and by increasing $CH_4$ transport to the surface due to shifting rooting zones [*Strack et al.*, 2006]. Higher water table positions caused by increasing precipitation, runoff, or permafrost thaw in peatlands also generally increase $CH_4$ emissions [*Dise et al.*, 1993; *Turetsky et al.*, 2002; *Weltzin et al.*, 2000] by simultaneously increasing methanogenesis in saturated soils as well as graminoid abundance and/or productivity, which stimulates $CH_4$ transport to the atmosphere through aerenchymous tissue.

[5] Warming also has the potential to affect methane production and transport from Alaskan wetlands [*Zhuang et al.*, 2007]. While methanotrophy can be significant in reducing net $CH_4$ emissions in northern wetlands [e.g., *Moosavi and Crill*, 1998; *Pearce and Clymo*, 2001; *Whalen and Reeburgh*, 1990], increasing temperatures are predicted to influence rates of methanogenesis more than rates of $CH_4$ oxidation [*Dunfield et al.*, 1993] and thus are expected to stimulate $CH_4$ emissions.

[6] In many regions, northern wetlands are expected to experience warmer and drier climatic conditions under climate change. Interior Alaska already is experiencing large changes in climate including increases in surface annual temperatures [*Hinzman et al.*, 2005; *Houghton et al.*, 2001; *McGuire et al.*, 2002, 2007; *Serreze et al.*, 2000], small increases in annual precipitation [*Hinzman et al.*, 2005], longer growing seasons [*Euskirchen et al.*, 2006; *Goetz et al.*, 2005; *Serreze et al.*, 2000], and altered snowpack dynamics [*Dye*, 2002; *Serreze et al.*, 2000]. Across interior Alaska, the surface area of open water bodies within wetland-rich landscapes is declining, likely due to increased summer moisture deficits and permafrost degradation [*Hinzman et al.*, 2005; *Oechel et al.*, 2000; *Riordan et al.*, 2006; *Yoshikawa and Hinzman*, 2003]. However, Alaskan wetlands are strongly influenced by landscape topography, and thus may be influenced by permafrost degradation and runoff from surrounding upland systems. For example, expansion of open water and saturated wetland habitat in the Tanana Flats region is occurring due to increased groundwater discharge associated with meltwaters from the Alaska Range [*Jorgenson et al.*, 2001; *Osterkamp et al.*, 2000]. Though future climate change will influence both thermal and moisture regimes in wetlands, the net effect on atmospheric $CH_4$ emissions is not clear because controls on $CH_4$ fluxes, such as production, oxidation, and transport to the peat surface, may be affected differentially and/or to different magnitudes.

[7] To test the effect of changing climatic conditions on feedbacks between northern wetlands and climate systems, we recently initiated an ecosystem-scale experiment designed to test soil hydroclimate controls on short- and longer-term vegetation and carbon cycling responses in an Alaskan fen. Our experiment included a factorial design of water table position (three treatments including a control, a lowered or drying treatment, and a raised or flooded treatment) and surface soil temperature (two treatments including a control or no warming treatment, and surface soil warming via open top chambers) manipulations. Our goal was to create three distinct water table regimes, without minimizing the ambient seasonal fluctuations in water table position that typically characterize northern peatland environments.

[8] Here we present the short-term responses (first two years) in soil hydroclimate variables, $CH_4$ emissions, and methanogen activity across our experimental treatments. We recognize that in the short term, changes in $CH_4$ emissions across our soil hydroclimate manipulations are likely to be driven primarily by changing microbial activity, while vegetation-mediated controls on $CH_4$ fluxes (enhanced plant transport of $CH_4$, increased productivity, and changes in rooting zones) will become increasingly important controls on $CH_4$ flux as vegetation communities reach equilibrium with the manipulated water table levels [e.g., *Bubier*, 1995]. Using the first two years of data from this experiment, we determined whether our experimental manipulations of soil climate affected $CH_4$ flux while maintaining the same fundamental relationship between ambient water table position and $CH_4$ flux, or whether our experimental manipulations 'pressed' the system across a threshold yielding new relationships between ambient water table position $CH_4$ flux. We predicted that the latter would be evidenced by a significant interaction between experimental treatment and water table position on $CH_4$ flux.

## 2. Materials and Methods

### 2.1. Description of Study Site and Experimental Treatments

[9] Our study, the Alaska Peatland Experiment (APEX; http://www.apex.msu.edu), was conducted in a rich fen located outside the boundaries of the Bonanza Creek Experimental Forest, situated approximately 35 km southeast of Fairbanks, Alaska, USA (64.82°N, 147.87°W). The area is classified as continental boreal, with a mean annual temperature of −2.9°C and mean annual precipitation of 269 mm (30% as snow) [*Hinzman et al.*, 2006]. The APEX site is a moderate rich fen (mean pH = 5.3) located in the floodplain of the Tanana River. Rich fens represent one of the most common peatland types in western boreal North America [*Vitt et al.*, 2000]. The APEX site lacks trees and is dominated by a diverse community of brown moss, *Sphagnum* and emergent (*Equisetum*, *Carex*) species. The fen contains no distinct microtopography (hummocks or hollows), and maximum peat depth is approximately 1 m.

[10] In 2004, we created three large experimental plots (each 120 $m^2$ area) within the APEX fen and randomly assigned each plot to one of three water table treatments,

including a control, lowered, and raised water table treatment. There were no significant differences in early growing season water table position, species composition, or baseline C fluxes across these three plots prior to our manipulations, though it is possible that our raised water table plot is located in a slightly wetter microclimate than the other two plots. In April 2005, when soils were still frozen, we used a small excavator to create drainage channels (~40 cm wide, 1 m deep) to divert surface water from the lowered water table plot. Our goal was to reduce water table position inside the lowered plot by ~10–15 cm, in line with the level of predicted future drying [*Roulet et al.*, 1992]. In June 2005, we installed solar-powered bilge pumps to pump water into the raised water table plot from a surface well immediately downslope. The chemistry of water additions is similar to ambient pore water in our raised plot (no significant differences in pH, electrical conductivity, anion/cation or organic acid concentrations; data not shown). Mean DOC concentrations measured in surface waters of the supply well to the raised plot (64.8 ± 1.1 mg/L) fell within the range of values measured in 20 and 80 cm piezometers within the control plot (79.1 ± 3.6 and 47.8 ± 0.3 mg/L, respectively; TOC-V Analyzer, Shimadzu Scientific Instruments, Columbia, MD, USA). Likewise, concurrent measurements of Specific Ultraviolet Absorbance (SUVA; Beckman DU-640 Spectrophotometer, Beckman Coulter, Inc., Fullterton, CA, USA) did not differ between the supply well (6.9 ± 0.9 L (mg C)$^{-1}$ m$^{-1}$) and the control plot (6.6 ± 1.1 L (mg C)$^{-1}$ m$^{-1}$) (1- way ANOVA, $F = 0.04$, $p = 0.86$). While our flooding treatment does not involve a dilution of DOC concentrations as would be expected with increased precipitation, our treatment does not lead to major changes in pore water chemistry in the raised plot and is probably a reasonable simulation of flooding involved in wetland thermokarst formation in this region.

[11] Within each of the three water table plots (control, lowered, raised), triplicate open top chambers (http://www.geog.ubc.ca/itex/) were installed with the goal of passively increasing incoming solar radiation and surface soil temperatures by about 1°C. Open top chambers were constructed out of 0.16 cm thick Lexan, with base dimensions of 0.8 m$^2$. To minimize snowpack disturbance, OTCs were removed right before snow accumulation at the site (October), and were re-installed in identical locations in each water table plot following snowmelt (May). During the growing seasons of 2005 and 2006, OTCs passively warmed surface soil (2 cm beneath moss) at our site by an average of 0.7, 0.9, and 0.6°C in the control, lowered, and raised plots, respectively. Our experimental design represents a full factorial design, and allows us to examine the influence of water table (control, lowered, raised), warming (control, warmed with OTCs), and water table × soil warming interactions on peatland C fluxes.

### 2.2. Characterizing Soil Hydroclimate and Vegetation Composition

[12] Mean hourly measurements of soil temperature and water table position were logged across our experimental treatments beginning June 2005. At each water table × warming plot (and adjacent to each gas flux collar, see section 2.3), we used thermistors to monitor air temperature just above the peat surface as well as peat temperatures at 2, 10, 25, and 50 cm beneath the moss surface. We also used quantum sensors (Apogee Instruments, Logan, UT) to monitor mean hourly photosynthetic active radiation (PAR) at each gas sampling collar. All environmental data were logged using Campbell CR10x data loggers (Campbell Scientific, Logan, UT).

[13] Mean hourly water table position in each water table treatment was monitored using pressure transducers (Campbell Scientific, Logan, UT) installed at the bottom of 5 cm diameter, 1 m deep PVC wells. Water table measurements were calibrated against manual water table measurements within each of the plots. In 2006, our lowered and control plot water table data were incomplete due to data logger malfunction. We used weekly manual water table measurements, our continuous raised plot data, and calculations of peat storativity to model continuous water table data in the lowered (23 July to 30 September 2006) and control (14 July to 20 September 2006) plots.

[14] The percent cover of all vascular and bryophyte species was visually estimated within each gas flux collar (section 2.3) in July 2005 and August 2006. Dominant vascular species included *Carex utriculata, Equisetum fluviatile* and *Potentilla palustris*. Dominant bryophyte species at our site include *Sphagnum* (*Sphagnum obtusum, Sphagnum platyphyllum)* and brown moss (*Hamatocaulis vernicosus, Drepanocladus aduncus*) species. Canonical discriminant analysis showed that percent species cover within each gas flux collar did not vary across our experimental treatments in 2005, and showed no significant shifts in species composition in the early stages of our experiment (comparison of species composition in 2005 versus 2006 across treatments). However, upon visual observation the abundance of mosses appeared to decline in the lowered water table plot. Given that many peatland vegetation species occupy relatively narrow niches defined largely by height above the water table [*Bubier*, 1995; *Bubier et al.*, 2006; *Gignac et al.*, 1991; *Nykanen et al.*, 1998; *Strack et al.*, 2006], we do anticipate future shifts in species composition across our experimental manipulations.

### 2.3. $CH_4$ Flux Measurements

[15] $CH_4$ fluxes were measured weekly from June to September in 2005 and 2006 using conventional static chamber techniques [*Carroll and Crill*, 1997]. Chambers for gas sampling were constructed of 0.64 cm thick Lexan (area 0.362 m$^2$; volume 0.227 m$^3$). Chambers were placed on Lexan collars that were permanently embedded into the peat surfaces by approximately 7 cm. Gas tight seals were created using foam tape around the chamber base during each flux campaign. Small fans within the chamber gently mixed the headspace gas. Four 20 mL gas samples were taken using plastic syringes equipped with 3-way stopcocks over a period of 30–40 min. Samples were returned to the lab and analyzed for $CH_4$ concentrations, typically within a 24-h period, using a Varian 3800 gas chromatograph with an FID detector with a Haysep N column (Varian Analytical Inc., Palo Alto, CA, USA). Flux rates were calculated as the slope of linear regressions of $CH_4$ concentrations versus time. Nonlinear regressions, likely due to chamber leakage or soil disturbance were discarded from our subsequent analyses (7% of data). Our static chamber measurements captured two ebullition events [*Strack et al.*, 2005] that

released large quantities of $CH_4$. These events represent statistical outliers, and thus are excluded from the majority of our statistical analyses though ebullition events are discussed in greater detail in section 4.2. $CH_4$ fluxes were ln-transformed to help normalize data and model errors.

[16] All statistical analyses of $CH_4$ fluxes were performed using general linear models (Proc Mixed) in SAS 8.1 (SAS Institute Inc., Cary, NC, USA). We used a repeated measures analysis of variance and Tukey post hoc comparison of means tests to determine the effects of water table treatment, soil warming, year, and all interactions among these fixed effects on $CH_4$ fluxes. We also used a general linear model that included environmental variables (water table position, peat temperatures), year, experimental treatments (water table and soil warming treatments), and all possible interactions to predict $CH_4$ fluxes. If significant interactions were present between environmental variables and experimental treatments or year, we estimated slopes for all relevant treatment groups separately. We started with a full model that included all interactions between environmental variables and treatment, and removed terms sequentially from the model in a backward, stepwise procedure based on changes in likelihood. We used the final model and continuous records of mean daily water table position and peat temperatures at 25 cm depth to model $CH_4$ fluxes across the 2005 and 2006 growing seasons. Mean daily $CH_4$ fluxes were summed over the growing season period to calculate cumulative seasonal $CH_4$ fluxes within each water Table 10 soil warming treatment (Table 3).

### 2.4. Methanogen Population Abundance

[17] Surface peat cores were obtained from our experimental plots in September of 2005. We collected a surface peat core adjacent to each of our 18 gas flux collars using a 4.70 cm diameter sharpened stainless steel core barrel. The core barrel was attached to a cordless drill; the spinning action allowed the core to cut through soil organic material with minimal disturbance. Peat samples were extruded from the soil, sectioned into 0–5 and 5–15 cm segments, placed in plastic bags, and kept at 4°C for 2–4 h after which point they were frozen at −20°C.

[18] We estimated the abundance of methanogenic bacteria in soil using quantitative PCR of the $\alpha$-subunit of the mcr operon. The mcr operon codes for the enzyme methyl coenzyme M reductase, an enzyme critical to methanogenesis [*Hales et al.*, 1996]. We used the forward PCR primer ME1 (5′ GCM ATG CAR ATH GGW ATG TC) and the reverse primer ME2 (5′ TCA TKG CRT AGT TDG GRT AGT) [*Hales et al.*, 1996]. DNA was extracted from soil using the Powersoil DNA extraction kit according to manufacturer's instructions (Mobio Laboratories, Carlsbad, CA). DNA was quantified using the Picogreen assay (Invitrogen, Carlsbad, CA), and diluted to 1 ng/$\mu$L using DNase free water. Gradient PCR was conducted in order to determine the optimal annealing temperature for PCR. The size of the PCR product was confirmed at 760 bp by gel electrophoresis. Our qPCR reactions consisted of 2 $\mu$L DNA, 9 $\mu$L DNase free water, 2 $\mu$l of each primer (10 $\mu$M), 0.5 $\mu$L ROX dye (10,000 X dilution), and 12.5 $\mu$L Sybrgreen master mix (Stratagene, La Jolla, CA). The qPCR thermal cycling program consisted an initial step of 95°C for 10 min, then 40 cycles of 94°C for 40 s, 52°C for 1 min, and 72°C for 2 min. The PCR product was confirmed using a melting curve following the PCR program. Standards were made by quantifying multiple PCR products of the mcr operon and making serial dilutions down to 1.0 attogram/ $\mu$l. Samples were run on an MX3005P qPCR machine and data were analyzed using the MX3005P v2.02 software (Stratagene, Carlsbad, CA). Samples and standards were run in duplicate. The standard curve had an $r^2$ of 0.98 and an efficiency of 95%. Most samples amplified between 20 and 28 cycles. Positive and negative controls were run simultaneously. We used a three way analysis of variance model to explore the effects of peat depth (0–5 and 5–15 cm), water table treatment (raised, lowered, and control), soil warming treatment (control, warmed via OTCs), and all possible interactions on methanogen abundances.

## 3. Results

### 3.1. Soil Hydroclimate

[19] Observations of mean daily air temperatures at the Bonanza Creek LTER Tanana River floodplain site (http://www.lter.uaf.edu/data_detail.cfm?datafile_pkey = 1), which is close to the APEX fen, showed that air temperatures (1 May to 30 September) on average were warmer in 2005 (13.4 ± 0.1°C) than in 2006 (12.3 ± 0.1°C; F = 53.06, df = 1, 7337, $p < 0.0001$). Our site also was much wetter in 2005 than in 2006, likely due to more precipitation received as snowfall (snow water equivalent = 120 mm in 2005; 73 mm in 2006). Mean annual or growing season precipitation, however, did not vary between years (F = 1.61, df = 1, 304, $p > 0.10$).

[20] Despite the interannual differences between our study years, our hydrologic manipulations maintained differences in water table regimes between the control, raised, and lowered water table treatments in both years (Figure 1). In 2005 (the warmer and wetter year), water table position in the lowered water table treatment was 5 cm lower than the control plot on average across the growing season. In 2006 (the cooler and drier year), the lowered plot had an average water table position 8 cm lower than the control plot. In 2005 and 2006, the raised water table plot had an average water table position 9 and 11 cm higher than the control plot, respectively.

[21] Surface peat temperatures varied more across water table treatments than across sampling years. Most notably, both surface peat (2 cm beneath the moss surface) and deeper peat (25 cm beneath the moss surface) temperatures were consistently higher in the raised water table plot than in the lowered or control plots (Figure 2). In 2005, growing season peat temperatures (from 14 July to 30 September) at 2 cm depth averaged 12.5 ± 0.1°C, 12.5 ± 0.1°C, and 16.9 ± 0.0°C in the control, lowered and raised plots, respectively. These peat temperatures were slightly lower in 2006, averaging 11.9 ± 0.1°C, 11.8 ± 0.1°C, and 16.4 ± 0.1°C in the control, lowered, and raised plot, respectively.

### 3.2. Methane Fluxes

[22] Methane fluxes across the experimental treatments ranged from −13 to 813 mg $CH_4$ $m^{-2}$ $d^{-1}$ in 2005 and −3 to 3045 mg $CH_4$ $m^{-2}$ $d^{-1}$ in 2006 (negative values represent $CH_4$ consumption). A repeated measures analysis

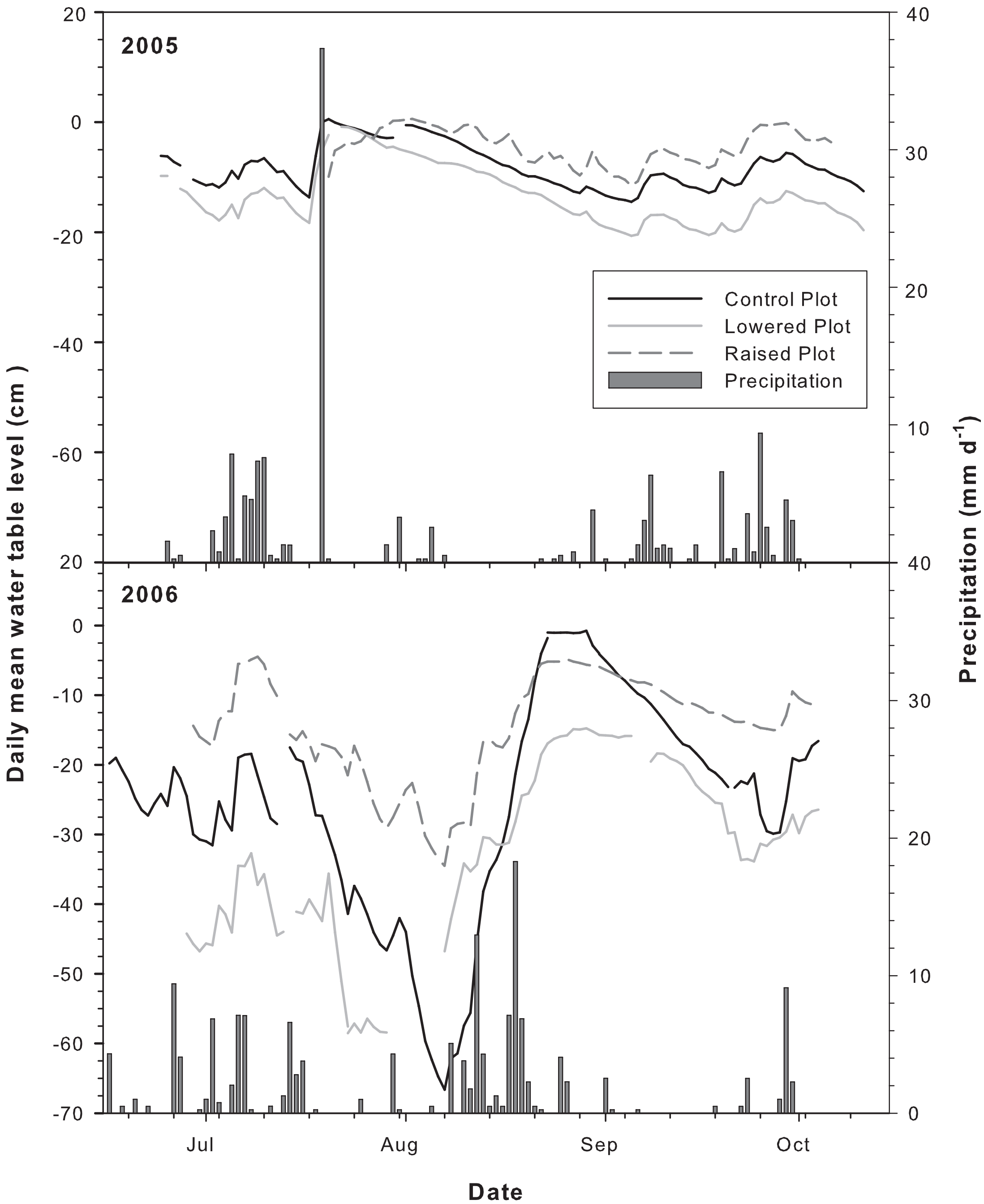


**Figure 1.** Water table levels and precipitation at the manipulation plots in 2005 and 2006. Positive values denote water table position above the peat surface (inundated). Bars represent precipitation events. Precipitation was not significantly different between the two study years (F = 1.61, df = 1, $p$ = 0.21).

of variance model showed that daily $CH_4$ fluxes varied by a water table treatment (raised, lowered, control) × year (2005, 2006) interaction (Table 1). Generally, $CH_4$ fluxes were lower in 2006 than 2005 (Figure 3a) due to drier conditions and lower water table position at the site (Figure 1). In 2005, daily $CH_4$ fluxes were highest in the raised treatment and lowest in the lowered treatment. In 2006, daily $CH_4$ fluxes were highest in the raised treatment and did not differ between the control and lowered treatments.

[23] Daily $CH_4$ fluxes also varied by a soil warming × water table treatment interaction (Table 1 and Figure 3b). Soil warming increased daily $CH_4$ fluxes in the raised and the lowered water table treatments, with no significant effect of warming on $CH_4$ fluxes in the control treatment. Averaged across sampling years, warming increased daily $CH_4$ fluxes by 80%, 8%, and 75% in the raised, control, and lowered water table treatments, respectively. In general, the highest $CH_4$ fluxes were from plots that received both soil warming and flooding (raised water table treatment) and were lowest in the unwarmed, drained plots (Figure 3b).

[24] Last, daily $CH_4$ fluxes varied by a soil warming × year interaction (Table 1; data not shown). Soil warming

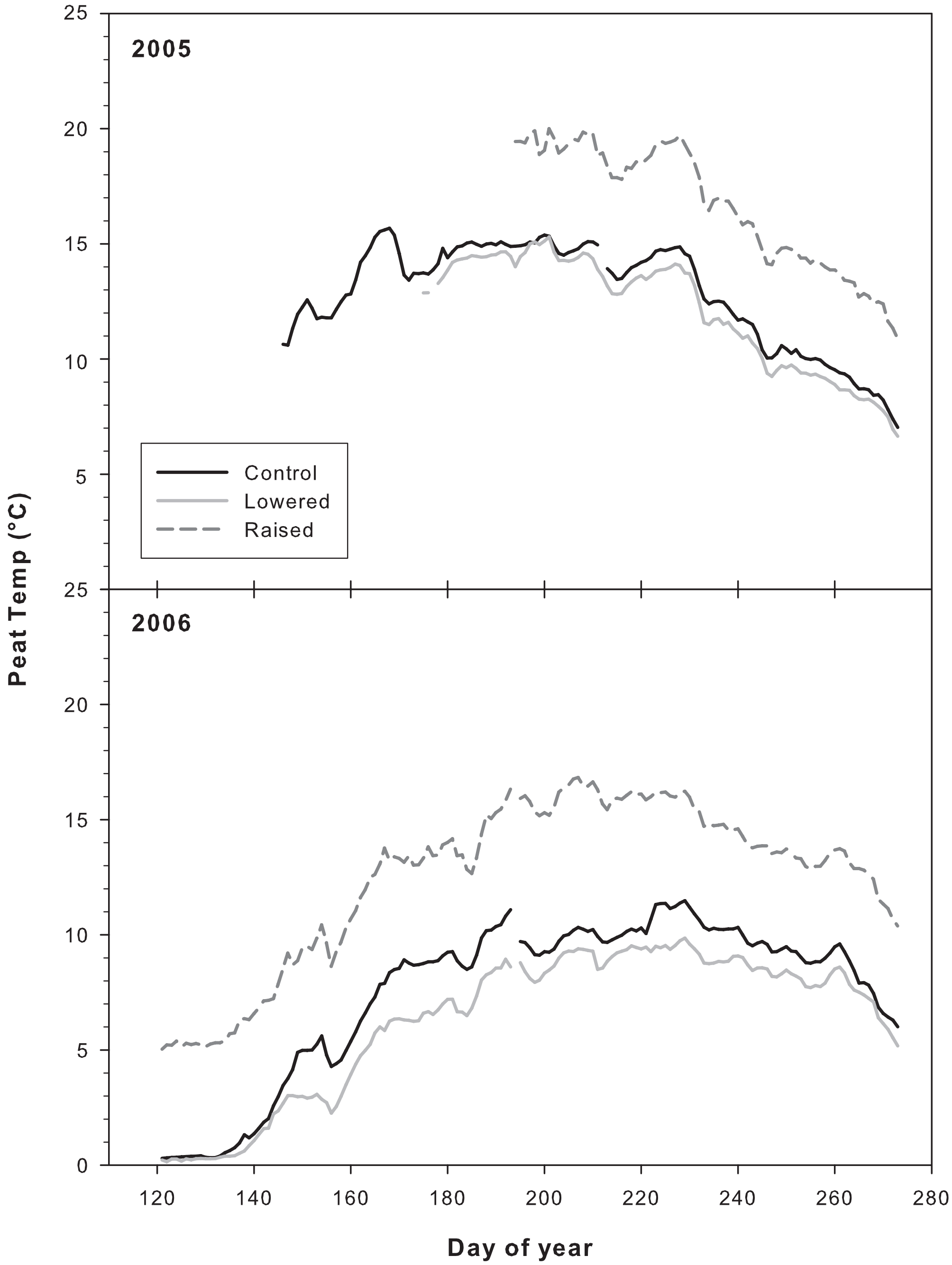


**Figure 2.** Mean peat temperatures at 25 cm beneath the moss surface in (a) 2005 and (b) 2006 across the three water table plots (corresponding to the control, lowered, raised water table treatments).

significantly increased fluxes in 2005, with no significant effects on $CH_4$ fluxes in 2006 (warmed plots: 118.6 ± 7.7[a] and 31.5 ± 3.3[c] mg $CH_4$ $m^{-2}$ $d^{-1}$ in 2005 and 2006, respectively; unwarmed plots: 75.2 ± 5.8[b] and 22.3 ± 2.5[c] mg $CH_4$ $m^{-2}$ $d^{-1}$ in 2005 and 2006, respectively; data are means ± one standard error; same letter superscripts denote nonsignficant post hoc comparisons).

[25] A combination of experimental treatments (control, lowered, raised water table treatments; warmed and unwarmed treatments), year, and continuous soil climate variables (water table position, peat temperature at 25 cm depth) explained more than 70% of variability in ln-transformed daily $CH_4$ fluxes (Table 2). Daily mean water table position was the most important predictor, explaining 48% of variation in $CH_4$ fluxes. No significant interactions between treatment and water table position or peat temperatures were retained in our final model. We used this model to estimate seasonal $CH_4$ fluxes for each water table × soil warming treatment. The seasonal modeling highlights the water table × soil warming interaction that govern daily $CH_4$ fluxes (Table 1), though the differences in seasonal

**Table 1.** Results of a Repeated Measures Analysis of Variance Model Analyzing $CH_4$ Fluxes Across Our Experimental Treatments[a]

| Effect | Numerator df | Denominator df | F | *P* |
|---|---|---|---|---|
| Warming treatment | 1 | 5 | 39.93 | 0.0015 |
| Water table treatment | 2 | 8 | 43.29 | <0.0001 |
| Day of year | 31 | 130 | 4.76 | <0.0001 |
| Year | 1 | 5 | 63.31 | 0.0005 |
| Warming treatment × water table treatment | 2 | 8 | 18.59 | **0.0010** |
| Warming treatment × year | 1 | 5 | 14.55 | **0.0124** |
| Water table treatment × year | 2 | 8 | 6.56 | **0.0206** |
| Warming treatment × water table treatment × year | 2 | 8 | 2.27 | 0.1659 |

[a]Units are in mg $CH_4$ $m^{-2}$ $d^{-1}$. Significant higher-level interactions are marked in bold.

fluxes among our treatments were smaller in 2006 than in 2005 (Table 3).

### 3.3. Methanogen Activities

[26] There was a peat depth × soil warming interaction for both the relative abundance of methanogens (attogram mcr/ng DNA, $F = 7.2$, df = 1, $p = 0.014$; Figure 5a) and the total abundance of methanogens (attogram mcr/g dry soil, $F = 5.7$, df = 1, $p = 0.026$; Figure 5b), with no water table treatment effect or additional interactions among main effects for either of these variables. In the unwarmed plots, methanogen relative abundance was greater in the 5–15 compared to the 0–5 cm depth increment. Soil warming increased relative methanogen abundance in the 0–5 cm increment, suggesting that our soil warming treatments increased methanogen abundance in the surface-most peat layer, but did not significantly affect abundances in the 5–15 cm increment (Figure 5a). Similar trends were found for total methanogen abundances (Figure 5b), though our measurements were associated with large error terms.

[27] There was a positive relationship between 2005 $CH_4$ fluxes across the water table × soil warming treatments and the abundance of the mcr gene (Figure 6). The relative abundance of the mcr gene at 5–15 cm peat depth also was a strong predictor of mean $CH_4$ fluxes, explaining 40% of the variability in $CH_4$ fluxes (data not shown, df = 1,15; $F = 9.34$, $p = 0.008$). There was no significant relationship between $CH_4$ fluxes and ME abundance expressed per g wet soil ($p > 0.05$; data not shown). Additionally, there was no significant relationship between $CH_4$ fluxes and total DNA extracted from soil (which can be used as an estimator of total microbial biomass belowground).

## 4. Discussion

### 4.1. Hydroclimate Controls on $CH_4$ Emissions and Methanogens

[28] Our sampling characterized $CH_4$ fluxes across two years representing very different climatic conditions in interior Alaska (Figure 3). Our in situ experimental design was intended to manipulate soil hydroclimate (water table position, soil temperature) without minimizing ambient variation to better understand vegetation and carbon cycle responses to changing soil climate conditions beyond the scope of contemporary environmental variability. Differences in soil hydroclimate between our sampling years had large consequences for daily $CH_4$ fluxes, resulting in significant water table treatment × year and soil warming × year interactions (Table 1). These interactions in the controls on $CH_4$ emissions also are evident in the seasonal estimates of $CH_4$ fluxes (Table 3). A shallow snowpack and lower snow water equivalent in the winter of 2005–2006 likely led to less runoff and lower water table positions (Figure 1) at our site in 2006, which likely contributed to the lower $CH_4$ fluxes measured in 2006 than in the previous year (Figure 3). Water table drawdown influences the major zones of methanogenesis and methanotrophy, but also could increase microbial competition for labile C substrate (i.e., root exudates) between methanotrophic and methanogenic

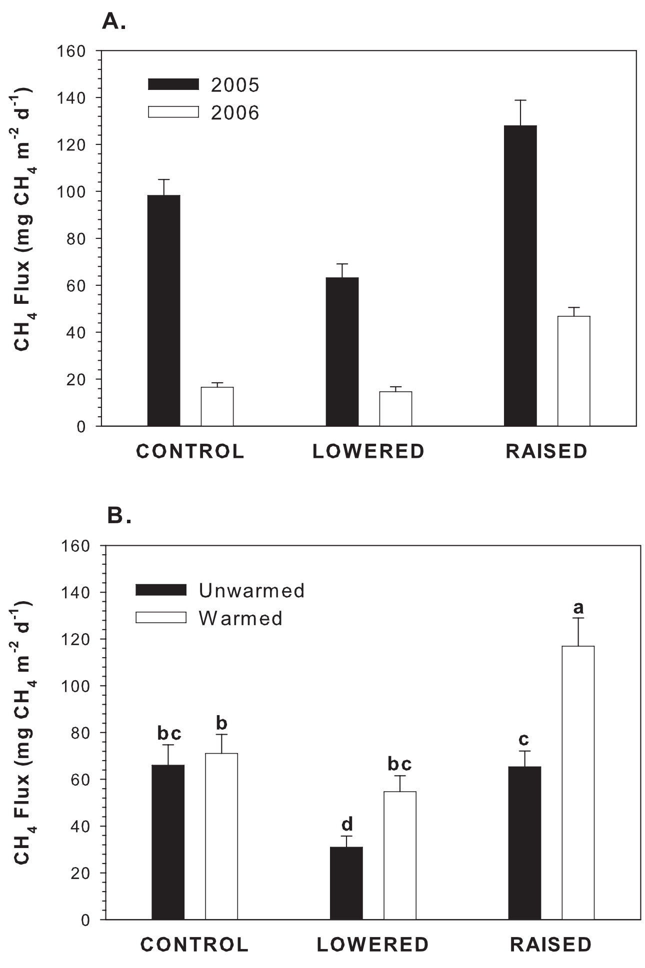


**Figure 3.** Results of a repeated measures analysis of variance model analyzing $CH_4$ fluxes across experimental treatments. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscript denote nonsignificant differences from post hoc comparison of means tests.

**Table 2.** Results of a General Linear Model Using Experimental Treatments and Environmental Parameters to Predict ln Transformed $CH_4$ Fluxes[a]

| | df | Type III SS | F | *P* |
|---|---|---|---|---|
| Model | 11 | 148.49 | 38.80 | <0.001 |
| Year | 1 | 4.105 | 11.80 | <0.001 |
| Mean daily water table position | 1 | 8.294 | 23.84 | <0.001 |
| Year × water table treatment | 4 | 3.435 | 2.47 | 0.047 |
| Peat temperature (25 cm) × warming treatment | 1 | 4.304 | 12.37 | <0.001 |
| Peat temperature (25 cm) × year | 1 | 1.490 | 4.28 | 0.040 |
| Peat temperature (25 cm) × water table treatment | 2 | 2.203 | 3.17 | 0.045 |
| Error | 180 | 62.619 | | |

[a]The model explained 72% of the variation in $CH_4$ fluxes. Mean daily water table position alone explained the majority of variability in $CH_4$ fluxes (48%).

bacteria by stimulating C mineralization more so than plant productivity and root exudation [*Blodau et al.*, 2004]. In addition to water table controls on $CH_4$ fluxes, a thinner snowpack in 2006 likely led to reduced soil insulation and lower soil temperatures during shoulder seasons [*Osterkamp and Romanovsky*, 1999; *Zhuang et al.*, 2001], which can reduce nutrient cycling and microbial activity in northern wetland ecosystems well into the growing season [*Schimel et al.*, 2004]. Given that a combination of water table position and peat temperatures were significant predictors of daily $CH_4$ fluxes, both of these interannual differences in hydroclimate likely led to lower overall $CH_4$ emissions in our second year of sampling (Table 3).

[29] Despite these large interannual differences, our results showed strong responses in $CH_4$ fluxes and methogen abundances to our soil climate manipulations. Soil flooding (raised water table treatment) led to increased $CH_4$ fluxes (Figure 3 and Table 3), though the magnitude of response varied among sampling years. Averaged across our soil warming treatments, mean daily $CH_4$ fluxes were 30% and 180% greater in the raised water table plot than in the control plot in 2005 and 2006, respectively. Water table drawdown or lowering of water table position also affected $CH_4$ fluxes, resulting in a significant decline in fluxes in 2005 but not in 2006. Averaged across our soil warming treatments, mean daily $CH_4$ fluxes were 12% and 36% lower in the drought or lowered water table plot than in the control plot in 2005 and 2006, respectively. Thus, independent of soil warming, water table manipulations that led to soil inundation (flooding) had a stronger effect on $CH_4$ fluxes than water table drawdown, which contributed to a nonlinear relationship between $CH_4$ fluxes and water table position (Figure 4a).

[30] While water table position often is hypothesized to serve as the dominant control on $CH_4$ fluxes from peatlands, $CH_4$ production and emissions from peatlands also are dependent on soil temperature [cf. *Christensen et al.*, 2003b; *Dunfield et al.*, 1993; *Moore and Dalva*, 1993; *Segers*, 1998]. However, few studies, particularly in the field, have investigated the interaction between temperature and water table levels as controls on peatland $CH_4$ fluxes (Table 4). Soil warming increased concentrations of methanogens in surface peat (Figure 5) and $CH_4$ fluxes across all water table plots, though this effect was not significant in the control water table treatment (Figure 3b). Averaged across water table treatments, our soil warming treatments increased $CH_4$ fluxes in both sampling years, though differences between the warmed and unwarmed plots were larger in 2005 than in 2006. The largest fluxes of $CH_4$ occurred in plots that received both soil warming and flooding. Soil warming in the raised water table treatment increased daily $CH_4$ fluxes by 0–325% (mean increase of 79%) above the effects of soil flooding alone (Table 3). *Updegraff et al.* [2001] found similar results in a bog monolith experiment, in which soil warming and flooding treatments together increased growing season $CH_4$ fluxes by about 175% compared to an increase of 100% with flooding alone.

[31] While both methanogenesis and methanotrophy could increase with peat temperatures, here we focused on potential climatic controls on methanogen communities [*Dunfield et al.*, 1993; *Sundh et al.*, 1995]. Our results showed rapid increases in methanogen abundance to soil climate manipulations, with significant increases in the soil

**Table 3.** Cumulative Seasonal $CH_4$ Emissions (±Standard Errors) Across the Water Table and Soil Warming Treatments[a]

| | | Cumulative Seasonal $CH_4$ Fluxes (g $CH_4$ $m^{-2}$ $season^{-1}$) | |
|---|---|---|---|
| Water Table Treatments | Soil Warming Treatments | 20 Jul to 1 Sep 2005 | 29 Jun to 10 Sep 2006 |
| Control | Warmed | 5.4 ± 0.7 | 1.2 ± 1.1 |
| | No warming | 4.1 ± 0.7 | 0.9 ± 1.2 |
| Lowered | Warmed | 3.2 ± 0.7 | 1.0 ± 1.1 |
| | No warming | 2.3 ± 0.7 | 0.8 ± 1.1 |
| Raised | Warmed | 7.4 ± 0.7 | 3.5 ± 1.2 |
| | No warming | 4.8 ± 0.7 | 2.5 ± 1.2 |

[a]Seasonal emissions were derived from the general linear model presented in Table 2. Error terms are standard errors that represent within-treatment variability compounded with model error.

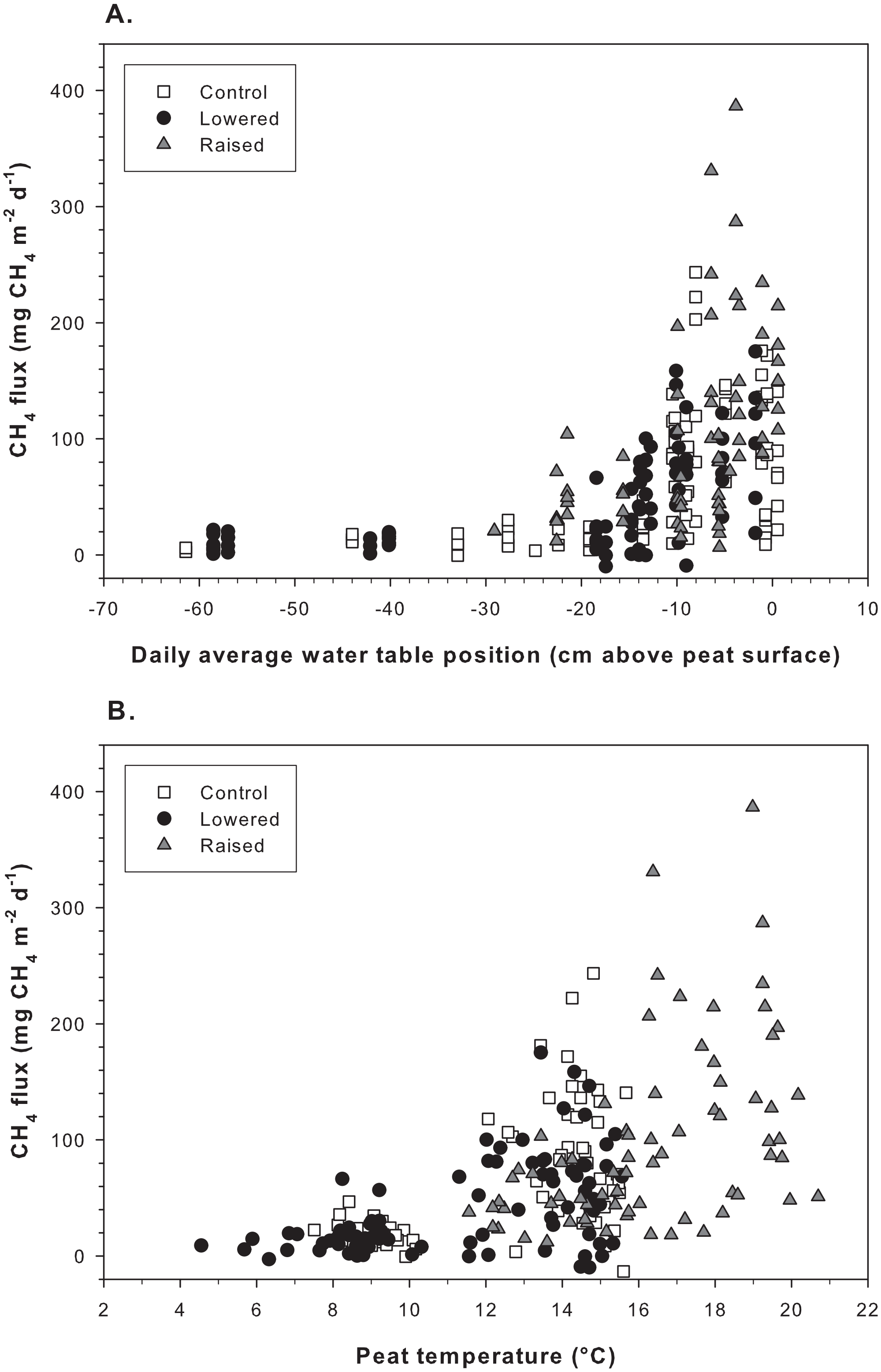


**Figure 4.** (a) Effect of water table position and (b) peat temperature at 25 cm depth beneath the moss surface on $CH_4$ fluxes across the three water table treatments.

warming treatment in the first year of the experiment (Figure 5). To our knowledge, this is one of the first studies to show increases in methanogen population size in response to field-based soil warming experiments. While we did not observe any effects of water table treatment on methanogen abundance, the relationship between observed average $CH_4$ fluxes and relative methanogen abundance (Figure 6) suggests that increases in

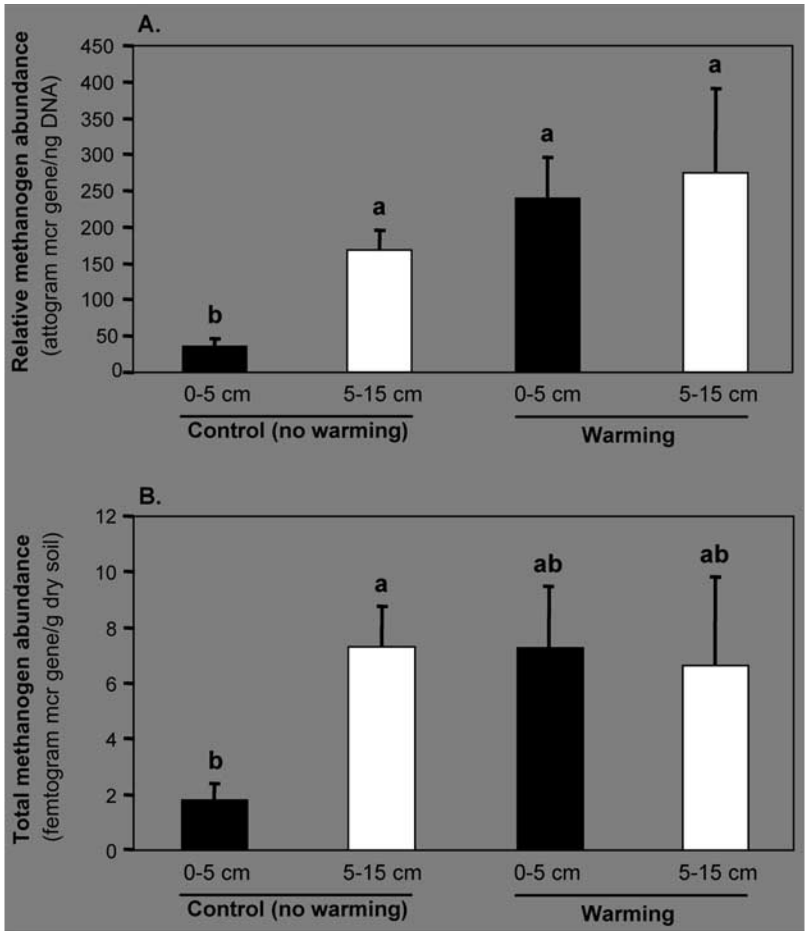


**Figure 5.** Results of an analysis of variance model analyzing (a) the relative abundance and (b) the total abundance of methanogens estimated by qPCR in surface (0–5 cm) and deeper (5–15 cm) peat across the soil warming treatments. Data are means ± one standard error. Same letter superscript denote nonsignificant differences from post hoc comparison of means tests.

methanogen population size was at least partially responsible for increases in flux rates under more saturated conditions (Figure 4). Future work should also investigate the sensitivity of methanotrophic populations to soil climate variation as well as implications of climate change for redox sink-source relationships.

[32] In addition to directly controlling the zones of methanogenesis and $CH_4$ oxidation, the water table position controls the transfer of heat to deeper peat layers through thermal conductivity. Thus, fluctuating water table position can have both direct (via redox status) and indirect (heat transfer) controls on the biological processes leading to $CH_4$ emissions. Surface and deeper peat temperatures within our raised water table treatment tended to remain much warmer than the other experimental plots (Figure 2), likely as a result of heat transfer from surface water to deeper peat layers. Greater heat transfer in these flooded conditions likely contributed to the strong increase in daily (Figure 3) and seasonal (Table 3) $CH_4$ fluxes associated with the raised water table treatment. The linkages between water table position and peat temperatures driven by thermal conductivity likely contribute to the often interactive controls of these soil hydroclimate variables in governing $CH_4$ fluxes from peatland soils.

[33] Climate change is expected to alter soil climate dynamics beyond the scope of contemporary variability. A key question is whether our current models will be able to accurately represent C cycle responses and $CH_4$ emissions under these changing climatic conditions, or whether ecosystems will undergo threshold changes that create new controls on and/or new trajectories of $CH_4$ fluxes that are not represented in current models. Our experiment allowed us to determine whether this ecosystem showed evidence of such threshold changes to affect $CH_4$ emissions in the first few years of experimentation. Mean daily water table position was the strongest predictor of daily $CH_4$ fluxes, and our analysis revealed no significant interactions between treatment (i.e., water table or soil warming treatments) and water table position. Thus, at this point, it seems that our treatments have simply extended the scope of ambient water table fluctuations as controls on $CH_4$ fluxes, without ‘pressing’ the system into fundamental new relationships between water table and $CH_4$ fluxes. However, processes operating at longer timescales, such as changes in plant community structure and soil organic matter quality may invoke such threshold changes in future years of this in situ experiment (see section 4.3 for related discussion on longer-term responses).

**Table 4.** Synthesis of Short- Versus Longer-Term Methane and Vegetation Responses to Manipulations of Water Table (WT) and Soil Temperature in Northern Peatlands[a]

| Reference | Scale (Peat Type) | Treatment Magnitude | Duration | Description of Response |
|---|---|---|---|---|
| | | *Short-Term WT Manipulations* | | |
| *Strack and Waddington* [2007] | Ecosystem (poor fen) | WT: −20 cm drawdown | 3 years | Reduced $CH_4$ flux by ∼80%; Increase in vascular vegetation; stronger response with time |
| *Dise et al.* [1993] | Ecosystem (bog) | WT: +6 to +10 cm flooding | 2 years | Increased $CH_4$ flux by 200–250% |
| *Blodau et al.* [2004] | Core (bog) | WT: −36 cm drawdown | 30 weeks | Reduced $CH_4$ flux by 80–90% |
| *Aerts and Ludwig* [1997] | Core (fen) | WT: −10 cm drawdown | 7 weeks | Reduced $CH_4$ flux by 80–90% in mesotrophic and eutrophic fen |
| *Funk et al.* [1994] | Core (bog) | WT: −15 cm drawdown | 10 weeks | Reduced $CH_4$ flux by 90% |
| | | *Short-Term Warming Manipulations* | | |
| *Granberg et al.* [2001] | Ecosystem (poor fen) | Temp: +2.0°C (soil) | 3 years | Warming increased $CH_4$ fluxes by 14% in plots with high sedge cover; no effect in plots without high sedge cover |
| *Verville et al.* [1998] | Ecosystem (tundra) | Temp: +1.5°C (soil) | 2 years | No response in $CH_4$ fluxes |
| | | *Factorial Short-Term WT × Warming Manipulations* | | |
| *Updegraff et al.* [2001] | Mesocosm (bog and poor fen) | WT set at +1, −10, −20 cm; Temp: +1.6 to +4.1°C (soil) | 3 years | **Poor fen:** $CH_4$ fluxes were ∼375–550% greater at +1 than at −20 cm WT; Warming increased $CH_4$ fluxes by 0 and 40% in −20 and the +1 WT treatments, respectively. **Bog:** $CH_4$ fluxes were ∼100% greater at +1 than at −20 cm; Warming increased $CH_4$ fluxes by 40% both at +1 and −20 cm. |
| *Moore and Dalva* [1993] | Core (bog, poor fen) | WT set at 0 and −40 cm; Temp set at 10 and 22.6°C (air) | 6 weeks | **Poor fen:** WT drawdown increased $CH_4$ fluxes by ∼250% at 10°C, but decreased fluxes by ∼90% at 22.6°C. Warming increased $CH_4$ fluxes by ∼2800% at 0 cm but no change at −40 cm. **Bog:** Lower WT decreased $CH_4$ fluxes by ∼90% in both warming treatments; Warming increased $CH_4$ fluxes by ∼120% and 60% when WT at 0 cm (surface) and −40 cm, respectively |
| This study | Ecosystem (rich fen) | WT: −5 to −8 cm drawdown, +9 to +11 cm flooding; Temp: +0.6 to 1°C (soil) | 2 years | Flooding increased $CH_4$ fluxes by 75% and 0% with and without warming, respectively. WT drawdown decreased $CH_4$ fluxes by 17% and 53% with and without warming, respectively. No vegetation response to treatments, though moss dieback noted. |

**Table 4.** (continued)

| Reference | Scale (Peat Type) | Treatment Magnitude | Duration | Description of Response |
|---|---|---|---|---|
| | | *Long-Term WT Manipulations* | | |
| *Strack et al.* [2004] | Ecosystem (poor fen) | WT: −20 cm drawdown | 8 years | Reduced $CH_4$ fluxes by 55%; Increase in herbaceous and shrub spp., decrease in *Sphagnum* (except in hollows) |
| *Roulet et al.* [1993] | Ecosystem (fen and bog) | WT: −10 cm to −60 drawdown | 7 years | Reduced $CH_4$ fluxes by 98–105% in fen sites and 100–200% in bog sites |
| *Laine et al.* [1995] (a); *Laine et al.* [1996] (b); *Martikainen et al.* [1995] (c); *Nykanen et al.* [1998] (d) | Ecosystem (fen, bog) | WT: −15 cm to −25 cm drawdown | 30 years | Reduced $CH_4$ fluxes by 50 (a,b)–100% (a,c,d) in a fen and by 25–80% (c,d) in a bog; Decrease in *Sphagnum* cover (c), increase in woody vegetation (a,c) |
| | | *Long-Term Factorial WT and Warming Manipulations* | | |
| *Keller et al.* [2004] | Core/incubation (bog and fen) | See *Updegraff et al.* [2001][b] | 11 wk incubation after 6 yr treatment | **Fen:** WT drawdown decreased $CH_4$ production, with no change in $CH_4$ production rates due to temperature manipulations. **Bog:** No change in $CH_4$ production rates with WT or temperature treatments |

[a]WT drawdown and flooding manipulations are denoted by negative and positive WT level changes relative to the soil or moss surface, respectively. The magnitude of warming manipulations is described as changes in surface soil or air temperatures. For ecosystem-scale manipulations, changes in vegetation structure are reported when possible.
[b]*Keller et al.* [2004] indicates WT set at ∼−3, −16, −25 cm below peat surface.

### 4.2. Diffusive Versus Episodic (Ebullition) Fluxes of $CH_4$

[34] Our static chamber measurements characterize diffusive fluxes of $CH_4$ at the peatland surface. Recent studies, however, have shown that the episodic ebullition of entrapped gas bubbles may account for as much, or more, seasonal $CH_4$ release as diffusive fluxes in northern peatlands [*Baird et al.*, 2004; *Christensen et al.*, 2003a; *Strack et al.*, 2005; *Tokida et al.*, 2007]. While our methods were not designed to capture these episodic events, we did measure several ebullition events that led to large $CH_4$ fluxes to the atmosphere. For example, an ebullition event in 2006 released >3 g $CH_4$ $m^{-2}$ $d^{-1}$ from the control plot, approximately 160 times larger than the daily diffusive flux on that sampling day. Together, the two episodic fluxes that we captured were equivalent to 0.1% and 46.3% of the cumulative seasonal $CH_4$ flux (Table 3) in 2005 and 2006, respectively. *Kellner et al.* [2006] suggest that ebullition will be greater in warm and wet peat soils due to a higher entrapped gas content from higher $CH_4$ production and lower $CH_4$ solubility. Surprisingly, we did not observe any ebullition in our warmed and raised water table treatment, although this might have been due to biases in our chamber-based sampling. Given the importance of ebullition in contributing to total $CH_4$ fluxes from peatlands, more detailed characterization of the spatial and temporal variation in $CH_4$ ebullition across our experimental treatments will be necessary to resolve the overall peatland-atmosphere exchange of $CH_4$ under our various experimental soil climate regimes.

### 4.3. Short Versus Longer-Term Ecosystem Responses to Changing Soil Climate

[35] Our experiment was designed to examine both short- and longer-term responses in hydrology, vegetation composition, and carbon cycling to soil climate manipulations beyond the scope of ambient hydroclimate variability in a rich fen. Seasonal $CH_4$ fluxes measured so far across our experimental treatments (Table 3) are on the low end but well within the range of $CH_4$ fluxes observed for North American peatlands (0.6–129.0 g $CH_4$ $m^{-2}$ $yr^{-1}$) [*Roulet et al.*, 1994; *Vitt et al.*, 1990; *Whalen and Reeburgh*, 1988, 1992]. Our data also agree with previous studies that have shown strong relationships between $CH_4$ fluxes and water table position in peatlands [cf. *Bubier et al.*, 1995; *Moore and Roulet*, 1993]. Most field studies that have examined the effects of inundation or flooding on $CH_4$ emissions have focused on natural spatial and/or temporal variability in water table position; few studies have experimentally raised water table position in situ [see *Dise et al.*, 1993; *Updegraff et al.*, 2001] (Table 4). *Dise et al.* [1993] found that a flooding treatment of similar magnitude to our experimental design (Table 4) caused 200–250% increases in $CH_4$ emissions in a Minnesota peatland.

[36] Numerous field and laboratory studies have examined $CH_4$ fluxes under experimentally lowered water table positions. Short-term experiments (i.e., 7 weeks to 3 years) typically show reductions in $CH_4$ fluxes from peatland soils by 80–90% with water table drawdown (Table 4). However, the response of $CH_4$ emissions to water table drawdown typically are sustained or can grow stronger over time; measurements conducted over longer time frames (>5 years)

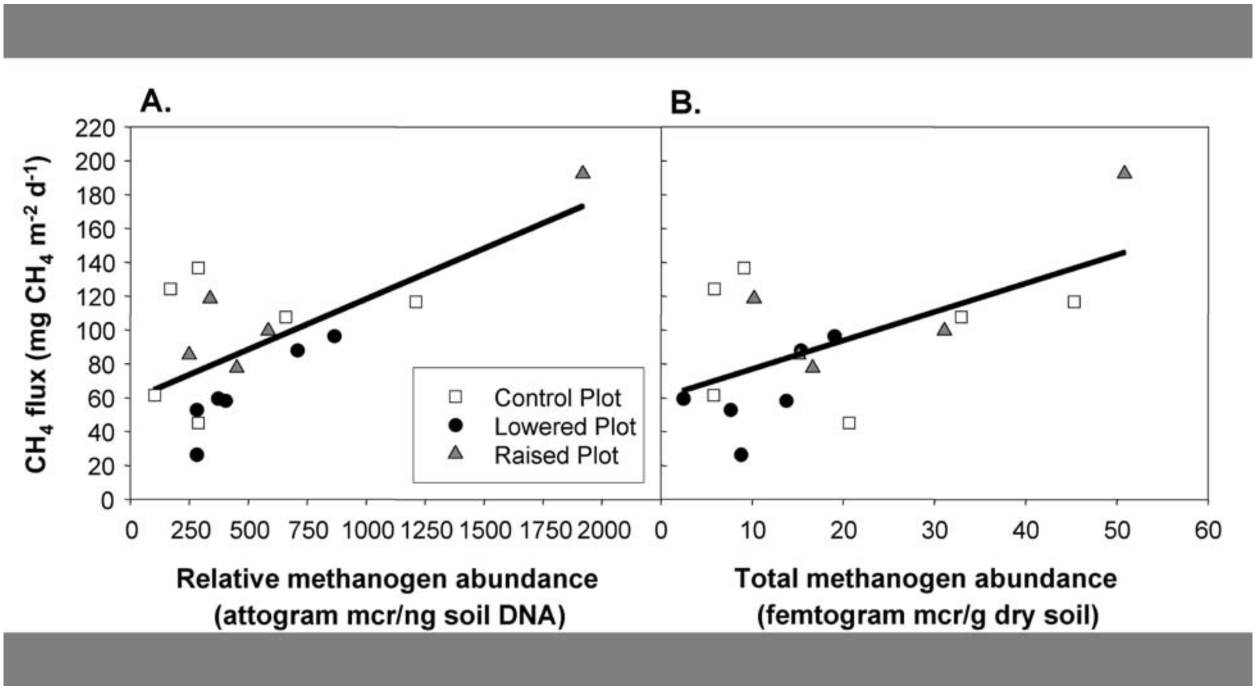


**Figure 6.** (a) Effect of mean methanogen abundance in surface peat layers cm on mean daily $CH_4$ fluxes from 2005 (slope = 0.06 ± 0.02; intercept = 58.80 ± 11.99; F = 11.94, d.f. = 1, 15, $p$ = 0.004, $R^2$ = 0.44). (b) Effect of mean total abundance of methanogens in surface peat layers on mean daily $CH_4$ fluxes from 2005 (slope = 1.68 ± 0.61; intercept = 60.17 ± 13.82; F = 7.69, d.f. = 1, 15, $p$ = 0.01, $R^2$ = 0.34).

have shown reductions in $CH_4$ fluxes ranging anywhere from 25%–200% (Table 4). Variation in the response of $CH_4$ fluxes to water table drawdown across these studies over both short- and longer- time periods likely is driven by treatment magnitude and length of study, changing vegetation productivity and plant-mediated transport under drier conditions, peatland type (bog, fen) [cf. *Moore and Dalva*, 1993; *Updegraff et al.*, 2001], and differential response across peatland microforms (hummocks, hollows) [*Strack and Waddington*, 2007].

[37] Unlike long-term peatland drainage experiments, long-term warming experiments are rare in boreal peatlands despite the observed [*Christensen et al.*, 2003b; *Treat et al.*, 2007] and simulated [*Bergamaschi et al.*, 2007; *Zhuang et al.*, 2007] sensitivity of $CH_4$ emissions to warmer temperatures. *Granberg et al.* [2001] observed strong interactions between sedge cover and experimental warming, in which $CH_4$ emission increased with soil warming only in plots with high sedge cover. Long-term warming experiments in Alaskan tundra have documented no net change in plant productivity but did show enhanced shrub productivity, decreased graminoid productivity, decreased moss cover, and increased N mineralization with soil warming [*Chapin et al.*, 1995]. The several studies that have used factorial designs of water table and warming manipulations have found significant interactions among these main effects in governing $CH_4$ fluxes to the atmosphere (Table 4). Here, our results show that soil warming effects on $CH_4$ fluxes in a boreal rich fen are coupled to water table dynamics, as warming had the greatest influence on $CH_4$ fluxes in our raised water table treatment (Figure 3b). However, over the next several years to decade, we predict further enhancements of $CH_4$ emissions with soil warming in our lowered water table plot accompanied by succession from moss- to sedge-dominated communities [cf. *Granberg et al.*, 2001].

### 4.4. Implications of Changing Hydroclimate for $CH_4$ Emissions in Alaskan Wetlands

[38] In a regional modeling study, *Zhuang et al.* [2007] estimate that current $CH_4$ emissions from Alaskan soils are approximately 3 Tg $CH_4$ $yr^{-1}$, of which the majority of emissions were attributed to wet tundra ecosystems. Methane emissions across Alaska are predicted to increase by more than 75% in the next 100 years, largely due to temperature controls on $CH_4$ emissions [*Zhuang et al.*, 2007]. Additional modeling of regional $CH_4$ dynamics in this region could be improved by a better understanding of peatland distributions across Alaska, as current estimates range from 0.13–0.6 million $km^2$ depending on various criteria used for defining peat soils [*Bridgham et al.*, 2006; *Gorham*, 1991; *Kivinen and Pakarinen*, 1981]. Wetland areas in Alaska also are changing due to thermokarst formation [*Osterkamp*, 2005; *Osterkamp et al.*, 2000] and changes in surface moisture balance [e.g., *Hinzman et al.*, 2005; *Riordan et al.*, 2006] that appear to be exacerbated by ongoing climate change in Alaska.

[39] Our results show that seasonal $CH_4$ fluxes could increase by 80–300% under both wetter and warmer soil climates. Thus, higher water table positions caused by increases in precipitation or disturbances that affect near surface hydrology and soil thermal regimes such as permafrost thaw [*Jorgenson et al.*, 2001; *Turetsky et al.*, 2007] likely will stimulate $CH_4$ emissions beyond the effects of soil warming alone. On the other hand, $CH_4$ fluxes were substantially reduced by water table drawdown, with only small increases with soil warming in our lowered water

table treatment. Together, these results suggest that modeling the response of wetland $CH_4$ emissions to climate change in Alaska needs to consider the interactive effects of soil warming and water table position on $CH_4$ production and transport.

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## References

Aerts, R., and F. Ludwig (1997), Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils, *Soil Biol. Biochem.*, *29*, 1691–1698.

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

Baird, A. J., C. W. Beckwith, S. Waldron, and J. M. Waddington (2004), Ebullition of methane-containing gas bubbles from near-surface Sphagnum peat, *Geophys. Res. Lett.*, *31*, L21505, doi:10.1029/2004GL021157.

Bergamaschi, P., et al. (2007), Satellite chartography of atmospheric methane from SCIAMACHY on board ENVISAT: 2. Evaluation based on inverse model simulations, *J. Geophys. Res.*, *112*, D02304, doi:10.1029/2006JD007268.

Blodau, C., N. Basiliko, and T. R. Moore (2004), Carbon turnover in peatland mesocosms exposed to different water table levels, *Biogeochemistry*, *67*, 331–351.

Bolin, B., R. Sukumar, P. Ciais, W. Cramer, P. G. Jarvis, H. Kheshgi, C. Nobre, S. Semenov, and W. Steffen (2000), Global perspective, in *IPCC Special Report on Land Use, Land-Use Change and Forestry*, edited by R. T. Watson et al., chap. 1, IPCC, Geneva.

Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. C. Trettin (2006), The carbon balance of North American wetlands, *Wetlands*, *26*, 889–916.

Bubier, J. L. (1995), The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands, *J. Ecol.*, *83*, 403–420.

Bubier, J. L., T. R. Moore, L. Bellisario, N. T. Comer, and P. M. Crill (1995), Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, *9*, 455–470.

Bubier, J. L., T. R. Moore, and G. Crosby (2006), Fine-scale vegetation distribution in a cool temperate peatland, *Can. J. Bot. Rev. Can. Bot.*, *84*, 910–923.

Carroll, P., and P. Crill (1997), Carbon balance of a temperate poor fen, *Global Biogeochem. Cycles*, *11*, 349–356.

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

Chen, Y.-H., and R. G. Prinn (2006), Estimation of atmospheric methane emissions between 1996–2001 using a 3D global chemical transport model, *J. Geophys. Res.*, *111*, D10307, doi:10.1029/2005JD006058.

Christensen, T. R., N. Panikov, M. Mastepanov, A. Joabsson, A. Stewart, M. Oquist, M. Sommerkorn, S. Reynaud, and B. Svensson (2003a), Biotic controls on $CO_2$ and $CH_4$ exchange in wetlands - a closed environment study, *Biogeochemistry*, *64*, 337–354.

Christensen, T. R., A. Ekberg, L. Strom, M. Mastepanov, N. Panikov, O. Mats, B. H. Svensson, H. Nykanen, P. J. Martikainen, and H. Oskarsson (2003b), Factors controlling large scale variations in methane emissions from wetlands, *Geophys. Res. Lett.*, *30*(7), 1414, doi:10.1029/2002GL016848.

Clymo, R. S., J. Turunen, and K. Tolonen (1998), Carbon accumulation in peatland, *Oikos*, *81*, 368–388.

Dise, N. B., E. Gorham, and E. S. Verry (1993), Environmental-factors controlling methane emissions from peatlands in Northern Minnesota, *J. Geophys. Res.*, *98*, 10,583–10,594.

Dunfield, P., R. Knowles, R. Dumont, and T. R. Moore (1993), Methane production and consumption in temperate and Sub-Arctic peat soils - Response to temperature and pH, *Soil Biol. Biochem.*, *25*, 321–326.

Dye, D. G. (2002), Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000, *Hydrol. Process.*, *16*, 3065–3077.

Euskirchen, E. S., et al. (2006), Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems, *Global Change Biol.*, *12*, 731–750.

Frolking, S., N. Roulet, and J. Fuglestvedt (2006), How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration, *J. Geophys. Res.*, *111*, G01008, doi:10.1029/2005JG000091.

Funk, D. W., E. R. Pullman, K. M. Peterson, P. M. Crill, and W. D. Billings (1994), Influence of water-table on carbon-dioxide, carbon-monoxide, and methane fluxes from taiga bog microcosms, *Global Biogeochem. Cycles*, *8*, 271–278.

Gignac, L. D., D. H. Vitt, S. C. Zoltai, and S. E. Bayley (1991), Bryophyte response surfaces along climatic, chemical, and physical gradients in peatlands of western Canada, *Nova Hedwigia*, *53*, 27–71.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton (2005), Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance, *Proc. Natl. Acad. Sci. U.S.A.*, *102*, 13,521–13,525.

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

Granberg, G., I. Sundh, B. H. Svensson, and M. Nilsson (2001), Effects of temperature, and nitrogen and sulfur deposition, on methane emission from a boreal mire, *Ecology*, *82*, 1982–1998.

Hales, B. A., C. Edwards, D. A. Ritchie, G. Hall, R. W. Pickup, and J. R. Saunders (1996), Isolation and identification of methanogen—Specific DNA from blanket peat by PCR amplification and sequence analysis, *Appl. Environ. Microbiol.*, *62*, 668–675.

Hinzman, L. D., et al. (2005), Evidence and implications of recent climate change in northern Alaska and other arctic regions, *Clim. Change*, *72*, 251–298.

Hinzman, L., L. Viereck, P. C. Adams, V. Romanovsky, and K. Yoshikawa (2006), Climate and permafrost dynamics of the Alaskan boreal forest, in *Alaska's Changing Boreal Forest*, edited by F. Chapin et al., pp. 39–61, Oxford Univ. Press, New York.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu (2001), *Climate Change 2001: The Scientific Basis*, 944 pp., Intergovernmental Panel for Climate Change, Cambridge Univ. Press, UK.

Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp (2001), Permafrost degradation and ecological changes associated with a warming climate in central Alaska, *Clim. Change*, *48*, 551–579.

Keller, J. K., J. R. White, S. D. Bridgham, and J. Pastor (2004), Climate change effects on carbon and nitrogen mineralization in peatlands through changes in soil quality, *Global Change Biol.*, *10*, 1053–1064.

Kellner, E., A. J. Baird, M. Oosterwood, K. Harrison, and J. M. Waddington (2006), Effect of temperature and atmospheric pressure on methane ($CH_4$) ebullition from near-surface peats, *Geophys. Res. Lett.*, *33*, L18405, doi:10.1029/2006GL027509.

Kivinen, E., and P. Pakarinen (1981), Geographical distribution of peat resources and major peatland complex types in the world, *Ann. Acad. Sci. Fenn. A.*, III.

Kuhry, P., and J. Turunen (2006), The postglacial development of boreal and subarctic peatlands, in *Boreal Peatland Ecosystems*, edited by R. K. Wieder and D. H. Vitt, pp. 25–46, Springer, New York.

Laine, J., H. Vasander, and R. Laiho (1995), Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland, *J. Appl. Ecol.*, *32*, 785–802.

Laine, J., J. Silvola, K. Tolonen, J. Alm, H. Nykanen, H. Vasander, T. Sallantaus, I. Savolainen, J. Sinisalo, and P. J. Martikainen (1996), Effect of water-level drawdown on global climatic warming: Northern peatlands, *Ambio*, *25*, 179–184.

Martikainen, P. J., H. Nykanen, J. Alm, and J. Silvola (1995), Change in fluxes of carbon-dioxide, methane and nitrous-oxide due to forest drainage of mire sites of different trophy, *Plant Soil*, *169*, 571–577.

McGuire, A. D., J. M. Melillo, D. W. Kicklighter, and L. A. Joyce (1995), Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates, *J. Biogeogr.*, *22*, 785–796.

McGuire, A. D., J. M. Melillo, D. W. Kicklighter, Y. D. Pan, X. M. Xiao, J. Helfrich, B. Moore, C. J. Vorosmarty, and A. L. Schloss (1997), Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration, *Global Biogeochem. Cycles*, *11*, 173–189.

McGuire, A. D., et al. (2002), Environmental variation, vegetation distribution, carbon dynamics, and water/energy exchange in high latitudes, *J. Veg. Sci.*, *13*, 301–314.

McGuire, A. D., et al. (2007), Responses of high latitude ecosystems to global change: Potential consequences for the climate system, in *Terrestrial Ecosystems in a Changing World*, *IGBP Ser*, edited by J. G. Canadell, D. E. Pataki, and L. F. Pitelka, pp. 297–310, Springer, Heidelberg.
Moore, T. R., and M. Dalva (1993), The influence of temperature and water-table position on carbon-dioxide and methane emissions from laboratory columns of peatland soils, *J. Soil Sci.*, *44*, 651–664.
Moore, T. R., and N. T. Roulet (1993), Methane flux - water-table relations in northern wetlands, *Geophys. Res. Lett.*, *20*, 587–590.
Moosavi, S. C., and P. M. Crill (1998), $CH_4$ oxidation by tundra wetlands as measured by a selective inhibitor technique, *J. Geophys. Res.*, *103*, 29,093–29,106.
Nykanen, H., J. Alm, J. Silvola, K. Tolonen, and P. J. Martikainen (1998), Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates, *Global Biogeochem. Cycles*, *12*, 53–69.
Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane (2000), Acclimation of ecosystem $CO_2$ exchange in the Alaskan Arctic in response to decadal climate warming, *Nature*, *406*, 978–981.
Osterkamp, T. E. (2005), The recent waning of permafrost in Alaska, *Global Planet. Change*, *49*, 187–202.
Osterkamp, T. E., and V. E. Romanovsky (1999), Evidence for warming and thawing of discontinuous permafrost in Alaska, *Permafrost Periglac, Processes*, *10*, 17–37.
Osterkamp, T. E., L. Viereck, Y. Shur, M. T. Jorgenson, C. Racine, A. Doyle, and R. D. Boone (2000), Observations of thermokarst and its impact on boreal forests in Alaska, USA, *Arct. Antarct. Alp. Res.*, *32*, 303–315.
Pearce, D. M. E., and R. S. Clymo (2001), Methane oxidation in a peatland core, *Global Biogeochem. Cycles*, *15*, 709–720.
Riordan, B., D. Verbyla, and A. D. McGuire (2006), Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images, *J. Geophys. Res.*, *111*, G04002, doi:10.1029/2005JG000150.
Roulet, N., T. Moore, J. Bubier, and P. M. Lafleur (1992), Northern fens: Methane flux and climatic change, *Tellus, Ser. B*, *44*, 100–105.
Roulet, N. T., R. Ash, W. Quinton, and T. Moore (1993), Methane flux from drained northern peatlands: Effect of a persistent water-table lowering on flux, *Global Biogeochem. Cycles*, *7*, 749–769.
Roulet, N. T., A. Jano, C. A. Kelly, L. F. Klinger, T. R. Moore, R. Protz, J. A. Ritter, and W. R. Rouse (1994), Role of the Hudson-Bay lowland as a source of atmospheric methane, *J. Geophys. Res.*, *99*(D1), 1439–1454.
Schimel, J. P., C. Bilbrough, and J. A. Welker (2004), Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities, *Soil Biol. Biochem.*, *36*, 217–227.
Segers, R. (1998), Methane production and methane consumption: A review of processes underlying wetland methane fluxes, *Biogeochemistry*, *41*, 23–51.
Serreze, M. C., J. E. Walsh, F. S. Chapin, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry (2000), Observational evidence of recent change in the northern high-latitude environment, *Clim. Change*, *46*, 159–207.
Shurpali, N. J., S. B. Verma, J. Kim, and T. J. Arkebauer (1995), Carbon-dioxide exchange in a peatland ecosystem, *J. Geophys. Res.*, *100*, 14,319–14,326.
Strack, M., and J. M. Waddington (2007), Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment, *Global Biogeochem. Cycles*, *21*, GB1007, doi:10.1029/2006GB002715.
Strack, M., J. M. Waddington, and E.-S. Tuittila (2004), The effect of water table drawdown on northern peatland methane dynamics: Implications for climate change, *Global Biogeochem. Cycles*, *18*, GB4003, doi:10.1029/2003GB002209.
Strack, M., E. Kellner, and J. M. Waddington (2005), Dynamics of biogenic gas bubbles in peat and their effects on peatland biogeochemistry, *Global Biogeochem. Cycles*, *19*, GB1003, doi:10.1029/2004GB002330.
Strack, M., M. F. Waller, and J. M. Waddington (2006), Sedge succession and peatland methane dynamics: A potential feedback to climate change, *Ecosystems (N.Y., Print)*, *9*, 278–287.
Sundh, I., C. Mikkela, M. Nilsson, and B. H. Svensson (1995), Potential aerobic methane oxidation in a Sphagnum-dominated peatland—Controlling factors and relation to methane emission, *Soil Biol. Biochem.*, *27*, 829–837.
Tokida, T., O. Nagata, F. Takakai, A. Kagemoto, and R. Hatano (2007), Falling atmospheric pressure as a trigger for methane ebullition from peatland, *Global Biogeochem. Cycles*, *21*, GB2003, doi:10.1029/2006GB002790.
Treat, C. C., J. L. Bubier, R. K. Varner, and P. M. Crill (2007), Timescale dependence of environmental and plant-mediated controls on $CH_4$ flux in a temperate fen, *J. Geophys. Res.*, *112*, G01014, doi:10.1029/2006JG000210.
Turetsky, M. R., R. K. Wieder, and D. H. Vitt (2002), Boreal peatland C fluxes under varying permafrost regimes, *Soil Biol. Biochem.*, *34*, 907–912.
Turetsky, M. R., M. Mack, J. Harden, and K. L. Manies (2005), Terrestrial carbon storage in boreal ecosystems: Causes and consequences of spatial heterogeneity, in *Proceedings of the 10th Cary Conference*, edited by G. M. Lovett et al.
Turetsky, M. R., R. K. Wieder, D. H. Vitt, R. J. Evans, and K. D. Scott (2007), The disappearance of relict permafrost in boreal north America: Effects on peatland carbon storage and fluxes, *Global Change Biol.*, *13*, 1922–1934.
Turunen, J., E. Tomppo, K. Tolonen, and A. Reinikainen (2002), Estimating carbon accumulation rates of undrained mires in Finland—Application to boreal and subarctic regions, *Holocene*, *12*, 69–80.
Updegraff, K., S. D. Bridgham, J. Pastor, P. Weishampel, and C. Harth (2001), Response of $CO_2$ and $CH_4$ emissions from peatlands to warming and water table manipulation, *Ecol. Appl.*, *11*, 311–326.
Vasander, H., and A. Kettunen (2006), Carbon in boreal peatlands, in *Boreal Peatland Ecosystems*, edited by R. K. Wieder and D. H. Vitt, pp. 165–194, Springer, New York.
Verville, J. H., S. E. Hobbie, F. S. Chapin, and D. U. Hooper (1998), Response of tundra $CH_4$ and $CO_2$ flux to manipulation of temperature and vegetation, *Biogeochemistry*, *41*, 215–235.
Vitt, D. H. (2006), Function characteristics and indicators of boreal peatlands, in *Boreal Peatland Ecosystems*, edited by R. K. Wieder and D. H. Vitt, pp. 9–24, Springer, New York.
Vitt, D. H., S. E. Bayley, T.-L. Jin, L. A. Halsey, B. Parker, and R. Craik (1990), Methane and carbon dioxide production from wetlands in boreal Alberta, report, contract 90–0270, 83 pp., Alberta Environ., Edmonton.
Vitt, D. H., L. A. Halsey, I. E. Bauer, and C. Campbell (2000), Spatial and temporal trends of carbon sequestration in peatlands of continental western Canada through the Holocene, *Can. J. Earth Sci.*, *37*, 683–693.
Weltzin, J. F., J. Pastor, C. Harth, S. D. Bridgham, K. Updegraff, and C. T. Chapin (2000), Response of bog and fen plant communities to warming and water-table manipulations, *Ecology*, *81*, 3464–3478.
Whalen, S. C., and W. S. Reeburgh (1988), A methane flux time series for tundra environments, *Global Biogeochem. Cycles*, *2*(4), 399–409.
Whalen, S. C., and W. S. Reeburgh (1990), Consumption of atmospheric methane by tundra soils, *Nature*, *346*, 160–162.
Whalen, S. C., and W. S. Reeburgh (1992), Interannual variations in methane emissions: A four year time-series at fixed sites, *Global Biogeochem. Cycles*, *6*, 139–159.
Wieder, R. K., D. H. Vitt, and B. W. Benscoter (2006), Peatlands and the boreal forest, in *Boreal Peatland Ecosystems*, edited by R. K. Wieder and D. H. Vitt, pp. 1–8, Springer, New York.
Yoshikawa, K., and L. D. Hinzman (2003), Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska, *Permafrost Periglac, Processes*, *14*, 151–160.
Zhuang, Q., V. E. Romanovsky, and A. D. McGuire (2001), Incorporation of a permafrost model into a large-scale ecosystem model: Evaluation of temporal and spatial scaling issues in simulating soil thermal dynamics, *J. Geophys. Res.*, *106*, 33,649–33,670.
Zhuang, Q., J. M. Melillo, D. W. Kicklighter, R. G. Prinn, A. D. McGuire, P. A. Steudler, B. S. Felzer, and S. Hu (2004), Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: A retrospective analysis with a process-based biogeochemistry model, *Global Biogeochem. Cycles*, *18*, GB3010, doi:10.1029/2004GB002239.
Zhuang, Q., J. M. Melillo, M. C. Sarofim, D. W. Kicklighter, A. D. McGuire, B. S. Felzer, A. Sokolov, R. G. Prinn, P. A. Steudler, and S. Hu (2006), $CO_2$ and $CH_4$ exchanges between land ecosystems and the atmosphere in northern high latitudes over the 21st century, *Geophys. Res. Lett.*, *33*, L17403, doi:10.1029/2006GL026972.
Zhuang, Q., J. M. Melillo, A. D. McGuire, D. W. Kicklighter, R. G. Prinn, P. A. Steudler, B. S. Felzer, and S. Hu (2007), Net emissions of $CH_4$ and $CO_2$ in Alaska: Implications for the region's greenhouse gas budget, *Ecol. Appl.*, *17*, 203–212.

J. W. Harden and M. P. Waldrop, U.S. Geological Survey, Menlo Park, CA 94025, USA.

A. D. McGuire, Alaska Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

C. C. Treat, Department of Plant Biology, Michigan State University, East Lansing, MI 48824, USA. (treatc@msu.edu)

M. R. Turetsky, Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada. (mrt@uoguelph.ca)

J. M. Waddington, School of Geography and Earth Sciences, McMaster University, Hamilton, ON L8S 4K1, Canada.