



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

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[1] Growing season CH₄ 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 CH₄ 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 In-transformed CH₄ fluxes, with mean daily water table position representing the strongest predictor. We used quantitative PCR of the *a*-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 CH₄ fluxes. Our results show that water table manipulations that led to soil inundation (flooding) had a stronger effect on CH₄ fluxes than water table drawdown. Seasonal CH₄ fluxes increased by 80–300% under the combined wetter and warmer soil climate treatments. Thus, while warming is expected to increase CH₄ 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 CH₄ emissions beyond the effects of soil warming alone. Consequently, we argue that modeling the effects of climate change on Alaskan wetland CH₄ emissions needs to consider the interactive effects of soil warming and water table position on CH₄ production and transport.

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1. Introduction

[2] Boreal ecosystems cover 14% of the earth's vegetated surface (14–18.5 million km²) [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 km² [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 accumula-

tion 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 (CH₄), releasing an estimated 30 to 50 Tg CH₄ yr⁻¹ [Chen and Prinn, 2006; Zhuang *et al.*, 2004, 2006], approximately 20% of the estimated 190 Tg CH₄ yr⁻¹ emitted from wetlands globally [Bergamaschi *et al.*, 2007]. Given that CH₄ has a net radiative capacity 23 times greater than CO₂ on a 100-year timescale [Houghton *et al.*, 2001], large-scale changes in CH₄ 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 CH₄ emissions through complex controls on CH₄ production, oxidation, and plant mediated transport. Methane emissions

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are the net result of CH₄ production (methanogenesis) through anaerobic microbial respiration and CH₄ oxidation (methanotrophy) in aerobic soil layers. Water table position often serves as the dominant control on CH₄ 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 CO₂ emissions and reduce atmospheric CH₄ fluxes, and can cause individual peatlands to switch from net C sinks to sources [e.g., *Aim 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 CH₄ emissions in wetlands by increasing the availability of labile substrates in soil via root exudation and by increasing CH₄ 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 CH₄ 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 CH₄ 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 CH₄ 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 CH₄ oxidation [*Dunfield et al.*, 1993] and thus are expected to stimulate CH₄ 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 slimmer 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 CH₄ emissions is not clear because controls on CH₄ fluxes, such as produc-

tion, 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, CH₄ emissions, and methanogen activity across our experimental treatments. We recognize that in the short term, changes in CH₄ emissions across our soil hydroclimate manipulations are likely to be driven primarily by changing microbial activity, while vegetation-mediated controls on CH₄ fluxes (enhanced plant transport of CH₄, increased productivity, and changes in rooting zones) will become increasingly important controls on CH₄ 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 CH₄ flux while maintaining the same fundamental relationship between ambient water table position and CH₄ flux, or whether our experimental manipulations 'pressed' the system across a threshold yielding new relationships between ambient water table position and CH₄ flux. We predicted that the latter would be evidenced by a significant interaction between experimental treatment and water table position on CH₄ 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 m² 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., Fullerton, CA, USA) did not differ between the supply well (6.9 ± 0.9 L (mg C)⁻¹m⁻¹) and the control plot (6.6 ± 1.1 L (mg C)⁻¹m⁻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 m². 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 $\times$ 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 $\times$ 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 CRI0x 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 vemicosus*, *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. CH₄ Flux Measurements

[15] CH₄ 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 m²; volume 0.227 m³). 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 CH₄ 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 CH₄ 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 CH₄. 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. CH₄ fluxes were ln-transformed to help normalize data and model errors.

[16] All statistical analyses of CH₄ 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 CH₄ 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 CH₄ 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 tinalmodel and continuous records of mean daily water table position and peat temperatures at 25 cm depth to model CH₄ fluxes across the 2005 and 2006 growing seasons. Mean daily CH₄ fluxes were summed over the growing season period to calculate cumulative seasonal CH₄ 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 *a*-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 TOG 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/μL 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 continued at 760 bp by gel electrophoresis. Our qPCR reactions consisted of 2 μL DNA, 9 μL DNase free water, 2 μL of each primer (10 μM), 0.5 μL ROX dye (10,000 X dilution), and 12.5 μL Sybr-green 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/μL. 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 ($13.4 \pm 0.1^\circ\text{C}$) than in 2006 ($12.3 \pm 0.1^\circ\text{C}$; $F = 53.06$, $df = 1, 7337$, $P < 0.0001$). 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 $12.5 \pm 0.1^\circ\text{C}$, $12.5 \pm 0.1^\circ\text{C}$, and $16.9 \pm 0.0^\circ\text{C}$ in the control, lowered and raised plots, respectively. These peat temperatures were slightly lower in 2006, averaging $11.9 \pm 0.1^\circ\text{C}$, $11.8 \pm 0.1^\circ\text{C}$, and $16.4 \pm 0.1^\circ\text{C}$ 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 CH₄ m⁻² d⁻¹ in 2005 and -3 to 3045 mg CH₄ m⁻² d⁻¹ in 2006 (negative values represent CH₄ consumption). A repeated measures analysis

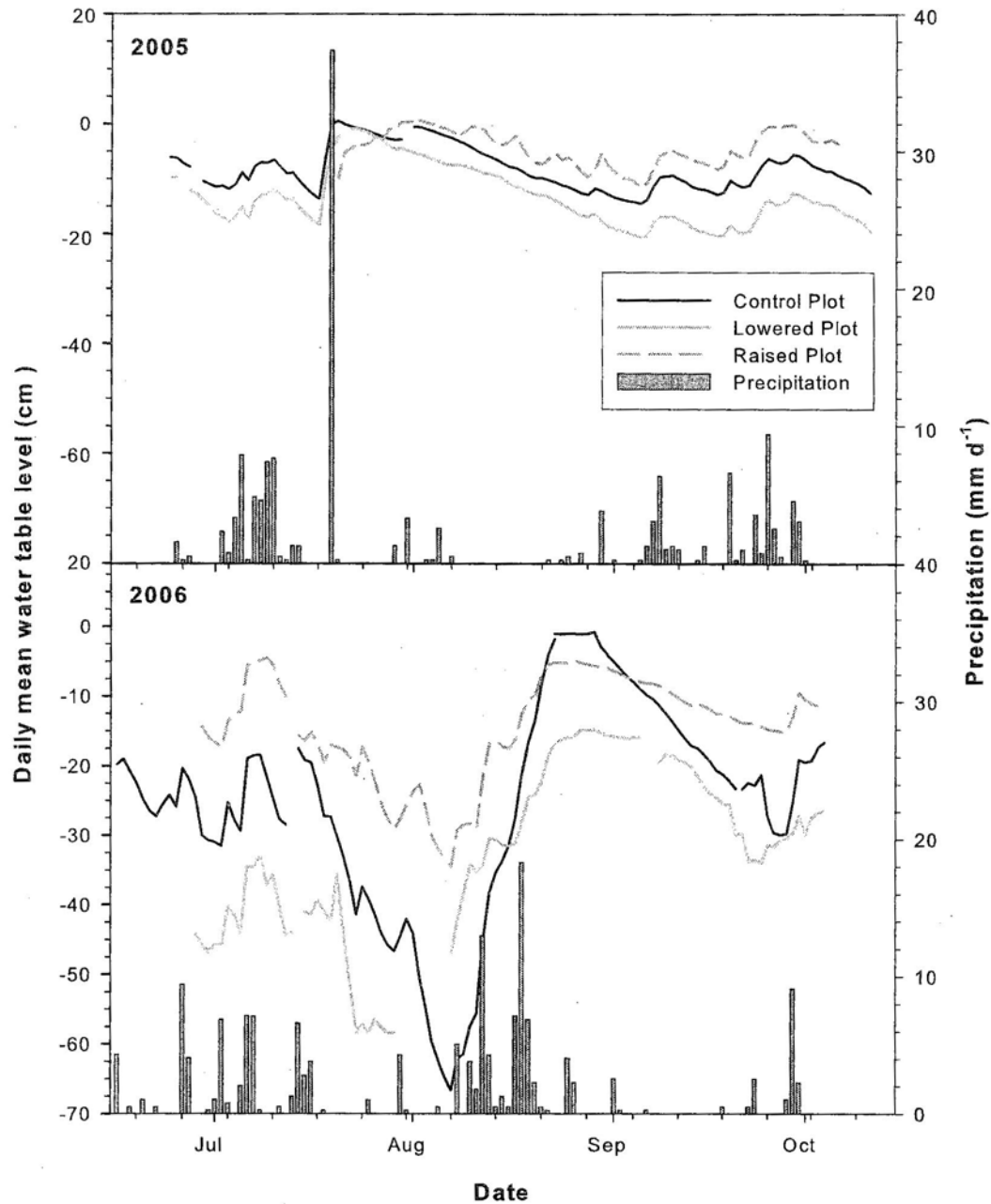


Figure 1. Water table levels and precipitation at the manipulation plots in 2005 and 2006. Positive values denote water table position above the peat surface (inundated). Bars represent precipitation events. Precipitation was not significantly different between the two study years ($F = 1.61$, $df =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

of variance model showed that daily CH_4 fluxes varied by a water table treatment (raised, lowered, control) $\times$ 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.

[21] Daily CH_4 fluxes also varied by a soil warming $\times$ 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 $\times$ year interaction (Table 1; data not shown). Soil warming

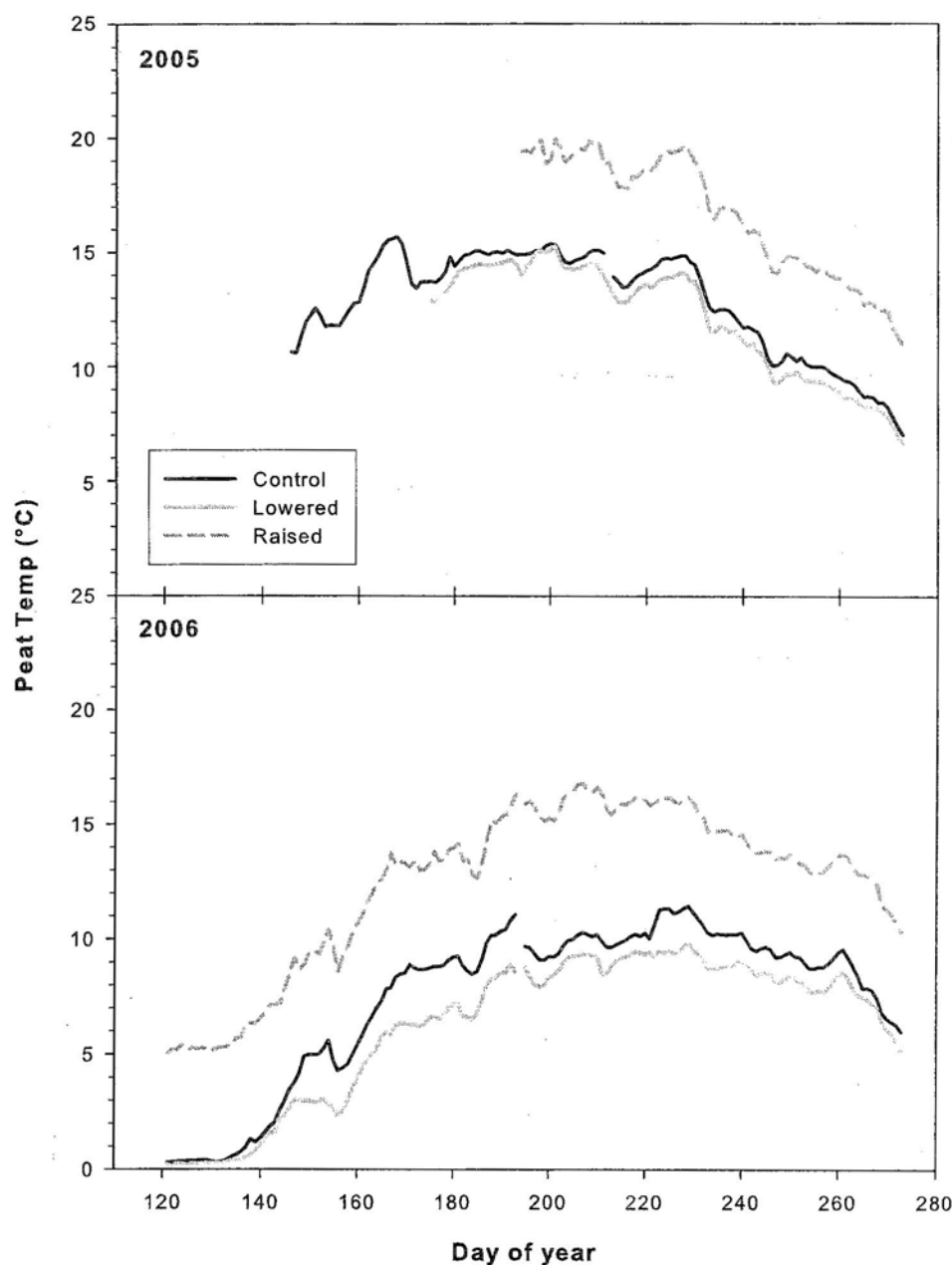


Figure 2. Mean peat temperatures at 25 cm beneath the moss surface in (a) 2005 and (b) 2006 across the three water table plots (corresponding to the control, lowered, raised water table treatments).

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 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ in 2005 and 2006, respectively; unwarmed plots: 75.2 ± 5.8^b and 22.3 ± 2.5^e $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ in 2005 and 2006, respectively; data are means $\pm$ one standard error; same letter superscripts denote nonsignificant 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 In-transferred 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 $\times$ soil warming treatment. The seasonal modeling highlights the water table $\times$ 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 CH₄ 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

^aUnits are in mg CH₄ 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 [or either of these variables. In the unwarmed plots, methanogen relative abundance was greater in the 5-15 cm compared to the 0-5 cm depth increment. Soil warming increased relative ethanogen 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 CH₄ 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 CH₄ fluxes, explaining 40% of the variability in CH₄ fluxes (data not shown, $df = 1, 15$; $F = 9.34$, $p = 0.008$). There was no significant relationship between CH₄ fluxes and ME abundance expressed per g wet soil ($p > 0.05$; data not shown). Additionally, there was no significant relationship between CH₄ 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 CH₄ Emissions and Methanogens

[28] Our sampling characterized CH₄ 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 CH₄ fluxes, resulting in significant water table treatment × year and soil warming × year interactions (Table 1). These interactions in the controls on CH₄ emissions also are evident in the seasonal

estimates of CH₄ 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 CH₄ 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

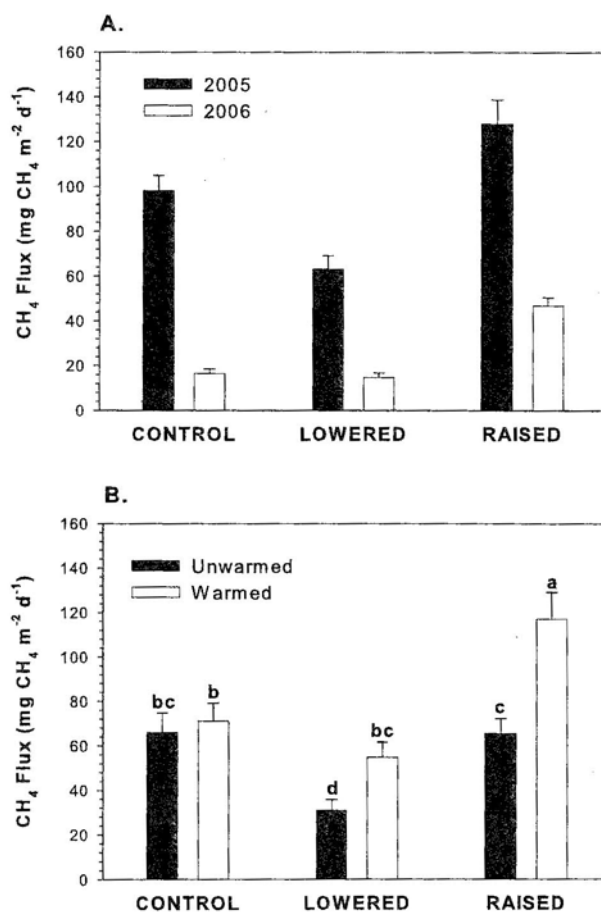


Figure 3. Results of a repeated measures analysis of variance model analyzing CH₄ fluxes across experimental treatments. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscript denote nonsignificant differences from post hoc comparison of means tests.

Table 2. Results of a General Linear Model Using Experimental Treatments and Environmental Parameters to Predict In Transformed CH₄ 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		

^aThe model explained 72% of the variation in CH₄ fluxes. Mean daily water table position alone explained the majority of variability in CH₄ 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 CH₄ 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 CH₄ fluxes, both of these interannual differences in hydroclimate likely led to lower overall CH₄ emissions in our second year of sampling (Table 3).

[29] Despite these large interannual differences, our results showed strong responses in CH₄ fluxes and methanogen abundances to our soil climate manipulations. Soil flooding (raised water table treatment) led to increased CH₄ fluxes (Figure 3 and Table 3), though the magnitude of response varied among sampling years. Averaged across our soil warming treatments, mean daily CH₄ 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 CH₄ fluxes, resulting in a significant decline in fluxes in 2005 but not in 2006. Averaged across our soil warming treatments, mean daily CH₄ 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 CH₄ fluxes than water table drawdown, which contributed to a

nonlinear relationship between CH₄ fluxes and water table position (Figure 4a).

[30] While water table position often is hypothesized to serve as the dominant control on CH₄ fluxes from peatlands, CH₄ 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 CH₄ fluxes (Table 4). Soil warming increased concentrations of methanogens in surface peat (Figure 5) and CH₄ 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 CH₄ fluxes in both sampling years, though differences between the warmed and unwarmed plots were larger in 2005 than in 2006. The largest fluxes of CH₄ occurred in plots that received both soil warming and flooding. Soil warming in the raised water table treatment increased daily CH₄ 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 CH₄ 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 CH₄ Emissions (±Standard Errors) Across the Water Table and Soil Warming Treatments^a

Water Table Treatments	Soil Warming Treatments	Cumulative Seasonal CH ₄ Fluxes (g CH ₄ m ⁻² season ⁻¹)	
		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

^aSeasonal 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.

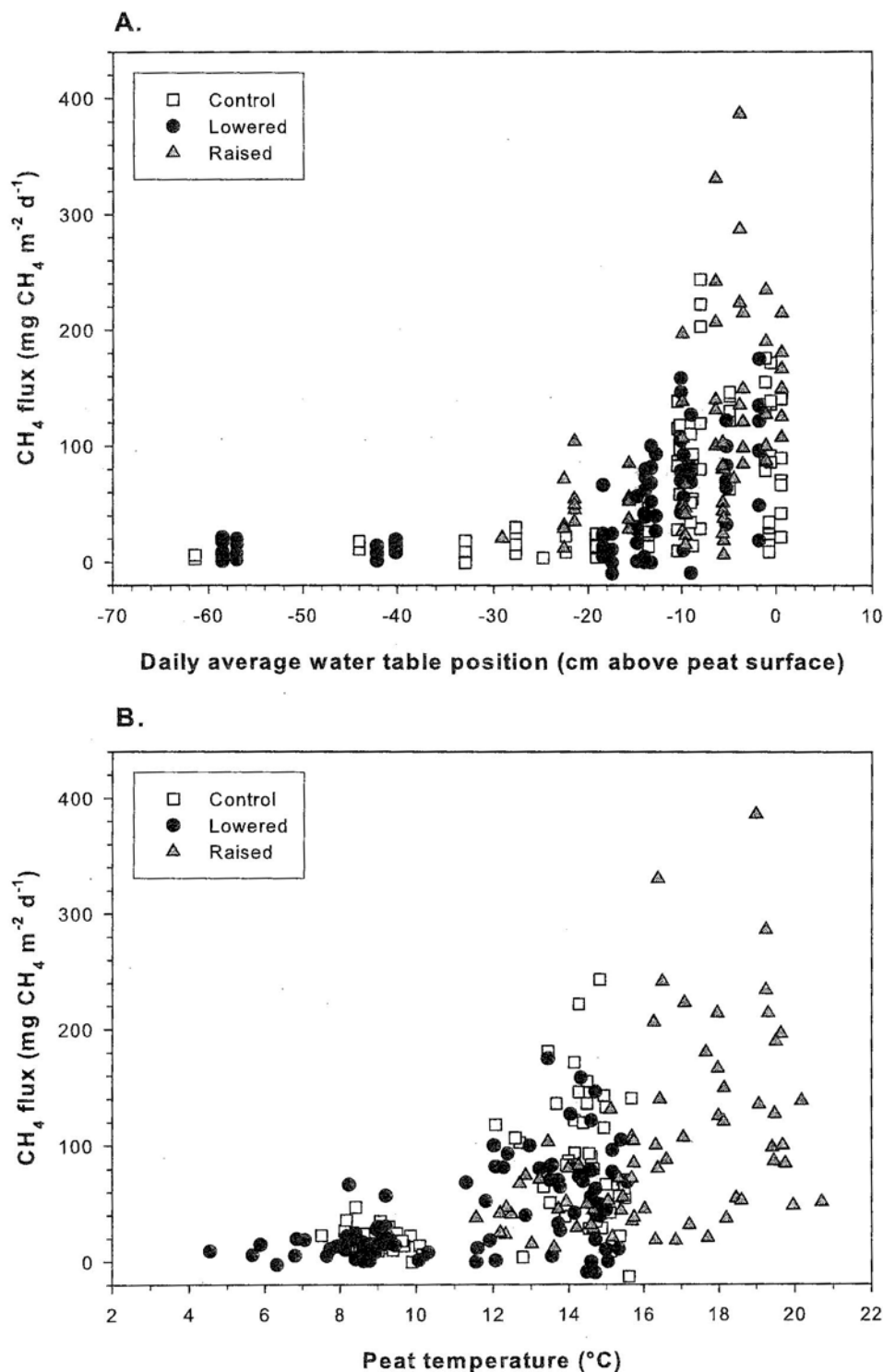


Figure 4. (a) Effect of water table position and (b) peat temperature at 25 cm depth beneath the moss surface on CH_4 fluxes across the three water table treatments.

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

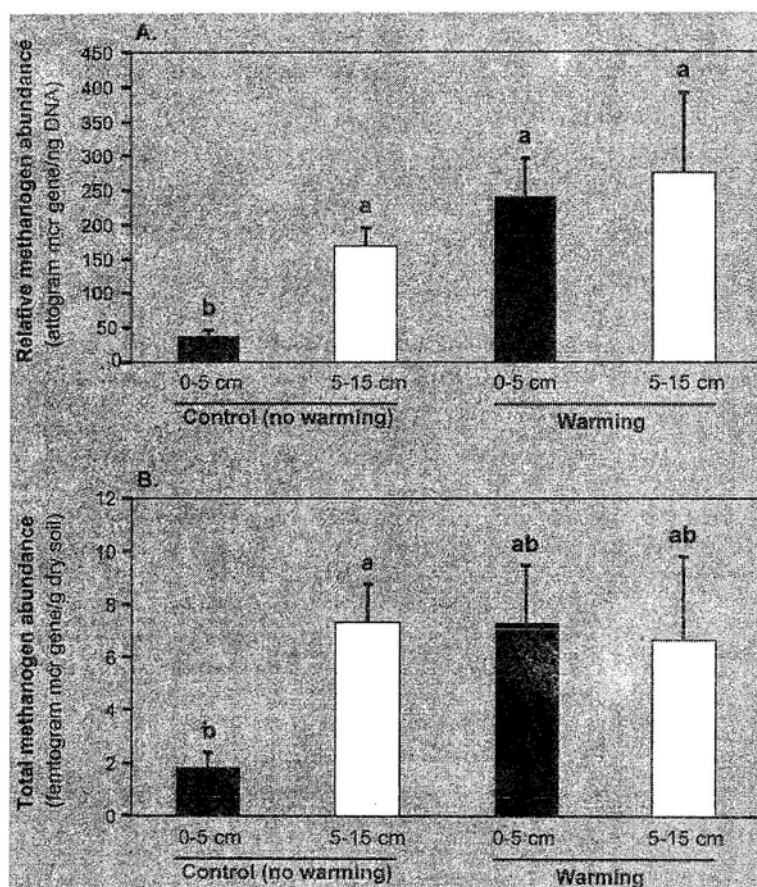


Figure 5. Results of an analysis of variance model analyzing (a) the relative abundance and (b) the total abundance of methanogens estimated by qPCR in surface (0–5 cm) and deeper (5–15 cm) peat across the soil warming treatments. Data are means $\pm$ one standard error. Same letter superscript denote 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
<i>Short-Term WT Manipulations</i>				
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%
<i>Short-Term Warming Manipulations</i>				
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
<i>Factorial Short-Term WT × Warming Manipulations</i>				
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
<i>Strack et al.</i> [2004]	Ecosystem (poor fen)	WT: -20 cm drawdown	Long-Term WT Manipulations 8 years	Reduced CH ₄ fluxes by 55%; Increase in herbaceous and shrub spp., decrease in <i>Sphagnum</i> (except in hollows)
<i>Roulet et al.</i> [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
<i>Laine et al.</i> [1995] (a); <i>Laine et al.</i> [1996] (b); <i>Marikainen et al.</i> [1995] (c); <i>Nykanen et al.</i> [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 <i>Sphagnum</i> cover (c), increase in woody vegetation (a,c)
<i>Keller et al.</i> [2004]	Core/incubation (bog and fen)	See <i>Updegraff et al.</i> [2001] ^b	Long-Term Factorial WT and Warming Manipulations 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

^aWT 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 CH₄

[34] Our static chamber measurements characterize diffusive fluxes of CH₄ 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 CH₄ release as diffusive fluxes in northern peatlands [*Baird et al.*, 2004; *Christensen et al.*, 2003 a; *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 CH₄ fluxes to the atmosphere. For example, an ebullition event in 2006 released >3 g CH₄ 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 CH₄ 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 CH₄ production and lower CH₄ 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 CH₄ fluxes from peatlands, more detailed characterization of the spatial and temporal variation in CH₄ ebullition across our experimental treatments will be necessary to resolve the overall peatland-atmosphere exchange of CH₄ 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 CH₄ fluxes measured so far across our experimental treatments (Table 3) are on the low end but well within the range of CH₄ fluxes₂ observed for North American peatlands (0.6–129.0 g CH₄ 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 CH₄ 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 CH₄ 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). *Disc et al.* [1993] found that a flooding treatment of similar magnitude to our experimental design (Table 4) caused 200–250% increases in CH₄ emissions in a Minnesota peatland.

[36] Numerous field and laboratory studies have examined CH₄ fluxes under experimentally lowered water table positions. Short-term experiments (i.e., 7 weeks to 3 years) typically show reductions in CH₄ fluxes from peatland soils by 80–90% with water table drawdown (Table 4). However, the response of CH₄ emissions to water table drawdown typically are sustained or can grow stronger over time; measurements conducted over longer time frames (>5 years)

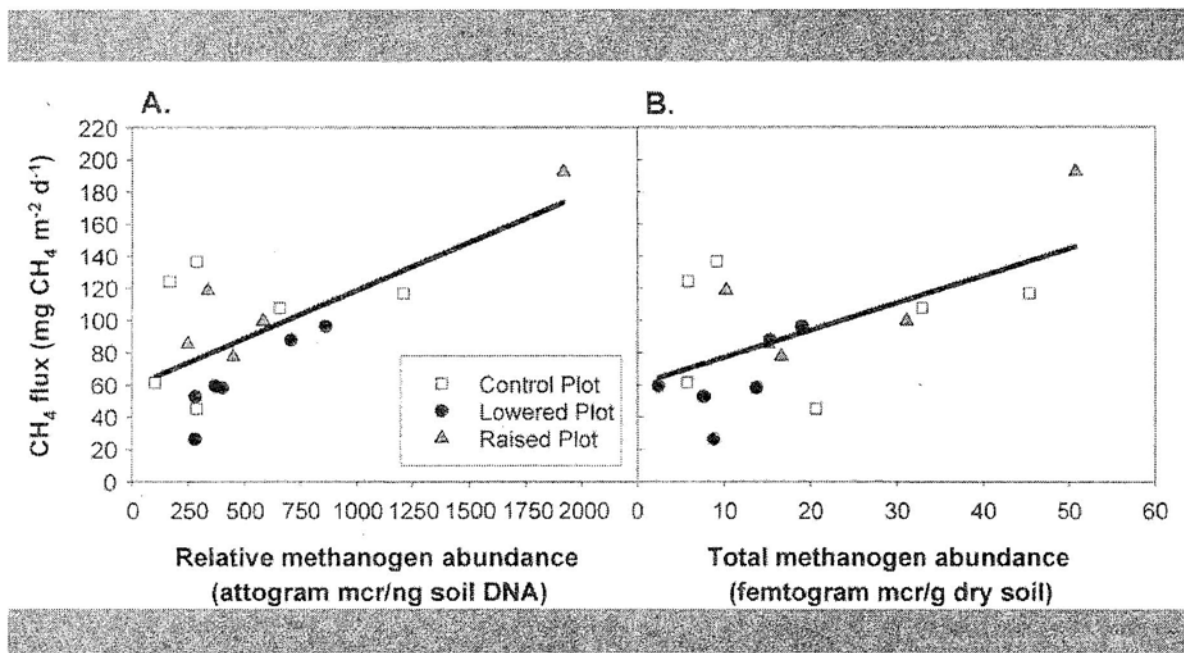


Figure 6. (a) Effect of mean methanogen abundance in surface peat layers cm on mean daily CH₄ fluxes from 2005 (slope = 0.06 ± 0.02 ; intercept = 58.80 ± 11.99 ; $F = 11.94$, d.f. = 1, 15, $p = 0.004$, $R^2 = 0.44$). (b) Effect of mean total abundance of methanogens in surface peat layers on mean daily CH₄ 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 CH₄ fluxes ranging anywhere from 25%-200%, (Table 4). Variation in the response of CH₄ 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, 2001]

[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 CH₄ emissions to warmer temperatures. Granberg et al. [2001] observed strong interactions between sedge cover and experimental warming, in which CH₄ 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 CH₄ fluxes to the atmosphere (Table 4). Here, our results show that soil warming effects on CH₄ fluxes in a boreal rich fen are coupled to water table dynamics, as warming had the greatest influence on CH₄ fluxes in our raised water table treatment (Figure 3b). However, over the next several years to decade, we predict further enhancements of CH₄ 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 Hydroclimatic for CH₄ Emissions in Alaskan Wetlands

[38] In a regional modeling study, Zhuang et al. [2007] estimate that current CH₄ emissions from Alaskan soils are approximately 3 Tg CH₄ 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 CH₄ emissions [Zhuang et al., 2007]. Additional modeling of regional CH₄ 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 km² depending on various criteria used for defining peat soils [Bridgman 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 CH₄ 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 CH₄ emissions beyond the effects of soil warming alone. On the other hand, CH₄ 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 CH₄ emissions to climate change in Alaska needs to consider the interactive effects of soil warming and water table position on CH₄ production and transport.

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