

## A MULTI-YEAR PERSPECTIVE ON METHANE CYCLING IN A SHALLOW PEAT FEN IN CENTRAL NEW YORK STATE, USA

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**Abstract:** Minerotrophic sedge fens are common in sub-arctic regions and are a significant source of atmospheric methane (CH<sub>4</sub>), yet they have received less attention than other peatlands, such as boreal ombrotrophic bogs, which are smaller sources of CH<sub>4</sub>. At the process level, CH<sub>4</sub> fluxes in sub-arctic systems are limited primarily by cold temperatures, and thus are sensitive to potential climate change. This study examined CH<sub>4</sub> dynamics in a temperate sedge-fen to determine controls on the spatial and temporal variability in CH<sub>4</sub> fluxes and, therefore, how the biogeochemistry of CH<sub>4</sub> in sedge-fen peatlands may respond to predicted changes in climate. We used flux chambers and laboratory peat incubations over a six to seven-year period (1994–2000) to study fluxes, pools, and potential production of CH<sub>4</sub> in a peat-forming wetland in central New York State, USA. Results showed that precipitation (i.e., dry years and depth to water table) exerted an important control on annual and seasonal patterns of CH<sub>4</sub> fluxes. Mean summer flux rates ranged from 2258 nmol m<sup>-2</sup> s<sup>-1</sup> in the wettest year to -934 nmol m<sup>-2</sup> s<sup>-1</sup> (net consumption) in the driest year. CH<sub>4</sub> concentrations in the surface peat were as low as 0.01 μatm and as high as 10 matm in the summer months depending on precipitation patterns. In contrast, CH<sub>4</sub> concentrations were consistently two to three times greater in sub-surface than in surface peat, and pools persisted during dry years and were temporally less variable. Fluxes were only weakly associated with potential CH<sub>4</sub> production rates, which showed little seasonal variation. *In-vitro* measurements of potential CH<sub>4</sub> production did not sufficiently explain fluxes, suggesting a need for improved *in-situ* methods for measuring CH<sub>4</sub> production. Site differences associated with different dominant vegetation had a significant effect on CH<sub>4</sub> cycling in all years except the driest, suggesting sensitivity to vegetation changes. These results indicate that predicting responses of fen peatlands to environmental requires an improved understanding of the underlying microbial processes and mechanisms that control CH<sub>4</sub> cycling.

**Key Words:** methane flux, peatlands, fens, temperate, minerotrophic, microbial processes, climate, methane oxidation

### INTRODUCTION

Despite considerable effort to quantify methane (CH<sub>4</sub>) fluxes from peatland ecosystems to the atmosphere (e.g., Harriss et al. 1985, Bartlett and Harriss 1993), flux estimates are fraught with large measurement variability (temporally and spatially) that spans several orders of magnitude (Bubier and Moore 1994). Temporal patterns generally follow seasonal cycles, with greater fluxes during warmer months, yet the magnitude and timing of peak CH<sub>4</sub> fluxes can vary widely from year to year (Frolking and Crill 1994).

Moreover, spatial variability occurs at the landscape scale and down to the plot scale (Bartlett and Harriss 1993). Because of the array of complex biological and physical processes that control flux, predicting CH<sub>4</sub> emissions therefore has been problematic and has hindered our ability to predict how these systems will respond to global environmental changes (Gorham 1991). The most successful approach has been the establishment of *in situ* empirical relationships with environmental or plant-based variables.

The most widely recognized controls on CH<sub>4</sub> fluxes are peat and air temperature (Crill et al. 1993, Gran-

berg et al. 2001), water-table level (Moore and Knowles 1989, Moore and Roulet 1993), vegetation (Whiting and Chanton 1993, Bubier 1995), and peat quality (Svensson and Sundh 1992, Yavitt et al. 2000); yet, these variables explain only a portion of the observed variation in flux measurements (Segers 1998). Process-based approaches that examine the biological mechanisms that produce and consume  $\text{CH}_4$  *in situ* have also been used to explain flux rates (e.g., Svensson and Rosswall 1984, Yavitt et al. 1988, Yavitt et al. 1997, Whalen and Reeburgh 2000). Nevertheless, much uncertainty concerning controls on  $\text{CH}_4$  fluxes remains.

Flux measurements that span multiple years (e.g., Frohking and Crill 1994) provide more insight into spatial and temporal patterns and potential controls on those patterns than single time-point or one-year studies. Multi-year studies, in general, capture more of the climatic variability seen in nature. Because  $\text{CH}_4$  is produced biologically under anoxic conditions, climatic variability could impact long-term microbial population and community dynamics. For example, we could intuitively expect low fluxes during dry years and greater fluxes during wet-years, yet it is uncertain how peat microbial communities would respond to cycles of wet and dry years. Flux measurements that encompass temporal and spatial variability are therefore useful for elucidating such mechanisms and processes.

Here, we report six years of  $\text{CH}_4$  flux data for a peat-forming sedge fen in central New York State, USA. In addition, we report seven years of data for peat-porewater  $\text{CH}_4$  concentrations and potential  $\text{CH}_4$  production. Minerotrophic sedge fens (*Carex*-dominated) have received less attention than *Sphagnum*-dominated systems that are common in the boreal regions. Sedge fens are more extensive on the landscape in sub-arctic regions where persistent cold climate and very short growing season appear to be the most important factors limiting  $\text{CH}_4$  fluxes (Roulet et al. 1992). Unlike *Sphagnum*-dominated peatlands, these *Carex*-dominated systems have higher overall rates of  $\text{CH}_4$  cycling (Yavitt et al. 1990), thin peat accumulations, and relatively open and rapid (short residence time) hydrology compared to bog systems. These “wet” (term used to represent relative annual water budget) peatland systems have high net primary productivity (NPP) and are large  $\text{CO}_2$  sinks, yet are significant sources of  $\text{CH}_4$  (Whiting and Chanton 1992). In terms of greenhouse gas equivalents, these sites will have a greater impact on global warming than “dry” boreal bogs that are net sinks of  $\text{CO}_2$  but small sources of  $\text{CH}_4$ . Since cold temperatures limit  $\text{CH}_4$  production in these sites and consequently  $\text{CH}_4$  fluxes, we would expect our cool-temperate study site to be on the very high end of  $\text{CH}_4$  point sources, providing potential insight into

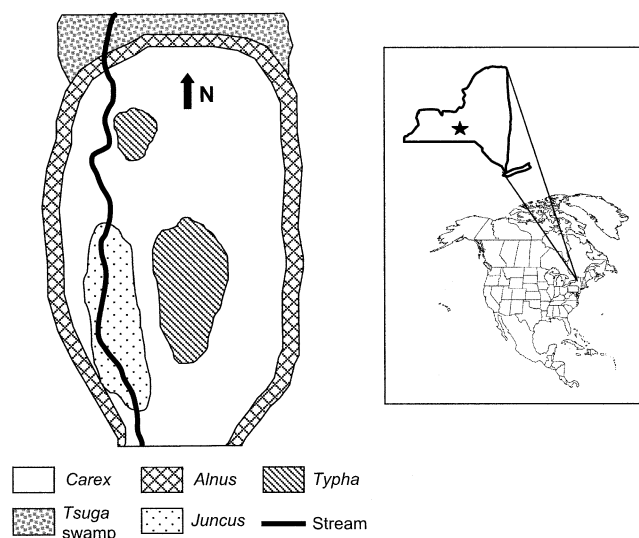


Figure 1. Study site map of Michigan Hollow showing vegetation zones, stream location, and geographic location in North America and New York State.

how northern counterparts might respond to environmental changes.

The primary objective of our study was to examine patterns and controls of  $\text{CH}_4$  flux variability in low latitude shallow sedge fens. In particular, we wanted to investigate the relationship among  $\text{CH}_4$  fluxes, peat porewater  $\text{CH}_4$  pools, and microbial  $\text{CH}_4$  cycling, and how these relationships are influenced by climate and vegetation. We hypothesized that  $\text{CH}_4$  fluxes, pools, and potential production rates would be greatest in the summer months and in years with high summertime precipitation and that  $\text{CH}_4$  fluxes would therefore be correlated with precipitation and peat temperature patterns. In addition, we hypothesized that  $\text{CH}_4$  cycling process rates would be highest in sites dominated by more highly decomposable *Carex* vegetation (Yavitt and Lang 1990). We used both an environmental variable (e.g., Chanton and Dacey 1991, Crill et al. 1993, Moore and Roulet 1993, Yavitt et al. 2000) and a process-based approach (e.g. Svensson and Rosswall 1984, Yavitt et al. 1988, Yavitt et al. 1997, Whalen and Reeburgh 2000) to address these relationships using correlation and regression analyses.

## METHODS

### Study Site

Our study site, Michigan Hollow, is a 15-ha minerotrophic, peat-forming, riverine sedge fen located in central New York State, USA ( $42^{\circ} 21' \text{N}$ ,  $76^{\circ} 28' \text{W}$ ). The wetland sits in the lowest part of a small, forested watershed (Figure 1). The upland directly adjacent to the wetland has secondary forest species, and there is

Table 1. Climate characteristics and sampling effort summary for each study year. Measurements of CH<sub>4</sub> flux and CH<sub>4</sub> pools (porewater [CH<sub>4</sub>]) were made in the field. Potential CH<sub>4</sub> production was measured in the laboratory. NA denotes unavailable data.

Year	<sup>1</sup> Average Summer Air Temperature (°C)	<sup>2</sup> Average Summer Peat Temperature (°C)	<sup>3</sup> Summer Precip Departure (cm)	<sup>4</sup> Porewater [CH <sub>4</sub> ]		CH <sub>4</sub> Flux Chambers		Potential CH <sub>4</sub> Production	
				# Sampling Dates	Total n	# Sampling Dates	Total n	# Sampling Dates	Total n
1994	NA	16.7	NA	14	210	0	0	1	24
1995	19.3	18.3	-16.5	13	195	4	48	8	96
1996	18.7	17.4	9.8	9	81	9	81	8	96
1997	17.9	17.8	-5.2	3	45	3	45	3	36
1998	19.1	18	-5.7	3	45	3	45	3	36
1999	19.6	17.2	-2.9	0	0	2	48	2	96
2000	17.8	15	-3.5	4	96	4	96	2	96

<sup>1</sup> Summer (mid-June through mid-August) temperature measured in the field.

<sup>2</sup> Peat temperature measured at 15 cm.

<sup>3</sup> Summer precipitation departure from normal (~36 cm) from the Northeast Regional Climate Center.

<sup>4</sup> Both surface and sub-surface peat porewater (only surface porewater in 2000).

a narrow alder thicket (*Alnus rugosa* L.) around the edge of the wetland. In the 1970s, the wetland was covered by a mono-specific stand of *Carex lacustris* Willd. (Bernard and Macdonald 1974). Around 1990, associated with an increase in beaver activity, areas in the wetland became dominated by *Typha latifolia* L. Following removal of the beaver, previously flooded areas developed lush stands of *Juncus effusus* L. Our investigation focused on these distinct vegetation zones and will be referred to as the *Carex*, *Typha*, and *Juncus* sites.

Peat accumulations at Michigan Hollow are ~1 m, and peat depth has likely varied due to previous land-use practices such as cattle grazing. The peatland receives surface and sub-surface flow from the surrounding forested uplands, and drains south into the upper Susquehanna watershed and ultimately into the Chesapeake Bay. Bernard and Macdonald (1974) described this site previously.

#### Field and Laboratory Techniques

We collected data over a 6 to 7-year period from 1994 to 2000. The data were collected monthly in 1994 and 1995, but late fall, winter, and early spring measurements were suspended due to low activity and little inter-annual variation during that period. Concentration of dissolved CH<sub>4</sub> in peat porewater was measured from 1994 to 1998 and in 2000 and used as an estimate of the peat CH<sub>4</sub> pool (Table 1). Data for 1999 were not used because of drought and methodological problems. Field CH<sub>4</sub> flux measurements *in-vitro* potential CH<sub>4</sub> production began in 1995 and continued through 2000. Additionally, in 1999 and 2000, we measured potential aerobic CH<sub>4</sub> oxidation in surface peat samples. All measurements were replicated in three sampling sites and five (1994 through 1998)

to eight times (1999 and 2000) within sampling sites (Table 1). At each site and on each date, we took measurements of peat temperature, air temperature, and depth to water table (at the surface in normal years). During occasional drought years, the water table dropped to a maximum depth of 40 cm. Therefore, we used monthly precipitation departure from normal data (Northeast Regional Climate Center, Cornell University) as a surrogate of water-table depth in this study.

Methane flux measurements were made using methods similar to those of Moore and Knowles (1990) and Yavitt et al. (1990). We used static chambers made from large plastic water bottles (~15 L headspace volume; 27 cm dia. × 37 cm height) with the bottoms removed. For each sampling date, we placed chambers at 5–8 random sampling points in each site within the wetland (15–24 total). Chambers were carefully inserted 3 cm into the peat surface in order to maintain a gas-tight seal and allowed to equilibrate for 10 minutes. Tall stems of *Typha*, *Juncus*, or *Carex* were carefully rolled up and released inside the chamber in order to account for plant transport in the flux measurements. This method allowed us to capture spatial variability in fluxes within the site as opposed to taking measurements in one location with a fixed base, although some methane could have been released when inserting the chamber. Chambers were then capped with rubber stoppers that were connected to 2-m-long Nalgene<sup>®</sup> tubing (1-mm internal diameter) and fitted with a 3-way stopcock. A 60-ml syringe was used to mix air in the headspace (~5×) and draw the sample. Samples were collected four times (0, 15, 30, and 60 minutes) over a one-hour period and transferred to a 10-ml syringe for transport to the lab for CH<sub>4</sub> analysis. Flux rates were calculated as the slope of the CH<sub>4</sub> concentration over time.

Peat CH<sub>4</sub> pools were estimated by extracting pore-

water using a stainless steel porewater sampler connected to a 60-ml syringe fitted with a 3-way stopcock. Syringes were filled with O<sub>2</sub>-free N<sub>2</sub> (ultra-high purity N<sub>2</sub> (Airgas, Inc.)), and the steel tube connected and flushed just prior to insertion into the peat. Porewater (30 ml) was drawn into each syringe and the stopcock closed before removing the collection tube. Gases were stripped from the porewater by filling the remaining headspace in the syringe with N<sub>2</sub>, shaking vigorously for 5 minutes, and transferring the headspace volume to a 10-ml syringe prior to transport to the lab for CH<sub>4</sub> analysis. We collected porewater samples from two depths: 0–5 cm (surface) and 20–30 cm (sub-surface). For each sampling date, porewater CH<sub>4</sub> was collected from 5–8 random sampling points in each site within the wetland (15–24 total). Peat porewater CH<sub>4</sub> concentrations are reported as dissolved CH<sub>4</sub> ( $p\text{CH}_4\text{-matm}$ ) by using a version of Henry's law (Flett et al. 1976) and Bunsen solubility coefficients (Yamamoto et al. 1976).

Assays for potential CH<sub>4</sub> production were carried out with freshly collected peat samples. Peat cores were extracted using a Russian style peat bore (Aquatic Research Instruments, Inc.) with a 10-cm-diameter barrel. For each sampling date, we randomly collected 3–16 cores from each site within the wetland. Each core was sectioned into 0–15 and 15–35 cm depths. Samples were placed in sealed bags and stored on ice for no more than 2 hours, transported to the lab, immediately transferred to sterile mason jars, and flushed with O<sub>2</sub>-free N<sub>2</sub> before being sealed. Potential CH<sub>4</sub> production was then estimated using a modification of the method of Yavitt et al. (1988). Thirty grams of wet peat (two analytical replicates for each field sample) was placed in sterile ~250 ml mason jars. Jars were flushed with O<sub>2</sub>-free N<sub>2</sub> and sealed with canning lids fitted with replaceable rubber septa set in silicone sealant. Jars were evacuated to –67 kPa and then overpressurized with N<sub>2</sub> to 135 kPa, with this process being repeated 10 times for each jar. Each jar was then overfilled with N<sub>2</sub> and equilibrated to atmospheric pressure through a syringe filled with O<sub>2</sub>-free water. All incubations were performed at laboratory temperatures of ~23°. Gases were sampled every 12 hours from the headspace. Potential aerobic CH<sub>4</sub> oxidation was measured in a similar fashion with 1% CH<sub>4</sub> and 20% O<sub>2</sub> added to the headspace.

Methane was analyzed on a Varian 3400cx gas chromatograph equipped with a flame ionization detector (FID) and a Chromosorb 102 column. Injection, detector, and column temperatures were 130°C, 180°C, and 50°C, respectively. The FID was calibrated at each sampling period by analyzing triplicate external samples of certified 10, 100, 1000, and 10,000  $\mu\text{L L}^{-1}$

(1%) CH<sub>4</sub> standards. Standard reproducibility was generally  $\pm 0.25\%$ .

### Data Analyses

Descriptive statistics and a lack-of-fit test were used to determine whether data satisfied assumptions of normality and equal variance. Flux and pool data were log-transformed in order to satisfy these assumptions. Since our data set was not continuous and had missing values, we used statistical procedures that allowed us to measure random effects and account for missing data. Therefore, we used an analysis of variance (ANOVA) and general linear model procedure (PROC GLM; SAS v.8.2) to examine temporal patterns of CH<sub>4</sub> fluxes, pools, and potential production using season and year as independent variables. Pair-wise comparisons were made using a Tukey procedure. We also used ANOVA to examine spatial patterns in summertime (mid-June to mid-September) fluxes, pools, and production using year and site as independent variables. Sites were categorized according to the dominant vegetation (i.e., *Typha*, *Carex*, or *Juncus*). Pearson correlation coefficients were calculated to determine correlations between and among measured variables (summertime means) and environmental variables (peat temperature and precipitation). In addition, we used linear regression techniques to examine predictors of summer CH<sub>4</sub> emissions and peat CH<sub>4</sub> pools. Non-normal data were log-transformed in order to meet normality requirements.

## RESULTS

### Temporal Patterns

Methane flux rates varied over several orders of magnitude (Figure 2) from a maximum flux rate of 2258  $\text{nmol m}^{-2} \text{s}^{-1}$  to a net consumption rate of –934  $\text{nmol m}^{-2} \text{s}^{-1}$ . Rates were temporally variable and significantly different between years and seasons, and the seasonal variability changed among years as indicated by the significant interaction term in the ANOVA (Table 2). The highest rates were in the summer of 1996, corresponding to high precipitation, whereas rates were very low throughout 1995, an extremely dry year. This significant temporal pattern was driven by the difference between wet years, as Tukey comparisons suggested that the 1996 rates were not significantly higher than the next wettest year (2000). Although rates were generally higher during the warmer months, significant CH<sub>4</sub> flux was measured year-round depending on ice and snow cover.

Porewater CH<sub>4</sub> concentrations in surface peat varied annually and seasonally (Figure 3; Table 2). Surface

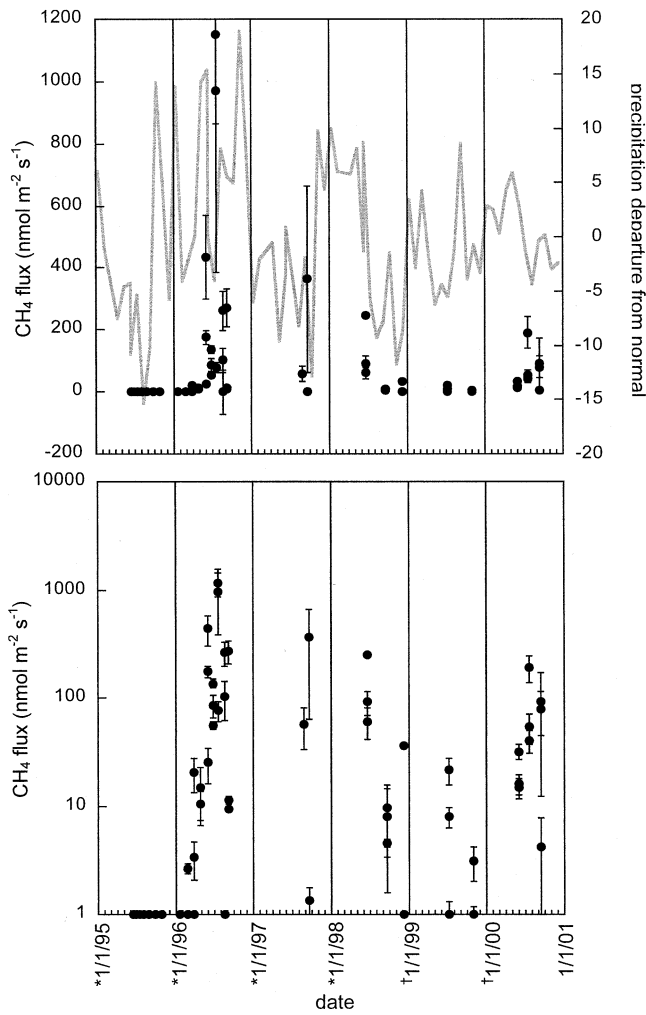


Figure 2. Michigan Hollow CH<sub>4</sub> flux rates from 1995 to 2000. Data are presented in normal (A) and log scale (B). Data points are mean CH<sub>4</sub> flux rate ±SE from three different sampling sites on individual sampling dates. Years with\*, n=5 for each site and date; years with†, n=8 for each site and date. Gray line is the monthly precipitation departure from normal data from the Northeast Regional Climate Center, Cornell University.

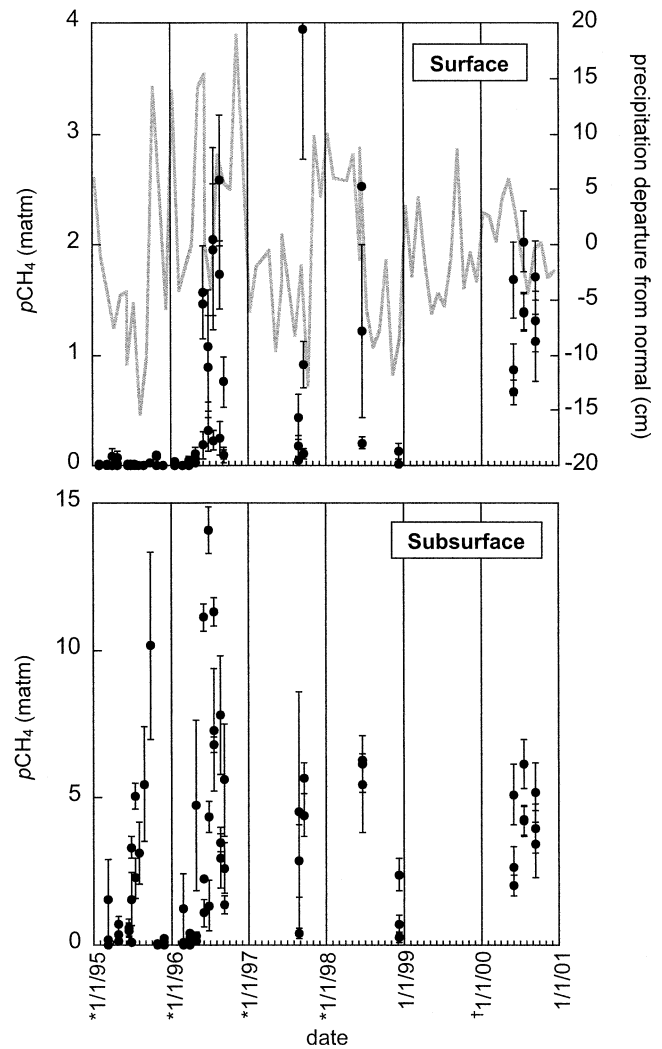


Figure 3. Michigan Hollow porewater CH<sub>4</sub> concentrations in surface (0–15 cm) and subsurface (20–35 cm) peat from 1994 to 2000. Data points are mean pCH<sub>4</sub> ±SE from three different sampling sites on individual sampling dates. Years with\*, n=5 for each site and date; years with†, n=8 for each site and date. Gray line is the monthly precipitation departure from normal data from the Northeast Regional Climate Center, Cornell University.

Table 2. Results of two-way Analysis of Variance procedure to test for temporal differences in CH<sub>4</sub> dynamics. Values are the computed F-statistic (df in parentheses) and symbols denote significant effects. Season defined as mean winter, spring, summer or autumn values.

	CH <sub>4</sub> Flux	Peat CH <sub>4</sub> pools		Potential CH <sub>4</sub> Production	
		Surface	Sub-surface	Surface	Sub-surface
Year	158.53* (5)	271.9* (5)	35.35* (5)	5.43* (5)	1.82 (5)
Season	30.72* (3)	26.22* (3)	0.8 (3)	1.8 (3)	1.38 (3)
Year*Season	88.83* (2)	59.57* (6)	8.14* (6)	0.23 (6)	4.37† (6)

\* Significant at p < 0.0001.  
 † Significant at p < 0.05.

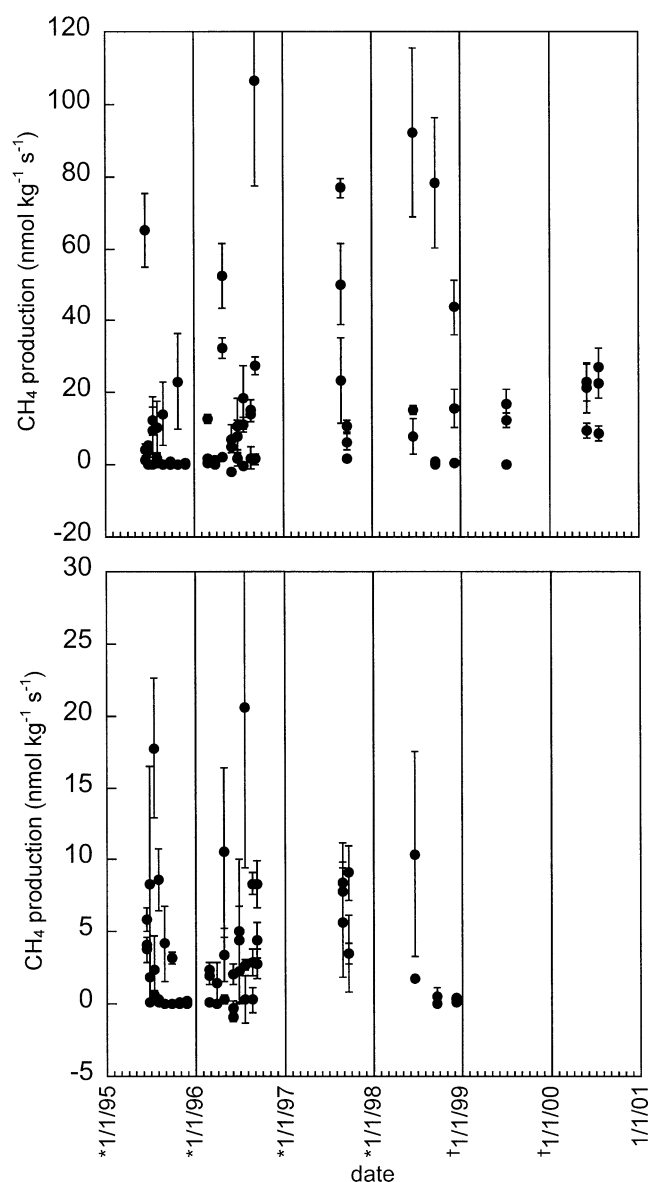


Figure 4. Annual and seasonal potential  $\text{CH}_4$  production rates from anoxic laboratory incubations of Michigan Hollow surface (0–15 cm) and subsurface (20–35 cm) peat. Data points are mean headspace  $\text{CH}_4$  flux  $\pm$ SE from three different sampling sites on individual sampling dates. Years with \*,  $n=5$  for each site and date; years with †,  $n=8$  for each site and date.

$\text{CH}_4$  concentrations were as low as  $0.01 \mu\text{atm}$  in the winter months and as high as  $10 \text{ matm}$  in the summer months. Years with above normal summertime precipitation had the highest  $\text{CH}_4$  concentrations in the surface peat ( $df=2$ ,  $F=4.74$ ,  $p=0.0079$ ). Similar seasonal patterns were observed in the sub-surface peat, yet  $\text{CH}_4$  concentrations were consistently 2–3 times greater in sub-surface than in the surface peat (Figure 3). Sub-surface  $\text{CH}_4$  pools were seasonally less variable than surface pools depending on the year (Table 2) and,

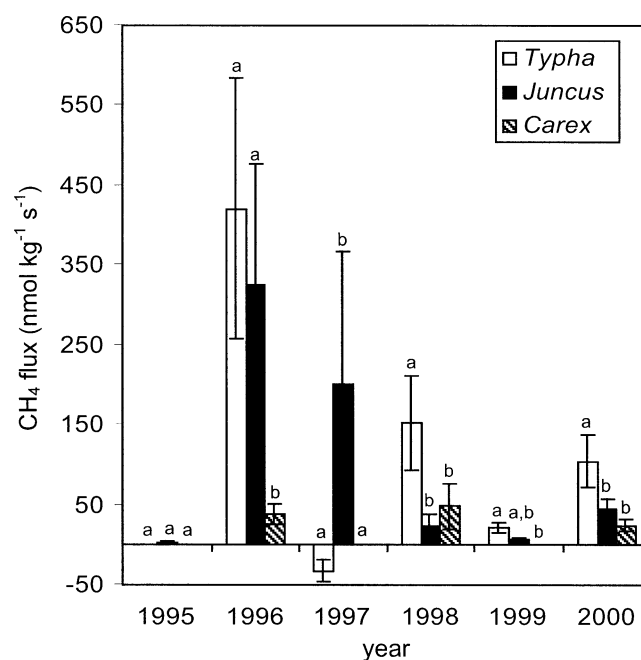


Figure 5. Mean summer  $\text{CH}_4$  flux rates  $\pm$ SE for each sampling site during the study period. Sites are denoted by the dominant vegetation. Bars with different letters within years are significantly different at  $p < 0.01$ .

unlike surface concentrations, remained at  $\sim 1 \text{ matm}$  on average and as high as  $8 \text{ matm}$  during the winter.

Potential  $\text{CH}_4$  production assays (performed at  $23^\circ\text{C}$ ) suggested a seasonal pattern for  $\text{CH}_4$ -producing organisms, with rates ranging from  $135$  to  $-38 \text{ nmol kg}^{-1} \text{ s}^{-1}$  (Figure 4). Potential  $\text{CH}_4$  production rates in surface peat were generally three times greater than in sub-surface peat. Mean production rates over the study period were  $14.9 \text{ nmol kg}^{-1} \text{ s}^{-1}$  in the surface versus  $4.1 \text{ nmol kg}^{-1} \text{ s}^{-1}$  in the subsurface. Potential microbial activity was often lowest in the colder months and greatest in the summer, yet mean potential  $\text{CH}_4$  production rates were not significantly different between seasons (Table 2). Annual variability was significantly different only in surface peat, and a slight year-dependent seasonal effect was observed in the sub-surface peat samples (Table 2).

#### Spatial Patterns

Daily measurements were highly spatially variable, and coefficients of variations for each sampling date ranged from  $480$  to  $<1\%$ . Mean summertime  $\text{CH}_4$  flux rates were not significantly different between the *Typha* and *Juncus* sites in half of the years (Figure 5) but were significantly greater than the *Carex* sites except in dry years (1995 and 1999)(Figure 5). Flux rates were not different among the three sites in the dry years, with the exception of the *Carex* site, which was

Table 3. Summer CH<sub>4</sub> flux rates, pools, and potential production rates for each sampling site. Data are mean summertime values ± SE. Values with different letters are significantly different using a Tukey comparison.

Variable	df	F	p	Site		
				<i>Typha</i>	<i>Juncus</i>	<i>Carex</i>
CH <sub>4</sub> flux (nmol m <sup>-2</sup> s <sup>-1</sup> )	2	3.4	0.0356	113 (44.8) <sup>A</sup>	103 (36.8) <sup>A</sup>	17 (6.3) <sup>B</sup>
Surface CH <sub>4</sub> pool (matm)	2	13.33	<.0001	1.8 (0.2) <sup>A</sup>	1.1 (0.2) <sup>B</sup>	1.1 (0.2) <sup>B</sup>
Sub-surface CH <sub>4</sub> pool (matm)	2	13.12	<.0001	3.8 (0.5) <sup>A</sup>	2.2 (0.3) <sup>B</sup>	1.3 (0.3) <sup>C</sup>
Surface CH <sub>4</sub> prod (nmol kg <sup>-1</sup> s <sup>-1</sup> )	2	4.71	0.0098	19.6 (3.1) <sup>A</sup>	13.4 (1.9) <sup>B</sup>	12.8 (2.1) <sup>B</sup>
Sub-surface CH <sub>4</sub> prod (nmol kg <sup>-1</sup> s <sup>-1</sup> )	2	0.35	0.7056	5.7 (2.5) <sup>A</sup>	4.6 (0.9) <sup>A</sup>	3.7 (1.1) <sup>A</sup>

significantly less than the other sites in 1999. Mean summertime surface peat porewater CH<sub>4</sub> concentrations were significantly greater in the *Typha* site over the study period (Table 3) but not significantly different in any given year. Sub-surface CH<sub>4</sub> pools overall were significantly greater in the *Typha* peat and lowest in the *Carex* peat (Table 3), and site differences were important in all years except the driest (year by site interaction data not shown). Potential CH<sub>4</sub> production showed significant site differences regardless of the year, yet rates were not significantly different between the *Carex* and *Juncus* sites in any year. The pattern was more complicated in the subsurface peat. Year and site had no significant effect alone, but the interaction was significant and showed that site was important in wet years.

#### Environmental Factors

Correlation analysis demonstrated that summertime CH<sub>4</sub> emissions were positively correlated with surface and sub-surface CH<sub>4</sub> pools, aerobic CH<sub>4</sub> oxidation rate, and precipitation (Table 4). Emission rates were negatively correlated with peat temperature. Surprisingly, no relationship between CH<sub>4</sub> emissions and potential CH<sub>4</sub> production rates was apparent. Surface-peat CH<sub>4</sub>

pools were weakly correlated with potential CH<sub>4</sub> production in surface and sub-surface peat but were most positively correlated with precipitation and sub-surface CH<sub>4</sub> pool and negatively correlated with peat temperature. Surface pools did not correlate with potential aerobic oxidation. Sub-surface pools also showed weak correlation with production rates but were most strongly correlated with precipitation.

Regression analyses demonstrated that variation in CH<sub>4</sub> flux rates could be explained by precipitation ( $r^2=0.56$ ) and surface CH<sub>4</sub> pools ( $r^2=0.63$ ). However, this relationship was strongly driven by the low emission rates in the driest year (1995). When this year was excluded from the analysis, the strength of the relationship weakened considerably. Variation was more consistently predicted by a positive relationship with sub-surface CH<sub>4</sub> pools ( $r^2=0.32$ ) and aerobic CH<sub>4</sub> oxidation rates ( $r^2=0.37$ ; Figure 6). Regression calculations to predict CH<sub>4</sub> pools were also highly driven by the 1995 data, and no relationships between pools and production rates were observed.

#### DISCUSSION

CH<sub>4</sub> fluxes varied by at least five orders of magnitude during the study period. The highest mean flux

Table 4. Pearson Correlation Coefficients for correlates of CH<sub>4</sub> fluxes and CH<sub>4</sub> pools. Symbols denote significant coefficients.

	CH <sub>4</sub> Flux	Surface CH <sub>4</sub> Pool	Sub-surface CH <sub>4</sub> Pool	Surface CH <sub>4</sub> Prod	Sub-surface CH <sub>4</sub> Prod	CH <sub>4</sub> Oxidation	Peat Temp	Summer Precip Depart
CH <sub>4</sub> flux	—	0.79*	0.57*	0.16†	0.17	0.52*	-0.38	0.75*
Surface CH <sub>4</sub> pool	0.79*	—	0.75*	0.24†	0.25†	-0.07	-0.47*	0.71*
Sub-surface CH <sub>4</sub> pool	0.56*	0.75*	—	0.24†	0.26*	ND	0.03	0.54*

\* Significant at  $p < 0.0001$ . † Significant at  $p < 0.05$ .

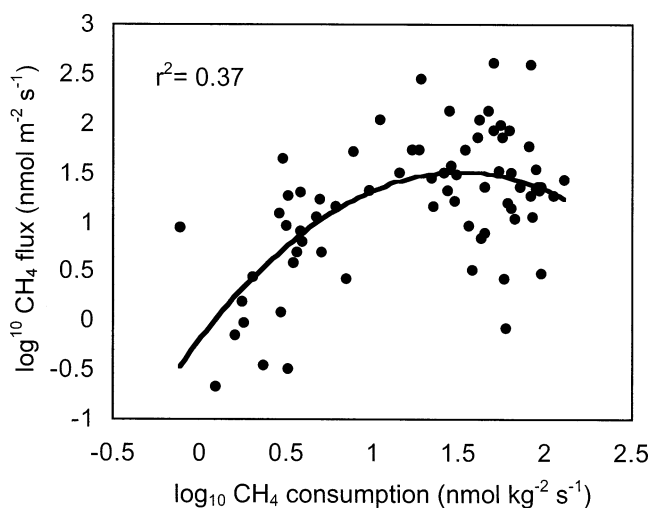


Figure 6. Quadratic line fit for  $\log_{10}$ -CH<sub>4</sub> flux rate (y-axis) and  $\log_{10}$ -potential CH<sub>4</sub> consumption rate (x-axis) from 1999 and 2000.

rate from 1996 and the highest single flux rate were similar to the high rates reported by Harriss et al. (1985) for Minnesota bogs. However, our mean flux rates over the study period were not different from those reported for open graminoid bogs and fens in the discontinuous permafrost zone (Bubier et al. 1995) or sub-arctic sedge-fens (Moore and Knowles 1990), both of which have only moderately high CH<sub>4</sub> flux rates. Mean summer flux rates were surprisingly low given our *a priori* predictions concerning “wet” sedge fens in more temperate climates. Our lowest flux rates were actually negative (i.e., net oxidation) during the driest years. “Wet” peatlands may therefore be sinks for CH<sub>4</sub> during periods of prolonged drought. The more rapid hydrology (short residence time) in our site compared to northern counterparts may act to reduce CH<sub>4</sub> fluxes at the decadal scale. Nevertheless, the system ranged from a large CH<sub>4</sub> source to a moderate sink.

One of the most significant observations in this study was the lack of an increase in CH<sub>4</sub> flux rates in the wettest year (1996). Given the highly reducing conditions (Smemo 2003) and high CH<sub>4</sub> concentrations in the surface and sub-surface peat in 1996 (Figure 3), flux rates were not nearly as high as expected given our predictions and hypotheses about “wet” sedge fens and were not very different from years with normal precipitation. High water table and peat temperatures, large CH<sub>4</sub> pools, and high NPP (Yavitt and Williams *unpublished data*) should have conspired to generate extremely high CH<sub>4</sub> flux rates. It is possible that high plant NPP actually increased transport of O<sub>2</sub> to the rhizosphere and, hence, CH<sub>4</sub> oxidation (Yavitt and Knapp 1998). Given our low potential methane production measurements in the same years, it is also

possible that other processes that influence net production are constraining fluxes.

Climate exerts an inherently strong control on temporal patterns of peatland CH<sub>4</sub> flux (Moore et al. 1998). As described by Frohling and Crill (1994), temperature and precipitation variability influences seasonal and inter-annual patterns of CH<sub>4</sub> flux. The flux data presented here agree with those observed patterns. Flux rates were clearly highest in the summer months of most years, and average summer flux among years was greatest during periods of higher than normal precipitation (Figure 2). Surface CH<sub>4</sub> pools also followed this pattern. CH<sub>4</sub> fluxes and surface CH<sub>4</sub> pools were positively correlated and are both seasonally influenced by peat temperature and subsequent low CH<sub>4</sub> production rates (Dise 1993). Inter-annual variability of flux and surface pools appeared to correlate best with precipitation patterns. Sub-surface pools, conversely, did not show a strong seasonal pattern, suggesting that temperature changes have less influence on deeper older peat that is permanently saturated and below the primary influence of plant roots.

Although several studies have shown that peat temperature is positively correlated with CH<sub>4</sub> flux (Svensson and Rosswall 1984, Crill et al. 1988, Dise 1993), we found no such relationship in our system (Table 4). In fact, CH<sub>4</sub> flux and peat temperature were weakly negatively correlated, likely due to a temperature effect on aerobic CH<sub>4</sub> oxidation rates in surface peat (Crill et al. 1993) (i.e., CH<sub>4</sub> escape from peat is reduced at higher temperatures by aerobic CH<sub>4</sub> oxidation). Instead, precipitation departure from normal was the most important environmental variable describing the variability of flux rates and CH<sub>4</sub> pool concentration (a correlate of flux). Precipitation, due to landscape position, directly influences water-table elevation in Michigan Hollow, and depth to water table has previously been described as an important predictor of CH<sub>4</sub> flux (Svensson et al. 1975, Moore and Roulet 1993). Water-table depth could also exert control on redox gradients and CH<sub>4</sub> exchange within the peat profile (Romanowicz et al. 1995).

Our results also showed distinct within-wetland site differences for CH<sub>4</sub> fluxes, pools, and potential production (Table 3). One possible explanation for site differences is distance from the stream running through the wetland. Since the stream would be a likely source of oxygenated water to the peat profile, sites closest to the stream would have the lowest flux and production rates and the smallest pools. The opposite pattern was actually observed, suggesting alternative controls on site differences. We hypothesize that site differences are related to the presence, growth, and decomposition of the dominant vegetation in each site.

It is well known that vegetation can affect CH<sub>4</sub> flux-

es and pools indirectly via carbon quality or NPP control of CH<sub>4</sub> production (Chanton and Dacey 1991, Svensson and Sundh 1992, Bergman et al. 2000) or directly through plant-mediated transport (Bubier et al. 1995, Yavitt and Knapp 1995). In our system, fluxes were significantly greater in the *Typha*- and *Juncus*-dominated sites than in the *Carex*-dominated site (Table 3). Yavitt and Knapp (1998) reported the same pattern when they measured CH<sub>4</sub> flow through emergent aquatic plants in a central New York wetland and associated the pattern with differences in leaf physiology. Significant differences in surface CH<sub>4</sub> pools might also be explained by differences in CH<sub>4</sub> transport through aquatic plants or by differences in potential CH<sub>4</sub> production rates in surface peat fueled by decomposition products of the dominant plants (Yavitt et al. 2000). Sub-surface pools, on the contrary, were not significantly different, suggesting that CH<sub>4</sub>-producing organisms are C-limited in older, highly decomposed peat.

CH<sub>4</sub> fluxes are the net result of a variety of soil biological and physical processes (Segers 1998, and references therein), including biological CH<sub>4</sub> production under anoxic conditions. We might, therefore, expect CH<sub>4</sub> fluxes to be correlated with potential rates of CH<sub>4</sub> production. When summertime flux rates were compared to summertime production rates (in order to control for temperature effects on laboratory incubations), we found that potential CH<sub>4</sub> production was a poor predictor of CH<sub>4</sub> fluxes and pools ( $r^2 < 0.1$ ). When summertime production rates were converted to an area basis integrated across a depth of 1 m (0.25 m at surface rate, 0.75 m at sub-surface rate), potential CH<sub>4</sub> production per unit area nearly always exceeded flux rates suggesting that a significant portion of production is lost to other processes such as aerobic CH<sub>4</sub> oxidation (Priemé 1994).

Potential CH<sub>4</sub> production rates also showed little seasonal pattern when incubated at 23°C. This suggests that seasonal differences in CH<sub>4</sub> pools are the result of temperature regulation of microbial activity and redox status and not microbial population changes. It is therefore possible that low CH<sub>4</sub> production is a bigger constraint on fluxes than is aerobic CH<sub>4</sub> oxidation. The same may hold true during periods of drought. Most CH<sub>4</sub> production occurs in surface peat, and this CH<sub>4</sub> source is shut off when peat is dry. In other words, CH<sub>4</sub> production regulates fluxes in “wet” peatlands more than the balance between production and aerobic oxidation, such as in “dry” peatlands with distinct oxic zones. This necessitates better measurements of CH<sub>4</sub> production rates *in situ* rather than *in vitro* in order to provide more realistic and quantitative estimates of the relationship between CH<sub>4</sub> production and ecosystem CH<sub>4</sub> fluxes.

Although we found low R-square values in our process-based predictions of CH<sub>4</sub> flux, we were able to explain some of the measurement variance ( $r^2 = 0.37$ ) when we created a regression model (quadratic curve fit) using log-transformed potential CH<sub>4</sub> consumption rate data from 1999 and 2000 (Figure 6). Our results suggest a positive relationship between CH<sub>4</sub> flux and potential CH<sub>4</sub> consumption at low flux rates but also suggest that this relationship becomes more negative when flux rates are high. Sundh et al. (1995), however, found that CH<sub>4</sub> consumption was negatively correlated with CH<sub>4</sub> flux in a *Sphagnum*-dominated peatland. This makes sense since greater CH<sub>4</sub> consumption would decrease the amount of CH<sub>4</sub> that could potentially be emitted to the atmosphere. In our system, high NPP of emergent aquatic plants increases the delivery of oxygen to the peat through roots, thus increasing CH<sub>4</sub> consumption rates while at the same time increasing plant-mediated CH<sub>4</sub> transport to the atmosphere. This mechanism would be particularly important in the *Typha* and *Juncus* sites, where diffusive flux through plants is most important (Yavitt and Knapp 1998), and might ultimately decrease fluxes as oxygen delivery increases CH<sub>4</sub> consumption. Thus, plant physiology might alter the relationship between fluxes and microbial processes.

In conclusion, these results imply that studies of CH<sub>4</sub> cycling in shallow peat-forming fens provide insight into how peatland ecosystems respond to variations in short and long-term climate. This study showed that seasonal and annual patterns of CH<sub>4</sub> cycling could be explained by a variety of factors, including temperature and precipitation. Our inability to make process-based predictions of CH<sub>4</sub> fluxes is likely explained by high variability between sites and questions pertaining to the usefulness of *in-vitro* potential CH<sub>4</sub> production measurements. Better methods for making *in-situ* measurements are clearly needed. Although aerobic CH<sub>4</sub> oxidation explained some of the variability in summertime CH<sub>4</sub> fluxes, the process may not be as important of a control on flux rates as low CH<sub>4</sub> production during drought. We also found that summertime CH<sub>4</sub> flux rates in this system were not as high as hypothesized given the “potential” of the system to produce CH<sub>4</sub>. This suggests that predicting responses of “wet” peatlands in sub-arctic regions to environmental changes will be complex and may require a better understanding of underlying processes and mechanisms.

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