

University of New Hampshire
University of New Hampshire Scholars' Repository

Earth Sciences Scholarship

Earth Sciences

1-2014

Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions

Genevieve L. Noyce
University of Toronto

Ruth Varner
University of New Hampshire - Main Campus, ruth.varner@unh.edu

Jill L. Bubier
Mount Holyoke College

Steve Frolking
University of New Hampshire - Main Campus, steve.frolking@unh.edu

Follow this and additional works at: https://scholars.unh.edu/earthsci_facpub

 Part of the [Biogeochemistry Commons](#)

Recommended Citation

Noyce, G. L., R. K. Varner, J. L. Bubier, and S. Frolking (2014), Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions, *J. Geophys. Res. Biogeosci.*, 119, 24–34, doi:10.1002/2013JG002474.

This Article is brought to you for free and open access by the Earth Sciences at University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Earth Sciences Scholarship by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact nicole.hentz@unh.edu.

Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions

Genevieve L. Noyce,^{1,2} Ruth K. Varner,¹ Jill L. Bubier,³ and Steve Frolking¹

Received 12 August 2013; revised 3 December 2013; accepted 7 December 2013; published 10 January 2014.

[1] Peatlands are a large natural source of atmospheric methane (CH₄), and the sedge *Carex rostrata* plays a critical role in the production, oxidation, and transport of CH₄ in these systems. This 4 year clipping experiment examined the changes in CH₄ emissions from a temperate peatland after removing all aboveground *C. rostrata* biomass. Methane fluxes, dissolved CH₄, and environmental variables were measured during spring, summer, and fall from 2008 to 2011. Clipping and removing the *C. rostrata* leaves and stems caused an immediate decrease in CH₄ emissions that persisted over 4 years of this study. There was a strong seasonal trend in CH₄ flux, with the largest treatment effects occurring during the fall months when the sedges were senescing. As expected, there was a strong positive correlation between *C. rostrata* green-leaf area and CH₄ flux, implying that the presence of *C. rostrata* increases CH₄ emissions from this peatland. Large interannual variability in vegetation distribution and biomass, water table depth, and temperature was observed in this study, indicating the importance of multiyear studies for understanding the interactions among these factors to determine how they could be incorporated into biogeochemical models to predict CH₄ emissions under changing environmental conditions.

Citation: Noyce, G. L., R. K. Varner, J. L. Bubier, and S. Frolking (2014), Effect of *Carex rostrata* on seasonal and interannual variability in peatland methane emissions, *J. Geophys. Res. Biogeosci.*, 119, 24–34, doi:10.1002/2013JG002474.

1. Introduction

[2] Peatlands contain one third of the global soil carbon (C) pool [Gorham, 1991] and release around 30 Tg of methane (CH₄) per year [Frolking et al., 2011]. The magnitude of CH₄ emission varies widely depending on a variety of controls, including vegetation, temperature, and precipitation patterns; and peatlands can shift from net sources to net sinks of C from year to year [e.g., Carroll and Crill, 1997; Bubier et al., 2003; Roulet et al., 2007]. The net amount of CH₄ released to the atmosphere depends on the difference between CH₄ production in the saturated zone of the peat and CH₄ oxidation in the unsaturated surface layer. High CH₄ emissions occur when a concentration gradient allows for diffusion from belowground and when there is a mechanism for CH₄ to be transported aboveground, either through plants or ebullition (bubbling).

[3] Many studies have reported a positive correlation between the presence of aerenchymous vegetation, including

sedges, and high CH₄ emissions when compared to sites dominated by shrubs [Shannon and White, 1994; Bubier et al., 1995; Bubier, 1995; Bellisario et al., 1999; Joabsson and Christensen, 2001; Ström and Christensen, 2007; Miao et al., 2012]. Similarly, CH₄ fluxes increased after aerenchymous plants emerged and decreased after they senesced [Wilson et al., 1989; Dise et al., 1993; Leppälä et al., 2011]; and in clipping experiments, CH₄ emissions were highest from sites with intact sedges [e.g., Whiting and Chanton, 1992; King et al., 1998; Verville et al., 1998; Strack et al., 2006].

[4] Sedges release high-quality carbon as root exudates, which promote CH₄ production through the acetate fermentation pathway, and sites dominated by sedges have more acetate fermentation than *Sphagnum*-dominated sites [Bellisario et al., 1999; Popp et al., 1999; Prater et al., 2007; Rooney-Varga et al., 2007]. High CH₄ emissions are correlated with periods of active plant growth and with autumnal litter fall, both of which are inputs of carbon [Wilson et al., 1989; Moore et al., 2011]. In addition, sedges provide a conduit to the atmosphere that bypasses the main zone of CH₄ oxidation, making plant-associated transport the foremost method of CH₄ release in sedge-dominated wetlands [Chanton, 2005].

[5] While many sedge clipping experiments have included CH₄ measurements, these studies have generally been conducted over a single growing season [e.g., Whiting and Chanton, 1992; Shannon et al., 1996; Waddington et al., 1996; Kelker and Chanton, 1997; Frenzel and Karofeld, 2000; Greenup et al., 2000; Strack et al., 2006] or as a single measurement [e.g., Schimel, 1995; Kutzbach et al., 2004]. When CH₄ fluxes have been measured during subsequent

¹Earth Systems Research Center, Institute for the Study of Earth, Oceans, and Space and Department of Earth Sciences, University of New Hampshire, Durham, New Hampshire, USA.

²Department of Geography, University of Toronto, Toronto, Ontario, Canada.

³Environmental Studies Department, Mount Holyoke College, South Hadley, Massachusetts, USA.

Corresponding author: G. Noyce, Department of Geography, University of Toronto, 100 St. George St. Toronto, ON M5S 3G3, Canada. (genevieve.noyce@mail.utoronto.ca)

years of clipping experiments, data have still only been collected during the growing season [e.g., King *et al.*, 1998; Verville *et al.*, 1998].

[6] This study investigated the links between *Carex rostrata*, a circumboreal wetland sedge species found in North America, Asia, and Europe, and CH₄ fluxes from a temperate fen in the northeast U.S. during a 4 year clipping experiment. Data were collected from the month before the clipping experiment was implemented through 41 months after, covering four *C. rostrata* growing seasons in addition to including data from spring and fall months. We examined the clipping effect over 4 years with varying temperatures and levels of precipitation and also analyzed seasonal trends. In addition, we estimated the role of *C. rostrata* in CH₄ transport. We hypothesized that CH₄ emissions would always be highest from the *C. rostrata*-dominated plots, especially during the growing season, but that this effect would be mitigated during periods of low water table depth when sedge roots are in the unsaturated zone. In addition, we hypothesized that vegetation-assisted transport would be the main release of CH₄ from the *C. rostrata*-dominated plots.

2. Methods

2.1. Site Description

[7] Sallie's Fen is a temperate, mineral-poor fen located in Barrington, New Hampshire (43°12.5'N, 71°3.5'W). This 1.7 ha peatland receives water from runoff, rainfall, and a small ephemeral stream that runs along the northern edge. The biologically active season runs from late April to October, with senescence of most deciduous plant species beginning in late August. The ground layer is dominated by *Sphagnum* moss species (e.g., *Sphagnum fallax* and *Sphagnum magellanicum*). Dominant vascular plants include ericaceous evergreen shrubs such as leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*), and cranberry (*Vaccinium oxycoccus* and *Vaccinium macrocarpon*), and deciduous shrubs such as speckled alder (*Alnus incana* ssp. *rugosa*) and highbush blueberry (*Vaccinium corymbosum*), as well as sedges (*Carex rostrata* and *Carex aquatilis*) and three-leaved Solomon's-plume (*Maianthemum trifolium*). Red maple (*Acer rubrum*) is the dominant tree and lines the edges of the fen.

2.2. Experimental Design

[8] In April 2008, we inserted six aluminum collars (60 × 60 × 25 cm frames) into the northeast part of the fen, where *C. rostrata* is the dominant vascular plant species. Each plot had nearly 100% *Sphagnum* moss cover and other vegetation included *C. calyculata*, *V. oxycoccus*, *M. trifolium*, and *A. rubrum*. The collars were distributed in pairs such that each pair had comparable temperature and water table conditions. June 2008 served as a calibration period to determine the similarity of the plots prior to clipping.

[9] On 2 July 2008, around the peak of the *C. rostrata* growing season, the aboveground *C. rostrata* was removed from one collar in each pair. *C. rostrata* plants were clipped to just below the *Sphagnum* surface. The remaining aerenchymous stems were covered with small plastic bags filled with petroleum jelly and sealed at their base to prevent CH₄ and oxygen transport through the aerenchyma. The

three remaining plots were left as undisturbed controls. Prior to CH₄ flux measurements, any *C. rostrata* stubble visible above the *Sphagnum* surface in the clipped plots was re-clipped and resealed as needed. By 2010, *C. rostrata* growth in these plots was minimal and re-clipping was rarely necessary.

2.3. Methane Flux Measurements

[10] Methane fluxes were measured once or twice per week from June through August and once or twice per month from September through November in 2008, 2009, 2010, and 2011. In 2010 and 2011, CH₄ fluxes were also measured weekly or twice-monthly from March through May, just after the emergence of green *C. rostrata* growth. Most fluxes in this study were measured in late morning: von Fischer *et al.* [2010] determined that CH₄ flux rates are generally stable over a 6 h time period and thus that an individual flux measurement can be representative of the daily rate of CH₄ emission through diffusive pathways. Fluxes were measured using a static chamber technique [e.g., Frolking and Crill, 1994]. A clear Teflon chamber measuring 60 × 60 × 90 cm (see Carroll and Crill [1997] for description) was placed in the grooved aluminum collars. The chambers contained fans to circulate the internal air and a climate control system to keep relative humidity and temperature close to ambient conditions. After placement, the chamber was left open for 5–10 min to minimize disturbance effects and allow the air inside the chamber to return to ambient conditions. To measure CH₄ flux, the chamber was closed and covered with a shroud designed to block out all light and to further minimize changes in temperature and relative humidity during the measurement period. Five 60 mL headspace samples were taken from inside the chamber every two minutes for a 10 min period using polypropylene syringes (BD, Franklin Lakes, New Jersey) equipped with three-way stopcocks. Ambient air outside the chambers was also sampled.

[11] The air samples were analyzed on a Shimadzu GC-14A gas chromatograph equipped with a flame ionization detector (GC-FID) within 6 h. The GC-FID operates with the following conditions: 130°C injector and detector temperatures, 50°C column temperature, and an Ultra High Purity nitrogen carrier gas flow rate of 30 mL min⁻¹ through a 2 m ¹/₆ inch o.d. stainless steel packed column (HayeSepQ 100/120). The GC-FID was calibrated using a standard of 1.8612 ppm CH₄ (2008–2010) or 3.266 ppm CH₄ (2010–2011). The standard error of 10 standard injections on any sampling day was less than 0.1%. Standards are breathing air cylinders calibrated against standards from NOAA's Earth System Research Laboratory's Global Monitoring Division's Carbon Cycle Greenhouse Gases Group. Each sample was run twice and the average concentration was used for the final calculations. Fluxes were calculated as the slope of the linear regression of CH₄ concentration versus time. Nonlinear regressions, most likely due to chamber leakage, disturbance, or episodic ebullition, were discarded from subsequent analyses (approximately 10% of data). Nonlinearity was determined as data falling outside the 95% confidence level for linear regressions. Other discarded data included any measurements where the initial CH₄ concentration in the chamber was substantially above ambient concentrations and any negative fluxes because these were presumed to be due to disturbance from placing the chamber.

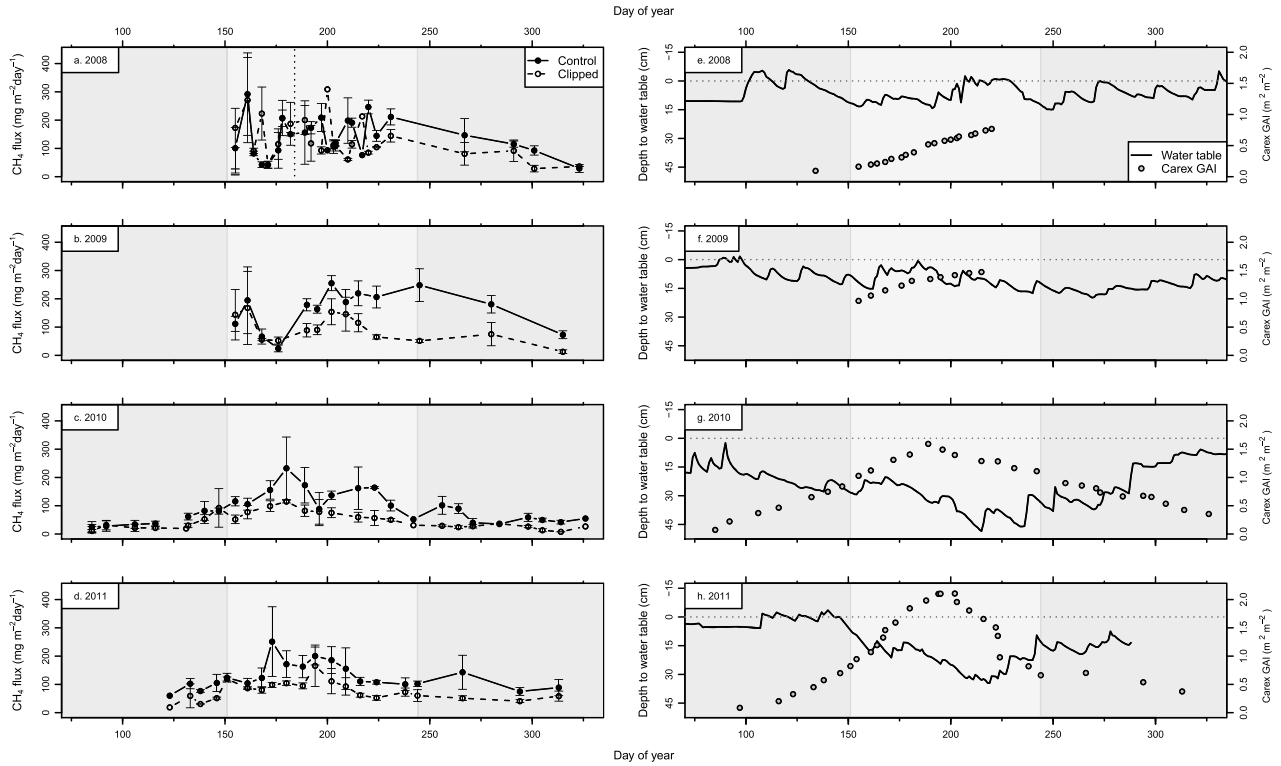


Figure 1. (a–d) Time series of mean CH₄ fluxes (black) for 2008 through 2011. Solid circles and lines indicate the control plots; open circles and dashed lines indicate the clipped plots. Error bars indicate standard error. The vertical dotted line in Figure 1a indicates the clipping date. (e–h) Time series of mean *C. rostrata* Green Area Index (GAI) in control plots (points) and mean daily water table depth across both treatments (lines) for 2008 through 2011. The horizontal dotted line indicates the peat surface. Shading denotes spring, summer, and fall seasons.

2.4. Peat Pore Water Methane Measurements

[12] Two stainless steel sippers (3 mm diameter) were perforated at the end and inserted inside each collar in June 2008, adjacent to a *C. rostrata* plant, to sample peat pore water at 18 and 60 cm below the peat surface. Eighteen centimeters was determined to be the dominant rooting zone for *C. rostrata*, while 60 cm is presumably below the bulk of the *C. rostrata* roots and always below the water table. During dry periods, we were unable to collect 18 cm pore water for analysis. After flux measurements, any water in the sippers was drawn up and discarded, after which a 30 mL sample was drawn and stored in a plastic syringe. Peat pore water was collected during every sampling season except fall 2008.

[13] To determine the dissolved CH₄ concentration in the pore water samples, each syringe was filled with 30 mL of ambient air and shaken vigorously for 2 min to allow the dissolved CH₄ to equilibrate with the air. Two 10 mL replicates of the headspace air were then immediately analyzed on a GC-FID that had been calibrated using 1000.6 ppm CH₄ (Scott Specialty Gases, Plumsteadville, Pennsylvania). The average of these replicates was used as the sample concentration. Occasionally, samples were stored at 4°C for 24 h instead of being analyzed on the same day as collection. In these cases, the samples were returned to room temperature before being analyzed.

2.5. *Carex rostrata* Measurements

[14] Every other week throughout summer 2008 and 2009 and spring through fall 2010 and 2011, *C. rostrata* Green Area Index (GAI) was measured in each plot using a technique similar to that described by *Wilson et al.* [2007]. Each *C. rostrata* leaf in the plots was measured and assigned to an approximate height class (0–20 cm, 21–40 cm, 41–60 cm, 61–80 cm, and 81+ cm). Widths of five *C. rostrata* leaves from each height class were measured. These widths were averaged together and multiplied by the midpoint of each height class and the number of leaves in that class to approximate *C. rostrata* GAI in each plot in m² *C. rostrata* per m² ground. *C. rostrata* GAI was linearly interpolated between measurement days. In addition, the maximum and minimum heights of *C. rostrata* green-leaf area were measured for 10 *C. rostrata* plants in three sections of the fen twice a month during the growing season for all years.

[15] Following the initial clipping in 2008, the clipped *C. rostrata* leaves were dried and weighed for a biomass estimate. These weights were plotted with corresponding GAI measurements to give an equation for calculating biomass from GAI: *C. rostrata* dry biomass (g m⁻²) = 107.03 × *C. rostrata* GAI (m² m⁻²) + 14.04 (*R*² = 0.98). This equation was then used to approximate *C. rostrata* biomass in the unclipped collars.

Table 1. Summer Means, Minimums, and Maximums (June, July, and August) for 2008 Through 2011

	2008	2009	2010	2011
<i>Control Water Table Depth (cm)</i>				
Minimum	0.1	5.2	3.4	2.4
Mean	13.5 ^a	16.7 ^b	27.2 ^c	18.6 ^d
Maximum	22.7	26.7	49.5	40.5
<i>Clipped Water Table Depth (cm)</i>				
Minimum	0.0	-0.7	-1.5	-3.5
Mean	13.3 ^a	10.8 ^b	22.3 ^c	12.7 ^a
Maximum	22.5	20.8	44.6	34.5
<i>Air Temperature (°C)</i>				
Minimum	13.3	12.0	12.7	14.5
Mean	19.3 ^{ab}	18.4 ^a	20.0 ^b	23.8 ^c
Maximum	25.2	24.0	27.4	35.5
<i>Peak C. rostrata Biomass (g m⁻²)</i>				
	7 Aug	3 Aug	8 Jul	7 Jul
	96	172	185	246
<i>Control CH₄ Flux (mg CH₄ m⁻² day⁻¹)</i>				
Minimum	44.2	12.4	29.4	70.5
Mean	184.3 ^a	156.7 ^a	133.2 ^b	152.7 ^a
Maximum	686.7	312.7	448.9	497.1
<i>Clipped CH₄ Flux (mg CH₄ m⁻² day⁻¹)</i>				
Minimum	55.0	32	25.8	36.8
Mean	131.9 ^a	105.2 ^a	73.5 ^b	92.8 ^a
Maximum	389.7	322.2	134	312.4
<i>Control 18 cm Pore Water CH₄ (ppm CH₄)</i>				
Minimum	255	959	766	728
Mean	4,087 ^a	4,034 ^a	2,838 ^b	3,832 ^a
Maximum	10,625	8,226	6,159	7,531
<i>Clipped 18 cm Pore Water CH₄ (ppm CH₄)</i>				
Minimum	480	1,750	1,239	2,043
Mean	6,141 ^a	4,508 ^b	3,787 ^c	3,962 ^b
Maximum	10,710	8,083	6,859	7,774
<i>Control 60 cm Pore Water CH₄ (ppm CH₄)</i>				
Minimum	2,794	2,903	1,101	1,513
Mean	6,714 ^a	6,115 ^a	6,748 ^a	5,514 ^a
Maximum	11,060	13,389	10,608	9,098
<i>Clipped 60 cm Pore Water CH₄ (ppm CH₄)</i>				
Minimum	21	2,073	1,015	1,091
Mean	6,324 ^{ab}	6,688 ^{ab}	7,235 ^a	5,416 ^b
Maximum	11,005	16,806	17,669	11,857

Letters indicate statistically significant ($P < 0.05$) differences between yearly means.

2.6. Environmental Variables

[16] Meteorological data were collected continuously at Sallie's Fen using an automated meteorological station located in the approximate center of the fen. Daily mean water table depth and air temperature from the met station were used in this analysis. When continuous temperature data were not available, we interpolated using a linear relationship with data from a secondary temperature probe ($R^2 = 0.91$).

[17] Perforated PVC wells were inserted next to each collar for water table measurements. Water table depth was measured manually relative to the peat surface on the same days as flux measurements. The average difference in water table depth at each collar relative to the continuous data was used to calculate collar water table depth between measurement days. Air and peat temperature, at the surface and at 10 cm below the peat surface, were manually measured at the same time as the CH₄ fluxes.

2.7. Data Analysis

[18] R Project for Statistical Computing (version 2.15.1) was used for all statistical analyses. For correlations and

regressions, a natural-log transformation was used on the CH₄ flux data to more closely approximate a normal distribution. Pearson's product moment correlation coefficients were calculated between ln CH₄ flux, 18 cm dissolved CH₄, 60 cm dissolved CH₄, *C. rostrata* GAI, water table depth, air temperature, and peat temperature. Correlations were calculated using all the data combined and then separating the data into control and clipped plots, but always including all 4 years. One-way analyses of variance (ANOVAs) were conducted between yearly means of water table depth and air temperature. Post-hoc analysis with Tukey's Honestly Significant Difference (HSD) test was used to identify years with significant differences.

[19] Data were divided into seasons based on *C. rostrata* growth; *C. rostrata* begins to produce green leaves and grow rapidly in spring (1 March to 31 May), reaches maximum biomass in summer (1 June to 31 August), and senesces during the fall (1 September to 30 November). This allowed for analysis during the growing seasons to compare with other experiments, as well as investigation of effects during other major phenological periods, including green-up and senescence.

[20] Instances where a data point was missing for one collar in a pair were removed from the data set prior to statistical analysis (resulting in the exclusion of 41 out of 481 CH₄ fluxes and 36 out of 782 pore water CH₄ concentrations). This kept means from being skewed toward collars with fewer missing data.

[21] To determine the effect of treatment on CH₄ fluxes, dissolved CH₄ concentration, water table depth, or peat temperature across the entire experiment, paired *t* tests were conducted between the clipped collars and their corresponding control collar. One-way ANOVAs were conducted between yearly means of CH₄ fluxes and dissolved CH₄ concentration and Tukey's HSD test was used to identify the significantly different means. To determine the interaction between treatment and season, a two-way repeated measures ANOVA was conducted using data from all 4 years, with season as a within-subject factor and treatment as a between-subject factor. Ratios of CH₄ fluxes were calculated between paired collars on a daily basis and averaged per collar for each measurement season. One-sample, one-sided *t* tests were used to determine which seasons had mean ratios that were significantly negative, implying a reduction of CH₄ flux from the clipped plots.

2.8. Methane Transport Estimates

[22] To estimate the role of *C. rostrata* in CH₄ emissions from Sallie's Fen, we assumed that all CH₄ emitted from the clipped plots occurred through diffusion. The rate of diffusive flux can be approximated using a known gradient of CH₄ and the following equation

$$F_{\text{diff}} = K_{\text{eff}} * \frac{\Delta\text{CH}_4}{z} \quad (1)$$

where F_{diff} is the diffusive flux of CH₄, ΔCH_4 is the change in CH₄ concentration along the gradient, z is the depth of the layer, and K_{eff} is an effective diffusion coefficient that incorporates the net rates of CH₄ oxidation and diffusion at this site [Lerman, 1979]. The gradient was estimated using the difference between the 18 cm pore

Table 2. Correlation Coefficients Among CH₄ Fluxes, *C. rostrata* Green Area, and Environmental Variables Across All 4 Years

	ln CH ₄ Flux	18 cm CH ₄	60 cm CH ₄	<i>Carex</i> GAI	Water Table Depth	Air Temperature	10 cm Temperature
ln CH ₄ flux	1	0.24 ^c	-0.15 ^c	<i>All Data</i> 0.43 ^c	-0.05	0.54 ^c	0.46 ^c
ln CH ₄ flux	1	0.38 ^c	-0.16 ^a	<i>Control Plots</i> 0.46 ^c	-0.16 ^a	0.60 ^c	0.46 ^c
<i>Carex</i> GAI	0.46 ^c	0.13	-0.22 ^c	1	0.04	0.46 ^c	0.31 ^c
ln CH ₄ flux	1	0.26 ^c	-0.13	<i>Clipped Plots</i> -	-0.12	0.67 ^c	0.54 ^c

^aindicates significance at $\alpha = 0.05$.

^bindicates significance at $\alpha = 0.01$.

^cindicates significance at $\alpha = 0.001$.

Units: ln CH₄ flux (mg CH₄ m⁻² day⁻¹), pore water CH₄ (ppm CH₄), *Carex* GAI (m² m⁻²), water table depth (cm), temperature (°C).

water CH₄ concentration and the ambient surface CH₄ concentration, which is a very coarse approximation. F_{diff} was assumed to equal the measured CH₄ flux from the clipped plots. K_{eff} was calculated using monthly means of CH₄ flux and dissolved CH₄ concentration and then averaged across the entire data set to get an effective diffusion coefficient of $8.0 \pm 1.1 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$. This

coefficient was assumed to be unaltered by treatment and the mean value was used to estimate monthly diffusive fluxes from the control plots, again using the simplified gradient from 18 cm to the peat surface. The mean monthly CH₄ flux from *C. rostrata* transport was then approximated as the difference between the mean monthly flux and the estimated diffusive flux.

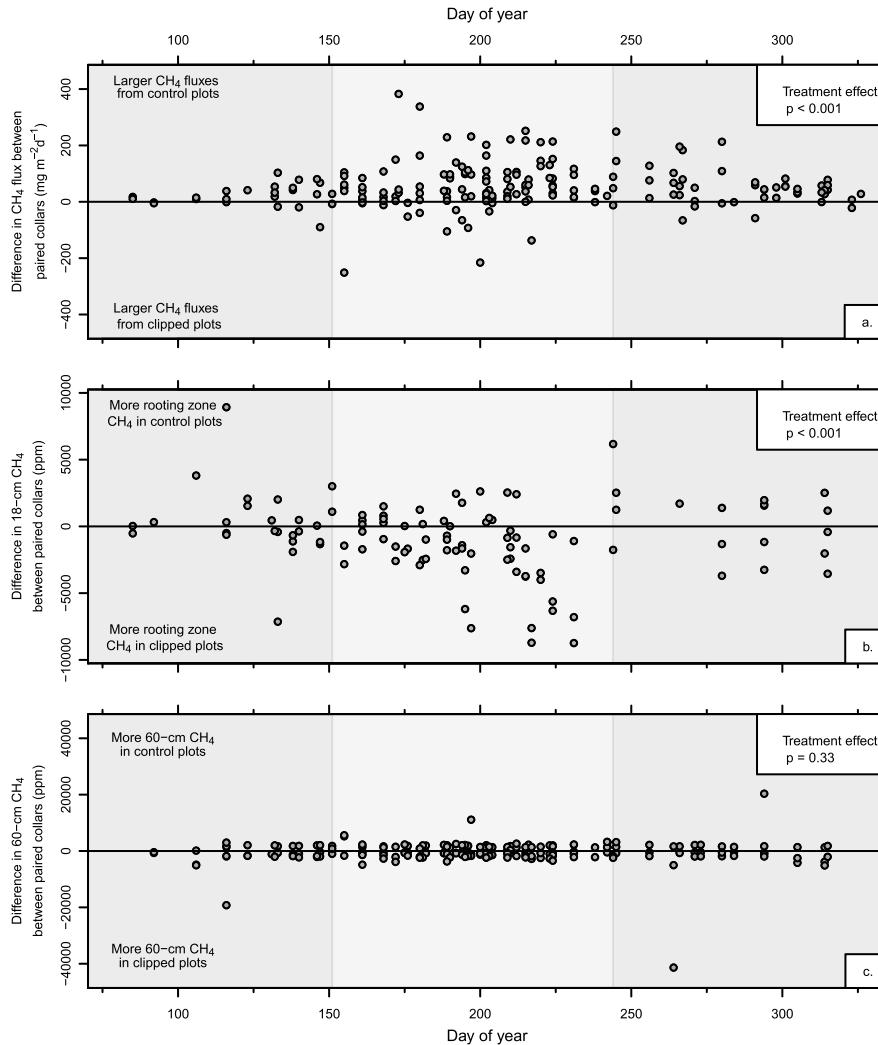


Figure 2. Time series of differences (control minus treatment) between paired collars throughout all 4 years in (a) CH₄ fluxes, (b) 18 cm dissolved CH₄, and (c) 60 cm dissolved CH₄. Shading denotes spring, summer, and fall seasons.

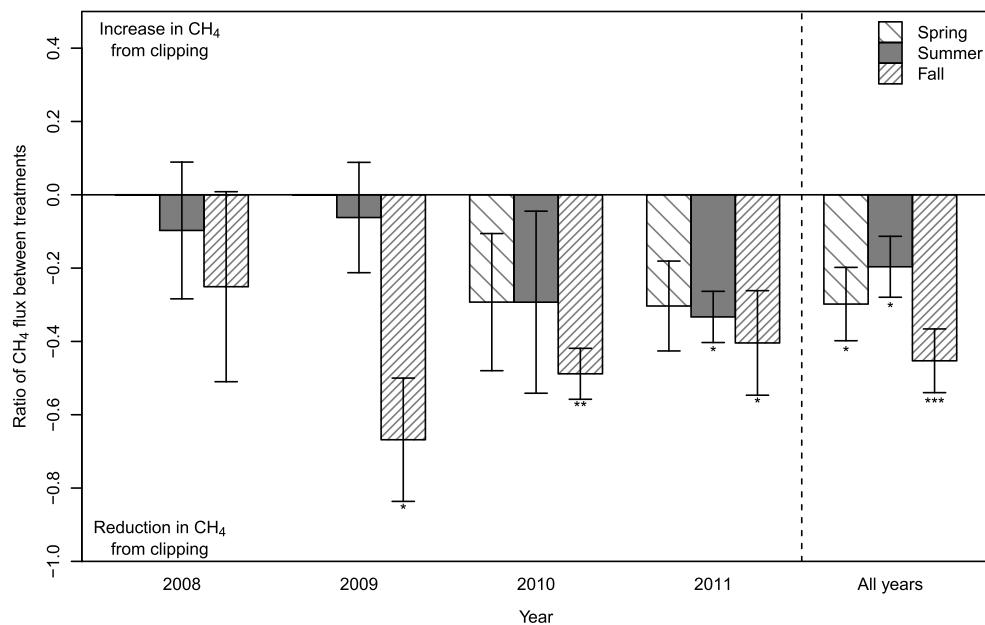


Figure 3. Effect of clipping on CH₄ flux for 2008 through 2011. The treatment ratio is the CH₄ flux from each control collar divided by the CH₄ flux from its paired clipped collar, minus one, so a value of zero is no treatment effect. Bars represent seasonal averages for each year and across all 4 years combined. Error bars represent standard error. Symbols indicate means that are significantly nonzero: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

3. Results

3.1. Hydrological and Temperature Conditions

[23] Depth to water table and the magnitude of seasonal fluctuations varied by year (Figures 1e–1h), resulting in significant ($P < 0.001$) interannual variability in mean summer water table depth (Table 1). The year 2010 was very dry, with the mean summer water table averaging almost 33 cm below the peat surface, which was 11 to 26 cm deeper than in the other years (Table 1). Air temperature varied across the 4 years but followed the same general seasonal trend. The most interannual variability occurred during spring and fall, but 2011 had a mean summer air temperature of 23.8°C, which was 3.8 to 5.4°C higher than the mean temperatures for the other 3 years (Table 1). Mean summer air temperatures were significantly ($P < 0.05$) different between most years (Table 1). Overall, 2008 was a wet summer with average temperatures, 2009 was cooler and slightly drier, 2010 was very dry with similar temperatures to 2008, and 2011 was the warmest year but between 2009 and 2010 in terms of moisture.

[24] Removing the sedges altered water table depth but had no significant effect on peat temperature. There was no significant difference in water table depth between the treatments in 2008, but for 2009 through 2011, the water table was significantly ($P < 0.05$) higher in the clipped plots compared to their paired control plot by an average of 4 cm (Table 1).

3.2. *Carex rostrata* Growth

[25] In each year, *C. rostrata* began to produce green leaves in March or April and continued to grow throughout the summer. In 2008 and 2009, even though *C. rostrata* started senescing in mid-July to late July (around day 200), overall green-leaf area increased because new shoots continued to emerge (Figures 1e–1f). In 2010 and 2011, however, *C. rostrata* biomass in the control plots peaked in the beginning of July and

tailed off through the summer and fall (Figures 1g–1h). The maximum height of *C. rostrata* was similar across all four summers (around 90 cm), but the maximum *C. rostrata* biomass in the control collars during the measurement period (as approximated by GAI) was much lower in summer 2008 and much higher in summer 2011 compared to the other years. Peak *C. rostrata* biomass during the growing season was estimated as 96 g m⁻² in 2008, 172 g m⁻² in 2009, 185 g m⁻² in 2010, and 246 g m⁻² in 2011 (Table 1). *C. rostrata* growth was significantly ($P < 0.001$) correlated with both air temperature and peat temperature but not with water table depth (Table 2).

3.3. Comparison of Plots Prior to Experiment Implementation

[26] Plots were set up as spatially correlated pairs to ensure similar environmental conditions within a pair and reduce variability in fluxes, thus highlighting the treatment effect. Prior to clipping, CH₄ fluxes ranged from 19.3 to 563.6 mg CH₄ m⁻² day⁻¹ in the clipped collars and from 9.7 to 580.0 mg CH₄ m⁻² day⁻¹ in the control collars (Figure 1a). On average, CH₄ fluxes from the treatment collars prior to clipping were almost 40 mg CH₄ m⁻² day⁻¹ higher than CH₄ fluxes from the control collars, but the means were not significantly different ($P = 0.974$). Despite the observed differences in CH₄ flux magnitude, there were no similar trends in mean dissolved CH₄ concentrations between the two sets of plots at either 18 or 60 cm below the peat surface during the preclipping period.

3.4. Treatment Effect on Methane Fluxes

[27] Over 4 years, CH₄ fluxes after clipping ranged from 6.6 to 497.1 mg CH₄ m⁻² day⁻¹ in the control collars, with a mean flux of 125.3 mg CH₄ m⁻² day⁻¹ and from 1.8 to 322.2 mg CH₄ m⁻² day⁻¹ in the clipped collars, with a mean flux of 74.4 mg CH₄ m⁻² day⁻¹ (Figures 1a–1d). Across the entire experiment, CH₄ fluxes from the control collars were significantly

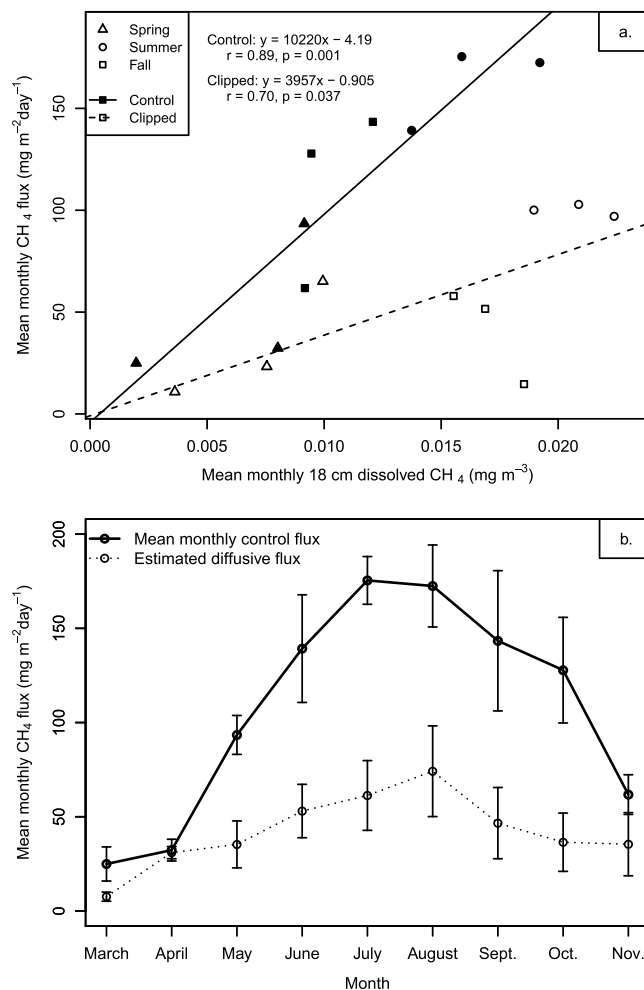


Figure 4. (a) Relationship between mean monthly CH₄ fluxes and mean monthly 18 cm dissolved CH₄ concentration for control and clipped plots. (b) Mean monthly CH₄ flux from control plots across all 4 years (solid line) and estimated monthly means of CH₄ emitted through diffusion in the control plots (dashed line). Error bars indicate standard error.

($P < 0.001$) higher than from their paired clipped collar (Figure 2a). The treatment difference in CH₄ flux magnitude varied throughout the experiment, with the largest average difference in CH₄ flux between paired collars during the *C. rostrata* growing season occurring in 2010 (67.9 mg CH₄ m⁻² day⁻¹) and the smallest difference occurring in 2008 (42.8 mg CH₄ m⁻² day⁻¹). Across all measurement seasons, the largest difference occurred in fall 2009 (111.3 mg CH₄ m⁻² day⁻¹) and the smallest occurred in spring 2010 (14.5 mg CH₄ m⁻² day⁻¹).

[28] After clipping in 2008, the mean CH₄ flux over the remainder of the summer increased by 30% in the control plots and decreased by 22% in the clipped plots, though these responses were not significantly different from each other. Throughout the rest of the experiment, summer CH₄ fluxes from the clipped plots were 10% less than fluxes from the control plots in 2008, 6% less in 2009, 30% less in 2010, and 33% less in 2011, though the average treatment effect was largest during the fall months (Figure 3). While summer clipped fluxes averaged between 67% and 94% of the magnitude of summer CH₄ fluxes from the control plots, fall clipped fluxes ranged from 33% of control fluxes in 2009 to 75% in 2008. For individual years and seasons, there was a significant ($P < 0.05$) reduction of CH₄ emissions from the clipped

collars compared to their paired control collars in summer 2011 and fall 2009, 2010, and 2011 (Figure 3). Though both treatment ($F_{1,420}$, $P < 0.001$) and season ($F_{2,420}$, $P < 0.001$) significantly affected CH₄ fluxes across the entire data set, there was no significant interaction between treatment and season.

[29] Overall, CH₄ flux was significantly ($P < 0.001$) positively correlated with *C. rostrata* green area, 18 cm pore water CH₄ concentrations, and air and peat temperature (Table 2). CH₄ flux from the control plots was also significantly ($P < 0.05$) correlated with water table depth, though there was no significant correlation between water table and fluxes from the clipped plots (Table 2). The control CH₄ fluxes were more strongly correlated with pore water CH₄ concentrations than the clipped CH₄ fluxes were (Table 2), while the clipped fluxes were more strongly correlated with air temperature than the control fluxes were (Table 2), though these treatment effects were not significant. Even when the dissolved CH₄ concentrations were similar between the treatments, the control plots still had higher CH₄ fluxes and both control and treatment plots had strong linear correlations between 18 cm dissolved CH₄ concentrations and flux (Figure 4a and Table 2). Between 40 and 70% of CH₄

emissions from the control plots may occur through plant transport (Figure 4b). The ratio of CH₄ flux from the clipped plots compared to their paired control plots was not significantly correlated with water table depth or air temperature.

3.5. Treatment Effect on Pore Water Methane

[30] Over 4 years, the concentration of dissolved CH₄ at 18 cm below the peat surface ranged from 199 to 10,625 ppm in the control collars with a mean concentration of 3192 ppm and from 107 to 10,710 ppm in the clipped collars with a mean concentration of 4099 ppm. After clipping in 2008, the mean dissolved CH₄ concentration at 18 cm below the peat surface increased by 105% from June (before clipping) to July and August (after clipping) in the clipped plots while the mean concentration in the control plots only increased by 35%, which was a significant treatment effect ($P < 0.05$). Across all 4 years, 18 cm dissolved CH₄ was significantly ($P < 0.001$) higher in the clipped plots compared to their paired controls (Figure 2b). Over 4 years, the concentration of dissolved CH₄ at 60 cm below the peat surface ranged from 35.8 to 38,245 ppm in the control collars with a mean concentration of 4872 ppm and from 21.0 to 51,921 ppm in the clipped collars with a mean concentration of 5268 ppm (Table 1). Clipping did not significantly affect 60 cm dissolved CH₄ concentrations (Figure 2c).

4. Discussion

4.1. Effect of *Carex rostrata* Clipping on Methane Emissions

[31] As expected, summer CH₄ fluxes were generally higher from the control plots than from the clipped plots in all 4 years (Figure 2a) and clipping significantly reduced CH₄ flux across all four summers (Figure 3). In particular, a large effect was observed in summer 2008, directly after the initial clipping. Even though plots in both treatments experienced similar temperatures and water table levels throughout the initial treatment year (2008), CH₄ fluxes increased by 30% in the control plots from June (preclipping) to July and August (postclipping) but decreased by 22% in the clipped plots. Despite day-to-day variability in CH₄, after clipping there was a significant trend of larger fluxes occurring from the controls compared to the clipped collars (Figures 1 and 2a). Treatment had a significant effect across the entire data set, which indicates that clipping and sealing *C. rostrata* reduces overall CH₄ emissions from this peatland. A large percent of the annual CH₄ flux occurs during the peak growing season; vegetation-related controls most likely dominate annual fluxes and thus are important to consider in biogeochemical models [von Fischer et al., 2010]. Riutta et al. [2007] also concluded that plant community is very important in predicting CH₄ flux, even across otherwise homogenous sites, and Moore et al. [2011] found that vegetation was the most important predictor of individual CH₄ fluxes throughout their 5 year study.

[32] Our results are consistent with those found in other sedge-removal experiments. For example, Kelker and Chanton [1997] and Waddington et al. [1996] both saw reductions in CH₄ flux when *Carex* species were removed from Canadian fens. Other studies observed a more pronounced response, with CH₄ emissions from clipped plots totaling only 3 to 40% of those from nearby control plots

[Whiting and Chanton, 1992; King et al., 1998; Verville et al., 1998; Frenzel and Karofeld, 2000; Strack et al., 2006]. Frenzel and Karofeld [2000], in particular, saw a 97% decrease in CH₄ flux after clipping *Scheuchzeria palustris* and *Eriophorum vaginatum*. This variability may be related to the amount of sedge biomass removed in these experiments or to the particular sedge species [Ström et al., 2005].

[33] Contrary to expectations, the effect of *C. rostrata* clipping, as shown by the ratio of CH₄ flux from the clipped plots compared to CH₄ flux from the control plots, did not vary with water table depth. Even though the water table was significantly higher in the clipped plots in 2009 through 2011, presumably because removing the sedges reduced evapotranspiration rates in the clipped plots, these later years still showed a stronger treatment effect on CH₄ emissions than the initial clipping year when the water table depths were the same in both treatments. Both control and clipped plots tended to have lower CH₄ emissions in drier years, but CH₄ fluxes were still higher from the control plots. This may be because *C. rostrata* has long rhizomes and roots that remain partially in the anoxic zone even when the water table is low [Hultgren, 1989a], as in summer 2010, so the plants could still enhance CH₄ emissions.

4.2. Seasonal Effects

[34] Clipping *C. rostrata* significantly decreased summer CH₄ emissions across the experiment, but there was also a particularly strong effect of *C. rostrata* on fall (September through November) CH₄ emissions (Figure 3). The fall CH₄ emissions were usually larger in the control plots than in their paired clipped plots across all 4 years (Figure 2a), even though *C. rostrata* plants generally started to senesce during that time period (Figures 1e–1h). The ratios of CH₄ flux illustrate the strong treatment effect in fall, both in individual years and throughout the entire experiment (Figure 3). This implies that the effects of *C. rostrata* are not limited to only its active growing period, especially when the water table is high, as in fall 2009. Neither of the 2 years of spring data showed treatment effects (Figure 3); spring CH₄ fluxes from the control and clipped plots were very similar (Figures 1c, 1d, and 2a). Consequently, even though both seasons had similar amounts of *C. rostrata* green area, *C. rostrata* was more important in enhancing CH₄ emissions in fall. Moore et al. [2011] observed a similar trend of strong vegetation effects on fall CH₄ fluxes from a long-term study in a Canadian bog. While the presence of the sedge *Eriophorum vaginatum* was significantly correlated with CH₄ emissions in the summer months, it became the most important predictor of CH₄ emissions in September and October, presumably because the higher water table in fall means the dominant rooting zone is more likely to be saturated, enhancing root effects on CH₄ production and transport.

[35] In our study, there was no significant interaction between treatment and season for CH₄ fluxes, implying that seasonal trends in CH₄ flux are not dependent on the presence of *C. rostrata*. This is in contrast to Miao et al., [2012], who found that CH₄ fluxes from a boreal peatland only showed seasonal trends in sedge-dominated sites. Methane diffusion (whether through the peat or through sedge aerenchyma) is driven by a concentration gradient, so fluxes are dependent on the buildup of CH₄ in the peat through the temperature-dependent process of methanogenesis and thus fluxes exhibit

seasonal patterns that follow the belowground CH₄ concentration regardless of the presence of *C. rostrata* (Table 2).

4.3. Long-Term Effects and Interannual Variability

[36] Summer *C. rostrata* biomass was much lower in 2008 than in later years of the experiment (Table 1 and Figures 1e–1h). This is most likely related to *C. rostrata* shoot density; in 2008, the maximum *C. rostrata* density during the growing season was 336 green shoots per m², compared to nearly double that the following year. Biomass may have slightly increased after measurements of *C. rostrata* growth ended in early August in 2008 and 2009, but given the lower number of shoots in 2008 and the fact that *Carex* reached the same maximum height in all years, 2008 almost certainly had the lowest *C. rostrata* biomass of all 4 years. When the CH₄ flux collars were inserted in April 2008, a 10 to 20 cm slit was cut into the peat, including through coarse and fine roots. Previous studies have indicated a loss of vascular-plant density as a result of collar insertion [Heijmans *et al.*, 2004] and because one of the sources of new *C. rostrata* roots is horizontally growing rhizomes [Hultgren, 1989a], cutting through these structures may have had a large effect on the emergence of new shoots during the immediately following growing season. The largest peak in new *C. rostrata* shoots also generally occurs in the beginning of the growing season [Gorham and Somers, 1973; Hultgren, 1989a; Saarinen, 1998] which was shortly after the collars were installed in 2008 and thus presumably when the disturbance effect was largest.

[37] Interannual variability in peat temperature and saturation can also affect the growth rate and maximum biomass of emergent *C. rostrata* [Gorham and Somers, 1973; Hultgren, 1989b]. In 2008, the peat temperature remained below freezing until mid-April, which may have contributed to the lower overall *C. rostrata* biomass. Later spring flooding may have limited early shoot growth as well. The timing of *C. rostrata* senescence also varied between years, with browning occurring earlier in 2010 and 2011. This may be a result of the low water table level throughout most of 2010 (and in 2011, to a lesser extent) (Figures 1e–1h), which can have a significant effect on *C. rostrata* height and leaf and root biomass [Kennedy *et al.*, 2003]. Field observations also indicate that large interannual variations in water table can affect shoot length and density, with the shortest shoots observed in low water years and the tallest observed in high water years [Hultgren, 1989b].

[38] There was a stronger treatment effect on summer CH₄ emissions in the later years of the experiment compared to 2008 and 2009 (Figure 3). This may indicate that the system is approaching a steady state as residual effects of the experiment implementation are no longer affecting the clipped collars, which has been seen in other studies [e.g., Verville *et al.*, 1998; Riutta, 2008]. In this experiment, the treatment difference may also have been limited in the first year after clipping due to an increase in available substrate from decomposing *C. rostrata* belowground. Sedge rhizomes start to decompose after only 4 days under anoxic conditions [Barclay and Crawford, 1982] and 10 to 45% of the total mass of *C. rostrata* roots and rhizomes decompose during the first 12 months after separation from the aboveground shoots [Scheffer and Aerts, 2000]. Increased substrate availability is consistent with the high concentrations of dissolved CH₄ around the *C. rostrata* rooting area in the clipped plots,

especially because this trend was less apparent in the subsequent years of the experiment.

4.4. *Carex rostrata* as a Methane Transport Mechanism

[39] In July and August 2008, the clipping treatment significantly ($P < 0.05$) affected the concentration of rhizospheric dissolved CH₄; CH₄ concentrations more than doubled in the clipped plots, while control-plot concentrations increased by only 35%. An increase in dissolved CH₄ was expected because the late summer conditions are more favorable for methanogenesis [Treat *et al.*, 2007], but the magnitude of the difference implies that clipping and sealing the *C. rostrata* plants had a substantial effect on the buildup of dissolved CH₄. Most likely, this indicates a disruption in the clipped plots; if CH₄ transport mechanisms were equal between the two treatments, then the higher dissolved-CH₄ concentrations in the clipped plots (Figure 2b) ought to have resulted in larger CH₄ emissions. Instead, daily CH₄ fluxes from the control plots were consistently higher across all 4 years (Figures 1a–1d, and 2a), implying that more CH₄ is transported in the presence of *C. rostrata*. This is consistent with results from other clipping experiments [e.g., Waddington *et al.*, 1996] that also observed lower concentrations of dissolved CH₄ at sites with high CH₄ emissions and concluded that it was the result of the transport effect of aerenchymous vegetation. The higher dependence of CH₄ flux on pore water CH₄ in the control plots compared to the clipped plots (Figure 4a) also indicates that plant transport in these plots is likely to be supplementing diffusion. Similarly, fluxes were typically higher from the control plots than from the clipped plots, even when the dissolved CH₄ concentrations were similar (Figure 4a), again suggesting a substantial effect of plant transport. Given these data, we wanted to approximate the role of plant transport in enhancing CH₄ emissions from Sallie's Fen.

[40] Methane emissions are the net result of production, oxidation, ebullition, diffusion through the peat, and plant transport. Some CH₄ may be removed from the plots via horizontal flow [Waddington and Roulet, 1997; Billett and Moore, 2007], but that should also be consistent within a pair and is probably very low at this site, except during large precipitation events. Enhanced CH₄ production in the control plots relative to the clipped plots is quite likely, given the labile root exudates from the sedges, but does not explain why there is more 18 cm CH₄ in the clipped plots despite presumed lower production rates. The aerenchymous nature of sedges means that higher rates of CH₄ oxidation could be occurring in the control plots, but given the observed strong correlation between sedge cover and CH₄ flux (Table 2), this is most likely only a minor component of the sedge effects of CH₄ dynamics. At Sallie's Fen, ebullition is responsible for less than 12% of the annual CH₄ emissions [Santoni *et al.*, 2012], ebullition rates do not correlate with sedge fractional cover [Goodrich, 2010], and very few ebullition events occur during daytime [Goodrich *et al.*, 2011], meaning that ebullition is unlikely to be a major component of the measured CH₄ emissions in this study. This leaves diffusion through the peat (in both sets of plots) and plant transport (in only the control plots) as the likely controls on the observed treatment differences in CH₄ flux.

[41] By approximating the monthly diffusive fluxes from the control collars, we estimated that 40 to 70% of the CH₄ emitted from Sallie's Fen may occur through plant transport.

This range is comparable to that of *Kutzbach et al.* [2004] who estimated plant-mediated CH₄ flux to account for 66 ± 20% of total CH₄ emissions. *King et al.* [1998] also found that adding straw-like tubing to clipped plots increased CH₄ emissions substantially, to about half the magnitude of the CH₄ fluxes from the unclipped plots, which argues for the importance of vegetation-mediated transport in controlling CH₄ emissions from sedge-dominated systems. The estimated transport role of *C. rostrata* is largest in the summer months, but still substantial in September and October (Figure 4b). This may again indicate the importance of the presence of *C. rostrata* in controlling CH₄ emissions even during fall months when the plants are no longer actively growing. *Moore et al.* [2011] suggest this may be because the transport of CH₄ through sedges can continue in cooler months when peat and air temperature have less effect on CH₄ emissions. In addition, *Carex* species emit CH₄ from the plant base where leaves bundle together and thus vegetation height (i.e., the green area measurement in this study) may not be a factor in the ability of *C. rostrata* to transport CH₄ [*Kelker and Chanton, 1997*].

[42] However, these are rough estimations and incorporate many simplifying assumption, especially by relying on the coarse resolution of the effective diffusion gradient, which may be the reason our estimated effective diffusion coefficient is several orders of magnitude larger than coefficients for CH₄ diffusion in saturated peat typically reported in the literature [e.g., *Lerman, 1979; Rothfuss and Conrad, 1994; Arah and Stephen, 1998; Clymo and Bryant, 2008*]. However, Sallie's Fen is mainly unsaturated above 18 cm and our estimated coefficient is closer to reported CH₄ diffusion rates in air (e.g., 1.9–2.3 × 10⁵ m² s⁻¹) [*Arah and Stephen, 1998; Matsunaga et al., 1998*]. Diffusion through the unsaturated peat is also likely to be substantially affected by turbulent mixing, which may also explain our high estimated effective diffusion coefficient. In addition, because the clipped collars had a significantly higher water table depth, the diffusion rates may not actually be the same for both treatments. Nonetheless, the strong linear correlations between 18 cm CH₄ concentration and CH₄ flux across an order of magnitude in each variable (Figure 4a) indicate that an effective diffusion model is plausible. These approximations imply that it is likely that a substantial portion of the annual CH₄ emissions from Sallie's Fen occur through plant transport and that this theory should be further investigated, using a more detailed CH₄ profile within the peat column to accurately characterize the actual diffusion rates within each treatment.

5. Conclusions

[43] Over a 4 year clipping experiment, we observed a strong reduction in CH₄ flux from the clipped plots. Removing the aboveground *C. rostrata* biomass caused an immediate decrease in CH₄ emissions that persisted for the rest of the growing season and continued over the next 3 years of the study. There was a strong seasonal trend in CH₄ flux, with the largest treatment effects on CH₄ flux occurring in summer and fall, suggesting that a longer summer or warmer fall could lead to larger total CH₄ emissions. Overall, we observed a strong positive relationship between *C. rostrata* green area and CH₄ flux indicating that the presence of *C. rostrata* increases CH₄ emissions at Sallie's Fen. We propose that plant transport is

the driving mechanism behind this trend and may account for 40 to 70% of the total CH₄ flux at this site, but this theory needs further research to be conclusive. We also found a strong correlation between air temperature and CH₄ flux, regardless of the presence of *C. rostrata*.

[44] Peatlands are an important source of atmospheric CH₄ and changes in these ecosystems will result in positive or negative feedback to future climate. To have accurate predictions, controls on CH₄ emissions from peatlands need to be thoroughly understood and implemented in biogeochemical models. Models consistently predict warming for temperate and boreal peatlands [*Frolking et al., 2011*], which would potentially increase CH₄ emissions if saturation conditions do not change. Changes in seasonality, in particular, are likely to affect CH₄ emissions from sedge-dominated sites. Large interannual variability in vegetation distribution and biomass, water table depth, and temperature was observed in our study. Overall, these data indicate the importance of conducting experiments over a multiyear period in order to observe the likely long-term effects on the ecosystem, as opposed to just the initial disturbance effects, as well as the importance of measurements that span a range of environmental conditions.

[45] **Acknowledgments.** This research was supported by a UNH-NASA Research and Discover Fellowship and a Mount Holyoke College HHMI Summer Research Fellowship (HHMI #52005134) to G. Noyce, NSF grants DEB 0346625 to J. Bubier and DEB 0316326 to P. Crill and R. Varner, and USDA grant 2011-67003-30373 to S. Frolking. We thank Patrick Crill (Stockholm University) for establishing the long-term research at Sallie's Fen, Eduardo Miranda, Tom O'Dowd, Libby Szarkowski, and Bianca Young for field and lab assistance, and Jack Dibb, Nicola Blake, and Sallie Whitlow for allowing access to Sallie's Fen, as well as Nigel Roulet, Dennis Baldocchi, and an anonymous reviewer for their comments that improved the manuscript.

References

- Arah, J. R. M., and K. D. Stephen (1998), A model of the processes leading to methane emission from peatland, *Atmos. Environ.*, **32**(19), 3257–3264.
- Barclay, A. M., and R. M. M. Crawford (1982), Plant growth and survival under strict anaerobiosis, *J. Exp. Bot.*, **33**(3), 541–549.
- Bellisario, L. M., J. L. Bubier, T. R. Moore, and J. P. Chanton (1999), Controls on CH₄ emissions from a northern peatland, *Global Biogeochem. Cycles*, **13**, 81–91.
- Billett, M. F., and T. R. Moore (2007), Supersaturation and evasion of CO₂ and CH₄ in surface waters at Mer Bleue peatland, Canada, *Hydrol. Process.*, **22**(12), 2044–2054, doi:10.1002/hyp.6805.
- Bubier, J. L. (1995), The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands, *J. Ecol.*, **83**, 403–420.
- Bubier, J. L., T. R. Moore, L. Bellisario, N. T. Comer, and P. M. Crill (1995), Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, **9**, 455–470.
- Bubier, J., P. Crill, A. Mosedale, S. Frolking, and E. Linder (2003), Peatland responses to varying interannual moisture conditions as measured by automatic CO₂ chambers, *Global Biogeochem. Cycles*, **17**, GB001946, doi:10.1029/2002GB001946.
- Carroll, P., and P. Crill (1997), Carbon balance of a temperate poor fen, *Global Biogeochem. Cycles*, **11**, 349–356.
- Chanton, J. P. (2005), The effect of gas transport on the isotope signature of methane in wetlands, *Org. Geochem.*, **36**(5), 753–768.
- Clymo, R. S., and C. L. Bryant (2008), Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised peat bog, *Geochim. Cosmochim. Acta*, **72**, 2048–2066, doi:10.1016/j.gca.2008.01.032.
- Dise, N. B., E. Gorham, and E. S. Verry (1993), Environmental-factors controlling methane emissions from peatlands in Northern Minnesota, *J. Geophys. Res.*, **98**, 10,583–10,594.
- Frenzel, P., and E. Karofeld (2000), CH₄ emission from a hollow-ridge complex in a raised bog: The role of CH₄ production and oxidation, *Biogeochemistry*, **51**, 91–112.

- Frolking, S., and P. Crill (1994), Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: Measurement and modeling, *Global Biogeochem. Cycles*, *8*, 385–397.
- Frolking, S., J. Talbot, M. C. Jones, C. C. Treat, J. B. Kauffman, E.-S. Tuittila, and N. Roulet (2011), Peatlands in the Earth's 21st century climate system, *Environ. Rev.*, *19*, 371–396.
- Goodrich J. (2010), Identifying temporal patterns and controlling factors in methane ebullition at Sallie's Fen, a temperate peatland site, using automated chambers, MS thesis, Dept. of Earth Sci., Univ. of New Hampshire, Durham, New Hampshire, USA.
- Goodrich, J. P., R. K. Varner, S. Frolking, B. N. Duncan, and P. M. Crill (2011), High-frequency measurements of methane ebullition over a growing season at a temperate peatland site, *Geophys. Res. Lett.*, *38*, L07404, doi:10.1029/2011GL046915.
- Gorham, E. (1991), Northern peatlands: role in the carbon cycle and probable responses to climate warming, *Ecol. Appl.*, *1*, 182–195.
- Gorham, E., and M. G. Somers (1973), Seasonal changes in the standing crop of two montane sedges, *Can. J. Bot.*, *51*, 1097–1108.
- Greenup, A. L., M. A. Bradford, N. P. McNamara, P. Ineson, and J. A. Lee (2000), The role of *Eriophorum vaginatum* in CH₄ flux from an ombrotrophic peatland, *Plant Soil*, *227*, 265–272.
- Heijmans, M. M. P. D., W. J. Arp, and F. S. Chapin III (2004), Carbon dioxide and water vapor exchange from understory species in boreal forest, *Agr. For. Meteorol.*, *123*, 135–147, doi:10.1016/j.agrformet.2003.12.006.
- Hultgren, A. B. C. (1989a), Above-ground biomass variation in *Carex rostrata* stokes in two contrasting habitats in central Sweden, *Aquat. Biol.*, *34*, 341–352.
- Hultgren, A. B. C. (1989b), Growth in length of *Carex rostrata* shoots in relation to water level, *Aquat. Biol.*, *34*, 353–365.
- Joabsson, A., and T. R. Christensen (2001), Methane emissions from wetlands and their relationship with vascular plants: An Arctic example, *Global Biogeochem. Cycles*, *7*, 919–932.
- Kelker, D., and J. Chanton (1997), The effect of clipping on methane emissions from *Carex*, *Biogeochemistry*, *39*, 37–44.
- Kennedy, M. P., J. M. Milne, and K. J. Murphy (2003), Experimental growth responses to groundwater level variation and competition in five British wetland plant species, *Wetlands Ecol. Manage.*, *11*, 383–396.
- King, J. Y., W. S. Reeburgh, and S. K. Regli (1998), Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment, *J. Geophys. Res.*, *103*, 29,083–29,092.
- Kutzbach, L., D. Wagner, and E.-M. Pfeiffer (2004), Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia, *Biogeochemistry*, *69*, 341–362.
- Leppälä, M., J. Oksanen, and E.-S. Tuittila (2011), Methane flux dynamics during mire succession, *Oecologia*, *165*, 489–499, doi:10.1007/s00442-010-1754-6.
- Lerman, A. (1979), *Geochemical Processes: Water and Sediment Environments*, John Wiley, Inc., New York.
- Matsunaga, N., M. Hori, and A. Nagashima (1998), Diffusion coefficients of global warming gases into air and its component gases, *High Temp. High Pressures*, *30*, 77–83.
- Miao, Y., C. Song, L. Sun, X. Wang, H. Meng, and R. Mao (2012), Growing season methane emission from a boreal peatland in the continuous permafrost zone of Northeast China: Effects of active layer depth and vegetation, *Biogeochemistry*, *9*, 4455–4464.
- Moore, T. R., A. De Young, J. L. Bubier, E. R. Humphreys, P. M. Lafleur, and N. T. Roulet (2011), A multi-year record of methane flux at the Mer Bleue Bog, southern Canada, *Ecosystems*, *14*, 646–657, doi:10.1007/s10021-011-9435-9.
- Popp, T. J., J. P. Chanton, G. J. Whiting, and N. Grant (1999), Methane stable isotopic distribution at a *Carex* dominated fen in north central Alberta, *Global Biogeochem. Cycles*, *13*, 1063–1077.
- Prater, J. L., J. P. Chanton, and G. J. Whiting (2007), Variation in methane production pathways associated with permafrost decomposition in collapse scar bogs of Alberta, Canada, *Global Biogeochem. Cycles*, *21*, GB4004, doi:10.1029/2006GB002866.
- Riutta, T. (2008), Fen ecosystem carbon gas dynamics in changing hydrological conditions, Dissertation Forestales, *67*.
- Riutta, T., J. Laine, M. Aurela, J. Rinner, T. Vesale, T. Laurila, S. Haapanala, M. Pihlatie, and E.-S. Tuittila (2007), Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem, *Tellus*, *59B*, 838–852, doi:10.1111/j.1600-0889.2007.00302.x.
- Rooney-Varga, J. N., M. W. Giewat, K. N. Duddleston, J. P. Chanton, and M. E. Hines (2007), Links between archaeal community structure, vegetation type, and methanogenic pathway in Alaskan peatlands, *FEMS Microbiol. Ecol.*, *60*, 240–251.
- Rothfuss, F., and R. Conrad (1994), Development of a gas diffusion probe from the determination of methane concentrations and diffusion characteristics in flooded paddy soil, *FEMS Microbiol. Ecol.*, *14*, 307–318.
- Roulet, N. T., P. M. Lafleur, P. J. H. Richards, T. R. Moore, E. R. Humphreys, and J. Bubier (2007), Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, *Global. Change Biol.*, *13*(2), 397–411, doi:10.1111/j.1365-2486.2006.01292.x.
- Santoni, G. W., B. H. Lee, J. P. Goodrich, R. K. Varner, P. M. Crill, J. B. McManus, D. D. Nelson, M. S. Zahniser, and S. C. Wofsy (2012), Mass fluxes and isofluxes of methane (CH₄) at a New Hampshire fen measured by a continuous wave quantum cascade laser spectrometer, *J. Geophys. Res.*, *117*, D10301, doi:10.1029/2011JD016960.
- Saariinen, T. (1998), Demography of *Carex rostrata* in a boreal mesotrophic fen: Shoot dynamics and biomass development, *Ann. Bot. Fennici*, *36*, 203–209.
- Scheffer, R. A., and R. Aerts (2000), Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems, *Oikos*, *91*, 541–549.
- Schimel, J. P. (1995), Plant transport and methane production as controls on methane flux from arctic wet meadow tundra, *Biogeochemistry*, *28*, 183–200.
- Shannon, R. D., and J. R. White (1994), A three-year study of controls on methane emissions from two Michigan peatlands, *Biogeochemistry*, *27*, 35–60.
- Shannon, R. D., J. R. White, J. E. Lawson, and B. S. Gilmour (1996), Methane efflux from emergent vegetation in peatlands, *J. Ecol.*, *84*, 239–246.
- Strack, M., M. F. Waller, and J. M. Waddington (2006), Sedge succession and peatland methane dynamics: A potential feedback to climate change, *Ecosystems*, *9*, 278–287, doi:10.1029/2003GB002209.
- Ström, L., and T. R. Christensen (2007), Below ground carbon turnover and greenhouse gas exchanges in a sub-arctic wetland, *Soil Biol. Biochem.*, *39*, 1689–1698.
- Ström, L., M. Mastepanov, and T. R. Christensen (2005), Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands, *Biogeochemistry*, *75*, 65–82.
- Treat, C. C., J. L. Bubier, R. K. Varner, and P. M. Crill (2007), Timescale dependence of environmental and plant-mediated controls and CH₄ flux in a temperate fen, *Geophys. Res. Lett.*, *112*, G01014, doi:10.1029/2006JG000210.
- Verville, J. H., S. E. Hobbie, F. S. Chapin III, and D. U. Hooper (1998), Response of tundra CH₄ and CO₂ flux to manipulation of temperature and vegetation, *Biogeochemistry*, *41*, 215–235.
- von Fischer, J. C., R. C. Rhew, G. M. Ames, B. K. Fosdick, and P. E. von Fischer (2010), Vegetation height and other controls of spatial variability in methane emissions from the Arctic coastal tundra at Barrow, Alaska, *J. Geophys. Res.*, *115*, G00I03, doi:10.1029/2009/JG001283.
- Waddington, J. M., and N. T. Roulet (1997), Groundwater flow and dissolved carbon movement in a boreal peatland, *J. Hydrol.*, *191*, 122–138, doi:10.1016/S0022-1694(96)03075-2.
- Waddington, J. M., N. T. Roulet, and R. V. Swanson (1996), Water table control of CH₄ emission enhancement by vascular plants in boreal peatlands, *J. Geophys. Res.*, *101*(D17), 22,777–22,785.
- Whiting, G. J., and J. P. Chanton (1992), Plant-dependent CH₄ emission in a subarctic Canadian fen, *Global Biogeochem. Cycles*, *6*, 225–31.
- Wilson, D., J. Alm, T. Riutta, J. Laine, K. A. Byrne, E. P. Farrell, and E.-S. Tuittila (2007), A high resolution green area index for modeling the seasonal dynamics of CO₂ exchange in peatland vascular plant communities, *Plan. Ecol.*, *190*, 37–51.
- Wilson, J. O., P. M. Crill, K. B. Bartlett, D. I. Sebacher, R. C. Harriss, and R. L. Sass (1989), Seasonal variation of methane emissions from a temperate swamp, *Biogeochemistry*, *8*, 55–71.