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Timescale dependence of environmental and plant-mediated controls on CH₄ flux in a temperate fen

Claire C. Treat,^{1,2} Jill L. Bubier,¹ Ruth K. Varner,³ and Patrick M. Crill⁴

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[1] This study examined daily, seasonal, and interannual variations in CH₄ emissions at a temperate peatland over a 5-year period. We measured net ecosystem CO₂ exchange (NEE), CH₄ flux, water table depth, peat temperature, and meteorological parameters weekly from the summers (1 May to 31 August) of 2000 through 2004 at Sallie's Fen in southeastern New Hampshire, United States. Significant interannual differences, driven by high variability of large individual CH₄ fluxes (ranging from 8.7 to 3833.1 mg CH₄ m⁻² d⁻¹) occurring in the late summer, corresponded with a decline in water table level and an increase in air and peat temperature. Monthly timescale yielded the strongest correlations between CH₄ fluxes and peat and air temperature ($r^2 = 0.78$ and 0.74 , respectively) and water table depth (WTD) ($r^2 = 0.53$). Compared to daily and seasonal timescales, the monthly timescale was the best timescale to predict CH₄ fluxes using a stepwise multiple regression ($r^2 = 0.81$). Species composition affected relationships between CH₄ fluxes and measures of plant productivity, with sedge collars showing the strongest relationships between CH₄ flux, water table, and temperature. Air temperature was the only variable that was strongly correlated with CH₄ flux at all timescales, while WTD had either a positive or negative correlation depending on timescale and vegetation type. The timescale dependence of controls on CH₄ fluxes has important implications for modeling.

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1. Introduction

[2] Methane (CH₄) is a greenhouse gas with 62 times the global warming potential (GWP) of carbon dioxide at 20 year timescales [Houghton *et al.*, 2001]. Wetlands comprise the largest and most variable source of CH₄ released to the atmosphere. Wetlands store approximately one-third of global soil carbon as peat [Alm *et al.*, 1997; Gorham, 1991], which has the potential to be released to the atmosphere with higher temperatures and changing water table levels [Carroll and Crill, 1997; Houghton *et al.*, 2001; Roulet *et al.*, 1992].

[3] Many studies have found that differences in peat temperature and water table position affect CH₄ emissions both within a site and over a range of wetland types [e.g., Bubier *et al.*, 1995; Moore and Dalva, 1993; Updegraff, 2001], while others have found that substrate availability

and temperature are the strongest determinants of this variation [Christensen *et al.*, 2003a]. Seasonal average water table has been proposed as a predictor of CH₄ emissions across a wide range of sites [Bubier, 1995; Dise *et al.*, 1993; Moore and Roulet, 1993; Waddington *et al.*, 1996].

[4] Higher CH₄ emissions have been observed coincident with water table levels at or near the peat surface [Aerts and Ludwig, 1997; Bubier, 1995; Dise *et al.*, 1993; Moore and Dalva, 1997]. Others have reported opposite or insignificant trends during periods of low water table position or when the average water table was within 15 cm of the peat surface [Bellisario *et al.*, 1999; Kettunen *et al.*, 1996; Moosavi and Crill, 1997; Shannon and White, 1994; Yavitt *et al.*, 1993]. This is possible because of the decrease in overlying hydrostatic pressure causing the release of stored CH₄ induced by either a water table drop or a change in barometric pressure [Glaser *et al.*, 2004; Rosenberry *et al.*, 2003; Strack *et al.*, 2004].

[5] Plant productivity influences CH₄ production by providing substrate from root exudates [Joabsson *et al.*, 1999; King *et al.*, 2002; Öquist and Svensson, 2002; Ström *et al.*, 2003]. CH₄ fluxes have been correlated with vascular plant biomass [Bellisario *et al.*, 1999; Christensen *et al.*, 2003b; King *et al.*, 1998; Whiting *et al.*, 1991], species composition [Bubier, 1995; Joabsson and Christensen, 2001], net ecosystem productivity (NEP) across a variety of wetlands with water table levels at or near the soil surface

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Table 1. Collar Height Above 2004 Mean Water Table Level, Total Above-Ground Plant Biomass, Dominant Species Composition, and Mean Seasonal Values of Net Ecosystem CO₂ Exchange (NEE), Respiration, Photosynthesis, CH₄ Flux, and Dissolved CH₄ by Each Collar for Grouped Years (May–August 2000–2004)^a

Collar	Height Above Water Table, cm	Total Biomass, g m ⁻²	Species Composition, Biomass in g m ⁻²			NEE, μmol CO ₂ m ⁻² s ⁻¹	Respiration, μmol CO ₂ m ⁻² s ⁻¹	Photosynthesis, μmol CO ₂ m ⁻² s ⁻¹	CH ₄ Flux, mg CH ₄ m ⁻² d ⁻¹	Dissolved [CH ₄] at 10 cm, ppm
			Sedge	Leatherleaf	Other Woody Species					
1	9.4	170.4	0	81.2	78.6	-5.1 (2.9) a	5.4 (1.3) ab	-10.5 (2.3) a	680.6 (746) a	10385 (9062) a
2 l	17.8	210.4	0	128.6	51.4	-6.3 (2.3) abc	5.0 (1.3) b	-11.3 (2.2) a	266.6 (290) b	7420 (3254) ab
3	19.3	221.6	23.5	24.0	0	-7.9 (3.0) bc	7.5 (1.7) c	-15.3 (2.8) b	214.9 (168) b	5460 (3149) b
4	20.1	1065.1	0	27.5	972.7	-7.8 (2.9) bc	7.5 (1.8) c	-15.3 (2.7) b	260.5 (203) ab	7706 (4820) ab
5 s	26.5	326.2	185.5	46.3	88.3	-6.7 (2.1) ac	4.8 (1.4) b	-11.5 (2.5) a	222.3 (290) b	8566 (5831) ab
6 l	29.9	595.3	0	161.1	403.2	-7.6 (3.0) bc	7.2 (2.5) c	-14.8 (3.8) b	295.9 (388) b	5013 (3345) b
7 s	26.4	209.1	57.8	78.2	31.6	-5.8 (2.0) a	5.7 (2.0) ab	-11.5 (3.1) a	181.1 (589) b	5600 (3556) b
8 s	21.8	251.6	44.8	80.2	85.1	-7.0 (2.5) ac	4.7 (1.3) b	-11.7 (3.3) a	259.2 (259) b	7687 (8417) ab
10	13.6	241.4	21.2	111.9	80.7	-5.5 (3.1) a	6.5 (2.3) ac	-12.0 (3.0) a	191.0 (219) b	4775 (2699) b
11 l	17.1	213.1	18.3	162.3	0	-5.7 (1.9) a	5.2 (1.4) b	-10.8 (2.2) a	247.2 (257) b	4866 (2937) b

^aDry biomass is given in g m⁻². Parentheses indicate standard deviation. Occurrence of the letters s, l denotes sedge dominated and leatherleaf collar grouping, respectively. Occurrence of the letters a, b, c indicates significant differences between collars ($\alpha = 0.05$).

[Waddington *et al.*, 1996; Whiting and Chanton, 1993] and net ecosystem CO₂ exchange (NEE) [Bellisario *et al.*, 1999; Joabsson and Christensen, 2001]. CH₄ fluxes have also been linked to photosynthesis, especially in wet sites [Joabsson *et al.*, 1999; King and Reeburgh, 2002; Nykänen *et al.*, 2003; Ström *et al.*, 2003]. Ecosystem respiration may also be related to CH₄ fluxes as both CO₂ and CH₄ are products of decomposition, and both gases are constrained by the same physical factors of gas phase exchange. Few studies have documented the dynamics among plant productivity, NEE, species composition and CH₄ fluxes on different timescales.

[6] We examined the links among CH₄ fluxes and physical (e.g., water table, air, and peat temperature) and biological variables (e.g., NEE, photosynthesis, respiration, and plant species composition) across a variety of temporal and spatial scales. While several studies have taken this integrative approach to looking at CH₄ fluxes, most have been limited to one or two growing seasons [Bellisario *et al.*, 1999; Bubier *et al.*, 2005; Frolking and Crill, 1994; Heikkinen *et al.*, 2004; Waddington *et al.*, 1996]. Here we present 5 years of CH₄, NEE, air and peat temperature, and water table measurements at Sallie's Fen in New Hampshire, USA. We compared differences among years, as well as within years and between plant communities.

2. Materials and Methods

2.1. Site Description

[7] Sallie's Fen is a temperate peatland located in Barrington, New Hampshire, USA (43°12.5'N, 71°3.5'W), approximately 20 km from Durham, New Hampshire. It is a mineral poor fen of approximately 1.7 ha that receives most of its water from runoff, rainfall and a small ephemeral stream [Melloh and Crill, 1996]. The pH ranges from 4.1 to 5.7. The fen receives an average of 1100 mm of precipitation annually. The annual average temperature is 8.1°C and the average annual growing season temperature is 17.1°C [Frolking and Crill, 1994]. The biologically active season lasts from late April through October with plant senescence beginning in late August. The dominant vegetation of the fen is composed of *Sphagnum* mosses in the ground layer, with evergreen shrub leatherleaf (*Chamaedaphne calyculata*) and deciduous shrubs alder (*Alnus incana* spp. *rugosa*)

and blueberry (*Vaccinium corymbosum* and *V. angustifolium*), sedges (*Carex rostrata* and *C. aquatilis*), cranberry (*Vaccinium oxycoccus*) and bog lily (*Maianthemum trifolium*) in the shrub and herbaceous layers. A few red maple trees (*Acer rubrum*) line the edges of the fen.

2.2. Net Ecosystem CO₂ Exchange Measurements

[8] We measured net ecosystem CO₂ exchange (NEE), respiration and CH₄ fluxes at 10 locations within the fen on a weekly basis from 1 May through 31 August 2000–2004. The sampling sites span a range of heights above the water table and vegetation types (Table 1). NEE was measured using the static chamber method described by Carroll and Crill [1997]. The transparent chamber enclosed 0.401 m³, and consisted of an aluminum frame covered on three sides with 1.27 mm Teflon FEP film, while the fourth side and removable lid were made with 3.2 mm Lexan. The Teflon and Lexan used in the chambers reduced incident photosynthetically active radiation (PAR) less than 10% (P. Czepiel, personal communication, 1997). The chamber had three 12 V brushless muffin fans for circulating the air within the chamber across a heat exchanger through which ice water was circulated on sunny, hot days in order to maintain headspace temperature to within 1°C of ambient. The climate control system also kept relative humidity low enough to prevent condensation from forming on the chamber walls. The chambers were placed on aluminum collars (63 cm × 63 cm) permanently embedded 10–15 cm into the peat surface with a groove for chamber placement and sealing with water. We recorded the air temperature, peat temperature at a depth of 10 cm and the pH of the surface water during each flux measurement.

[9] CO₂ concentrations were measured for a period of 2 min using a LICOR-6200 photosynthesis system (LiCor Inc., Lincoln, Nebraska), which included an LI-6250 infrared gas analyzer, data logger, PAR sensor and sensor head with thermocouples and a relative humidity sensor. NEE was calculated from the change in headspace CO₂ concentration over the measurement period and was corrected for moisture fluxes using methods described by Hooper *et al.* [2002].

[10] In order to define a photosynthetic light response curve, NEE was measured at four light levels; at full light and using shrouds to block approximately half, three-quarter

ters, and all PAR. Because of the uncertainties in quantifying net ecosystem production from weekly chamber CO₂ data for the whole growing season [Bubier *et al.*, 1999] and uncertainties in measuring NEE at low light levels using shade cloths [Burrows *et al.*, 2005], we used gross photosynthesis at full light (PSN_{max} = net ecosystem CO₂ flux at PAR > 1000 μmol photons m⁻² s⁻¹ minus respiration) as an estimate of maximum plant productivity. NEE measurements with a relative humidity greater than 80% were discarded because of plant stress leading to observed decreased rates of photosynthesis. The dark measurement of NEE using the shroud to block all light from entering the chamber was considered a measure of ecosystem respiration. Although this technique overestimates nighttime respiration due to higher chamber temperatures, our goal was to measure daytime CO₂ respiration and CH₄ flux simultaneously.

2.3. CH₄ Flux Measurements

[11] CH₄ flux measurements were made during the dark chamber run during and after the respiration measurements to avoid changes in temperature during the necessarily longer enclosure times. Five headspace samples were taken every 2 min from the chamber for a 10-min period with 60 ml polypropylene syringes equipped with polycarbonate/nylon stopcocks. We also sampled the concentration of CH₄ equilibrated with pore water at 10 cm depth. This was accomplished by extracting pore water in the field, returning the syringes to the laboratory to equilibrate to room temperature. The syringes were filled with 30 ml of pore water and 30 ml of room air then shaken by hand for 2 min immediately prior to analysis. Mixing ratios of CH₄ in both chamber headspace and pore water samples were determined by analysis with a gas chromatograph equipped with a flame ionization detector (GC-FID, Shimadzu GC-14A). Ultra High Purity Nitrogen (UHP N₂) carried the sample through an analytical separation column of 2 m × 1/16" OD stainless steel packed with HayeSepQ held isothermally at 50°C. Mixing ratios were determined by comparing sample peak areas with breathing air standards calibrated with NOAA ESRL Global Monitoring Laboratory's Carbon Cycle Greenhouse Gases Group (formerly CMDL). Precision for this analysis was ±0.5%. Fluxes were calculated using a linear regression of the change in CH₄ mixing ratios over the 10-min period. The coefficient of determination had to be significant to the 95% confidence limit for n = 3 (r² = 0.95), n = 4 (r² = 0.87), or n = 5 (r² = 0.75); otherwise the sample was rejected. Approximately 17% of CH₄ fluxes were discarded using these criteria, but the mean of the discarded fluxes was not significantly different from the sample mean. Low CH₄ flux rates were included if they were significantly different than 0. The chamber was vented prior to starting the CH₄ flux measurement period, and only fluxes with the initial concentrations near ambient were used in the analyses to ensure that disturbance was not a factor.

2.4. Environmental Variables

[12] Meteorological and water table data were collected continuously at Sallie's Fen using an automated meteorological (MET) station. Hourly average MET data and daily average water table data were used in the analyses. During periods when meteorological data were unavailable, we used air temperature and precipitation data from a weather station in Durham, New Hampshire, approximately 20 km

away. Daily water table data were linearly interpolated between manual well measurements from 7 June to 6 July 2003 when continuous well measurements were unavailable (S. Frolking, personal communication, 2004). Water table depths (WTD) were calibrated using manual measurements of water table depth relative to the peat surface for all years. Depth to water table from the peat surface for each collar was determined using a tube level in August 2004 (Table 1). We measured WTD and air and peat temperature at each collar at the same time we measured CO₂ and CH₄ fluxes.

[13] Plant species composition and biomass estimates of each collar were made during August 2003. Species composition was measured using a quadrat and visually estimating percent coverage within the collar. Biomass estimates were derived from counting stem height and number of each species within the collar using algorithms from previous studies at the site [Burrows *et al.*, 2005]. We divided sites into two main vegetation groups determined by collar species composition and biomass (Table 1): sedge (primarily *Carex rostrata*) and leatherleaf (*Chamaedaphne calyculata*). The leatherleaf collars were designated as the three collars with the highest leatherleaf biomass (collars 6, 2, 11). Sedge collars were those with the highest percentage of sedge biomass (collars 5, 7, 8).

2.5. Data Analysis

[14] For analysis, NEE, photosynthesis and respiration are considered metrics of plant and microbial activity, while air temperature, peat temperature and water table depth data are referred to as environmental measurements. Throughout the manuscript we adopt the convention that CO₂ and CH₄ fluxes to the atmosphere are positive and CO₂ uptake by the ecosystem is negative.

[15] We examined relationships between the independent variables and CH₄ flux on a seasonal scale using individual fluxes (representing the measurement period), monthly means across all collars, and the seasonal means for individual collars and all collars combined, in individual years and combined data from all years (grouped years). A natural log transformation was used on the CH₄ flux data to reduce skewness and to approximate a normal distribution for all analyses.

[16] SPSS 12.0 software (SPSS Inc., Chicago, Ill.) was used for statistical analyses. One-way ANOVA tests were conducted at α = 0.05 (two-tailed) to determine differences between the independent variables in different years, as well as differences between collars. A Bonferroni post hoc analysis was used to determine where differences occurred between the groups. We used regressions (α = 0.05) to determine the relationships between independent variables and CH₄ fluxes. Stepwise multiple regressions (α = 0.05) for three different timescales included parameters for NEE, maximum photosynthesis, respiration, air and peat temperature, and water table level. Variables that were not statistically significant were omitted from the reported results of the multiple regression analyses.

3. Results

3.1. Environmental Conditions

[17] Mean summer air temperature at Sallie's Fen ranged from 15.8°C in 2004 to 18.3°C in 2001, with July and

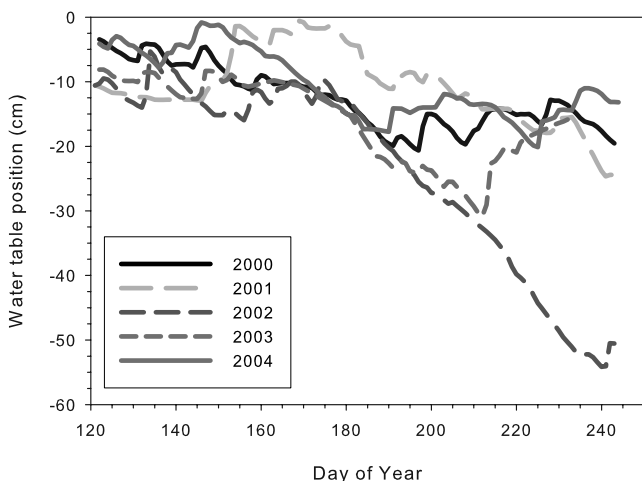
Table 2. Monthly and Seasonal (1 May to 31 August) Mean Air Temperature, Water Table Depth, and Seasonal Cumulative and Monthly Precipitation

	Year					Mean ^a
	2000	2001	2002	2003	2004	
<i>Air Temperature, °C</i>						
Season	16.7	18.3	17.8	17.0	15.8	18.5
May	12.3	13.6	12.1	11.4	12.9	13.5
June	17.5	19.4	16.8	17.4	16.2	18.6
July	18.6	19.0	21.3	20.5	18.8	21.5
August	18.6	21.0	21.0	19.9	20.4	20.5
<i>Water Table Depth, Centimeters Beneath Peat Surface</i>						
Season	12.5	10.6	23.4	15.9	9.0	
May	5.9	12.0	11.2	10.0	4.0	
June	11.1	2.6	12.3	11.4	8.8	
July	17.6	10.0	24.3	23.9	14.5	
August	15.4	17.6	45.4	19.4	14.7	
<i>Cumulative Precipitation, mm</i>						
Season	337	287	331	275	465	334
May	85	42	124	89	144	92
June	80	142	149	52	48	91
July	114	75	21	37	90	64
August	57	28	37	97	183	86

^aMean reflects 30-year mean temperature (1971–2001) at Durham, New Hampshire (U.S. climate normals 1971–2000, www.ncdc.noaa.gov/normals.html) and 5-year mean precipitation at Sallie's Fen, Barrington, New Hampshire.

August usually the warmest months (Table 2). The seasonal mean air temperatures were lower at Sallie's Fen than the 30-year climate normals at Durham, New Hampshire, probably due to differences in microclimate from topographic differences and effects of surrounding trees. Water table level fell over the course of the summer, starting at 5–10 cm below the peat surface in early May and falling to 15–55 cm below the peat surface by the end of August (Figure 1). Monthly mean depths ranged from 3 cm below the peat surface in June 2001, the year with the highest mean water table, to as much as 45 cm below peat surface in August 2002, the driest year in our study (Table 2).

[18] Interannual variability in water table position was determined by both the total amount of precipitation and the

**Figure 1.** Daily average water table position (cm) below peat surface for May through August 2000–2004.

timing. In 2001, Sallie's Fen received 286.8 mm of precipitation during the growing season, with the majority falling in June and July, resulting in the water table staying near the peat surface (Figure 1). The water table fell dramatically in 2002 despite receiving 330.5 mm of precipitation over the season because the rainfall was concentrated in the months of May and June with less than 60 mm falling in July and August (Table 2).

3.2. NEE, Photosynthesis, and Respiration

[19] Maximum NEE (at PAR > 1000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) gradually increased through midseason, then declined toward the end of the season. The components of NEE, photosynthesis and respiration followed a similar trend but with respiration initially lagging NEE and photosynthesis (data not shown). Individual NEE fluxes ranged from 0.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to a peak value of $-14.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Photosynthesis ranged from -3.8 to $-22.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and respiration ranged from 1.3 to 12.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Results of a one-way ANOVA ($\alpha = 0.01$)

Table 3. Seasonal (1 May to 31 August) and Monthly Mean Measurements for (a) NEE, (b) Respiration, (c) Photosynthesis, and (d) Methane Flux^a

	Year				
	2000	2001	2002	2003	2004
<i>NEE ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)</i>					
Season	-6.1 (3.1)	-6.1 (2.5)	-6.7 (2.7)	-6.9 (2.3)	-6.8 (2.8)
May	-2.8	-4.6	-4.2		-4.4
June*	-5.4 a	-5.5 a	-8.3 b	-7.4 ab	-7.9 b
July	-7.2	-7.6	-7.7	-7.4	-7.6
August	-6.9	-5.7	-5.2	-5.9	-5.2
<i>Respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)</i>					
Season	5.7 (2.0)	5.6 (2.0)	5.9 (2.2)	6.4 (2.1)	6.3 (1.8)
May	3.8	3.9	2.4		3.9
June	6.2	5.6	5.0	6.6	6.4
July*	5.3 a	5.8 ab	6.4 ab	6.1 ab	6.6 b
August	6.4	5.8	7.0	6.6	6.3
<i>Photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)</i>					
Season*	-11.8 (3.7) a	-11.7 (3.1) a	12.6 (2.5) a	-13.3 (3.4) a	-13.2 (3.3) a
May	-6.6	-8.6	-6.6		-8.3
June*	-11.6 ab	-11.0 ab	-13.3 abc	-13.9 bc	-14.3 c
July	-12.6	-13.4	-14.0	-13.5	-14.2
August	-13.3	-11.5	-12.2	-12.4	-11.5
<i>CH₄ Flux ($\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$)</i>					
Season*	204 (164) a	316 (356) ab	423 (581) b	244 (405) ab	241 (320) a
May	76	112	57		92
June	145	123	146	150	151
July	202	385	418	392	344
August*	349 ab	562 ab	751 a	183 b	257 b
<i>[CH₄] Dissolved in 10 cm Pore Water (ppm)</i>					
Season*	8067 (4931) a	8754 (4572) a	7790 (8143) a	4634 (2321) b	3835 (2675) b
May	4315	6465	18503		
June	6678	7209	6427	4794	4794
July*	8594 ab	10352 a	9117 ab	4716b c	2095 c
August*	10872 a	8769 ab	4662 b	4371 b	4246 b

^aPhotosynthesis was calculated using NEE measured at maximum PAR (>1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). Occurrence of *, a, b denotes significant differences between individual years at $\alpha = 0.01$ level; numbers in parentheses denote standard deviation of the mean.

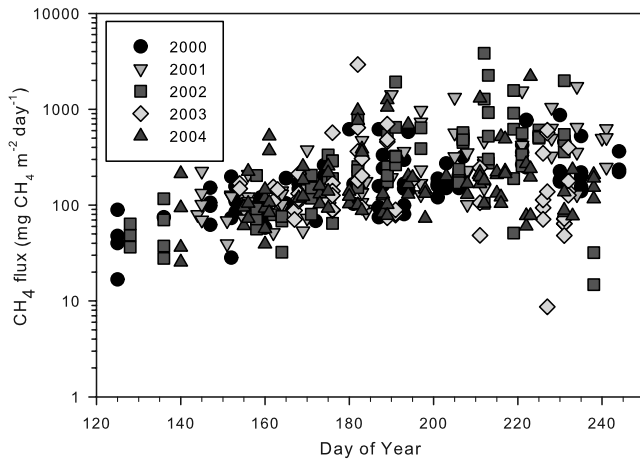


Figure 2. Individual CH₄ fluxes from all collars during May through August 2000 to 2004.

indicated significant differences among seasons for photosynthesis ($F(4, 382) = 3.831, p = 0.005$) and at a monthly level for NEE and photosynthesis in June and for respiration in July (Table 3).

3.3. CH₄ Fluxes

[20] CH₄ fluxes increased in magnitude and variability during the season in all years (Figure 2), ranging from an efflux of 8.7 to 3833.1 mg CH₄ m⁻² d⁻¹. The seasonal increase in flux is linear and normally distributed when logarithmically transformed (results not shown). Results of a one-way ANOVA ($\alpha = 0.01$) indicated significant differences among all years ($F = 4.180, d.f. = 4, 382, p = 0.003$; Figure 3), which were greatest during the month of August. Years 2002 and 2000 had the highest (423 mg CH₄ m⁻² d⁻¹) and lowest (204 mg CH₄ m⁻² d⁻¹) seasonal average CH₄ flux, respectively (Table 3).

[21] The strength and sign of the correlations between CH₄ flux and the suite of abiotic and biotic variables varied by timescale (minutes, months, seasons; Table 4). There were significant linear relationships ($\alpha = 0.05$) between individual CH₄ flux measurements and each of the independent variables except NEE. Peat temperature, air tem-

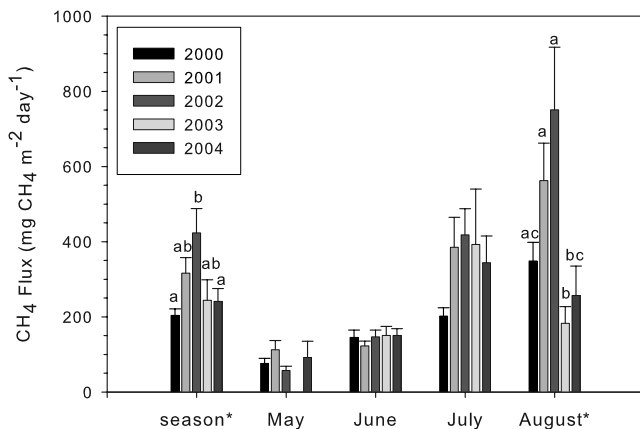


Figure 3. Monthly and seasonal mean CH₄ fluxes. Error bars indicate standard error. Different letters indicate significant differences ($\alpha = 0.05$) between years.

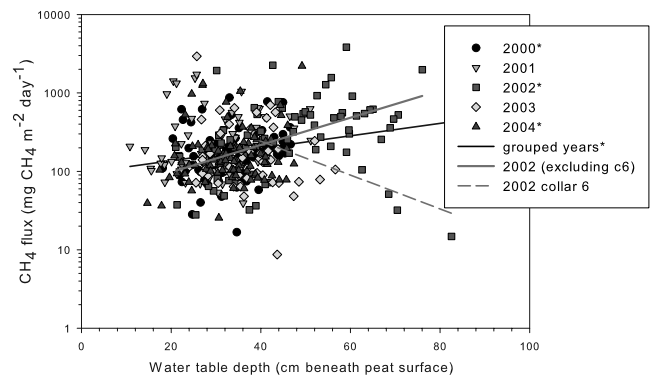


Figure 4. Individual water table depth (WTD) versus CH₄ flux for all collars. Asterisk indicates significant relationship ($\alpha = 0.05$). Regression lines shown for grouped years* ($\ln(\text{CH}_4 \text{ flux}) = 0.02 (\text{WTD}) + 4.55, r^2 = 0.05$) and for 2002, all collars but 6 and for collar 6 only $\ln(\text{CH}_4 \text{ flux}) = 0.04 (\text{WTD}) + 3.78, r^2 = 0.28$; $\ln(\text{CH}_4 \text{ flux}) = -0.05 (\text{WTD}) + 7.47, r^2 = 0.37$.

perature and respiration showed the strongest correlations with individual CH₄ fluxes ($r^2 = 0.12, 0.11, 0.10$ respectively). CH₄ fluxes increased significantly with a decline in water table in several individual years and in combined years (Figure 4), with the regressions having similar slope of 0.02 to 0.03 each year. In 2002, CH₄ flux increased with greater WTD at all locations except collar 6 (the driest hummock), where fluxes decreased with a falling water table (Figure 4). CH₄ fluxes were positively correlated with air temperature in individual years (2000–2003) and weakly correlated in all 5 years combined. Peat temperature had a slightly stronger positive relationship with CH₄ fluxes than air temperature ($r^2 = 0.12$ versus 0.11) in grouped years. CH₄ fluxes increased significantly with higher rates of respiration in both individual and grouped years (Table 4). A stepwise multiple regression revealed that factors differed in importance depending on the timescale. The strongest predictive model included monthly means of air temperature and WTD, explaining 81% of variability in CH₄ fluxes (Table 5).

3.4. Collars and Vegetation Groups

[22] The 10 collars varied in species composition, biomass, height above water table and location within the fen (Table 1). Similarly, mean seasonal NEE, photosynthesis, respiration and CH₄ fluxes differed significantly among collars when the years were combined (Table 1). Collars 3, 4 and 6 had the highest mean seasonal NEE (-7.6 to $-7.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), respiration (7.2 to $7.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and photosynthesis (-14.8 to $-15.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Mean seasonal photosynthesis at these three collars also differed significantly from all other collars while respiration differed significantly from other locations except collar 10. Collars 4 and 6 had the highest total biomass and woody biomass, 1065 g m⁻³ and 595 g m⁻³, respectively. Collar 1 had the highest seasonal mean CH₄ flux for the 5 years combined (680.6 mg CH₄ m⁻² d⁻¹) while collar 7 had the lowest mean CH₄ flux (181 mg CH₄ m⁻² d⁻¹). Collars 1 and 7 also had the lowest amounts of total above

Table 4. Correlations (*r*) of Simple Regressions Between Variables Listed and ln (CH₄ Flux) at Different Timescales and Vegetation Types for Grouped Years (2000–2004)^a

	Seasonal	Individual	Mean Monthly	Mean Seasonal	Sedge Collars	Leatherleaf Collars
NEE _{max}		0.03	0.47	0.14	−0.08	0
Respiration		0.32	0.74	0.02	0.33	0.35
Photo		−0.17	0.67	0.08	−0.24	−0.22
Air T		0.33	0.86	0.30	0.34	0.27
Peat T		0.34	0.88	0.06	0.54	0.23
WTD		0.22	0.73	−0.16	0.56	0.09

^aCorrelations for sedge and leatherleaf collars are based on individual fluxes. Bold font denotes significance ($\alpha = 0.05$). Sign (positive or negative) indicates the direction of the relationship with CH₄ flux.

ground biomass but collar 1 was much wetter with a mean water table position 17 cm above that of collar 7.

[23] The mean CH₄ emission of the collars with the most sedge biomass (collars 5, 7, 8) was 250.8 mg CH₄ m^{−2} d^{−1} and was not significantly different than the CH₄ emission from leatherleaf-dominated collars (6, 2, 11), 268.6 mg CH₄ m^{−2} d^{−1} ($p = 0.682$). Mean respiration was significantly higher at leatherleaf collars (5.77 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than sedge collars (5.08 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) using all years ($p = 0.004$), though the respiration was the same when considered on a per gram of above ground biomass basis (0.02 $\mu\text{mol s}^{-1} \text{ g}^{-1}$). The water table at leatherleaf collars averaged 39.9 cm below the peat surface, making them significantly drier than sedge collars (36.3 cm, $p = 0.007$).

[24] At sedge collars, we found significant correlations between individual CH₄ fluxes and respiration, photosynthesis, air and peat temperature, and water table depth for all years combined (Table 4), as well as for 2000–2002. Sedge collars had higher correlation coefficients between CH₄ fluxes and each of the variables than leatherleaf collars and all collars combined. CH₄ fluxes at sedge collars were positively correlated with water table level for the grouped years, and showed the strongest correlation between two variables of any group at the individual timescale ($r^2 = 0.31$). Water table depth accounted for anywhere from 31% of the variability of CH₄ fluxes from sedge collars in all years, to a maximum of 51% of the variability in 2000.

4. Discussion

4.1. Water Table Controls on CH₄ Flux

[25] We expected a lower water table to produce lower CH₄ fluxes because the deeper water table level favors aerobic respiration and CH₄ oxidation [Aerts and Ludwig, 1997; Bubier et al., 1995; Dise et al., 1993; Moore and

Roulet, 1993]. We observed the opposite, a lower water table associated with higher individual and monthly CH₄ fluxes (Table 4 and Figure 5b). Bellisario et al. [1999] also found inverse relationships from those expected between water table level and CH₄ flux. Most likely, the high CH₄ fluxes we observed in the late season are due to a combined effect of higher rates of CH₄ production in warmer peats and episodic fluxes of stored CH₄. Bubble releases can be produced by lowered pressure due to a falling water table and changes in barometric pressure [Glaser et al., 2004; Strack et al., 2005].

[26] When the water table drops, several conflicting processes may be important: (1) the pressure gradient with a subsequent release of stored CH₄, (2) decreased CH₄ production, and (3) increased or decreased CH₄ oxidation. Most collars showed the trend of increasing CH₄ fluxes with a falling water table with a coincident increase in temperature, indicating that the lowering of the water table has a larger influence on CH₄ fluxes through changes in pressure gradients and increased production due to warming than by limiting microbial CH₄ production and increasing oxidation. There were no differences in the concentration of CH₄ dissolved in pore water at 10 cm between months (Table 3), suggesting that CH₄ production is relatively constant over the season despite a falling water table. Rather than a direct link to water table level, CH₄ fluxes may be primarily related to peat temperature and secondarily to soil moisture content rather than WTD, as has recently been found with CO₂ respiration in peatlands [Lafleur et al., 2005]. We found that only the driest collar (#6) in the driest year showed decreasing CH₄ fluxes on an instantaneous scale (Figure 4), indicating that there maybe a threshold soil moisture content to switch off CH₄ production. Additionally, water table lowering and subsequent drying might more severely dry and inhibit methanotrophs within water-hold-

Table 5. Coefficients, Standard Error of Coefficient, t-Scores, p-Values, and r^2 for Stepwise Multiple Regression at Three Different Timescales With Independent Variables NEE, Photosynthesis, Respiration, Water Table, Air and Peat Temperature, with ln CH₄ as the Dependent Variable^a

Timescale	Variable	Coefficient	Standard Error	T-Value	P	Cumulative r^2
Individual	Peat temperature	0.04	0.01	7.08	<0.01	0.12
	Respiration	0.07	0.03	4.44	<0.01	0.16
	Air temperature	0.03	0.01	2.22	0.03	0.17
	WTD	0.01	<0.01	2.06	0.04	0.18
Monthly	Air temperature	0.15	0.03	4.99	<0.01	0.74
	WTD	0.03	0.01	2.56	0.02	0.81
Seasonal	Air temperature	0.07	0.03	2.14	0.04	0.09

^aVariables not shown were not significant in the regression ($\alpha = 0.05$); each model includes the variables from the previous model.

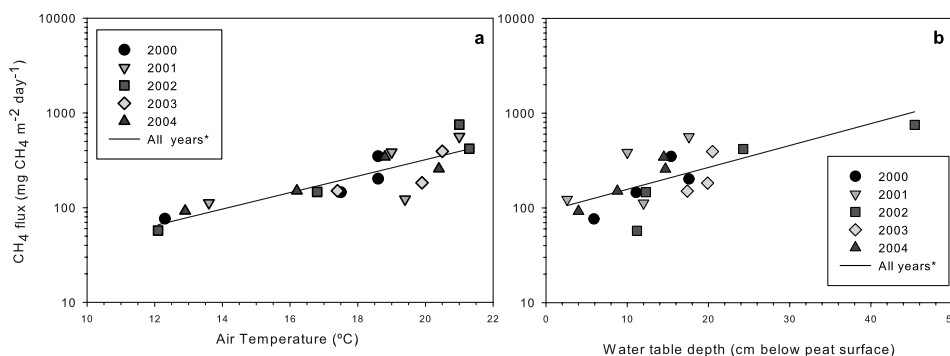


Figure 5. (a) Monthly mean air temperature versus CH₄ flux. Asterisk indicates significant relationship ($\alpha = 0.05$). Regression lines shown for grouped years ($\ln(\text{CH}_4 \text{ flux}) = 0.20(\text{airT}) - 1.78$, $r^2 = 0.74$); (b) Monthly mean water table depths versus CH₄ flux; ($\ln(\text{CH}_4 \text{ flux}) = 0.54(\text{WTD}) - 4.52$, $r^2 = 0.82$).

ing *Sphagnum* moss hyaline cells [Raghoebarsing *et al.*, 2005; Basiliko *et al.*, 2004].

[27] At the seasonal scale, we observed lower CH₄ fluxes at sites with lower water table levels, in contrast to the individual or monthly measurement scale (Table 4). We found stronger correlations between CH₄ and WTD at the seasonal scale in 2001 and 2003 ($r = -0.64$ for both) than any yearly individual flux relationships (r ranged from 0.21 to 0.33; data not shown). The relationship between increased WTD and decreased CH₄ flux at the seasonal scale is the generally observed pattern [Bubier *et al.*, 1995; Dise *et al.*, 1993; Moore and Dalva, 1997; Waddington *et al.*, 1996] and suggests that over longer timescales than days or weeks, the water table exerts a strong control on the extent of anaerobiosis in the peat.

[28] The collar with the highest water table level, collar 1, consistently showed the highest mean seasonal CH₄ fluxes (Table 1) indicating that average water table position determines CH₄ fluxes over a variety of sites. However, as discussed above, there are also other factors that affect fluxes on shorter timescales, e.g., this collar received the least amount of sunlight, spending many mornings and late afternoons in shade and consequently had a low plant biomass. Higher CH₄ fluxes from this wet site suggest that water table, not plant productivity, controls CH₄ fluxes.

4.2. Interannual Climate Variability

[29] We found that seasonal mean CH₄ flux for the 5 years combined showed a significant relationship only with air temperature (Table 4), and in several individual years with both WTD and temperature. However, in the cool and wet years of 2000 and 2004, there were no significant relationships between CH₄ fluxes and any variables at a seasonal scale. These 2 years had very similar water table dynamics (Figure 1), with no large drop in water table (<20 cm), were both cool (a mean seasonal temperature of 16.7°C in 2000 and 15.8°C in 2004; Table 2) and had the lowest seasonal average CH₄ fluxes (Table 3). The combination of high water table with continuing input of fresh water and low peat temperature may have inhibited methanogenesis.

[30] 2002 was an exceptionally dry year in terms of the seasonal mean water table level (Table 2). Precipitation was high in the early season but water table was exceptionally low by the end of August, falling to an average of 60 cm below the peat surface and as much as 90 cm below the peat

surface at some measurement sites. In association with this dry season, we measured the largest, most variable CH₄ fluxes (Figure 3), probably owing to episodic fluxes and other causes previously discussed. For these reasons, August 2002 average flux was the highest monthly average in the study.

4.3. Vegetation Control on CH₄ Flux

[31] Mean seasonal methane fluxes from the sedge-dominated and leatherleaf-dominated collars were not significantly different despite differences in the physiology of sedges that enhance CH₄ flux by increasing transport and bypassing the CH₄ oxidation zone [King *et al.*, 1998; Shannon and White, 1994]. Relationships between CH₄ fluxes and independent variables were much stronger in the sedge collars than the leatherleaf collars (Table 4), and were highly positively correlated with water table depth at sedge collars. The largest flux measured in the whole study was from a sedge collar in August 2002, 3811 mg CH₄ m⁻² d⁻¹, which increased the standard deviation of the average flux from the sedge collars and illustrates the relative importance of episodic fluxes at sedge-dominated sites.

[32] Somewhat surprisingly, CH₄ fluxes from sedge collars were not significantly correlated with plant productivity or environmental variables in 2003 or 2004 even though these years had the highest rates of NEE and photosynthesis. These 2 years also had the highest CO₂ respiration measurements and lower concentrations of dissolved CH₄ in pore water at 10cm. Compared with other years, the proportion of carbon emitted as aerobic respiration was much larger than that produced through anaerobic respiration, perhaps because of less-than-average June rainfall. Lower rainfall in the beginning of the summer may influence the ratio of aerobic to anaerobic respiration by altering soil moisture while not affecting WTD. With the inclusion of cumulative monthly precipitation in a stepwise multiple regression, peat temperature, monthly precipitation and air temperature were the significant predictors of mean monthly CH₄ fluxes.

4.4. Modeling CH₄ Fluxes

[33] We observed fluxes to be highly variable through the year at the individual scale (Figure 2), which is reflected in the large standard deviation of the seasonal mean measurements (Figure 3). There were different relationships between CH₄ flux and the suite of measured biological and

physical variables depending on the timescale (Table 4), indicating that relationships between CH₄ and simple abiotic and biotic factors are complex and that any modeling approach will need to integrate numerous parameters and processes. Additionally, variability in CH₄ flux between years was attributed to significant interannual differences in August of each year (Figure 3) driven by accumulating climatic effects (such as WTD and temperature interactions) and episodic fluxes through the growing season that are difficult to describe through simple parameters.

[34] The strength of modeling CH₄ fluxes depends on the timescale and the grouping of vegetation types. Over a multiple year time period using all collars, air temperature was the only consistent predictor of CH₄ fluxes across all timescales (Table 4) in Sallie's Fen. On a monthly timescale, mean air temperature (Figure 5a), water table (Figure 5b) and respiration were the best predictors of CH₄ flux (Table 4). This intermediate time period produced the strongest predictive power using a multiple regression approach, explaining 81% of the variation in monthly CH₄ fluxes (Table 5).

5. Conclusions

[35] Five years of data at Sallie's Fen demonstrate the complexity of processes that contribute to the spatial and temporal variability in CH₄ fluxes. Temporal variation of individual CH₄ fluxes was high, ranging 100-fold in magnitude. Aggregated CH₄ fluxes on monthly and seasonal scales showed lower variation and stronger relationships with abiotic and biotic variables. Similarly, spatial variability of CH₄ fluxes was reduced by classifying sites by vegetation type. Interannual differences in CH₄ fluxes were driven by elevated and variable late summer emissions, which appeared to be caused by low water table levels and high temperatures. Air temperature was the only variable that was strongly correlated with CH₄ fluxes at all timescales, while WTD had either a positive or negative correlation depending on timescale and vegetation type. Using a stepwise multiple regression, the monthly timescale produced the strongest predictive relationships among CH₄ flux, air temperature and water table level ($r^2 = 0.81$).

[36] This study shows that the strength and even the direction of the predictive relationships are completely dependent on the timescale and time period of measurement. Given the weak correlations between CH₄ flux and environmental variables at shorter timescales than months or seasons, research integrating both these measurements and mechanistic modeling is needed to understand the processes that control CH₄ production, oxidation and transport.

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