

Stand-specific diurnal dynamics of CH₄ fluxes in boreal lakes: Patterns and controls

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[1] Diurnal variation in methane fluxes can cause systematic errors in flux estimates, particularly at places with aquatic vegetation. Closed chamber measurements were made during the ice-free period in central Finland. Methane fluxes were quantified at an interval of a few hours for several boreal lakeshore communities consisting of *Phragmites australis* (Cav.) Trin. ex Steud. and of wetland sedges, grasses, and herbs. The automated measurement system was operated for 4 months in a *P. australis* stand and for 2 months in a site with mixed wetland vegetation. Additional manual measurements lasted for a few days. In *P. australis* stands the CH₄ fluxes were typically highest around noon. On the average, efflux of CH₄ measured during office hours (0800–1600 local time (LT)) should be corrected using a factor 0.68 to obtain a more reliable estimate of daily CH₄ release. The fluctuation magnitude varied between different locations and over the study period, being the greatest in the most productive parts of the stands in August. A harmonic regression model, scaled with temperature and stand biomass, was successfully applied to reconstruct CH₄ flux in *P. australis* stand. In the sedge, grass and herb stands the diurnal fluctuation in CH₄ flux was generally small. Commonly, daily maximum in efflux occurred during evening or night and large (threefold) diurnal differences were occasionally found. Daytime measurements alone can result in a slight or moderate underestimate of the total flux for the wetland communities. These results recommend that spatial and seasonal differences in diurnal CH₄ flux dynamics should be considered when planning measuring or modeling CH₄ fluxes.

INDEX TERMS: 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1845 Hydrology: Limnology; 1851 Hydrology: Plant ecology; 1890 Hydrology: Wetlands; **KEYWORDS:** *Phragmites australis*, CH₄, littoral wetland, stem convective flow, gas transport, harmonic regression model

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1. Introduction

[2] Decomposition of organic residues in waterlogged sediments of the littoral zone results in the production of methane (CH₄), an effective infrared absorbing gas. Productive land-water interfaces commonly have large fluxes of CH₄ at a local scale [Bartlett *et al.*, 1992; Smith and Lewis, 1992; Hyvönen *et al.*, 1998; Striegl and Michmerhuizen, 1998; Juutinen *et al.*, 2003]. Thus gaining of an overall understanding of littoral carbon cycling is essential in order to obtain regional carbon and greenhouse gas budgets in lake-rich temperate, boreal and arctic regions. Diurnal variation in CH₄ fluxes can cause systematic errors in emission estimates, particularly at

places with aquatic vegetation. It should be quantified in order to design sampling and modeling or possibly to correct existing estimates.

[3] Diurnal variation in the fluxes of CH₄ is associated with the dynamics of production, oxidation and transportation of CH₄, and its pattern appears to be specific for individual species or stands. Transportation of CH₄ through aquatic plants has particular importance in the diurnal variability. Gas molecules either move through plants by diffusion along a concentration gradient or are transported by convective (or bulk) flow, the latter mechanism exhibiting strong diurnal dynamics [Dacey and Klug, 1979; Chanton *et al.*, 1992]. Plant-mediated transportation of CH₄ is associated with the adaptation of wetland and aquatic species to live in oxygen depleted sediments. It takes place through a continuous air space inside the plant, which allows the transfer of atmospheric oxygen to the roots and the leakage of sediment gases upward. Ventilation by convective flow is assumed to be a competitive advantage and occurs commonly among species colonizing relatively deep waters, for example, *Nuphar lutea* (L.) Sibth. & Sm. and *Phragmites australis* (Cav.) Trin. ex Steud. [cf. Brix *et*

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Table 1. Sites and Periods of the CH₄ Flux Measurements

Site ^a	Dominant Species (Aboveground Biomass)	Measurement Period	N ^b
1	L. Heposelkä: transect through <i>Phragmites australis</i> stand, automatic measurements	1995	
1.1	<i>P. australis</i> , inner (landward) margin	10 July to 20 Oct	1
1.2	<i>P. australis</i> , middle (~217 g m ⁻²)	10 July to 20 Oct.	1
1.3	<i>P. australis</i> , outer margin (~58 g m ⁻²)	10 July to 20 Oct.	1
1.4	<i>P. australis</i> , outer margin (~67 g m ⁻²)	10 July to 20 Oct.	1
2	L. Kevätön: transect from temporarily flooded meadow to <i>P. australis</i> belt, automatic measurements	1998	
2.1	<i>Calamagrostis canescens</i> (Weber) Roth (227 g m ⁻²)	2 July to 28 Aug.	1
2.2	<i>Calamagrostis canescens</i> (202 g m ⁻²)	2 July to 28 Aug.	1
2.3	<i>Calla palustris</i> L., <i>Potentilla palustris</i> (L.) Scop. (44 g m ⁻²)	2 July to 28 Aug.	1
2.4	<i>P. palustris</i> , <i>C. palustris</i> , <i>Carex aquatilis</i> Wahlenb. (567 g m ⁻²)	2 July to 28 Aug.	1
2.5	<i>P. australis</i> (31 g m ⁻²)	2 July to 28 Aug.	1
2.6	<i>P. australis</i> (16 g m ⁻²)	2 July to 28 Aug.	1
3	L. Heposelkä: Temporarily flooded shore, manual measurements	1995	
	<i>Carex vesicaria</i> L., <i>Calamagrostis canescens</i>	15–17 Aug.	1
	<i>Carex rostrata</i> Stokes	15–17 Aug.	1
4	L. Mekrijärvi: temporarily flooded lacustrine fen, manual measurements	1999	
	<i>Eriophorum angustifolium</i> Honckeney, <i>Molinia caerulea</i> (L.) Moench	14–18 June and 16–19 Aug.	2
	<i>Carex aquatilis</i> , <i>Potentilla palustris</i>	14–18 June and 16–19 Aug.	2
5	L. Mekrijärvi: temporarily flooded shore, manual measurements	1999	
	<i>Agrostis canina</i> L.	14–18 June and 16–19 Aug.	2
	<i>Carex aquatilis</i>	14–18 June and 16–19 Aug.	2

^aAutomatically measured plots have subnumbering.

^bN indicates the number of plots.

al., 1996; Vretare Strand, 2002]. Convective through flow presupposes a pressure gradient within a plant or several rhizome-connected specimens. Typically, the direction of flow is from young, pressurized leaves or culms through the rhizomes and roots toward nonpressurized dead, old or cracked leaves and culms [Dacey, 1981; Armstrong and Armstrong, 1991; Grosse et al., 1996; Yavitt and Knapp, 1998]. Internal pressurization is mainly powered by solar irradiance that heats the plant surfaces above the ambient temperature so that thermal transpiration and humidity-induced diffusion increase the pressure in the lacuna [Dacey, 1981; Armstrong and Armstrong, 1991; Chanton et al., 1993]. Therefore convective flow occurs during daylight, while diffusion only occurs at night, and the efflux of CH₄ through *P. australis* and *N. lutea* at midday can be manifold compared to that during night [Dacey and Klug, 1979; Kim et al., 1998a, 1998b; Käki et al., 2001]. Convective flow is found in many genera, for example, in *Nymphaea*, *Nelumbo*, *Typha*, *Eleocharis* and *Potamogeton*, but there is a considerable difference in flow rates between species [Dacey, 1987; Brix et al., 1992; Heilman and Carlton, 2001; Vretare Strand, 2002].

[4] Among wetland species, like *Carex* spp., ventilation of the roots is based on diffusion, and the diurnal variation in fluxes of CH₄ is associated with changes in temperature, oxygen supply, or availability of photosynthates that regulate the production and oxidation of CH₄. The highest CH₄ effluxes have often been measured during the afternoon, evening or night hours [Whalen and Reeburgh, 1988; King, 1990; Whiting and Chanton, 1992; Mikkilä et al., 1995; Waddington et al., 1996]. Diurnal fluctuation of CH₄ fluxes may bias emission estimates even in wetland communities venting by diffusion [Mikkilä et al., 1995]. Vegetation communities from both categories are considered here, but the main focus in this study is on *Phragmites australis*. It is a common lakeshore and wetland species and it causes strong diurnal variation in CH₄ fluxes. Intensive studies over short periods are numerous, but season long observation series at frequent intervals are needed to properly

characterize the patterns and controls of diurnal variation in the CH₄ flux. Such series are still few [Kim et al., 1998a, 1998b].

[5] Here we report closed chamber measurements of CH₄ fluxes, consisting of both short-term campaigns and long-term series of automatically controlled measurements in stands of *Phragmites australis* and in stands of mixed wetland species. Our aim is to quantify the diurnal fluctuation in fluxes of CH₄ and effects of environmental factors regulating diurnal variability. Using this information, a simple harmonic regression model is developed in order to predict the course of hourly CH₄ fluxes in *P. australis* stands. We also discuss the reliability of estimates obtained using closed chamber techniques for ecosystems of species that employ pressurized ventilation.

2. Materials and Methods

2.1. Study Sites

[6] Diurnal dynamics of CH₄ fluxes were studied in several sites with littoral vegetation typical of the study lakes. The lakes are located at the transition of the south and middle boreal zones in eastern central Finland. The lakes were mesotrophic Lake Heposelkä (62°30'N, 29°30'E), mesotrophic L. Mekrijärvi (62°45'N, 31°00'E), and eutrophic L. Kevätön (63°06'N, 27°38'E). The lakes in this region are typically ice free from early May to early November.

[7] Methane fluxes were measured with an automated measurement system at two sites (Table 1): at 4 plots within a *Phragmites australis* stand (water depth 50–100 cm) in site 1, and at 6 plots along a moisture and vegetation gradient in site 2. The gradient consisted of a temporarily flooded upper part, a wetter transient, and a sparsely vegetated fringe of constantly inundated *P. australis*. In the site 1, the automated measurements lasted from July to October (1995) with a gap of three weeks in August/September. In the site 2, the system was operated during July and August (1998). Three-day manual measurement

Table 2. Ratio of the CH₄ Flux Estimate Obtained by Measuring During the Whole Day (24 Hours) Relative to the Estimates Obtained by Measuring Only During Midday (1000–1400 LT) and During Office Hours (0800–1600 LT)^a

Site	Community	Integration Period	Flux for 24 Hours/ 0800–1600 LT	Flux for 24 Hours/ 1000–1400 LT
3	<i>Carex, Calamagrostis</i>	3 days, Aug.	1.03	1.07
3	<i>Carex</i>	3 days, Aug.	1.11	1.13
4	<i>Eriophorum, Molinia</i>	3 days, June	1.00	0.94
4	<i>Eriophorum, Molinia</i>	3 days, Aug.	0.92	0.92
4	<i>Carex, Potentilla</i>	3 days, June	1.05	0.98
4	<i>Carex, Potentilla</i>	3 days, Aug.	1.07	1.07
5	<i>Agrostis</i>	3 days, June	1.00	1.00
5	<i>Carex</i>	3 days, June	1.10	1.18
5	<i>Carex</i>	3 days, Aug.	1.00	1.40
5	<i>Carex</i>	3 days, Aug.	0.94	1.00
2.1	<i>Calamagrostis</i>	July–Aug.	1.00	1.00
2.2	<i>Calamagrostis</i>	July–Aug.	1.21	1.26
2.3	<i>Calla, Potentilla</i>	July–Aug.	1.07	1.10
2.4	<i>Potentilla</i>	July–Aug.	1.08	0.98
2.5	<i>Phragmites</i>	July–Aug.	0.62	0.54
2.6	<i>Phragmites</i>	July–Aug.	0.64	0.75
1.1	<i>Phragmites</i>	July–Oct.	0.91	0.88
1.2	<i>Phragmites</i>	July–Oct.	0.58	0.56
1.3	<i>Phragmites</i>	July–Oct.	0.66	0.67
1.4	<i>Phragmites</i>	July–Oct.	0.69	0.59

^aA value below 1 means that, on the average, a measurement (e.g., during office hours) overestimates daily CH₄ flux and vice versa. Note that the integration periods vary from days to months.

campaigns were carried out in three sites having a total of 10 plots within the temporarily flooded littoral zone. These measurements were performed in August 1995 in the site 3, and in both June and August 1999 in the sites 4 and 5. Automatic and manual measurements were made *c.* every fifth and fourth hour, respectively (Time GMT+2).

2.2. Methane Flux Measurements

[8] The automated and manual measurements were made using a closed chamber method [Crill *et al.*, 1988]. During the measurement, aluminum chamber (60 × 60 × heights 20–70 cm) was fitted airtightly into the water-filled groove of the preinstalled collars. During the 20-min measurement period, four gas samples were drawn from the chamber at 5-min interval. Gas samples were analyzed using a gas chromatograph (Shimadzu GC-14-A, Japan, or Perkin-Elmer F-22, Germany) equipped with a 1 m Porapak Q80–100 column and a FID. Gas fluxes were calculated from the linear ($r^2 > 0.90$) change in chamber CH₄ concentration. The automated measurement system consisted of a PC with a controlling program, data acquisition board, gas chromatograph, and up to six aluminum measurement collars and chambers. A trailer at the lakeshore housed the PC and GC, to which the chambers were connected with 50 m long gas tubing. Opening and closing of the chambers was performed pneumatically, and during the closing and opening stages, the chambers were vented through a valve in order to minimize the pressure changes. When a chamber was closed the magnetic valves were opened and the headspace gas was circulated continuously between the chamber and the laboratory cabin at a rate of 1 L min⁻¹ by means of pumps. Fans mixed the air in the chamber. During a 20-min closure a subsample of chamber air was injected for analysis at 5-min interval. Each chamber was closed and the flux measured approximately every fifth hour. Some measurements had to be rejected due to an occasional failure in the mechanism or due to sample loss in

the detector. The system is described in detail by *Silvola et al.* [1992], and has been applied earlier also in a mire [Kettunen *et al.*, 2000] and in farmed lands [Maljanen *et al.*, 2002].

[9] Temperature in the air, headspace and sediment and the height of the water level were recorded at the same time with the gas measurements. Solar irradiance (Li-Cor pyranometer sensor LI-200SB) was measured in the middle of the *Phragmites australis* stand at the automate measurement site. Above ground biomass in the automate plots was harvested in the end of August in the site 2, and was estimated for the plots in the site 1. Wind speed, relative humidity and air temperature data were obtained from Joensuu airport for the site 1. The weather station located within 20 km from the study site.

[10] In order to evaluate the effect of the closed chamber on the ventilation of *Phragmites australis*, and to study the roles of a single plot and adjacent stand on gas fluxes, culms in the measurement plots and adjacent stand were manipulated in the site 1. This was done in plots close to the site of the primary measurements. In order to exaggerate the culm destruction in a plot and to prevent gas ventilation in the vicinity of measurement plot the culms in the measurement collars were cut 5 cm above the water surface, and the surrounding culms, within a radius of 1 m, were cut 5 cm below the water surface. We hypothesized that this attenuates the diurnal differences in CH₄ fluxes. Later, the culms in the measurement collar were also cut 5 cm below the water surface.

2.3. Data Analyses

[11] Differences in CH₄ flux estimates calculated from all measurements round the clock and measurements conducted only specific times of day were investigated. Values in Table 2 represent the ratio of the mean CH₄ flux on the basis of several measurements over 24 h relative to the mean flux on the basis measurements only during office

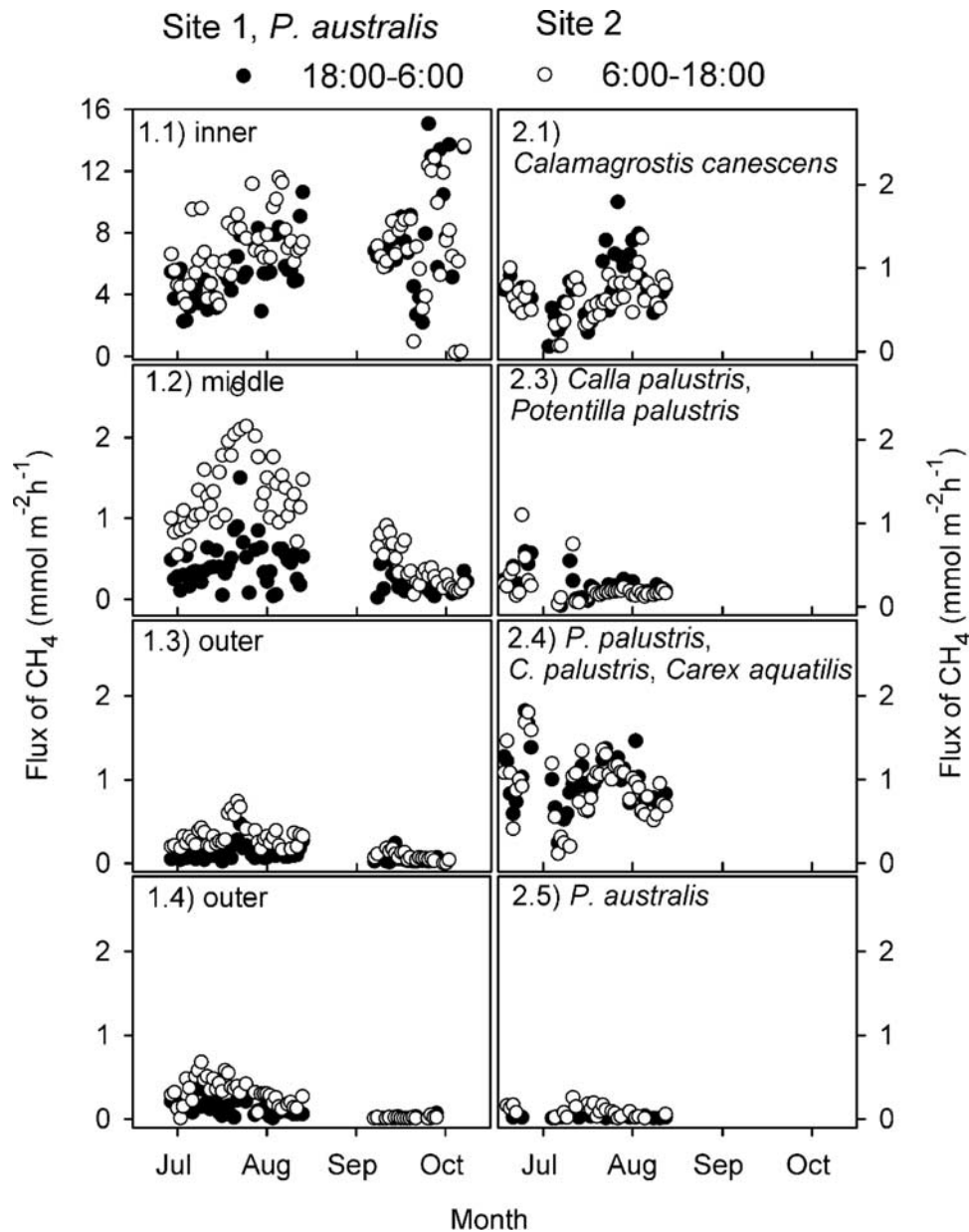


Figure 1. Automatically measured CH₄ fluxes averaged for 12-hour periods in (left) site 1 and (right) site 2. Day and night periods are indicated with open and closed symbols, respectively. Note the different scale on the y axis for plot 1.1.

hours (0800–1600 local time (LT)) and only during midday (1000–1400 LT), for example, mean flux of whole day (24 hour)/mean flux between 0800 and 1600 LT. The closer the ratio is to value 1, the closer the two estimates are. Comparisons were made with periods as long as possible (up to months) and with shorter ones. The automatically recorded data were analyzed chamber by chamber, and the manual data were reduced to average values for each vegetation community. The possible contribution of environmental factors as dynamic regulators of the CH₄ flux were investigated in more detail in the *Phragmites australis* community using the long observation series from the site 1. Stepwise linear regression was used to quantify the effect of environmental factors driving the fluctuation in the fluxes.

The innermost plot (1.1) in the site 1 was excluded from the analysis due to its extremely high CH₄ emission, which diminished the diurnal variation. The contributions of solar irradiance, air temperature and relative humidity, and wind speed to the variation were subsequently tested using regression analysis. In order to eliminate the causes of temporal variation other than the diurnal ones, the data from each of the three remaining plots were divided into 7-day blocks, conforming to calendar weeks. The dependent variable (CH₄ flux) and irradiance were both log_e transformed.

[12] A sample set consisting of 70% of the observations from three measurement plots was used to develop a more simple predictive model, based on harmonic regression, for

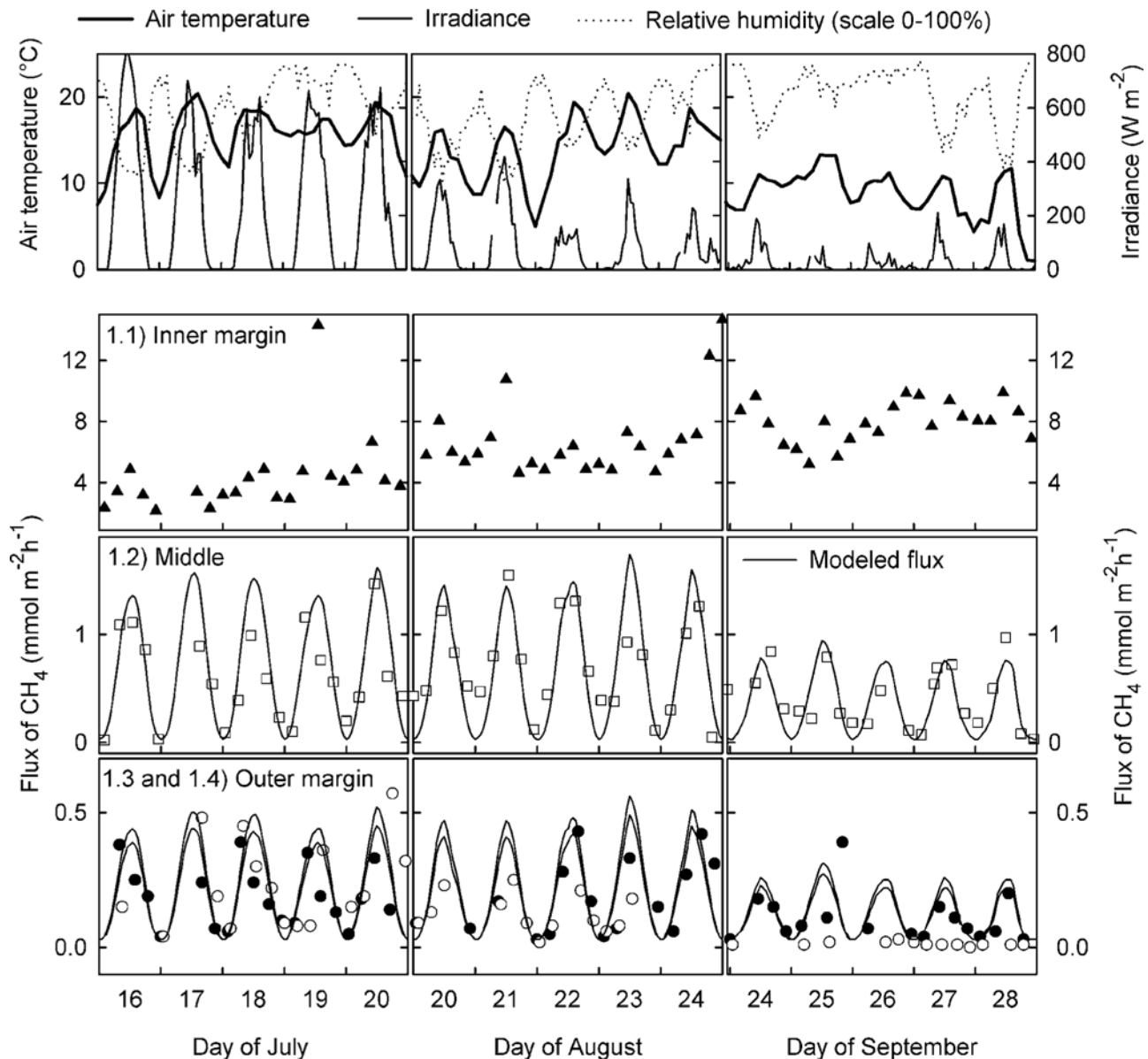


Figure 2. Air temperature, irradiance, relative humidity, and CH₄ fluxes during 5-day periods in July, August, and September in the *Phragmites australis* stand of site 1. (top) Weather data and (bottom) measured instantaneous CH₄ flux (open and closed symbols) and modeled flux (line) are given. Symbols indicate different plots. For the model, see Table 4. Note the different scales on the y axes.

diurnal fluxes of CH₄ (mmol m⁻²h⁻¹) over the open water period for the stand of *Phragmites australis* stand (site 1):

$$CH_4 = a + b_1 \times BM \times T_{sed} \times T_{air} \times \sin\left[\frac{\pi(b_2 - h)}{24}\right]^2, \quad (1)$$

where a , b_1 and b_2 are parameters, BM denotes the end season aboveground biomass, T_{sed} and T_{air} , sediment (–20 cm) and air temperature (°C), respectively, and h is running hour. The rest of the data were used for validation. Calculations were made using SPSS, version 10.1.0 [SPSS inc.].

3. Results

[13] Diurnal fluctuation in CH₄ emissions was strong in the *Phragmites australis* plots, while the fluctuation in other

communities dominated by wetlands species, for example, *Calamagrostis canescens*, *Calla palustris*, *Carex* spp., *Eriophorum angustifolium*, and *Potentilla palustris*, was generally weak (Figure 1). The *P. australis* plots showed the highest effluxes of CH₄ around noon, at which time the effluxes were even more than tenfold the lowest effluxes during the night (Figure 2). However, the magnitude in the diurnal fluctuation of CH₄ flux varied in different *P. australis* plots, even within the same stand. The ratio of mean midday (1000–1400 LT) CH₄ flux relative to the mean daily (24 hour) flux was on average 0.67 in six plots, but it varied from 0.54 to 0.98 (Table 2). The day-night difference was largest in the middle and densest part of the site 1, and in the plot with larger biomass in the site 2. The difference was clearly smallest in the inner stand margin of site 1 (plot 1.1), where CH₄ efflux was very high, also

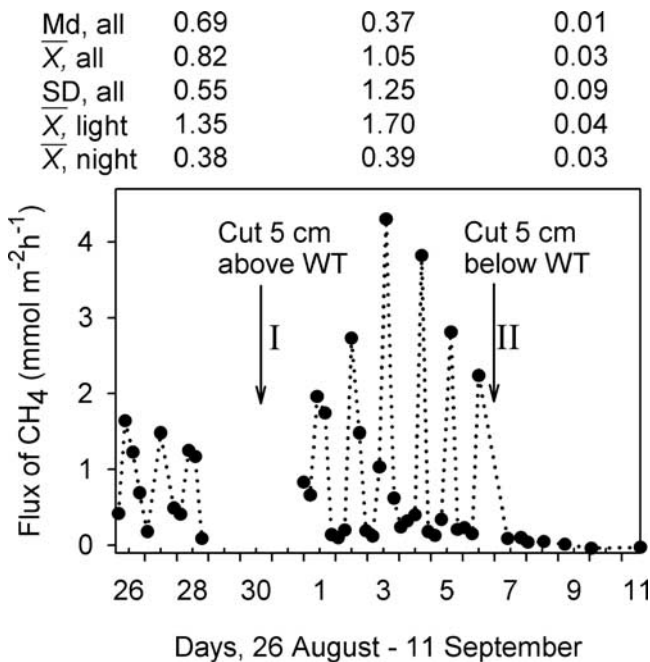


Figure 3. Example of the effect of culm manipulation on CH₄ fluxes in a *Phragmites australis* plot. Arrow I indicates the time when the culms in the measurement plot were cut 5 cm above the water surface and culms within a 1-m radius outside the plot were cut 5 cm below the surface. Arrow II indicates when the culms in the measurement plot were cut 5 cm below the water table. Median (Md), mean (\bar{X}), and standard deviation (SD) of the CH₄ flux are given for each phase. Mean values are also given separately for daylight and night times.

during the nighttime (Figure 1). An average flux of CH₄ measured during office hours should be corrected with a factor 0.68 (range 0.58–0.91) to obtain more reliable CH₄ flux estimate for a day (Table 2). It seemed that diurnal fluctuation in CH₄ efflux weakened toward the end of the season. In the plot 1.2 having a large diurnal fluctuation, for example, the mean flux of CH₄ over 24 hours was 0.52 times the mean efflux of CH₄ during midday (1000–1400 LT) in August, and 0.69 times that in October. The corresponding values were 0.81 and 1.01 in the plot with the smallest daily differences in fluxes of CH₄.

[14] Cutting the culms 5 cm above the water surface in the plots and 5 cm below the water surface (no influx or efflux) within a 1-m radius surrounding the plot did not attenuate the diurnal flux dynamics of CH₄ (Figure 3). In addition, the mean flux of CH₄ and its standard deviation increased compared to the situation preceding the cutting, while the median decreased. The efflux of CH₄ was attenuated when the culms in the measurement plots were cut below the water surface.

[15] Weekly variation in the fluxes of CH₄ were correlated with the variation in solar irradiance, air temperature, relative humidity, wind speed, and, to a lesser extent, occasionally with sediment temperature at a depth of 20 cm below the sediment surface. These variables correlated strongly with each other so that air temperature often followed, with a certain time lag, the changes in irradiation

(Figure 2). Further, the diurnal pattern of relative humidity was often reverse to that of irradiance, and wind speed was frequently highest during the daylight hours. In stepwise linear regression, the variation of solar irradiance alone explained 39–73% of the weekly variation in the fluxes of CH₄ during midseason (Table 3 and Figure 4). Relative humidity, in turn, explained 10–72% of the weekly variation in the fluxes, particularly at the end of the season and in the outermost plot, that is, in cases where the fluxes of CH₄ were the smallest. In some cases, air temperature and wind speed gave additional explanation. Seasonal variation in the flux of CH₄ between July and October followed the changes in the sediment temperature. Standing biomass seemed to explain spatial differences in CH₄ fluxes (Figure 4). However, aboveground biomass alone cannot explain very high CH₄ effluxes in the inner stand margin.

[16] The hourly CH₄ fluxes from the site 1 were reconstructed over the latter half of the open water season by using Equation 1 (Figure 2 and Table 4). The model reasonably well captured seasonal, spatial (three plots), and hourly variation in fluxes of CH₄ ($r^2 = 0.73$) (Figure 5). The model produced underestimates for the highest CH₄ effluxes, and overestimates for October especially in the plot with the smallest measured effluxes (the outermost plot). Cumulative fluxes of CH₄ reconstructed using the model equaled 87%, 103%, and 103% of the corresponding seasonal estimates calculated using mean values of the measured fluxes in the plot in the middle of the stand, and in the outer margin of two plots, respectively. The cumulated fluxes were compared only over those weeks for which measured values were available.

[17] The range of diurnal variation in the CH₄ fluxes was much smaller in the plant communities of the temporarily flooded littoral zone than that in the *Phragmites australis* communities (Figure 1). Often the maximum in CH₄ efflux occurred during the afternoon, evening, midnight or even shortly after midnight, while the minimum occurred in the morning or midday. The mean CH₄ efflux over 24 h was 0.92–1.20 times the efflux during the office hours (Table 2). In about one half of the cases measuring only between 0800 and 1600 LT lead to a slightly too low estimate of daily CH₄ efflux. Sporadically, however, there were substantial differences in the daytime and night fluxes of CH₄. The automated measurements made over July and August revealed that two adjacent *Calamagrostis canescens* plots and one nearby *Calla palustris*/*Potentilla palustris* plot had a large day to night variation in the CH₄ fluxes during the first half of August (Figures 1 and 6). During this period, the mean efflux of CH₄ over 24 hours was 1.4 and 1.5 times that during the midday (1000–1400 LT) in the two *C. canescens* plots, while the corresponding values over the whole 2-month period were 1 and 1.26 (Table 2). The period of large diurnal differences was associated with an overall increase in the efflux of CH₄, caused by a rise in the water level. The temperature in deep sediment (>20 cm) showed low diurnal fluctuation, with a maximum at night, but no significant correlation was found between the sediment temperature and the flux of CH₄.

4. Discussion

4.1. *Phragmites Australis*

[18] Systematic diel fluctuation in CH₄ flux was recognized in every *P. australis* plot. It seems that often the

Table 3. Regression Models, $\ln [\text{CH}_4 \text{ flux} + 1] = a + b_1X_1 + \dots + b_nX_n$, Explaining the Weekly Variation of CH₄ Fluxes in *P. australis* Plots 1.2, 1.3, and 1.4^a

Site	Week ^b	<i>a</i>	ln [solar irradiance], W m ⁻²		<i>T</i> _{air} , °C		RH, %		Wind Speed, m s ⁻¹		Degrees of Freedom		<i>F</i>
			<i>r</i> ²	<i>b</i>	<i>r</i> ²	<i>b</i>	<i>r</i> ²	<i>b</i>	<i>r</i> ²	<i>b</i>	Regression	Residual	
1.2	28	0.153 ^c	0.58	0.073 ^c							1	15	23 ^c
1.2	29	0.162 ^d	0.65	0.084 ^c							1	26	51 ^c
1.2	30	0.235 ^c	0.71	0.105 ^c							1	25	66 ^c
1.2	31	0.500 ^c	0.44	0.098 ^c							2	24	19 ^c
1.2	34	0.968 ^d	0.52	0.066 ^d			0.10	-0.009 ^c			2	24	22 ^c
1.2	39	0.795 ^c			0.13	0.028 ^d	0.58	-0.009 ^c			2	26	36 ^c
1.2	40	1.379 ^c					0.64	-0.013 ^c			1	22	43 ^c
1.3	28	0.033	0.59	0.021 ^d							1	11	19 ^d
1.3	29	0.105 ^c	0.49	0.024 ^c							2	22	17 ^c
1.3	30	0.097 ^c	0.44	0.022 ^c							1	21	18 ^c
1.3	31	0.205 ^c	0.39	0.042 ^d							1	21	18 ^c
1.3	34	0.733 ^c	0.60	0.042 ^c							1	17	27 ^c
1.3	39	-0.079			0.39	0.019 ^d					1	23	17 ^c
1.3	40	0.276 ^c					0.43	-0.003 ^c			1	26	22 ^c
1.4	28	0.387 ^c					0.32	-0.003 ^c			2	13	15 ^c
1.4	29	0.972 ^c					0.43	-0.009 ^c			2	22	19 ^c
1.4	30	0.489 ^c					0.71	-0.006 ^c			2	29	59 ^c
1.4	31	0.648 ^d	0.73	0.049	0.04	-0.013 ^c	0.03	-0.005 ^d	0.08	0.041 ^d	3	22	35 ^c
1.4	34	0.213 ^d			0.13	0.007 ^d	0.72	-0.003 ^c			2	14	41 ^c
1.4	40	0.155 ^c					0.41	-0.001 ^c			1	7	6 ^c

^aIndependent variables tested were solar irradiance, air temperature (*T*_{air}) at height of 2 m, relative humidity (RH), and wind speed. Probability of 0.05 for *F* was used as a stepping method criterion in stepwise regression. Partial coefficients of determination (*r*²) are given before the regression coefficients.

^bWeek 28 is 9–15 July, week 29 is 16–22 July, week 30 is 23–29 July, week 31 is 30 July to 5 August, week 34 is 20–26 August, week 39 is 24–30 September, and week 40 is 1–7 October.

^cSignificance level is *P* < 0.05.

^dSignificance level is *P* < 0.01.

^eSignificance level is *P* < 0.001.

magnitudes of diurnal variation in CH₄ flux are comparatively similar, but that spatial and seasonal variations in fluctuation magnitude do exist. In a Nebraskan *P. australis* stand, measured by eddy correlation technique, the average CH₄ efflux during nighttime (2000–0600 LT) was 47% of the efflux during daytime (0800–1800 LT) over late May to mid-September, varying from 36% to 63% during the season [Kim *et al.*, 1998a]. In a Danish mesocosm study the corresponding percentage, calculated from values in study of Grünfeld and Brix [1999], ranged from 60 to 75% in September. In our study the mean nighttime fluxes in different plots were from 29% to 85% (mean of six plots was 42%) of mean daytime fluxes over July to October. A distinct diurnal pattern in the fluxes of CH₄ was found only occasionally in boreal lake littoral belts of *P. australis* and *Typha latifolia*, as determined in several campaigns, and in the case of *P. australis* the pattern did not become evident until August [Käki *et al.*, 2001].

[19] Seasonal mean CH₄ efflux increased with increasing aboveground biomass, which indicates that vegetation has positive effect on CH₄ production and emission, in line with previous works [Torn and Chapin, 1993; King *et al.*, 2002]. An exception was, however, the plot with very high CH₄ release. In that place accumulated litter could explain great CH₄ formation as the plot located in inner stand margin [cf. Juutinen *et al.*, 2003; Kankaala *et al.*, 2004]. Spatial variation in the daily fluctuation magnitude of the CH₄ flux between different plots showed no clear relationship with CH₄ flux or with aboveground biomass of plots. It may, however, conform to the vegetation pattern affecting both the CH₄ production and convective flow pattern of the stand, that is, relationship between CH₄ production rate

and rate of convective flows. For example, the diurnal differences in CH₄ efflux were strikingly small (Table 2) in the inner margin plot (1.1) of the stand even though diurnal fluctuation pattern was detectable (Figure 2). A reason may be very high production of CH₄, and the subsequently large storage of CH₄ in the sediment, that is not exhausted by convections in daylight, and that enables strong diffusive flux of CH₄. Similarly, the sparsely vegetated, detritus accumulating outer margin of a *P. australis* stand in a boreal lake Vesijärvi had comparatively high effluxes of CH₄ with no diurnal pattern as a consequence of sporadic ebullition of CH₄ [Käki *et al.*, 2001]. Sporadic ebullition, however, was not a striking feature in the inner margin plot (1.1) of the present study.

[20] The largest diurnal differences in the flux of CH₄ occurred in most plots during August when the overall release rate of CH₄ was the greatest (Figure 1). In autumn the diurnal differences leveled off. Similar patterns of seasonal variation in the diurnal CH₄ flux dynamics in a *P. australis* stand have been reported by Kim *et al.* [1998a]. We did not measure the fluxes of CH₄ before July. However, the diurnal dynamics in CH₄ fluxes only appear after the emergence of new culms that enable the formation of internal pressurization [Kim *et al.*, 1998a]. Development of vegetation further enhances the capacity as the highest internal pressures and flow rates occur during or slightly after the seasonal biomass maximum [Arkebauer *et al.*, 2001]. At the same time, apparently, higher organic matter supply in warm conditions supports a larger CH₄ production, increasing the amount of CH₄ that can be flushed out by convective flow. In autumn the senescent tissues of *P. australis* apparently become brittle and can no longer

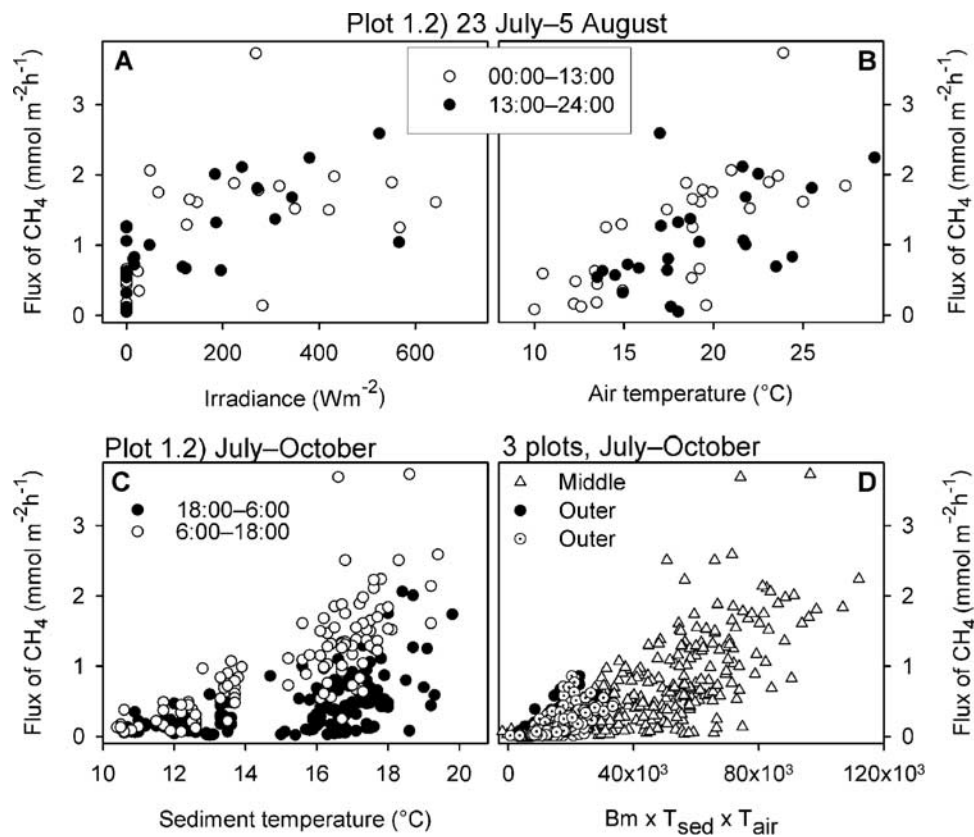


Figure 4. Relationship between the CH₄ flux and certain environmental variables in the *Phragmites australis* stand of site 1 (a and b) during two weeks of August in one plot and between July and October (c) in one plot and (d) in three plots. $Bm \times T_{sed} \times T_{air}$ denotes the product of approximated end season aboveground biomass (in g) in a plot and sediment and air temperature (°C).

fully support the pressurization. Cracking sounds in senescent *P. australis* and *Typha latifolia* L. stands, which we also heard in our study sites, on clear autumn mornings have been interpreted as rupturing due to increasing internal pressure [Sebacher et al., 1985; Kim et al., 1998a]. The longest observation series in the present study, lasting from mid-July to mid-October, did not cover the early part of the summer. However, if the early and late halves of the season are similar with respect to the diurnal differences in the CH₄ fluxes, the data can be used to represent the whole ice-free season.

[21] Solar irradiance was the most important environmental variable driving the daily course of CH₄ flux within *Phragmites australis* (Table 3). However, when the overall effluxes of CH₄ were low, that is, at the end of the season and in the outermost plot, the variation in relative humidity and air temperature explained much of the diurnal fluctuation in CH₄ release. Overall, the same factors were found to correlate with the CH₄ fluxes also in a Nebraskan *P. australis* marsh. Also there, irradiance became a less important factor at the end of the season [Kim et al., 1998b]. The relationship between irradiance and the CH₄ flux is apparent. However, it is not linear, because the release of CH₄ to the atmosphere is proportional to the production of CH₄ in the rhizosphere and storage in the plant, and the rate limiting step is the diffusion rate of CH₄ into the root aerenchyma [Chanton et al., 1993; Kelker and Chanton, 1997; Yavitt and Knapp, 1998; Beckett et al., 2001].

Therefore a vigorous increase in CH₄ release follows an increase in light intensity after dawn, but the daily maximum in the efflux of CH₄ can occur earlier than that in irradiance (Figure 4), [Whiting and Chanton, 1996; Yavitt and Knapp, 1998; van der Nat et al., 1998; Käki et al., 2001]. Furthermore, the amount of CH₄ flushed during the daylight hours can possibly determine the residual flux for the evening and night.

[22] The suitability of closed chambers for measuring in ecosystems of species that vent by means of convective flows, for example, *Phragmites australis*, has been questioned because the internal pressure and convective flow is generated by differences in temperature and humidity, induced by irradiance, between the ambient air and internal lacunae [Brix et al., 1996; Arkebauer et al., 2001]. Closure of the chamber may increase the relative humidity in the headspace or decrease the temperature difference between plant and its surroundings. In addition, immediate light

Table 4. Parameters for the CH₄ Reconstruction Model (Equation (1))

Parameter	Coefficient	Asymptotic SE
a	0.029864	0.0154
b_1	0.000023	0.0000007
b_2	0.242187	0.1626
r^2	0.73	
Degrees of freedom (regression)	3	
Degrees of freedom (residual)	466	

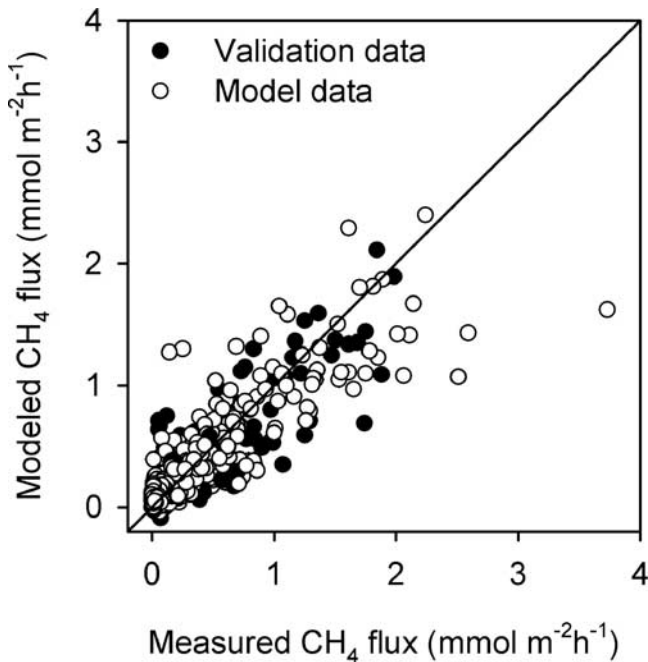


Figure 5. Comparison of measured and modeled fluxes of CH₄ for three *Phragmites australis* plots in site 1.

variations and therefore use of dark chambers have been reported to affect CH₄ flux measured in *P. australis* stands [van der Nat et al., 1998; van der Nat and Middelburg, 2000]. However, in our measurements a typical diurnal fluctuation in CH₄ flux was found in the *P. australis* communities. The pattern and magnitude was similar to that measured elsewhere using, for example, the eddy correlation technique that keeps vegetation intact (see the first paragraph of discussion). Apparently, the effect of the chamber on the fluxes of CH₄ can be small or negligible. One explanation for this can be that convective through flow of the *P. australis* stand is integrated via rhizome connections [see Armstrong et al., 1996]. More limited flow connections were suggested, however, in an experiment where ethane was injected into green *P. australis* culm, and found only in its nearest brown culm, not in any others [Chanton et al., 2002].

[23] In our culm experiment, diurnal flux dynamics of CH₄ was not attenuated even though the culms in the plot were radically shortened and when the gas exchange of culms surrounding the measurement plots was blocked by cutting them below the water surface (Figure 3). This suggests that even the stumps maintained gas flow dynamics within a chamber. Alternatively, the intact stand one meter apart from the measurement plot supported pressurized ventilation, which contrast with result of the above mentioned ethane injecting experiment of Chanton et al. [2002]. The increase in daytime CH₄ fluxes and in magnitude of the diurnal fluctuation following the culm manipulation could be associated with a reduced number of efflux sites per unit area, or with increased CH₄ production following some plant death and release of labile compounds and decreased CH₄ oxidation due to attenuated oxygen transport into rhizosphere. A feature of *Typha* sp. and Nymphaeaceae is that gas circulation occurs within an individual plant only [Dacey and Klug, 1979; Sebacher et al., 1985; Dacey, 1987; Chanton et al., 1993; Yavitt and Knapp,

1998]. In those cases the use of an opaque chamber could attenuate convective flows, as suggested by results of Whiting and Chanton [1996].

[24] We tested a simple harmonic regression model for reconstructing the hourly fluxes of CH₄ over seasonal and spatial scales. In the model easily measurable variables affecting the seasonal and spatial pattern of the production of CH₄—temperature of the sediment and air and above-ground biomass—determined the daily flux and fluctuation magnitude. The reconstruction occasionally deviated significantly from the measured instantaneous values, because the model was not capable of capturing the highest episodic fluxes of CH₄, as well as because the fluctuation amplitude was fixed (24 hours) while there was real variation in the timing of the CH₄ flux maximum. Nevertheless, the CH₄ fluxes accumulated from the hourly model estimates fell within 13 percentage units of the flux estimate on the basis of the observed values. It is worth noting that our data covered only the latter half of the open water season.

4.2. Communities of Wetland Species

[25] Communities of wetland species in the temporarily flooded littoral zone generally showed only small diurnal variation, and evidently, convective flow was not involved in ventilation. Occasionally, however, there was substantial diurnal variation in the CH₄ fluxes and, during these periods, the daytime measurements alone would lead to an underestimated CH₄ efflux for the whole day. We captured a period with large diurnal variation in three plots that were monitored automatically (Figures 1 and 6). An increase in diurnal differences in the CH₄ fluxes could be caused by the enhanced oxidation of CH₄ in the sediment surface during daytime as a consequence of benthic primary production and oxygen release [King, 1990]. The observation was made after the water had risen up to 10–15 cm above the soil surface in early August. In the study of King [1990], nighttime emissions were 3.1–3.7 times higher than the emissions during the light period in marsh sediment cores with an algal mat, while the difference was smaller in cores without an obvious algal mat. The occurrence of such a strong phenomenon may

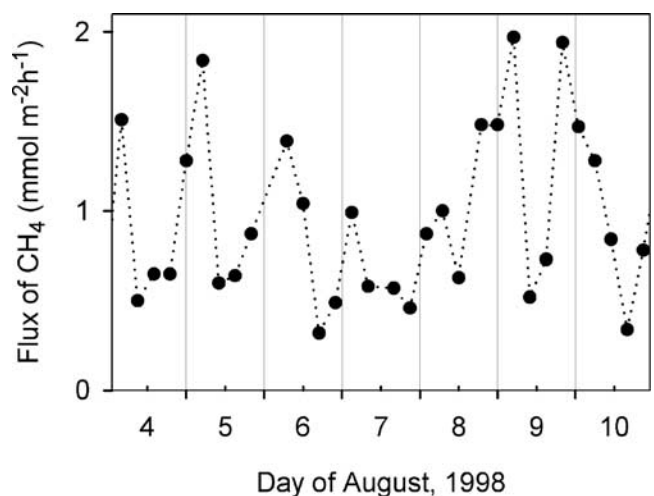


Figure 6. Fluxes of CH₄ in the *Calamagrostis canescens*-dominated plot (2.1) during early August. The grid lines indicate midnight.

be restricted to certain conditions that only persist for shorter periods of time.

[26] A marked diurnal fluctuation in the fluxes of CH₄ has also been reported in some mire sites. Mikkelä *et al.* [1995] found higher nighttime effluxes in dry, but not in wet communities of a boreal mire. In a *Carex rostrata* dominated mire the nighttime fluxes of CH₄ were 3–4 times greater than the 24-hour average [Waddington *et al.*, 1996]. Decreased oxidation of CH₄ as a consequence of lower night temperatures was suggested to cause the diurnal variation in dry mire sites [Mikkelä *et al.*, 1995]. In a *C. rostrata* site, the nighttime maximum in the CH₄ flux coincided with a maximum in the pore water CH₄ concentration, indicating that the substrate supply regulated the diurnal dynamics, apparently following the daily photosynthetic CO₂ fixation with a time lag [Waddington *et al.*, 1996]. Higher release of CH₄ during the evenings and nighttime were found to be independent of the fluctuation in peat temperature also in a wet tundra and in an *Eriophorum angustifolium* lawn [Whalen and Reeburgh, 1988; Thomas *et al.*, 1996]. However, the effect of temperature on production and diffusion of CH₄ might explain the small maximum in the efflux of CH₄ in late afternoon hours, as found in a *Carex* dominated subarctic fen and in a nonvegetated sediment surface [Whiting and Chanton, 1992; van der Nat *et al.*, 1998]. The eddy correlation measurements of Fan *et al.* [1992] showed that efflux of CH₄ from a lake dominated landscape was 50% higher during daytime due to higher wind speeds compared to night. No diurnal trends in CH₄ fluxes were found in *Carex* and *Calamagrostis* dominated wetland sites or in an *Equisetum fluviatile* L. stand [Moosavi and Crill, 1997; Hyvönen *et al.*, 1998]. The diurnal fluctuation in CH₄ follows different modes in individual wetland communities, and appears to depend on a large number of factors.

4.3. Conclusion

[27] These results suggest that the modeling and integration of CH₄ fluxes should be based on several observations of CH₄ fluxes per day. If continuous measurements of CH₄ fluxes with frequent interval are not available, diurnal fluctuation in CH₄ fluxes could be quantified by conducting intensive campaigns. Ideally, such a sampling should be conducted in several locations and several times per the chosen site and season. Particularly this is needed in the case of aquatic species venting by convective flow, because within those species CH₄ fluxes vary within a day in a range comparable to seasonal variation in CH₄ release. In addition, other reasons can sometimes result in substantial diurnal variation in communities venting only by diffusion.

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