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Diurnal variation in methane emission in relation to the water table, soil temperature, climate and vegetation cover in a Swedish acid mire

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Abstract. Diurnal variation in the rate of methane emission and its relation to water table depth and macro climate was studied in several plant communities within an acid, *Sphagnum* dominated, mixed mire in Northern Sweden. Provided that diurnal variation in solar radiation and air temperature occurred, methane fluxes differed during day and night. Diurnal patterns in methane emission rates were found to differ among mire plant communities. In relatively dry plant communities (ridges, minerotrophic lawn), the average nighttime emission rates were 2–3 times higher than the daytime rates during the two periods with high diurnal variation in solar radiation and air temperature. Methane emission was significantly ($p < 0.05$) related to solar radiation and soil temperature at depths of 5 and 10 cm at all sampling points in the dry plant communities. In the wetter plant communities, no significant difference between daytime and nighttime average methane emission rates were found even though methane emissions were significantly related with radiation and soil temperature at approximately 70% of the sampling points. The increased emission rate for methane at night in the comparatively dry plant communities was probably caused by an inhibition of methane oxidation, owing to the lower nighttime temperatures or to a delay in the supply of root-exuded substrate for the anaerobic bacteria, or by both. The pattern observed in the wet plant communities indicated that methane production were positively related either to soil temperature or light-regulated root exudation.

Introduction

On a global scale, CH_4 release from wetlands should affect the global budget of atmospheric CH_4 (Fung et al. 1991). However there is great uncertainty regarding the magnitude of emissions from wetlands (Roulet et al. 1992). Any factor influencing the processes by which CH_4 is produced by methanogenic microorganisms or oxidized by methanotrophic microorganisms can influence net emission rates. Temporal variability in CH_4 flux within ecosystems is high owing to variations in factors such as groundwater level (Svensson et al. 1975; Sebacher et al. 1986; Moore & Roulet 1993), soil temperature (Svensson 1984; Moore & Knowles 1987; Crill et al. 1988), photosynthetic activity (Whiting & Chanton 1992; Happell et al. 1993; Chanton et al. 1992) and methane oxidation (Yavitt et al. 1990a; Whalen et al. 1991; Sundh et al. 1994a, b).

Diurnal variation in net methane emission rates has been observed in several different methane-emitting environments. In a temperate wetland, the CH_4 flux rate differed significantly between day and night (Yavitt et al. 1990b). During the summer period, nocturnal CH_4 emissions were twice as high as daytime rates, whereas in the autumn the relation was vice versa. Similarly, in a study of Arctic tundra soils, the methane emission rate differed between day and night; however, methane flux was not consistently related to soil temperature or time of day (Whalen & Reeburgh 1988). In *Carex*-dominated fens in Quebec, the diurnal fluctuation in CH_4 emission was related to changes in sediment temperature (Whiting & Chanton 1992). Diurnal changes in CH_4 flux from rice paddy fields in USA (Sass et al. 1991), Italy (Schütz et al. 1990a), China (Seiler et al. 1984) and Japan (Yagi & Minami 1990) have also been reported. In most of the rice paddies studied, emissions were in most cases higher during the day than at night.

The presence of vascular plants on mires may influence net methane emission rates. Vascular plants translocate photosynthate to their root and, subsequently, to the rhizosphere (cf. Van Veen et al. 1989). This process also has been shown to occur in species growing on mires (Wallén 1986). During anaerobic conditions, part of the exudate will be decomposed to methane. Vascular plants may also mediate gas mass transport from the anaerobic zone to the atmosphere. Up to 95% of the emissions may represent plant-associated transport (e.g. Dacey & Klug 1979; Cicerone et al. 1981; Whiting & Chanton 1992; Morrissey et al. 1993). A further possible process is that plants can attenuate emissions by transporting oxygen from the atmosphere to the rhizosphere, that supports methane oxidation and thus reduces CH_4 emissions (Conrad 1989).

Aerobic methane oxidation is an important regulator of methane emissions from mire ecosystems (Yavitt et al. 1990a). The impact of methane oxidation on net emission rates is largely determined by the degree to which the aerated zone extends above the water table level and by the pore-water concentration of methane, i.e. the supply of methane to the methanotrophs (Sundh et al. 1994a, b). Actual rates of methane production and oxidation at a given site will be influenced by the peat temperature (Dunfield et al. 1993; Sexstone & Mains 1990; Whalen et al. 1990). In a preliminary report, Mikkelä et al. (1992) provided evidence for temperature-regulated methane emission coupled to the temperature response of the methanotrophic bacteria in certain peat areas.

The aim of the study was: (I) To compare the diurnal pattern in CH_4-emission during different weather conditions. (II) To reveal if the variation in CH_4-emission is related to the environmental parameters, which change during a 24-hour period. To achieve this above described goals we measured the diurnal fluctuations in methane emission on three occasions in seven different plant communities on an acid mixed mire in central Sweden.

Materials and methods

Site description

The study area is a largely ombrotrophic, Sphagnum-dominated mixed mire 15 km south of Umeå in the boreal zone in Sweden (63°44′ N, 20°06′ E, 35 m altitude). A small part of the mire is minerotrophic. Seven plant communities were distinguished on the basis on the dominant vegetation. The nomenclature follows Lid (1963) for the phanerogams and Koponen et al. (1977) for the *Sphagnum* mosses. The terms used for classifying the plant communities were taken from Gore (1983).

1. Low ridges dominated by *Sphagnum fuscum* in the bottom layer and with *Rubus chamaemórus* and *Oxycoccus quadripétalus* in the field layer. The water table fluctuated over the growing season from ca 5 cm to ca 20 cm below the vegetation surface.
2. Raised ridges dominated by *S. fuscum* in the bottom layer. The water table level fluctuated between 10 and 30 cm below the vegetation surface during the spring and autumn periods, and between 20 and 40 cm depth during the summer.
3. A minerotrophic lawn dominated by *S. majus* and *S. balticum* in the bottom layer. *Carex rostrata, C. limosa* and *O. quadripétalus* dominated the field layer. The water table level ranged from ca 0 cm, in the spring and autumn, to ca 20 cm depth in summer.
4. Lawns dominated by *Sphagnum* (several species, but mainly *S. balticum*) and sparse stands of *Eriophorum vaginatum* in the field layer. The water level ranged from ca 0 cm, in the spring and autumn, to ca 10 cm depth at the end of the summer.
5. Carpets dominated by *S. majus*, with scattered *E. vaginatum*. This community was waterlogged throughout most of the measurement period.
6. Mud-bottom communities with dead *S. majus* covered by a thin layer of liverworts. The water surface was at or close to the vegetation surface throughout the measurement period.
7. Open pool, 8–10 m in diameter. The pool is 1–2 m deep in the center and has *S. majus* growing at the bottom and edges.

Climate, soil temperature and water table level measurements

Global radiation (0.3–4 μm) was measured by a pyrradiometer and air temperature by a glass-thermometer, similar to those commonly used by the Swedish national weather service (SMHI), positioned 1.5 meter above the ground. Precipitation were measured by at tipping-bucket (ARG 100, Campell SCI). Global radiation and air temperature were recorded every 10 min, and precipitation was recorded continuously, then saved as hourly means on a data logger (Model CR10, Campell Scientific Inc. Utah USA) in the center of the research area on the mire. Soil temperatures at 5, 10, 20 and 40 cm depth was registered simultaneously on the three measurement occasions at the 12 sampling points used for diurnal CH_4 flux measurements during August 30–31, 1992. The depth of the water table level at every emission measurement point was manually measured in plastic tubes, with small holes, inserted into the peat. To minimize disturbance, all sampling points, except those along the ridges, could be reached using boardwalks.

Emission measurements and CH_4 analysis

Diurnal emission measurements were made on three occasions: July 17–18 and September 10–11, 1991, and August 30–31, 1992. The rate of CH_4 emission was measured with static metal chambers (surface area 3.8 dm^2, volume 7.2 dm^3) with a hole (1 cm diam) at the closed end. The chambers were gently pushed ca 5 cm into the peat surface, and the holes were closed with gastight rubber stoppers. The chambers were sampled after one hour and were not inserted back into the vegetation surface until it was time for the next measurement, about an hour later. At all plant communities but the low and raised ridges the accumulation of methane is linear ($r^2 > 0.95$, $n = 4$) for one hour. At the low emitting communities the accumulation of methane is linear at $r^2 > 0.9$, $n = 4$ for accumulation rates above 0.3 mg*h^{-1}*m^{-2}. Pre-evacuated bottles (8 ml) with gastight butyl rubber stoppers were used to collect gas samples from the chambers. A double needle was inserted through the chamber membrane and then through the butyl stopper in the bottle. Methane was analyzed on a gas chromatograph (Nilsson & Bohlin 1993). External standards of 10 and 100 ppm CH_4 in N_2 (AGA Gas, AB, Skellefteå, Sweden) were used for calibration.

For the 1991 measurements, three chambers were used in each of the seven plant communities; in 1992, three chambers were used for the low ridges (plant community no. 1) and carpets (no. 5), two chambers each in the raised ridge (no. 2) and the mud-bottom (no. 6) and one chamber each in the minerotrophic (no. 3) and the lawn (no. 4). The open pool (no. 7) was not sampled in 1992. On July 17–18, 1991, the sampling was started at 11.00, and the second measurement period started at 14.00. Emission was then measured every second hour until 12.00 the next day. During September 10–11, 1991, samples were collected at 11.00, 14.00, 16.00, 18.00, 20.00, 22.00, 04.00, 08.00 and 11.00. In 1992, measurements started at 16.00 August 30, and samples were collected every second hour until 14.00 the next day.

Data treatment and statistics

To evaluate the difference between daytime and nighttime CH_4-flux averages, an independent-sample t-test was used (Zar 1984). Differences were considered significant in cases where $p < 0.05$. For the July 1991 and August 1992 measurements, the daytime averages were calculated from flux measurements collected between 10.00 and 20.00; the basis for the day/night division was changes in incoming radiation and air temperature. On September 10, 1991, the radiation was already low at 18.00, so the daytime averages for this date were calculated from 10.00 to 18.00. Nighttime averages were based on the flux rates from 22.00 to 08.00 for July 1991 and August 1992, and from 20.00 to 08.00 for September 1991.

The relationships between soil temperature at the four chosen depths and methane emission were evaluated by linear regression separately for each sampling point. The relation between methane and solar radiation was analyzed by linear regression for all sampling points. The methane emissions were filtered by moving averages, two points wide. The radiation and temperature curves were shifted forward by up to 12 hours relative to the methane measurements to find the highest r^2-value.

Results

July 17–18, 1991

On July 17–18, 1991, the weather was clear, with a maximal air temperature of about 20 °C decreasing to 6 °C at night (Fig. 1A). In all plant communities, changes in the soil temperature at 5 cm depth closely paralleled changes in air temperature (Figs. 1A, 3). The mire was relatively dry, and the water level was 15–40 cm below the vegetation surface at the ridges and in the minerotrophic lawn, and 1–7 cm below the vegetation surface in the *S. balticum* lawns, the carpets and the mud-bottoms (Table 1).

The average daytime and nighttime rates of CH_4 emission differed by a factor of between 2 and 20, depending on the plant community (Fig. 2A). In the ridges and the minerotrophic plant communities, the methane emission rate at night significantly ($p < 0.05$) exceeded the daytime emission (Fig. 2A). At

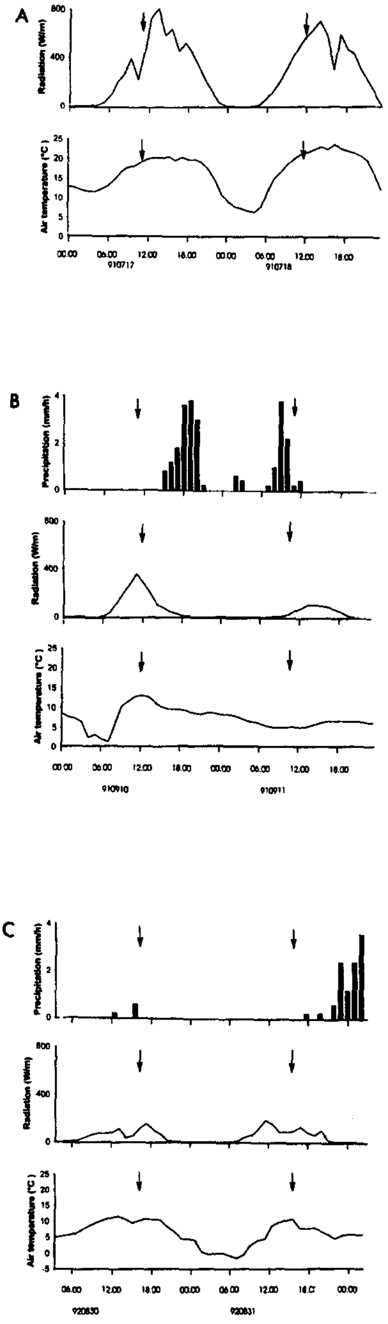

Fig. 1. Air temperature, global radiation and precipitation at Storåmyran on A. July 17–18, 1991, B. September 10–11, 1991, C. August 30–31, 1992. There were no precipitation on July 17–18, 1991, so no precipitation curve is shown. The arrows indicate the time for start and end of the measurements.

Table 1. Water table level in all plant communities, except the pool, during the three measurement periods of diurnal variation in methane emission rates.

	Water table level (cm below vegetation surface)			
Sampling points	91 July 17–18	91 Sept 10	91 Sept 11	92 Aug 30–31
Low ridge	16–21	16–22	8–14	6–10
Raised ridge	28–40	28–38	22–30	13–19
Minerotrophic	15–18	20–22	14–16	3
S. balticum lawn	6–7	6–9	3–6	0
Carpets	2–3	2–3	0	0
Mud-bottom	1	1	0	0

one mud-bottom sampling point, the daytime average exceeded the nighttime average ($p < 0.05$); however, significant differences were not found at the other mud-bottom sampling points or in the *S. balticum* lawn or the carpet (Fig. 2A). At the open pool, the daytime averages were 10–20 times higher than the nighttime averages. However, they were not significantly different because of the large standard deviation caused by the irregular release of methane during the day (Figs. 2A, 3).

The linear regression of methane emission on soil temperature at 5 and 10 cm below the vegetation surface was significant for 10 of 12 sampling points (Table 2A). No significant relations were observed between methane emission and temperature at 20 and 45 cm depth for any sampling point or date; thus, these regressions are not shown. The linear regression of methane emission on incoming radiation resulted in significant relations for 15 of 21 sampling points (Table 2A). Without any forward shift, the relations between methane emission and the soil temperature and radiation for the ridges and the minerotrophic plant communities were negative (temperature or radiation maxima coincided with minimum methane emission). At all except three of these sampling points, the regressions gave higher r^2-values and the relations became positive when the temperature and radiation curves were shifted forward 2–12 h.

September 10–11, 1991

Climatic conditions were mixed during sampling on September 10, 1991, with a clear sky initially before a rainstorm moved in that afternoon, The water level rose between 3 and 8 cm during the sampling period (Table 1). The air temperature decreased slowly from 12 °C at noon the first day to 5 °C at noon the next day (Fig. 1B). Soil temperatures at 10, 20 and 40 cm

Table 2A. Linear regression of methane emission rate, filtered by two points wide moving average, on soil temperature at 5 and 10 cm depth for the points with continuous temperature registration, and on global radiation for all points. Storåmyran July 17–18, 1991. *b*, the slope coefficient; *h*, the number of hours that the temperature and radiation curves has been shifted forward in the regression.

	Temperature 5 cm				Temperature 10 cm				Radiation			
Sampling point	r^2	p	b	h	r^2	p	b	h	r^2	p	b	h
Low ridge 1	0.91	0.000	0.11	10	0.89	0.000	0.25	8	0.35	0.044	0.10	8
Low ridge 2	0.80	0.000	0.20	6	0.85	0.000	0.40	4	0.83	0.000	0.20	10
Low ridge 3	0.70	0.000	0.22	6	0.69	0.001	0.43	4	0.73	0.000	0.19	10
Raised ridge 1									0.95	0.000	0.12	12
Raised ridge 2	0.80	0.000	0.05	10	0.85	0.000	0.10	8	0.90	0.000	0.08	12
Raised ridge 3	0.70	0.001	0.15	6	0.60	0.003	0.20	4	0.59	0.004	0.15	10
Minerotrophic lawn 1									0.84	0.000	−0.43	0
Minerotrophic lawn 2									0.81	0.000	−0.45	0
Minerotrophic lawn 3	0.83	0.000	2.90	10	0.87	0.000	6.25	8	0.81	0.000	−0.91	2
S. balticum lawn 1									0.66	0.001	0.11	4
S. balticum law 2									0.34	0.048	0.11	10
S. balticum law 3	0.68	0.001	0.22	0	0.57	0.004	−0.54	8	0.59	0.004	0.14	4
Carpets 1	0.39	0.031	0.17	8	0.36	0.040	0.24	6	0.40	0.028	−0.11	0
Carpets 2	0.63	0.002	−0.35	8	0.73	0.000	−0.71	6	0.19	0.155	n.s.	n.s.
Carpets 3	0.00	0.928	n.s.	n.s.	0.00	0.817	n.s.	n.s.	0.01	0.828	n.s.	n.s.
Mud-bottom 1	0.30	0.068	n.s.	n.s.	0.26	0.090	n.s.	n.s.	0.12	0.160	n.s.	n.s.
Mud-bottom 2									0.55	0.006	−0.34	4
Mud-bottom 3	0.48	0.012	0.22	0	0.68	0.001	−1.92	2	0.31	0.058	n.s.	n.s.
Open pool 1									0.32	0.055	n.s.	n.s.
Open pool 2									0.36	0.040	1.18	0
Open pool 3									0.32	0.054	n.s.	n.s.

n.s. – not significant at $p < 0.05$

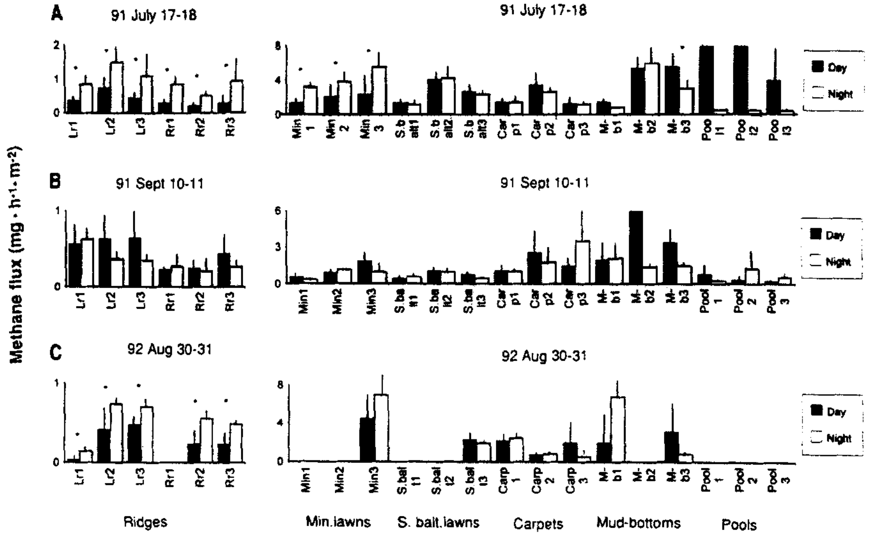

Fig. 2. Day and night methane emission average, in all sampling points, during the three measurements occasions. * indicate significant ($p < 0.05$) difference. The thin bars is standard deviation (SD). A. July 17–18, 1991, $n = 11$, B. September 10–11, 1991, $n = 7$, C. August 30–31, 1992, $n = 11$, the empty space is not measured. Lr is low ridge, Rr is raised ridge, Min is minerotrophic lawn, S. balt is S. balticum lawn, Carp is carpet, M-b is mud-bottom, Pool is open pool. In July 1991 the Pool 1 mean was 15 ± 8.5 mg*h^{-1}*m^{-2} and Pool 2 was 10 ± 8.0 mg*h^{-1}*m^{-2}. In September 1991 the M-b 2 mean was 8.0 ± 7.0 mg*h^{-1}*m^{-2}). In August the M-b 1 SD was 9.0 mg*h^{-1}*m^{-2}. Note the different scales for the y-axes.

depths were very similar, and the soil temperature curves at 5 cm depth had an amplitude 3–4 °C in all plant communities (Fig. 4).

Mean rates of CH_4 emission did not differ significantly for the daytime and nighttime measurements at any of the sampling points (Fig. 2B). In the afternoon, when it started to rain and blow, the methane flux peaked in some of the carpet, mud-bottom and open pool communities (Fig. 4).

Compared to the previous sampling date the methane emission rate was overall low but significantly related to soil temperature at 5 and 10 cm depth for 8 of 12 and 10 of 12 sampling points respectively ($p < 0.05$) with linear regression, shifted forward 2–8 h (Table 2B). Most of these relations were negative. The linear regression of methane emission on solar radiation resulted in significant correlations for 14 of 21 sampling points (shifted forward 2–12 h). Almost all the relations were positive between radiation and methane emission.

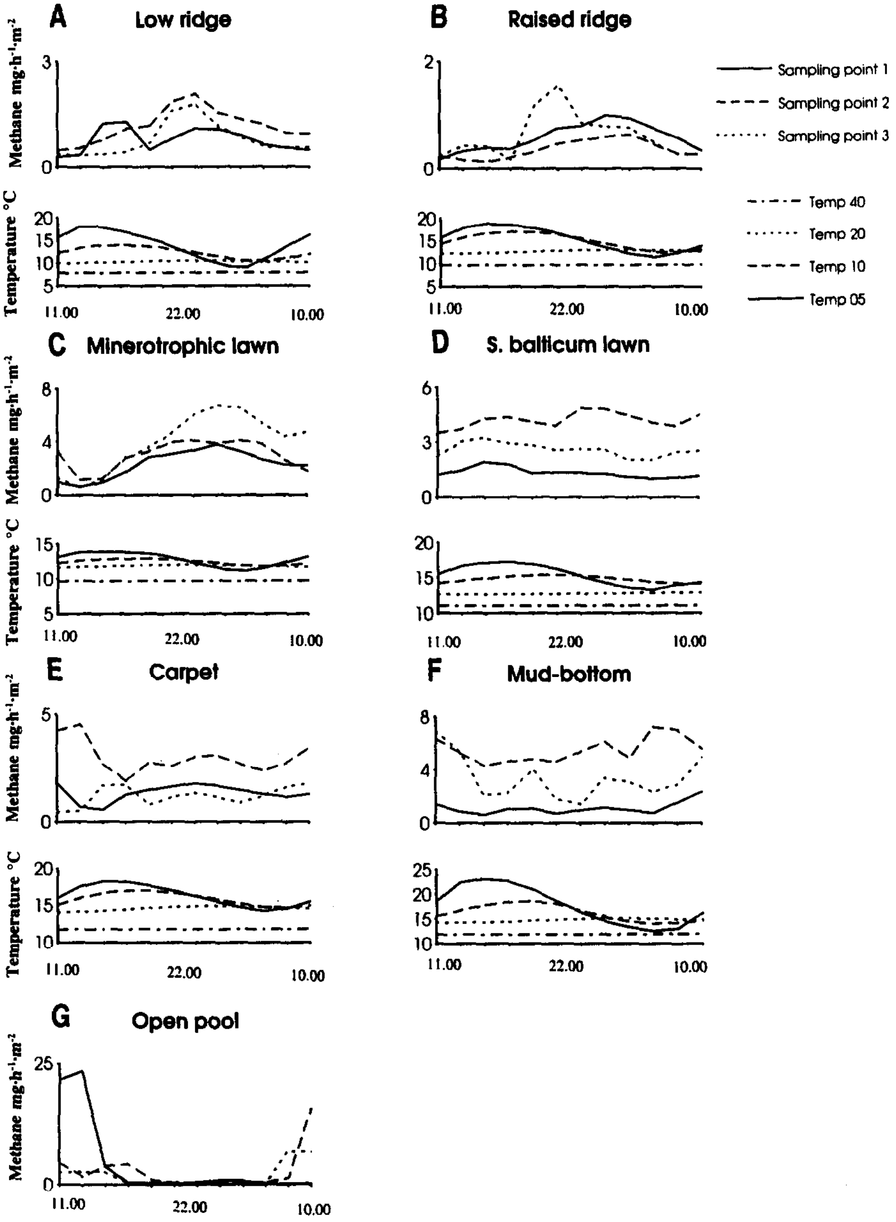

Fig. 3. Methane emission and soil temperature at four depths at all sampling points at Storåmyran on July 17–18, 1991. Note the different scales for the methane flux and temperature axis.

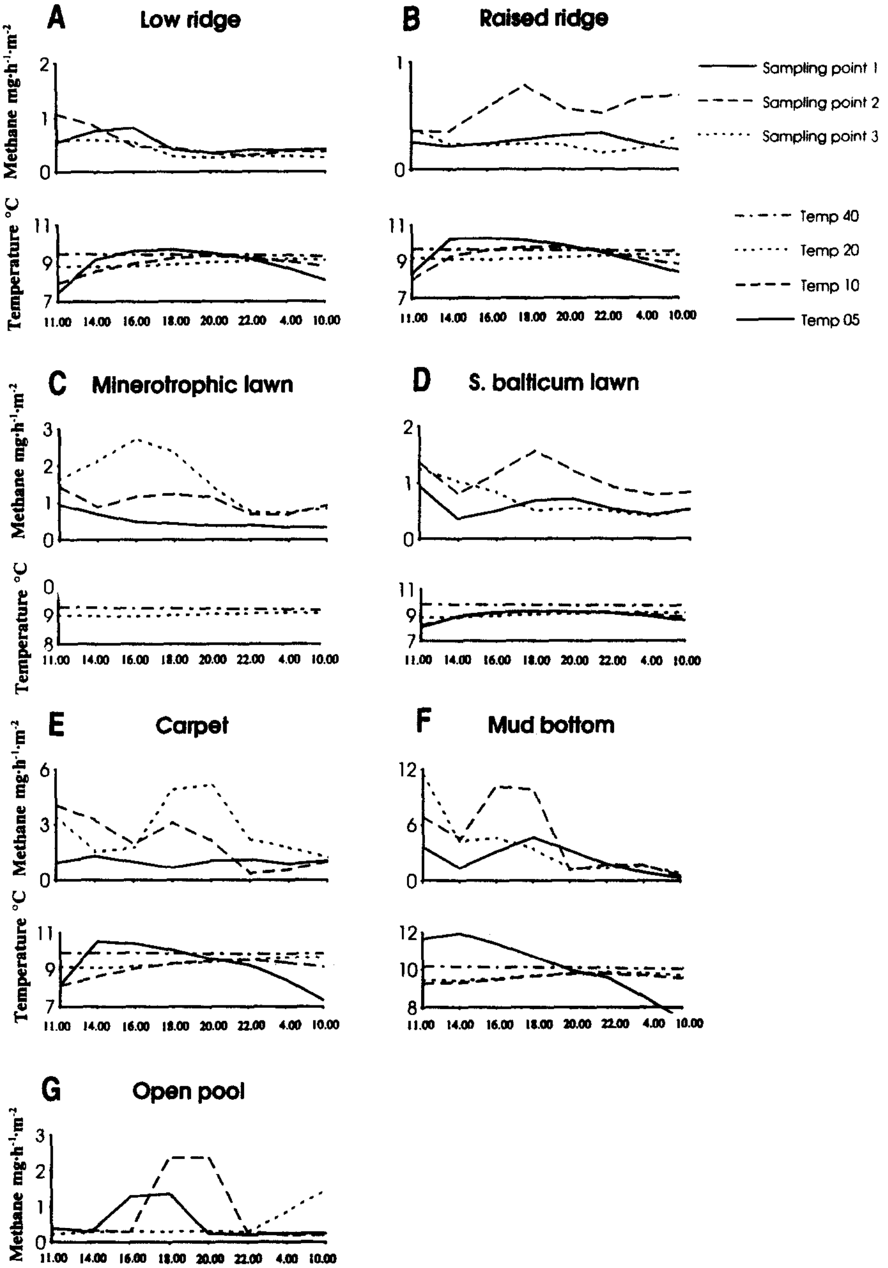

Fig. 4. Methane emission and soil temperature at four depths at all sampling points at Storåmyran on September 10–11, 1991. Note the different scales for the methane flux and temperature axis.

Table 2B. Linear regression of methane emission rate, filtered by two points wide moving average, on soil temperature at 5 and 10 cm depth for the points with continuous temperature registration, and on global radiation for all points. Storåmyran September 10–11, 1991. *b*, the slope coefficient; *h*, the number of hours that the temperature and radiation curves has been shifted forward in the regression.

	Temperature 5 cm				Temperature 10 cm				Radiation			
Sampling point	r^2	p	b	h	r^2	p	b	h	r^2	p	b	h
Low ridge 1	0.71	0.009	−0.13	4	0.64	0.017	−0.51	4	0.79	0.003	0.13	4
Low ridge 3	0.95	0.000	−0.44	2	0.92	0.000	−0.84	0	0.85	0.001	0.21	0
Low ridge 3	0.96	0.000	−0.12	4	0.87	0.001	−0.24	2	0.77	0.004	0.11	2
Raised ridge 1									0.13	0.376	n.s.	n.s.
Raised ridge 2	0.69	0.010	0.08	4	0.55	0.034	0.15	2	0.60	0.025	−0.09	2
Raised ridge 3	0.56	0.032	−0.04	2	0.64	0.017	−0.09	0	0.61	0.023	0.05	0
Minerotrophic lawn 1									0.92	0.000	0.17	0
Minerotrophic lawn 2									0.62	0.020	−0.17	12
Minerotrophic lawn 3	m.d.	m.d.	m.d.	m.d.	m.d.	m.d.	m.d.	m.d.	0.74	0.006	0.53	4
S. balticum lawn 1									0.37	0.110	n.s.	n.s.
S. balticum lawn 2									0.35	0.123	n.s.	n.s.
S. balticum lawn 3	0.88	0.001	−0.50	2	0.92	0.000	−0.63	2	0.79	0.003	0.22	0
Carpets 1	0.00	0.964	n.s.	n.s.	0.02	0.716	n.s.	n.s.	0.39	0.100	n.s.	n.s.
Carpets 2	0.60	0.023	−1.01	6	0.60	0.024	−1.87	2	0.51	0.046	0.79	0
Carpets 3	0.44	0.073	n.s.	n.s.	0.56	0.033	−2.73	8	0.29	0.172	n.s.	n.s.
Mud-bottom 1	0.67	0.013	−1.75	6	0.66	0.015	−4.46	4	0.55	0.034	0.88	6
Mud-bottom 2									0.52	0.045	2.22	6
Mud-bottom 3	0.47	0.062	n.s.	n.s.	0.61	0.022	−13.25	0	0.92	0.000	2.70	0
Open pool 1									0.81	0.001	0.35	6
Open pool 2									0.45	0.068	n.s.	n.s.
Open pool 3									0.17	0.307	n.s.	n.s.

m.d. – missing data; n.s. – not significant at $p < 0.05$

August 30–31, 1992

The weather was dry and sunny during August 30–31, 1992, but there was 135 mm of rain during the two preceding weeks and 0.8 mm of rain prior to sampling (Fig. 1C). The water table was closer to the mire surface than on the other measurement dates as a result of the high precipitation during August (Table 1). The air temperature was about 10 °C when the measurements were started and decreased to −2 oC at night. In all plant communities, nighttime soil temperatures did not drop as much as nighttime air temperatures (Figs. 1C, 5).

Diurnal patterns of CH_4 emission were similar to the findings in July 1991. Thus, at the ridges and the minerotrophic lawn, the mean nocturnal emission exceeded the daytime mean (Fig. 2C). However, for the minerotrophic sampling point the difference between daytime and nighttime emission rates was not statistically significant ($p > 0.05$). In the *S. balticum* lawn, carpet and mud-bottom communities, the average CH_4 emission did not differ significantly between day and night.

At most sampling points there was a significant relation between methane emission and soil temperature at 5 or 10 cm depth (shifted forward 2–10 h) below the peat surface (Table 2C). All the significant relations between soil temperature and methane emission rate were positive. The linear regression of methane emission on solar radiation gave significant relations for 7 of 12 points (shifted forward 2–6 h). The significant relations between emission and radiation were negative at the ridges and the minerotrophic plant communities (shifted forward 2 h) and positive in the carpet no. 2 sampling point (shifted forward 6 h) (Table 2C).

Discussion

General considerations

Fluctuations in rates of methane emission across time scales of hours and days, may be caused by temporal changes in several factors, including (i) temperature effects on decomposition and subsequent methane production, (ii) methane production coupled to plant photosynthesis and carbon translocation to roots, (iii) plant-mediated gas transport, mainly regulated by the intensity of photosynthetically active light that in turn regulates stomatal conductance, (iv) temperature effects on methane oxidation in the oxic zone.

According to our results, the specific pattern of variation in emission rate during a 24-h period varies among different plant communities as well as the amplitudes of diurnal variation in air and soil temperatures and light intensity.

Table 2C. Linear regression of methane emission rate filtered by two points wide moving average, on soil temperature at 5 and 10 cm depth for the points with continuous temperature registration, and on global radiation for all points. Storåmyran August 30–31, 1992. *b*, the slope coefficient; *h*, the number of hours that the temperature and radiation curves has been shifted forward in the regression.

	Temperature 5 cm				Temperature 10 cm				Radiation			
Sampling point	r^2	p	b	h	r^2	p	b	h	r^2	p	b	h
Low ridge 1	0.90	0.000	0.22	6	0.94	0.000	0.63	4	0.52	0.012	−0.26	0
Low ridge 2	0.83	0.000	0.18	6	0.80	0.000	0.29	4	0.62	0.004	−0.16	0
Low ridge 3	0.81	0.000	0.11	6	0.80	0.000	0.23	6	0.57	0.007	−0.15	0
Raised ridge 2	0.85	0.000	0.04	10	0.84	0.000	0.09	8	0.74	0.001	−0.09	0
Raised ridge 3	0.79	0.000	0.18	8	0.84	0.000	0.31	8	0.57	0.007	−0.26	2
Minerotrophic lawn 3	0.78	0.000	2.08	6	0.83	0.000	3.33	6	0.43	0.028	−2.19	2
S. balticum lawn 3	0.11	0.320	n.s.	n.s.	0.42	0.031	1.44	10	0.13	0.275	n.s.	n.s.
Carpets 1	0.57	0.008	0.55	2	0.52	0.013	1.03	6	0.32	0.069	n.s.	n.s.
Carpets 2	0.68	0.002	0.13	0	0.58	0.007	0.27	0	0.38	0.043	0.21	6
Carpets 3	0.09	0.365	n.s.	n.s.	0.42	0.032	13.04	10	0.19	0.178	n.s.	n.s.
Mud-bottom 1	0.12	0.306	n.s.	n.s.	0.34	0.060	n.s.	n.s.	0.09	0.380	n.s.	n.s.
Mud-bottom 3	0.34	0.059	n.s.	n.s.	0.21	0.160	n.s.	n.s.	0.30	0.085	n.s.	n.s.

n.s. – not significant at $p < 0.05$

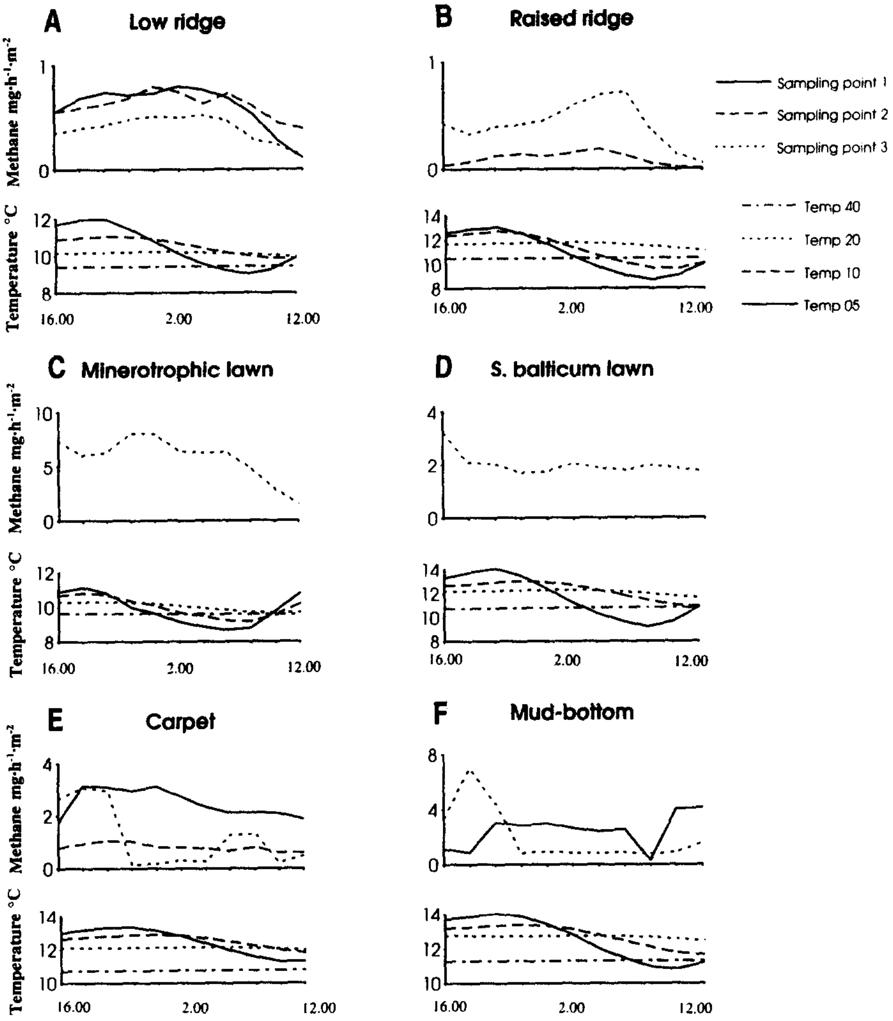

Fig. 5. Methane emission and soil temperature at four depths at all sampling points at Storåmyran on August 30–31, 1992. Note the different scales for the methane flux and temperature axis.

The groundwater level is important since it determines the extent to which methane production and oxidation are affected by changes in temperature and radiation. In plant communities with the groundwater level at the vegetation surface, diurnal variation in soil temperature will affect the anaerobic zone. However, in areas where the groundwater level is more than 5–10 cm below the vegetation surface diurnal temperature variation will occur mainly in the aerobic zone.

Measurements of methane oxidation rates made by incubating peat slurries indicated that the rates were strongly temperature dependent at methane concentrations above substrate saturation. At the plant communities inhabiting ridges, the methane oxidation rate showed temperature dependence at concentrations of 0.03 μM CH_4, with the Q_{10} (10–20 °C)-value being approximately 2 (M. Nilsson, pers. comm.). The fact that actual methane concentrations at groundwater level in this plant community were 30–300 μM CH_4 (Sundh et al. 1994a) further supports the hypothesis that methane oxidation in this mire plant community is strongly regulated by temperature.

The degree of diurnal variation in the transport of methane from the anaerobic zone to the atmosphere varies depending on the plant species. In *Typha latifolia* (Chanton et al. 1993; Knapp & Yavitt 1992) and yellow waterlily (Dacey 1981; Dacey & Klug 1979) there is a close relationship between stomatal conductance and methane emission. In these two species the methane emission is much higher during daytime than at night. On the other hand, plants that rely solely on molecular diffusion for gas transport do not show large fluctuations in methane emission rates between day and night, e.g. rice (Seiler et al. 1984; Schütz et al. 1989) and *C. rostrata* and *C. limosa* (Whiting & Chanton 1992). In contrast Morrissey et al. (1993) found a close relation between methane flux rates and stomatal conductance in *C. aquatilis*- and *C. rostrata*-dominated communities. Our use of dark chambers for accumulating emitted methane may have decreased the plant-mediated transport of methane because light regulates stomatal conductance. Thus, we may have missed emission peaks around midday in some of the plant communities. The short incubation time used although minimize this problem. Further more roots below the accumulation chamber only partly comes from the plant inside the chamber. Most of the roots is from surrounding plants.

Dry plant communities

In the relatively dry plant communities, nighttime emissions significantly exceeded daytime emissions during two of the measurement periods. In September 1991 the air temperature successively decreased through whole the measurement period and obviously not caused distinct differences between day and night in the soil temperature. This may be the main reason why no elevated emission rates showed up at this time. Higher emission rates at night have also been observed in temperate wetlands (Yavitt et al. 1990b), tundra wetlands (Whalen & Reeburgh 1988), Florida everglades (Happell et al. 1993) and Chinese rice paddy fields (Schütz et al. 1990b).

Vascular plants dominate the vegetation cover on the ridges and in the minerotrophic plant communities. In a subarctic fen, both the pore-water concentration of methane and net emission rates were reduced drastically when the vascular plants were experimentally removed (Whiting & Chanton 1992). It is therefore likely that the vascular plants contribute to the diurnal fluctuations, caused by variation in substrate supply to the anaerobic microbial community. Translocation experiments with ^{14}C-labelled carbon dioxide uptake by *Empetrum hermaphroditum, Andromeda polifolia* and *Rubus chamaemorus*, often dominating the hummock and ridge vegetation of subarctic mires, showed that more than 90% of the photosynthetic assimilate was found below ground three days after labelling (Wallén 1986). The carbon translocated below ground was found down to 10–15 cm depth in *E. hermaphroditum* and *A. polifolia*, whereas it was distributed below 25 cm (i.e. into the permanently anaerobic zone) in *R. chamaemorus*. Therefore, reason why the methane emission rate in this study peaked several hours after the diurnal maxima in air temperature or light intensity could be delayed production of CH_4 from exuded substrate (Table 2A, B and C, Figs. 1, 3, and 5).

In these dry plant communities, there was a pronounced variation in soil temperature in the aerated zone, but not in the anaerobic zone (Table 1, Figs. 3, 4 and 5). A positive relation between methane consumption rates and temperature has been observed in taiga forests soils (Whalen et al. 1991) as well as in laboratory measurements and incubations of a mixed deciduous-coniferous forest soil (Crill 1991) and peat soils (Dunfield et al. 1993). Thus a decrease in temperature in the aerobic zone may reduce the rate of aerobic methane oxidation, resulting in a higher methane emission rate at night. The potential for methane oxidation is markedly higher on the ridges and in the minerotrophic lawn plant communities than in the lawn, carpet and mud-bottoms, indicating that populations of methanotrophic organisms are larger in the drier communities (Sundh et al. 1994a). Methane emissions in these plant communities should therefore be regulated by temperature. Conversely, King & Adamsen (1992) found that forests soil cores incubated at ambient methane concentrations responded only slightly to a change in temperature. They argued that the low temperature sensitivity was due to the fact that the transport of methane from the atmosphere to the methanotrophic organisms (i.e. diffusion) was the rate-limiting step. In the aerobic zone of peat and landfill cover soils with much higher methane concentrations, temperature-sensitive enzymatic processes probably become more important. However, the maximal emission rates on the ridges and in the minerotrophic lawn communities in July 1991 and August 1992, occurred before the soil temperatures at 5 and 10 cm depths dropped to their minima (Figs. 3, 5). Thus it is unlikely that temperature inhibition of methane oxidation alone caused the increase in emission rate at night.

Wet plant communities

Among the plant communities with the groundwater level close to the vegetation surface, no difference in average methane emission rates between day and night occurred except at one mud-bottom sampling point in July 1991. However, several significant relations were found between methane emission and soil temperature or radiation (Table 2A, B, C). The diurnal temperature variation in the anaerobic layer suggests that temperature regulates methane production. Reported Q_{10} responses for methane production in natural habitats vary between 1.0 and 6.0 (Svensson 1984; Sexton & Mains 1990; Westerman & Ahring 1987; Westerman et al. 1989; Dunfield et al. 1993). If we were correct in assuming that methane production is the only process varying diurnally in the *S. majus* and mud-bottom communities, then the amplitude of the methane emission is well within the range of reported Q_{10}-values. In addition, the exudation of organic materials coupled to photosynthetic carbon fixation by *Sphagnum* plants and benthic algae may cause a peak in methane emission coinciding with the maximum air temperature or light intensity.

The low and constant rate of methane emission from the open pool at night in July 1991 indicates that diffusion was the major transport mechanism (Fig. 3). During daytime, the methane emission rate was 10–20 times higher and very variable, suggesting that methane was transported to the pool surface by ebullition. Bubbles in the pool water were frequently seen. The high methane emission rates coincided with the period of photosynthetic activity. The pool bottom is mostly covered by *S. majus* that is overgrown by epiphytic algae. Svensson (1986) found that the production of methane peaked around midday in *Sphagnum* moss samples colonized by epiphytic cyanobacteria incubated in the field. The peak in the nitrogenase activity of the cyanobacteria preceded methane production by 2–3 h. A possible interaction via hydrogen, released from the nitrogen system between the two organism groups, was proposed to explain the pattern observed. Such phenomena may influence the diurnal patterns of emission rates, at least in the wet communities and in the pool. Alternatively, the high daytime values at the pool could be caused by the wind, that started to blow in the mornings in July and in the afternoon during September 10–11, 1991 (Figs. 3, 4). Wind induces the mixing of pool water and may help to transport methane-rich bottom water to the surface.

Conclusion

Our study revealed several different patterns of diurnal variation in methane emission during the same period. The patterns differed among the plant communities but were relatively consistent within them. Short-term variation in methane emission rates may result from one or several processes, depending on the plant community. For the sites used in our study we suggest that the main regulatory processes were as follows: (i) ridges and the minerotrophic lawn – probably the most complex system, with diurnal changes caused by the delayed production of CH_4 from exuded substrate in combination with time lags in rates of methane oxidation; (ii) *S. balticum* lawn, *S. majus*-dominated carpet and mud-bottom communities – temperature-regulated decomposition and light-regulated exudation; (iii) Open-pool – light-regulated exudate production by submerged *Sphagnum* and epiphytic algae without any delay between production and exudation and/or methane release through the stirring of the water by wind and rain.

Diurnal variation in the CH_4 emission rate may bias the values used for estimating CH_4 emissions on regional and global levels. More specifically, short daytime measurements of methane flux will result in a consistent underestimation of the methane emission from ridges and sedge fens. For the Swedish mire types, use of a daily mean value corrected for the difference between daytime and nighttime means will increase the annual emission, as estimated by Svensson et al. (1991), by about 25%. The corrected daily average is only used on mire types with appropriate vegetation types (Hånell 1989) and 50% of the season used for estimation of methane emission is accounted to have diurnal variation in the surface soil temperature. In the ridge plant communities studied, a diurnal temperature variation of more than 5°C occurred at 5 cm depth on about 75% of the days during July and August.

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