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Predicting variations in methane emissions from boreal peatlands through regression models

Anu Kettunen[1], Veijo Kaitala[2], Jukka Alm[3], Jouko Silvola[3],
Hannu Nykänen[4] and Pertti J. Martikainen[4]

[1] *Peatland Forestry, Department of Forest Ecology, P.O. Box 24, FIN-00014 University of Helsinki, Finland*
[2] *Department of Biological and Environmental Sciences, University of Jyväskylä, P.O. Box 35, FIN-40351 Jyväskylä, Finland*
[3] *Department of Biology, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland*
[4] *Laboratory of Environmental Microbiology, National Public Health Institute, P.O. Box 95, FIN-70701 Kuopio, Finland*

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Frequently measured data from a boreal fen was used to test how regression models predict the spatial and temporal variations in methane emissions. In the spatial microscale, emissions were lowest from high hummocks with low water table and highest from the intermediately moist lawn with a high sedge cover. Seasonal variations were strong, but diurnal variations weak. The importance of episodic emissions increased from wet microsites to hummocks. The regression models explained the temporal pattern of methane emissions quite satisfactorily for flarks and low hummocks, but less satisfactorily for high hummocks. For independent data sets, the goodness of fit values were usually low. Episodic pulses and diurnal variations were not captured by the models and the models overestimated the spring emissions and underestimated midsummer high emissions.

Introduction

Methane fluxes from peatlands show high temporal and spatial variations (Whalen and Reeburgh 1988, 1992, Moore *et al*. 1990, Morrissey and Livingston 1992, Windsor *et al*. 1992, Dise 1993, Moosavi *et al*. 1996, Waddington and Roulet 1996). The temporal variations consist of interannual variation related to varying weather conditions (Mattson and Likens 1990, Whalen and

Reeburgh 1992, Frolking and Crill 1994, Shurpali and Verma 1998), the seasonal cycle of methane emissions with high summer and low winter fluxes (Dise *et al.* 1993, Shurpali *et al.* 1993, Frolking and Crill 1994, Alm *et al.* 1998, Mast *et al.* 1998), the diurnal flux cycle (Silvola *et al.* 1992, Mikkelä *et al.* 1995, Thomas *et al.* 1996, Van der Nat *et al.* 1998), and episodic high fluxes (Windsor *et al.* 1992, Christensen 1993, Frolking and Crill 1994). The variations occur because the basic processes, methane production, methane oxidation and transport from peat to atmosphere, depend on environmental factors (Conrad 1989).

Methane flux from wetlands is controlled by the dynamical balance between methane production and oxidation processes in different peat layers and the transport from peat to atmosphere (Bubier and Moore 1994, Conrad 1989, 1996). Methane production requires suitable carbon source (Conrad 1989, 1996, Morrissey and Livingston 1992, Valentine *et al.* 1994) and anaerobic conditions (Conrad 1989, 1996, Segers 1998). The root exudates by plants apparently promote methane production which increases with the photosynthetic activity of plants (Schütz *et al.* 1991, Whiting *et al.* 1991, Whiting and Chanton 1992, 1993, Schimel 1995, Thomas *et al.* 1996, Megonigal and Schlesinger 1997, Shurpali and Verma 1998). Changes in substrate availability and redox conditions are suggested to control the growth and death of methanogenic bacteria (Grant 1998, Segers and Kengen 1998). In addition, in principle an increase in temperature enhances methane production rate but *in situ* conditions substrate availabilty strongly affects the temperature response (Dunfield *et al.* 1993, Valentine *et al.* 1994, Bergman *et al.* 1998). Population of methane oxidizing bacteria develop where methane and oxygen profiles in peat overlap (Conrad 1989, 1996, Segers 1998). Temperature control has been suggested to be less important for methane oxidation than for methane production (Dunfield *et al.* 1993). In methane transport from vegetated surfaces, flux via plants seems to dominate the diffusive flux whenever suitable sedge species exist (Chanton and Dacey 1991, Morrissey and Livingston 1992, Whiting and Chanton 1992, Verville *et al.* 1998) and bubbling, which dominates in unvegetated surfaces, is rare (Van der Nat *et al.* 1998).

Correlation techniques have been widely used to relate methane emissions to environmental factors, such as temperature and soil hydrology (Crill *et al.* 1988, Moore *et al.* 1990, Dise *et al.* 1993, Shurpali *et al.* 1993, Shannon and White 1994, Christensen and Cox 1995, Kettunen *et al.* 1996, Suyker *et al.* 1996). Regression analysis has quite often been succesfully applied to predict mean seasonal fluxes among microsites but it is much more difficult to predict the temporal variations in methane emissions using regressions to temperatures and water tables (Whalen and Reeburgh 1992, Bubier *et al.* 1993, Roulet *et al.* 1992, 1993, Torn and Chapin 1993, Vourlitis *et al.* 1993, Moore *et al.* 1990, 1994). In addition, the lack of frequent measurements has made analyses of temporal patterns difficult in previous studies. Different relationships between methane emissions and environmental factors have been obtained depending on the spatial scale and temporal frequency of measurements. Some studies have emphasized the temperature control (Moore and Knowles 1987, Crill *et al.* 1988, Dise *et al.* 1993, Shannon and White 1994, Moosavi *et al.* 1996, Suyker *et al.* 1996), while others have found vegetation type and hydrology to be of importance (Svensson and Rosswall 1984, Morrissey and Livingston 1992, Bubier *et al.* 1993, 1995, Roulet *et al.* 1994, Bubier 1995, Nykänen *et al.* 1998) The various and partly contradictory results from earlier studies indicate that interactions between environmental factors and methane emissions are complex, and any single environmental factor can hardly be expected to predict the methane flux satisfactorily (*see* Whalen and Reeburgh 1992, Christensen 1993, Kettunen *et al.* 1996, Granberg *et al.* 1997).

The purpose of the study is to detect the modes of spatial and temporal variations in temporally intense measurements of methane emissions and to test how well regression model approaches with environmental factors as independent variables describe and predict the detected variations. In particular, we analyze how the commonly used linear and exponential models of methane emissions vs. peat temperatures perform when we have a large number of temporally intense measurements. In this stydy, we use measurements of methane emissions, peat temperature profile and water tables from six different microsites with various hydrological and botanical characteristics within a Finnish low sedge *Sphagnum papillosum* pine fen during summer 1993.

Materials and methods

Mire and microsite classification

The methane emissions, peat temperature profiles (T_0, T_{10}, T_{20}, T_{50}, *see* Table 1 and explanation below) and water tables (WT) were measured during summer 1993 in a low sedge *Sphagnum papillosum* pine fen that is situated in the margin area of the mire complex Salmisuo. The mire complex Salmisuo (62°47´N, 30°56´E) in eastern Finland is an oligotrophic bog, split by some minerotrophic strips (Tolonen 1967).

Six microsites were selected to represent different vegetation surfaces of the mire with increasing moisture (hummocks, lawns and flarks) (Tables 2 and 3). Two microsites represented high hummocks with low water tables (hummocks A and B in Tables 2 and 3). Hummock B was situated immediately at the mire edge. The water table in hummock B was not reliable due to measurement problems and was not included in the analyses. One collar was situated in a lawn surface which contained a low hummock with typical hummock vegetation (lawn/low hummock B). One collar was located on a *Sphagnum* lawn surface with a high sedge cover (lawn A). The water table remained persistently close to the *Sphagnum* surface and even exceeded the surface for flarks A and B that represented differently vegetated wet microsites. At flark A, the abundance of *Carex rostrata* indicated less standing water conditions than those prevailing at flark B. As field layer species with aerenchyme tissues capable of transporting methane were not dominant in hummocks A and B, lawn/low hummock B, and flark B, plant flux is apparently negligible in these microsites. In flark A and lawn A, the abundance of *Carex rostrata* and *Eriophorum vaginatum* with aerenchymatous root systems indicate the plant flux to be important in these microsites (Schütz *et al.* 1991, Torn and Chapin 1993, Schimel 1995, Thomas *et al.* 1996).

Measurements at the hummock B, lawn/low hummock B and flark B covered the period from

Table 1. Average peat temperatures were measured close to the collars in one additional site similar to lawn A in relation to water tables and vegetation.

	Ranges of peat temperatures	
	May–Jul.	Aug.–Oct.
T_0	11.7 (from –2.3 to +28.3)	6.2 (from –8.4 to +26.6)
T_{20}	9.9 (from +3.1 to +13.9)	8.7 (from +3.0 to +14.3)
T_{50}	6.7 (from +0.2 to +10.6)	8.8 (from +4.8 to +11.4)

Table 2. Average water tables (minima and maxima in parentheses) in the microsites. Negative values are used for water tables below the peat surface. The water table measurements from hummock B were unreliable and are not shown. For flark A, lawn A and hummock A, virgin data were available till the end of July.

Microsite	Ranges of water tables (cm) in the microsites	
	May–Jul.	Aug.–Oct.
Flark A	–1.5 (from –4.0 to +2.0)	
Flark B	–3.1 (from –8.0 to +2.0)	–2.5 (from –4.8 to +1.0)
Lawn A	–4.6 (from –8.0 to +2.0)	
Lawn/low hummock B	–7.6 (from –12.0 to –3.0)	–7.3 (from –10.0 to –5.0)
Hummock A	–28.0 (from –33.0 to –22.0)	

the beginning of May to the middle of October. Measurements at the hummock A, lawn A and flark A were usable from early May to the end of July as depths of water table and other factors were manipulated in these microsites during the late summer months (August–October).

Measurements of methane fluxes and environmental variables

Gas fluxes were measured from six different collars (Tables 2 and 3), situated within a few tens of meters apart from each other. Permanent 60 × 60 cm light transparent collars were driven into the peat in the spring and an automatic flux chamber (height 20 cm) system mounted on the collars for a 20 minute measurement period recorded methane emissions once every five to six hours. Air was circulated from the chambers to Shimadzu GC-14-A gas chromatograph equipped with a flame ionization detector. A PC program controlled the chambers pneumatically. The fluxes were calculated from the linear least square fits of four headspace concentration values to incubation times. The flux measurement was rejected if the initial headspace methane concentration was higher than 4 ppm or if $r^2 < 0.90$. This method (Silvola *et al.* 1992) is appropriate for measuring diffusive flux. Bubbling, which resulted in nonlinear increase in headspace methane concentration ($r^2 < 0.90$), led to rejection of the measurement and was detected only very rarely.

The water table near each collar and the chamber temperature were automatically detected immediately before the methane flux. The device for water table measurement consisted of a 10 cm diameter ground water well, a float on the water surface, and a counterbalance in a string turning a wheel to adjust a potentiometer connected to a PC. The peat temperature profile at different depths (0–2, 10, 20 and 50 cm) was measured for one additional selected site a few meters away from the collars (Table 1). The surface temperature (T_0) and peat temperatures at depths of 20 and 50 cm (T_{20} and T_{50}) were chosen for the analyses as the chamber temperature and temperature at 10 cm were strongly correlated with T_0 and T_{20}, respectively ($r^2 = 0.96$) and were thus omitted in calculations.

Diurnal variation

To normalize the measurements for the analysis of the diurnal pattern, the deviations of individual measurements from the daily average were divided by the daily average ($n = 4$). The normal-

Table 3. Dominant species in the bottom and field layers (coverage percentages in parentheses) in the microsites. In the bottom layer *S.* = *Sphagnum* and *P.* = *Polytrichum* and in the field layer *A.* = *Andromeda*, *C.* = *Carex*, *Ch.* = *Chamaedaphne*, *Dr.* = *Drosera*, *Em.* = *Empetrum*, *Er.* = *Eriophorum*, *R.* = *Rubus*, *Sc.* = *Scheuzcheria* and *V.* = *Vaccinium*.

Microsite	Vegetation in the microsites	
	Bottom layer	Field layer
Flark A	*S. angustifolium* (100%)	*C. rostrata* (10%) and *Er. vaginatum* (10%)
Flark B	*S. angustifolium* (60%) and *S. majus* (40%)	*Sc. palustris* (2%)
Lawn A	*S. angustifolium* (85%) and *S. magellanicum* (10%)	*Er. vaginatum* (12.5%)
Lawn/low hummock B	Low *S. fuscum* (70%) hummock with *S. angustifolium* (10%), *S. russowii* (10%) and *S. magellanicum* (10%)	*A. polifolia* (10%)
Hummock A	*S. fuscum* (85%) hummock with *S. angustifolium* (10%)	*A. polifolia* (10%) and *R. chamaemorus* (10%)
Hummock B	*S. fuscum* (90%)	*Em. nigrum* (12.5%)

ized measurements were classified into six diurnal classes covering four hours each (from 00.00 to 04.00 solar time = UTC + 2, from 04.00 to 08.00 etc.). Monthly averages were calculated for each four-hour group and ANOVA were used to test whether the averages differed from each other i.e. whether the measurements showed any pattern in relation to the time of day.

Episodic values

A centered moving average including all measurements within a seven–day window was used as a reference level of methane emission. If the measured value was more than two standard deviations higher (the 95% confidence interval of the normal distribution) than the moving average, it was classified as episodic, i.e. an episodic value x_k was detected when

$$x_k - \hat{x}_k > 2s_k \qquad (1)$$

where

$$\hat{x}_k = \frac{1}{Nb_k + Nf_k}\left(\sum_{i=1}^{Nb_k} x_{k-i} + \sum_{i=1}^{Nf_k} x_{k+i}\right) \qquad (2)$$

$$s_k^2 = \frac{1}{Nb_k + Nf_k - 1}\left(\sum_{i=1}^{Nb_k} x_{k-i}^2 + \sum_{i=1}^{Nf_k} x_{k+i}^2\right) \qquad (3)$$

and Nb_k and Nf_k were the numbers of measurements backwards and forwards within the centered window. The contribution of episodic values C_e to the growing period emissions was studied by comparing the cumulative moving average estimates including and excluding the episodic values.

Regression models

Methane emissions were related to peat temperatures at various depths and water tables through linear and exponential regression equations ($CH_4 = a_j + b_jT_j + c_j$ (WT) and ln (CH_4) = $d_j + e_jT_j + f_j$ (WT) where $j = 0$, 20 and 50). As microscale differences in depth of water table and vegetation are related to methane flux (Morrissey and Livingston 1992, Christensen 1993, Bubier and Moore 1994), the regression models were estimated separately for each study plot. The variations in water tables were extremely small during the summer 1993 compared to average growing season. As the water tables remained practically constant, it was obvious that variations in methane emissions could not be related to the constant water level.

To study the time lags between temperatures and methane emissions the measurements were classified into six diurnal classes covering four hours each (from 00.00 to 04.00, from 04.00 to 08.00 etc.) to achieve equally spaced time series. Linear and expontential regression models of type ($CH_4 = a_j + b_jT_j + c_j$(WT) and ln ($CH_4$) = $d_j + e_jT_j + f_j$(WT) where $j = 0$, 20 and 50) with lagged temperatures as independent variables were then applied to the measurements.

Models were tested by dividing data to two parts, one of which was used in parameter estimation and the other in model validation (independent data sets). One period at a time, each one week, each two weeks and each four weeks period was left out from the estimation and used as independent data sets for model validation. In addition, for flark B, lawn/low hummock B and hummock B, the model estimated from the May–July data was tested against the August–October data. The model outputs were compared to measured values of the independent data set using goodness of fit values (r^2) and the average of absolute prediction error (average error).

Calculation of cumulative emissions

The cumulative emissions were calculated using both the moving average approach and the regression model approach. The values obtained applying the moving average or the regression models were summed using the measurement periods as integration steps. In the regression model approach, the missing values were obtained by interpolation if single measurements were missing. If the temperature and water table measurements for longer periods (up to several days) were missing, interpolated daily averages of temperatures and water tables were used.

Results

Variability captured by seasonal regression models

Even though the study plots were situated within a few meters of each other, the methane emissions from the microsites differed considerably (Table 4 and Fig. 1). Intermediately moist lawn A with a high sedge cover showed the highest average, maximum and cumulative emissions among the microsites during the May–July period (Tables 4 and 5). Also the cumulative estimates for the May–Oct period by regression models were highest for lawn A. Lawn/low hummock B and flarks A and B showed slightly lower emissions than lawn A and hummocks A and B had the lowest average and cumulative emissions.

Overall, the cumulative estimates obtained by seasonal regression models were relatively close to the estimates obtained by the moving average approach and estimates by linear models matched slightly better to moving average estimates than estimates by exponential models (Table 5). The predicted cumulative emissions from flarks B and A were close to each other for the linear model but the exponential model produced a very high estimate for flark A for the August–October period as compared to the linear estimate or to the estimates for flark B.

The regression models captured reasonably well the strong seasonal pattern of methane emissions with highest fluxes during the midsummer (Fig. 1). The emission levels were about three times as high in July–August as in June. At the beginning of the growing season in May and June, the emissions lagged behind the increase in peat temperatures and were lower than in September. By October, the emissions decreased to average values of 1–3 mg CH_4 m^{-2} h^{-1}.

Methane emissions in all microsites increased with increasing peat temperatures. The temperatures at depths of 20 and 50 cm explained the seasonal variations in methane emissions better than the peat surface temperature for which $r^2 < 0.20$ in all microsites. The explanatory power of the best seasonal regression models was quite good for flarks A and B, lawn A, and lawn/low hummock B ($r^2 > 0.60$ for the linear and > 0.70 for the exponential models in Table 6). For the methane emissions from hummocks A and B, the peat temperatures were not a large source of variations in methane emissions ($r^2 < 0.40$ in Table 6). The average values of the absolute prediction error were between 1.0 and 2.0 mg CH_4 m^{-2} h^{-1} for flarks

Table 4. Average methane emissions (minima and maxima in parantheses) (mg CH_4 m^{-2} h^{-1}) from the microsites. For flark A, lawn A and hummock A virgin data were available till the end of July.

Microsite	May–Jul.	Aug.–Oct.
Flark A	7.9 (0.6–19.2)	
Flark B	6.5 (0.5–25.7)	8.2 (1.3–31.3)
Lawn A	10.9 (1.2–33.8)	
Lawn/ low hummock B	5.8 (0.5–16.9)	8.7 (0.8–26.6)
Hummock A	3.5 (0.6–16.0)	
Hummock B	2.2 (0.2–9.5)	2.8 (0.2–14.5)

Table 5. The predicted cumulative methane emissions (g CH_4 m^{-2} a^{-1}) from the different microsites using moving averages of the methane measurements and linear and exponential models from Table 4. For flark A, lawn A and hummock A virgin data were available till the end of July.

Microsite	May–Jul.			Aug.–Oct.			May–Oct.		
Flark A	17.3^{a}	16.5^{b}	17.0^{c}	–	12.2^{b}	22.6^{c}	–	29.2^{b}	39.1^{c}
Flark B	14.4^{a}	15.9^{b}	11.8^{c}	13.9^{a}	11.7^{b}	14.8^{c}	28.3^{a}	27.7^{b}	26.6^{c}
Lawn A	23.5^{a}	23.4^{b}	21.7^{c}	–	29.7^{b}	31.9^{c}	–	53.2^{b}	53.7^{c}
Lawn/low hummock B	12.9^{a}	11.9^{b}	11.0^{c}	14.7^{a}	16.2^{b}	15.1^{c}	27.6^{a}	28.0^{b}	26.1^{c}
Hummock A	7.7^{a}	7.7^{b}	6.4^{c}	–	5.5^{b}	5.2^{c}	–	13.2^{b}	11.6^{c}
Hummock B	4.7^{a}	5.4^{b}	4.5^{c}	4.9^{a}	4.1^{b}	3.7^{c}	9.5^{a}	9.5^{b}	8.3^{c}

[a)] Moving average
[b)] Linear model
[c)] Exponential model

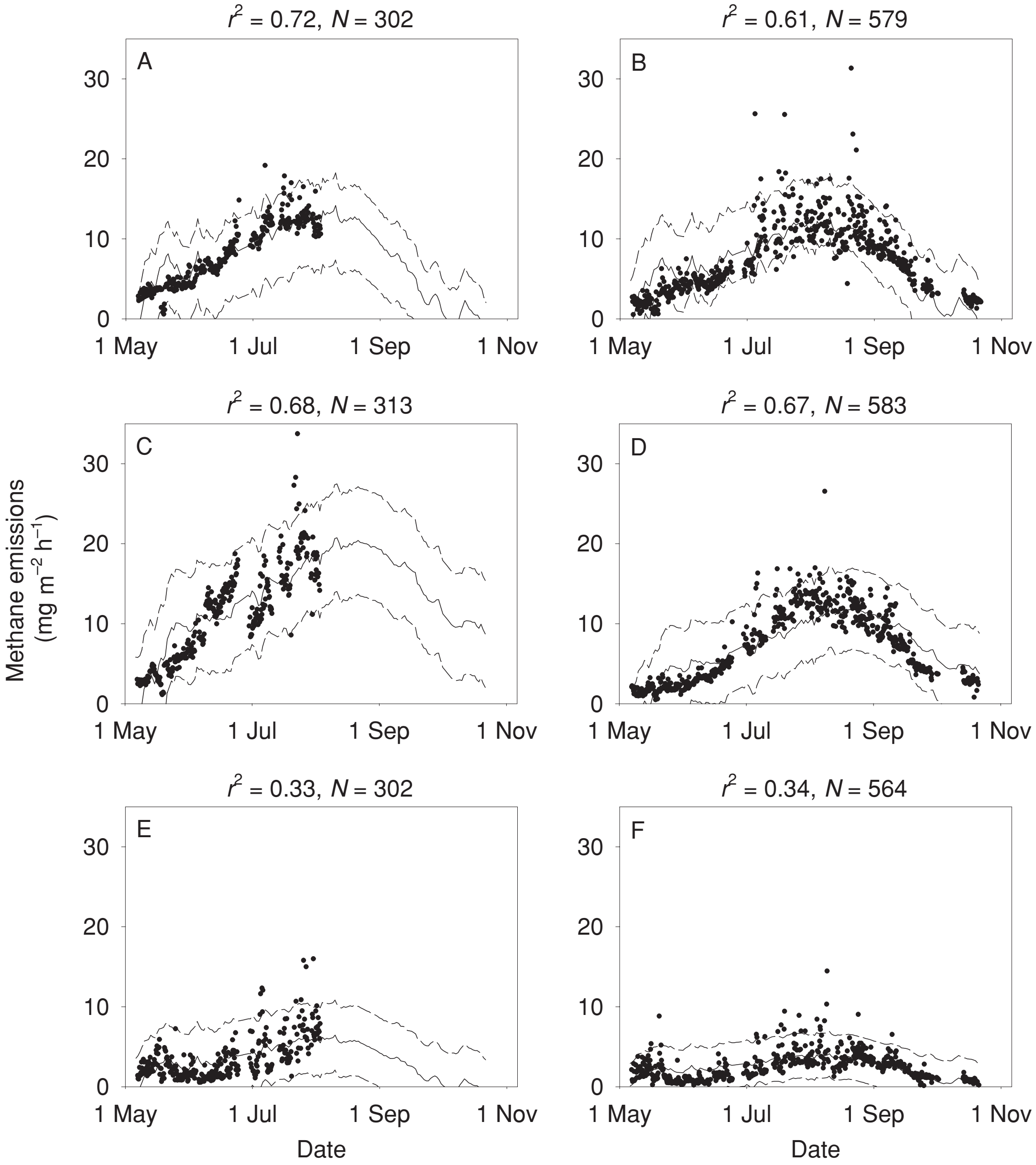

Fig. 1. The measured (black circles) and the predicted (solid lines) methane emissions with ± 95% confidence intervals (dashed line) for the modelled values in the microsites. Linear dependence of the methane emissions on the peat temperatures was assumed using T_{20} as independent variable for flarks A (panel A) and B (panel B) and hummocks A (panel E) and B (panel F) and T_{50} as independent variable for lawn A (panel C) and lawn/low hummock B (panel D). The model parameters were estimated using the measurements presented here and the estimates can be found in Table 6. For flark A, lawn A, and hummock A, virgin data were available till the end of July.

A and B, lawn/low hummock B and hummocks A and B and 3.0 mg CH_4 m^{-2} h^{-1} for flark A.

The methane emissions showed a two-tailed pattern with respect to peat temperatures at depths of 20 and 50 cm (Fig. 2). Methane emissions integrate methane production from the whole peat pro-

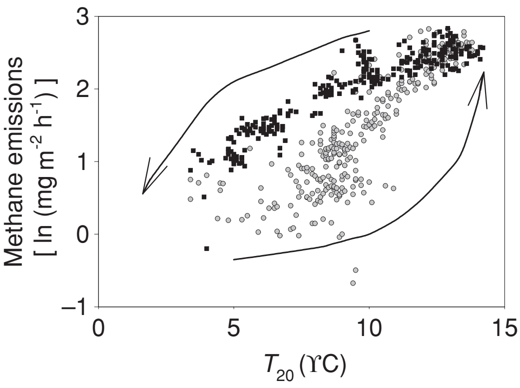

Fig. 2. Methane emissions from lawn-low hummock B versus peat temperature at a depth of 20 cm. The grey circle symbols stand for the measurements from May to the end of July and the black square symbols for the August–October measurements. The arrows indicate the temporal pattern that from May to the end of July emissions grow to their maximal values and from August to October they decrease.

file and in spring when the surface is warmest and lowest layers are nearly frozen the active parts of the profile are on average cooler (warmer) than the temperature at 20 cm (50 cm) and in autumn when the surface cools, the deep layers remain warm and the active parts of the profile are warmer (cooler) than the temperature at 20 cm (50 cm). The seasonal pattern in methane emissions hence differs from the pattern in peat temperatures at certain depth. As a result, the seasonal regression models tended to predict higher emissions as compared to the measurements at the beginning of summer, in May and in the first half of June (Fig. 1). The regressions with peat temperature at depth of 50 cm predicted too high estimates at the end of summer, in September and October (Fig 1A and D). One possible reason for the pattern in Fig. 2 is a lag between peat temperature and methane emissions, but the use of lagged peat temperatures with lags of several days up to two weeks did not improve the explanatory power of the regression models (never more than 0.05). Consequently, the use of lagged temperatures with lags greater than 24 hours were not studied further.

The water table in individual microsites only varied within 6–11 centimeters during the summer 1993 (Table 2), i.e. remained practically constant compared to average season. The seasonal variations in methane emissions were not related to variations in water table. The multiple regression of flux versus temperature and water table showed only very little improvment in r^2 (never more than 0.04) compared to the regression of flux versus temperature in individual microsites. However, when data from all microsites were considered, methane fluxes showed a positive relation to water tables with high fluxes occurring when water level was high and water table improved the goodness of fit compared to models with only peat temperatures as independent variables (for example, r^2 was 0.35 for the model $CH_4 = a_{20} + b_{20}T_{20}$ and 0.54 for the model $CH_4 = a_{20} + b_{20}T_{20} + c_{20}(WT)$).

Variability not captured by seasonal regression models

When data sets covering different one, two and four week periods were left out from the estimation (independent data sets), the parameter estimates were not much different from the estimates from the whole data e.g. the maximum and minimum estimate for temperature coefficient in the exponential model differed less than 0.05 in flarks

Table 6. The best linear and exponential models.

Microsite	N	r^2	CH_4 =	r^2	ln (CH_4) =
Flark A	302	0.72	$-6.79 + 1.49T_{20}$	0.72	$+0.54 + 0.21T_{50}$
Flark B	579	0.61	$-5.03 + 1.27T_{20}$	0.70	$-0.06 + 0.23T_{50}$
Lawn A	313	0.68	$-3.39 + 2.16T_{50}$	0.74	$+0.51 + 0.25T_{50}$
LAwn/low hummock B	583	0.67	$-4.67 + 1.50T_{50}$	0.78	$-0.45 + 0.28T_{50}$
Hummock A	302	0.33	$-3.22 + 0.69T_{20}$	0.32	$-0.74 + 0.18T_{20}$
Hummock B	564	0.34	$-1.21 + 0.38T_{20}$	0.37	$-1.03 + 0.17T_{20}$
All microsites	2640	0.54	$-3.17 + 1.21T_{20} + 0.22WT$	0.56	$-0.13 + 0.22T_{20} + 0.04(WT)$

A and B, lawn A and lawn/low hummock B. Of course, the longer the data set to be left out, the larger the change in the parameter estimates on average. The goodness of fit values for data used in estimation did not differ from the values with whole data in the estimation but for the independent data sets the goodness of fit values were in most cases remarkably lower ($r^2 < 0.30$), (for typical examples see Fig. 3C and E). In some cases, the goodness of fit values for the independent data set were as good as for the dependent data set (Fig. 3A shows an example). Generally speaking, the highest goodness of fit values for the independent data sets were obtained when data from the late summer period was chosen as the independent data. Interestingly, the goodness of fit values for the August–October independent data set were higher (Fig. 3B, D and F) than for the independent data sets of one, two and four week periods, even though the hysteresis between temperature and methane emissions in Fig. 2 would suggest relatively low goodness of fit values for the independent data set covering the period August–October. The average errors were slightly higher for the different independent data sets than for the dependent data sets, i.e. between 3.0 and 4.0 mg CH_4 m^{-2} h^{-1} for flarks A and B, lawn A, lawn/low hummock B and hummock A. For hummock B, the average error was typically about 2.0 mg CH_4 m^{-2} h^{-1}.

Diurnal variations in methane emissions occurred early in the growing season at all sites except lawn A and flark A but the pattern was no longer evident by July (Fig. 4). In hummocks and flarks, methane fluxes were highest during the afternoon from 12.00 to 20.00 h and lowest between 00.00 and 08.00 h. Maxima were up to 30% higher and minima up to 20% lower than the daily averages in these microsites. The ANOVA analysis resulted in statistically significant differences ($p < 0.01$) in May for flark B, lawn/low hummock B and hummocks A and B, in June for hummocks A and B and in July for hummock B. The lawn/low hummock B pattern was significant in June with $p < 0.05$. During the August–October period, the diurnal patterns were not significant. In the four microsites with a significant diurnal pattern (hummocks A and B, lawn/low hummock B and flark B) field layer species capable of transporting methane do not dominate, but in the two microsites (lawn A and flark A) with no clear diurnal pattern the abundance of sedges was significant (Table 3).

During the period when diurnal variations were strongest (8–14 May represented in Fig. 4A, C and E), methane emissions correlated to peat surface temperature (correlation coefficients between 0.60 for flark A and 0.80 for hummock B) suggesting that peat temperature near the surface might control diurnal changes in the diffusion and methane production rate. The relationship, however, was not obvious even during the next week or generally later in the growing season. The correlation of methane emissions to lagged peat surface temperatures with lags from 4 to 24 hours never increased from the value of methane emissions vs. unlagged temperature as the diurnal maxima and minima in peat surface temperature and methane emissions occurred quite simultaneously.

The diurnal variations found in methane emissions from some microsites during the early season were not reproduced by the seasonal regression models as the temperatures at depths of 20 and 50 cm showed only weak diurnal variations. Similarly to normalized measurements, the residuals of seasonal regression models showed a diurnal pattern with maxima between 12.00 and 16.00 h and minima between 04.00 to 08.00 h. The residuals correlated strongly to peat surface temperature during the period 8–14 May (correlation coefficient ranged between 0.53 for flark B and 0.80 for hummock B). However, correlation between the residuals and peat surface temperature could be observed only for very short periods of time. For example, during the next week, 15–22 May, the correlation had decreased to 0.31 for flark B and 0.36 for hummock B. For this reason, the peat surface temperature or its deviations from the daily mean could neither be used to reduce the diurnal fluctuations in residuals nor to improve the explanatory power of the seasonal regression models.

The contribution of diurnal variations to total variations was evaluated comparing the goodness of fit (r^2) of the best seasonal models estimated for all measurements and for daily averages of measurements. For lawn A, flark A, and lawn/low hummock B, the goodness of fit was improved very little (less than 0.05) when daily averages were used, indicating that diurnal cycle is a negligible source of variation in these microsites. For

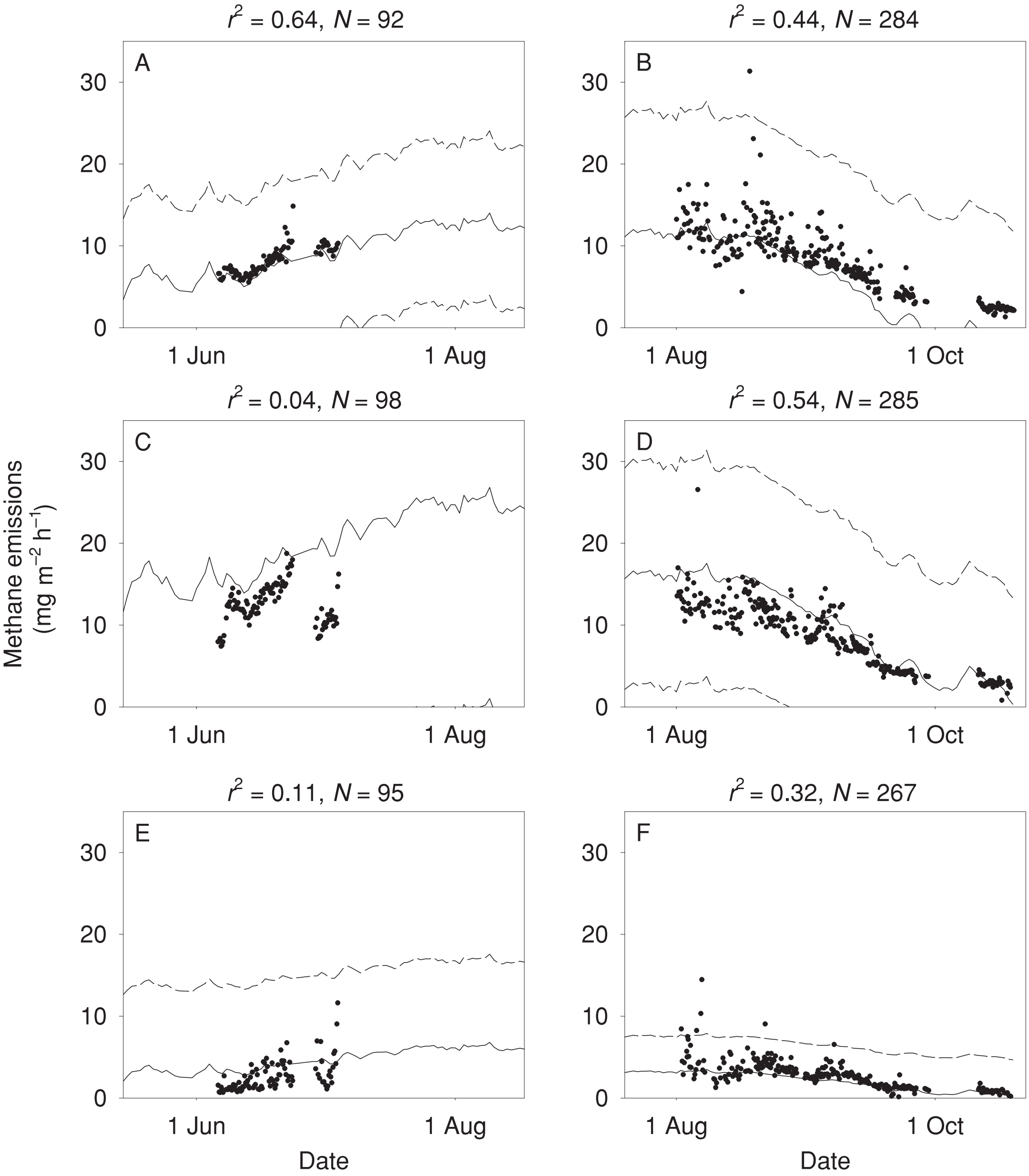

Fig. 3. The measured (black circles) and the predicted (solid lines) methane emissions with ± 95% confidence intervals (dashed line) for the modelled values in the microsites. Linear dependence of the methane emissions on the peat temperatures was assumed using T_{20} as independent variable for flarks A (panel A) and B (panel B) and hummocks A (panel E) and B (panel F) and T_{50} as independent variable for lawn A (panel C) and lawn/low hummock B (panel D). The measurements presented here were not used in parameter estimation. The *N* and r^2 give the number of independent measurements and the goodness of fit between model output and the independent data set. For flark A (panel A), lawn A (panel C) , and hummock A (panel E), a four week period from 6 June till 3 July and for flark B (panel B), lawn/low hummock B (panel D), and hummock B (panel F), data from August–October period was used as the independent data set.

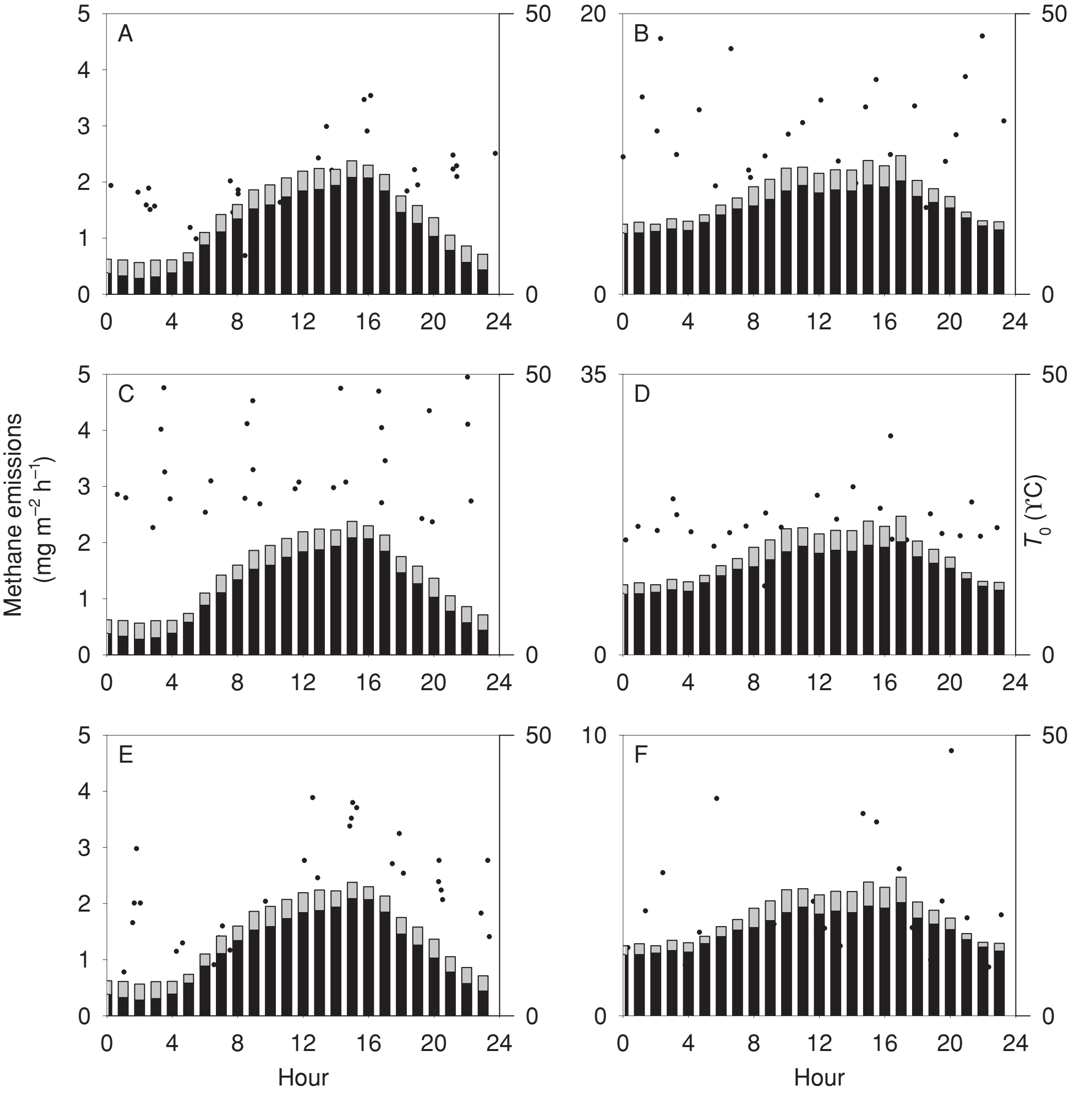

Fig. 4. Methane emission measurements (black circles) and hourly averages and standard deviations of diurnal peat surface temperature from 0–2 cm (bars) in flark B during (A) 8–14 May and (B) 12–19 July, in lawn A during (C) 8–14 May and (D) 12–19 July and in hummock B during (E) 8–14 May and (F) 12–19 July. The 8–14 May period shows the clearest diurnal patterns found in our data and the 12–19 July period represents a typical midsummer period. Note differences in methane emissions scale.

flark B, the explanatory power increased from 0.61 to 0.71 suggesting that diurnal variations cannot be neglected. For the hummocks A and B the goodnesses of fit for the daily averages were 0.56 and 0.49 (compared to 0.33 and 0.34) indicating that in hummocks the diurnal fluctuations are a significant source of variation.

The number of episodic emissions and their contribution to the seasonal estimate increased from the flarks to the hummocks for the May–July period (Table 7 and Fig. 5). During the August–October season, neither the number of episodic values nor their contribution differed much among the microsites. The episodic values increased the cumulative estimate by a few percent in the flarks and lawns and in the hummocks their effect rose up to 10%. The episodic emissions occurred throughout the measurement period in flark B, in lawn/low hummock B and in hummocks A and B (Fig. 5B and D–F). In flark A and lawn A with sedges capable of methane transport, the episodic emissions appeared at the end of July (Figs. 5A and C). The seasonal regression models failed to predict the high episodic peaks.

Discussion

The average emissions and calculated cumulative annual emissions were of the same order of magnitude (between 10 g CH_4 m^{-2} a^{-1} from the hummocks and 50 g CH_4 m^{-2} a^{-1} from the lawn) as previously measured boreal forested fen emissions (Crill *et al.* 1988, Moore *et al.* 1990, Bartlett and Harriss 1993, Dise 1993, Dise *et al.* 1993, Shurpali *et al.* 1993, Frolking and Crill 1994, Martikainen *et al.* 1995, Laine *et al.* 1996, Granberg *et al.* 1997, Shurpali and Verma 1998). Similarly to large scale spatial variations that have been related to vegetation and average water table (Christensen 1993, Dise *et al.* 1993, Roulet *et al.* 1994, Bubier *et al.* 1996), the microscale variations in methane emissions increased with increasing average water table and increasing sedge cover. In hummocks with low water table, most of the easily degradable carbon is supplied to unsaturated layers above the water table where it is aerobically degraded and not converted to methane and consequently the flux would be low. In wet microsites, carbon supplied to peat profile by the plants meets anaerobic conditions and promotes methane production resulting in high methane emissions. Among the microsites, water table was hence an important distinguishing factor and improved the explanatory power of the regression models. The temporal variations in methane emissions could not be related to water tables, as the water tables at invidual sites showed only very small temporal variations (see Dise *et al.* 1993, Shannon and White 1994). The abundance of sedges is connected to fluxes as the sedges provide both substrate for methanogenesis as root exudates and also an efficient pathway for methane to liberate from peat to atmosphere (Chanton and Dacey 1991, Schimel 1995, Verville *et al.* 1998) while diffusion in peat matrix (water phase) is very slow. In addition, methane flux via plants escapes oxidation that otherwise decreases the flux (Frenzel and Rudolph 1998).

The methane emissions showed a relatively strong relation to peat temperatures for the lawn and the flarks but not for the hummocks as also observed by Shannon and White (1994). Nevertheless, it is possible that the extremely low variations in water tables in our data may result in overemphasizing the importance of temperature control in methane emissions especially in flarks and lawns where practically the whole peat profile remained water saturated throughout the season. The weak temperature relationship in hummocks can at least partly be explained by the contribution of episodic emissions and diurnal variations that were not related to peat temperature and were strongest in hummocks. The poor fit for hummocks can also be due to the fact that the temperature profile used in regressions was measured in a wet site and hence, may not be representative

Table 7. The contribution of episodic emissions in the microsites. *N* is the total number of measurements, N_e is the number of measurements that are classified as episodic and C_e is the contribution of episodic values to annual flux. For flark A, lawn A and hummock A virgin data were available till the end of July.

Microsite	May–Jul.			Aug.–Oct.		
	N	N_e	C_e	N	N_e	C_e
Flark A	305	5	1%			
Flark B	298	8	3%	276	10	3%
Lawn A	316	12	3%			
Lawn/low hummock B	302	15	4%	287	8	2%
Hummock A	304	11	7%			
Hummock B	299	18	13%	270	6	5%

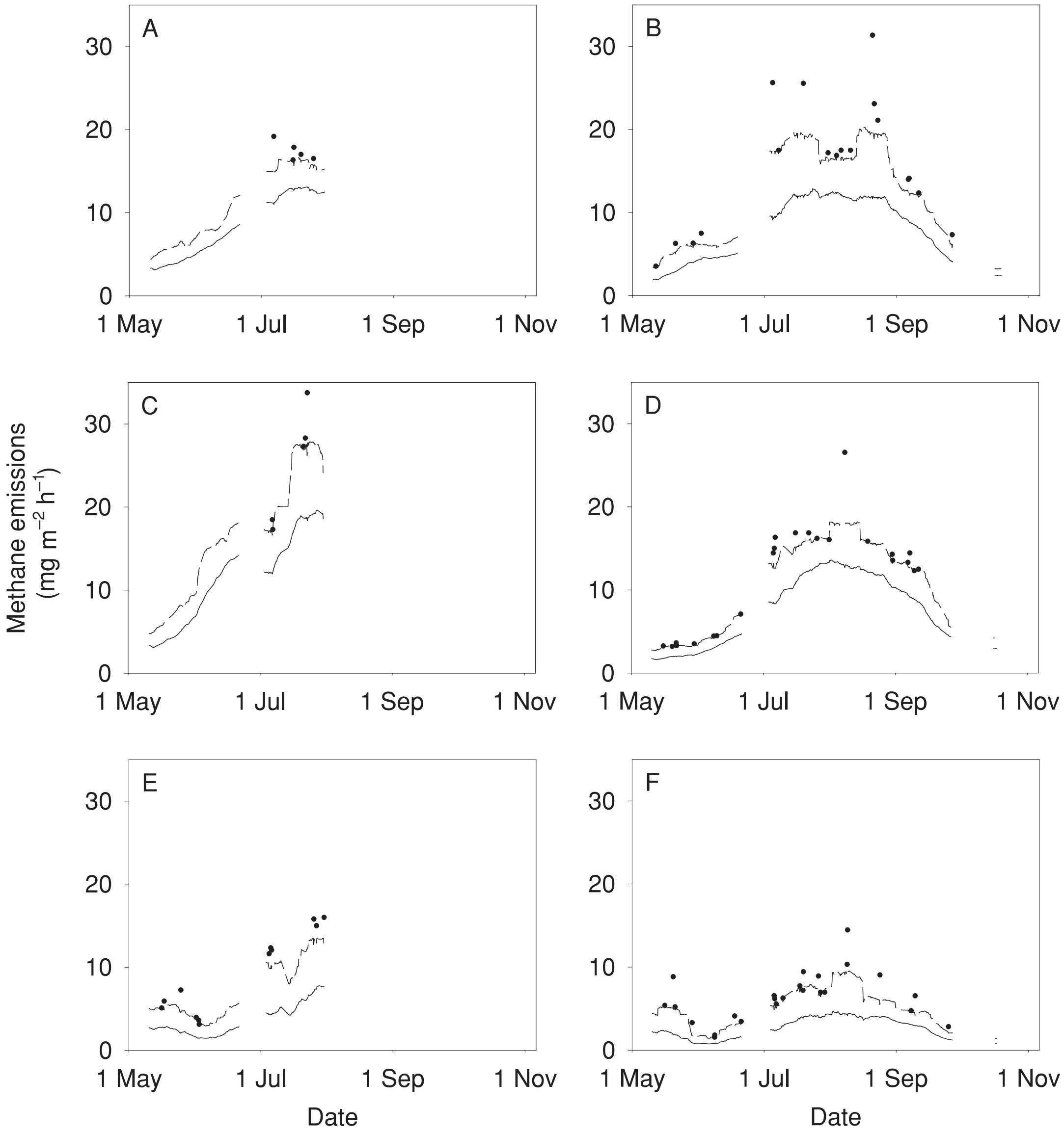

Fig. 5. The episodic pulses in methane emissions (black circles) compared to the basic emission level obtained by moving average approach (solid line) from the microsites. For flark A (panel A), lawn A (panel C), and hummock A (panel E), virgin data were available till the end of July and for flark B (panel B), lawn/low hummock B (panel D), and hummock B (panel F) till early October.

for hummocks. Even though it has been found that the permanently unsaturated hummock layers above the water table do not show significant methane oxidation potential (Kettunen *et al.* 1999), methane oxidation in *in situ* conditions may still play a more important role in hummocks than in lawns and flarks. In addition, the total variation in methane emissions is lower in hummocks than in other microsites due to low basic emission level and hence, the relative contribution of error terms becomes larger.

In our data, the relationship between peat temperatures and methane emissions was not highly non-linear inside the range of observations and hence, the linear and exponential models performed similarly. In earlier studies, both linear

(Whalen and Reeburgh, Shannon and White 1994, Granberg *et al.* 1997) and exponential (Moore and Knowles 1987, Moore and Knowles 1990, Moore *et al.* 1990, Dise *et al.* 1990, Granberg *et al.* 1997) relations between peat temperatures and methane emissions have been reported with similar goodness of fit values and similar or lower regression slopes. The observation that linear and exponential models perform similarly is not suprising as the relationship between measured temperature and methane emissions depends on all temperature effects on the basic processes, possibly with a lag. The temperature dependence of methane production and oxidation as microbial processes should follow the Arrhenius exponential form, and diffusion should show an almost linear temperature dependence. Regression models do not capture the temperature dependence of the basic processes, but only simulate the resulting sum effect of temperature on the methane flux. Linear models are, however, at least in our data better in relation to heteroscedasticity than exponential. On the other hand, at low temperatures, linear models may predict negative emissions not consistent with observations.

The seasonal pattern of methane emissions could, to some extent, be reproduced by the regressions with peat temperatures as independent variables. However, when only part of the data were used in parameter estimation, the model outputs did not predict satisfactorily the independent data sets not used in parameter estimation. As the model predictions for data from the same microsites and the same mire for a relatively short time period are not accurate, the models definitely cannot be generalized to predict emissions from different microsites, different mires or for longer time periods. Furthermore, because other environmental variables, such as the photosynthetic activity of plants, follow a similar seasonal cycle, the correlation between peat temperature and methane emissions does not necessarily imply that methane emissions are controlled by temperature but rather may reflect the dynamic effects of plants on the methane flux that have been emphasized recently (Chanton and Dacey 1991, Schütz *et al.* 1991, Whiting and Chanton 1992, 1993, Bubier 1995, Schimel 1995, Shurpali & Verma 1998, Verville *et al.* 1998). The systematic early summer overestimation and midsummer underestimation of the fluxes by the temperature driven models might result from the fact that methane emissions integrate methane production from the whole peat profile and the temperature at fixed depth is not the same as the average temperature of the active part of the profile. On the other hand, the observed difference may indicate that the availability and quality of substrate, and the temporal changes in microbial populations active in methane production and oxidation are more important controls of methane fluxes than the peat temperature. The availability of suitable substrate for methanogenesis is connected to the development of vegetation during the growing season (Schütz *et al.* 1991, Whiting and Chanton 1993, Schimel 1995). In spring when the peat temperatures rise, lack of suitable substrates for methanogenesis possibly restricts methane production while during midsummer, substrate availability apparently no more limits the methane production. The hypothesis that substrate control of the methane flux is more important than the temperature control during the early season is further supported by the observation that when temperature time series were differentiated to remove the effects of the seasonal cycle, methane emissions no longer correlated with temperatures (Kettunen *et al.* 1996). During the late season, emissions correlated also to differentiated temperature series (Kettunen *et al.* 1996). The importance of substrate control is further strengthened if the apparent connection of growth and death of methanogenic bacteria to the changes in substrate availability is considered (Grant 1998, Segers and Kengen 1998). In addition, the pore water methane concentration builds up only gradually and causes a lag before the methane formed in the soil is released to the atmosphere (Christensen 1993, Shurpali *et al.* 1993) which partly explains the difference between the present model predictions and measurements.

Weak diurnal fluctuations with maxima during late afternoon and minima during the night were present only during the early season in our data and unlike Mikkelä *et al.* (1995), we did not find a late summer diurnal pattern. However, the control of diurnal patterns is complex and seasonal variation in any single control mechanism, e.g. the carbon allocation pattern within plants, would result in different diurnal patterns during the early and late season. In our study, a diurnal pattern was found in the microsites where plant transport was apparently negligible and the diffusive flux thus dominated the emissions. This was in line with the observation that drier microsites show stronger diurnal patterns than wetter microsites (Mikkelä *et al.* 1995), an observation apparently related to differences in sedge dominance. As methane emissions from microsites with sedges capable of transporting methane did not show any diurnal rhythm, it seems that the flux via *Carex* and *Eriophorum* (Table 3) species is not controlled by changes in the air flow due to opening or closure of stomata (cf. Koncalova *et al.* 1988, Chanton *et al.* 1992, Whiting and Chanton 1992). In our data, diurnal fluctuations in methane emissions seemed to occur when the difference between the air temperature and the peat temperature was large, i.e. during the warm days in the early season when deep peat layers had not warmed up. The large diurnal variations in peat temperatures are apparently reflected to the diffusion rate of methane in peat (Jähne *et al.* 1987) and possibly also to methane production (e.g. Dunfield *et al.* 1993, Westerman 1993) causing diurnal variations in methane flux. The result that diurnal fluctuations in the microsites, where they occurred, could be correlated to peat surface temperatures only for short time periods indicates that the control mechanisms for methane fluxes change over the growing season.

Conclusion

We reported temporally frequent measurements from six microsites within a single mire and used them to analyze the different modes of variations in methane emissions. Temporally less frequent measurements would have resulted in differences in regression slopes, goodness of fit values and cumulative emissions. Based on the measurements presented here, the difference in cumulative emissions in lawn A and lawn/low hummock B, e.g., would rise to 3 g CH_4 m^{-2} a^{-1} ($\approx$ 10 %) if measurements were taken at two-week intervals. If the microscale measurements are to be generalized to obtain areal estimates, too long measurement intervals may underestimate methane emissions. Furthermore, long measurement interval would most probably miss diurnal patterns and short term episodic fluxes. The observed differences in diurnal patterns, contribution of short term episodic fluxes and explanatory power of regression models among the microsites that are situated within a few tens of meters from each other indicate that microscale variability associated with water table levels, abundance of sedges and microtopography is strongly reflected to processes behind methane emissions. Our results are consistent with the idea that abundance of sedge species affects the substrate availability and the mode of transport process and its control mechanisms. It also seems likely that the *in situ* methane production and oxidation rates in the microsites are controlled by the substrate availability and moisture conditions. Intense field measurements of fluxes and climatic variables help reveal relationships and responses which are valuable in understanding the underlying process mechanisms controlling methane fluxes.

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