

Vegetation heterogeneity and ditches create spatial variability in methane fluxes from peatlands drained for forestry

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Abstract Drainage of peatlands for forestry starts a succession of ground vegetation in which mire species are gradually replaced by forest species. Some mire plant communities vanish quickly following the water-level drawdown; some may prevail longer in the moister patches of peatland. Drainage ditches, as a new kind of surface, introduce another component of spatial variation in drained peatlands. These variations were hypothesized to affect methane (CH₄) fluxes from drained peatlands. Methane fluxes from different plant communities and unvegetated surfaces, including ditches, were measured at the drained part of Lakkasuo mire, Central Finland. The fluxes were found to be related to peatland site type, plant community, water-table position and soil temperature. At nutrient-rich fen sites fluxes between plant communities differed only a little: almost all plots acted as CH₄ sinks (−0.9 to −0.4 mg CH₄ m^{−2} d^{−1}), with the exception of *Eriophorum angustifolium* Honck. communities, which emitted 0.9 g CH₄ m^{−2} d^{−1}. At nutrient-

poor bog site the differences between plant communities were clearer. The highest emissions were measured from *Eriophorum vaginatum* L. communities (29.7 mg CH₄ m^{−2} d^{−1}), with a decreasing trend to *Sphagna* (10.0 mg CH₄ m^{−2} d^{−1}) and forest moss communities (2.6 mg CH₄ m^{−2} d^{−1}). CH₄ emissions from different kinds of ditches were highly variable, and extremely high emissions (summertime averages 182–600 mg CH₄ m^{−2} d^{−1}) were measured from continuously water-covered ditches at the drained fen. Variability in the emissions was caused by differences in the origin and movement of water in the ditches, as well as differences in vegetation communities in the ditches. While drainage on average greatly decreases CH₄ emissions from peatlands, a great spatial variability in fluxes is emerged. Emissions from ditches constantly covered with water, may in some cases have a great impact on the overall CH₄ emissions from drained peatlands.

Keywords Bog · CH₄ · Drainage · Emission · Fen · Plant community

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Introduction

In Finland, ca. 5.7 million ha of peatlands have been drained for forestry since the 1920s, an amount equal to 40% of the global estimate of 15 million ha (Paavilainen and Päivänen 1995).

This drainage has resulted in clearly reduced emissions of methane (CH_4) from these ecosystems (Nykänen et al. 1998; Minkkinen et al. 2002). However, the estimates of the reduced emissions from drained peatlands contain a great deal of uncertainty, since they are based on data that show large spatial and temporal variation, but are insufficient for analyzing the factors behind the variation.

CH_4 emission is the balance of two counteracting processes: methanogenesis in anoxic conditions and oxidation of produced CH_4 in the unsaturated surface layers of peatlands (e.g., Bubier and Moore 1994). Water-level drawdown results in decreased emissions (Nykänen et al. 1998) by directly reducing production and enhancing oxidation rates (Kettunen et al. 1999) but also through vegetation changes that take place after drainage (Laine et al. 1995). Drainage causes a shift in the physiognomy of the vegetation from sedges and grasses to arboreal species (trees and dwarf shrubs) (Laiho et al. 2003). Since sedges are the most important plant group in producing substrate for methanogenesis and providing fast transport for the produced gas (Joabsson et al. 1999; Kettunen 2003), it can be hypothesized that post-drainage dynamics (temporal and spatial) of this plant species group have an important role in controlling the emissions.

Although drained peatlands are hydrologically less variable ecosystems than undisturbed mires, they are far from being homogenous in this sense. Depending on the original site type, slope of the terrain and condition of the drainage, some mire plant species, including some *Sphagna* and sedges (e.g., *Eriophorum* sp.), may remain vigorous in the moist patches of the peatland, decades after drainage (Laine and Vanha-Majamaa 1992; Laine et al. 1995). Such spatial variation in soil moisture and vegetation is most likely also reflected in soil aeration, and consequently, in the production and consumption of CH_4 in these sites.

Ditches create another component of spatial variation in drained peatlands. Firstly, they represent very different conditions for microbial processes compared to the peat soil in the area between ditches, and secondly, there is a large variation in shape and condition among ditches.

Depending on the original conditions (mire site type, peat thickness, ditch depth and slope, underlying mineral soil, etc.) and ditching technique, ditches may stay functional for decades or they may deteriorate and fill with vegetation in less than 10 years after drainage (Keltikangas et al. 1986).

The condition of the ditch is reflected in many factors, causing variation in the CH_4 emissions, such as vegetation, water-table position in the ditch, water movement, origin of the water in the ditch and origin of the substrate for methanogenesis. The variation in the reported CH_4 fluxes from ditches is therefore vast (0–595 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$; Roulet and Moore 1995; Schiller and Hastie 1996; Minkkinen et al. 1997), but it has not been quantitatively attributed to measurable factors. Since CH_4 emissions from ditches may sometimes totally alter the overall emission-reducing impact of drainage (Roulet and Moore 1995), a better understanding of the mechanisms behind emissions from ditches is needed.

The aims of the study were (1) to relate the CH_4 fluxes in drained forested peatlands to spatial heterogeneity caused by moisture induced vegetation patterns; (2) to compare fluxes from drained plant communities with those from pre-drainage communities of different nutrient levels; and (3) to analyse the factors behind the vastly differing CH_4 emissions from ditches.

Material and methods

Experimental design and site descriptions

The measurements were done at Lakkasuo mire in Central Finland, in 1996–1997. Lakkasuo is an eccentric, raised-bog complex where a large number of Finnish mire site types are found (Laine et al. 2004). Approximately half of the peatland was drained in 1961, resulting in water-level drawdown in the drained part and in a shift from mire vegetation towards a species composition common in upland forests (Minkkinen et al. 1999). This change is especially distinct in the minerotrophic, originally fen part of the mire, whereas the ombrotrophic part is still rather wet and largely dominated by the original mire vegetation.

Four experimental sites were set up to cover the variation in soil nutrient levels (three in the minerotrophic fen part, sites 1–3, and one in the ombrotrophic bog part, site 4), and ditch conditions (stagnant/moving water, vegetation) (Fig. 1). Each site consisted of a plot of CH₄ sampling points on the drained areas and a plot in drainage ditches. The sites also had three “control” plots in the undrained part of the mire, one for each nutrient-level. Each drained plot had 2–8 CH₄ flux sampling points with different vegetation communities and/or microtopography (Fig. 1). Prior to drainage, the drained plots had been of the same site type as their control plots. As the undrained, pristine part is topographically above the drained one, ditches have had only a minor impact on the undrained part, making comparisons between the two parts possible.

Sites 1–3 are situated on the minerotrophic, fen part of the peatland and are thus referred to as fen sites. In its natural state site 1 is classified as a herb-rich flark fen (RhRiN), representing the highest nutrient level (mesotrophy) in the experiment. The undrained control plot is treeless, and the field layer is dominated by two sedge species

Carex livida (Wahlenb.) Willd. and *Carex lasiocarpa* Ehrh.. There is a lot of sedge litter on the peat surface, and the moss layer is negligible. The drained part has developed into *Vaccinium myrtillus* type (Laine 1989) with a dense tree stand dominated by *Betula pubescens* Ehrh. with some *Picea abies* (L.) H. Karst. as the secondary tree layer (Table 1). The soil surface is covered by a thick layer of *Betula* leaf litter, and thus is nearly vegetationless. The peat layer is shallow (30–50 cm) and the water table usually remains below the peat layer during summer months.

The ditches draining the plot are vegetationless, and there is on average 15 cm of slowly moving water on the ditch bottoms.

Sites 2 and 3 were originally oligotrophic tall sedge fens (Laine et al. 2004). Prior to drainage they were similar to each other, being dominated by *Carex lasiocarpa*, *C. rostrata* Stokes and *Eriophorum angustifolium* Honck. in the field layer, with *Sphagnum papillosum* Lindb., *S. magellanicum* Brid. and *S. fallax* (H.Klinggr.) H.Klinggr. in the moss layer. There is one common control plot for both drained sites on the undrained part (Fig. 1).

Fig. 1 Location of the sites, plots and CH₄ sampling points in the drained strips, ditches and undrained parts of Lakkasuo mire. DR = Drained, UD = Undrained. The direction of water movement in the ditches is marked by arrows

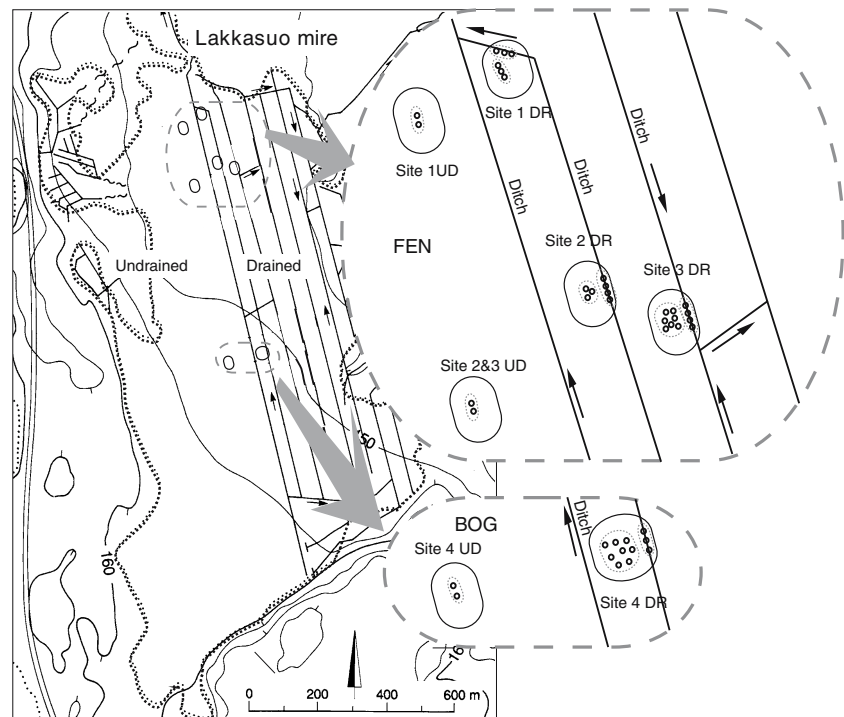


Table 1 General description of the sites

Site number	Site type		Tree stand vol., m ³ ha ⁻¹		Tree species		Peat thickness, cm		Ditch water movement/depth	Ditch vegetation
	UD	DR	UD	DR	UD	DR	UD	DR		
1	RhSN	Mtkg	-	39	birch 100% (spruce seedlings)	50	35	Moving/15 cm	No vegetation	
2	VSN	Ptkg	-	86	pine 70%, birch 30%	170	140	Stagnant/50 cm	Green algae	
3	VSN	Ptkg	-	95	pine 80%, birch 20%	170	150	Moving/15 cm	No vegetation	
4	RaTR	Vatkg	5	20	pine 100 %	270	250	Stagnant/20 cm	<i>Carex rostrata</i> , <i>Eriophorum vaginatum</i> , <i>Sphagnum riparium</i>	

UD = Undrained, DR = drained. Site types: RhSN = herb-rich sedge fen, VSN = tall-sedge fen, RaTR = Cottongrass pine bog with *Sphagnum fuscum* hummocks, Mtkg = *Vaccinium myrtillus* pine forest, Ptkg = *Vaccinium vitis-idaea* pine forest and Vatkg = Dwarf shrub pine forest

The drained part has developed into *Vaccinium vitis-idaea* site type. The tree stands in both drained sites are dominated by *Pinus sylvestris* L. with some *Betula pubescens* in the tree layer (Table 1). In site 2, the field layer is characterized by *Eriophorum angustifolium* as relict from the undrained situation. The moss layer is dominated by forest moss communities, such as *Pleurozium shreberi* (Willd. ex Brid.) Mitt., *Dicranum polysetum* Sw. and *Polytrichum commune* Hedw. Site 3 is similar to site 2, except for the occurrence of *Sphagnum angustifolium* (C.E.O.Jensen ex Russow.) C.E.O.Jensen and *S. russowii* Warnst. communities in the moss layer. In the field layer *Eriophorum vaginatum* L. tussocks are common (Table 2).

The ditch crossing site 2 is vegetationless except for some green algae growing on the water. Because of insufficient slope, the water in the ditch is rather stagnant. The depth of the water is 50 cm on average.

The ditch at site 3 is steeper and water is running constantly throughout the year, indicating that the ditch may also drain waters from the surrounding upland and possibly even from the groundwaters connected to the undrained mire. There is no vegetation, and the depth of the water is 20 cm, on average.

Site 4 is situated at the southern, ombrotrophic part of the mire. The undrained part is classified as cottongrass pine bog with *Sphagnum fuscum* (Schimp.) H.Klinggr. hummocks (RaTR). Ground vegetation is dominated by *Sphagnum fuscum* and *S. balticum* (Russow.) Russow. ex C.E.O.Jensen with *Eriophorum vaginatum* in the field layer. The tree stand consists purely of *Pinus sylvestris*. Drainage has increased the tree stand biomass, decreased the coverage of Sphagna and increased that of forest mosses and dwarf shrubs (e.g. *Vaccinium uliginosum* L.) while the coverage of cottongrass (*Eriophorum vaginatum*) has not changed (Minkkinen et al. 1999). The *Sphagnum* communities still present at the drained part consist mostly of *S. fuscum*, *S. angustifolium* and *S. balticum*. *Pleurozium shreberi* is the dominant forest moss (Table 2). The drained part is classified as a dwarf shrub type.

The ditch crossing the drained plot is filled with vegetation. Sedge communities of *Carex rostrata*

Table 2 Site codes, surface classes, average CH₄ flux (mg CH₄ m⁻² d⁻¹) and water-table position (WT, cm, negative values indicate position below soil surface) during the measurements in 1996–1997, and coverage (%) of main plant species^a (and litter) on the drained measurement points

Site	Point	Fen/ Bog	Surface class	CH ₄ flux	WT	Litter		Sedges		Sphagna			Forest mosses			Dwarf shrubs					Herbs									
						ang ^a	ang ^a	Eri	Eri	Sph ang	Sph ang	Sph bal	Sph fus	Sph rub	Sph rus	Dic pol	Ple sch	Pol com	Pol str	And pol	Bet nan	Bet nan	Emp nig	Emp nig	Vac oxy	Vac uli	Rub cha	Rub cha	Tri eur	
1	D1	Fen	Litter	-0.24	-53		100																							
1	D2	Fen	Litter	-0.56	-53		96																							
1	D3	Fen	Litter	-0.32	-53		99																							
2	D1	Fen	For moss	-0.13	-39		5																							
2	D2	Fen	Eri ang	0.76	-37		15	20																						
2	D3	Fen	Eri ang	0.96	-38		38	10																						
3	D1	Fen	For moss	-1.73	-54		5																							
3	D2	Fen	Eri vag	-1.87	-52			95	1																					
3	D3	Fen	For moss	-1.19	-52																									
3	D4	Fen	Sphagnum	-1.36	-48					50																				
3	D5	Fen	Sphagnum	-0.72	-45					100																				
3	D6	Fen	Sphagnum	-0.72	-37					2	100																			
3	D7	Fen	Eri vag	0.37	-41			95	15																					
4	D1	Bog	Sphagnum	5.14	-30			5		90	9																			
4	D2	Bog	Sphagnum	9.65	-15			2	100																					
4	D3	Bog	Eri vag	40.07	-24			90																						
4	D4	Bog	Eri vag	28.94	-24			70	2																					
4	D5	Bog	Sphagnum	14.44	-15			5		99	1																			
4	D6	Bog	For moss	3.24	-35			95																						
4	D7	Bog	Eri vag	20.31	-36			95																						
4	D8	Bog	For moss	1.84	-25			2																						

^aPlant species: Eri ang = *Eriophorum angustifolium*, Eri vag = *E. vaginatum*, Sph ang = *Sphagnum angustifolium*, Sph bal = *S. balticum*, Sph fus = *S. fuscum*, Sph rub = *S. rubellum*, Sph rus = *S. russowii*, Dic pol = *Dicranum polysetum*, Ple sch = *Pleurozium schreberi*, Pol com = *Polytrichum commune*, Pol str = *Polytrichum strictum*, And pol = *Andromeda polifolia*, Bet nan = *Betula nana*, Emp nig = *Empetrum nigrum*, Vac oxy = *Vaccinium oxycoccos*, Vac uli = *V. uliginosum*, Rub cha = *Rubus chamaemorus*, Tri eur = *Trientalis europaea*

and *Eriophorum vaginatum* with submerged *Sphagnum riparium* Angstr. on the bottom are found along the ditch. The average depth of water on the ditch is 20 cm.

Measurements

CH₄ fluxes were measured biweekly during the snow-free seasons 5.6.1996–10.11.1997, and twice during the winter 1996–1997. Measurements were done using static chambers made of metal tubes (diameter 31.5 cm, height 30–42 cm, depending on the plant community). Measurement points were prepared by pressing a 5-cm deep groove of the size of the chamber into the peat. In the beginning of each measurement the chamber was installed on the groove, thereby making an airtight seal with the peat.

The fluxes from the ditch water surface were measured with floating chambers, allowing continuous waterflow under the chambers during the measurements. In 1997 CH₄ fluxes were also measured from the ditch bottoms (using normal chambers) to study whether the CH₄ emitted from ditch water surface could be produced in the underlying sediment. The chambers were carefully installed on the ditch bottom in a way that water could not be exchanged anymore by water flow in the ditch. Thus the CH₄ sampled from the chamber headspace is the sum of CH₄ produced in and released from the underlying sediments and the standing water column. To reduce the disturbance impact caused to the ditch bottom, the chamber was left to stabilize for ca. 5 min before the air vent was closed and timekeeping started.

Four gas samples of 50–60 ml were taken from the chamber headspace with plastic syringes during a measuring period of 35 min (5, 15, 25 and 35 min.); they were analyzed for CH₄ within 24 h with a gas chromatograph equipped with a flame ionization detector. For ditches, shorter measurement periods (12–20 min) were sometimes used because of very high fluxes. Before sampling, the air in the chamber headspace and pipeline was mixed by pumping the syringes a few times.

Air (T_{air}) and soil temperature (T_{soil}) at 10-cm intervals (down to 70 cm) and water-table position (WT) were measured from each point during the flux measurements. Continuous weather data for

the measurement years 1996–1997 were collected by a weather station situated close to sites 2 and 3.

The release of bubbles (ebullition) from the ditch water was measured with floating inverted funnels using a collecting period of two weeks. The funnels were equipped with a syringe with a 3-way stop cock fastened at the narrow end of the funnel. The bottom of the funnel was inserted 1 cm below the water surface, and it was filled with ditch water by sucking air through the syringe. The volume of the collected gas was measured, and CH₄ concentration was determined by a gas chromatograph equipped with a thermal conductivity detector. Because of the dilution and possible oxidation of the trapped CH₄ gas during the collection period, CH₄ concentration was also analyzed from fresh bubbles.

Calculations

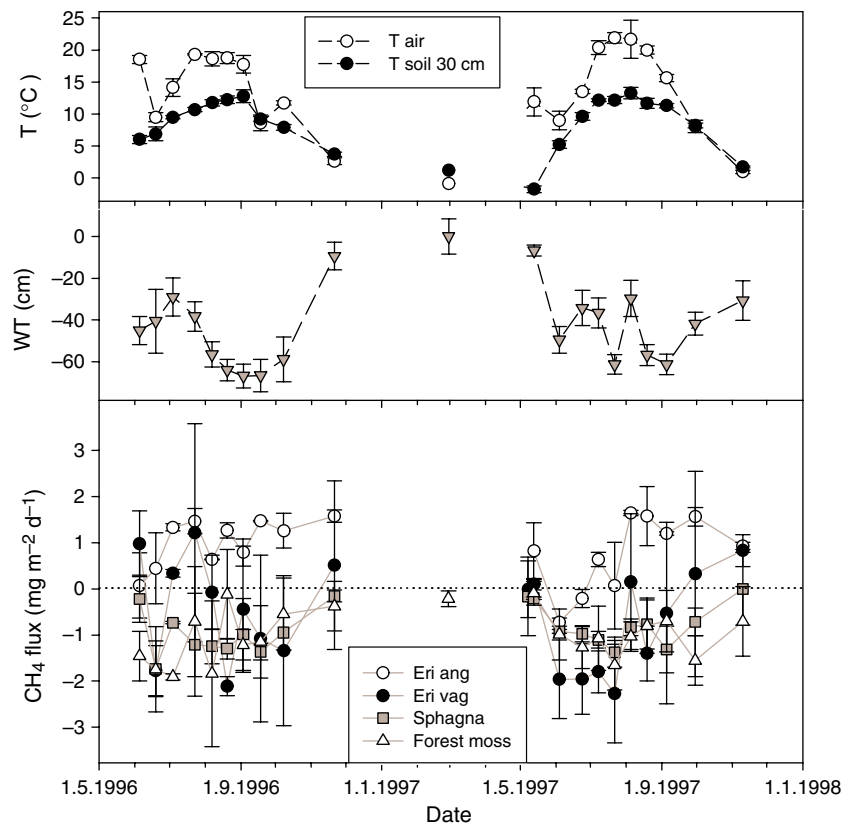
The daily fluxes of CH₄ were calculated by linear regression of the concentration change in the four samples drawn from chamber headspace, using at least two replicate injections from each sample. Distinct ebullition events were excluded from the data, but otherwise all data were included. The bubble fluxes from ditches were calculated using the volume of collected gas in the funnels and the CH₄ concentration of the fresh samples.

Annual CH₄ fluxes for each bog and fen plant community were estimated by two methods: (1) integrating from the daily emissions and (2) using nonlinear regression models (Systat 10, SPSS Inc., USA) with T_{soil} and WT as explanatory variables. Continuous soil temperature data was derived from a weather station near site 2 after calibration ($T_{\text{site}} = T_{\text{station}} + b$) to each site. The manually-measured WT data were interpolated for the days between measurement events.

Statistical analyses

Since the experimental design was hierarchical, the spatial and temporal variation in the flux data was statistically analyzed using hierarchical multi-level models (MLwiN 2.01, Centre for Multilevel modeling, University of Bristol, UK) with fixed (WT, T_{soil} , plant community) and random effects (measurement events, points, plots and sites).

Fig. 2 Average (mean \pm SD) air and soil temperatures and water-table position (WT); and CH_4 emissions (mean \pm SE) from the different vegetation communities at the drained fen sites 1–3



Results

Overall variation

Variation in the CH_4 fluxes over the whole data was, as expected, very high. In the drained plots fluxes varied from -3.6 to 89.7 ; in undrained control plots, from -1.6 to 319.0 ; and in the ditches, from -1.1 to 3512.2 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. This variation was caused by (1) temporal dynamics in soil temperature, water-table position and vegetation communities and (2) by spatial variation in the same variables among the experimental plots.

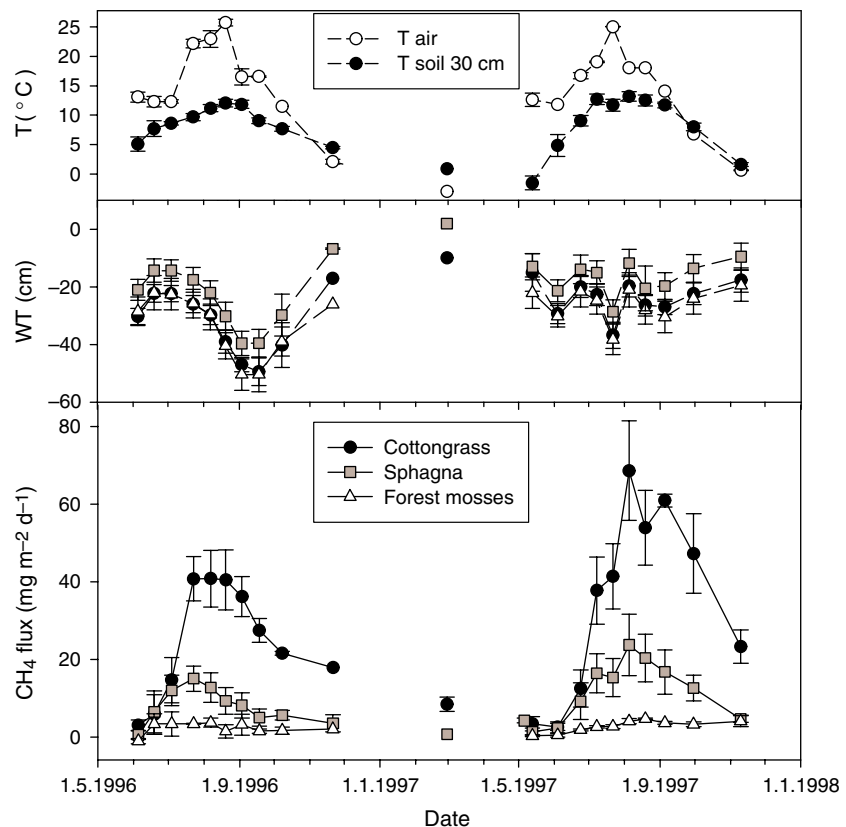
Variation within and between vegetation communities of the drained plots

CH_4 fluxes from the drained fen (1–3) and bog (4) sites were clearly different; the bog communities were emitting CH_4 , while the fen communities were mainly consuming it (Figs. 2, 3). At the bog site the highest fluxes were emitted from *Eriophorum*

vaginatum tussocks, decreasing to less than half in *Sphagnum*-communities and being quite low in forest moss communities (Table 3). The CH_4 fluxes from these plant communities were significantly different from each other also when WT and T_{soil} were included in a multilevel model (Table 4). Higher WT and T_{soil} increased CH_4 emissions from all plant communities. The response to WT was similar in all three plant communities, but the response to T_{soil} was different between the communities: increasing T_{soil} increased fluxes most from *Eriophorum vaginatum* communities, and least from forest moss communities (Table 4). The best temperature correlation was found at the depth of 30 cm, which was also the average WT (Table 3).

At the fen sites (1–3), the differences between communities were much smaller (Fig. 2, Table 3). *Eriophorum angustifolium* was the only community continuously emitting CH_4 in the fen sites (Fig. 2, Table 3). Other fen communities were consuming CH_4 at average rates (Table 3) that

Fig. 3 Average (mean \pm SD) air and soil temperatures and water-table position (WT); and CH_4 emissions (mean \pm SE) from the different vegetation communities at the drained ombrotrophic pine bog, site 4



were not statistically significantly different from each other (Table 4). WT was positively correlated with CH_4 flux, similarly to the bog site, but the response to T_{soil} was negative, with the exception of the *Eriophorum angustifolium* community. Highest correlations with T_{soil} were found at the depth of 10 cm. Of the random effects in the model, measurement site and measurement plot were not statistically significant, whereas measurement event was significant within both fen and bog sites (Table 4).

The estimated annual fluxes in different plant communities varied between -0.28 and $0.28 \text{ g CH}_4 \text{ m}^{-2} \text{ a}^{-1}$ in the fen sites and between 0.48 and $6.74 \text{ g CH}_4 \text{ m}^{-2} \text{ a}^{-1}$ in the bog sites (Table 5). The two estimation methods, integration and regression, gave similar outcomes.

Ditch fluxes; chamber measurements

Emissions from the ditch water in the minerotrophic sites were higher than from any vege-

tated surfaces in the drained and undrained control plots, whereas at the bog site they were of similar magnitude as the undrained control plots. There was great variation in the fluxes between different ditches, related to water movement. Fluxes were highest from ditch plots 1 and 3 where water moved constantly. Average warm season fluxes (1 May–31 August) from the sites 1 and 3 were 350 and $600 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, respectively, and extremely high fluxes (up to $3512 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) were recorded from ditch plot 3 in spring and summer 1997. Fluxes from ditches with stagnant water were much smaller, on average 182 and $50 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ from the ditch plots 2 and 4, respectively (Figs. 4, 5). During winter 1997 the ditch surfaces were partly unfrozen, and high fluxes, from 96 to $137 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, were measured from the open ditch water at sites 2 and 3 (Fig. 4), and $48 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, even through the ice cover, at site 3. Integrating from these instantaneous values, extremely high annual fluxes were

Table 3 Measured instantaneous CH₄ fluxes (mg CH₄ m⁻² d⁻¹), water table positions (WT, cm, negative values indicate position below soil surface), soil (30 cm depth) and air temperatures (°C) in 1996–1997 at the different plant communities in the drained fen and bog sites at Lakkasuo mire

CH ₄ flux	n	Fens					Bog				
		Litter		Eriang	Erivag	Sphagnum	Forest moss	Erivag	Sphagnum	Forest moss	
		Mean ± SD	Range	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	
WT	46	-0.41 ± 0.68	-1.84 to 1.36	0.86 ± 0.79	-0.66 ± 1.71	-0.91 ± 0.77	-1.02 ± 1.16	29.73 ± 21.59	9.97 ± 8.54	9.97 ± 8.54	2.56 ± 1.98
T _{Soil}	46	-46 ± 8	-27 to -53	-38 ± 17	-3.34 to 3.57	-2.77 to 1.45	-3.56 to 1.69	0.21–89.74	-0.75 to 32.11	-0.75 to 32.11	-1.71 to 6.50
T _{air}	46	7.7 ± 3.5	7.7 to 13.0	8.6 ± 4.0	8.5 ± 4.3	8.9 ± 4.3	8.6 ± 4.0	8.6 ± 4.0	8.4 ± 4.4	8.4 ± 4.4	8.2 ± 4.2
Range	46	14.0 ± 6.4	14.0 to 23.0	14.7 ± 6.3	14.0 ± 6.0	14.5 ± 5.9	13.9 ± 6.6	14.7 ± 7.1	14.8 ± 6.8	14.8 ± 6.8	15.2 ± 6.5
Range	46	1.7–23.0	1.3–26.0	0.7–21.8	0.7–21.8	0.7–21.8	-0.9 to 26.0	-3.0 to 26.6	-3.0 to 25.5	-3.0 to 25.5	0.6–26.6

estimated for the ditches at fen sites, whereas the flux from the bog ditch was clearly smaller (Table 6).

The fluxes from ditch bottoms (5–210, mean 45 mg CH₄ m⁻² d⁻¹) were clearly lower than those from the moving water on sites 1 and 3, but at the same level (50–265, mean 157 mg CH₄ m⁻² d⁻¹) with stagnant water at site 2 (Fig. 4).

At site 4 where the ditch was vegetated, there was a very clear connection between vegetation (sedge vs. moss) communities and CH₄ flux: the flux was high from the *Eriophorum vaginatum* (summertime average 93 mg CH₄ m⁻² d⁻¹) and *Carex rostrata* (48 mg CH₄ m⁻² d⁻¹) communities, whereas the flux was close to zero (0.5 mg CH₄ m⁻² d⁻¹) from the neighboring point with pure *Sphagnum riparium* community (Fig. 5).

Ditch fluxes; bubble collectors

There were large differences between ditches in the bubble gas concentration and volume. Ebullition was clearly highest in the ditch with stagnant water (site 2). Concentration of CH₄ in the trapped bubbles varied by ditch from an average of 2.2 (site 1) to 10.4% (site 2). However, concentration in the fresh bubbles was much higher (15–22% on average), indicating a considerable dilution of CH₄ gas during the collecting period. The flux estimates, corrected with the CH₄ concentration in fresh bubbles, were on average 9 mg CH₄ m⁻² d⁻¹ for site 1, 35 mg CH₄ m⁻² d⁻¹ for site 2, and 10 mg CH₄ m⁻² d⁻¹ for site 3. Temporal variation was not very distinctive, but the highest fluxes were measured in the warmest months, July and August.

Undrained control plots

Of the undrained control plots the sedge fen (plot 2) showed the highest CH₄ emissions: daily emissions varied from 0.2 to 319 mg CH₄ m⁻² d⁻¹ (Fig. 6). The average daily emission for the summer months (June–August) was 102 mg CH₄ m⁻² d⁻¹, and the integrated annual emission 13.2 g CH₄ m⁻². The water table at the site was constantly close to the peat surface (on average –2 cm) and never deeper than –10 cm. At the mesotrophic site (control plot 1), the water table

was 10 cm deeper and much more dynamic than at the oligotrophic site (control plot 2); it dropped below the peat layer of 30 cm several times during the summer months (Fig. 6). Consequently, site 1 had much lower daily emissions, on average $13 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, and the annual integrated emission was $1.6 \text{ g CH}_4 \text{ m}^{-2}$. The bog site emitted on average $39 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ during the summer months, and the annual emission was $6.6 \text{ g CH}_4 \text{ m}^{-2}$. WT varied between 0 and 30 cm, being on average 11 cm below the peat surface.

There were no replicates for different vegetation surfaces in the undrained sites. However, if single collars are examined, a similar trend can be seen as on the drained sites: collars with more sedge vegetation emitted more CH_4 . At the mesotrophic site 1 the collar with *Carex lasiocarpa* as the dominant species emitted three times

as much as the one with similar coverage of *Carex livida*. At the bog site the collar with ca. 10% coverage of *Eriophorum vaginatum* emitted four times the amount compared to the collar with ca. 2% coverage of the same species.

Discussion

Plant communities

CH_4 fluxes were measured in a partly-drained mire in Central Finland. Drainage has clearly lowered CH_4 emissions at the mire. The bog sites are emitting half of the emissions found in a natural state, while at the fen sites the emissions have ceased and sites are mainly consuming atmospheric CH_4 .

As commonly seen in drained peatlands in Finland (Laine et al. 1995), some mire plant communities (*Eriophorum vaginatum* and *E. angustifolium* in the field layer and *Sphagnum angustifolium* and *S. russowii* in the bottom layer) have remained at the drained fen sites. It was therefore reasonable to assume that these microhabitats could maintain more vigorous methanogen populations, which could be reflected in CH_4 emissions from the plant communities present at such sites.

Plants themselves affect methane emissions in many ways. For example, deep-rooted wetland plants (e.g. sedges) produce substrate for methanogenesis and provide pathways for oxygen and CH_4 through their aerenchyma (Joabsson et al. 1999). At sedge-rich sites CH_4 is mainly produced from labile carbon compounds (e.g. acetate, Ström et al. 2003) and a close correlation has been found with NEE and CH_4 emissions (e.g. Whiting and Chanton 1993). Despite similar functions of these aerenchymous sedges, the contribution of different species on CH_4 emissions varies in different studies. Plant species dependent variability has been found for example in the CH_4 oxidation in the rhizosphere (Ström et al. 2005) and inside the aerenchyma (Frenzel and Rudolph 1998), in the gas transport mechanisms (Schimel 1995) and in the formation rates of acetate, the substrate for methanogenesis (Ström et al. 2005). It is therefore evident that

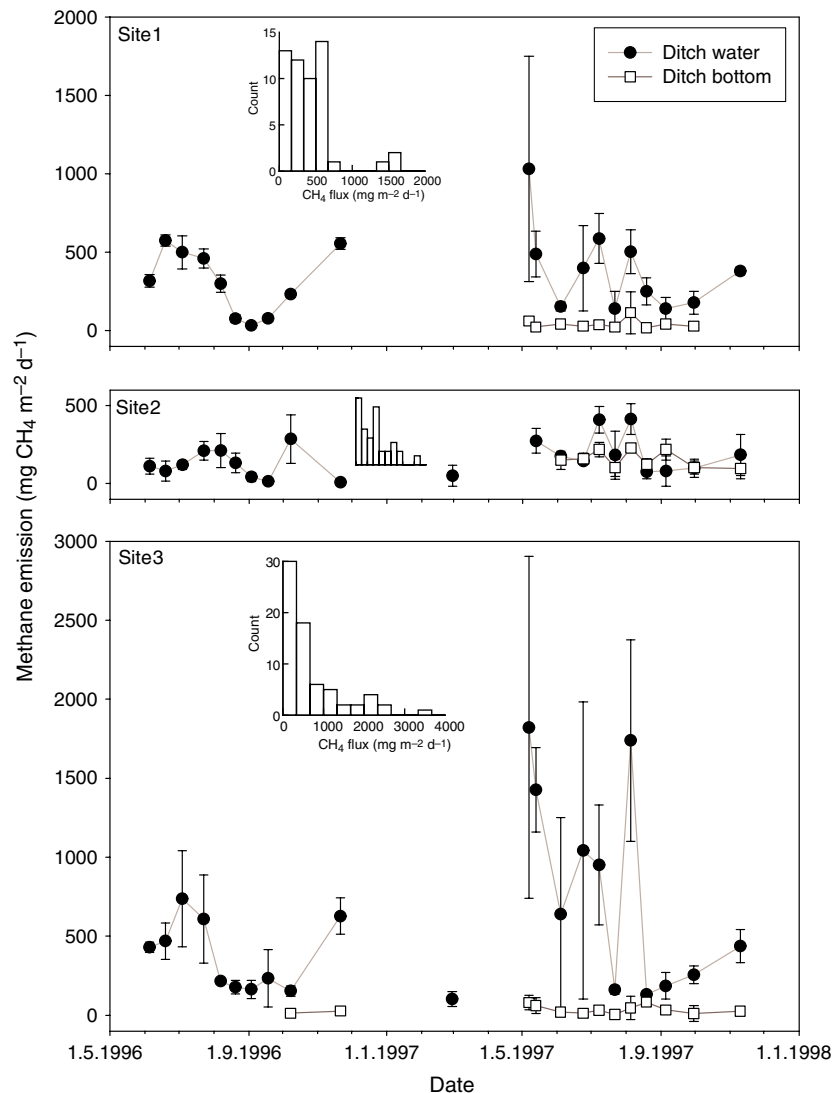
Table 4 Results of hierarchical multilevel variance analysis for the drained bog (a) and fen sites (b); fixed parameters included only if statistically significant (i.e., mean estimate $>2 \times \text{SEM}$. (standard error of the mean))

	Mean estimate	SEM
(a) Bog		
<i>Fixed effects</i>		
Constant	2.1070	0.1303
WT	0.0112	0.0038
$T_{\text{soil}_{30 \text{ cm}}}$	0.0322	0.0143
$\text{Sphagnum} \times T_{\text{soil}_{30 \text{ cm}}}$	0.0575	0.0165
$\text{Eri vag} \times T_{\text{soil}_{30 \text{ cm}}}$	0.1231	0.0167
<i>Random effects</i>		
Measurement point	0.0491	0.0290
Measurement event	0.1782	0.0209
(b) Fen		
<i>Fixed effects</i>		
Constant	1.6724	0.0862
WT	0.0024	0.0010
$T_{\text{soil}_{10 \text{ cm}}}$	-0.0107	0.0036
$\text{Eri ang} \times T_{\text{soil}_{10 \text{ cm}}}$	0.0182	0.0074
<i>Random effects</i>		
Measurement site	0.0115	0.0141
Measurement point	0.0195	0.0098
Measurement event	0.0446	0.0043

The response variable is CH_4 flux ($\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$), which was transformed before the analysis [$\ln(\text{CH}_4 \text{ flux} + 5)$] to reach linearity and to also include negative flux values. Dummy coding was used for vegetation communities; constant represents forest moss community. T_{soil} is soil temperature °C. WT is water table position (cm, negative values indicate position below soil surface). *Eri vag*: *Eriophorum vaginatum*; *Eri ang*: *Eriophorum angustifolium* community

Table 5 Estimated annual fluxes ($\text{g CH}_4 \text{ m}^{-2}$) and mean values of the driving variables for the regression model (calibrated soil 30-cm temperatures $^{\circ}\text{C}$, and water-table positions, cm) for the different plant communities in the drained fen and bog sites

	Fen_eriang	Fen_erivag	Fen_Sph	Fen_for.moss	Fen_litter	Bog_eri.vag	Bog_Sph	Bog_for.moss
Integrated CH_4 flux	0.20	-0.11	-0.16	-0.21	-0.07	6.74	1.91	0.48
Modeled CH_4 flux	0.28	-0.15	-0.24	-0.28	-0.06	6.73	2.29	0.72
WT_mean (1 June–31 Oct)	-40	-51	-47	-51	-46	-29	-21	-35
T_{mean}	4.42	4.52	4.52	4.52	4.42	4.52	4.52	4.52

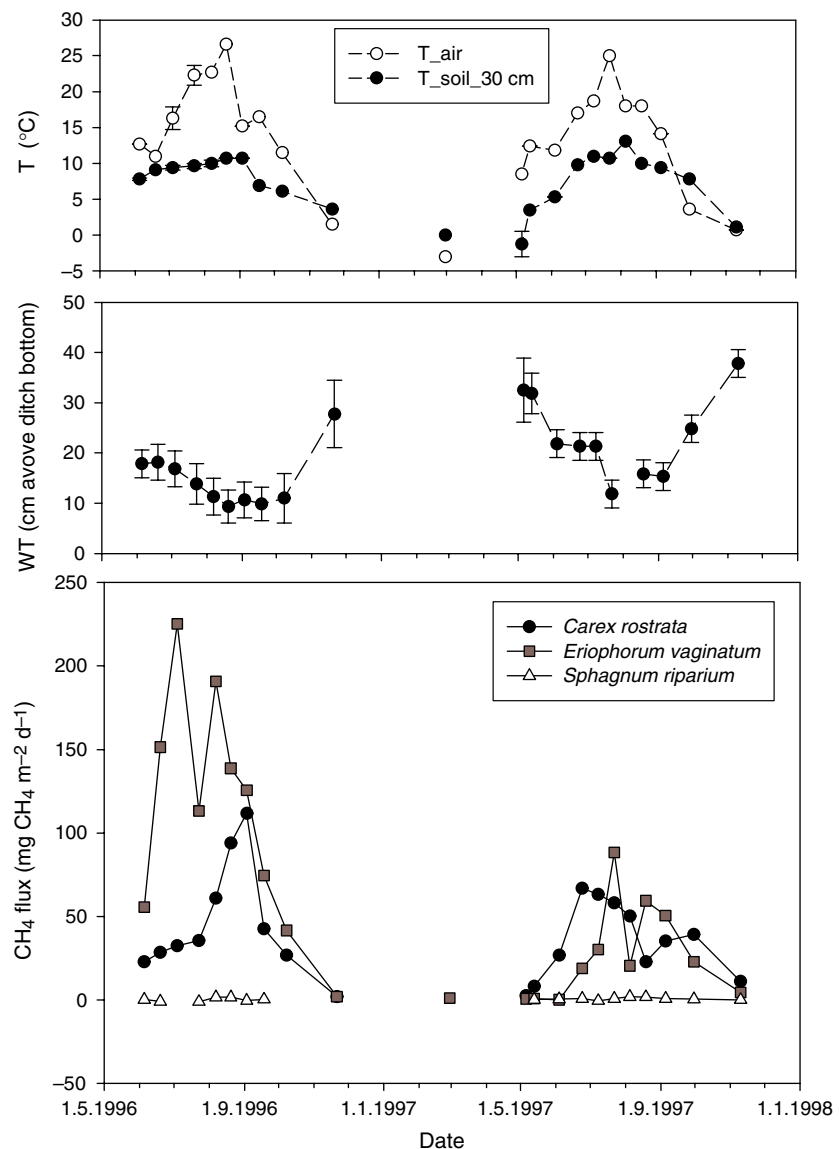
Fig. 4 CH_4 emissions (mean \pm SD) from ditches (ditch water and ditch bottom) at the fen sites 1–3. Frequency distributions of the measured fluxes are also shown as insertions

plant communities may have a great impact on CH_4 dynamics in drained peatlands, where the community structures are highly variable.

Fluxes from the drained sites were expectedly low in the fen sites where drainage had caused a

notable change in plant communities and water-table position (Glenn et al. 1993; Crill et al. 1994; Martikainen et al. 1995; Roulet and Moore 1995; Nykänen et al. 1998; Huttunen et al. 2003). The differences in CH_4 emissions among different

Fig. 5 Air and soil temperature, water table position (WT) above the ditch bottom and CH₄ emissions from different vegetation communities in the ditch at the bog site 4



plant communities in the fen sites were small, and nearly all communities acted as small CH₄ sinks throughout the measurement period. However, one plant community (*Eriophorum angustifolium*) at site 2 continuously emitted CH₄, although the adjacent forest moss community at the same site was consuming it. This indicates that the presence of deep-rooted sedges is important in providing a non-oxidative pathway for CH₄ to the atmosphere (Joabsson et al. 1999), even in drained peatlands. On the other hand, while one *Eriophorum vaginatum* community at site 3 (D2;

Table 2) showed a small uptake of CH₄, an adjacent point with similar vegetation and slightly higher mean WT (D7, Table 2) emitted it. It can be concluded, that the occurrence of deep-rooted mire plants (sedges) may, but does not always indicate raised levels of CH₄ emissions if drainage is sufficiently efficient.

In the drained bog (site 4) the water table as well as CH₄ fluxes were clearly and constantly higher than in the fen sites, and the differences between plant communities were clear. *Eriophorum vaginatum* communities showed the

highest CH₄ emissions, even though the water table relative to tussocks was ca. 10 cm deeper than in the *Sphagnum* communities. This indicates that the roots of the sedge *Eriophorum vaginatum* still reach to anaerobic peat layers, transporting part of the produced methane unoxidized (Frenzel and Rudolph 1998) to the atmosphere. Forest moss communities were the driest spots and emitted the least CH₄. The differences between the emissions from the communities were clearest in summer during high soil temperatures (Fig. 4), as indicated also by the significant interaction between T_{soil} and plant community in the bog site (Table 4). Thus, in the drained bog with poorer drainage the different plant communities show clear differences in CH₄ emissions, a fact which is important to take into consideration if areal emissions from drained bogs should be estimated.

The impact of plant community was very clear at the ditch that was filled with submerged *Sphagnum riparium* with spots of *Eriophorum vaginatum* and *Carex rostrata*. No CH₄ was emitted through the *S. riparium* community, while a great deal was emitted through the adjacent sedges ca. 1 m away. It is probable that the produced CH₄ is being oxidized in the cells of *Sphagnum riparium* (Fritze, H., unpublished data); CH₄ oxidation by endophytic methanotrophic bacteria has been detected in the leaves of *Sphagnum cuspidatum* (Raghoebarsing et al. 2005)—a species also adapted to wet hollow-conditions. Instead, no oxidation potential has

been found in the leaves of *Eriophorum vaginatum* or *E. angustifolium* (Frenzel and Rudolph 1998).

Water-table position was closely correlated with CH₄ efflux at all sites: deeper water tables caused lower emissions, as expected (Waddington et al. 1996, Daulat and Clymo 1998). This caused temporal flux variation within sampling points and spatial variation among similar plant communities. The emissions from the drained sites were, however, less sensitive to WT dynamics than those from undrained sites, as shown by Nykänen et al. (1998). This phenomenon may be related to plant community dynamics after drainage (Laine et al. 1995) and to the concurrent changes in the microbial community structures (Borgå et al. 1994; Fisk et al. 2003) associated with production (Galand et al. 2005) and oxidation (Jaatinen et al. 2005) of CH₄. High rates of CH₄ oxidation in the rooting zone of, especially, the drained sites were clearly indicated as high oxidation potentials at those depths by Jaatinen et al. (2005). Within similar nutrient levels (fen/bog) the impact of the plant community exceeded the impact of the WT, which is seen as significantly different emissions between the communities with similar water tables, especially at the bog site (Tables 4, 6).

Ditches

The emissions of CH₄ from ditches were highly variable, and this variability was connected to the amount and movement of water and occurrence of vegetation in the ditch. Ditches with moving water had overall higher fluxes, higher flux peaks and also higher variability in fluxes than the ditches with standing water. The fluxes from the ditch bottoms under moving water were clearly smaller than those measured from the water surface (Fig. 4). This suggests that major part of the measured CH₄ fluxes from the ditches with moving water are not produced at the underlying ditch sediment, but are transported by the drainage waters from surrounding areas, possibly even from the adjacent undrained mire through ground water flow. On the other hand, at site 2 where stagnant and warm water maintains a vital algal community in the ditch, new carbon may be

Table 6 The estimated annual CH₄ emissions by site (g CH₄ m⁻² a⁻¹)

Site	Strip	Ditch, diffusive	Ditch, ebullition	Total DR	UD
1	-0.01	95	2.2	2.8	2.1
2	0.28	42	8.4	1.7	13.1
3	-0.22	164	2.3	4.5	13.1
4	3.24	7	0.0	3.4	6.5

All vegetation communities present at the site have equal weight. Values for the drained strips and undrained mires have been estimated using regression functions, ditch values have been integrated from daily values. Ditch width was 1 m and ditch spacing was 35 m in the calculations of Total DR values

sequestered and deposited down on the ditch bottom, providing substrate for CH_4 production.

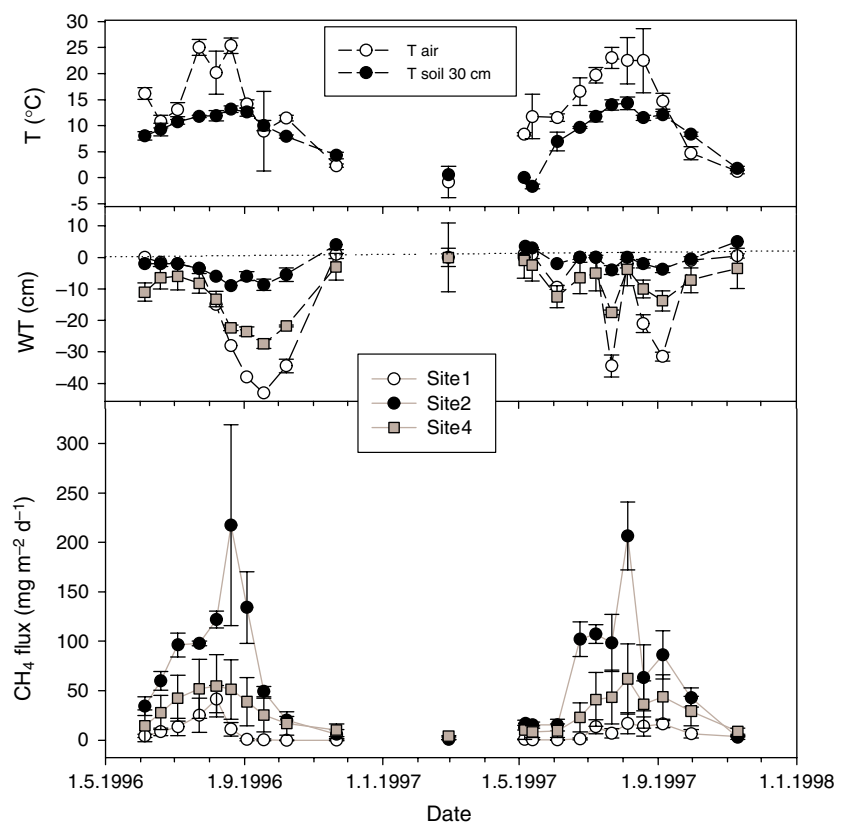
Extremely high instantaneous fluxes (up to $3512 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) were measured with chambers from the ditch plot 3 in 1997. The concentration increases within chamber headspace were linear, excluding the possibility of large CH_4 ebullition events during the measurement. To evaluate whether the flux could be derived solely from diffusion we calculated the potential diffusion rate of CH_4 from water surface to air using the boundary layer diffusion equations presented by Kling et al. (1992). An average concentration difference between water and air of $50 \mu\text{mol l}^{-1}$ measured at the ditch plot 3 in 1997 would produce a flux of $254\text{--}464 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ assuming windless conditions and water temperature range of $0\text{--}20^\circ\text{C}$. However, the diffusion rate is extremely sensitive to the thickness of the boundary layer, which is regulated by wind velocity. The measured flux rates of over $3500 \text{ mg m}^{-2} \text{ d}^{-1}$ would be possible only if wind

velocity exceeds 7 m s^{-1} . Since such wind velocity inside the closed chamber during measurement is unlikely, another possibility is that the turbulent water movement under the chamber decreases the boundary layer thickness and increases the potential diffusion rate. Since we did not measure water velocity, it remains unresolved whether the high fluxes were derived from diffusion only, or if a continuous steady bubble flux of CH_4 took place during the measurements. Such bubbling was, however, never observed on the field.

Because of the turbulences in the ditch water very high spatial and temporal variation in emissions (Fig. 4) may be expected. It is, however, possible that the floating chambers themselves cause additional turbulence into moving water and therefore such measurements could overestimate the average emissions from ditches.

Ebullition of CH_4 from ditches with moving water (sites 1 and 3) was rather small: it was estimated to form only $0.2\text{--}2.3\%$ of the diffusive flux. At site 2 with standing water, ebullition was

Fig. 6 Average (mean \pm SD) air and soil temperatures and water-table position (WT); and CH_4 emissions (mean \pm SE) from the different vegetation communities at the undrained 'control' plots. Site 1 is mesotrophic, site 2 oligotrophic, and site 4 ombrotrophic by nutrient-level



10–22% of the diffusive flux, which is similar to results by Minkkinen et al. (1997). No ebullition was detected in vegetated ditches (site 4). The results suggest that ebullition is important only from ditches with stagnant water where CH₄ may be produced in the sediments of the ditch bottom.

Overall, the CH₄ fluxes from ditches were considerably higher than estimated earlier for the same peatland (Minkkinen et al. 1997) or those estimated for ditches in forestry-drained peatlands in Canada (Roulet and Moore 1995; Schiller and Hastie 1996) or for ditches in peat mining areas in Sweden and Finland (Nykänen et al. 1996; Sundh et al. 2000). Some ditches (site 1 and 3) emitted considerable amounts of CH₄ even during the winter (Fig. 4), and annual fluxes estimated by integrating daily fluxes were thus extremely high, up to 164 g CH₄ m⁻² a⁻¹ (Table 6). If these fluxes were divided evenly over the whole drained area (the distance between ditches being 35 m) the drained fen would be a source of CH₄ instead of being a small sink. For site 1 particularly, thus calculated total emissions would exceed those from the undrained control site. At sites 2 and 3 these would be 10–35% of “natural” emissions. In the bog site, however, the average ditch emissions for the three different plant communities would not raise the areal estimate markedly (Table 6).

Roulet and Moore (1995) suggested that areal emissions from drained peatlands would be a function of ditch spacing; higher density of ditches would increase areal CH₄ emissions, and in their case ditch spacing <38 m resulted in increased areal CH₄ emissions after drainage. This would, however, be true only if the CH₄ emitted was produced in the ditch sediments, which was not the case in our study. Instead, the higher ditch density would deepen the average water table, produce drier conditions and lead to more rapid changes in vegetation composition and therefore decrease in CH₄ emissions.

Conclusions

Drainage decreases CH₄ emissions considerably and usually stops them totally from well-drained nutrient rich peatlands, where ditches remain

functional for decades. In bogs where post-drainage vegetation changes are smaller, CH₄ emissions will continue, but at a lowered level, and they are strongly dependent on the prevailing plant community. CH₄ emissions may also continue from nutrient rich sites, if moist patches supporting deep-rooted sedge species remain, which is not uncommon in Finnish peatlands. Emissions from these surfaces are, however, low compared to those of natural mires. On the other hand, drainage ditches draining nutrient-rich peatlands may emit vast amounts of CH₄ if they remain constantly covered by standing water or if CH₄-rich waters are fed to ditches from surrounding mires. At such sites the emissions from ditches may negate much of the emission-reducing impact of drainage. Normally, however, in a well-planned and constructed drainage system, the ditch bottoms are flooded only after rainfall events, and CH₄ emissions may thus have less importance (Minkkinen et al. 1997).

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