CH₄ emissions from a West Siberian mire

Metaanivuo länsi-siperialaiselta suolta

Ulrike Bosse and Peter Frenzel

Ulrike Bosse, Biology Department, Carleton University, Ottawa, ONK1S 5B6, Canada. Tel (819) 776-9008, e-mail: ubosse@yahoo.ca Peter Frenzel, Max-Planck-Institut für Terrestrische Mikrobiologie, 35043 Marburg, Germany, email: frenzel@mailer.uni-marburg.de

Northern wetlands are an important source of the greenhouse gas CH_4 . We studied CH_4 turnover in an oligotrophic mire near the Yenisej River in West Siberia in July 1996. CH_4 emissions were determined using closed chambers. CH_4 production and CH_4 oxidation potentials were estimated from flask incubations. Mean CH_4 emissions from lawn and mudbottoms were 117 ± 19 mg m⁻² d⁻¹ (SE; n=47). CH_4 concentrations, CH_4 production and CH_4 oxidation potentials in lawn samples were high, indicating that CH_4 oxidation might be important in controlling CH_4 emissions. The area-weighted estimate for the mire was 80 mg m⁻² d⁻¹, which makes this an area of medium to high CH_4 emission. For the surrounding pine forest soil, a CH_4 sink of about -1 mg m⁻² d⁻¹ was estimated, a value similar to that in other boreal forest soils. The area-weighted estimate for ca. 360 km² of mire and forest around the site was a CH_4 emission of at least 25 mg CH_4 m⁻² d⁻¹ during summertime.

Keywords: CH₄ emission, CH₄ oxidation, CH₄ production, Siberia

INTRODUCTION

Northern wetlands cover large areas of the world, and they are an important source of the greenhouse gas methane (Matthews & Fung 1987, Aselman & Crutzen 1989, Bartlett & Harriss 1993). The two single largest northern wetlands are the Hudson Bay Lowlands in Canada and the West Siberian Lowlands in Russia (Gorham 1991). In general, CH_4 emissions from wetlands vary widely both in space and in time (e.g. Harriss et al. 1985, Moore et al. 1990, Dise 1993, Bubier et al. 1995, Inoue et al. 1995, Liblik et al. 1997). Therefore, attempts to quantify and predict CH_4 emissions will eventually require mechanistic models with parameters that can be remotely measured. However, there is also a need for basic flux data from areas which have so far received less attention — at least in the English language literature— such as the West Siberian Lowlands (Inoue et al. 1995, Toshjima et al. 1995, Panikov et al. 1995, 1997, Panikov & Dedysh 2000) as well as for more studies on CH_4 production and CH_4 oxidation, the two biological processes underlying CH_4 emission.

 CH_4 can be produced when organic matter is degraded under anoxic conditions, for example in waterlogged soils. The amount of CH_4 emitted from a wetland is then modified by CH_4 oxidation in oxic zones within the wetland: the surface

(Yavitt et al. 1988) and the rhizosphere (Fechner & Hemond 1992, Calhoun & King 1997, Frenzel 2000). Plants growing in waterlogged conditions have an aerenchyma, or gas-transporting tissue. As some O_2 usually diffuses from the roots into the rhizosphere, it can stimulate CH₄ oxidation there. The rhizosphere is also important for CH₄ emission in other ways. O₂ can stimulate chemical or biological reoxidation of HS-, reduced Ncompounds or Fe²⁺. This will increase the availability of alternative electron acceptors for degradation of organic matter, and reduce CH4 production (Achtnich et al. 1995, Frenzel et al. 1999). Plants also provide C-sources in the form of exudates or root cap sloughing. Since CH₄ production is often C-limited, it may increase as a result of that. Because diffusion is facilitated in the aerenchyma, plants can represent the main route of CH₄ emission in a wetland. In general, extreme temperatures and low pH will restrict microbial activities in northern wetlands. Thus, water table and temperature (Moore et al. 1990, Dise 1993, Moosavi et al. 1996, Bellisario et al. 1999), plant cover (Whiting & Chanton 1992, Shannon & White 1994, Bellisario et al 1999), peat type and pH (Valentine et al. 1994) are all likely to influence CH₄ production and CH₄ oxidation in a wetland.

While most of the CH₄ emitted to the atmosphere is eventually oxidized there photochemically, an estimated 5% are oxidized in upland soils (soils not usually waterlogged) such as most forest soils (reviewed in Conrad 1995). In northern latitudes, boreal forest covers much of the land that is not covered by wetlands. Soils in those forests might thus be important for oxidation of atmospheric CH₄. Temperate and boreal forest soils tend to show CH₄ oxidation rates within 0.5–2 mg CH₄ m⁻² d⁻¹ (King 1997); however, we found no reports for boreal forest soils in Siberia. Forest fires and logging activities (clear cutting) represent the main disturbances in boreal forests.

This paper reports the results of an expedition to West Siberia in July 1996 to study CH_4 turnover in an area close to the Yenisej River. The study was part of a carbon flux study (see, for example, Kelliher et al. 1998, Kelliher et al. 1999, Schulze et al. 1999, Wirth et al. 1999, Valentini et al. 2000). In view of the above-mentioned scarcity of data from this area, our first objective was to get a measure of the CH_4 flux from mire, most likely the main CH_4 source in the area. Together with this we measured CH_4 production and CH_4 oxidation potentials to get information about the biological controls of CH_4 fluxes. Our second objective was to estimate the supposed CH_4 sink in upland soils that may partially compensate for the emissions from wetlands.

MATERIALS AND METHODS

Area

The study area (61°N, 89° E) is an area with both wetland and forest habitats 40 km west of the Yenisej River in Central Siberia. For a description of the area see Kelliher et al. (1998) and Valentini et al. (2000). All measurements were done between July 1 and July 27, 1996. The following climate data for the area are summarized from Kelliher et al. (1999), Wirth et al. (1990) and Valentini et al. (2000): mean annual temperature -3.8 °C; mean annual rainfall ca. 500 mm with more than half of that falling as rain, mostly during summer thunderstorms; July usually the wettest and the hottest month with an average temperature of 18 °C; growing season 147 days. During the period of this study, temperatures seemed to be somewhat higher than normal; rain patterns appeared to be normal (Kelliher et al. 1999).

Site description and physical parameters

We studied an acidic, oligotrophic mire of approximately 1 km² with forested edges. General phenology, the low pH and the species of *Sphagnum* and other vegetation supported the oligotrophic character of the mire. The central area showed three structures, ridges, lawn and mudbottoms. Ridges were structures of 1–5 m width and a height of 40–50 cm rising above the surrounding flat area, lawn and mudbottoms. Ridges were between 2 and 50 m long and characterized by various Ericaceae, *Betula nana*,

Carex ssp., E. vaginatum, Rubus chamaemorus and Pinus sylvestris. The surface of lawn consisted mostly of Sphagnum ssp., the surface of mudbottoms consisted of a ca. 1 cm thick layer of, most likely, Zygnematales or Liverwort (pers. communication E. Karofeld, J. Bubier). Otherwise, both areas were characterized by Scheuchzeria palustris, Rhynchospora sp., Drosera ssp., Eriophorum vaginatum and Carex ssp.. The dominating Sphagnum-species were S. fallax and S. angustifolium (L. Kannukene, pers. communication). Carex-species included C. rostrata, C. limosa and C. pauciflora. Throughout the study period, the water table in the flat areas (lawn or mudbottom) was 0-5 cm below the surface. All studies of mire were done in this central nonforested area.

The forest in the area is pine forest (*Pinus sylvestris*), also called dark Taiga. Forest fires are frequent and of varying intensity. Together with logging activities, this has created relatively small patches of forest of different age. One of our study sites was a dry, 215 year old open stand ("old stand"), the other was a 28 year old, relatively dense stand ("young stand"). Litter and lichens covered most of the ground. The soil was mostly sand with a very thin topsoil layer (ca. 5 cm).

Measurements were also made on July 19 in Bor Island. Bor Island is a forested mineral island surrounded by mire. During a fire experiment in 1993 the forest was severely burnt (FIRESCAN Science Team 1996). Before the fire, its overstory was apparently composed of trees of at least 2 age groups, 130 and 180 years old (FIRESCAN Science Team 1996). Three years after the fire, the central area appeared almost completely dead (only 3 seedlings were found during one hour of walking).

Temperature profiles in mire were measured with an electric thermometer (Omega Engineering, Inc.) and a stainless-steel probe (60 cm long, 5 mm diameter) with a built-in thermistor. A total of 26 profiles were measured, 13 in lawns and mudbottoms and 13 in ridges (303 data points, depth intervals 5 cm, sampling depth 0 to 45–65 cm). Sampling dates were July 4, 7, 11 and 12, 1996. All profiles were measured between 10:00 and 12:00. The pH was measured *in-situ* with a battery-operated pH-meter. The water content W was defined as W = (fw-dw) / dw where dw is the weight of the sun-dried sample (field experiment) and fw is the weight of the fresh sample. In the field, samples were dried in the sun until weight was constant. The biomass of sun-dried samples was determined for 625 cm² plots and converted to m². Aboveground biomass included all plants. Belowground biomass was *Scheuchzeria* only, *Carex/Rhynchospora* only or the black surface layer of holes only (the layer that easily separated from the *Sphagmum* below). In the laboratory, samples were dried at 80 °C.

Concentration profiles (mire and forest)

Concentration profiles were measured using metal probes. For water samples, a probe with a sideport opening behind the tip was used (1 m long, 1.2 mm diameter, 0.8 ml dead volume). At the top, a syringe could be connected to the probe. Sample volume was 1 ml to flush the probe and 1 ml as sample. For analysis, the syringe volume was increased to 10 ml with N_2 , and the CH_4 was extracted into this headspace by vigorous shaking for 60 s. For gaseous samples, we used a probe with a pointed, closed tip (1 m long, 3.3 mm diameter, 2.5 ml dead volume). It had 12 holes of 1 mm diameter over a distance of 5 to 15 mm behind the tip. At the top, a needle could be inserted through a septum to take samples. Sample volume was 5 ml to flush the probe and 5 ml for analysis.

In the mire, water samples were taken at a depth of 5–30 cm in lawn (n=24) and 5–15 cm below the water table of a ridge (n=12). Gaseous samples were taken at a depth of 5–70 cm above the water table of a ridge (n=18). Profiles from mire were used to determine general patterns of CH₄ distribution.

In the forest, a total of 18 profiles were measured, 10 in an old stand, 5 in a young stand and 3 on Bor Island (142 data points, depth intervals 5–10 cm, sampling depth 0 to 25–80 cm). Profiles from forest soil were used to estimate the CH₄ flux using Fick's first law

 $J = -D_a dc dx^{-1},$

with J the flux of a gas over a surface $-[nl cm^{-2} s^{-1}]$, D_a the diffusion coefficient of that gas in air $[cm^2 s^{-1}]$

and dc dx⁻¹ the concentration gradient of the gas [ppm_v cm⁻¹]. In soil, the diffusion coefficient changes due to porosity and tortuosity. The diffusion coefficient was estimated using the correction proposed by Millington & Quirk (1960). For our soil, their equation $J = -D_{a} f_{a}^{2} f_{t}^{-0.66} dc dx^{-1}$ gives $J = -0.06 \text{ dc } \text{dx}^{-1}$ using the diffusion coefficient $D_a = 0.207 \text{ cm}^2 \text{ s}^{-1}$ (for $15 \pm 2^{\circ}\text{C}$; average of values in 1,10 and 20 cm depth measured Jul 9-24; pers. communication F. Kelliher), the pore volume of gas $f_a = 0.40$ and the total pore volume $f_t = 0.43$. Pore volume and total pore volume were calculated from the bulk density $\delta_{\rm B}{=}\,1.5$ gdw ml $^{-1}$ (B. Lühker, pers. communication), the specific gravity of quartz sand $\delta_F = 2.65 \text{ g ml}^{-1}$ (Vomocil 1965) and the water content W = 0.02 (measured) using $f_a = 1 - \delta_B \delta_F^{-1} - f_w$, and $f_w = W \delta_B$. For comparison, a diffusion coefficient of CH4 determined experimentally for a sandy soil of similar texture was used (effective diffusion coefficient, Koschorreck & Conrad 1993), giving J = -0.03dc dx⁻¹. Both equations were used to estimate the CH₄ flux in soil (see Discussion).

Emission measurements (mire)

CH₄ fluxes were measured with the closed chamber technique adapted to mire conditions. The transparent chambers were made from Plexiglas® and covered an area of 625 cm². Plexiglas® panes were fixed between two metal frames and sealed with silicone. Frames either had sharp edges on one side and were used as bottom parts, or had been pre-assembled as top parts complete with a movable Plexiglas® lid and a fan. Gas volume was 13 or 261. To avoid disturbances from walking, chambers were set up 5-24 h before measurements and were operated from the nearest ridges or from about 5 m distance. The fans and the lids were connected to cable and string, respectively, and Teflon tubing (5 m long, 2 mm diameter, 3.9 ml dead volume) was connected to a sampling port with flanged fittings. Sample volume was 5 ml to flush the tube, and 5 ml as a sample. In addition, each chamber had a butyl rubber septum with a needle to avoid gas pressure changes when samples were taken. For a flux measurement, samples were taken every 5 min for 25 min (n=5-6 samples per flux), and a linear regression was performed. In two cases, fluxes on a ridge were measured for 135 min (n=6 samples each). In 4 cases (found in ridge, lawn and mudbottoms), values indicated the emission of gas bubbles. These values were excluded from the linear regression but used to estimate the gas bubble flux. Because the chambers were moved to another site after each flux measurement except in the case of diurnal measurements, a total area of 3.94 m^2 was covered.

Production measurements (mire)

Production measurements were done in 150 ml flasks. Samples were filled into the flasks, then the flasks were flushed with N₂ and closed with rubber septa. The increase in CH₄ concentration was followed over time by taking 0.5 ml samples with a syringe. After the end of the experiment, the dry weight of the samples was determined. Samples were bulk samples from 5–10 cm deep (mostly Sphagnum), 0-30 cm (Scheuchzeria roots) and 10-30 cm (Scheuchzeria leaves, a mixed sample) for lawn; ridge samples were all 10-30 cm (Sphagnum, woody roots). Scheuchzeria leaves and ridge Sphagnum were measured in duplicate. Experiments were done in Siberia (n=3 samples per rate, incubation time 46 h, 2 flasks) or in Germany (n=6 samples per rate, incubation time 1630 h or as indicated, 6 flasks). In Siberia, the flasks were incubated in a soil pit of ca. 20 cm depth covered with a white plastic sheet. Temperatures in the pit fluctuated with daytime between 20 and 30°C. For measurements in Germany, peat samples were taken on Jul 29 from a depth of 10-30 cm from ridge and from lawn, and transported at in-situ moisture content in polyethylene bottles. The samples were transported in aluminum boxes as cargo to Germany. They arrived August 16 and the experiment was started the same day at an incubation temperature of 25°C.

Oxidation measurements (mire)

Oxidation measurements were done in 150 ml flasks. Samples were filled into the flasks within 4 hours after sampling. The flasks were closed with rubber septa. CH_4 was added to give final concentrations between 4 and 6000 ppm_v (5 nM-8 μ M) and then the decrease in CH_4 concentra-

tion was followed over time by taking 0.5 ml samples with a syringe. For *Scheuchzeria* leaves from lawn and top layer from mudbottoms, oxidation kinetics were measured. For *Scheuchzeria* leaves, 9 flasks at CH₄ concentrations between 8 and 4900 ppm_v (11 nM–7 μ M) were tested. For top layer, 6 flasks with CH₄ concentrations between 4 and 4200 ppm_v (5 nM–6 μ M) were tested. After the end of the experiment, the dry weight of the samples was determined. Experiments were done in Siberia. Oxidation potentials were estimated from the decrease in CH₄ concentration in the flask (n=2 or 3 sampling data per rate as indicated). The flasks were incubated as described for the production measurements.

Gas analyses

In the field, CH₄ was measured on a SRI 9300A gas chromatograph (GC) equipped with a flame ionization detector. The GC was set up in a tent, a generator (Honda) provided electricity. Synthetic air (80% N₂, 20% O₂, no hydrocarbons) was used as carrier gas. CH₄ calibration gases were prepared from a 49.5 ppm_v calibration gas (AirLiquide) or from 100% CH₄. For CH₄ concentrations below 10 ppm_v, we used a 8.25 ppm_v calibration gas. For concentrations above 10 ppm_v, we prepared 3-8 CH₄ calibration mixtures to cover the range encountered in a particular experiment. Because ambient conditions changed, the GC was calibrated every 10 min during all measurements. All samples were taken with plastic syringes stoppered with silicone rubber stoppers and measured within 3 h except for the Bor Island samples (8 h). We used either a sample loop (injection volume 3 ml, sample port volume 2 ml) or direct injection (volume 0.5 ml). In the laboratory in Germany, a Carlo Erba and a SRI 9300A equipped with an FID were used.

RESULTS

Site description and physical parameters (mire)

In the top 5–10 cm of lawn, the *Sphagnum* ssp. usually appeared little degraded and fine sedge roots were abundant. Below that depth, *Sphag*-

num ssp. was increasingly degraded, and throughout the top 30–40 cm, we found a lot of *Scheuchzeria* parts, both living and dead. In mudbottoms, *Sphagnum* ssp. was found only below the dark top layer and was usually more degraded than the *Sphagnum* ssp. in the corresponding depth of lawn. The distribution of *Carex* ssp. and *Scheuchzeria* parts was similar to that in lawn.

Above ground biomass was 40 ± 4 g(dry weight) m⁻² (SE; n=4) in lawn, 18±5.8 (SE; n=3) in mudbottoms and 188±30 (SE; n=5) in ridges. The belowground biomass (0-30 cm depth) of Scheuchzeria was 5-6x that value for both lawn and mudbottoms. For experiments, the dead belowground biomass (old leaves and sheaths, "leaves" in the text) was usually separated from the living belowground biomass (roots, rhizomes and stems, "roots" in the text). The belowground biomass of Carex ssp. and Rhynchospora was sampled once and was found to be less than 10% of the total Scheuchzeria value. Biomass of the black surface layer of mudbottoms was 65-117 g(dry weight) m⁻² (range, n=2). Temperature profiles differed between flat areas and ridge, but were similar within each type. In lawns and mudbottoms, surface temperatures of 20–30 °C (depending on the day) decreased almost linearly to 13-17 °C in 50 cm depth. In ridges, temperature gradients were steeper and temperatures could reach <5 °C at water level in the center of the ridges. In one case, we found ice. Towards the edges, temperature gradients approached those of the flat areas. The pH in the top 5 cm of peat ranged from 2.8-3.3 in the ridges and from 3.2–3.9 in lawn and mudbottoms.

Concentration profiles (mire)

CH₄ concentrations in lawn are shown in Fig. 1. The mean value for 0–30 cm depth was 377±89 μ M (SE; n=24). Digging revealed more gas bubbles at 30–40 cm depth and more dead *Scheuchzeria* parts than above. In ridges, CH₄ concentrations above the water table were just above atmospheric concentrations and showed no trend over depth (mean of 2.88±0.15 ppm_v or 4±0.24 nM, SE; n=18). At 5 cm below the water table, values had increased sharply to about 130 μ M and were similar to those in lawn at 15 cm (total n=12).



Fig. 1. CH_4 concentration (mean \pm SE) in lawn in a mire in West Siberia. Water table was at 0 cm. Values from several profiles were combined, for details see text.

Kuva 1. Turvekerroksen metaanipitoisuus (tasapinta) länsi-siperialaisella suolla (useiden profiilien keskiarvo). Vedenpinnan syvyys 0 cm.

Emission rates (mire)

In total, 62 fluxes were measured (Table 1). This includes fluxes that were not significant on the 5% level i.e. fluxes with low r² values, as well as negative fluxes indicating CH₄ uptake. Ambient CH₄ mixing ratios above ground were often between 2 and 5 ppm_v. Average fluxes from lawn and mudbottoms were very similar, around 117 mg m⁻² d⁻¹. Eight of the 47 fluxes measured there showed CH₄ uptake; none of the 8 was statistically significant. Fluxes from lawn and mudbottoms were measured at 34 different sites and were normally distributed. Ridges showed a much lower flux than lawn or mudbuttom with an average of only 5 mg CH_4 m⁻² d⁻¹. Eight of the 15 fluxes measured there showed CH₄ uptake and again, none of the 8 was statistically significant. Fluxes from ridges were measured at 6 different sites. Measurements during a 24 h period did not show a diurnal pattern (fluxes measured at 04:40, 10:00, 16:00, 22:30, 05:00 in 2 chambers in lawn, and one in ridge). Occasionally, gas bubbles were detected in the chambers by a sudden increase in the CH₄ concentration. The amount of CH₄ released was 0.20 mg per event (\pm 0.04, SE; n=4 [2 in ridge, 2 in lawn]). For a total measuring time of 1.25 d this gives a bubble flux of only 0.16 mg m⁻² d⁻¹.

Production rates (mire)

Under anoxic conditions, CH_4 was produced in material from lawn and ridges. In lawn, rates were high (300–1500 ng CH_4 gdw⁻¹ h⁻¹, n=4 for a mixed sample and *Scheuchzeria* samples; 30 for a Sphagnum sample), rates in ridges were low (around 0.1 ng CH_4 gdw⁻¹ h⁻¹; n=3). Transporting might have had an effect on samples, but transported lawn samples were apparently active without a lag (but t1=90h). CH_4 production was also observed in CH_4 oxidation experiments with top layer of mudbottoms or roots, when the flasks accidentally became anoxic (5 samples in total). The samples had been treated as oxic samples and thus been exposed to O₂ before anoxic conditions presumably set in.

Oxidation rates (mire)

CH₄ oxidation potentials are shown in Table 2. In general, oxidation started immediately. CH₄ oxidation was above the detection limit for all plant samples tested except for ridge samples at low CH₄ concentrations. Within one CH₄ concentration range, *Carex* samples had the highest rates. CH₄ oxidation kinetics were measured with *Scheuchzeria* leaves and with the top layer of mudbottoms (Fig. 2). Rates of about 13 μ g CH₄ gdw⁻¹ h⁻¹ at 4000 ppm_v CH₄ confirmed the rates measured in other experiments (see Table 2). The

Table 1. CH₄ emission from various habitats in a mire in West Siberia. CH₄ emissions were determined using closed chambers. The value for "Mire" is an estimate assuming 1/3 of the mire is covered by ridge and 2/3 by flat areas. See Text for details.

Taulukko 1. Metaaniemissiot erilaisilta suokasvupaikoilta. Emissiot mitattiin suljetuilla kammioilla. Koko suon keskiarvo ("Mire") on laskettu mättäiden (1/3) ja tasapintojen (2/3) pinta-alaosuuksilla painotettuna.

Habitat type	$\begin{aligned} mean \pm SE \\ [mg \ m^{-2} \ d^{-1}] \end{aligned}$	range [mg m ⁻² d ⁻¹]	n
Ridge	5 ± 5.9	-22 to 78	15
Flat areas	117 ± 19	-22 to 621	47
-mudbottoms only	106 ± 31	-18 to 621	23
-lawn only	128 ± 23	-22 to 387	24
Mire (estimate)	80		62

oxidation in the top layer was consistent with Michaelis Menten kinetics with the maximum rate $V_{\rm max}$ =4.7 µg gdw⁻¹ h⁻¹ and an apparent Michaelis Menten constant $K_{\rm app}$ =1.4 µM (Fig. 2). In contrast to *Sphagnum* ssp., the top layer had dried up during the hot days preceding the experiment, and we assume that there was little or no gasphase transfer limitation. The results show that rates were similar between top layer and *Scheuchzeria* leaves at low, but not at high CH₄ concentrations.

Concentration profiles (forest)

Fig. 3 shows CH_4 mixing ratio in forest soils. At all sites, CH_4 mixing ratios decrease with depth. The zone of linear decrease indicates diffusion, the changing gradient in about 20–30 cm depth indicates CH_4 consumption. We found no consistent differences between areas with and without lichen, i.e. at varying distances from trees (data not shown). The CH_4 threshold in soil from the old stand seemed to be the lowest.

DISCUSSION

Concentration profiles (mire)

Lawns had high CH_4 concentrations (Fig. 1). The high SE and a maximum value of 2240 μ M in 35 cm depth is indicative for gas bubbles that were also observed when taking peat samples. CH_4 concentrations in ridges agreed well with profiles measured in hummocks by Benstead & Lloyd (1994) and by Frenzel & Karofeld (2000). In a study by Fechner & Hemond (1992), walking to the sampling site increased gaseous CH_4 concen-

Table 2. Potential CH_4 oxidation rates in belowground samples from a mire in West Siberia, estimated using flask incubations. See also Fig. 2. A CH_4 concentration of 7 μ M corresponds to 5400 ppm_v, 0.3 μ M to 230 ppm_v.

Taulukko 2. Metaanin hapetuspotentiaali turve- ja kasvinäytteissä (maanalaiset osat). Hapetusnopeudet mitattu inkuboimalla näytteitä laboratoriopulloissa (ks. myös kuva 2). Metaanipitoisuus 7 μ M vastaa 5400 ppm, ja 0.3 μ M vastaa 230 ppm,

Experimental details (sampling depth 0–30 cm or as indicated)	n	Oxidation rate $[\mu g CH_4 gdw^{-1} h^{-1}]$
Lawn and mudbottoms		
at 7 μ M CH ₄ , rates for n=2-3		
lawn only: Sphagnum ssp. (0-5 cm),	6	6-50
Scheuchzeria (roots, roots + leaves together),		mean 25
Carex ssp. (roots)		
at 0.3 μ M CH ₄ , rates for n=3 ¹		
Scheuchzeria (roots, both lawn		0.2-1.1
and mudbottoms), Carex ssp. (roots)	4	mean 0.7
Ridge		
at 7 μ M CH ₄ , rates for n=2		
woody $roots^2$	3	0.5-0.8
		mean 0.6
<u>at 0.3 μM CH₄, rates for n=2</u>		
Sphagnum ssp. (0-5 cm), woody roots	2	< 0.2
		(detection limit)

¹ minimum rates: CH_4 was oxidized faster than expected so that concentrations were too low to continue when the first sample was taken at t=6.5h and the experiment had to be restarted after 10 and 20 h.

² Chamaedaphne caliculata, Andromeda polifolia, Ledum palustris measured individually



Fig. 2. Kinetics of CH₄ oxidation in a mire in West Siberia. Upper figure: old leaves of *Scheuchzeria* (lawn). The solid line is a linear regression. Lower figure: top layer (mudbottoms). The solid line is a Michaelis Menten fit. Data points are rates measured in individual flasks, for details see text.

Kuva 2. Metaanin hapetusnopeuden suhde metaanipitoisuuteen. Hapetusnopeudet mitattu kasvi- ja turvenäytteistä yksittäisissä laboratoriopulloissa. Yläkuva: Scheuchzerian vanhoja lehtiä (tasoitus: lineaarinen regressio), alakuva: pintaturvetta kasvittomilta kuljupinnoilta (tasoitus: Michaelis-Menten funktio).

trations dramatically in one case. In our study, as gaseous samples in ridges had a low mean value just above atmospheric concentrations, sampling them from adjacent lawn areas seems not to cause such artifacts.

Emission rates (mire)

On average, ridges were a very small source of CH_4 emission, lawns and mudbottoms were a very large source, and results indicated that there was occasional CH_4 uptake in all three surface structures. Lawn and mudbottoms were not different in terms of CH_4 emission, even though they were

different in appearance as well as in biomass (see below). Since ridge and lawn have very different CH_4 emissions, the average emission from this mire should be calculated using the percentage area of each type of mire surface. From an aerial photograph provided by D. Mollicone & R. Valentini, we estimated that two thirds of the area are lawn or mudbottoms, one third ridge. This gives an area-weighted emission of 80 mg CH_4 m⁻² d⁻¹ for this mire. Since the forest in the adjacent area is a sink, the estimated emission for the region would be lower (see below).

The high variability in our measurements makes comparisons difficult; however, as we included the different surface structures found in most such mires (except ponds) and also measured at many different sites within each type, the variability may well be realistic, and is not unusual (Harriss et al. 1985, Inoue et al. 1995, Liblik et al. 1997). Also, as pointed out below, there are not many basic data from different areas of West Siberia. Still, comparisons can only be approximate at this stage. The area-weighted value may best be compared with studies where fluxes were integrated over areas described as "open bogs" or "ombrotrophic bogs" or "poor fens".

In such a comparison, fluxes in the Hudson Bay Lowlands tend to be lower than or similar to our values (means for open graminoid bog of 33– 68 CH₄ m⁻² d⁻¹ in Bubier et al. (1993), of *ca.* 20 and 38 (in bogs and fens; recalculated for a 100 d season) in Klinger et al. (1994), and of 10–110 in Bellisario et al. 1999), but values in other areas also fall into that group, such as Scotland (mean of 9 mg CH₄ m⁻² d⁻¹ in an ombrotrophic blanket bog in Beverland et al. 1996), and to some extent Finland (means of 5–140 in ombrotrophic bogs and 23–345 in oligo and oligo-mesotrophic fens in Nykänen et al. 1998).

In other studies, especially studies from Minnesota, fluxes tend to be similar to or higher than in our study. For example, one may find means of 50–190 mg CH₄ m⁻² d⁻¹ in ombrotrophic bogs (Harriss et al. 1985) and means of 126–657 in different bogs, fen laggs and a poor fen, respectively (Dise 1993; values recalculated for a 100 d season). But similar or higher values are also found in most studies we know of for West Siberia. These values all come from the Plotnikovo



Fig. 3. Depth profiles of CH_4 mixing ratios in forest soil in West Siberia. Bor Island is a forest severely burnt 3 years before these measurements. For details see text.

Kuva 3. Metsämaan metaanipitoisuus eri syvyyksissä. Bor Island on metsikkö, joka on palanut voimakkaasti 3 vuotta ennen mittauksia.

field station near Tomsk and include 234±326 mg CH₄ m⁻² d⁻¹ for mostly non-forested, ombrotrophic and mesotrophic bogs (Inoue et al. 1995), *ca.* 230 for open, mostly ombrotrophic bog with a thin forested edge (Panikov et al. 1995) and 397±23, also in mostly ombrotrophic bog but weighted for plant coverage (Panikov et al. 1997). However, values from another area near Tomsk are low (22 mg CH₄ m⁻² d⁻¹ in an ombrotrophic bog with patchy forest in Panikov et al. 1995).

Where microtopography is given instead, we compared "hollows", "depressions" or "carpets" to our flat areas (which have a very high water table); and "hummocks" or "hillocks" to our ridges. Results in Bubier et al. (1995), Moore et al. (1994) and Slobodkin et al. (1992) confirmed the trends described above.

Thus, our study supports earlier results that the area could be a significant CH_4 source compared to the Hudson Bay Lowlands. Given that these two areas are the largest wetland areas in the world, such a difference in emission would be important. However, our values were not as high as some others reported for West Siberian wetlands, and in the same range as or lower than values from areas other than the Hudson Bay Lowlands. One reason for this might be temperature, as CH_4 fluxes (Moosavi & Crill 1997) and specifically CH_4 production (Dunfield et al. 1993) decrease with decreasing temperature. In the Hudson Bay Lowlands, the average temperature in 20 cm depth in 39 different sites was between 6.0 and 13.6 °C (Moore et al. 1994). At our site, it was between 18 and 26 °C. Soil temperature may correlate to water table, and water table at our site was indeed high. A high water table usually implies high fluxes, although not always (Bellisario et al 1999).

All our measurements were done in July; most other flux values also come from studies during summer, ranging from 1 to 6 months. Dise found that the maximum flux was in July (Dise 1993), while the winter (Nov–Mar) flux represented 4– 11% of the total annual flux in open bogs and poor fens, but up to 21% in a forested bog (Dise 1992). If we assume that between 79 and 96% of the value in Dise (1993) were emitted within 150 days, their fluxes are still as high or higher than ours. Results indicated there was no diurnal pattern, similar to results by Klinger et al. (1994).

Plants in waterlogged conditions are usually good gas conduits; so a difference in biomass such as that between lawn and mudbottoms would suggest a difference in CH_4 emission (e.g. Bellisario et al. 1999, Saarnio & Silvola 1999). Also, *Scheuchzeria* and all other plant species tested had a high CH_4 oxidation capacity (see below), indicating that they were supplied with enough O_2 and CH_4 to support an active community of methanotrophic bacteria. This would suggest that they indeed function as a conduit for CH_4 and thus influence CH_4 emissions. However, there was no difference in emission between lawn and mudbottom (Table 1).

In some studies fluxes are rejected below a certain r^2 value (e.g. Bellisario et al. 1999). Since that might include very low fluxes or — usually high — gas bubble fluxes, the effect of this on a mean value is difficult to predict. Liblik et al. (1997) mentioned that while fluxes below a certain r^2 value are generally rejected, this was not the case if gas bubbles seemed to be the cause rather than an overall low flux. In our case, we excluded the few bubble fluxes instead (s. above), so our estimate is probably an underestimate.

Production rates (mire)

CH₄ production potentials measured in various kinds of peat usually span 3-4 orders of magnitude. Our lawn rates, including the relatively low Sphagnum ssp. rates, were higher than those reported in a number of other studies (e.g. Yavitt et al. 1990 or Moore & Dalva 1997), and in the same range as those reported in some others (e.g. Moore et al. 1994, Valentine et al. 1994). CH₄ production is very temperature sensitive, and much of the work cited was done at 20 °C, while our field experiment permitted only 25 °C. Q₁₀ values range mostly from 1-6 (see e.g. Williams & Crawford 1984, Dunfield et al. 1993, Yavitt et al. 1997). However, if we somewhat arbitrarily reduce our values to 30% to correct for the temperature difference, our rates would still be in the middle to upper range compared to other peat values. [Note: we used a water content of 90% to convert rates in the literature from fresh weight to dry weight if necessary].

Exposure to oxygen and the pH are also important for CH_4 production. Our results with "oxic" flasks showing CH_4 production indicated that methanogenic bacteria were quite resistant to oxic conditions. This confirms studies in other systems (Fetzer et al. 1993, Bosse & Frenzel 1997) as well as results by Kettunen et al. (1999) in a high latitude mire in Finland. Our study also confirms CH_4 production in peat at the lower end

of the pH ranges reported (e.g. Williams & Crawford 1984 pH 3.8–4.0, Moore & Knowles 1990 pH 2.8–5.3, Dunfield et al. 1993 pH 3.5–6.0).

Rates of 0.3–1.0 μ g CH₄ gdw⁻¹ h⁻¹ for 80– 230 gdw Scheuchzeria biomass per m² translate into 1–6 mg CH₄ m⁻² d⁻¹ produced in 0–30 cm depth. A rate of 0.03 μ g CH₄ gdw⁻¹ h⁻¹ for 30,000 gdw peat (i.e. mostly Sphagnum) per m² of the same depth interval translates into 22 mg CH_4 $m^{-2} d^{-1}$. Together, this is equal to only about 20% of lawn or mudbottom emission (Table 1). But because some CH₄ was probably oxidized before emission (see below), production should have been higher than emission. We can only speculate about the reasons for this low value. There might be significant CH₄ production below 30 cm depth. While CH₄ production will be increasingly limited by temperature or labile organic C with increasing depth, emission might depend on accumulated CH₄ and would then not directly reflect production. This example shows how important it is to analyze processes to fully understand CH₄ emissions from wetlands.

Oxidation rates (mire)

In Watson et al. (1997), a model based on measured CH_4 and O_2 profiles indicated subsurface CH_4 oxidation in the presence of roots. At high CH_4 concentrations, all of our belowground samples showed in fact a potential for CH_4 oxidation.

Overall, the $K_{\rm m}$ of 1.4 μ M found in our study reflects the high-CH₄ environment of the site in that it is clearly not in the nM range (reviewed in Conrad 1996). $K_{\rm m}$ values measured in peat range from a few nM to 60 µM (e.g. Yavitt et al. 1988, Watson et al. 1997, Kravchenko 1999). Both Scheuchzeria leaves and top layer readily oxidized CH₄ to below atmospheric concentrations, down to about 1 and 0.3 ppm_v, respectively. The latter value is more typical for the high-affinity CH₄ oxidation activity (Conrad 1996). The low threshold was reflected in the negative fluxes measured occasionally in lawn. During dry spells, the surface of the lawn may thus become a small sink despite presumably high CH4 fluxes from below.

 $V_{\rm max}$ values and oxidation rates measured at 0.3% CH₄ (which would be roughly comparable to our V_{max}) range from 4 to 60 µg gdw⁻¹ h⁻¹ (e.g. Sundh et al. 1994, Whalen & Reeburgh 1996, Watson et al. 1997). Our measured $V_{\rm max}$ is at the lower end of this. CH₄ oxidation, like CH₄ production, can take place at low pH values (e.g. Moore & Knowles 1990 pH \ge 2.8, Dunfield et al. 1993 pH \geq 3.5, Dedysh & Panikov 1997 pH \geq $3.3 \ge 4$ if only *in-situ* pH values are considered]), but shows a pH optimum at least somewhat higher than the *in-situ* value (Dunfield et al. 1993, Dedysh & Panikov 1997). There is only one report of an acidophilic methanotrophic culture (Dedysh et al. 1998). So a low V_{max} could, in part, be due to the low pH. But since in fact CH₄ oxidation rates in Scheuchzeria leaves were still increasing linearly and had reached 12 µg gdw⁻¹h⁻¹, their V_{max} was probably more in the middle range of the literature values, and CH₄ oxidation in the top layer might have been limited by some other factor.

Looking at the CH_4 oxidation potential measured at a lower concentration (1000 ppm_v CH_4) supports this, as rates were the same or higher than other values reported. Fig. 2 gives CH_4 oxidation potentials of 2500–3500 ng gdw⁻¹ h⁻¹ for top layer and *Scheuchzeria* leaves, respectively, which is higher than for example values in Dunfield et al. (1993) and Moore & Dalva (1997).

Dedysh & Panikov (1997) show that the temperature optimum of CH₄ oxidation is 15–20 °C. and that there was a drop in activity above 20 °C in their samples. This might have been the case in our samples, too. Due to the different temperature sensitivity, the high *in-situ* temperatures in our site during at least part of the summer (compare discussion of emissions above) might favor CH₄ production relatively more than CH₄ oxidation (Dunfield et al. 1993). But potential activities measured at those temperatures still gave a much higher potential for CH₄ oxidation (mean of 25 µg gdw⁻¹ h⁻¹) than for CH₄ production (mean of 1 µg gdw⁻¹ h⁻¹), suggesting CH₄ oxidation could still be important. In-situ, O2 availability will restrict CH₄ oxidation to the top layer and the rhizosphere. There, however, CH₄ oxidation rates may be high. Oxidation rates at 0.3 μ M CH₄ would be equal to 1–4 mg CH_4 m⁻² d⁻¹ oxidized in 0–30 cm depth by plant material, oxidation rates at 7 μ M CH₄ would correspond to 40–160 mg CH₄ oxidized m⁻² d⁻¹. The later potential is considerable compared to the fluxes measured.

We were surprised that *Scheuchzeria* leaves we considered to be dead (see Methods section) still supported instantaneous and high rates of CH_4 oxidation. It is unlikely these half degraded leaves were oxygenated, and so the methanotrophic bacteria are probably not active *in-situ*. However, they became active in <6.5h (Table 2), indicating that they are able to react very quickly if conditions become favorable.

 CH_4 oxidation rates in ridges were lower than in lawn and mudbottoms (Table 2), and CH_4 concentration profiles in ridges indicated that the oxidation horizon was near the water table. It has been shown that the CH_4 oxidation potential is negligible within the acrotelm of hummocks (Saarnio et al. 1997, Frenzel & Karofeld 2000), and that CH_4 concentrations decrease sharply near the water table (Benstead & Lloyd 1994, Frenzel & Karofeld 2000).

Concentration profiles (forest)

In forest sites studied by Savage et al. (1997), the CH_4 oxidation layer was closer to the surface than in our soil. However, CH_4 profiles measured by Whalen et al. (1992) were similar to ours. At a water content of only 2%, this would most likely be due to water stress, which can determine the distribution of a population (Schnell & King 1996).

From the combined profiles, the size of the CH₄ sink was estimated using Fick's first law (see Methods section). The dc dx⁻¹ was determined for the 0–20 cm interval. The correction proposed by Millington & Quirk (1960) gave J = -0.06 dc dx⁻¹. Using that value and the empirical values of Koschorreck & Conrad (1993) for a sandy soil, fluxes ranged from 0.5 to1.7 mg CH₄ m⁻² d⁻¹ (Table 3). This is similar to results in other forest soil, which ranged mostly from 0.5–2 mg CH₄ m⁻² d⁻¹ (reviewed in King 1997). Table 3 shows lowest values for the young site, highest values for Bor Island, but differences between sites are small. But clearly the profiles from Bor Island indicate CH₄ consumption, 3 years after a very

intensive fire. This is in agreement with a study by Burke et al. (1997). They found that burnt sites even tended to be slightly stronger methane sinks than unburnt controls after a few years.

CH₄ emission on the landscape scale

A regional estimate of the relative area of mires, riparian wetlands (marshes, deciduous forest with willows and birches) and upland forests was derived from a Russian map (1:50,000). 1-km²quadrants were classified as mires if their coverage was >50%, and as riparian wetlands, if the total length of a river within the quadrant was >1km. The remaining quadrants were taken as forest. Only the lowlands west of the river Yenisej within an area of 361km² were taken into account. Using these criteria, upland forest, mires and riparian wetlands cover 53, 32 and 15% of the area, respectively. Using mean emissions of -1, 80 and 0 mg CH_4 m⁻² d⁻¹ for the three landscape types, we get an average emission of 25 mg CH_4 m⁻² d⁻¹ for July 1996. Because the riparian wetlands (as well as ponds in mires) are expected to be CH₄ sources, the real source strength may be higher.

 CH_4 emission for the area was also estimated from CH_4 mixing ratios measured during flights

Table 3: CH₄ oxidation rates in soil calculated from CH₄ profiles measured in pine forest soil in West Siberia. Low and high indicate the range of fluxes resulting from different ways to estimate the diffusion coefficient (see text for details). All fluxes are negative and indicate CH₄ uptake. The number of profiles used in each type of stand is given in the Materials and Methods section.

Taulukko 3. Metaanin hapetusnopeus metsämaassa, pitoisuusprofiilien mukaan laskettuna. 'Low' ja 'high' ovat minimi- ja maksimiarvoja hapetusnopeuksille, jotka on saatu laskemalla diffuuusiovakiot eri laskutavoilla (ks. teksti). Kaikki arvot ovat negatiivisia, eli merkitsevät metaanin vuota ilmakehästä maahan.

site	slope [ppm _v cm ⁻¹]	$\begin{array}{c} low \ flux \\ [mg \ m^{-2} \ d^{-1}] \end{array}$	high flux [mg m ⁻² d ⁻¹]
young	0.031	-0.52	-1.05
old	0.047	-0.80	-1.59
Bor Island	0.049	-0.83	-1.66
all sites	0.044	-0.74	-1.49

above the same area and during the same period. It was remarkably similar with 32 mg CH_4 m⁻² d⁻ ¹ (F. Kelliher, pers. comunication). This suggests that these estimates might be realistic despite their large error margin. Liblik et al. (1997) estimated 18 mg CH_4 m⁻² d⁻¹ as summer flux for the landscape around Fort Simpson, NWT, Canada; an area of discontinuous permafrost with upland forest on sandy dunes and about 35% wetlands similar to the area we studied except that almost half of that wetland is frozen peat plateau with low emission. Roulet et al (1994) estimated 14-16 CH₄ m⁻² d⁻¹ for the High Boreal regions of the Hudson Bay Lowlands. But for wetlands in West Siberia, airborne measurements by Tohjima et al. (1995, 1996) gave an estimate of 40–146 mg CH₄ m⁻² d⁻¹. The highest values, however, co-occurred with oil production sites.

CONCLUSION

We found that CH_4 emissions from this mire are probably rather on the high end compared to CH_4 emissions from the Hudson Bay Lowlands, but not higher than those from a number of other areas such as Scandinavia or Minnesota. They were also not as high as what has been found in the few other studies from the West Siberian Lowlands. CH_4 profiles in forest soils surrounding the mire indicated consumption of atmospheric CH_4 in the same order of magnitude as found in other boreal forests.

The area-weighted estimate of the regional source strength indicated that CH_4 oxidation in the forest did not compensate for the CH_4 emissions from the mire. Considering the good agreement between our estimate and another one derived from airborne measurements, this study indicates that ground-based techniques that take into account spatial heterogeneity may give reasonable results even on a larger scale.

ACKNOWLEDGMENTS

This study could not have been realized without the experience and knowledge of the rest of the group, and our thanks go to them all. We would like to express our special thanks to E.D. Schulze, the head of the expedition, for stimulating discussions and an excellent organization, to D. Mollicone and R. Valentini who let us use their aerial photography of the mire, and to B. Lühker who measured the bulk density of the forest soil. For helpful and constructive comments, many thanks go to T. Moore who looked at an earlier draft of the manuscript, and to two anonymous reviewers.

REFERENCES

- Achtnich, C., Bak, F. & Conrad, R. 1995. Competition for electron donors among nitrate reducers, ferric iron reducers, sulfate reducers and methanogens in anoxic paddy soil. Biology & Fertility of Soils 19: 65–72.
- Aselmann, I. & Crutzen, P.J. 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. Journal of Atmospheric Chemistry 8: 307–358.
- Bartlett, K.B. & Harriss, R.C. 1993. Review and assessment of methane emissions from wetlands. Chemosphere 26: 261–320.
- Bellisario, L.M., Bubier, J.L. & Moore, T.R. 1999. Controls on CH₄ emissions from a northern peatland Global Biogeochemical Cycles 13: 81–91.
- Benstead, J. & Lloyd, D. (1994) Direct mass spectrometric measurement of gases in peat cores. FEMS Microbiology Ecology 13: 233–240.
- Beverland, I.J., Moncrieff, J.B., Ónéill, D.H., Hargreaves, K.J. & Milne, R. 1996. Measurement of methane and carbon dioxide fluxes from peatland ecosystems by the conditional-sampling technique. Quarterly Journal of the Royal Meteorological Society 22: 819–838.
- Bosse, U. & Frenzel, P. 1997. Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*). Applied & Environmental Microbiology 63: 1199–1207.
- Bubier, J.L, Moore, T.R. & Roulet, N.T. 1993. Methane emissions from wetlands in the midboreal region of northern Ontario, Canada. Ecology 74: 2240–2254.
- Bubier, J.L., Moore, T.R., Bellisario, L., Comer, N.T. & Crill, P.M. 1995. Ecological controls on CH₄ emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. Global Biogeochemical Cycles 9(4): 455–470.
- Burke, R.A., Zepp, R.G., Tarr, M.A., Miller, W.L. & Stocks, B.J. 1997. Effect of fire on soil-atmosphere exchange of methane and carbon dioxide in Canadian boreal forest sites. Journal of Geophysical Research-Atmospheres 102: 29289–29300.
- Calhoun, A. & King, G.M. 1997. Regulation of root-associated methanotrophy by oxygen availability in the rhizosphere of two aquatic macrophytes. Applied & Environmental Microbiology 63: 3051–3058.
- Conrad, R. 1996. Soil microorganisms as controllers of atmospheric trace gases (H₂, CO, CH₄, OCS, N₂O, and NO). Microbiological Reviews 60: 609–640.

- Conrad, R. 1995. Soil microbial processes involved in production and consumption of atmospheric trace gases. *In J. Gwynfryn Jones (ed.) Advances in Microbial Ecol*ogy. Plenum Press, New York, USA.
- Dedysh, S.N. & Panikov, N.S. 1997. Effect of pH, temperature, and concentration of salts on methane oxidation kinetics in *Sphagnum* peat. Microbiology 66: 476–479
- Dedysh, S.N., Panikov, N.S., Liesack, W., Grosskopf, R., Zhou, J.Z. & Tiedje, J.M. 1998. Isolation of acidophilic methane-oxidizing bacteria from Northern peat wetlands. Science 282: 281–284.
- Dise, N.B. 1992. Winter fluxes of methane from Minnesota peatlands. Biogeochemistry 17: 71–83.
- Dise, N.B. 1993. Methane emission from Minnesota peatlands: spatial and seasonal variability. Global Biogeochemical Cycles 7: 123–142.
- Dunfield, P., Knowles, R., Dumont, R. & Moore, T.R. 1993. Methane production and consumption in temperate and subarctic peat soils — response to temperature and pH. Soil Biology & Biochemistry 25: 321–326.
- Fechner, E.J. & H.F. Hemond 1992. Methane transport and oxidation in the unsaturated zone of a Sphagnum peatland. Global Biogeochemical Cycles 6: 33–44.
- Fetzer, S., Bak, F. & Conrad, R. 1993. Sensitivity of methanogenic bacteria from paddy soil to oxygen and dissipation. FEMS Microbiology Ecology 12 : 107–115.
- FIRESCAN Science Team (1996) Fire in ecosystems of boreal Eurasia: The Bor Forest Island Fire Experiment Fire Research Campaign Asia-North (FIRESCAN) p. 848–873. In J. S. Levine (ed.) Biomass Burning and Global Change. Vol 2. MIT Press Cambridge, Massachusetts, USA.
- Frenzel, P. (2000) Plant-associated methane oxidation in ricefields and wetlands. Advances in Microbial Ecology 16: 85–114.
- Frenzel, P., & Karofeld, E. 2000. CH₄ oxidation controls CH₄ emission from a hollow-ridge complex in a raised bog. Biogeochemistry 51 : 91–112.
- Frenzel, P., Bosse, U. & Janssen, P.H. 1999. Rice roots and methanogenesis in a paddy soil: ferric iron as an alternative electron acceptor in the rooted soil. Soil Biology & Biochemistry 31: 421–430.
- Gorham, E. 1991. Northern peatlands Role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1: 182–195.
- Harriss, R.C., Gorham, E., Sebacher, D.I., Bartlett, K.B. & Flebbe, P.A. 1985. Methane flux from northern peatlands. Nature 315: 652–654.
- Inoue, G., Maksyutov, S. & Panikov, N. 1995. CO₂ and CH₄ emission from wetlands in West Siberia. 37–43. *In* Takahasi, K., Osawa, A. & Kanazawa, Y. (eds.) Proceedings of the third symposium on the joint Siberian permafrost studies between Japan and Russia in 1994. Sapporo, Japan.
- Kelliher, F.M., Lloyd, J., Arneth, A., Byers, J.N., McSeveny, T.M., Milukova, I., Grigoriev, S., Panfyorov, M., Sogatchev, A., Varlargin, A., Ziegler, W., Bauer, G &

112 Bosse & Frenzel

Schulze, E. D. 1998. Evaporation from a Central Siberian pine forest. Journal of Hydrology 205: 279–296.

- Kelliher, F.M., Lloyd, J., Arneth, A., Lühker, B., Byers, J.N., McSeveny, T.M., Milukova, I., Grigoriev, S., Panfyorov, M., Sogatchev, A., Varlargin, A., Ziegler, W., Bauer, G, Wong, S.-C. & Schulze, E.-D. 1999. Carbon dioxide efflux density from the floor of a central Siberian pine forest. Agricultural and Forest Meteorology 94: 217–232.
- Kettunen, A., Kaitala, V., Lehtinen, A., Lohila, A., Alm, J., Silvola, J. & Martikainen, P.J. 1999. Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires. Soil Biology and Biochemistry 31: 1741–1749.
- King, GM. 1997. Responses of atmospheric methane consumption by soils to global climate change. Global Change Biology 3: 351–362.
- Klinger, L.F., Zimmerman, P.R., Greenberg, J.P., Heidt, L.E. & Guenther, A.B. 1994. Carbon trace gas fluxes along a successional gradient in the Hudson Bay Lowland. Journal of Geophysical Research 99(D1): 1469–1494.
- Koschorreck, M. & Conrad, R. 1993. Oxidation of atmospheric methane in soil: Measurements in the field, in soil cores and in soil samples. Global Biogeochemical Cycles 7: 109–121.
- Kravchenko, I.K. 1999. The inhibiting effect of ammonium on the activity of the methanotrophic microbial community of a raised Sphagnum bog in west Siberia. Microbiology 68: 203–208 (translated from Mikrobiologiya 68: 241–246).
- Liblik L.K., Moore, T.R., Bubier, J.L. & Robinson, S.D. 1997. Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. Global Biogeochemical Cycles 11: 485–494.
- Matthews, E. & Fung, I. 1987. Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources. Global Biogeochemical Cycles 1: 61–86.
- Millington, J.R., Quirk, J.P. 1960. Transport in porous media. p. 97–106. In Van Beren, F.A. (ed.) Transactions of the International Congress of Soil Sciences 7th. Elsevier, Amsterdam.
- Moore, T.R.& Dalva, M. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil Biology & Biochemistry 29: 1157–1164.
- Moore, T. R. & Knowles, R. 1990. Methane emissions from fen, bog and swamp peatlands in Quebec. Biogeochemistry 11: 45–61.
- Moore, T.R., Roulet, N. & Knowles, R. 1990. Spatial and temporal variations of methane flux from subarctic/ northern boreal fens. Global Biogeochemical Cycles 4: 29–46.
- Moore, T.R., Heyes, A. & Roulet, N.T. 1994. Methane emissions from wetlands, southern Hudson Bay Lowland. Journal of Geophysical Research 99: 1455–1467

- Moosavi, S.C. & Crill, P.M. 1997. Controls on CH₄ and CO₂ emissions along two moisture gradients in the Canadian boreal Zone. Journal of Geophysical Research-Atmospheres 102: 29261–29277.
- Moosavi, S.C., Crill, P.M., Pullman, E.R., Funk, D.W. & Peterson, K.M. 1996. Controls on CH₄ flux from an Alaskan boreal wetland. Global Biogeochemical Cycles 10: 287–296.
- Nykänen, H., Alm, J., Silvola, J., Tolonen, K. & Martikainen, P.J. 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochemical Cycles 12: 53–69.
- Panikov, N.S. & Dedysh, S.N. 2000. Cold season CH₄ and CO₂ emission from boreal peat bogs (West Siberia): winter fluxes and thaw activation dynamics. Global Biogeochemical Cycles 14(4): 1071–1080.
- Panikov, N.S., Sizova, M.V., Zelenev, V.V., Machov, G.A., Naumov, A.V. & Gadzhiev, I.M. 1995. Methane and carbon dioxide emission from several Vasyugan wetlands: spatial and temporal flux variations. Ecological Chemistry 4(1): 13–23.
- Panikov, N.S., Glagolev, M.V., Kravchenko, I.K., Mastepanov, M.A., Kosych, N.P., Mironycheva-Tokareva, N.O., Naumov, A.V., Inoue, G & Maxutov, S. 1997. Variability of methane emission from West-Siberian wetlands as related to vegetation type. Ecological Chemistry 6(1): 59–67.
- Roulet, N.T., Jano, A., Kelly, C.A., Klinger, L.F., Moore, T.R., Protz, R., Ritter, J.A. & Rouse, W.R. 1994. Role of the Hudson Bay Lowland as a source of atmospheric methane. Journal of Geophysical Research 99: 1439– 1454.
- Saarnio, S. & Silvola, J. 1999. Effects of increased CO_2 and N on CH_4 efflux from a boreal mire: a growth chamber experiment. Oecologia 119: 349–356.
- Saarnio, S., Alm, J., Silvola, J., Lohila, A., Nykanen, H. & Martikainen, P.J. 1997. Seasonal variation in CH₄ emissions and production and oxidation potentials at microsites on an oligotrophic Pine fen. Oecologia 110: 414–422.
- Savage, K., Moore, T.R. & Crill, P.M. 1997. Methane and carbon dioxide exchange between the atmosphere and Northern boreal forest soils. Journal of Geophysical Research-Atmospheres 102: 29279–29288.
- Schnell, S. & King, GM. 1996. Responses of methanotrophic activity in soils and cultures to water stress. Applied & Environmental Microbiology 62: 3203– 3209.
- Schulze, E.-D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I., Schulze, W., Ziegler, W., Varlagin, A., Sogachov, A., Valentini, R., Dore, S., Grigorief, S., Kolle, O., Tchebakova, N. Vygodskaya, N. 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink — a synthesis. Global Change Biology 5(6):703–722.

- Slobodkin, A.I., Panikov, N.S. & Zavarzin, G.A. 1992. Microorganism methane formation and consumption in tundra and middle taiga bogs. Microbiology 61: 486– 493 (translated from Mikrobiologiya 61: 683–691).
- Sundh, I., Nilsson, M. Granberg, G & Svensson, B.H. 1994. Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. Microbial Ecology 27: 253–265.
- Tohjima, Y., Maksyutov, S., Machida, T. & Inoue, G 1995. Airborne measurements of atmospheric CH₄ over the West Siberian Lowland during the 1994 Siberian Terrestrial Ecosystem-Atmosphere-Cryosphere Experiment (STEACE). p. 50–57. *In* Takahasi, K., Osawa, A. & Kanazawa, Y. (eds.) Proceedings of the third symposium on the joint Siberian permafrost studies between Japan and Russia in 1994. Sapporo, Japan.
- Tohjima, Y., Maksyutov, S., Machida, T. & Inoue, G 1996. CO₂ and CH₄ from wetlands in west Siberia. Geophysical Research Letters 23: 37–43.
- Valentine, D.W., Holland, E.A. & Schimel, D.S. 1994. Ecosystem and physiological controls over methane production in northern wetlands. Journal of Geophysical Research 99: 1563–1571.
- Valentini, R., Dore, S., Marchi, G., Mollicone, D., Panfyorov, M., Rebmann, C., Kolle, O., Schulze, E.-D. 2000. Carbon and water exchanges of two contrasting central Siberia landscape types: regenerating forest and bog. Functional Ecology 14:87–96.
- Vomocil, J.A. 1965. Porosity. *In* Black, C.A., Evans, D.D., Ensminger, L.E., White, J.L., Clark, F.E. (eds.) Methods of soil analysis. Part 1. American Society of Agronomy. Madison, Wisconsin, USA.
- Watson, A., Stephen, K.D., Nedwell, D.B. & Arah, J.R.M.

1997. Oxidation of methane in peat — kinetics of CH_4 and O_2 removal and the role of plant roots. Soil Biology & Biochemistry 29: 1257–1267.

- Whalen, S.C. & Reeburgh, W.S. 1996. Moisture and temperature sensitivity of CH₄ oxidation in boreal soils. Soil Biology & Biochemistry 28: 1271–1281.
- Whalen, S.C., Reeburgh, W.E. & Barber, V.A. 1992. Oxidation of methane in boreal forest soils: a comparison of seven measures. Biogeochemistry 16: 181–211.
- Whiting, G.J. & Chanton, J.P. 1992. Plant-dependent CH₄ emission in a subarctic Canadian fen. Global Biogeochemical Cycles 6: 255–231.
- Williams, R.T. & Crawford, R.L. 1984. Methane production in Minnesota peatlands. Applied & Environmental Biology 47: 1266–1271.
- Wirth, C., Schulze, E.-D., Schulze, W., von Stunzner-Karbe, D., Ziegler, W., Miljukova I.M., Sogatchev, A., Varlagin, A.B., Panvyorov, M., Grigoriev, S., Kusnetzova, W., Siry, M., Hardes, G., Zimmermann, R. & Vygodskaya, N.N. 1999. Above-ground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. Oecologia 121(1):66– 80.
- Yavitt, J.B., Lang, GE. & Downey, D.M. 1988. Potential methane production and methane oxidation rates in peatland ecosystems of the Appalachian Mountains, United States. Global Biochemical Cycles 2: 253–268.
- Yavitt, J.B., Downey, D.M., Lancaster, E. & Lamg, GE. 1990. Methane consumption in decomposing Sphagnum-derived peat. Soil Biology & Biochemistry 22: 441–447.
- Yavitt, J.B., Williams, C.J. & Wieder, R.K. 1997. Production of methane and carbon dioxide in peatland ecosystems across North America — effects of temperature, aeration and organic chemistry of peat. Geomicrobiology Journal 14: 299–316.

TIIVISTELMÄ

Metaanivuo länsi-siperialaiselta suolta

Boreaalisen vyöhykkeen suot ovat merkittävä metaanin lähde ilmakehään. Tässä tutkimuksessa selvitettiin metaanin vaihtoa Yenisey-joen ympäristössä Länsi-Siperiassa heinäkuussa 1996. Päätutkimusalue oli vähäravinteinen suo, mutta myös viereisen kangasmaalla olevan metsäalueen metaanin kulutusta mitattiin. Metaanivuo mitattiin suljetuilla kammioilla. Metaanin tuotos- ja hapetuspotentiaaleja estimoitiin inkuboimalla turvenäytteitä lasiastioissa laboratoriossa. Kangasmaametsän metaanin vaihtoa estimoitiin määrittämällä metaanin pitoisuuspfofiili metsämaassa.

Metaanivuo tasapinnoilta (saraisten tasapintojen ja kasvittomien kuljupintojen keskiarvo) oli 117 \pm 19 mg m⁻² d⁻¹ (SE; n=47). Metaanin pitoisuudet sekä tuotos- ja hapetuspotentiaalit olivat korkeita tasapinnoilta otetuissa turvenäytteissä, mikä viittaa siihen että metaanin hapetus saattaa olla merkittävä metaanivirtauksia säätävä tekijä ko. suolla. Emissiot mättäiltä olivat hyvin pieniä (5 ± 5.9 mg m⁻² d⁻¹, SE; n=15), ja jopa metaanin kulutusta esiintyi. Kasvillisuuspinnoilla painotettu (1/3 mätäs, 2/3 tasapinta) keskiarvo koko suon metaanivuolle oli 80 mg m⁻² d⁻¹, ollen samalla tasolla muualla mitattujen vastaavien soiden metaaniemissioiden kanssa.

Metaanipitoisuudet metsämaassa pienenivät pinnasta (2 ppm) syvempiin maakerroksiin (n. 0,5 ppm). Pitoisuusprofiilien mukaan estimoituna metsämaa toimii pienenä metaanin nieluna (–1 mg m⁻² d⁻¹); nielun suuruus on samaa luokkaa muiden boreaalisten metsämaiden kanssa. Suoja kangasmaiden pinta-aloilla painotettu kesäajan metaaniemissioiden keskiarvo 360 km²:n suuruiselle suoalueelle tutkimusalojen ympäristössä oli 25 mg CH₄ m⁻² d⁻¹.

Received 25.9.2001, Accepted 9.11.2001