

Microbial Controls on Methane Fluxes from a Polygonal Tundra of the Lena Delta, Siberia

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ABSTRACT

Permafrost soils of high-latitude wetlands are an important source of atmospheric methane. In order to improve our understanding of the large seasonal fluctuations of trace gases, we measured the CH₄ fluxes as well as the fundamental processes of CH₄ production and CH₄ oxidation under *in situ* conditions in a typical polygonal tundra in the Lena Delta, Siberia. Net CH₄ fluxes were measured from the polygon depression and from the polygon rim from the end of May to the beginning of September 1999. The mean flux rate of the depression was 53.2 ± 8.7 mg CH₄ m⁻² d⁻¹ with maximum in mid-July ($100\text{--}120$ mg CH₄ m⁻² d⁻¹), whereas the mean flux rate of the dryer rim part of the polygon was 4.7 ± 2.5 CH₄ m⁻² d⁻¹. The microbial CH₄ production and oxidation showed significant differences during the vegetation period. The CH₄ production in the upper soil horizon of the polygon depression was about 10 times higher (38.9 ± 2.9 nmol CH₄ h⁻¹ g⁻¹) in July than in August (4.7 ± 1.3 nmol CH₄ h⁻¹ g⁻¹). The CH₄ oxidation behaved exactly in reverse: the oxidation rate of the upper soil horizon was low (1.9 ± 0.3 nmol CH₄ h⁻¹ g⁻¹) in July compared to the activity in August (max. 7.0 ± 1.3 nmol CH₄ h⁻¹ g⁻¹). The results indicated clearly an interaction between the microbiological processes with the observed seasonal CH₄ fluctuations. However, the CH₄ production is primarily substrate dependent, while the oxidation is dependent on the availability of oxygen. The temperature plays only a minor role in both processes, probably because the organisms are adapted to extreme temperature conditions of the permafrost. For the understanding of the carbon dynamics in permafrost soils, a differentiated small-scale view of the microbiological processes and the associated modes of CH₄ fluxes is necessary, especially at key locations such as the Siberian Arctic. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: methane fluxes; microbial processes; CH₄ production; CH₄ oxidation; permafrost soils

INTRODUCTION

Wet tundra environments of the Arctic influence the global climate by the release of methane (CH₄) and other radiatively active trace gases into the atmosphere. Methane contributes to the enhanced greenhouse effect with a portion of approximately 20% (Wuebbles and Hayhoe, 2002). The world-wide

wetland area has a size of about 5.5×10^6 km² (Aselman and Crutzen, 1989), about half of it is located in high latitudes of the northern hemisphere (>50°N). The atmospheric input of methane from tundra soils of this region has been estimated between 20–40 Tg CH₄ yr⁻¹ (Christensen *et al.*, 1996), corresponding to about 25% of the methane emission from natural sources (Fung *et al.*, 1991). However, the strength of tundra environments as a methane source and the sensitivity of permafrost to potential changes in climate are still uncertain.

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In the last decades numerous studies on methane fluxes were focused on tundra environments in Northern America and Scandinavia (e.g. Svensson and Rosswall, 1984; Whalen and Reeburgh, 1988; Bartlett *et al.*, 1992; Liblik *et al.*, 1997; Reeburgh *et al.*, 1998; Christensen *et al.*, 2000). Since the early nineties, the large tundra areas of Russia were integrated into these investigations (e.g. Christensen *et al.*, 1995; Samarkin *et al.*, 1999; Panikov and Dedysch, 2000; Tsuyuzaki *et al.*, 2001). All these studies reveal temporal and spatial variability of methane fluxes, ranging between -1.9 and $360 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. To understand these dramatic fluctuations, some studies focused on the environmental conditions and soil characteristics. Water table position, soil moisture and temperature, type of substrate and vegetation as well as availability of organic carbon, which indirectly influences the methane dynamics of tundra environments, were studied (e.g. Torn and Chapin, 1993; Vourlitis *et al.*, 1993; Bubier *et al.*, 1995; Oberbauer *et al.*, 1998; Joabsson *et al.*, 1999; Yavitt *et al.*, 2000). Although 80–90% of total methane emission originates from microbial activities (Ehlt and Schmidt, 1978), only a few investigations dealt with methane production and methane oxidation caused by basically microbiological processes (Slobodkin *et al.*, 1992; Vecherskaya *et al.*, 1993; Samarkin *et al.*, 1994; Schimel and Gullede, 1998; Segers, 1998; Frenzel and Karofeld, 2000; Wagner *et al.*, 2001).

Approximately 14% of the global carbon is stored in permafrost soils and sediments (Post *et al.*, 1982). Due to this carbon pool, tundra environments play a major role in the global carbon cycle, even more since current climate models predict significant changes in temperature and precipitation patterns in these regions (Hansen *et al.*, 1988; Kattenberg *et al.*, 1996). The microbial methane production (methanogenesis) is one of the most prominent microbiological processes during the anaerobic decomposition of organic matter. A small group of strictly anaerobic organisms called methanogenic archaea is responsible for methanogenesis (Garcia *et al.*, 2000). Although methanogenic archaea are widespread in nature (e.g. permafrost soils, marshes, swamps, marine and freshwater sediments, flooded rice paddies, geothermal habitats), they show an extremely specialized metabolism. In permafrost soils two main pathways of energy-metabolism dominate: (i) the reduction of CO_2 to CH_4 using H_2 as a reductant and (ii) the fermentation of acetate to CH_4 and CO_2 (Deppenmeier *et al.*, 1996).

After its production methane is partly oxidized either in the aerobic top layer of permafrost soils

or in the aerobic rhizosphere by highly specialized *Proteobacteria*, belonging to the group of methanotrophic bacteria (Hanson and Hanson, 1996). They are using CH_4 as the sole carbon source, while energy is gained by the oxidation of CH_4 to CO_2 . Methanotrophic bacteria are common in almost all environments, where they can survive under unfavourable living conditions by the formation of spores. The oxidation of methane by methanotrophic bacteria as a sink for methane is probably just as important as the production of methane by methanogenic archaea. Both processes determine the methane fluxes of natural wetlands. It is well known that the methane oxidation in rice soils amounts to 45–90% and in freshwater ecosystems to 80–90% of the produced methane (Frenzel *et al.*, 1990; van Bodegom *et al.*, 2001; Khalil *et al.*, 1998). Thus a better understanding of methane fluxes of natural wetlands requires the knowledge of the function, physiology and population dynamics of the involved microorganisms.

The purpose of this study was to verify the role of the microbial processes for the seasonal fluctuation of methane fluxes from tundra environments. The analysis included measurements of seasonal methane fluxes and environmental parameters as well as the quantification of methane production and oxidation under *in situ* conditions within the active layer of permafrost soils.

STUDY SITE

The study site of Samoylov Island, Siberia, lies within the Lena Delta, which represents the largest delta of the circum-arctic land masses, formed by the Lena River. The Lena Delta is located at the Laptev Sea coast between the Taimyr Peninsula and the New Siberian Islands (Figure 1). The delta occupies an area of about $32,000 \text{ km}^2$ and is characterized by a network of smaller and larger rivers and channels as well as more than 1500 islands. The delta can be divided into three geomorphologically different terraces (Are and Reimnitz, 2000; Schwamborn *et al.*, 2002): (i) the oldest terrace was formed in the middle to late Pleistocene and is fragmentarily exposed (30–55 m a.s.l.) in the southern part of the delta. The terrace consists of ice-complexes containing fine-grained silty sediments with a high content of segregated ice. The ice-complex moreover includes enormous layers of organic-rich material and less decomposed peaty material, (ii) Arga Island, the western part of the delta (20–30 m a.s.l.) is characterized by coarse-grained sandy sediments and a multitude of deep lakes, which were formed in

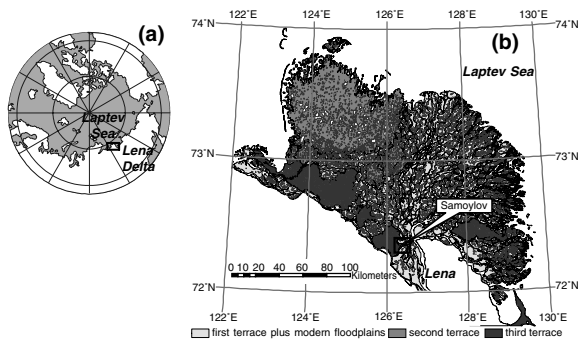


Figure 1 Map showing the Lena Delta, northeast Siberia (N 72°22, E 126°28). (a) circum polar map with the details of the Lena Delta; (b) location of the study area Samoylov Island within the Lena Delta.

the late Pleistocene to late Holocene, (iii) the eastern terrace is regarded as the currently active part of the Lena Delta. The latter is of a middle Holocene age with several modern flood plains (1–12 m a.s.l.) at the base. The landscape of the delta is characterized by the patterned ground of ice-wedge polygons in different development stages (Müller, 1997). The entire delta is situated in the zone of continuous permafrost with a thickness of about 500–600 m (Romanovskii and Hubberten, 2001).

Samoylov (N 72°22, E 126°28) is a representative island in the active and youngest part (8000–9000 years) of the Lena Delta and covers an area of about 1200 ha. The western coast of the island is characterized by modern accumulation processes (fluvial and aeolian sedimentation). Three flood plains can be distinguished, which differ in their flooding frequency and vegetation coverage.

The texture of accumulated sediments is dominated by the sand fraction (fine to medium). In contrast, the eastern coast of Samoylov is dominated by erosion processes, which form an abrasion coast. This part is composed of middle Holocene deposits, which cover about 70% of the total area of the island. Our studies of methane fluxes and microbial activity were carried out within this terrace, which is dominated by active ice wedges with low-centred polygons. The topography is determined by this patterned ground and shows a distinct micro-relief of polygon rims and polygon depressions.

Due to the micro-relief, soil and vegetation characteristics vary in rapid succession. The soils of the investigation site are characterized by very homogeneously spread soil units: the polygon rims were dominated by *Glacic Aquiturbels* (Ajj, Bjjg, Bjjf), whereas the prevalent soil type of the polygon depressions were *Typic Historthels* (Oi, A, Bg, Bf) classified according to the US Soil Taxonomy (Soil Survey Staff, 1998). The peaty soils of the polygon depression are characterized by a water level near the soil surface and the predominantly anaerobic accumulation of organic matter. The drier soils of the polygon rim show a distinctly deeper water level, lower accumulation of organic matter and pronounced cryoturbation properties. The vegetation of the polygon rim is dominated by dwarf shrub *Dryas punctata* and the mosses *Hylocomium splendens* and *Timmia austriaca*, whereas the polygon depression is dominated by hydrophytes like various *Carex* species and different moss species (e.g. *Limprichtia revolvens*, *Meesia longiseta*). The thaw depth of the soils varied between 30 and 45 cm (rim, depression), respectively. A typical cross-section of a low-centred polygon is shown in Figure 2.

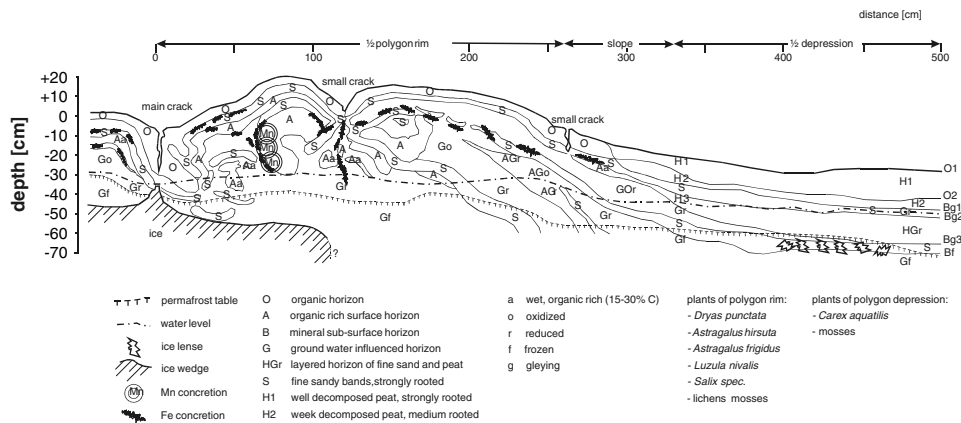


Figure 2 Cross section, across the border, of a typical low-centred polygon (Lena Delta, Siberia).

The climate of the southern Lena Delta is characterized by a low mean annual air temperature (-14.7°C) and a mean annual precipitation of 190 mm. The winter season lasts nine months, from the end of September to the end of May ($T_{\text{avg}} = -30^{\circ}\text{C}$, $T_{\text{min}} = -48^{\circ}\text{C}$) with insufficient light (polar night) and heavy snowstorms (140 km h^{-1} , Wein, 1999). The summer period of almost 12 weeks is characterized by higher temperatures ($T_{\text{avg}} = 7^{\circ}\text{C}$, $T_{\text{max}} = 18^{\circ}\text{C}$) and permanent light (polar day).

MATERIAL AND METHODS

CH₄ Fluxes

Net CH₄ fluxes presented in this paper were measured from the end of May to the beginning of September during the Expedition LENA 1999 (Pfeiffer *et al.*, 2000). This investigation pertained to an ongoing long-term study of trace gas emissions, which started in 1998. The flux measurements were determined using five static chambers (PVC transparent, 12.5 l) for the polygon rim and depression, respectively. The chambers consisted of a $50 \times 50\text{ cm}$ stainless steel base installed permanently 15 cm into the active layer. Water filled channels on top of the steel base provided airtight seals of the chamber components. Each chamber was fitted with four ports connected with two perforated pipes fixed inside the chamber. Chamber headspace was sampled over 30 min by pumping headspace air through a gas collecting jar connected with gastight tubes (Tygon). CH₄ fluxes were calculated from the chamber volume and the linear increase in CH₄ concentration.

Vertical profiles of soil CH₄ concentrations were obtained from both the polygon rim and depression by extracting CH₄ from soil pore water. Fresh soil (about 20 g) from each horizon was placed immediately after sampling into 50-ml glass jars containing 35 ml of saturated NaCl solution. Jars were closed gastight with a screw cap with septum, equilibrated by shaking the solution and analysed for CH₄ concentration by taking a sample with a gastight syringe from the jars headspace.

CH₄ Production and Oxidation

The CH₄ production and oxidation capacity of the soil typical for the polygon depression was analysed at the beginning of July and at the beginning of August 1999, while the microbial activity of the soil from the polygon rim was measured only in August 2000.

The CH₄ production was studied considering the *in situ* soil temperature gradient. Fresh soil material (20 g) from different soil horizons was weighed into 100-ml glass jars and closed with a screw cap containing a septum. The samples were evacuated and flushed with ultra pure N₂. The prepared soil samples were re-installed in the same layers of the soil profile from which the samples had been taken. Three replicates were used for each layer. Gas samples were taken every 24 h out of the jars headspace with a gastight syringe. CH₄ production rates were calculated from the linear increase in CH₄ concentration analysed by gas chromatography.

The CH₄ oxidation capacity was studied considering the *in situ* CH₄ concentration and the natural soil temperature gradient. Fresh soil material (5 g, well homogenized) from different soil horizons was weighed into 50-ml glass jars and closed with a screw cap with septum. All samples were supplied with about 2000 ppm CH₄ (corresponding to about $800\text{ }\mu\text{mol CH}_4\text{ l}^{-1}$ pore water). The samples were treated in the same way as described for measurement of methane formation, with the exception that gas samples were taken every 12 h. CH₄ oxidation capacities were calculated from the linear decrease in CH₄ concentration analysed by gas chromatography.

Calculation

In order to calculate the balance between both microbial processes and to compare these data with the measured CH₄ fluxes (F_{act}), the potential CH₄ fluxes (F_{pot}) were determined from the CH₄ production and oxidation rates according to the following equation:

$$F_{\text{pot}} = M_{\text{CH}_4} \sum_{i=1}^n (x_{pi} - x_{oi}) * BD_i * y_i$$

F_{pot}	potential CH ₄ flux from soils into the atmosphere [$\text{mg m}^{-2}\text{ d}^{-1}$]
n	number of horizons in the soil profile
x_{pi}	CH ₄ production rate in horizon i [$\text{mmol g}^{-1}\text{ d}^{-1}$]
x_{oi}	CH ₄ oxidation rate in horizon i [$\text{mmol g}^{-1}\text{ d}^{-1}$]
M_{CH_4}	molar mass of CH ₄ [g mol^{-1}]
BD_i	bulk density of horizon i [g m^{-3}]
y_i	thickness of horizon i [m]

Environmental Conditions

Daily soil temperature, water table and thaw depth were determined manually at the same time as CH₄ flux samples were taken. The soil temperature was measured at 5-cm increments from 0 to 15 cm depth at the polygon rim and depression. Additional temperature measurements were carried out during the experiments of *in situ* CH₄ production and oxidation (5-cm increments from 0 to 40 cm soil depth). The water table position relative to the soil surface was measured in a series of slotted wells distributed over the polygon. The thaw depth was determined by inserting a steel rod into the soil until permafrost was encountered. The pH of the soil pore water was measured after sampling the soil solution from different depths by suction lysimeters.

Carbon Analysis

Dissolved organic carbon (DOC) was extracted in July and in August, respectively, from soil samples of two vertical profiles (polygon depression and rim). Fresh soil material (9 g) was taken at 5-cm intervals down to a depth of 30 cm in the polygon depression and to a depth of 40 cm in the polygon rim. The samples from each layer were weighed into glass jars (50 ml) and mixed with 45 ml distilled water. The bottles were closed and shaken for 1 h in the dark. Afterwards the suspension was filtered (mesh 0.45 µm, Gelman Science) and the clear solution was inactivated by adding sodium azide. The DOC analysis was done with an Elementar High-TOC-II.

Total organic carbon (TOC) was analysed with an element analyser (Elementar Vario EL) using dried and homogenized soil samples. Prior to analysis the samples were treated with HCl (10%) at 80 °C for carbonate removal.

Gas Analysis

CH₄ concentrations were determined with a gas chromatograph (Chrompack GC 9003) in the field laboratory. The instrument was equipped with a Poraplot Q (100/120 mesh, 20 ft) capillary column, which operated with pure helium as carrier gas at a flow rate of 20 ml min⁻¹. CH₄ was analysed by a flame ionization detector. The injector/detector temperatures were set at 160 °C and the column oven at 80 °C. All gas sample analyses were done after calibration of the gas chromatograph with standard gases.

RESULTS

CH₄ Fluxes

The CH₄ fluxes of the depression differed strongly from those of the rim of a wet polygon tundra. The mean flux rate for the total vegetation period (June–September) of the depression was 53.2 ± 8.7 mg CH₄ m⁻² d⁻¹, whereas the mean flux rate of the dryer rim part of the polygon was 4.7 ± 2.5 mg CH₄ m⁻² d⁻¹. The emission of CH₄ from the depression covered dominantly by *Carex aquatilis* showed large seasonal fluctuations. Right from the start of soil thawing a relatively high CH₄ flux rate of more than 10 mg CH₄ m⁻² d⁻¹ was determined at the beginning of June (Figure 3a). This rate increased with advanced thawing of the active layer and reached the highest values with 100–120 mg CH₄ m⁻² d⁻¹ in the middle of July. During the second half of July, CH₄ fluxes decreased continuously and attained a constant rate of about 25 mg CH₄ m⁻² d⁻¹ in August, when the maximum thawing depth of the active layer was reached (Figure 3b). During the early vegetation period from the end of May to mid-July (99-05-25 to 99-07-15) the CH₄ fluxes were significantly correlated ($r = 0.937$) with the thawing of the active layer (Figure 4), whereas no correlation was observed between CH₄ fluxes and soil temperature (data not shown). In contrast to the polygon depression, CH₄ fluxes of the rim, which is dominated by a moss vegetation, showed no seasonal fluctuation. During the whole season the rate was lower than 10 mg CH₄ m⁻² d⁻¹.

CH₄ concentration of the pore water within the soils of both the rim and the depression of the polygon increased with depth. The concentrations for both soils were in the same order of magnitude. It varied between 0.1 and 489.3 µmol CH₄ l⁻¹ soil solution within the *Typic Historthel* and between 0.9 and 766.5 µmol CH₄ l⁻¹ soil solution within the *Glacic Aquiturbel*, respectively (Table 1).

Microbial CH₄ Production and Oxidation

The *in situ* CH₄ production of the *Typic Historthel* (polygon depression) showed significant differences in the upper soil layer (0–5 cm depth) measured in July and August (Figure 5a, 5b). At the beginning of August the CH₄ production was about 10 times lower (4.7 ± 1.3 nmol CH₄ h⁻¹ g⁻¹, Figure 5b) than the rate at the beginning of July, which was 38.9 ± 2.9 nmol CH₄ h⁻¹ g⁻¹ (Figure 5a). With increasing soil depth, CH₄ production rate decreased at both

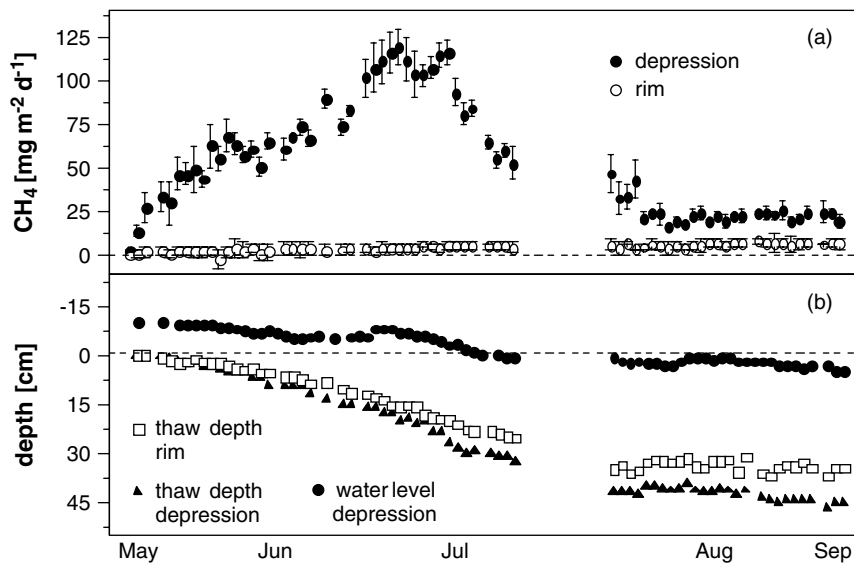


Figure 3 CH₄ flux and environmental variables of a low-centered polygon measured from the beginning of June to the beginning of September 1999. (a) CH₄ emission from the polygon depression and rim; mean \pm SE, $n = 5$; (b) water level of the polygon depression and thaw depth of the polygon depression and rim.

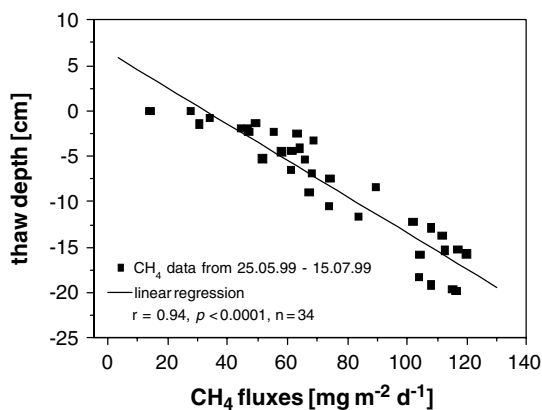


Figure 4 Relationship of CH₄ fluxes to the thaw depth of the active layer for the period 25 May to 15 July 1999.

measuring times. In contrast to the top soil, the production rates for the deeper soil layers were in the same order of magnitude (approximately between 1–4 nmol CH₄ h⁻¹ g⁻¹). The natural soil temperature gradient decreased from the top to the bottom of the soil. The temperature varied between 9.4 and 0.9 °C in July and was slightly lower in August with 7.5–0.4 °C.

Compared to the *in situ* CH₄ production, the CH₄ oxidation capacity of the studied soil was completely

different. At the beginning of July, CH₄ oxidation was only observed in the upper soil layer with a rate of 1.9 ± 0.3 nmol CH₄ h⁻¹ g⁻¹, while no CH₄ oxidation was detectable in the deeper soil layers (Figure 6a). In August CH₄ oxidation was registered through the entire vertical profile with the exception of the bottom layer (Figure 6b). The rates varied between 4.1 ± 0.3 and 7.0 ± 1.3 nmol CH₄ h⁻¹ g⁻¹, but in contrast to the CH₄ production the CH₄ oxidation did not decrease with the soil depth.

The potential CH₄ flux (F_{pot}) from the polygon depression calculated from the CH₄ production (119.1 mg CH₄ m⁻² d⁻¹) and oxidation rates (5.0 mg CH₄ m⁻² d⁻¹) was in the same order of magnitude (114.1 mg CH₄ m⁻² d⁻¹) compared to the measured CH₄ fluxes (approximately 110 mg CH₄ m⁻² d⁻¹) at the beginning of July. The calculated balance of CH₄ production and oxidation at the beginning of August revealed a negative flux rate ($28.7 - 66.4 = -37.7$ mg CH₄ m⁻² d⁻¹), suggesting a higher oxidation rate than the production rate.

The CH₄ production and oxidation activity of the *Glacis Aquiturbel* (polygon rim) was lower and showed another distribution within the profile compared to the *Typic Historthel*. The CH₄ production ranged from 0.2 ± 0.09 to 1.0 ± 0.2 nmol CH₄ h⁻¹ g⁻¹ (Figure 7). No CH₄ production was found in the upper soil layers between 0 and 20 cm depth, while the highest CH₄ production was detected

Table 1 Selected soil properties of the study sites.

Horizon*	Depth [cm]	CH ₄ concentration [$\mu\text{mol l}^{-1}$]	TOC [%]	DOC [†] [mg l ⁻¹]	DOC [‡] [mg l ⁻¹]	pH
Polygon depression (<i>Typic Historthel</i>)						
Oi1	0–5	0.1	18.4	17.4	11.7	n.d.
Oi2	5–10	6.4	14.0	13.6	8.8	7.9
Ajj	10–17	15.8	13.8	25.2	4.7	7.4
Bg1	17–23	39.9	8.1	12.0	9.5	n.d.
Bg2	23–30	116.9	4.6	9.3	11.9	n.d.
Bg2	30–35	280.5	3.6	7.2	12.8	n.d.
Bg3	35–40	489.3	4.3	10.5	n.d.	n.d.
Polygon rim (<i>Glacic Aquiturbel</i>)						
Ajj	0–5	0.9	2.1	7.3	7.3	n.d.
Bjgg1	5–12	0.7	2.0	7.1	6.8	n.d.
Bjgg2	12–20	98.2	2.4	9.0	4.0	7.9
Bjgg2	20–27	158.3	3.0	7.3	5.4	6.7
Bjgg2	27–35	441.6	2.4	4.0	6.4	6.8
Bjgg3	35–42	395.9	2.7	8.7	8.3	n.d.
Bjgg3	42–49	766.5	3.3	17.3	10.6	n.d.

* Horizon nomenclature and § soil classification according to Soil Survey Staff (1998). † First extraction of DOC at the beginning of July. ‡ Second extraction of DOC at the beginning of August 1999. TOC = total organic carbon; DOC = dissolved organic carbon; n.d. = not detected.

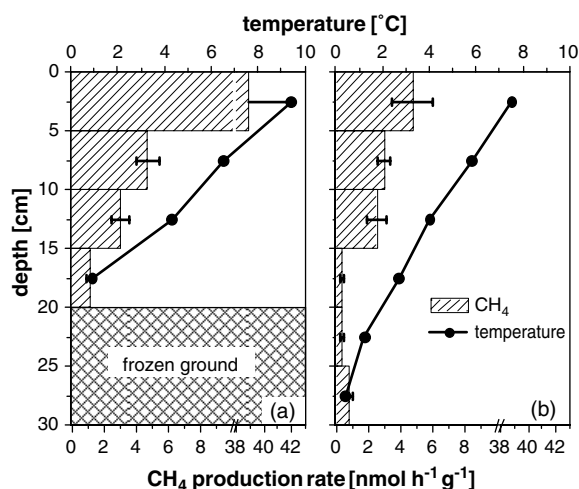


Figure 5 Vertical profile of CH₄ production and *in situ* soil temperature, polygon depression. CH₄ production rate and soil temperature determined at (a) the beginning of July 1999 and (b) the beginning of August 1999.

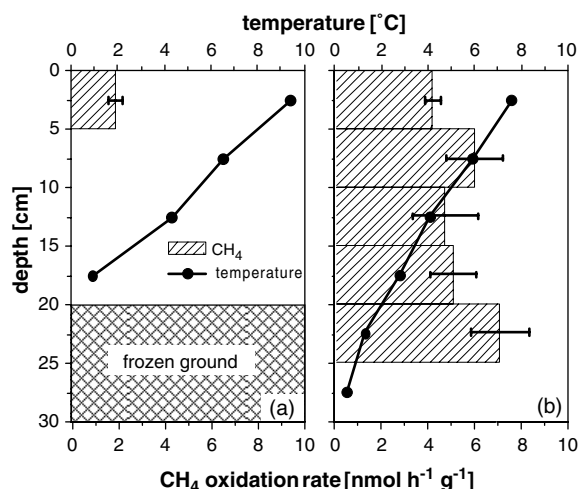


Figure 6 Vertical profile of CH₄ oxidation capacity and *in situ* soil temperature, polygon depression. CH₄ oxidation rate and soil temperature determined at (a) the beginning of July 1999 and (b) the beginning of August 1999 (b).

in the boundary to the frozen ground. The CH₄ oxidation capacity varied between 0.2 ± 0.05 and 0.9 ± 0.1 nmol CH₄ h⁻¹ g⁻¹ (Figure 7). The highest oxidation rates were observed in the bottom layers, where significant *in situ* CH₄ production prevails. The soil temperature decreased with the soil depth from 6.4 to 1.0 °C.

Soil Characteristics

In the upper 15 cm, average soil temperature in the polygon depression (*Typic Historthel*) systematically was about 3 °C higher than in the comparable depths of the polygon rim (*Glacic Aquiturbel*, Figure 8). While the upper soil temperature exhibited highly

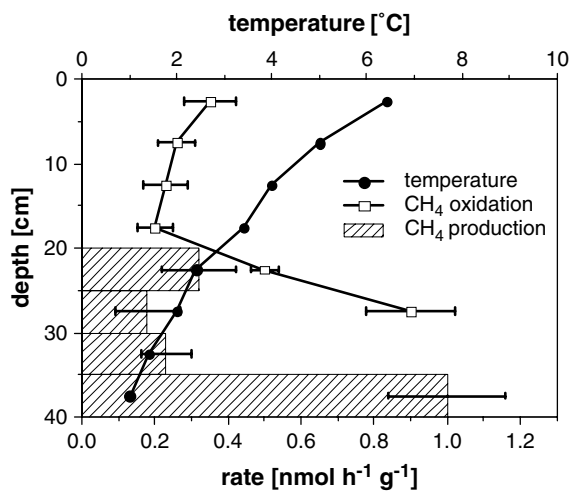


Figure 7 Vertical profile of CH₄ production and CH₄ oxidation capacity and *in situ* soil temperature within the polygon rim determined in August 2000.

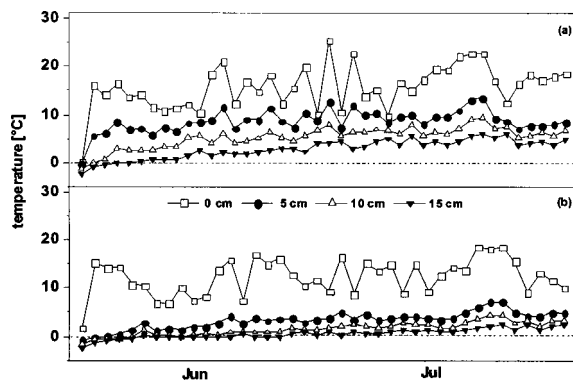


Figure 8 Soil temperature of a low-centred polygon measured in June and July 1999 at the CH₄ flux site: (a) depression; (b) rim.

diurnal fluctuations, the deeper soil layers showed a relatively constant temperature around 1.8 °C for the rim and 5.7 °C for the depression, which slightly increased to 3.6 and 6.8 °C, respectively, over the season.

The water level relative to the soil surface of the polygon depression decreased during the season. From the beginning of June to mid-July the polygon depression was water-filled. Afterwards the water level fell slowly under the soil surface and reached the lowest extent in August (Figure 3b). The maximum thaw depth of the soils was reached in August, with 35 cm in the polygon depression and 45 cm in the polygon rim (Figure 3b). The pH values measured in

the soil pore water during the field campaign ranged from pH 6.7 to 7.9 (Table 1).

The organic carbon (TOC) contents showed a large variability within the micro-relief (Table 1). The *Typic Historthel* of the polygon depression was characterized by a high amount of TOC, which ranged from 18.4 to 3.6% and decreased within the vertical profile of the soil. Contrary, the TOC content of the *Glacic Aquiturbel* was much lower (2.0–3.3%) and of small variability. Because of the different carbon pools of both soils, the average amount of DOC in the *Typic Historthel* was 13.6 mg l⁻¹ in July and 9.9 mg l⁻¹ in August, while the average amount of DOC in the *Glacic Aquiturbel* was 8.7 mg l⁻¹ in July and 6.9 mg l⁻¹ in August (Table 1). The DOC concentrations were remarkable higher in the upper soil layers of the polygon depression in July compared to the concentrations in August, while the DOC values of the polygon rim were similar in both months. A distinct tendency of DOC distribution could not be recognized in the vertical profile of the soils.

DISCUSSION

The CH₄ emission rates are from a tundra environment of the Lena Delta, northeastern Siberia, and were measured during the expedition *Lena 1999* for a period of 14 wk from the beginning to the end of the vegetation period. The CH₄ flux data were obtained within the scope of a long-term study of trace gas emissions carried out since 1998. The results revealed considerable variations of CH₄ emissions from the polygon depression during the vegetation period, while during the same time the polygon rim showed a relatively constant emission rate. The highest fluxes occurred in mid-July, the lowest in early spring as well as in autumn.

Although long-term studies of methane emission rates are necessary for the refinement of global CH₄ flux estimates (Matthews and Fung, 1987), few studies on CH₄ fluxes in the high arctic consider a measuring period of more than 4 wk (Bartlett *et al.*, 1992; Whalen and Reeburgh, 1992; Vourlitis *et al.*, 1993; Christensen *et al.*, 2000; Nakano *et al.*, 2000; Tsuyuzaki *et al.*, 2001). Most calculations are based on measurements made of a couple of days for the whole season (e.g. Torn and Chapin, 1993; Christensen *et al.*, 1995; Oberbauer *et al.*, 1998; Verville *et al.*, 1998). Investigations of CH₄ fluxes in the Russian Arctic over several years have not been published yet. However, the former studies (see above) yielded results that suggest

pronounced seasonal variations in CH₄ release, which were attributed to environmental variables like temperature and soil moisture. The essential CH₄ production and oxidation rates caused by the underlying microbiological processes in permafrost soils have been measured only in few studies under *in situ* conditions (Vecherskaya *et al.*, 1993; Samarkin *et al.*, 1999). Therefore the microbial activities are not well understood within the context of CH₄ flux analyses.

In this study, the microbiological processes of the polygon depression could be clearly correlated with the observed seasonal CH₄ fluctuations. At the beginning of July, the CH₄ production in the upper soil layer was unusually high with a rate of about 39 nmol CH₄ h⁻¹ g⁻¹. At the same time, CH₄ oxidation in the upper soil layer amounted to about 2 nmol CH₄ h⁻¹ g⁻¹, whereas no activity was found in the deeper soil layers. Considering the analysed CH₄ production and oxidation rates and the calculated potential fluxes within the soil profile, only 4% of the produced methane is oxidized by the methanotrophic bacteria in the upper soil layer. Compared with other ecosystems, where up to 90% of the formed CH₄ can be oxidized by methanotrophic bacteria (Frenzel *et al.*, 1990; Khalil *et al.*, 1998), their oxidation activity in the permafrost soil is very low at the beginning of the vegetation period. The high CH₄ production rate together with the low CH₄ oxidation rate explain the highest CH₄ fluxes determined in July 1999.

At the beginning of August, the CH₄ production and oxidation activity of the microorganisms differed completely from the July rates. The CH₄ production in the upper soil layer drastically decreased to about 4.5 nmol CH₄ h⁻¹ g⁻¹, while the CH₄ oxidation, which could be detected now in nearly the whole profile, strongly increased to rates between 4 and 7 nmol CH₄ h⁻¹ g⁻¹. The calculated balance of the CH₄ production and oxidation for the whole profile showed that the microbial CH₄ oxidation capacity (66 mg m⁻² d⁻¹) in this period was about twice as high as the microbial CH₄ production (29 mg m⁻² d⁻¹). Nevertheless, a significant CH₄ release from the polygon depression was also determined in August 1999, which can be attributed to the influence of the vegetation. It is well known that a substantial part of formed CH₄ is transported through the aerenchyma of vascular plants into the atmosphere (Whiting and Chanton, 1992; Morrissey *et al.*, 1993; Tsuyuzaki *et al.* 2001). L. Kutzbach (personal communication, 2003) demonstrated at the same investigation site a CH₄ transport through the dominating sedge *Carex aquatilis*, accounting for about 68% of the total CH₄

emission rates. Thus, the microbial oxidation of CH₄ in the aerobic soil zones is bypassed. Consequently, also at the shown ratio of CH₄ production and CH₄ oxidation, a significant CH₄ release had taken place.

The CH₄ fluxes and the microbial activities at the polygon rim were much lower than those appearing in the polygon depression. Our results underlined the influence of the micro-relief on CH₄ fluxes, as also described for a polygonal tundra setting on Taimyr Peninsula (Samarkin *et al.*, 1999). Thus, the top soil of the rim was much dryer than the depression with a distinct redox gradient. Therefore, CH₄ production was only found in the anaerobic bottom layer of the rim. Since the CH₄ oxidation was in the same range as the CH₄ production, and the plant-mediated CH₄ transport could be neglected at this site, the CH₄ emission rate at the rim of the polygon was low.

The seasonal changes of microbial activities are based on different environmental parameters. With the beginning of the vegetation season, a strong relationship between CH₄ fluxes and the thawing of the soil was deduced for the depression, whereas no correlation between CH₄ fluxes and the soil temperature was found over the whole season (data not shown). These results are in contrast to other investigations carried out by a number of authors (Morrissey and Livingston, 1992; Christensen *et al.*, 1995; Hargreaves and Fowler, 1998; Verville *et al.*, 1998), who found a strong relationship between the CH₄ emission and the air or soil temperature, respectively. Our investigations of the methanogenic activity under *in situ* conditions showed a substantial CH₄ production in the lower boundary of the active layer, which was characterized by a temperature of about 1 °C. Just as CH₄ oxidation by methanotrophic bacteria is independent from the temperature gradient of the soil. We assume that the microorganisms are well adapted to the extreme temperature regime of permafrost soils. Otherwise they would not have shown any activity at such low temperatures (Morita, 1992). This assumption was confirmed by the work of Omelchenko *et al.* (1993), who described a cold-adapted (psychrophilic) methane-oxidizing microbial community from Siberian tundra soils. Franzmann *et al.* (1997) described the only known strain of a psychrophilic methanogenic archaea isolated from Ace Lake, Antarctica. However, the *in situ* analyses showed that methanogenesis and methane consumption occurred with a high rate even at extremely low temperatures, whereby the temperature had only a subordinate relevance for the CH₄ fluxes of the investigated permafrost soils.

Furthermore, the adapted methanogenic archaeal community likely produced methane continuously during the back freezing of the soil in autumn. Apparently, this methane might be entrapped into the active layer and can be released in the thawing period of the following spring. Samarkin *et al.* (1999) already assumed that such back-stored methane adds to the emission of newly-produced methane. This process is evidenced by our results showing the coincidence of enhanced CH_4 fluxes and the onset of soil thawing in spring and early summer (Figure 4).

Further important factors affecting microbiological processes are the water table and the available substrate. The results revealed a high methane release in June/July, when water level is high and a low methane release at low water level in August/September (Figure 3). The measured CH_4 oxidation showed that the activity of the oxygen-dependent methanotrophic bacteria clearly increased with sinking water levels, because more oxygen was available for the oxidation process. The activity of the anaerobic methanogenic archaea in the permafrost soil was less affected by a falling water level, although methanogens are regarded as strictly anaerobic organisms. CH_4 production occurred in wetland soils in the presence of oxygen, because methanogenic bacteria are well protected against

oxygen by the activity of indigenous facultative anaerobic microflora (Wagner *et al.*, 1999).

In contrast to methanotrophic bacteria, which use methane as the only source of energy and carbon, the activity of methanogenic archaea mainly depends on the quality and quantity of available organic matter (Bergman *et al.*, 2000). The latter relationship is confirmed by our results, as the highest CH_4 production was determined in the upper soil horizons, in accordance with the highest measured TOC content. However, DOC concentrations were lower in these horizons in August than in July. Accordingly, the activity of methanogenic archaea decreased from July to August in the upper soil layers. Thus, the CH_4 production seems to be primarily controlled by the available substrate. This result is supported by the investigations of Bianchi *et al.* (1996), who reported that the CH_4 production in a river floodplain depends mainly on the quality and quantity of DOC.

CONCLUSION

Our results demonstrate the close relationship between CH_4 fluxes and the fundamental microbiological processes of CH_4 production and oxidation in polygonal tundra soils. An important finding is that in addition to the soil characteristics and the climate

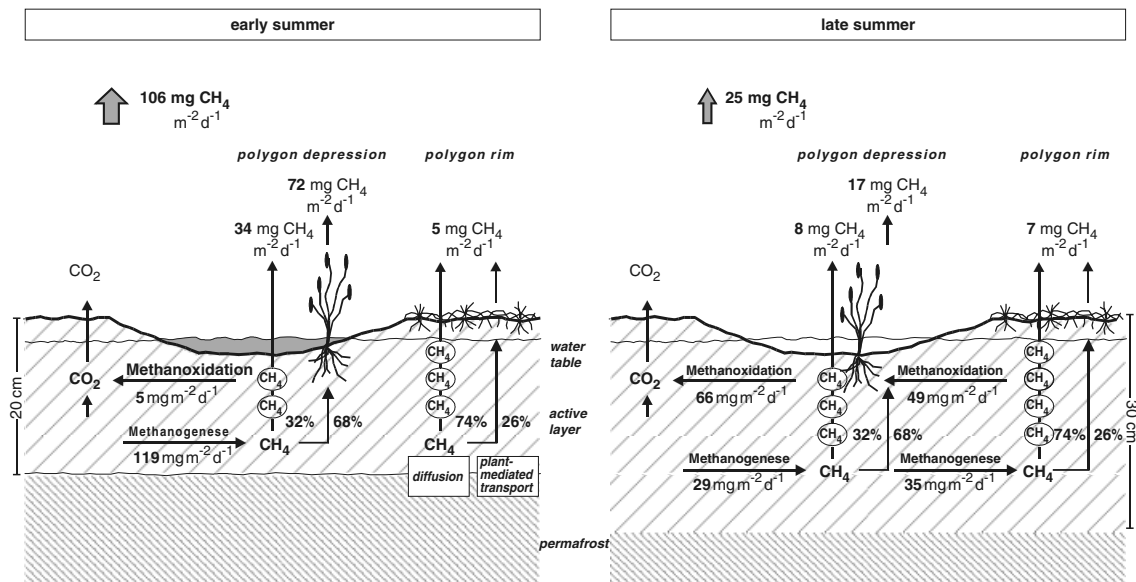


Figure 9 Illustration of the microbial processes associated with the methane cycle as well as the methane flux rates of a polygonal tundra on the basis of the spring and late summer conditions (explanations are given in the Discussion). The results of plant-mediated methane transport are included from L Kutzbach (personal communication, 2003).

conditions, a knowledge of the activity, physiology, and ecology of the bacteria community is fundamental for understanding trace gas fluxes in permafrost soils as compiled in Figure 9 for this case study. Such a sophisticated view of the small-scale microbiological processes in cold soils and the associated modes of methane release is needed also for other key locations in the Arctic. In outlook, this approach provides the basis for future environmental studies that deal with the fate of carbon stored in permafrost soils in the course of climate change.

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