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Methane turnover and temperature response of methane-oxidizing bacteria in permafrost-affected soils of northeast Siberia

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ABSTRACT

The abundance, activity, and temperature response of aerobic methane-oxidizing bacteria were studied in permafrost-affected tundra soils of northeast Siberia. The soils were characterized by both a high accumulation of organic matter at the surface and high methane concentrations in the water-saturated soils. The methane oxidation rates of up to 835 nmol CH_4 h^{-1} g^{-1} in the surface soils were similar to the highest values reported so far for natural wetland soils worldwide. The temperature response of methane oxidation was measured during short incubations and revealed maximum rates between 22 °C and 28 °C. The active methanotrophic community was characterized by its phospholipid fatty acid (PLFA) concentrations and with stable isotope probing (SIP). Concentrations of 16:1ω8 and 18:1ω8 PLFAs, specific to methanotrophic bacteria, correlated significantly with the potential methane oxidation rates. In all soils, distinct 16:1 PLFAs were dominant, indicating a predominance of type I methanotrophs. However, long-term incubation of soil samples at 0 °C and 22 °C demonstrated a shift in the composition of the active community with rising temperatures. At 0 °C, only the concentrations of 16:1 PLFAs increased and those of 18:1 PLFAs decreased, whereas the opposite was true at 22 °C. Similarly, SIP with $^{13}CH_4$ showed a temperature-dependent pattern. When the soils were incubated at 0 °C, most of the incorporated label (83%) was found in 16:1 PLFAs and only 2% in 18:1 PLFAs. In soils incubated at 22 °C, almost equal amounts of ^{13}C label were incorporated into 16:1 PLFAs and 18:1 PLFAs (33% and 36%, respectively). We concluded that the highly active methane-oxidizing community in cold permafrost-affected soils was dominated by type I methanotrophs under *in situ* conditions. However, rising temperatures, as predicted for the future, seem to increase the importance of type II methanotrophs, which may affect methane cycling in northern wetlands.

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1. Introduction

Wetlands are the major source of the climatically relevant trace gas methane, and their estimated contribution to global methane emissions is of 20–39% (Denman et al., 2007). Northern-latitude soils play a particular role in the global methane cycle because they contain one-third of the global organic carbon pool (Post et al., 1982). One-third of northern-latitude soils are underlain by permafrost (Zhang et al., 1999), and only a shallow surface layer (the active layer) thaws during the short summer period. Because water drainage is impeded by permafrost, water-saturated soils are widespread in northern lowlands. These soils are characterized by the accumulation of organic matter, anaerobic carbon turnover, and methane production. The effects of the observed and predicted climate changes will be stronger in the Arctic than the global average, and warming over the land in the Arctic north is expected to be twice as high as the global mean (Trenberth et al., 2007). As a result, increasing methane emissions from Arctic wetlands are expected (Wuebbles and Hayhoe, 2002). The most important sink for methane in wetland soils are aerobic methane-oxidizing bacteria, which use methane as their sole energy and carbon source. Depending on environmental conditions, methanotrophic bacteria may oxidize more than 90% of the methane produced before it reaches the atmosphere (Roslev and King, 1996; Popp et al., 2000). These microorganisms cluster taxonomically in the α-Proteobacteria (type II) and the γ-Proteobacteria (type I). Methane-oxidizing bacteria can be identified in environmental samples by their specific unsaturated phospholipid fatty acids (PLFAs) (Bowman et al., 1991; Börjesson et al., 2004). These PLFAs are 16:1ω8, which is synthesized almost exclusively by type I methanotrophs, and 18:1ω8, which is specific to type II methanotrophs. Besides their two signature fatty acids, type I and type II

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methanotrophs also exhibit an overall different PLFA pattern, with 16:1 PLFAs predominating in type I and 18:1 PLFAs in type II (Bowman, 2006), with only a few exceptions among the acido-, thermo-, and halophilic methanotrophs (Heyer et al., 2005; Tsubota et al., 2005; Dedysh et al., 2007). The strong seasonality in the Arctic means that temperatures in the active layer may fluctuate between about −30 °C in winter and +10 °C in summer (Boike et al., 2008). Our knowledge of how methanotrophs cope with these extreme temperatures is very limited. Which organisms are active at low *in situ* temperatures and how these communities will respond to the rising temperatures predicted for the future are unclear.

To improve our understanding of methane oxidation in cold permafrost-affected soils, we studied the abundance, activity, and temperature response of methane-oxidizing bacteria at two northeast Siberian tundra sites using activity measurements, PLFA distributions, and $\delta^{13}C$ signatures of PLFAs. The methane-oxidizing community active at low *in situ* temperatures and its response to rising temperatures was also characterized using stable isotope probing of bacterial PLFAs (PLFA–SIP) with $^{13}CH_4$. This method allows the differentiation of active microbial communities and their responses to changing environmental conditions (Boschker et al., 1998; Blumenberg et al., 2005; Shrestha et al., 2008). The results presented give new insights into the adaptation of methanotrophic communities to low temperatures in Siberian permafrost-affected soils and their responses to predicted warming.

2. Materials and methods

2.1. Investigation sites

Two study sites in the coastal lowlands of the Siberian Laptev Sea were investigated. The area belongs to the zone of continuous permafrost, and has a trans-Arctic, continental climate. The soils at both sites are completely frozen for more than 8 months of the year. Only during the short summer season does a shallow surface layer thaw to a depth of less than 50 cm. A mean annual air temperature of −14.7 °C and total summer precipitation of 72–208 mm (mean 137 mm) were recorded between 1999 and 2005 on Samoylov Island, the second sampling site. The soil temperature at a depth of 9 cm ranged between −34 °C and +10 °C (Boike et al., 2008). The main study site was situated in a hilly plain rising 25–55 m above sea level in the Lena-Anabar lowland, close to Cape Mamontovy Klyk (73.60°N, 117.13°E). The plain is of late Pleistocene origin but is dissected by thermoerosional valleys, formed in the Holocene, with water-saturated soils at the bottom. Three soils were sampled in a transect through a thermoerosional valley, one on the upslope (VU), the second on the downslope (VD), and the third at the bottom of the valley (VB). The landscape on the second site on Samoylov (72.22°N, 126.29°E), an island in the central part of the Lena River delta, is characterized by a microrelief of low-centred ice-wedge polygons (Fig. 1). Samples were collected from a soil profile in a polygon centre (PC). Further information on Samoylov Island has been given by Wagner et al. (2003).

2.2. Soil sampling and analysis

Soils at Mamontovy Klyk were sampled in August 2003, and at the PC on Samoylov in September 2003. For sampling, a pit was opened from the soil surface to the frozen permafrost table. Mixed samples were collected from the different soil horizons in sterile plastic bags. All collected samples were refrozen in the field in a letnik (cave in the frozen ground) and kept frozen until arrival in the laboratory. The refreezing of the samples was assumed to have only minor effects on the community composition and activity because the soil temperature drops below −30 °C every winter

Fig. 1. Aerial view of the low-centred ice-wedge polygonal tundra in the Lena river delta, the characteristic landscape of Samoylov island.

under natural conditions. To evaluate the impact of refreezing, we measured $^{13}CH_4$ incorporation into the microbial PLFAs in the same sample in the field and in the laboratory after the sample had been stored frozen during transport (see Supplementary material). Total carbon and nitrogen were measured with an elemental analyser (VarioMAX Elementar Analysensysteme GmbH, Hanau, Germany) after the soil samples had been sieved (<2 mm), milled, and dried at 105 °C. Soil pH was determined in a suspension of 10 g of fresh soil in 25 ml of 0.01 M $CaCl_2$ solution. Soil methane profiles were measured by transferring 40 g of fresh soil into a 130 ml glass bottle containing 70 ml of saturated NaCl solution. The bottle was immediately closed airtight and vigorously shaken. The methane concentration in the soil water was calculated from the methane concentration in the headspace, the headspace volume, and the water content of the sample. Methane was analysed using a gas chromatograph (GC-14B, Shimadzu Deutschland GmbH, Duisburg, Germany) equipped with a stainless steel Porapack-Q column and a flame ionization detector.

2.3. Potential methane oxidation rates

Potential methane oxidation rates (V_P) were measured in batch cultures. Fresh soil material (4 g) was placed in flat-walled culture bottles (50 ml) and distributed over the side wall as a thin layer. The bottles were sealed with rubber stoppers and incubated horizontally. The headspace contained 1% (v/v) methane in air. Triplicate samples were incubated in the dark at 5 °C (depth profiles of methane oxidation rates). Quadruplicate samples were incubated at 0 °C, 6 °C, 10 °C, 16 °C, 22 °C, 28 °C, 32 °C, 37 °C, and 42 °C to determine temperature profiles of methane oxidation in the surface samples from VB (0–14 cm) and PC (0–5 cm). Methane was measured repeatedly and the oxidation rates were calculated from the initial linear reduction in methane using multiple data points. Heat-sterilised samples were used as the control. After at least half the methane had been consumed, the experiment was stopped and the dry weights of the samples were determined. Methane concentrations in the heat-sterilised controls did not change during the incubation.

2.4. PLFA analysis

Bacterial lipids were extracted from triplicate freeze-dried peat samples (0.5 g) using a modified Bligh and Dyer extraction procedure (White et al., 1979), and fractionated into neutral, glyco-, and phospholipids by silica gel column chromatography (MEGA BE-SI, Varian Deutschland GmbH, Darmstadt, Germany). The separated phospholipids were transmethylated to fatty acid methyl esters

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