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Depth Distribution of Net Methanotrophic Activity at a Mountain Birch Forest–Tundra Heath Ecotone, Northern Sweden

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Abstract

Methanotrophy (the bacterial oxidation of CH_4) in soils is the major biological sink for atmospheric CH_4. Here we present results from a study designed to quantify the role of the physical diffusion barrier to CH_4, through surface soils, as a factor affecting methanotrophy. We used the mountain birch forest–tundra heath ecotone in subarctic northern Sweden as our study system. Our results show that, although CH_4 fluxes were generally low (around -20 μmol m^{-2} h^{-1}; a net flux from atmosphere to soil), the two adjacent communities responded in contrasting ways to *in situ* experimental reduction of the diffusion barrier (removal of the top 50 mm of soil): Uptake increased by 40% in forest soil in association with the removal, whereas it decreased marginally (by 10%) in tundra heath. Investigations of the depth-distribution of CH_4 oxidation *in vitro* revealed maximum rates at the top of the mineral soil for the forest site, whereas at the tundra heath this was more evenly spread throughout the organic horizon. The contrasting physicochemical properties and methanotroph activity in the organic horizons together explain the contrasting responses to the removal treatment. They also illustrate the potential role of vegetation for methane oxidation around this ecotone, exerted through its influence on the depth and properties of the organic horizons in these subarctic soils.

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Introduction

Methane (CH_4) is a potent greenhouse gas, contributing ca. 17% to climate warming (IPCC, 1990, 2001). Parts of the CH_4 budget are controlled by biological processes, for example CH_4 oxidation in aerobic soils (Mancinelli, 1995), and are estimated to amount to 5% of the global atmospheric CH_4 sink (Ehhalt et al., 2001). Soils in a wide range of ecosystems have been found to oxidize CH_4 (Mancinelli, 1995) including high altitude/latitude soils (Whalen and Reeburgh, 1990; Torn and Harte, 2006; Christensen et al., 1999). There are also indications that the CH_4 sink strength could increase in well-drained high latitude soils as a consequence of climate warming (Sjögersten and Wookey, 2002). However, the controls of high affinity CH_4 uptake in high latitude environments remain unclear. Despite the cold climate, neither temperature nor moisture seem to explain the fine scale spatial or temporal variation in uptake rates in mesic soils. This suggests more complex controls of CH_4 oxidation through, for example, the properties of the diffusion barrier, ammonium inhibition, and interaction with bacterivores (Mancinelli, 1995; Schlesinger, 1997; King, 1997). Indeed, one of the main constraints on CH_4 oxidization is the diffusion of CH_4 into microsites in the soil where the high affinity methanotroph population is active (Born et al., 1990; Dörr et al., 1993; Situala et al., 1995; Torn and Harte, 2006; Dong et al., 1998; Shrestha et al., 2004) and a thinning of the diffusion barrier could subsequently lead to increased CH_4 uptake (Dong et al., 1998; Saari et al., 1998) as long as other factors remain favorable. Furthermore, the depth distribution of methanotrophs is not well understood (King 1997), making it more difficult to identify the main controls on methanotrophic activity, and thus to predict the sink strength of CH_4 in high altitude/latitude soils.

In this study we chose the subarctic forest–tundra heath ecotone as a model system in order to evaluate the importance of the diffusion barrier for high affinity CH_4 oxidation rates. In these ecosystems the organic horizon differs markedly between adjacent forest and tundra heath vegetation types, with generally thicker and denser organic horizons beneath the tundra heath (Sjögersten et al., 2003). This contrast allows us to quantify the effect of the organic horizon on CH_4 oxidation in two different soil types in close proximity. The specific objectives of this study were (1) to assess whether the diffusion barrier limited CH_4 uptake rates, and (2) to determine the depth-distribution of methanotrophic activity in mesic forest and tundra heath soils. Although we cannot rule out the process of methanogenesis in these soil profiles (thus the net CH_4 flux could be the product of both methanotrophy in aerobic soil, and methanogenesis in anaerobic zones or microsites), previous observations in this area confirm that mesic/well-drained soils are predominantly net methane oxidizers (Christensen et al., 1999; Sjögersten and Wookey, 2002).

Methods

SITE DESCRIPTION

The two study sites were located at the mountain birch forest–tundra heath ecotone in the Abisko (Paddus) area at 560 m a.s.l., northern Sweden (68°21′N, 18°49′E); one site was within the mountain birch [*Betula pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti] forest and the other on subarctic tundra heath, approximately 50 m apart. The January and July mean temperatures at the nearby Abisko Research Station, 341 m a.s.l., are -11.9 and 11°C, respectively, and the annual precipitation is 304 mm. The study sites are mesic, and the soils are free-draining and classed as mature inceptisols/immature spodosols. The soil profile at the tundra site has a 10-mm-deep

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fibric (O_i) horizon underlain by a 122 mm hemic (O_e) horizon, and beneath that a ca. 63 mm albic (E) horizon overlying the parent material (till). The soils at the forest site are comprised of a 10 mm O_i horizon, underlain by a 38 mm O_e layer and a 90 mm albic horizon on top of the original till. The vegetation at the tundra site is dominated by *Empetrum hermaphroditum*; the few percent that make up the rest of the vegetation include *Vaccinium uliginosum*, *V. vitis-idaea*, *Betula nana*, graminoids, *Arctostaphylos alpinus*, *V. myrtillus*, *Salix glauca*, *Loiseleuria procumbens*, *Tofieldia pusilla*, *Bartsia alpina*, bryophytes, and lichens. The forest site has a sparse mountain birch canopy, the understory is comprised of 21% litter (mainly birch), 32% *Empetrum hermaphroditum*, 13% *V. myrtillus*, 4% *V. uliginosum*, and 5% *A. alpinus*. Also present at the site were *Juniperus communis*, *Betula nana*, *Linnaea borealis*, *Lycopodium annotinum*, bryophytes, and lichens.

METHANE SAMPLING AND EXPERIMENTAL DESIGN

In order to quantify the impact of the organic horizon as a diffusion barrier we established a soil removal experiment during July 2001. Twenty plots in each community, representative of the area with respect to soil and vegetation, were selected for the experiment. At each site 10 of the 20 plots were randomly allocated a treatment, but this was not applied until two baseline measurements (on 16 and 25 July) confirmed that there were no significant ($p > 0.3$) initial differences between plots. The treatment (applied on 25 July, after CH_4 sampling was completed) involved careful removal of the top 50 mm of the soil organic horizon. The soils were allowed to settle from the initial disturbance, and methane fluxes were then measured on three occasions within the following week. Methane fluxes were estimated by the closed-chamber technique, whereby an air-tight lid was placed on 100-mm-diameter collars that were inserted in the plots to form bases for the sampling (Sjögersten and Wookey 2002). Air samples (2 mL) were taken with syringes initially from the headspace air, and again after 1 h of incubation. These were analyzed the following day on a Perkin Elmer AutoSystem XL Gas Chromatograph. Soil moisture between 0–100 mm depth (ThetaMeter and probe: Delta-T Devices, Burwell, U.K.) and temperature at 100 mm (thermistor) were also measured adjacent to the collars as the CH_4 sampling was carried out.

To investigate further the depth distribution and activity of the methanotrophic community, both organic and mineral soil, as well as the transition between the two (i.e. the albic illuvial horizon in these profiles), were sampled for *in vitro* laboratory incubations. At each site, five representative plots were chosen for sampling, and from these soils were collected as 10 or 20 mm slices to ca. 250 mm depth, varying slightly depending on the nature of the horizon. The top of the organic horizon and the transition zone to the mineral soil were sampled as 10 mm slices of soil, and the rest of the profile as 20 mm slices at 20 mm intervals down the profile. The samples were passed through a 4 mm sieve in order to standardize and maximize the aeration, and hence the CH_4 oxidation of the different soil layers. For the incubations ca. 18 cm^3 of sieved soil were placed in clean glass serum bottles (41 cm^3), and the samples were allowed to settle at 10°C for ca. 12 h. Subsequently, the bottles were ventilated with laboratory air for 3 h, septum stoppers were added, and initial air samples (2 mL) were taken immediately, followed by another set after 1 h. The gas samples were then analyzed on the GC as described above. Soil moisture was determined gravimetrically after drying at 120°C.

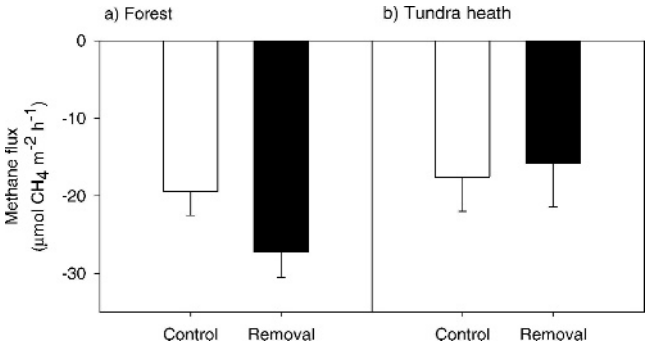

FIGURE 1. Methane fluxes in control plots and in plots where the top 50 mm of the organic horizon was removed, measured in (a) mountain birch forest and (b) tundra heath soils. Negative values indicate methane uptake by soils from the atmosphere. Mean values ± SE are shown.

DATA ANALYSIS

To identify systematic differences between the field sites and treatments, analyses were conducted on plot mean flux data following application of the soil removal treatment. Data were analyzed in SAS for Windows V. 8.2 using generalized linear mixed models (GLMM) with 'plot' as the random effect, vegetation type (site) and treatment (removal of organic material) as main effects, together with their interactions. Significant differences between means were thereafter tested with Tukey HSD (honest significant difference) *post hoc* analysis. The models were fitted by the method of residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite's approximation (Littell et al., 1996), and the residual variances were modeled as constant to the mean using PROC MIXED.

The results from the incubation experiment were analyzed in a similar way, but this time the data at each plot were grouped and averaged for the three main horizons, i.e. the organic, illuvial, and mineral, prior to the statistical analyses. A probability level of $P = 0.1$ was set as the upper limit for reporting P and F values from the statistical analyses of CH_4 flux.

Results

Both forest and tundra soils were weak net sinks of CH_4; −24.6 and −21.8 μg m^{-2} h^{-1}, respectively. The experimental removal of the organic horizon had contrasting effects on the CH_4 fluxes at the forest and tundra site (Fig. 1) as revealed by a site × treatment interaction ($F_{1,36} = 2.9$, $P = 0.096$) and subsequent *post hoc* analysis ($P = 0.06$). At the forest site the removal of the top organic layer was associated with a 40% increase in rates of CH_4 uptake, while at the tundra site CH_4 uptake was marginally (10%) lower. Average soil temperatures over the measurement period were 7.1 and 7.8°C at the tundra and forest sites, respectively. Soil moisture content was slightly higher ($F_{1,36} = 14.3$, $P < 0.001$) at the tundra site compared to the forest: 0.32 and 0.29 m^3 H_2O m^{-3}, respectively.

The laboratory incubation of the different profiles showed that the methanotrophic activity differed significantly between the horizons at the two different sites (Fig. 2). At the tundra heath site the highest CH_4 uptake was found in the organic horizon, while at the forest site, the illuvial transition zone between the organic and mineral horizon had the highest CH_4 oxidation rates. Soil moisture content varied significantly ($F_{2,16} = 223.6$, $P < 0.001$) between the organic and the mineral soil horizons, ca. 200 and

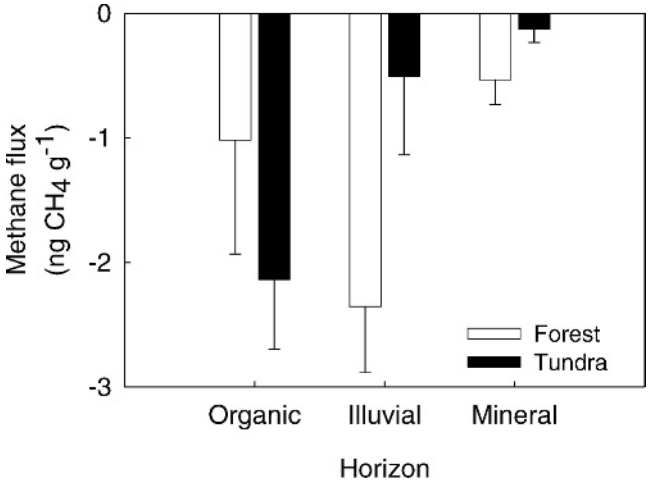

FIGURE 2. Depth distribution of methane uptake rates in soils from tundra heath and mountain birch forest. The illuvial layer is here a thin profile characterized by organic material transported into the mineral soil. Negative values indicate methane uptake. Mean values ± SE are shown.

50%, respectively, but did not differ between forest and tundra soils.

Discussion

The data presented here suggest that the upper 50 mm of predominantly organic soils in these profiles do, indeed, present a barrier to the diffusion of atmospheric CH_4 to sites where significant net methane oxidation by high-affinity methanotrophic bacteria occurs. This interpretation is consistent even with the contrasting response of CH_4 uptake in forest and tundra heath soil to the removal treatment.

Several studies of CH_4 fluxes in forests have reported maximum CH_4 oxidation at the top of the mineral horizons, while the organic horizons have not been considered sites of high activity (Crill, 1991; Torn and Harte, 1996; Koschorreck and Conrad, 1993; Schnell and King, 1994). By contrast, organic tundra soils studied by Whalen and Reeburgh (1990) supported an active methanotroph population. In our study, removal of the upper soil layer increased CH_4 oxidation at the forest site, while this was not noted at the tundra heath site. The 40% increase in CH_4 uptake in the forest compares with results from a similar removal of the organic horizon in a boreal forest system where CH_4 uptake rates increased by 50% (Saari et al., 1998). This suggests that CH_4 oxidation rates are more limited by diffusion at the forest site (where the maximum CH_4 oxidation occurs at the interface between the organic horizon and the mineral soil) than they are at the tundra heath. The contrasting nature of the soil profiles at the two sites, however, must be taken into account when interpreting the results. The removal of 50 mm of organic soil from the forest profiles effectively exposed the mineral albic horizons, where the *in vitro* measurements suggested that net methanotrophy was most active. If this treatment did not result in the development of any more adverse physical conditions for methanotrophs, then it seems a reasonable interpretation that *in situ* rates of net CH_4 oxidation would increase. Had this not occurred we might be led to conclude that removal of the organic horizons may have impaired methanotroph activity via mechanisms, which could include (1) increased desiccation stress, and/or (2) increased temperature variability near the surface of the exposed albic horizon. These factors might, indeed, be important, but the data do not suggest that they outweighed increased methanotrophy. Furthermore, there was also net CH_4 oxidation in the organic horizons of the forest soil (Fig. 2), and if the role of these horizons as a diffusion barrier for CH_4 transport was weak, or insignificant, we might expect the soil removal treatment actually to have *reduced* net CH_4 oxidation.

In the tundra heath soils, by contrast, our treatment removed around 38% of the organic horizon, but this did not translate into any significant reduction in the rate of CH_4 uptake, even though the strongest net methanotrophy noted *in vitro* was in the organic horizons (Fig. 2). This result suggests that methanotrophy in the lower parts of the organic (O_e) horizons might well have been constrained by poor CH_4 diffusion through intact profiles, and therefore been accelerated *in situ* with 50 mm of the upper soil removed. It is also important to note that although the CH_4 flux is substantially lower per unit mass in the tundra illuvial horizons (Fig. 2), the bulk density of these horizons is much higher (0.99 compared with 0.15 g cm^{-3}), thus making their contribution to surface CH_4 fluxes proportionally higher (especially when constraints on CH_4 diffusion were reduced).

The higher methanotrophic activity in the organic layer in the tundra heath soils compared with the forest might be linked to ammonium inhibition in the forest soils: The latter have higher ammonium mineralization rates than tundra soils (Schnell and King, 1994; Saari et al., 2004; Sjögersten and Wookey, 2005), and in a nearby tundra heath CH_4 oxidation was also strongly reduced in response to ammonium additions (Christensen et al., 1999), suggesting that this is a likely mechanism by which the nutrient cycling is tightly linked to CH_4 oxidation rates even in these strongly nitrogen-limited ecosystems (Press et al., 1998; Hobbie et al., 2002).

Although mountain birch forest and adjacent tundra heath soils differ in the depth distribution of net CH_4 oxidation, and in their response to removal of the upper soil, our results nonetheless provide evidence of a physical diffusion barrier to the movement of CH_4 from the atmosphere to sites of active methanotrophy. In order to improve the mechanistic understanding of the abiotic and biotic controls on CH_4 fluxes between soils and the atmosphere, it will be important to understand the depth distribution of the processes of CH_4 oxidation and production (in methanogenic systems). The implications for net CH_4 fluxes of environmental changes which result in alterations in the physicochemical properties (or extent) of contrasting soil horizons, and the biological processes occurring there, can also be more accurately predicted.

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