



Treeline soil warming does not affect soil methane fluxes and the spatial micro-distribution of methanotrophic bacteria



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ABSTRACT

The impact of a warmer climate on CH₄ fluxes from soils is highly uncertain, because soil warming may affect methanotrophic bacteria in two opposed ways: CH₄ assimilation in soils might be increased by the decreasing soil moisture often associated with soil warming. In contrast, CH₄ oxidation might be suppressed by higher NH₄⁺ concentrations in warmed soils resulting from an accelerated nitrogen mineralization. We investigated effects of soil warming on soil-atmosphere CH₄ fluxes in the last two years of a six-year long field experiment at a Swiss alpine treeline. Specifically, we measured CH₄ fluxes using static chambers, and characterized N cycling by quantifying soil N₂O emissions and NH₄⁺ and NO₃⁻ concentrations. We further labeled intact soil cores with ¹⁴CH₄ and traced the labeled bacteria using an auto-radiographic technique to study the potential warming-related changes in the micro-distribution of methanotrophic bacteria within the soils. Our results did not show a significant effect of soil warming on net CH₄ fluxes after five and six years of soil warming. In general, soils were a net sink for CH₄ but CH₄ emissions were observed occasionally. One reason for the unaltered CH₄ fluxes might be the negligible warming effects on soil water contents in the treeline environment with frequent rainfalls. In the warmed soils, soil moisture was lower in the litter layer, but not deeper in the soils. Therefore, soil warming did not affect gas transport rates into deeper soil layers where methanotrophic bacteria were located. Another reason might be the general absence of substantial warming effects on mineral N, with NH₄⁺ concentrations being marginally significantly higher in warmed soils only in ion exchange resin bags (*P* < 0.1) but not in soil extracts. Auto-radiographic image analysis of soil cores revealed an overall heterogeneous ¹⁴C distribution and a warming-induced shift of methanotrophic bacteria toward the soil surface. The absence of responses of CH₄ fluxes to warming in this alpine treeline ecosystem is likely related to the rather minimal changes in the putative drivers soil moisture and NH₄⁺ concentration.

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1. Introduction

Net land-atmosphere fluxes of methane (CH₄) are determined by the balance of CH₄ sources and sinks, which are both almost exclusively driven by soil microbial processes (Conrad, 2007; Shukla et al., 2013; but see Wang et al., 2013 for abiotic CH₄ sources). Methanogenic archaea produce CH₄ under conditions that are generally anaerobic (Mer and Roger, 2001; Conrad, 2007), although emissions are to a lesser degree also observed from some upland soils (Angel et al., 2012). On the other hand, soil CH₄ sinks are

driven by assimilation of CH₄ by methanotrophic bacteria, yielding organic carbon (C) that eventually is respired by methanotrophs, yielding CO₂, or that enters the soil C cycle as their biomass turns over (Hanson and Hanson, 1996; Semrau et al., 2010).

Methanogens and methanotrophs often co-occur in the same soils. CH₄ produced by methanogens in anoxic soil domains will diffuse through more oxic soil areas where part of it can be oxidized by methanotrophs before it reaches the atmosphere. Under these conditions, methanotrophs thrive on soil-internal CH₄ sources, functionally acting as a “biofilter” that reduces net CH₄ emissions to the atmosphere (Horz et al., 2001; Kammann et al., 2001; Urmann et al., 2009). However, some groups of methanotrophs can also assimilate atmospheric CH₄, turning soils into a net CH₄ sink. In many soils, methanotrophs in fact oxidize CH₄ both from internal sources and from the atmosphere, with one or the other process

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dominating depending on environmental conditions. The nature of the methanotrophic organisms consuming CH₄ at atmospheric and lower concentrations remains elusive since all isolation attempts have been unsuccessful to date. There is evidence from genetic markers that these organisms are distinct from the methanotrophic populations dominating CH₄ consumption in high-methane environments (Dunfield et al., 1999; Henckel et al., 2000; McDonald et al., 2008). On the other hand, some isolated methanotrophic strains are capable of oxidizing CH₄ over a wide range of concentrations (Knief and Dunfield, 2005), challenging this view (Dunfield, 2007). CH₄ fluxes are of interest because this greenhouse gas substantially contributes to anthropogenic radiative forcing and climate change (currently ≈30%; IPCC, 2013). A related important question is whether and how CH₄ dynamics in terrestrial ecosystems are altered under climate change, in particular warming. These effects are complicated to predict, on the one hand because CH₄ fluxes are controlled by a multitude of proximal (e.g. C supply and redox potential) and more distal factors (e.g. soil structure, climate), with only some of them affected by climate change. On the other hand, the net effect on fluxes manifest at the ecosystem level is the result of different responses of CH₄ fluxes.

Many previous studies have shown that methanogenesis increases with temperature (e.g. Moore and Dalva, 1993; Wang et al., 1999; Mer and Roger, 2001). This effect is driven by an accelerated metabolism of soil methanogens at higher temperatures. Also, the increase in general soil heterotrophic activity at higher temperatures increases the size of anaerobic domains with a redox potential sufficiently low for methanogenesis. However, experimental warming in field studies often not only leads to warmer but also drier soils (White et al., 2008; Luo et al., 2013). While one could consider this an undesired side effect of the experimental treatment, climate models in fact predict that warming will be accompanied by lower soil moisture in many regions, at least for part of the year (Luo et al., 2013). This potential drying effect could counteract positive warming effects on methanogenesis.

Direct temperature effects on CH₄ oxidation are comparably small (Hanson and Hanson, 1996; Price et al., 2004). However, soil CH₄ oxidation can be affected indirectly by warming via changes in plant and soil processes (Blankinship et al., 2011). CH₄ assimilation is generally substrate-limited, especially when CH₄ concentrations are low. In upland soils, soil CH₄ uptake rates therefore are often controlled by a diffusive supply from the atmosphere to the microsites where methanotrophic bacteria exist. Across sites, soil diffusivity is related to soil porosity. However, on a diurnal to seasonal basis, diffusivity is related to variation in soil moisture, which controls CH₄ transport rate by filling of pore networks (Dunfield et al., 1995; Billings et al., 2000; Luo et al., 2013). Drier soils under warming should therefore show higher soil CH₄ uptake, unless moisture is so low that methanotrophic activity is restricted due to physiological stress (e.g. Price et al., 2004).

A second important factor controlling soil CH₄ uptake is nitrogen (N) status, in particular ammonium (NH₄⁺) concentrations (e.g. Dunfield et al., 1995; Hartmann et al., 2010; Shukla et al., 2013). In laboratory settings, CH₄ oxidation is inhibited by NH₄⁺ (Dunfield and Knowles, 1995; Hanson and Hanson, 1996; Duan et al., 2013), most likely through an enzymatic effect (inhibition of methane mono-oxygenase by NH₃). In line with this finding, the soil CH₄ sink is often reduced under NH₄⁺ fertilizer application (Hütsch, 1996; Stiehl-Braun et al., 2011a). However, more complex ecological mechanisms are often at play in natural ecosystems, and soil CH₄ uptake is also sometimes correlated positively with N supply (Bodelier and Laanbroek, 2004). In grassland, Stiehl-Braun et al. (2011b) found that NH₄⁺ application inhibited CH₄ oxidation in some soil layers, but this effect did not translate into a smaller soil CH₄ sink because the reduced methanotrophic activity was

compensated by an increased sink activity in deeper soil layers. N-related effects on CH₄ oxidation are relevant in a climate change context because warming can accelerate organic matter mineralization and NH₄⁺ production (Rustad et al., 2001; Curtin et al., 2012; Bai et al., 2013). While this phenomenon may be transient (Butler et al., 2012), it nevertheless has the potential to reduce soil CH₄ uptake during this period. However, whether such an effect occurs also depends on whether NH₄⁺ can accumulate in the soil, or whether it is continuously removed by nitrification, plant uptake, or microbial immobilization. For example, Hartmann et al. (2010) reported increased NH₄⁺ concentrations after fertilization only under concomitant drought. Warming also may not affect mineralization if microbial activity drops because of reduced soil moisture (Carrillo et al., 2012).

Here, we present a study of simulated warming effects on soil CH₄ uptake in an afforestation located near the alpine treeline. We hypothesized that soil CH₄ uptake would increase due to reduced soil moisture, since these conditions would facilitate CH₄ diffusion into soils and thus CH₄ oxidation. We additionally expected that drier soils would decrease rates of methanogenesis if this process was important for the CH₄ balance in the soil. Alternatively, if higher soil temperatures were more influential on CH₄ fluxes than drying, we expected to find reduced soil CH₄ oxidation due to increased organic matter mineralization and consequently soil NH₄⁺ concentrations. We thus measured soil-atmosphere CH₄ fluxes, soil moisture and soil mineral N concentrations during the final two summers of a six year warming experiment. To disentangle mechanisms that involve changes in the spatial distribution of methanotrophic activity, we additionally labeled intact soil cores with ¹⁴CH₄ and studied the spatial distribution of the label using an auto-radiographic technique (Stiehl-Braun et al., 2011b).

2. Materials and methods

2.1. Study site and experimental design

We investigated soil warming effects on CH₄ transformations in a long-term experiment near the alpine treeline at Stillberg (2180 m a.s.l.) in the Central Alps near Davos, Switzerland. The warming experiment studied here was set up as an extra factorial treatment added in the course of a long-term elevated CO₂ study (Hagedorn et al., 2010).

In 2001, the original elevated CO₂ experiment was set up encompassing 20 plots with *Larix decidua* (European larch) and 20 plots with *Pinus mugo* ssp. *uncinata* (mountain pine). Each hexagonal 1.1 m² plot had a single tree in the center. Trees were surrounded by a dense cover of understory vegetation (for details, see Dawes et al., 2011).

These trees were part of an afforestation planted in 1975 on a steep north-east facing slope with 25–30° inclination). Plots were organized in five blocks, with each block consisting of two groups of four plots (two with *L. decidua* and two with *P. uncinata*). One group of plots per block was exposed to atmospheric concentrations of 550 μmol CO₂ mol⁻¹, while the other group was exposed to ambient CO₂. Details of the experimental set up with CO₂ enrichment were reported in Hättenschwiler et al. (2002). The CO₂ treatment was discontinued at the end of 2009 after 9 years of enrichment.

Starting in 2006, a soil warming treatment was established, using the same plots. The plots in which soils were warmed were chosen so that the former CO₂ exposure and the new warming treatment were orthogonal (Hagedorn et al., 2010). Warming was implemented with heating cables laid out on the ground surface of the plots in spirals with a 5 cm distance between cable loops. The soil warming treatment increased the soil temperature at 5 cm depth by 3–4 K. Each year, experimental warming began after snow

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