Wetting stimulates atmospheric CH₄ oxidation by alpine soil

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Abstract

Studies were done to assess the effects of soil moisture manipulations on CH₄ oxidation in soils from a dry alpine tundra site. When water was added to these soils there was a stimulation of CH₄ oxidation. This stimulation of CH₄ oxidation took time to develop. One to three days after water additions no stimulation was observed. Nine days after rewetting, CH₄ oxidation was greatly stimulated. This time delay suggests that methanotrophs grew in response to water additions, or that they take a long time to recover from metabolically inactive resting stages. © 1998 Federation of European Microbiological Societies. Published by Elsevier Science B.V.

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1. Introduction

Soil CH₄ oxidation consumes up to 45 Tg of the greenhouse gas CH₄ every year [1,2]. Although this quantity is small when compared with the total global CH₄ budget, the soil CH₄ sink is approximately equal to the annual excess of total CH₄ production over oxidation [2]. Therefore, any decrease in the global soil CH₄ sink would be expected to cause a proportional increase in the rate at which CH₄ is increasing in the atmosphere [3]. The importance of this sink necessitates understanding its biological mechanisms and how these mechanisms might change under various global change scenarios [4]. Yet, the ecology of the soil microorganisms which consume atmospheric CH₄ is poorly understood [5].

Soil moisture is the primary control on soil CH₄ oxidation [6], either by affecting gas diffusion [7] or because low soil moisture can cause osmotic stress on soil methanotrophs [8]. In wetter soils, CH₄ oxidation decreases with increasing soil moisture (e.g., [9–12]), but at lower soil moistures CH₄ oxidation is not highly correlated with soil moisture [13–15]. In fact, a few studies have shown that CH₄ oxidation can be stimulated by water additions and that maximum oxidation of CH₄ occurs at intermediate soil moistures [16–18]. In very dry soils such as in deserts, CH₄ oxidation is higher after precipitation [19]. In such soils osmotic stress may limit activity of CH₄-oxidizing bacteria more than diffusion of gases through the soil [8].

We have been studying CH₄ oxidation at high-elevation tundra sites on Niwot Ridge in the Colorado Rocky Mountains. There is little precipitation on Niwot Ridge in the summer, and soil moisture is provided largely by run-off from melting snow. However, in the meadows dominated by *Kobresia*
myosuroides, high winds prevent much snow accumulation. This makes Kobresia community soils very dry in the summer. July and August soil moisture contents average just above wilting point (−1.5 MPa or approximately 35% H2O). In these drier Kobresia sites, CH4 consumption is stimulated by rainfall and by artificial wetting (unpublished data). The present study was done to examine the effects of wetting and drying events on CH4 oxidation in these soils.

2. Materials and methods

2.1. Sites and soils

This study was conducted using soils from the Kobresia myosuroides-dominated plant communities of Niwot Ridge in the Colorado Front Range. Niwot Ridge is a UNESCO Biosphere Reserve and a National Science Foundation-sponsored Long-Term Ecological Research (LTER) Site, located near the University of Colorado Mountain Research Station. Soils at these sites have 20–30% soil organic matter (SOM) by weight and are described in more detail by Fisk and Schmidt [20].

Intact chunks (30 × 30 cm by 20 cm depth) of soil were collected during the period of plant senescence before development of substantial snowpack (in late February, 1996). At this time soil moisture was approximately 40–60 g H2O (100 g dry weight)−1. Before use, soil chunks were stored in an environmental chamber which simulated spring conditions (14 h of daylight, warming gradually during the daylight period from 8 to 15°C) until plants greened. Soils were wetted periodically to prevent excessive drying. Soils were then sieved (2 mm) and gravimetric moisture was determined on 6 subsamples by drying to a constant weight at 100°C. Replicate samples of 25 or 30 g dry weight equivalent of soil were placed in 170-ml specimen cups (diameter of 5–6 cm) within 1-l mason jars fitted with Teflon-coated silicone septa. Each time soil CH4 oxidation was measured, soil moisture was determined by weighing the cups of soil.

Before incubations to measure CH4 oxidizing activity, mason jars were opened and allowed to equilibrate with atmospheric CH4 concentrations (usually between 1.8 and 2.0 ppm). During the incubations, gas samples were taken at regular intervals with 10-cc syringes, for a total of 4–8 gas samples. Incubations lasted 5–30 h. Syringes were disassembled to equilibrate with atmospheric air for a minimum of 14 h before each new use. Gas samples were analyzed on a Hewlett Packard 5890A gas chromatograph using a flame ionization detector (FID) at 150°C. Variability of repeated injections of a 1751.8 ppb CH4 standard calibrated by the National Center for Atmospheric Research (NCAR) was ±10 ppb. Methane oxidation rates were calculated by linear regression of the changes in CH4 concentrations over time. Detection limit was 2 pmol (g dry weight soil)−1 h−1. Consecutive measurements of the same soil under similar moisture regimes and with similar sampling intervals usually varied by less than 4 pmol (g dry weight)−1 h−1, and never varied by more than 11 pmol (g dry weight)−1 h−1.

2.2. Experimental manipulations of soil moisture

CH4 oxidation rates were measured periodically during various manipulations of soil moisture. Soil moistures are reported as gravimetric moisture contents (% H2O). In the sieved soils used in these experiments, 100% water-filled porespace (WFPS) was measured by determining the moisture content of saturated soils and found to be 146 ± 17% (standard deviation) gravimetric H2O.

In order to differentiate between the effects of soil moisture and wetting, soils (three replicates for each treatment) originally at a moisture of 57% H2O were dried or wetted to obtain soil moistures of 12, 25, 37, 70, 84, and 97% H2O. Soils were dried over the course of 2–4 h by spreading them out in weighing boats at room temperature and mixing occasionally. Using this method, soils lost up to 8% gravimetric H2O per hour. Soils were wetted by adding water in small drops and mixing thoroughly. Loss of soil during wetting was minimal (less than 0.3%).

The effects of the above moisture manipulations on soil CH4 oxidation were observed for 11 days. Soil replicates were then wetted or dried to obtain soil moistures equal to that of the control soils, which were not deliberately manipulated, but had dried from 55 to 45% H2O during the 11 days. Soil structure was not obviously affected by changes in soil moisture content from 20 to 80% H2O. Aggre-
gates of soils wetted up to 95% H2O were larger. When these soils were dried to 45% H2O, these larger aggregates were broken into smaller ones such that the soil structure was not visibly different from the other replicates.

3. Results

Soils originally at 57% H2O were wetted or dried to a wide range of soil moistures (Fig. 1). Soil moisture affected CH4 oxidation differently depending on whether soils were wetted or dried.

When soils were dried below 35% H2O (approximately −1.5 MPa) (Fig. 1A), CH4 oxidation decreased within 12 h. This is consistent with the physiological response to water stress expected at such low water potentials [8]. Methane oxidation in soils dried to only 38% H2O (approximately −1 MPa) did not change significantly. Also, CH4 oxidation rates in control soils did not change significantly as they dried from 57% to 50% H2O over the course of 9 days (data not shown). Soils dried below 15% H2O did not oxidize any CH4 but emitted up to 11 pmol CH4 (g dry weight)−1 h−1.

In contrast to the effect of drying, CH4 oxidation was not significantly related to soil moisture immediately upon wetting (Fig. 1B, circles). Even 4 days after wetting (Fig. 1B, triangles), CH4 consumption in the wetted soils was not significantly higher with higher moisture. However, 9 days after wetting (Fig. 1B, diamonds) CH4 oxidation increased significantly to −29.5 (± 1.8), −48.2 (± 5.7), and −67.0 (± 1.6) pmol (g dry weight)−1 h−1 (for soil initially wetted to 70, 84, and 97% H2O, respectively). The largest increases in CH4 oxidation were observed in soils which received the most moisture. After this stimulation, soil CH4 oxidation rates decreased as soils dried for 2 more days (Fig. 1B, boxes). However, CH4 oxidation rates in soils stimulated by wetting remained significantly higher than CH4 oxidation in unstimulated soils that had been at the same soil moisture (Fig. 1B).

The above effects of drying and wetting could have been caused by either direct effects of soil moisture on cellular activity or by changes in the methanotrophic population. To distinguish between these, residual effects of the drying and wetting treatments on CH4 oxidation were measured after soils were dried or wetted back to approximately the same gravimetric H2O as the control soils. Control soils by this time had dried to 45% H2O as the control soils. Control soils by this time had dried to 45% H2O and their CH4 oxidation rates had declined to −11.2 (± 0.7) pmol (g dry weight)−1 h−1 (Fig. 2). The more soils had been wetted in the previous experiment the more they consumed CH4 (r² = 0.69, P < 0.01), but CH4 consum-
tion by soils which had been dried from 57% $H_2O$ were not significantly related to previous soil moisture.

4. Discussion

Wetting influences the microenvironment of soil methanotrophs in various ways. Two effects are well documented. (1) Wetting can slow the rate of diffusion of $CH_4$ and $O_2$ through soil, thus reducing $CH_4$ consumption [7]. (2) Wetting can decrease physiological water stress on soil microorganisms, and therefore may increase $CH_4$ consumption by increasing cellular activity [8].

The first possible effect of wetting on $CH_4$ oxidation was not observed in these alpine soils at the moistures tested. With diffusion limitation, wetting should decrease $CH_4$ oxidation, but we found the opposite. Methane consumption increased with increasing soil moisture (Fig. 1). Our data contrast with previous investigations where gas diffusion is the primary factor controlling $CH_4$ oxidation (e.g., [9–12]), probably because of the low soil moistures we investigated, and because our soils were sieved. Gas diffusion constraints become less important below 65% WFPS [13–15]. In all the experiments reported here, soil moistures never exceeded 100% gravimetric $H_2O$, which in these soils is roughly equivalent to 65% WFPS. The effects of wetting which we observed must be explained by mechanisms other than gas diffusion.

The second possible effect of wetting, a simple reduction in physiological stress, is also inconsistent with our data. Marked stimulation of $CH_4$ oxidation did not occur until more than 4 days after wetting (Fig. 1B). If relief of water stress simply increased activity of vegetative cells, $CH_4$ oxidation would be expected to increase within hours [21], but the delay of stimulation suggests a slower process, such as growth of the methanotrophic population. Alternatively, reactivation of sporulated or encysted methanotrophs may have been responsible. Whether because of growth or reactivation of inactive methanotrophs, $CH_4$ oxidation in wetted soils remained stimulated even after soils were dried back to control soil moistures (Fig. 2).

The mechanism by which wetting could stimulate methanotrophic growth or recovery from resting stages is as yet unclear. Wetting might simply relieve osmotic stress and allow soil methanotrophs to grow on the $CH_4$ available from the atmosphere, but wetting stimulated $CH_4$ oxidation even when original soil water potentials were greater than $-0.05$ MPa (Fig. 1B). This is well above the range at which osmotic stress has been shown to inhibit soil $CH_4$-oxidizing bacteria [8]. It is also above the range of water potentials at which $CH_4$ oxidation in these soils was inhibited by drying (Fig. 1A).

Alternatively, wetting may induce growth of methanotrophs or recovery from resting stages by increasing carbon supply [22]. Wetting increases the availability of water-soluble carbon substrates [23–26]. If soil methanotrophs could use this carbon, wetting would increase substrate for their growth or recovery from resting forms. Alternatively, these water-soluble carbon substrates might reduce $O_2$ concentrations and support soil methanogens which then supply $CH_4$ to methanotrophs.

This study demonstrates that changes in soil moisture have a profound effect on methane oxidation in soils from seasonally dry alpine meadows. Most im-

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Fig. 2. After the 11-day experiment shown in Fig. 1, soils were dried or wetted to the same soil moisture as the control soils (open circles). Soils initially wetted to higher soil moisture (closed diamonds) tended to have higher $CH_4$ oxidation rates when they were dried to the same moisture as control soils (regression line, $r^2 = 0.69$, $P < 0.01$). Soils which were wetted above 96% $H_2O$ were significantly higher than controls ($r^2 = 0.91$, $P < 0.005$). Methane oxidation rates of soils initially dried (crossed boxes) did not correspond with previous soil moisture.
portantly, there is a time delay in the effects of moisture additions on \( \text{CH}_4 \) oxidation. Such a long delay has not previously been reported. This time delay is best explained by growth or reactivation of methanotrophs after moderate water additions.

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