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Methane consumption by montane soils: implications for positive and negative feedback with climatic change

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Abstract. We report here three years of field observations of methane uptake, averaging 1.2 mg CH_4 m^{-2} d^{-1} in montane meadow soils. Surface soil moisture influenced diffusion of substrate while in deeper soil, where methane oxidation was maximum, moisture influenced both diffusion and microbial activity. Microbial oxidation of methane was maximum at an intermediate level of soil moisture, at this site at about 25% moisture by weight (50% water holding capacity). Laboratory incubations also showed inhibition below 20% moisture. These results provide *in situ* characterization of moisture limitation of methanotroph activity and evidence that soil drying may diminish the methane sink strength. The microbial limitation to methane consumption at low soil moisture provides a mechanism for positive feedback between methane flux and climate warming, as suggested by ice core data (Blunier et al. 1993; Chappellaz et al. 1990; Stauffer et al. 1985).

Introduction

Methane oxidation in soils and sediments is the single largest sink of methane, consuming significantly more methane than does the atmospheric OH sink ($\sim$ 600 Tg yr^{-1} in soil vs $\sim$ 450 Tg yr^{-1} by the atmospheric OH reaction; Reeburgh et al. 1993). Soil methane oxidation is an important modulator of terrestrial emissions, oxidizing almost half of all soil-produced methane. The net soil uptake of atmospheric methane is also significant; the sink strength, 30–60 Tg yr^{-1}, is roughly equal to the magnitude of the current imbalance between methane sources and sinks that gives rise to the current $\sim$ 1% per year increase in atmospheric methane concentration (Born et al. 1990; Dorr et al. 1993; Fung et al. 1991; Houghton et al. 1990). Therefore, changes in soil methane oxidation rates could significantly affect the global methane budget. The research reported here contributes to our understanding of microbial controls on soil methane oxidation, using field observations from aerobic soils.

Ice core data suggest positive feedback between net methane flux to the atmosphere and climatic change (Blunier et al. 1993; Chappellaz et al. 1990; Stauffer et al. 1985). Mechanisms for positive feedback to climate warming have been identified for methane emissions, which tend to increase with increasing temperature if moisture levels remain sufficient to maintain anaerobiosis (Bartlett et al. 1989; Bartlett et al. 1988; Bartlett & Harriss 1993; Dunfield et al. 1993; King & Adamsen 1992; Valentine et al. 1994; Westerman 1993).

In contrast, climatic controls over soil-methane oxidation are less well-understood. Negative feedback to global warming has been predicted because soil drying would increase diffusion rates (Jury et al. 1991; Torn & Chapin 1993; Whalen & Reeburgh 1990a). Most researchers find that uptake shows little response to temperature (Dorr et al. 1993; Keller et al. 1983; King & Adamsen 1992; Schimel et al. 1993; Steudler et al. 1989; Striegl et al. 1992; Tate & Striegl 1993; Torn 1994; Valentine et al. 1994) due to the small effect of temperature on substrate diffusion (Dorr et al. 1993; King & Adamsen 1992; Striegl et al. 1992) and a positive response to decreasing soil moisture (Bartlett et al. 1988; Delmas et al. 1992; Harriss et al. 1982; Moore & Roulet 1993; Roulet et al. 1992; Tathy et al. 1992), attributed to increases in gas diffusion rates. Soil methane consumption is widely thought to be limited by diffusion of the substrates, methane and oxygen (Bartlett and Harriss 1993; Dorr et al. 1993; King & Adamsen 1992; Striegl 1993).

Possible evidence for the role of soil moisture in positive feedback with methane consumption comes from observations of increased methane uptake by desert and short-grass prairie soils after rainfall (Mosier et al. 1991; Striegl et al. 1992), but in contrast with this study, soil moisture values were not reported and no controls for other environmental changes were invoked.

Methods

Our research site is a montane meadow on the western slope of the Rocky Mountains, Gunnison County, Colorado, USA. Each experimental plot (n = 10) extends from a dry ridge with sagebrush down to a moist meadow swale, labeled the dry zone and moist zone, respectively (Table 1). The soil, formed of glacial till, is rocky and high in organic matter without strongly differentiated horizons. For the entire snowfree season, zonal-averaged soil temperatures and moistures were 13.6 °C and 26% in 1991; 12.6 °C and 32% in 1992; and 13.6 °C and 23% in 1993.

Our research site includes sagebrush steppe habitat, a widespread ecosystem in which methane uptake has not been measured. Because global warming is predicted to dry soils in the interiors of continents (Schneider et

Table 1. **Site Characteristics.** Soil microclimate data in table are averages of two-hourly readings over depth (5, 12, 25 cm) and year (1991–93) from the end of snowmelt to late August

Site Description		
Elevation	2920 m	
Average annual precipitation	750 mm, 80% as snow	
Average summer air temperature	10 °C	
Typical snow-free season	May 20–November 1	
Climate during methane flux measurements:		
Range of soil temperature	7–31 °C	
Range of soil moisture	6–56 %	
Soil type	Cryoboroll (rocky glacial till)	
Soil pH	~ 6.3	
	Dry Zone	**Moist Zone**
Average summer soil temperature	14.0 °C	5 °C
Average summer soil moisture	22%	33%
Average heating effect during methane flux measurements:		
Soil temperature	+0.8 °C	−0.3 °C
Soil moisture (g H_2O/100 g soil)	−2.3	−0.2
Organic matter to 75-cm depth	12%	11%
Dominant vegetation	Sagebrush Steppe: *Artemisia tridentata, Mertensia fusiformis, Vicia americana, Lathyrus leucanthus, Festuca thurberi*	Montane Meadow: *Pentaphylloides floribunda, Claytonia lanceolata, Erythrocoma integrifolia, Melica spectabilis*

al. 1992), this type of habitat could be the location of significant feedback control on atmospheric methane levels. The soil moisture of this habitat is moister than at desert sites of methane flux measurements (Striegl et al. 1992) but our soils are seasonally drier than in short-grass prairie and the sites of most other methane studies (Adamsen & King 1993; Castro et al. 1993; Keller et al. 1990; Peterjohn et al. 1994; Steudler et al. 1989; Torn & Chapin 1993; Whalen & Reeburgh 1990a; Whalen & Reeburgh 1990b; Whalen et al. 1992).

We measured methane fluxes in the dry and moist zones of each plot in the spring and summer of 1991, 1992, and 1993, for a total of 11 sampling days in each zone. Measurements were made between 1100h and 1400h (MST). The flux value reported for each plot on each day is the average of 1–4 chambers per plot. In 1993, we also measured fluxes every four hours over two diurnal cycles in each zone, with one chamber per plot.

We measured methane flux using static chambers (Torn & Chapin 1993; Whalen & Reeburgh 1990b) accessed from elevated boards. Round, Plexiglas chambers (26-cm diameter) were placed on stainless steel collars for a total height of 24 cm. The collars were inserted 2–4 cm into the soil approximately one hour before sampling. A water-filled rim on each collar provided a methane-tight seal with the chamber. Headspace gas was sampled, with duplicate 10-ml glass syringes, 4 times during incubations of 21 to 45 minutes. Gas samples were analyzed within 12 hours by gas chromatography. We used a Carle gas chromatograph equipped with a flame ionization detector and helium carrier gas. Methane uptake was calculated by linear regression of the four measurements. In fewer than 10% of the incubations, methane depletion decreased uptake rates and the R^2 was improved by more than 0.1 units by omitting the last data point. In these cases, the last data point was dropped. Because the saturation effect was slight, non-linear methods were not used (Hutchinson & Livingston 1993).

Methane concentration in the soil atmosphere was sampled on three days in 1991. Stainless steel tubes (3 mm inner diameter) were inserted 10-, 20-, and 30-cm deep into soil with the aid of a mandrel that was removed before sampling (Whalen et al. 1992). Once in place, the tubes were capped with a rubber septa. A syringe was used to withdraw three times the tube volume of soil air before the sample was collected in a 10-ml glass syringe.

We recorded soil temperature and soil moisture within one meter of each chamber at depths of 5, 12, and 25 cm. Temperature was measured with thermocouples. Soil moisture was measured with gypsum blocks, calibrated to gravimetric moisture content (Harte et al. 1995). Moisture values are expressed as weight percent (g H_2O /100 g dry soil) rather than as percent of water-holding capacity. The water-holding capacity (WHC) of the soil is 42% for the dry zone and 52% for the moist zone. Soil moisture expressed as percent of WHC approximates that fraction of the soil pore space that is filled with water. This is only a relative measure of the diffusivity of the soil, since changes in air-filled pore space may not be related linearly to changes in diffusivity (Hillel 1980; Jury et al. 1991). The empirically determined relationship between gravimetric soil moisture and water matric potential is $\psi = -0.010*(\%\ \text{saturation})^{-3.2}$ and $\psi = -0.002*(\%\ \text{saturation})^{-3.4}$ for the dry and moist zones, respectively.

The experimental site is part of an investigation of ecological responses to meadow warming. Warming was achieved with infra-red heaters suspended

2.6 m above every-other plot, radiating approximately 15 W m^{-2} downward to the soil surface. The heaters advanced the date of snowmelt by an average of 10 days and significantly altered season-averaged soil temperature (increase of 1°C) and moisture (10 % decrease in moisture as measured gravimetrically; Harte et al. 1995). However, they had only a small effect on soil temperature or moisture during the specific hours when methane flux was measured (Table 1).

Laboratory incubations

In 1994, we measured methane consumption in laboratory incubations at two moisture levels, field moisture (control) and water-added. Separate trials were conducted for soils from each zone and three depths (centered at 5, 12, and 25 cm). Soils were collected just outside the north and south ends of the experimental plots, and composited. Soils were sieved (2 mm) just prior to the incubation, 48 hours after soil collection. Each 1-liter glass Mason canning jar was filled with 40 g sieved soil and capped with a lid with a septum for gas sampling. After an initial incubation at field moisture, four replicates of each zone-depth combination were incubated at field moisture and five replicates were incubated after being moistened with 4 ml (moist zone) or 8 ml (dry zone) distilled water. The 18-hr incubation started at ambient methane concentration ($\sim$ 1.8 ppm) and was maintained at 18°C. Consumption was determined by linear regression on measurements at 0, 6, 12, and 18 hours. The moisture content was 7–12% for dry zone soils and 12–15% for moist zone soils in controls, and 20–30% after water was added. Moisture content was determined gravimetrically for subsamples of soil immediately upon collection and for each replicate after the incubation ended. The behavior of controls did not change between the first and second incubations.

Results

Methane uptake in the meadow averaged 1.2 mg CH_4 m^{-2} d^{-1} (range = 0–3.4 mg CH_4 m^{-2} d^{-1}). Uptake was significantly greater in the dry zone (1.5 mg CH_4 m^{-2} d^{-1}) than in the moist zone (1.0 mg CH_4 m^{-2} d^{-1}) by t-test or ANCOVA with soil moisture ($p < 0.001$). These rates are greater than or comparable to those reported for most terrestrial ecosystems (Keller et al. 1990; Keller et al. 1993; Mosier et al. 1991; Mosier et al. 1993; Striegl et al. 1992; Tate & Striegl 1993; Whalen & Reeburgh 1990a; Whalen et al. 1992; Whalen et al. 1991), but lower than those reported for temperate hardwood forests (Castro et al. 1993; Steudler et al. 1989). Methane concentration in the soil atmosphere decreased with depth on each day sampled (Fig. 1).

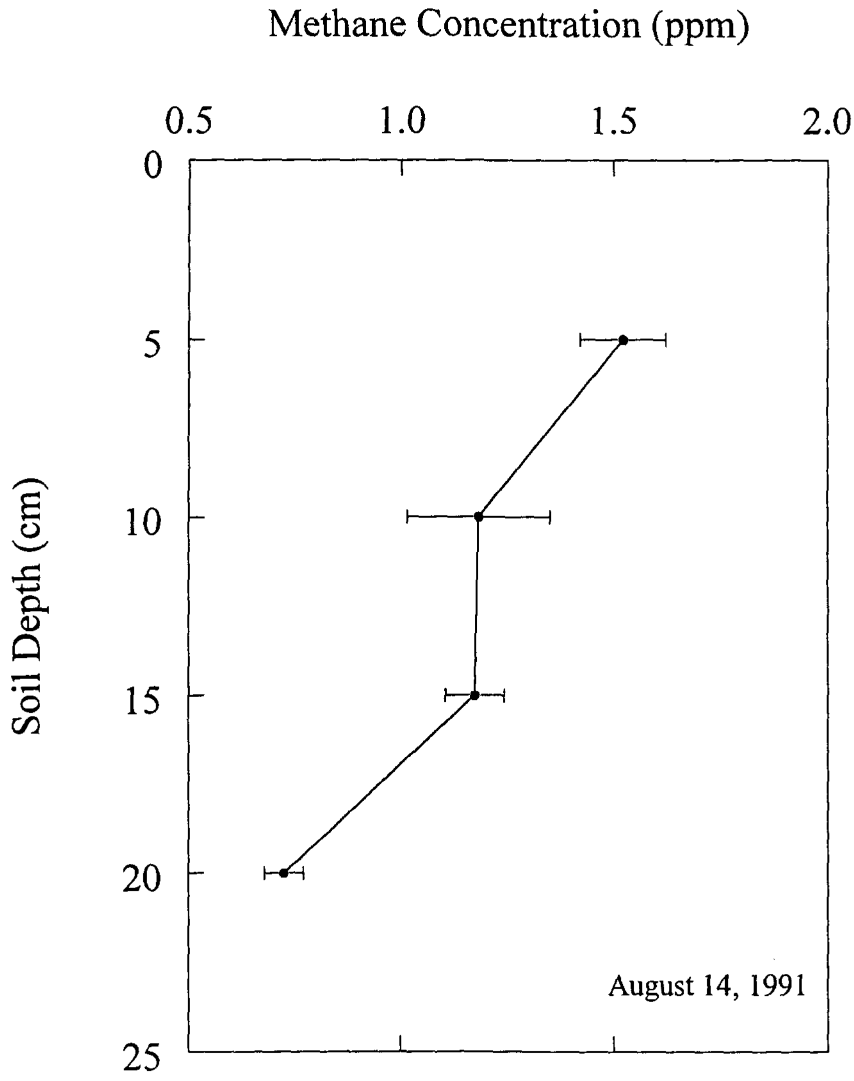


Fig. 1. A typical depth profile of methane concentration in the soil atmosphere, from August 14, 1991. Bars show standard error of measurements ($n = 3$ at 5 and 10 cm; $n = 2$ at 15 and 20 cm).

In none of the diel cycles was a significant effect of hour detected by ANCOVA with soil temperature and moisture as covariates and plot as categorical variable (i.e., repeated measure; $p > 0.112$). Moreover, no significant effect of the heaters on methane flux was detected in any year or zone. All subsequent analyses in this paper will use only the midday data, from both heated and control plots.

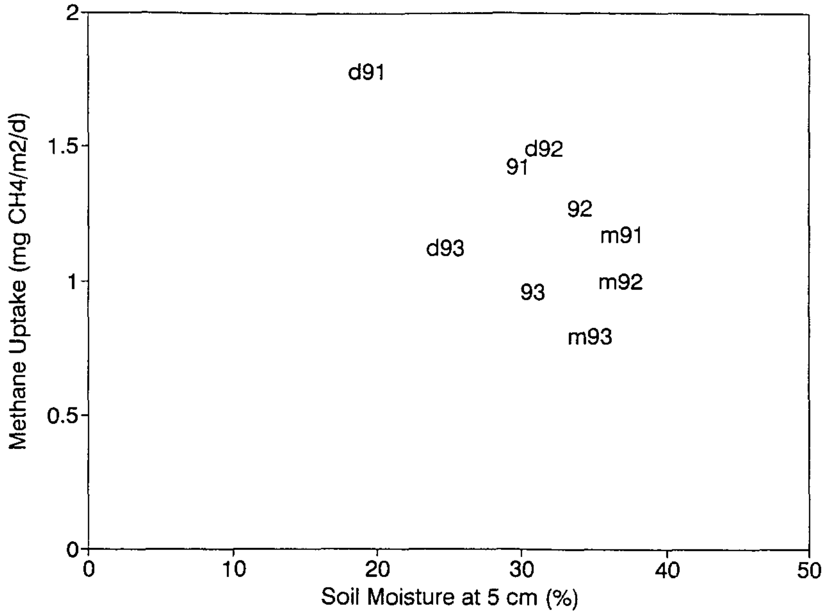


Fig. 2. Average of methane uptake measurements in each year vs average surface soil moisture (% by weight) during the methane measurements. Symbols show zone (d = dry zone; m = moist zone; no letter = both zones combined) and year (1991, 1992, and 1993).

Soil moisture had more influence over uptake rates than did soil temperature. Single-factor linear regressions gave a coefficient of determination and p-value of $R^2 = 0.43, p < 0.001$ for moisture at 5 cm and $R^2 = 0.28, p < 0.01$ for temperature at 5 cm; $n = 22$ sampling dates (11 sampling dates per zone, average of ten plots for each date). In multiple regression with both variables, only soil moisture was significant. The linear fit was poorer with soil moisture at 12 cm and 25 cm.

Both year and zone were significant factors in an ANCOVA with soil moisture as a covariate ($p < 0.001$ for each factor), and year was a significant factor in ANCOVA with dry zone data (Fig. 2).

In laboratory incubations, the consumption rate (mean = 0.98 ng CH_4 g^{-1} soil h^{-1}) was the same order of magnitude as the field uptake rates, assuming 30 cm of active soil. In both zones, soils from 12- and 25-cm deep had greater consumption rates than did soils from 5 cm ($p < 0.02$, $n = 4$; Fig. 3). Raising moisture levels (the water-added treatment) increased oxidation rates relative to the controls in the dry zone at all depths and in the moist zone at 5 cm ($p < 0.001$, except at 25 cm $p < 0.05$; Fig. 3). In other words, the four driest locations, which had low consumption rates, responded to added moisture and the two moister soils did not. The deeper moist-

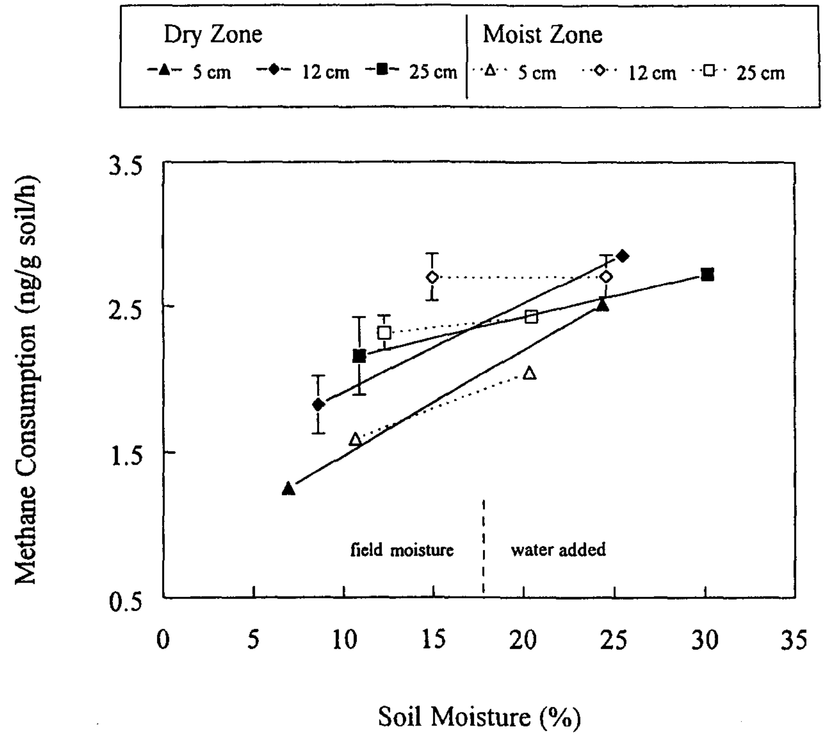


Fig. 3. Methane consumption versus soil moisture (% by weight) in laboratory incubations. The data on the left side of the graph are means of control jars at field moisture ($n = 4$); Data on the right side are means of moisture-added treatment ($n = 5$). Lines connect the control and treatment means for samples from the same site (zone and depth). All points are graphed with standard error bars; where the bars do not show, the standard error is very small.

zone soils, with field moisture of 25%, may already have been beyond the range of moisture-deficit inhibition. Methane oxidation by these soils reduced headspace concentrations to very low levels. After 48 hours of incubation, the moist zone 12-cm soils reduced headspace methane concentrations to 0.05 ppm.

To discern any effect of climate above the noise of spatial heterogeneity, we analyzed the field data using each plot mean separately ($n = 198$). The influence of soil moisture on uptake was significant over the natural variability in the 10 plots, two moisture zones and three snow-free seasons ($p < 0.001$ for a linear regression with moisture at 5 cm or a non-linear fit with 5 and 25 cm, discussed below).

To test if the field data contained a non-monotonic moisture response as seen in the laboratory, we compared the fit of quadratic and linear functions to a single linear regression of flux on moisture, using plot means ($n = 198$).

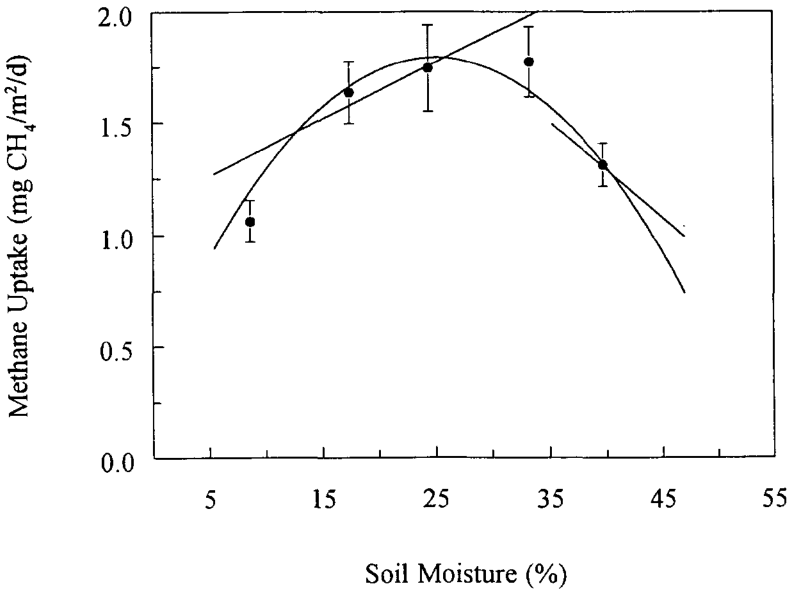
In both comparisons, described below, the non-monotonic fit was better than the single linear regression fit (Fig. 4).

While the linear fit of the disaggregated data with 5-cm moisture alone explains only 11% of the variance in flux, adding a quadratic 25-cm moisture term, representing a parabolic response function, explains 25% of the variance for both zones combined (Flux = Constant + $M_{5\ cm}$ + $(M_{25\ cm}\text{-}a)^2$; R^2 = 0.258; $p < 0.001$). No other combination of linear or quadratic moisture terms improved the fit of the linear 5-cm model (e.g., adding the square of 5-cm soil moisture or a linear 25-cm term). In a second test of non-monotonicity, we divided all of the flux data into two moisture classes, those above 35% moisture and those below. We repeated the analysis with moisture classes below 30%, 25% and 20% moisture. For the 35% division, the best-fit linear regressions for the two data classes form an upside-down "V" with maximum consumption in the center, at 35% moisture (Fig. 4; linear fit). The slope below 35% moisture is significantly greater than zero for the entire data set and for the dry zone alone. The moist zone data alone give a nearly significant positive slope; there are few "dry" data points, however, from this zone. The slopes were even more positive for the data below 25% and 20% soil moisture, for either zone or both combined, but these slopes were not significant.

Discussion

The positive slope on the left half of Figs. 4a–4c (linear or quadratic fits) and Fig. 3 indicates that soil drying under already dry conditions could reduce methane consumption. In contrast, the negative slope, seen above 25–35% soil moisture in Fig. 4 corroborates earlier reports that drying of moist soil could increase methane consumption (Peterjohn et al. 1994; Torn & Chapin 1993; Whalen & Reeburgh 1990a).

The observed pattern in methane flux–a linear relationship with 5-cm moisture and a downward U-shaped relationship at 25 cm–can be explained by considering that soil methanotrophs are less active near the soil surface than they are lower in the soil and that methanotroph activity peaks at mesic moisture levels. In laboratory incubations, we saw significantly higher consumption by soils collected at 12 and 25 cm than from soil sampled near the surface. A similar below-surface maximum in methane oxidation has been observed in aerobic soils of other temperate and boreal ecosystems (Adamsen & King 1993; Castro et al. 1995; Koschorreck & Conrad 1993; Valentine et al. 1994; Whalen et al. 1990). With this depth distribution of methanotroph activity, surface soil moisture would influence diffusion while lower-depth moisture would influence both diffusion and methanotroph activity. The influence of soil moisture on the diffusion component of consumption is always


2.0
1.5
1.0
0.5
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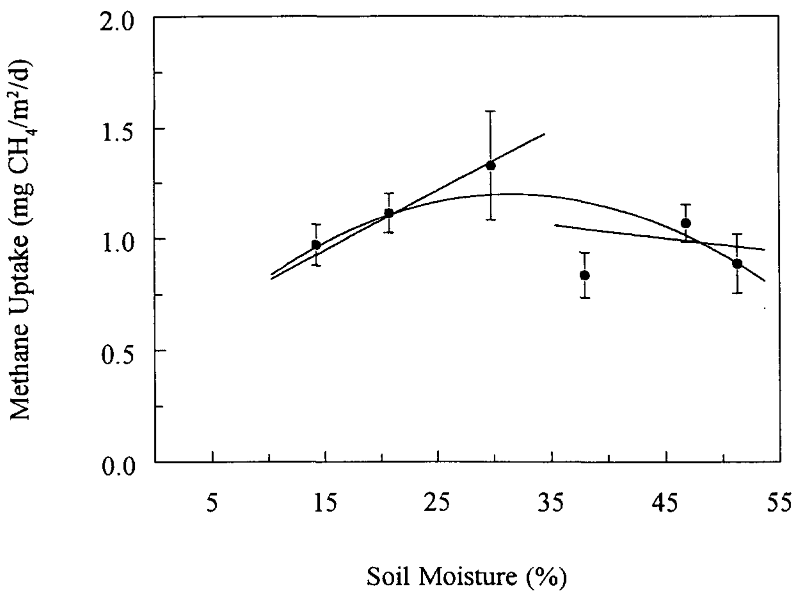
Methane Uptake (mg $CH_4/m^2/d$)
5
15
25
35
45
55
Soil Moisture (%)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Methane Uptake (mg $CH_4/m^2/d$)
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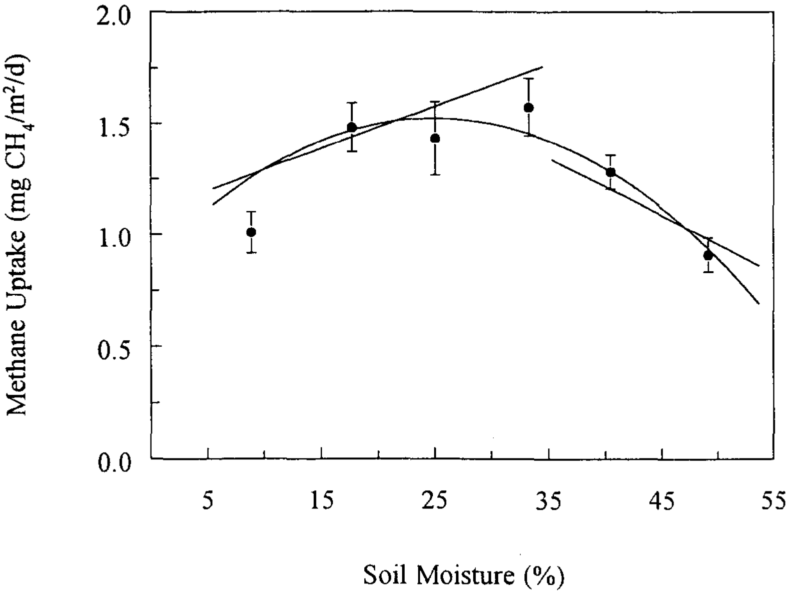

Fig. 4. This figure shows three ways of evaluating the non-monotonic fit of methane uptake to soil moisture at 25 cm: binned data clusters, best quadratic fit and linear fit of two moisture classes. Moisture is expressed as % by weight. Each approach suggests an upside-down U-shaped relationship (e.g., parabolic) between uptake and moisture. Figures show (a) dry zone, (b) moist zone, and (c) both zones combined. The clusters, quadratic equations, linear regressions, and statistical analyses were generated from all field data (n = 102 for dry zone, n = 96 for moist zone, n = 198 for both zones combined).

Data Clusters: The binned data clusters are averages (± SE) of clusters generated by dividing the moisture axis at 8% (g H2O/100 g soil) intervals. The circles show the average flux and moisture for each interval.

Quadratic Fit: The U-shaped curves show the quadratic fit (SYSTAT 6.0 NonLin; Wilkinson 1990), indicating maximum consumption around 25% moisture. For the dry zone data and the zones combined, the quadratic fits are significantly better than linear fits. The quadratic equations are (M_{25} = soil moisture at 25-cm depth):

(a) Dry zone: methane flux = $0.4072 + 0.1104*M_{25} - 0.0022*(M_{25})^2$
(b) Moist zone: methane flux = $0.4026 + 0.0505*M_{25} - 0.0008*(M_{25})^2$
(c) All Data: methane flux = $0.8900 + 0.0508*M_{25} - 0.0010*(M_{25})^2$

Linear Fit: The straight lines show linear regressions of flux on 25-cm soil moisture, for soil moisture <35% and soil moisture >35%. Regression model: Flux = constant + m* moisture at 25 cm;

		Slope (m) for regression Soil moisture <35%	p, one-tailed	n
(a)	Dry zone:	0.026	0.033	54
(b)	Moist zone:	0.027	0.057	25
(c)	All Data:	0.019	0.040	79

negative. The influence of soil moisture on methanotroph activity is more complex. Both our field and laboratory results show that the influence of soil moisture may also be positive; uptake rates *in situ* decrease at low moisture levels. Other laboratory studies have also found a non-monotonic response curve of methane oxidation to soil moisture (Reeburgh & Whalen 1993; Schimel et al. 1993; Whalen et al. 1990).

Although methane uptake is generally thought to be diffusion-limited (Bartlett & Harriss 1993; Dorr et al. 1993; Striegl 1993), at this site we observed that microbially-mediated oxidation was inhibited at moderately low moisture levels. The inhibition of microbial methane-oxidation by low soil moisture could be an important rate-limiting step in other soils and ecosystem types, although the soil-moisture level at which consumption begins to decrease may differ spatially and temporally.

Although methanotroph communities that oxidize soil-produced methane are found in moist soils, drying-induced reductions in consumption should be investigated as one possible explanation for observed methane-emission pulses from drying wetland soil (Moore & Roulet 1993). Studying the climatic controls over the activity of methanotroph communities in saturated environments is difficult because the net flux from these environments is the balance between both consumption and production. The mechanisms of oxidation-limitation in aerobic soils, described here, may help shed light on the controls over methane fluxes in other environments, particularly in landfills where methane consumption takes place in an aerobic layer well above the zone of production (Whalen et al. 1990).

The units chosen for reporting soil moisture, e.g., as percent by weight, water-filled pore space (%WFPS), or soil matric potential may differ, depending on the basis for limitation of oxidation. At higher soil moisture, where diffusion is limiting uptake rates, %WFPS has been shown to be a useful measure (e.g., van Breemen & Feitjal 1990). Water matric potential may be more directly related to microbial physiology, and it is a more sensitive measure of soil moisture at low soil moisture than is %WFPS.

The low R^2 for the flux-moisture regression with disaggregated data (R^2 = 0.120, linear; R^2 = 0.258, quadratic) indicates that other biotic and abiotic factors are also important in fluctuations in methane flux over time and space (the spatial factors being the primary difference between the aggregated ($n = 22$) and disaggregated ($n = 198$) regressions). Nevertheless, these results bear on climate change analyses because many potentially important factors, such as soil texture (Dorr et al. 1993), are unlikely to change rapidly or in a spatially-coherent fashion in response to climatic change or other global trends.

A climate feedback with methane consumption could affect two important aspects of the methane budget. First, soil uptake of atmospheric methane is roughly equal to the magnitude of the current imbalance between methane sources and sinks that is giving rise to a nearly 1% per year increase in atmospheric methane (Houghton et al. 1990). Second, methane consumption in soil and sediments is an important modulator of terrestrial emissions, oxidizing almost half of all soil-produced methane (Reeburgh et al. 1993). Hence, our observation that soil drying reduces methane consumption in soils with low moisture content suggests a potentially important positive feedback to climatic warming.

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