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Factors controlling atmospheric methane consumption by temperate forest soils

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Abstract. Over the past 6 years (1988-1993), we have examined the effects of soil temperature, soil moisture, site fertility, and nitrogen fertilization on the consumption of atmospheric CH_4 by temperate forest soils located at the Harvard Forest in Petersham, Massachusetts. We found that soil temperature is an important controller of CH_4 consumption at temperatures between -5° and 10°C but had no effect on CH_4 consumption at temperatures between 10° and 20°C. Soil moisture exerts strong control on CH_4 consumption over a range of 60 to 100% water-filled pore space (% WFPS). As moisture increased from 60 to 100% WFPS, CH_4 consumption decreased from 0.1 to 0 mg CH_4-C m^{-2} h^{-1} because of gas transport limitations. At 20 to 60% WFPS, site fertility was a strong controller of CH_4 consumption. High-fertility sites had 2 to 3 times greater CH_4 consumption rates than low-fertility sites. Nitrogen-fertilized soils (50 and 150 kg NH_4NO_3-N ha^{-1} yr^{-1}) had annually averaged CH_4 consumption rates that were 15 to 64% lower than annually averaged CH_4 consumption by control soils. The decrease in CH_4 consumption was related to both the years of application and quantity of nitrogen fertilizer added to these soils.

Introduction

Over the past 100 years, the concentration of CH_4 in the atmosphere has increased from 0.9 to 1.72 parts per million by volume (ppmv) [*Watson et al.*, 1990]. This increase is of concern because CH_4 is a greenhouse gas and is important in atmospheric chemistry [*Cicerone and Oremland*, 1988; *Lashof and Ahuja*, 1990]. This increase was caused by either greater emissions from natural and human sources or decreases in the strength of the CH_4 sinks.

The largest biological sink for CH_4 is the consumption by microbial processes in soils and sediments. Anaerobic CH_4 consumption is poorly understood but appears to be important in certain environments such as sulfate-reducing marine sediments and anoxic waters [*Reeburgh and Heggie*, 1977; *Reeburgh*, 1980]. Aerobic CH_4 consumption has recently been measured in many different ecosystems [*Steudler et al.*, 1989; *Keller et al.*, 1990; *Mosier et al.*, 1991; *Striegl et al.*, 1992] and appears to be a widespread sink for atmospheric CH_4. Global estimates of the total amount of atmospheric CH_4 consumed by aerobic soils range from 15 to 45 Tg yr^{-1} [*Watson et al.*, 1992] and is about 3 to 10% of the global emissions [*Watson et al.*, 1992]. Global estimates of the CH_4 sink are uncertain because measurements have been made at only a few locations and do not account for spatial features, such as land use history, that affect CH_4 consumption. Better predictions of future trends of this CH_4 sink require a more complete understanding of the processes responsible for CH_4 consumption and how these processes are influenced by environmental and biotic factors. In this paper, we describe how soil temperature, soil moisture, site fertility, and nitrogen fertilization affect CH_4 consumption by temperate forest soils.

Methods

Study Sites

This study was conducted at four sites located at the Harvard Forest in Petersham, Massachusetts (42°30'N,72°10'W). Two of our sites, a 66-year-old red pine (*Pinus resinosa* Ait.) plantation and an adjacent 84-year-old mixed hardwood stand, are located in the Prospect Hill Tract of the Harvard Forest and are part of

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the ongoing chronic nitrogen addition experiment [*Aber et al.*, 1993] and have a well-described history [*Bowden et al.*, 1990, 1991; *Aber et al.*, 1993]. These stands are located on well-drained loamy sand Entic Haplorthods (spodosol) of the Gloucester series. Ammonium is the dominant form of inorganic nitrogen in these soils. Nitrate concentrations are usually below the detection limit. Annual net nitrogen mineralization rates range from 70 to 80 kg N ha^{-1} yr^{-1} [*Aber et al.*, 1993; A.H. Magill et al., manuscript in preparation, 1994]. Net nitrification rates range from below the detection limits in the hardwood stand and up to 2.5 kg N ha^{-1} yr^{-1} in the pine stand.

Our other two study sites, a 70-year-old red pine (*Pinus resinosa* Ait.) plantation and 70-year-old mixed hardwood stand, were located in the Tom Swamp Tract of the Harvard Forest. Both of these stands are located on glacio-fluvial sand of the Merrimac soil series. Ammonium is also the dominant form of inorganic nitrogen in these soils. Annual net nitrogen mineralization rates range from 40 to 50 kg N ha^{-1} yr^{-1}. Net nitrification rates are below the detection limits (J.M. Melillo, unpublished data, 1994).

Treatments

Nitrogen additions. In 1988 the red pine and mixed hardwood stands in the Prospect Hill Tract were divided into three main 30 x 30 m plots; one plot was the untreated control, and the other two plots were fertilized with NH_4NO_3. Each of these main plots were subdivided into thirty-six 5 x 5 m subplots. The low-N plots received 37 kg N ha^{-1} yr^{-1} in 1988 and 50 kg N ha^{-1} yr^{-1} in 1989-1993. The high-N plots received 120 kg N ha^{-1} yr^{-1} in 1988 and 150 kg N ha^{-1} yr^{-1} in 1989-1993. The NH_4NO_3 was dissolved in 20 L of distilled water and applied to the forest floor with a backpack sprayer in six equal doses from May through October. We routinely measured CH_4 flux, soil moisture, soil temperature, and soil nitrogen dynamics in these plots from 1988 to 1993.

Water manipulations. We conducted soil moisture manipulation experiments in untreated plots adjacent to the control plots of the Prospect Hill Tract in 1992 and 1993. These experiments were designed to examine the effect of soil moisture on CH_4 consumption. In the summer of 1992, we lowered soil moisture by preventing precipitation from entering three replicate 1 x 1 m plots in the red pine and mixed hardwood stands for 12 weeks. Plastic tarps suspended 2 m above the forest floor prevented rain from directly entering these plots. In separate experiments, soil moistures in six 1 x 1 m plots adjacent to the control portion of the red pine stand were increased by adding 10 cm of groundwater to the forest floor in late summer of 1992 and, again, in the spring and summer of 1993. Plastic tarps suspended above the watered plots prevented precipitation inputs. We measured CH_4 flux, soil temperature, and soil moisture prior to and in a time series after the soil moisture manipulations.

Field Measurements

Prospect Hill tract. Methane fluxes were measured with an in situ static chamber incubation technique [*Steudler et al.*, 1989; *Bowden et al.*, 1990] from 1988 to 1993 at the same locations in all treatment and control plots of the chronic nitrogen addition experiment. We sampled three subplots from each treatment (control, low-N, and high-N) in each stand (red pine and mixed hardwood) for a total of 18 chambers. All chambers were sampled at the same time.

We measured CH_4 fluxes twice a month during the 1988 field season (May-December), once a month in the 1989 field season (March-December), and five to seven times in each of the 1990-1993 field seasons. In 1988, CH_4 fluxes were measured every six hours (0600, 1000, 1400, 1800, 2200, and 0200 LT) on each sampling date. In 1989, CH_4 fluxes were measured five times per day (0600, 1000, 1400, 1800, and 2200 LT). In 1990-1993, CH_4 fluxes were measured four times per day (0600, 1000, 1400, and 1800 LT). In this paper, we present monthly averaged CH_4 fluxes computed from all measurements made in each individual month and annually averaged fluxes computed from all measurements made each year.

Soil temperatures were measured with Omega dial thermometers placed at a depth of 5 cm. These measurements were made at the start and end of all of the 30-min incubation periods at one sampling chamber in each treatment plot.

We measured soil moisture of the organic horizon during all gas samplings and the upper 10 cm of mineral soil during 11 of 42 routine gas samplings and all of the moisture manipulation experiments. Average moisture contents for these horizons were determined from three to nine replicate 5.4-cm-diameter cores per treatment. After separating the cores into horizons, subsamples (10 to 20 g) of each horizon were weighed, dried at 105°C for 48 hours, and reweighed to determine the moisture content. Soil moisture contents of the mineral soil are expressed as a percentage of the total pore space that is filled with water (percent water-filled pore space, %WFPS) which is the ratio of the volumetric moisture content (cm^3 H_2O/cm^3 soil) to the total porosity of the soil. Volumetric moisture content was calculated by multiplying the ratio of the gravimetric moisture content to the density of water by the bulk density of the soil. Soil porosity was computed from the bulk and particle densities [*Blake and Hartge*, 1986a,b].

Net mineralization and net nitrification were measured using an in situ buried bag technique [*Nadelhoffer et al.*, 1983; *Pastor et al.*, 1984]. Briefly, we collected three pairs of two adjacent 5.4-cm-diameter cores to a depth of 10 cm of mineral soil. These cores were divided into organic and mineral horizons and placed into separate gas permeable polyethylene bags. One core from each pair was returned to the laboratory for analysis of the initial KCl, extractable NH_4 (Technicon Method 780-86T), and NO_3 (Technicon Method 782-86T) with a Traacs 800 autoanalyzer. The other core of each pair was wrapped in a 1-mm mesh fiberglass screen (to reduce puncture damage to the polyethylene bag) and placed back into the ground. In situ samples were incubated for 4 to 6 weeks during the 1988, 1989, and 1993 growing seasons and over the winter from November to April. One 6-week incubation was performed in the summer of 1990 and 1992. The net change in the extractable NH_4^+ plus NO_3^- and NO_3^- over the incubation period was used to estimate the net nitrogen mineralization and net nitrification rates, respectively.

Tom Swamp tract. We measured CH_4 consumption, soil temperature, and soil moisture simultaneously in the low-fertility Tom Swamp and the high-fertility Prospect Hill control plots in June 1993. Methane fluxes were measured twice (0700 and 1400 LT) at four different locations in each stand. Four soil cores (organic and upper 10-cm mineral soil) were collected at each site for soil moisture measurements.

Results

Prospect Hill Tract

Methane fluxes. During all gas samplings in 1988-1993, atmospheric CH_4 was consumed by forest soils in the Prospect Hill Tract of the Harvard Forest (Figures 1a and 1b). Methane consumption rates varied in a consistent seasonal pattern in all years (Figures 1a and 1b). Methane consumption was lowest (<0.05 mg CH_4-C $m^{-2}h^{-1}$) in the early spring and late fall (November-December). Methane consumption rates increased in late spring and early summer and the maximum rates (0.1 to 0.25 mg CH_4-C $m^{-2}h^{-1}$) were measured in late summer and early fall.

Soil temperature. Soil temperatures ranged from between -5° and 20°C in all years. Lowest temperatures were measured in the spring and late fall. Maximum temperatures were measured in either July or August.

We found a curvilinear relationship between CH_4 consumption and soil temperature (Figure 2). Methane consumption increased from 0 to 0.12 mg CH_4-C $m^{-2}h^{-1}$ as temperature increased from -5° to 10°C. Methane consumption was relatively constant at temperatures between 10° and 20°C.

Soil moisture. Average organic horizon soil moistures typically ranged from 50 to 200 g H_2O/g dry soil each year (Figure 3a). We usually observed the highest moisture contents in early spring and late fall. Low moisture contents were measured in the middle to late summer. Organic horizon soil moisture was not correlated with CH_4 flux, soil temperature, and mineral soil moisture.

Average mineral soil moistures measured during 11 of 42 routine gas samplings ranged from 14 to 57 g H_2O/g dry soil (20 to 80% WFPS). Most of the % WFPS values were between 25 and 45% WFPS.

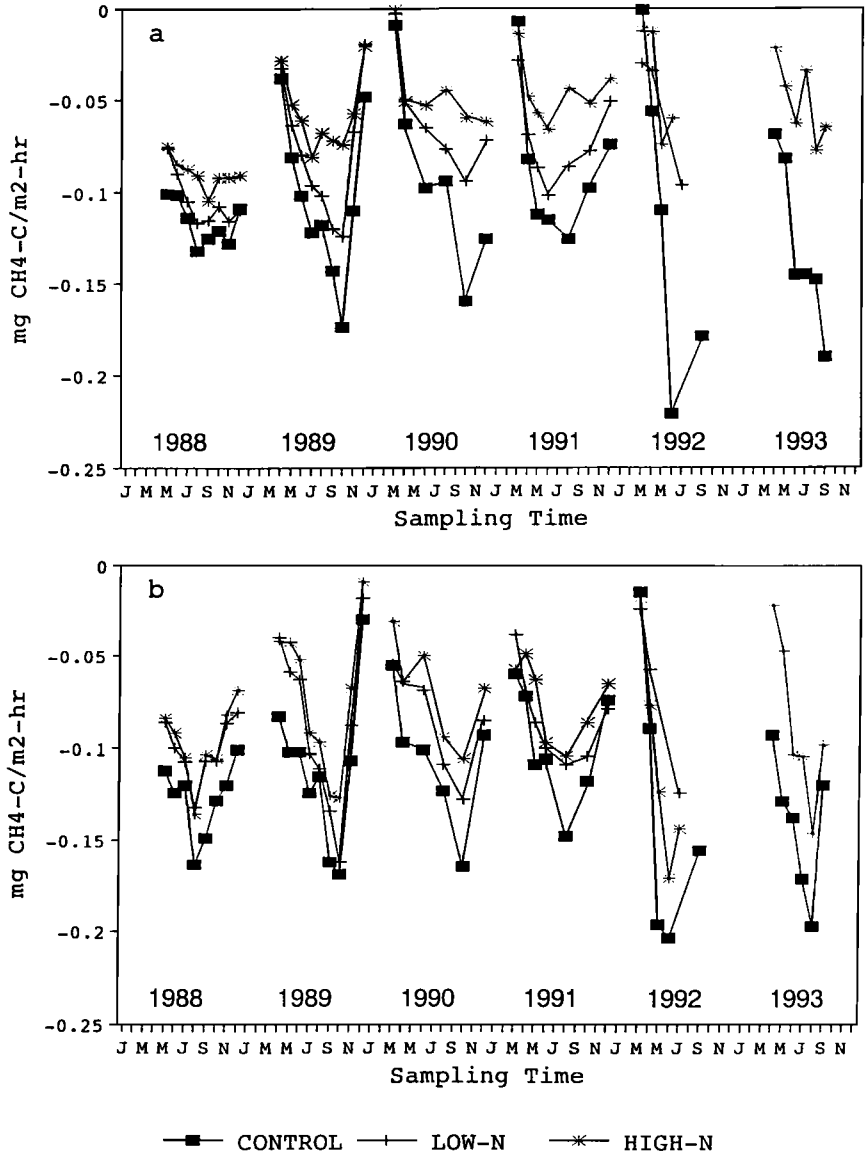

Figure 1. Monthly averaged methane consumption rates measured in (a) the Prospect Hill red pine plantation and (b) mixed hardwood stand.

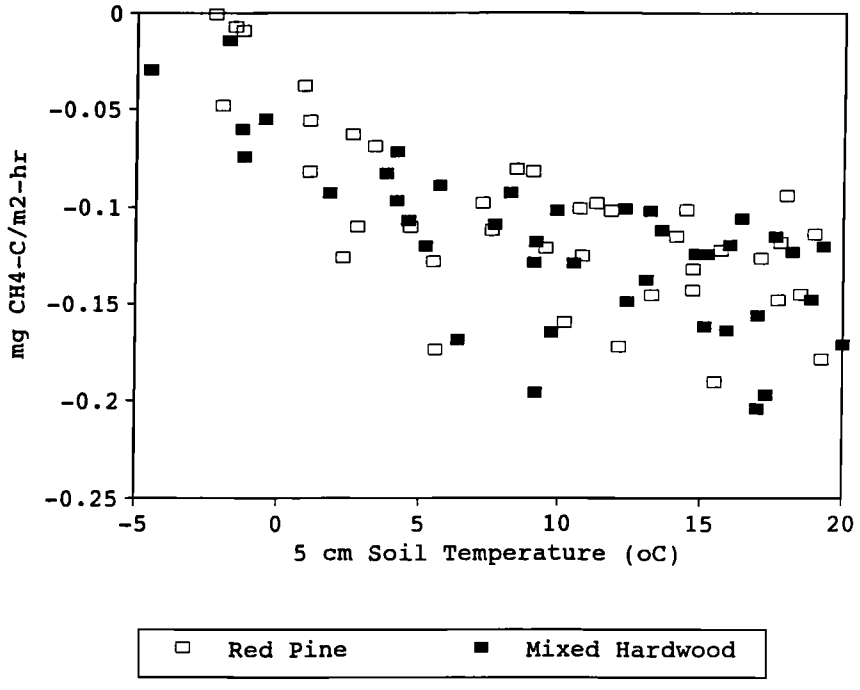

Figure 2. The relationship between monthly averaged methane consumption and soil temperature measured in the Prospect Hill control plots.

To increase the size of our mineral soil moisture data set, we conducted water addition [*Castro et al.*, 1994b] and exclusion experiments. Mineral soil moistures during the water addition experiments ranged from 20 to 100% WFPS. The addition of 10 cm of water immediately doubled the moisture content of the upper 10 cm of mineral soil in the watered plots. Mineral soil moisture contents returned to pretreatment levels about 48 hours after water additions in the summer and 72 to 216 hours after the water addition in early spring before bud burst [*Castro et al.*, 1994b]. Mineral soil moistures during the water exclusion experiment ranged from 20 to 55% WFPS, but most of the values were between 20 and 40% WFPS (Figure 3b). Mineral soil moisture in the water exclusion plots remained relatively constant (25 to 30% WFPS) for the entire 12-week dry-down period. In contrast, mineral moisture in the control plot varied from 30 to 55% WFPS.

We found that CH_4 consumption was affected by both high and low mineral soil moistures (Figure 4). As mineral soil moisture increased from 60 to 100% WFPS, CH_4 consumption steadily decreased from 0.1 to 0 mg CH_4-C $m^{-2}h^{-1}$. Over this moisture range, linear regression between CH_4 consumption and WFPS explained 75% of the variability. At low soil moistures (20 and 60% WFPS), we measured the highest CH_4 consumption rates (up to 0.25 mg CH_4-C $m^{-2}h^{-1}$).

Soil nitrogen. During all gas sampling in 1988-1993, soils fertilized with NH_4NO_3 consumed less CH_4 than control soils (Figures 1a and 1b). Soils in the high-N (150 kg N ha^{-1} yr^{-1}) plots always had the lowest consumption rates. Annually averaged CH_4 consumption by the high-N plots were 15 to 64% lower than annually averaged CH_4 consumption by control soils (Table 1). Soils in the low-N plots (50 kg N ha^{-1} yr^{-1}) always had intermediate rates that were 17 to 33% lower than rates in the control soils. Organic and mineral horizon NH_4^+ and NO_3^- pools, net nitrogen mineralization, and net nitrification were not correlated with CH_4 consumption. Details of these nitrogen data are presented by *Aber et al.* [1993] and A.H. Magill et al. (manuscript in preparation, 1994).

Tom Swamp Tract

Methane fluxes. To test our hypothesis that inherent site fertility is an important spatial controller of CH_4 consumption, we measured CH_4 consumption simultaneously at the Tom Swamp and Prospect Hill Tracts. In June 1993, CH_4 consumption by Prospect Hill control soils was 2 to 3 times higher than CH_4 consumption by Tom Swamp soils while at the same soil temperature (10° to 13°C) and moisture (Table 2). Both red pine stands had identical soil moisture (~40% WFPS), but the Prospect Hill Tract had 3 times higher CH_4 consumption than the Tom Swamp Tract. Similarly, both of the mixed deciduous stands had soil moisture of around 50% WFPS, but the Prospect Hill soils had 2 times higher consumption rates than the Tom Swamp soils.

Discussion

Temperate forest soils examined in this study consumed atmospheric CH_4 on all samplings dates in 1988-1993 (Figures 1a and 1b). Monthly averaged CH_4 consumption rates ranged from 0 to 0.23 mg CH_4-C $m^{-2}h^{-1}$. Annually averaged CH_4 consumption rates ranged from 0.09 to 0.14 mg CH_4-C $m^{-2}h^{-1}$ and were at the high end of the range in annual consumption rates (0.01 to 0.11 mg CH_4-C $m^{-2}h^{-1}$) reported for other temperate forests (Table 3).

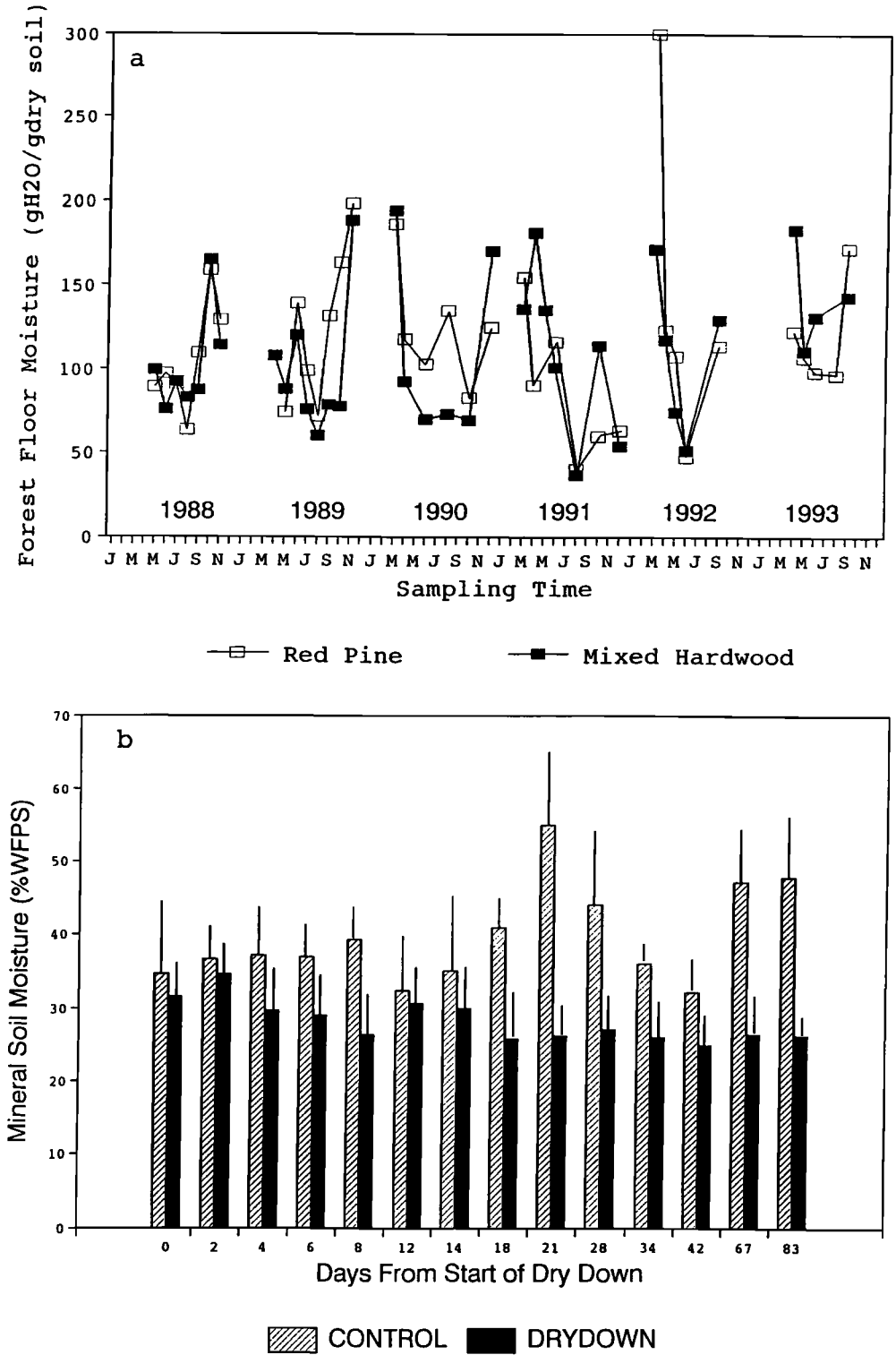

Figure 3. (a) Forest floor soil moisture in the Prospect Hill red pine and mixed hardwood control plots and (b) mineral soil moisture from a water exclusion experiment in the red pine stand.

Strong seasonal variations in CH_4 consumption (Figures 1a and 1b) may be related to seasonal variations in soil temperature and moisture. These factors appear to vary in their importance as controllers of CH_4 consumption. Soil temperature appears to be an important controller of CH_4 consumption at low temperatures (-5° to 10° C). As soil temperature increased from -5° to 10°C, CH_4 consumption increased from 0 to 0.12 mg CH_4-C $m^{-2}h^{-1}$ (Figure 2). Methane consumption was independent of soil

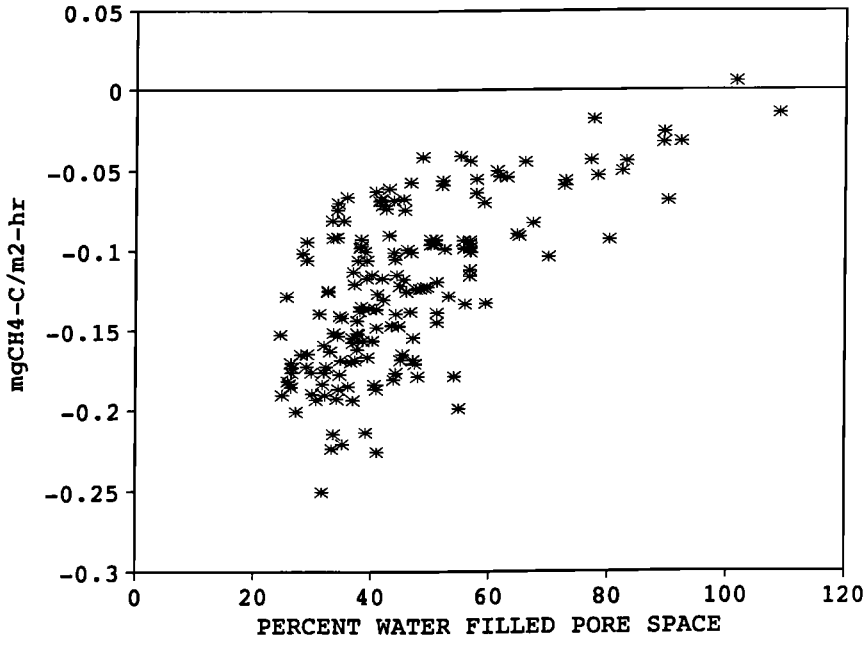

Figure 4. The relationship between methane consumption and soil moisture in the upper 10 cm of mineral soil from measurements made in control plots during routine gas samplings and all water manipulation experiments in the Prospect Hill Tract.

temperature between 10° and 20°C (Figure 2). This pattern is consistent with the results from other field [*Crill*, 1991] and laboratory studies [*King and Adamsen*, 1992; *Nesbit and Breitenbeck*, 1992]. *Crill* [1991] showed that in two consecutive years (1989 and 1990) monthly averaged CH_4 consumption rates by soils in a mixed coniferous-deciduous forest in New Hampshire increased from near zero (0.001 mg CH_4-C $m^{-2}h^{-1}$) in March to about 0.06 mg CH_4-C $m^{-2}h^{-1}$ in May as air temperature increased from 0°C to 15°C. However, monthly averaged CH_4 consumption changed by only 30% (0.07 to 0.09 mg CH_4-C $m^{-2}h^{-1}$ in 1989 and 0.08 to 0.11 mg CH_4-C $m^{-2}h^{-1}$ in 1990) as air temperature increased from 15° to 21°C [*Crill*, 1991]. *King and Adamsen* [1992] also showed that temperature increases from -2° to 2°C significantly increased CH_4 consumption by soil cores from a mixed deciduous-coniferous forest in Maine, while temperature increases from 2° to 30 °C had little effect on CH_4 consumption. Collectively, results from these studies support the idea that temperature is an important controller of CH_4 consumption by temperate forest soils in the winter and during the transition from spring to summer and fall to winter. In addition, future changes in soil temperature above our normal high of 20°C are not likely to increase the strength of this CH_4 sink.

The effect of temperature on CH_4 consumption may have been caused by temperature-induced changes in microbial activity. During cold times of the year (early spring and late winter),

Table 1. Methane Consumption by Forest Soils in the Prospect Hill Tract, Petersham, Massachusetts

	Annually Averaged Methane Consumption, mg CH_4-C m^{-2} h^{-1}			Percent Reduction in Methane Consumption	
Sampling Time	Control	Low-N	High-N	Low-N	High-N
		Red Pine Overstory			
May-Dec. 1988	-0.12	-0.10	-0.09	17	25
April-Dec. 1989	-0.10	-0.08	-0.06	20	40
March-Dec. 1990	-0.09	-0.06	-0.05	33	44
March-Dec. 1991	-0.09	-0.07	-0.05	22	44
March-Dec. 1992	-0.11	-0.07	-0.04	20	64
April-Dec. 1993	-0.13	----	-0.05	----	62
		Mixed Deciduous Overstory			
May-Dec. 1988	-0.13	-0.10	-0.10	23	23
April-Dec. 1989	-0.11	-0.09	-0.07	18	36
March-Dec. 1990	-0.11	-0.08	-0.07	27	36
March-Dec. 1991	-0.10	-0.08	-0.07	20	30
March-Dec. 1992	-0.13	----	-0.11	----	15
April-Dec. 1993	-0.14	----	-0.09	----	36

Table 2. Daily Averaged Methane Consumption Rates at Tom Swamp and Prospect Hill Control Plots in June 1993

Site	Vegetation	Methane Flux (Mean ± SE), mg CH_4-C m^{-2} h^{-1}
Tom Swamp	red pine	-0.054 ± 0.005
Prospect Hill	red pine	-0.146 ± 0.009
Tom Swamp	mixed deciduous	-0.094 ± 0.012
Prospect Hill	mixed deciduous	-0.138 ± 0.012

frozen temperate forest soil consume little or no atmospheric CH_4 probably because low temperatures significantly reduce microbial activity. We measured consumption rates of 0 to 0.02 mg CH_4-C $m^{-2}h^{-1}$ in early spring (March and April) when the soils were frozen (temperature < 0°C) and not covered with snow (Figures 1a and 1b). *Crill* [1991] also reported that frozen temperate forest soils in New Hampshire did not consume atmospheric CH_4 from January to March 1990. As temperature increases above 0°C, the activity of the soil microbial communities that consume atmospheric CH_4 increases and CH_4 consumption increases. When the microbial communities reach their optimum temperature in the late spring, other factors, such as soil moisture, become the most important controller of CH_4 consumption.

Soil moisture exerts a strong control over CH_4 consumption over the range from 60 to 100% WFPS (Figure 4). As soil moisture increased from 60 to 100% WFPS, CH_4 consumption decreased linearly from 0.1 to 0 mg CH_4-C $m^{-2}h^{-1}$. This pattern is consistent with results from other studies [*Steudler et al.*, 1989; *Nesbit and Breitenbeck*, 1992; *Koschorreck and Conrad*, 1993; *Adamsen and King*, 1993]. *Koschorreck and Conrad* [1993] reported that CH_4 consumption by forest soils in Germany decreased linearly from 0.03 to 0.006 mg CH_4-C $m^{-2}h^{-1}$ as soil moisture increased from about 40 to 90% water-holding capacity. At our study sites, the moisture-induced reduction of CH_4 consumption observed in our water addition experiments [*Castro et al.*, 1994b] has also been observed following precipitation events [*Steudler et al.*, 1989]. In these well-drained soils, the duration of the moisture-induced reduction of CH_4 consumption is likely to be affected by the preexisting soil moisture and evapotranspiration rates. We found that it took 24 to 48 hours for soil moisture and CH_4 consumption to return to the pretreatment levels when these soils were relatively dry (20 to 45% WFPS) and had high rates of evapotranspiration before the water addition. When there was less evapotranspiration before bud burst in May 1993, it took 72 to 216 hours to return to pretreatment soil moistures and CH_4 consumption rates. Our results suggest that the moisture-induced reduction of CH_4 consumption observed after our water manipulations and precipitation events is likely to be short-lived (1 to 5 days) when the soils are dry, regardless of the evapotranspiration rate. Although the moisture-induced reduction of CH_4 consumption is short-lived, the frequency at which it occurs under current climatic conditions is not well documented. Additional studies are necessary do determine (1) the minimum amount of precipitation necessary to cause the reduction, (2) the frequency of these precipitation events, and (3) the time required for these soils to dry down after precipitation events that occur when the soils are relatively wet (greater than 45% WFPS).

Potential explanations for the moisture-induced reduction of CH_4 consumption include (1) a shift in the net flux towards more CH_4 production at high soil moisture [*Yavitt et al.*, 1990; *Sexstone and Mains*, 1990], (2) physiological stress on the microbial communities that oxidize CH_4 at high soil moisture [*Adamsen and King*, 1993], and (3) alterations in soil gas transport rates at high soil moisture. Results from our moisture manipulation experiments [*Castro et al.*, 1994b] suggest that very little CH_4 is produced in these soils under wet conditions (60 to 100% WFPS) because CH_4 concentrations remained nearly constant at 0.2 ppm from 20 to 50 cm into the mineral horizon. In addition, soil microbial communities do not appear to be severely stressed by exposure to high soil moisture because these soils resumed the consumption of atmospheric CH_4 immediately after the 10-cm water additions [*Castro et al.*, 1994b]. Reduced CH_4 consumption is likely to be caused by slower transport of CH_4 from the atmosphere to the subsurface zone of consumption at high soil moisture because CH_4 transport is 10,000 times slower in water than in air.

Low soil moisture can also affect CH_4 consumption. Previous field studies in desiccated tropical forest [*Keller et al.*, 1990] and desert soils [*Striegl et al.*, 1992] suggest that low soil moisture (0.6-12% by weight) inhibits CH_4 consumption. At our temperate forest sites, however, low soil moistures (20 to 40% WFPS) coincided with high CH_4 consumption rates (Figure 4). In fact, our largest monthly averaged CH_4 consumption rate observed in June 1992 coincided with the lowest mineral soil moisture (20% WFPS) ever measured at this site. Thus over the duration of our 6-year study, we found that the Harvard Forest sites never had soil moistures low enough to inhibit CH_4 consumption even during the 12-week water exclusion experiments. Additional studies are needed to determine the effect that soil moistures below 20% WFPS have on CH_4 consumption by soils at our study sites. Future climatic conditions that create soil moistures between 20 to 40% WFPS for longer time periods relative to current conditions are likely to increase the annual strength of this sink.

At mineral soil moisture contents between 20 to 60% WFPS, CH_4 consumption ranged from 0.05 to 0.25 mg CH_4-C $m^{-2}h^{-1}$ (Figure 4). Potential reasons for this large variation include (1) constraints on CH_4 transport into soils [*Dorr et al.*, 1993; *Striegl*, 1993] and (2) spatial variations in site fertility. At low soil moisture, soil texture is an important controller of CH_4 transport because soil texture establishes the maximum possible rate at which CH_4 can be transported from the atmosphere to the subsurface zone of CH_4 consumption. Soil texture, however, could not explain why the coarser textured Tom Swamp soils had lower (2 to 3 times) consumption rates than our finer textured Prospect Hill soils (Table 2). In fact, soil texture considerations alone would predict that coarse texture soils should have higher consumption rates. We believe that our results can be explained by spatial variations in site fertility because site fertility affects the activity of the microbial communities in the soil. High-fertility sites, such as the Prospect Hill stands, may have higher consumption rates because they have either a more active population of CH_4 oxidizing bacteria or greater numbers of active CH_4 oxidizing bacteria relative to the lower fertility sites, such as Tom Swamp. Additional support for our hypothesis comes from measurements made at low-fertility soils in Acadia, Maine [*Castro et al.*, 1993]. These soils

Table 3. Results From Field Measurements of the Net Exchange of Methane Between the Atmosphere and Soils in Temperate Forest Ecosystems

Location	Overstory	Soil Texture	Sampling Period	Methane Flux, mg CH_4-C m^{-2} h^{-1}		Reference
				Range	Average	
United States						
New York and New England	spruce-fir	spodosol	May-Aug. 1990	+0.1 to -0.08	-0.02 to -0.05	*Castro et al.* [1993]
Durham , New Hampshire	mixed	inceptisol	March-Nov. 1989	-0.002 to -0.09	-0.06	*Crill* [1991]
	deciduous	loamy sand	April-Dec. 1990	-0.03 to -0.11	-0.07	*Crill* [1991]
Hubbard Brook, New Hampshire	mixed deciduous	sandy-loam	March-Nov. 1981	+0.007 to -0.02	-0.01	*Keller et al.* [1983]
Petersham, Massachusetts						
Tom Swamp	mixed deciduous	loamy sand	March-Dec. 1991	+0.005 to -0.105	-0.05	*Bowden et al.* [1993]
Soil Warming	mixed deciduous	loamy sand	April-Nov. 1992	-0.04 to -0.14	-0.10	*Peterjohn et al.* [1993]
Prospect Hill	mixed deciduous	loamy sand	May 1988-Dec. 1993	-0.09 to -0.13*	-0.11†	this study
	red pine	loamy sand	May 1988- Dec. 1993	-0.11 to -0.14*	-0.12†	this study
Germany						
Heidelberg	beech/spruce	sandy	April 1987-Dec. 1990	-0.03 to -0.25	-0.11	*Dorr et al.* [1993]
	beech/spruce	sandy	April 1987-Dec. 1990	-0.03 to -0.26	-0.09	*Dorr et al.* [1993]
	beech/oak/maple	loamy	April 1987-Dec. 1990	0 to -0.12	-0.05	*Dorr et al.* [1993]
	spruce	clay	April 1987-Dec. 1990	0 to -0.04	-0.01	*Dorr et al.* [1993]
	mixed deciduous	clay	April 1987-Dec. 1990	0 to -0.04	-0.01	*Dorr et al.* [1993]
Konstanz		silty loam	Feb. to Oct. 1992	0 to -0.06	-0.02	*Koschorreck and Conrad* [1993]

* Range of annually average CH_4 consumption rates over 6-year period.
† Grand mean from all annually averaged consumption rates (1988-1993).

had annual net mineralization rates of about 20 kg N ha^{-1} yr^{-1} and annually averaged CH_4 consumption rates (0.02 mg CH_4-C $m^{-2}h^{-1}$) that were about 5 times lower than annually averaged CH_4 consumption by Prospect Hill control soils (Table 3). These data suggest that inherent site fertility may account for the spatial variations in CH_4 consumption by forest soils with similar soil moistures. Thus we believe that site fertility and soil texture are the most important controllers of CH_4 consumption by forest soils.

Methane consumption was affected by NH_4NO_3 fertilization. Our fertilized plots always had lower CH_4 consumption than control soils (Figures 1a and 1b, and Table 1). This result is consistent with results from other fertilization studies [*Steudler et al.*, 1989; *Mosier et al.*, 1991; *Nesbit and Breitenbeck*, 1992; *Adamsen and King*, 1993; *Hutsch et al.*, 1993; *Castro et al.*, 1994a]. The suppression of CH_4 consumption appears to be associated with (1) high soil NH_4 concentrations [*Jones and Morita*, 1983; *Steudler et al.*, 1989; *Adamsen and King*, 1993; *King and Schnell*, 1994], (2) high nitrite concentrations [*King and Schnell*, 1994], and (3) changes in the soil nitrogen dynamics [*Mosier et al.*, 1991; *Nesbit and Breitenbeck*, 1992; *Hutsch et al.*, 1993]. Thus changes in the soil nitrogen cycle following fertilization may induce shifts in the relative activities of the microbial populations that oxidize atmospheric CH_4 from those dominated by methanotrophs in unfertilized soils to those dominated by ammonium oxidizers in fertilized soils [*Castro et al.*, 1994a]. Ammonium oxidizers have 100 to 10,000 times lower CH_4 oxidation rates the methanotrophs [*Jones et al.*, 1984].

Unlike the results from our NH_4NO_3 fertilization study, CH_4 consumption was not suppressed but increased along our fertility gradient. This increase may be because our highest-fertility site had inorganic nitrogen concentrations and/or soil nitrogen dynamics that were not high enough to suppress microbial processes responsible for CH_4 consumption. This suggestion is supported by laboratory studies. *Jones and Morita* [1983] showed that CH_4 oxidation by pure cultures of nitrifying bacteria increased ten-fold as NH_4 concentrations increased from 0 to 10 ppm but was suppressed at NH_4 concentrations above 10 ppm.

An important challenge is to predict how global changes, such as climate, land use, and atmospheric nitrogen deposition, will affect the exchange of greenhouse gases between the atmosphere and biosphere. Global climate models predict that the future climate of New England will have warmer air temperatures (4° to 8°C), more precipitation (1 mm d^{-1}) in the winter and less precipitation (2 mm d^{-1}) in the summer [*Mitchell et al.*, 1990]. These climate changes may increase the magnitude of the CH_4 sink because (1) warmer temperatures will increase the length of the season for CH_4 consumption and (2) greater CH_4 consumption will occur in the summer because of drier soils. This prediction is probably unrealistic because it does not account for other important environmental changes that may occur simultaneously with climate change. For example, fossil fuel use in the future is expected to increase the rates of atmospheric nitrogen deposition to terrestrial ecosystems [*Galloway et al.*, 1994]. Increased nitrogen deposition may lower the ability of these soils to consume atmospheric CH_4. In addition, land use has also been shown to reduce the rates of CH_4 consumption by a variety of temperate and tropical soils [*Keller et al.*, 1990; *Steudler et al.*, 1991; *Ojima et al.*, 1993]. Thus we need a better understanding of the interactions among climate, nitrogen deposition, and land use to make accurate predictions of changes in the magnitude of the terrestrial CH_4 sink.

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