

Methane flux in subalpine wetland and unsaturated soils in the southern Rocky Mountains

Kimberly P. Wickland¹, Robert G. Striegl²,
Steven K. Schmidt³, and M. Alisa Mast²

Abstract. Methane exchange between the atmosphere and subalpine wetland and unsaturated soils was evaluated over a 15-month period during 1995–1996. Four vegetation community types along a moisture gradient (wetland, moist-grassy, moist-mossy, and dry) were included in a 100 m sampling transect situated at 3200 m elevation in Rocky Mountain National Park, Colorado. Methane fluxes and soil temperature were measured during snow-free and snow-covered periods, and soil moisture content was measured during snow-free periods. The range of mean measured fluxes through all seasons (a positive value represents CH₄ efflux to the atmosphere) were: 0.3 to 29.2 mmol CH₄ m⁻² d⁻¹, wetland area; 0.1 to 1.8 mmol CH₄ m⁻² d⁻¹, moist-grassy area; -0.04 to 0.7 mmol CH₄ m⁻² d⁻¹, moist-mossy area; and -0.6 to 0 mmol CH₄ m⁻² d⁻¹, dry area. Methane efflux was significantly correlated with soil temperature (5 cm) at the continuously saturated wetland area during snow-free periods. Consumption of atmospheric methane was significantly correlated with moisture content in the upper 5 cm of soil at the dry area. A model based on the wetland flux-temperature relationship estimated an annual methane emission of 2.53 mol CH₄ m⁻² from the wetland. Estimates of annual methane flux based on field measurements at the other sites were 0.12 mol CH₄ m⁻², moist-grassy area; 0.03 mol CH₄ m⁻², moist-mossy area; and -0.04 mol CH₄ m⁻², dry area. Methane fluxes during snow-covered periods were responsible for 25, 73, 23, and 43% of the annual fluxes at the wetland, moist-grassy, moist-mossy, and dry sites, respectively.

1. Introduction

Increases in the atmospheric concentration of methane (CH₄) have prompted researchers to identify and quantify methane sources and sinks globally and to evaluate factors that control emissions of methane to the atmosphere [Schlesinger, 1991]. Water-logged soils and sediments are large sources of methane emission to the atmosphere [Cicerone and Oremland, 1988; Bouwman, 1991; Crill et al., 1991], while aerobic environments such as unsaturated soils and oxygenated sediments are large sinks of methane [Reeburgh et al., 1993; Torn and Harte, 1996]. The direction and rate of net methane exchange between soils and the atmosphere (methane flux) result from the balance between production and oxidation of methane, which commonly occur simultaneously and in close proximity in soils [Topp and Hanson, 1991; Tate and Striegl, 1993]. The direction and rate of methane exchange are commonly highly variable both spatially and temporally [Whalen and Reeburgh, 1988; Mosier et al., 1993; Bubier et al., 1995; Moosavi et al., 1996].

Soil temperature and soil moisture content influence methane exchange between soils and the atmosphere, although their relative importance varies among and within ecosystems. Soil temperature can be an important control on methane emissions in areas where sufficient moisture and anaerobic conditions are available for methanogenesis [Roulet et al., 1992b; Moosavi et al., 1996]. Soil temperature was positively correlated with methane emissions from Alaskan wet meadow tundra [Bartlett et al., 1992; Morrissey and Livingston, 1992], northern boreal peatlands [Crill et al., 1988; Moore and Knowles, 1990; Bubier et al., 1995; Kettunen et al., 1996], and freshwater rice paddies [Seiler et al., 1984; Schütz et al., 1989b]. Conversely, other studies of methane flux in similar environments reported weak or no significant correlation between soil temperature and methane flux [Sebacher et al., 1986; Born et al., 1990; Bubier et al., 1993; Glenn et al., 1993; Christensen et al., 1997], suggesting other factors had greater influence on methane flux than soil temperature.

Soil moisture content is a major determinant of whether soils are net methane emitters or consumers because it directly influences the availability of oxygen, gas diffusion rates, and microbial activity. Saturated soils generally emit methane unless they are covered by unsaturated oxic soils where methane may be consumed. Increasing thickness of the unsaturated soil layer is negatively correlated with methane emission [Roulet et al., 1992a; Bubier et al., 1993; Dise, 1993; Moore and Roulet, 1993; Nykänen et al., 1998]. Soils are net methane consumers if atmospheric methane is consumed in addition to methane produced in deeper saturated

¹U.S. Geological Survey, Boulder, Colorado.

²U.S. Geological Survey, Denver, Colorado.

³Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder.

Copyright 1999 by the American Geophysical Union.

Paper number 1998GB900003.

0886-6236/99/1998GB900003\$12.00

soils. Increasing soil moisture content inhibits consumption of atmospheric methane by decreasing gaseous diffusion of methane into the soil [Striegl, 1993]. However, methane consumption may be limited in soils having low moisture content due to water stress on methanotrophs [Striegl *et al.*, 1992; Adamsen and King, 1993; Torn and Harte, 1996; West and Schmidt, 1998].

The range in magnitude and controls of methane flux have been studied in several ecosystem types, but there are few studies in seasonally snow-covered subalpine soils and wetlands. Mountain systems cover about 20% of the Earth's continental areas [Haerberli and Beniston, 1998], and portions can be snow-covered most of the year, having a relatively short growing season. Methane exchange in high-elevation ecosystems may be particularly sensitive to changes in temperature and precipitation. Mosier *et al.* [1993] reported that methane production and consumption in Wyoming subalpine meadow and forest soils during snow-free periods were spatially and temporally controlled by soil moisture. Methane consumption in Colorado subalpine dry meadow soils was influenced by soil moisture effects on both diffusion and microbial activity [Torn and Harte, 1996]. Smith and Lewis [1992] measured methane emissions from subalpine lake-associated wetlands in Colorado and reported that methane flux variability across five sites was explained in part by differences in soil temperature and soil organic carbon content. Potential rates of methane production of incubated Appalachian Mountain peat cores were constrained by low temperatures, as seen in winter, and possibly by chemical quality of peat substrates during the summer [Yavitt *et al.*, 1988]. Methane emissions in alpine soils during snow-free periods were greater from soils having high soil moisture content [Sebacher *et al.*, 1986; Neff *et al.*, 1994]. Studies of trace gas exchange through seasonal snowpacks indicate that microbial activity can continue throughout snow-covered periods [Dise, 1993; Sommerfeld *et al.*, 1993, 1996; Brooks *et al.*, 1996, 1997; Melloh and Crill, 1996; Winston *et al.*, 1995, 1997]. However, little is known about the controlling processes, rates, and importance of winter gas emissions to the annual carbon budgets of different soil types [Sommerfeld *et al.*, 1993; Brooks *et al.*, 1995; Melloh and Crill, 1996; Mast *et al.*, 1998].

Knowledge of the seasonality of C fluxes and of factors influencing flux are important for estimating regional and global carbon cycling. This is particularly important for areas having seasonal snowpack, where differences in flux between snow-covered and snow-free periods may be considerable and where biological processes, such as plant growth, occur very quickly once snow melts [Briggs and MacMahon, 1983; Chapin and Oechel, 1983]. This paper documents the range in magnitude of methane flux that occurs in subalpine regions for soils having a range of soil moisture content and vegetation community types during a 15 month period, including snow-covered and snow-free periods. Methane fluxes were measured weekly (during snow-free periods) to monthly (during snow-covered periods) at four areas. Ancillary data include soil temperature and moisture content. The measurements were used to characterize temporal variation in methane fluxes of seasonally snow-covered subalpine soils; to quantify the importance of soil temperature

and soil moisture content as controls on methane exchange between subalpine soils and the atmosphere; and to calculate the annual methane emission from a subalpine wetland using a soil temperature model.

2. Site Description

The study site was conducted in the Loch Vale Watershed (40°18'N, 105°40'W), an alpine/subalpine basin on the east side of the continental divide in Rocky Mountain National Park, Colorado (Figure 1). The climate is characterized by long, cold winters and a 3-4 month snow-free period. Mean daily air temperatures range from -6.0°C in the winter to 13.7°C in the summer [Baron, 1992]. Average annual precipitation is 100 cm/yr, of which 70% falls as snow during October through May [Baron, 1992]. Spring snowmelt is the major hydrologic event of the year, with more than 60% of the annual streamflow occurring during snowmelt periods in June and July [Mast *et al.*, 1995].

The study site is located at an elevation of 3200 m and includes a 0.4 ha wetland and surrounding unsaturated soils (Figure 1). It is bordered by a steep talus slope to the north, and by streams to the south and east. Englemann spruce (*Picea engelmannii* Pargy), subalpine fir (*Abies lasiocarpa* Hook) forest extends to ~3250 m elevation and surrounds the study area. The wetland slopes downward (<1°) from the west and receives about 10 hours of direct sunlight per day in the summer months.

A 100 m transect spanning a moisture and vegetation gradient was established, and eight flux measurement sites within the transect were distributed among four community types designated: wetland (W), moist-grassy (MG), moist-mossy (MM), and dry (D) (Figure 1). The wetland area had three flux measurement sites, the moist-grassy and moist-mossy areas each had two sites, and the dry area had one site. These eight sites were also included in the ten sites used for winter CH₄ and CO₂ flux measurements discussed in Mast *et al.* [1998]. The number of flux measurement sites was limited by the remote location of the study area, which is ~6 km from the nearest road and accessible only by foot, and by sometimes harsh weather conditions. Boardwalks were not used because man-made structures are not allowed in the watershed. Extreme care was taken to avoid disturbance of the study area during flux measurements.

Table 1 describes characteristics of each site. Peat underlies the W, MG, and MM areas. It is 175 cm thick in the center of the wetland, and is underlain by coarse-sandy sediment. Table 2 lists approximate ages of peat and wood fragments collected from various depths within the peat profile.

3. Methods

3.1. Methane Flux

Methane flux measurements were made weekly or bimonthly during August-October 1995 and May-October 1996, and monthly during January-April 1996. Two different methods were used to estimate methane flux depending on the presence or absence of snowpack.

3.1.1. Methane flux measurements during snow-free periods. During snow-free periods, methane flux

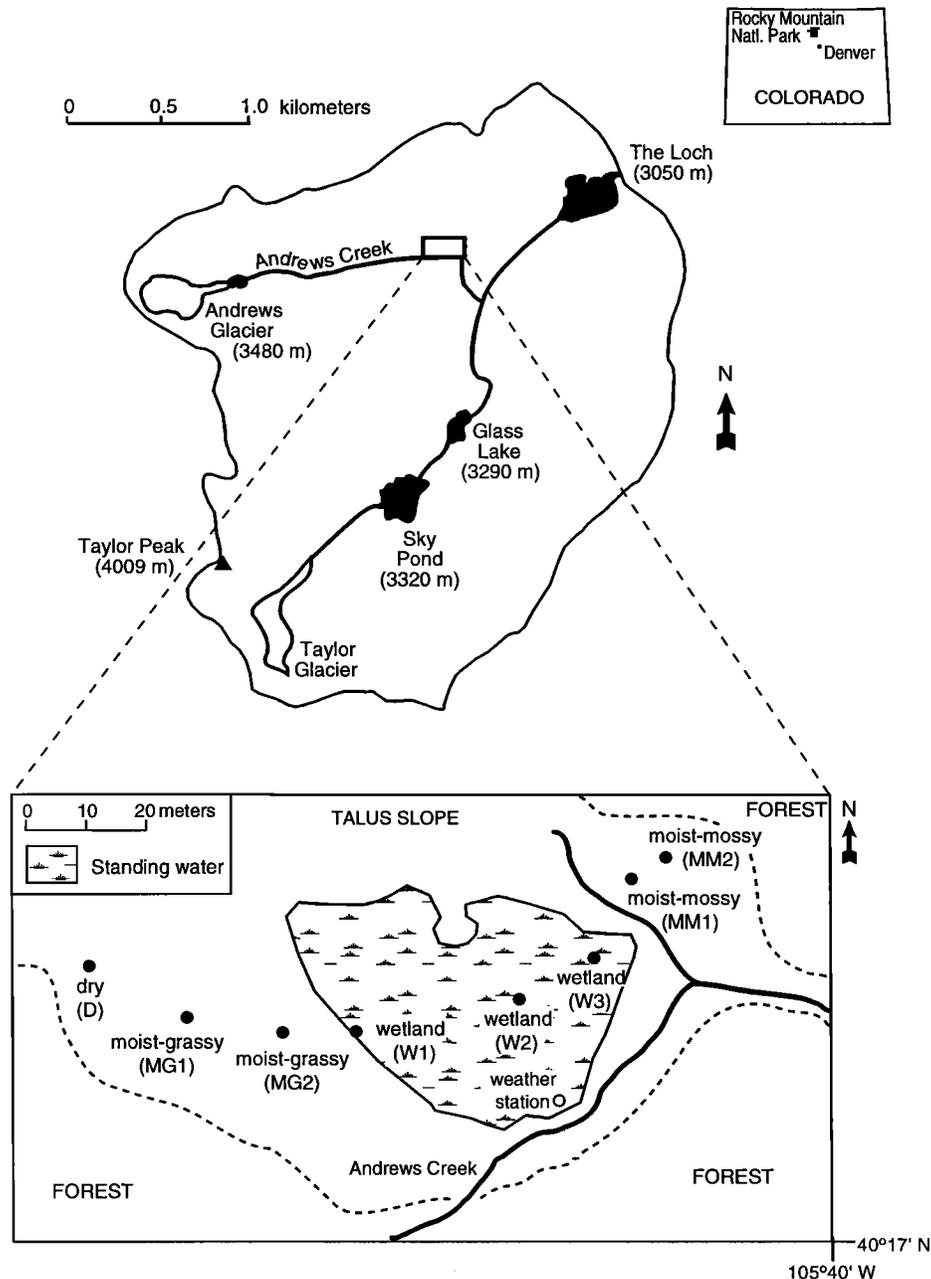


Figure 1. Map of the Loch Vale Watershed in Rocky Mountain National Park, Colorado, and the study site.

measurements were made using the closed chamber technique, in which the accumulation or loss of CH_4 in a chamber placed on the soil surface was measured over time [Healy *et al.*, 1996]. The cylindrical chamber (20 cm height, 19.5 cm inner diameter) having an open bottom and a closed top was constructed of clear polyvinyl chloride (PVC) and Lexan. A sample port fitted with a three-way stopcock was located at the top center of the chamber, and a coiled aluminum tube (1.6 mm inside diameter) was installed through the sidewall for pressure equalization. A small 12 volt computer fan improved chamber air circulation. A plastic skirt was attached around the chamber bottom and weighted with

sand-filled nylon stockings to prevent gas exchange between the chamber and the atmosphere during measurements.

Chambers were deployed for 8 min (W sites), 16 min (MG and MM sites), or 32 min (D site), depending on the anticipated time needed to detect methane flux. Sample times were increased by 2-4 min when methane fluxes decreased in September and October. Chamber air samples were collected five times at regular intervals during each deployment starting at time zero using gas-tight 20 mL nylon syringes. The samples were analyzed for methane concentration within 32 hours of collection using a Chrompack model 438A gas chromatograph (GC) having a 2 m 80-100 mesh Porapak-N

Table 1. Site Descriptions

Site	Soil (0-10 cm)	Average Percent Saturation (0-10 cm)	Vegetation
W1	64% organic (76% 0-5 cm)	100%	<i>Carex aquatilis</i> , <i>Carex utriculata</i> , <i>Juncus arcticus</i>
W2	88% organic	100%	
W3	79% organic	100%	
MG1	72% organic	74% (range 52-100%)	<i>Phleum commutatum</i> (alpine timothy), <i>Deschampsia cespitosa</i> (tufted hairgrass), scattered <i>C. aquatilis</i> and <i>Carex nigricans</i> , <i>Caltha leptosepala</i> (marsh-marigold)
MG2	67% organic	67% (range 51-99%)	
MM1	70% organic	76% (range 47-100%)	<i>Sphagnum</i> spp., <i>Kalmia microphylla</i> (alpine laurel), <i>Arctostaphylos uva-ursi</i> (kinnikinnik)
MM2	86% organic	75% (range 57-100%)	
D	25% organic	35% (range 16-59%)	Grasses, <i>Bistorta bistortoides</i> , <i>Chlorocrepis tristis</i> (hawkweed)

column, a flame ionization detector, nitrogen carrier gas, and an oven temperature of 40°C. Calibration tables were developed using four methane standards (0.49, 1.80, 21.1, and 604 ppm CH₄). Chromatographic data were integrated using a Hewlett-Packard HP 3365 Series II ChemStation computer program.

The net rate of methane emission or consumption was determined by

$$J = (dC/dt)h \quad (1)$$

where J is flux across the soil surface (mol m⁻² t⁻¹), C is the concentration of methane in the chamber at ambient temperature and pressure (mol m⁻³), t is time, h is chamber height (m), and dC/dt is the slope of the linear regression of methane concentration on time as time approaches zero [Rolston, 1993; Healy et al., 1996]. Flux is expressed in units of mmol CH₄ m⁻² d⁻¹. Chamber measurements reported here have a linear regression r^2 equal to or greater than 0.95.

Table 2. Age Dates and Species Identification of Peat and Wood Fragments Collected at Depth Near Site W2

Material	Depth, cm	Approximate Age, Years Before Present	Species
Peat	80	2300	--
Wood fragments	120-125	6200	<i>Picea engelmannii</i>
Wood fragments	138-155	7100	<i>Abies lasiocarpa</i>
Wood fragments	156-166	7500	<i>P. engelmannii</i>

Radiocarbon age dates via H. Haas (written communication, 1997). Species identification via P. Brown (written communication, 1997).

3.1.2. Methane flux measurements during snow-covered periods. During snow-covered periods, methane flux was calculated using the measured methane concentration gradient in the snowpack and physical snowpack properties [Mast et al., 1998]. Gas samples were collected from different depths in the snowpack at each site in 20 mL nylon syringes through a 3.5 m long stainless steel probe (3 mm inner diameter). Samples were taken at the air-snow interface, every 10-40 cm within the snowpack depending on total depth, and near the snow-soil interface when possible. The samples were analyzed for methane concentration as described earlier. Physical snowpack measurements were made within 2 days of each gas collection date. Snowpack density was measured from a vertical snowpit face using a 1 L stainless steel cutter, and snow temperatures were measured every 10 cm in the pit wall [Mast et al., 1998].

Methane flux to and from the soil through the snowpack was calculated using a one-dimensional form of Fick's law describing ordinary gaseous diffusion in porous unsaturated media [Striegl, 1993]:

$$J = -D_c \theta \tau (dC/dz) \quad (2)$$

where J is flux (mol m⁻² t⁻¹), D_c is the diffusion constant of methane through air at ambient temperature and pressure (m² t⁻¹), θ is snowpack porosity (dimensionless), τ is the tortuosity coefficient (dimensionless), and dC/dz is the measured concentration gradient of methane in the snowpack (mol cm⁻³ m⁻¹). The diffusion constant of methane through air at standard temperature and pressure, 1.69 m² d⁻¹, was corrected for temperature and pressure using the following equation [Striegl, 1993]:

$$D_c = 1.69(101,325/P)(T/273.15)^{1.823} \quad (3)$$

where P is atmospheric pressure (Pa), and T is temperature (K). Porosity was calculated from the average density of the snowpack (ρ_{snow}) and the density of ice (ρ_{ice}):

$$\theta = (1 - \rho_{\text{snow}}) / \rho_{\text{ice}} \quad (4)$$

The tortuosity coefficient was estimated as $\theta^{1/3}$, a theoretical value sometimes used when modeling diffusion through soils [Millington, 1959; Striegl, 1993]. Effective methane diffusivities, snow porosities, and tortuosities used in this study are reported by Mast *et al.* [1998].

Methane flux was calculated using the linear concentration gradient of methane and the average snowpack density. Nonlinear gradients were common in spring when midpack ice lenses altered methane diffusion. Detailed information on how methane fluxes were calculated from nonlinear gradients and examples of observed concentration gradients at the study site are described by Mast *et al.* [1998].

3.2. Soil Temperature

Soil temperatures during snow-free periods were measured for each site during flux measurements using a Fluke model 51 K/J Thermometer with a Type K Piercing Probe (length equal to 10.16 cm) inserted to 5 and 10 cm depths. Permanently installed thermistors continually measured soil temperatures at 1, 5, and 10 cm depths in a saturated area of the wetland, and temperatures were recorded hourly by a data logger at the weather station. The continuous temperature record began October 6, 1995, and continued through December 31, 1996.

3.3. Soil Moisture Content

Soil samples were collected from 0-15 cm below the soil surface at sites without standing water concurrent with methane flux measurements during 1996 snow-free periods. Blocks of soil (approximately 64 cm³) were cut at 5 cm increments and stored in air-tight containers until analysis. Gravimetric moisture content was calculated from the

difference in sample weights before and after oven-drying at 105°C for 24 hours. Dry bulk density was calculated by dividing the dry sample weight by the initial sample volume. Organic and mineral fractions were differentiated by burning the samples at 450°C for 24 hours. Solids density was calculated assuming the densities of organic matter and mineral matter are 1.55 and 2.65 g cm⁻³, respectively [Carter, 1993]. Percent saturation was calculated as the volumetric water content divided by pore space volume times 100.

4. Results

4.1. Site Conditions 1995-1996

The 1994-1995 winter season snowpack reached a maximum depth of 210 cm in mid-May 1995, and cold temperatures delayed the onset of snowmelt until mid-June. The 1995-1996 winter season snowpack began to accumulate in November and reached a maximum depth of 300 cm in late April 1996. Rapid snow accumulation in January triggered an avalanche that ran through the wetland and destroyed a portion of the surrounding forest. Snowmelt began in mid-May (snowpack was isothermal on May 15), and all of the flux measurement sites were snow-free by June 28. Mast *et al.* [1998] gives detailed descriptions of the 1994-1995 and 1995-1996 snowpacks and winter conditions.

The continuous soil temperature record indicates that wetland soils at 5 cm were never less than 0°C (Figure 2), which can be attributed to the insulating effects of the deep snowpack [Brooks *et al.*, 1996; Mast *et al.*, 1998]. Similar results were observed by Sommerfeld *et al.* [1996] at a subalpine site in Wyoming. Soil temperatures remained stable until the end of snowmelt, when they increased sharply about 12°C in 4 days at the wetland (Figure 2). Throughout July, snowmelt water from higher elevations flowed through the

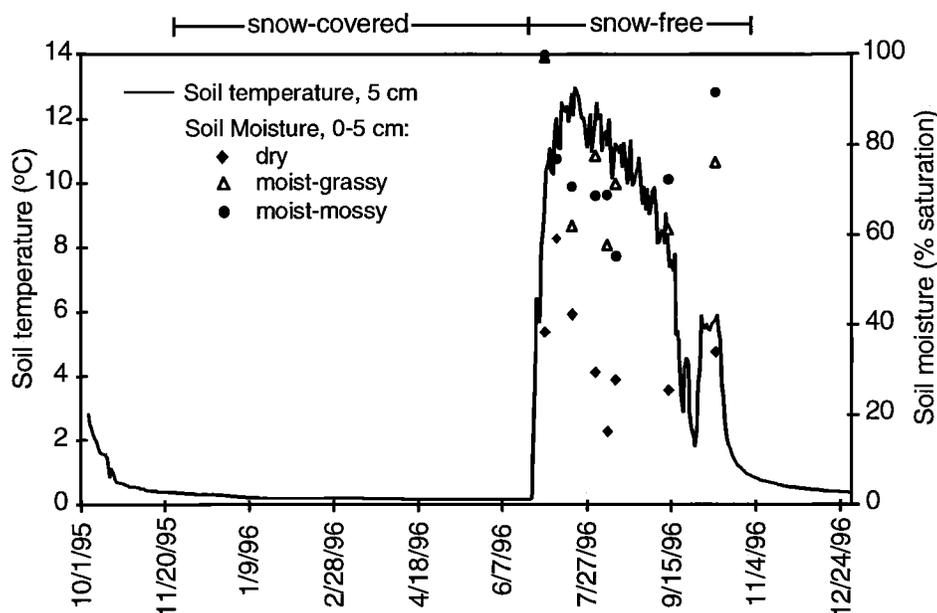


Figure 2. Wetland soil temperature at 5 cm depth recorded hourly at the weather station, 1995-1996; and soil moisture at the moist-grassy, moist-mossy, and dry sites, 1996.

Table 3. Mean Monthly Air and 5 cm Soil Temperatures

	Air Temperature, °C	Soil Temperature, °C 5 cm
Aug. 1995	13.4	--
Sept. 1995	6.5	--
Oct. 1995	0.5	1.3
June 1996	9.1	1.4
July 1996	12.8	13.1
Aug. 1996	11.8	12.2
Sept. 1996	5.9	7.2
Oct. 1996	1.6	3.9

study area. Soil moisture content at the moist and dry sites was greatest immediately after snowmelt, generally decreased through August, then increased in October (Figure 2). Mean air and 5 cm soil temperatures during the 1995 and 1996 snow-free periods are listed in Table 3.

4.2. Methane Flux 1995-1996

Mean methane fluxes are listed in Table 4; fluxes on each date represent one (D), two (MG, MM), or three (W) chamber measurements. Individual methane flux measurements are listed by Wickland [1997]. Methane fluxes were positive (methane was emitted from the soils) at W and MG, and at MM except on one occasion. Methane fluxes were always negative (atmospheric methane was consumed by the soils) or zero at D. Each site exhibited varying degrees of seasonality of methane flux during the 1995-1996 sampling period. Mean measured fluxes during 1996 snow-covered and snow-free periods (Table 4) sum to total annual fluxes of the following: W=2.35 mol CH₄ m⁻², MG=0.12 mol CH₄ m⁻², MM=0.033 mol CH₄ m⁻², and D=-0.042 mol CH₄ m⁻² for 1996. The percentages of the total annual methane fluxes occurring during snow-free periods (111 days) were as follows: W=75%, MG=27%, MM=77%, and D=57% (Figure 3).

4.3. Relationship Between Soil Temperature and Methane Flux

Linear regressions of mean methane fluxes and concurrently measured 5 cm soil temperatures (weather station temperatures used for W) during the entire 1995-1996 sampling period indicated a significant relationship at W ($r^2=0.73$, $p<0.001$) and MM ($r^2=0.41$, $p=0.01$), but not at MG or D ($p>0.05$). Methane fluxes during 1995-1996 snow-free periods were significantly related to 5 cm soil temperatures only at W ($r^2=0.55$, $p=0.02$). Individual soil temperatures are listed by Wickland [1997].

The relationship between 1996 methane emission rates at the wetland and 5 cm soil temperatures at the weather station is shown in Figure 4. Methane fluxes increased with rising soil temperatures immediately after snowmelt, then decreased in late July and August despite relatively high temperatures. As soil temperatures cooled, methane emission returned to

rates observed during snow-covered periods. The hysteretic flux-temperature relationship suggests that other factors in addition to soil temperature, such as increased methane oxidation and/or substrate limitation, were influencing methane flux from the wetland.

4.4. Relationship Between Soil Moisture Content and Methane Flux

Soil moisture content (percent saturation) at 0-5 cm depth was significantly correlated with 1996 snow-free methane fluxes at D (linear regression, $p=0.002$) and explained 87% of the variation in flux. Within the observed range of soil moisture content, the net consumption of methane at D increased exponentially as the soil became more saturated (Figure 5).

Soil in the wetland was considered to be saturated at all times because standing water was present, so it was assumed that soil moisture content did not change. Soil moisture (individual values listed by Wickland [1997]) was not significantly correlated with mean methane fluxes at MG or MM (linear regression, $p>0.05$). Multiple regressions of 1996 snow-free methane fluxes with soil temperature and soil moisture content showed no significant correlation at MG or MM and no improvement on the soil moisture-methane flux relationship at D ($p>0.05$).

4.5. Annual Methane Flux Estimate at the Wetland

Annual methane flux at the wetland was estimated using a flux-temperature model constructed from the 1996 mean fluxes and the hourly 5 cm soil temperature record at the weather station. The hysteretic flux-temperature relationship is best described by two equations (Figure 4). The period including snowcover through the onset of snowmelt and rising temperatures immediately following snowmelt, January 1 through July 2, is best described by a second-order polynomial equation ($r^2=1$):

$$J = -0.101x^2 + 3.5576x + 4.6281 \quad (5)$$

where J is mmol CH₄ m⁻² d⁻¹ and x is soil temperature (°C) at 5 cm. The following period, from July 23 through the expected return to similar winter values at the end of the year, is best described by the exponential relationship ($r^2=0.94$):

$$J = 1.7493e^{0.2007x} \quad (6)$$

These equations describe the seasonal shift in the flux-temperature relationship at the wetland more accurately than a single exponential fit ($r^2=0.8$).

Hourly methane fluxes were calculated by applying equations (5) and (6) to the 5 cm soil temperature record. Equation (5) was applied to soil temperatures during January 1 to July 7, 1996; and equation (6) was applied to soil temperatures during July 8 to December 31, 1996. Because there were no flux measurements made between July 2 and 23, it is difficult to predict when the shift in the flux-temperature relationship occurred. The two equations intersect at ~14.5°C (Figure 4); therefore the shift was designated as the first day having an hourly 5 cm soil temperature above 14°C.

Table 4. Mean Methane Fluxes, 1995-1996

Date	Wetland			Moist-Grassy			Moist-Mossy			Dry		
	CH ₄ Flux, mmol m ⁻² d ⁻¹	n	Range, mmol m ⁻² d ⁻¹	CH ₄ Flux, mmol m ⁻² d ⁻¹	n	Range, mmol m ⁻² d ⁻¹	CH ₄ Flux, mmol m ⁻² d ⁻¹	n	Range, mmol m ⁻² d ⁻¹	CH ₄ Flux, mmol m ⁻² d ⁻¹	n	
Aug. 10, 1995	--	--	--	1.84	2	1.37-2.31	--	--	--	--	--	
Aug. 16, 1995	16.94	3	10.03-23.76	0.94	1	--	--	--	--	-0.16	1	
Aug. 23, 1995	17.99	2	10.45-25.53	1.08	2	1.02-1.15	--	--	--	-0.62	1	
Sept. 7, 1995	29.23	3	11.87-38.19	0.70	2	0.27-1.12	--	--	--	-0.30	1	
Sept. 26, 1995	3.27	3	1.70-6.19	0.30	2	-0.16-0.75	0.095	1	--	-0.09	1	
Oct. 16, 1995	3.21	1	--	0.21	2	0.019-0.40	--	--	--	-0.026	1	
Oct. 29, 1995	0.29	2	0.24-0.34	0.49	2	-0.035-1.02	-0.04	1	--	0	1	
Jan. 9, 1996	0.78	3	0.38-1.37	0.09	2	0.001-0.18	0.001	1	--	-0.023	1	
Feb. 5, 1996	1.18	3	0.91-1.68	0.18	2	0.054-0.30	--	--	--	--	--	
March 20, 1996	0.86	3	0.46-1.10	0.43	2	0.056-0.80	0.015	2	0.002-0.028	-0.015	1	
April 8, 1996	1.98	3	1.28-2.35	0.32	2	0.31-0.33	0.014	2	-0.009-0.037	-0.011	1	
May 7, 1996	6.85	3	3.14-9.53	1.74	2	1.39-2.08	0.005	1	--	-0.013	1	
May 15, 1996	1.64	3	1.00-2.82	0.35	2	0.20-0.84	0.006	2	0.003-0.009	-0.021	1	
May 21, 1996	1.90	3	0.87-3.44	0.24	2	0.16-0.33	0.010	2	0.009-0.011	-0.014	1	
May 31, 1996	1.86	3	0.94-2.54	0.42	2	0.20-0.65	0.034	2	0.027-0.04	-0.018	1	
June 4, 1996	4.64	3	0.60-11.15	0.29	2	0.056-0.52	0.020	2	0.018-0.021	-0.010	1	
June 11, 1996	0.82	3	0.053-1.81	0.28	2	0.053-0.50	0.025	2	-0.014-0.064	-0.023	1	
June 18, 1996	3.77	2	3.74-3.80	0.25	2	0.013-0.48	0.21	2	0.10-0.32	-0.019	1	
June 28, 1996	20.17	3	6.21-29.07	0.37	2	0.025-0.70	--	--	--	-0.12	1	
July 2, 1996	27.85	3	25.09-30.61	0.26	2	0.21-0.30	--	--	--	-0.25	1	
July 23, 1996	22.31	3	18.43-27.57	0.41	2	0.40-0.41	0.67	2	0.01-1.33	-0.42	1	
Aug. 8, 1996	16.42	3	14.71-19.22	0.44	2	0.39-0.49	0.015	2	0-0.03	-0.05	1	
Aug. 15, 1996	15.59	3	9.88-24.28	0.21	2	0.090-0.32	--	--	--	-0.05	1	
Sept. 9, 1996	14.31	3	11.85-17.00	0.21	2	-0.029-0.45	0.17	2	0.039-0.30	-0.11	1	
Oct. 11, 1996	3.51	3	2.43-4.64	0.28	2	0.034-0.53	0.075	2	0-0.15	-0.36	1	
1996 mean	8.14	53		0.38	36		0.091	26		-0.09	17	
1996 snow-covered mean	2.39	32		0.42	22		0.014	18		-0.017	10	
1996 snow-free mean	17.17	21		0.31	14		0.23	8		-0.19	7	

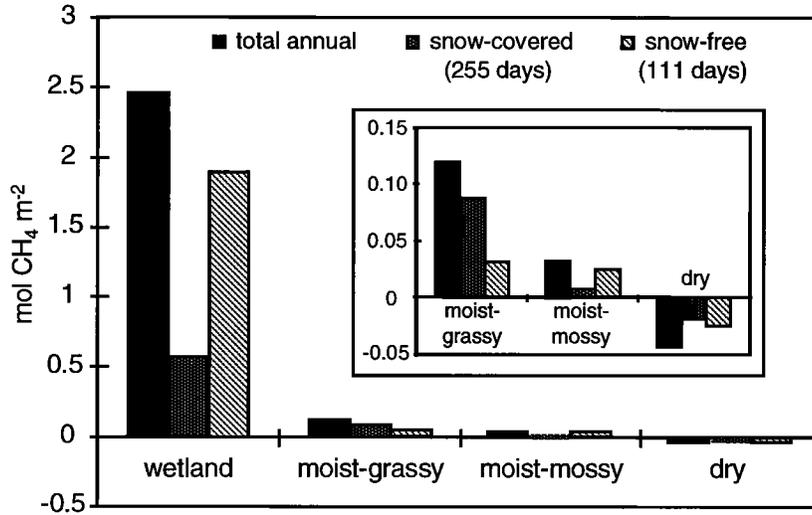


Figure 3. The 1996 annual, snow-covered, and snow-free methane fluxes at the four vegetation communities as determined by linear interpolation of the mean daily fluxes between the measurement dates. The inset shows fluxes at the moist and dry sites on a smaller scale.

Figure 6 shows the 1996 measured and predicted methane fluxes. Sensitivity analyses indicated that methane fluxes predicted by the two-equation model were within 12% of the measured rates during snow-free periods (6 of 7 within one standard deviation), whereas a single exponential model predicted fluxes that were 37% higher (3 of 7 within one standard deviation) than the measured rates during snow-free periods. The mean absolute difference between modeled and measured methane fluxes was 54% for snow-covered periods. The flux-temperature model did not predict the observed variability in fluxes during the snow-covered period because the 5 cm soil temperature record did not change appreciably (range equal to 0.15°-0.26°C, January 1 to June 23) (Figures 2 and 6).

The modeled annual methane flux from the wetland to the atmosphere during 1996 is 2.53 mol CH₄ m⁻² yr⁻¹. This is

about 8% greater than the annual flux estimated by linear interpolation (2.35 mol CH₄ m⁻² yr⁻¹) and 11% greater for the snow-free period only. Emissions during snow-free periods (111 days) account for 1.76 mol CH₄ m⁻² or 77% of the modeled annual flux, and emissions during snow-covered periods (255 days) account for 0.57 mol CH₄ m⁻² or 23% of the modeled annual flux.

5. Discussion

5.1. Soil Temperature and Methane Flux

The importance of soil temperature as a predictor of methane flux varied with site and season. Soil temperature was a significant predictor of flux during snow-free periods at the wetland, but not at the other sites. The positive relationship between soil temperature and methane flux

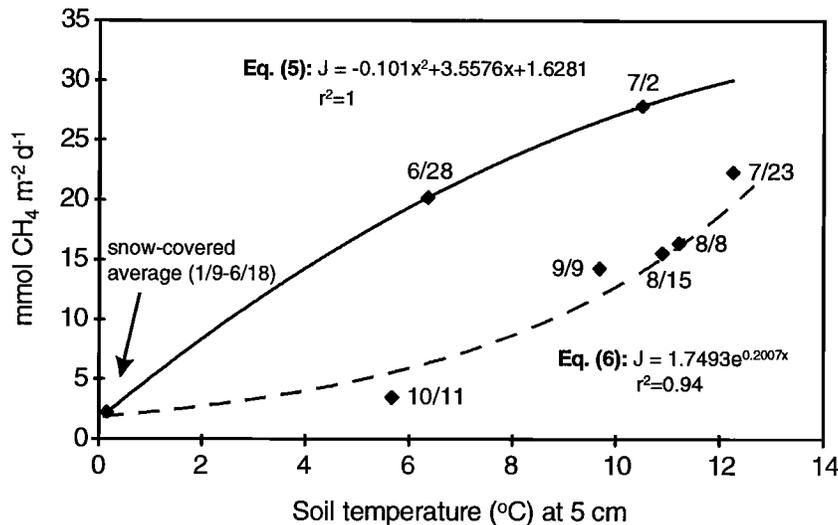


Figure 4. The 1996 mean daily emission rates at W versus soil temperature. Equation (5) is the second-order polynomial relationship between methane emission and temperature before and immediately after snowmelt, and equation (6) is the exponential relationship between emission and temperature as soils cool.

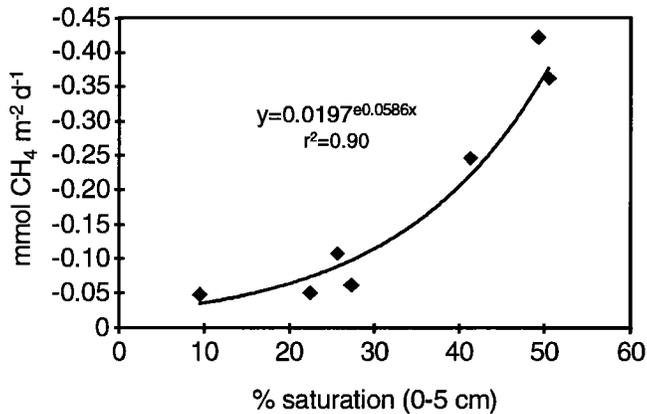


Figure 5. Mean net methane consumption at D versus percent soil saturation in the upper 5 cm during the snow-free period of 1996. The line represents the exponential relationship between methane consumption and percent soil saturation.

during snow-free periods at the wetland may result from direct stimulation of methanogenic activity and/or be a response to increased substrate availability from temperature-enhanced fermentation [Valentine *et al.*, 1994].

Temperature constraints on methanogenesis vary among studies. Methane production was optimal at 25°C and negligible below 10°C in laboratory manipulations of temperate and subarctic peat soils [Dunfield *et al.*, 1993]. However, methane production was detected in Appalachian peatland soils incubated at 6°C [Yavitt *et al.*, 1988]. Dise [1993] and Frohling and Crill [1994] detected methane emissions from snow-covered peat in situ that was at or below 0°C in the upper 20 cm. The wetland in our study emitted methane at temperatures as low as 0.1°C, the lowest 5 cm soil temperatures observed.

Periodic increases in methane emission from the wetland before and during snowmelt may have been caused by increases in microbial activity and/or microbial populations, release of methane stored within and beneath the snowpack,

and/or hydrologic change. Brooks *et al.* [1996, 1997] attributed increases in CO₂ and N₂O emissions from alpine soils before snowmelt to increased microbial activity due to substrate release as surface soils thawed under the snowpack as result of ground heat flux. This mechanism of substrate release probably does not apply to the wetland because soils did not freeze and did not warm until after snowmelt was complete. However, stable soil temperatures do not necessarily prohibit increased microbial activity or populations. Microbial activity can rise if free water is available under the snowpack. Lipson *et al.* [1998] observed that microbial biomass of alpine dry meadow soils generally increased through fall and winter under snowpack, and peaked during the spring before the soils were snow-free. The release of methane trapped beneath ice lenses within the snowpack and at the soil surface during snowmelt may have occurred. Melloh and Crill [1996] observed increases in near-surface soil methane stores under ice, and a build-up of methane in snowpack pore air beneath an ice layer. Mast *et al.* [1998] suggest that an episodic release of methane from the wetland through the snowpack may be related to influx of meltwater into the shallow groundwater system which may push methane-rich premelt water to the surface.

Methane fluxes at W increased sharply with soil temperature immediately after snowmelt. This is consistent with the observations of Yavitt *et al.* [1988] that the maximum annual potential for laboratory methane production in moss-dominated peatlands existed in the winter and early spring, but was constrained by temperature. Plant litter from the 1995 growing season may have provided high-quality substrates for the existing methanogens and other bacteria, and fueled the increase in microbial activity after snowmelt. Measured methane emission rates peaked 1 week after the wetland was snow-free, then declined in late July and August despite stable soil temperatures.

Methane emission from the wetland in mid to late summer was probably limited by factors other than soil temperature, such as substrate availability, aeration of sediments, and/or increased methane oxidation rates. The principal substrates used by methanogens are H₂, CO₂, and acetate, which result

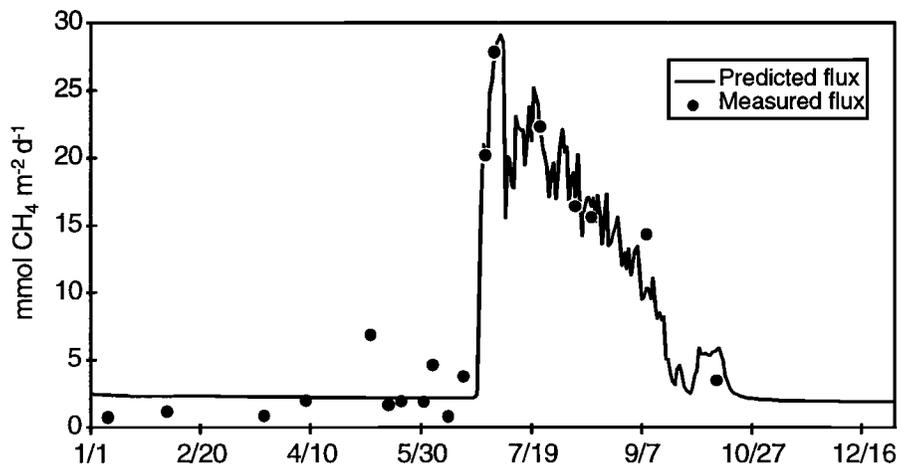


Figure 6. Predicted methane emissions, based on the flux-temperature model, and measured methane emissions at W, 1996.

from decomposition and fermentation of organic matter [Valentine *et al.*, 1994]. Rates of methanogenesis can be limited by rates of fermentation, which in turn are dependent on the amount and decomposability of organic matter, and temperature [Valentine *et al.*, 1994]. It is possible that fermentation became limited as labile plant decomposition products were consumed, resulting in substrate limitation of methanogenesis. Different components of plant litter have different decomposition rates, and the easily degradable nonlignocellulosic material in vascular plant litter can be utilized within days to weeks of deposition in aquatic systems [Moran *et al.*, 1989]. Labile substrates from litter deposition of the previous fall may have remained in the soil over winter until soil temperatures increased in the spring.

The decrease in methane fluxes after the observed peak rate may have been caused by aeration of the wetland sediments and/or increased rates of methane oxidation. Vascular plants can enhance methane emissions from sediments by serving as a conduit to the atmosphere, and can account for 75-90% of methane emissions from wetland ecosystems [Holzapfel-Pschorn *et al.*, 1986; Whiting and Chanton, 1992; Schimmel, 1995]. However, vascular plants transport oxygen to plant roots for root respiration, which may diffuse into the soil and fuel methane oxidation [Gerard and Chanton, 1993; Huang *et al.*, 1998]. Methane oxidation in the rhizosphere of rice plants and weeds consumed 77-95% of methane produced in rice paddies [Holzapfel-Pschorn *et al.*, 1986]. Schütz *et al.* [1989a] and Sass *et al.* [1992] observed that the emitted fraction of the methane produced in rice paddies declined with rice growth and development over the season [Huang *et al.*, 1998]. The measured maximum flux at the wetland occurred when aboveground plant biomass was relatively small. In the following 3 weeks, the aboveground biomass more than doubled (K. P. Wickland, unpublished data, 1997), and flux decreased more than 20%, while soil temperatures rose.

The effects of rising soil temperature on methane production at the moist sites may have been offset by increased methane oxidation in the upper soil layers. Substrate availability for methane production may have been a limiting factor at these sites as well. The magnitude of methane emissions was similar at the moist sites and the wetland during snow-covered periods. This suggests that there may have been temperature limitation of methane production in the surface soil while deep methane production continued in the underlying peat. Winston *et al.* [1997] observed similar conditions for winter CO₂ emission from boreal forest soils. Analysis of ¹⁴C in the forest soil CO₂ indicated that CO₂ produced during winter was much older than that produced during the growing season. They concluded that winter soil CO₂ originated from a deep, old carbon source where soil temperatures were high enough to maintain decomposition.

Net methane consumption at the dry site was not significantly related to soil temperature, agreeing with laboratory observations that methane consumption is less sensitive to changes in temperature than methane production [King and Adamsen, 1992; Dunfield *et al.*, 1993]. Tate and Striegl [1993] observed that less than 20% of the variation of in situ rates of net methane consumption in prairie soils were explained by soil temperature, and they attributed this to a masking of temperature sensitivity by the change in location

of methane consumption in the vertical soil profile and/or a change in the balance between methane production and consumption. It is possible that any temperature sensitivity of methane consumption at the dry site was masked in a similar manner.

5.2. Soil Moisture Content and Methane Flux

Methane emissions increased with increasing soil moisture content along the sampling transect. However, soil moisture content was a significant predictor of within-site temporal variability of methane flux only at the dry site. Physiological responses of methanotrophs to water stress may explain the positive relationship between soil moisture and net methane consumption at the dry site. Net consumption approached zero when soils in the top 5 cm were less than 30% saturated, and consumption increased about 4 times when soils reached 40-50% saturation. Torn and Harte [1996] and West and Schmidt [1998] noted similar correlations between soil moisture and methane consumption of Rocky Mountain soils. The dry site was never greater than ~50% saturated on sample days, but it is expected that net consumption would decrease at higher saturation levels.

5.3. Comparisons With Other Studies

Table 5 lists mean and annual methane fluxes from this study as well as from studies in similar environments. In general, both mean net methane emission and consumption rates in this study are greater than those measured in other subalpine soils. This may be due in part to between-site variability, climate variability, and/or differences in flux measurement technique. Mean methane flux during snow-free periods and the annual methane flux from the wetland are similar to those observed by Bubier *et al.* [1993] in some central Canadian wetlands. Mean methane flux during snow-covered periods from the wetland was the same as the 5-year average from a poor fen in New Hampshire [Melloh and Crill, 1996]. Mean net methane consumption during both snow-free and snow-covered periods at the dry site resembled those measured in an old-growth boreal forest in Canada [Wickland and Striegl, 1997].

5.4. Conclusions

Methane flux occurring during snow-covered periods in subalpine soils is a substantial portion of annual methane flux. Almost half of the annual net methane consumption at the dry site occurred during snow-covered periods, and 73% of the annual methane emission at the moist-grassy sites occurred during snow-covered periods. This indicates the importance of snow-covered periods when considering the annual methane flux of these types of subalpine soils. On an annual scale, subalpine wetland soils are a much greater source of methane to the atmosphere than other subalpine soils. Soil temperature was a significant predictor of the seasonality of methane emission from saturated subalpine wetland soils, and soil moisture content was an important predictor of seasonal variability of methane consumption from some unsaturated subalpine soils. Methane exchange in subalpine soils is therefore highly sensitive to short- and long-term local climate change.

Table 5. Comparison of Methane Fluxes

Location	Site Description	Elevation, m	Mean CH ₄ Flux, Snow-Free, mmol m ⁻² d ⁻¹	Mean CH ₄ Flux, Snow-Covered, mmol m ⁻² d ⁻¹	Annual CH ₄ Flux, mol m ⁻² yr ⁻¹	Reference
Colorado	wetland	3200	17.2	2.4	2.53	this study
Colorado	moist-grassy	3200	0.3	0.4	0.12	this study
Colorado	moist-mossy	3200	0.2	0.01	0.03	this study
Colorado	dry	3200	-0.2	-0.02	-0.04	this study
Colorado	alpine wet meadow	3500	0.003	n/a	n/a	<i>Neff et al.</i> [1994]
Colorado	alpine dry meadow	3500	-0.03	n/a	n/a	<i>Neff et al.</i> [1994]
Colorado	alpine/subalpine wetlands	2800-3600	2.1	0	n/a	<i>Smith and Lewis</i> [1992]
Colorado	subalpine dry meadow	2920	-0.08	n/a	n/a	<i>Torn and Harre</i> [1996]
Wyoming	subalpine meadow	3180	-0.02	-0.005	-0.004	<i>Mosier et al.</i> [1993]
West Virginia	sedge meadow	800-1000	n/a	n/a	16*	<i>Yavitt et al.</i> [1988]
Alaska	<i>Carex</i> stands	n/a	2	n/a	0.3	<i>Whalen and Reeburgh</i> [1988]
Canada	wetlands with standing water	n/a	5.7-21.9	n/a	0.8-3.4	<i>Bubier et al.</i> [1993]
Canada	boreal forest	n/a	-0.1	-0.08	n/a	<i>Wickland and Striegl</i> [1997]
New Hampshire	poor fen	n/a	n/a	2.4	n/a	<i>Melloh and Crill</i> [1996]

n/a, not available.

* Potential methane production of peat from 0-35 cm.

Acknowledgments. This research was funded by the Water, Energy, and Biogeochemical Budgets component of the Global Change Hydrology Program, U.S. Geological Survey; and EPA/NCERQA grant R82-3442-01. D. Clow graciously provided field assistance and weather station data, and P. Hern and A. Nutt provided field assistance. We thank the National Park Service for access to Rocky Mountain National Park. We thank P. Brooks and T. Huntington, and two anonymous referees for critical review of this paper.

References

- Adamsen, A.P.S., and G.M. King, Methane consumption in temperate and subarctic forest soils: Rates, vertical zonation, and responses to water and nitrogen, *Appl. Environ. Microbiol.*, 59(2), 485-490, 1993.
- Baron, J. (Ed.), *Biogeochemistry of a Subalpine Ecosystem: Loch Vale Watershed, Ecolo. Stud. Ser.*, vol. 90., 247 pp., Springer-Verlag, New York, 1992.
- Bartlett, K.B., P.M. Crill, R.L. Sass, R.C. Harriss, and N.B. Dise, Methane emissions from tundra environments in the Yukon-Kuskokwim Delta, Alaska, *J. Geophys. Res.*, 97(D15), 16,645-16,660, 1992.
- Born, M., H. Dorr, and I. Levin, Methane consumption in aerated soils of the temperate zone, *Tellus, Ser. B*, 42, 2-8, 1990.
- Bouwman, A.F. (Ed.), *Soils and the Greenhouse Effect: Proceedings of the International Conference Soils and the Greenhouse Effect*, 575 pp., John Wiley, New York, 1991.
- Briggs, G.M., and J.A. MacMahon, Alpine and subalpine wetland plant communities of the Uinta Mountains, Utah, *Great Basin Nat.*, 43(4), 523-530, 1983.
- Brooks, P.D., M.W. Williams, and S.K. Schmidt, Snowpack controls on soil nitrogen dynamics in the Colorado alpine, in *Biogeochemistry of Seasonally Snow-Covered Catchments*, edited by K. Tonnessen, M.W. Williams, and M. Tranter, *IAHS Publ.*, 228, 283-292, 1995.
- Brooks, P.D., M.W. Williams, and S.K. Schmidt, Microbial activity under alpine snowpacks, Niwot Ridge, Colorado, *Biogeochemistry*, 32, 93-113, 1996.
- Brooks, P.D., S.K. Schmidt, and M.W. Williams, Winter production of CO₂ and N₂O from alpine tundra: Environmental controls and relationship to inter-system C and N fluxes, *Oecologia*, 110, 403-413, 1997.
- Bubier, J.L., T.R. Moore, and N.T. Roulet, Methane emissions from wetlands in the midboreal region of northern Ontario, Canada, *Ecology*, 74(8), 2240-2254, 1993.
- Bubier, J.L., T.R. Moore, L. Bellisario, and N.T. Comer, Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, 9(4), 455-470, 1995.
- Carter, M.R. (Ed.), *Soil Sampling and Methods of Analysis*, 823 pp., A.F. Lewis, New York, 1993.
- Chapin, F.S., III, and W.C. Oechel, Photosynthesis, respiration, and phosphate absorption by *Carex aquatilis* ecotypes along latitudinal and local environmental gradients, *Ecology*, 64(4), 743-751, 1983.
- Christensen, T.R., A. Michelsen, S. Jonasson, and I.K. Schmidt, Carbon dioxide and methane exchange of a subarctic heath in response to climate change related environmental manipulations, *Oikos*, 79, 34-44, 1997.
- Cicerone, R.J., and R.S. Oremland, Biogeochemical aspects of atmospheric methane, *Global Biogeochem. Cycles*, 2, 299-327, 1988.
- Crill, P.M., K.B. Bartlett, R.C. Harriss, E. Gorham, E.S. Verry, D.I. Sebacher, L. Madzar, and W. Sanner, Methane flux from Minnesota peatlands, *Global Biogeochem. Cycles*, 2(4), 371-384, 1988.
- Crill, P.M., R.C. Harriss, and K.B. Bartlett, Methane fluxes from terrestrial wetland environments, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J.E. Rogers and W.B. Whitman, pp. 91-110, Am. Soc. for Microbiol., Washington, D. C., 1991.
- Dise, N.B., Methane emission from Minnesota peatlands: Spatial and seasonal variability, *Global Biogeochem. Cycles*, 7(1), 123-142, 1993.
- Dunfield, P., R. Knowles, R. Dumont, and T.R. Moore, Methane production and consumption in temperate and subarctic peat soils: Response to temperature and pH, *Soil Biol. Biochem.*, 25(3), 321-326, 1993.
- Frolking, S., and P. Crill., Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: Measurement and modeling, *Global Biogeochem. Cycles*, 8(4), 385-397, 1994.
- Gerard, G., and J. Chanton, Quantification of methane oxidation in the rhizosphere of emergent aquatic macrophytes: Defining upper limits, *Biogeochemistry*, 23, 79-97, 1993.
- Glenn, S., A. Heyes, and T. Moore, Carbon dioxide and methane fluxes from drained peat soils, southern Quebec, *Global Biogeochem. Cycles*, 7(2), 247-257, 1993.
- Haerberli, W., and M. Beniston, Climate change and its impacts on glaciers and permafrost in the Alps, *Ambio*, 27(4), 258-265, 1998.
- Healy, R.W., R.G. Striegl, T.F. Russell, G.L. Hutchinson, and G.P. Livingston, Numerical evaluation of static-chamber measurements of soil-atmosphere gas exchange: Identification of physical processes, *Soil Sci. Soc. Am. J.*, 60, 740-747, 1996.
- Holzappel-Pschorn, A., R. Conrad, and W. Seiler, Effects of vegetation on the emission of methane from submerged paddy soil, *Plant Soil*, 92, 223-233, 1986.
- Huang, Y., R.L. Sass, and F.M. Fisher Jr., A semi-empirical model of methane emission from flooded rice paddy soils, *Global Change Biol.*, 4, 247-268, 1998.
- Kettunen, A., V. Kaitala, J. Alm, J. Silvola, H. Nykanen, and P.J. Martikainen, Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland, *Global Biogeochem. Cycles*, 10(3), 457-471, 1996.
- King, G.M., and A.P.S. Adamsen, Effects of temperature on methane consumption in a forest soil and in pure cultures of the methanotroph *Methylobacter rubra.*, *Appl. Environ. Microbiol.*, 58, 2758-2763, 1992.
- Lipson, D.A., S.K. Schmidt, and R.K. Monson, Links between microbial population dynamics and nitrogen availability in an alpine ecosystem, *Ecology*, in press, 1998.
- Mast, M.A., C. Kendall, D.H. Campbell, D.W. Clow, and J. Back, Determination of hydrologic pathways in an alpine-subalpine basin using isotopic and chemical tracers, Loch Vale Watershed, Colorado, USA, in *Biogeochemistry of Seasonally Snow-Covered Catchments*, edited by K. Tonnessen, M.W. Williams, and M. Tranter, *IAHS Publ.*, 228, 263-270, 1995.
- Mast, M.A., K.P. Wickland, R.G. Striegl, and D.W. Clow, Winter fluxes of CO₂ and CH₄ from subalpine soils in Rocky Mountain National Park, Colorado, *Global Biogeochem. Cycles*, 12(4), 607-620, 1998.
- Melloh, R.A., and P.M. Crill, Winter methane dynamics in a temperate peatland, *Global Biogeochem. Cycles*, 10(2), 247-254, 1996.
- Millington, R.J., Gas diffusion in porous media, *Science*, 130, 100-102, 1959.
- Moore, T.R., and R. Knowles, Methane emissions from fen, bog and swamp peatlands in Quebec, *Biogeochemistry*, 11, 45-61, 1990.
- Moore, T.R., and N.T. Roulet, Methane flux: Water table relations in northern wetlands, *Geophys. Res. Lett.*, 20(7), 587-590, 1993.
- Moosavi, S.C., P.M. Crill, E.R. Pullman, D.W. Funk, and K.M. Peterson, Controls on CH₄ flux from an Alaskan boreal wetland, *Global Biogeochem. Cycles*, 10(2), 287-296, 1996.
- Moran, M.A., R. Benner, and R.E. Hodson, Kinetics of microbial degradation of vascular plant material in two wetland ecosystems, *Oecologia*, 79, 158-167, 1989.
- Morrissey, L.A., and G.P. Livingston, Methane emissions from Alaska Arctic tundra: An assessment of local spatial variability, *J. Geophys. Res.*, 97(D15), 16,661-16,670, 1992.
- Mosier, A.R., L.K. Klemmedtsson, R.A. Sommerfeld, and R.C. Musselman, Methane and nitrous oxide flux in a Wyoming subalpine meadow, *Global Biogeochem. Cycles*, 7(4), 771-784, 1993.
- Neff, J.C., W.D. Bowman, E.A. Holland, M.C. Fisk, and S.K. Schmidt, Fluxes of nitrous oxide and methane from nitrogen-

- amended soils in a Colorado alpine ecosystem, *Biogeochemistry*, 27, 23-33, 1994.
- Nykänen, H., J. Alm, J. Silvola, K. Tolonen, and P.J. Martikainen, Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates, *Global Biogeochem. Cycles*, 12(1), 53-69, 1998.
- Reeburgh, W.S., S.C. Whalen, and M.J. Alperin, The role of methylotrophy in the global CH₄ budget, in *Microbial Growth on C1 Compounds*, edited by J.C. Murrell and D.P. Kelly, pp. 1-14., Intercept Ltd., England, 1993.
- Rolston, D.E., Gas flux, in *Methods of Soil Analysis, Agron. Monogr.*, vol. 9, 2nd ed., Part 1, edited by A. Klute, pp. 1103-1120, Am. Stand. Assoc. and Soil Sci. Soc. of Am., Madison, Wis., 1993.
- Roulet, N.T., R. Ash, and T.R. Moore, Low boreal wetlands as a source of atmospheric methane, *J. Geophys. Res.*, 97(D4), 3739-3749, 1992a.
- Roulet, N., T. Moore, J. Bubier, and P. Lafleur, Northern fens: Methane flux and climatic change, *Tellus, Ser. B.*, 44, 100-105, 1992b.
- Sass, R.L., F.M. Fisher, Y.B. Wang, F.T. Turner, and M.F. Jund, Methane emission from rice paddies: The effect of floodwater management, *Global Biogeochem. Cycles*, 6, 249-262, 1992.
- Schimmel, J.P., Plant transport and methane production as controls on methane flux from arctic wet meadow tundra, *Biogeochemistry*, 28, 183-200, 1995.
- Schlesinger, W.H., *Biogeochemistry: An Analysis of Global Change*, 443 pp., Academic, San Diego, Calif., 1991.
- Schütz, H., W. Seiler, and R. Conrad, Processes involved in formation and emission of methane in rice paddies, *Biogeochemistry*, 7, 33-53, 1989a.
- Schütz, H., A. Holzapfel-Pschorn, R. Conrad, H. Renuenberg, and W. Seiler, A three-year continuous record on the influences of daytime, season and fertilizer treatment on methane emission rates from an Italian rice paddy, *J. Geophys. Res.*, 94, 16,405-16,416, 1989b.
- Sebacher, D.I., R.C. Harriss, K.B. Bartlett, S.M. Sebacher, and S.S. Grice, Atmospheric methane sources: Alaskan tundra bogs, and alpine fen, and a subarctic boreal marsh, *Tellus, Ser. B.*, 38, 1-10, 1986.
- Seiler, W.A., A. Holzapfel-Pschorn, R. Conrad, and D. Scharffe, Methane emissions from rice paddies, *J. Atmos. Chem.*, 1, 241-268, 1984.
- Smith, L.K., and W.M. Lewis Jr., Seasonality of methane emissions from five lakes and associated wetlands of the Colorado Rockies, *Global Biogeochem. Cycles*, 6(4), 323-338, 1992.
- Sommerfeld, R.A., A.R. Mosier, and R.C. Musselman, CO₂, CH₄ and N₂O flux through a Wyoming snowpack and implications for global budgets, *Nature*, 361, 140-142, 1993.
- Sommerfeld, R.A., W.J. Massman, R.C. Musselman, and A.R. Mosier, Diffusional flux of CO₂ through snow: Spatial and temporal variability among alpine-subalpine sites, *Global Biogeochem. Cycles*, 10(3), 473-482, 1996.
- Striegl, R.G., Diffusional limits to the consumption of atmospheric methane by soils, *Chemosphere*, 26, 715-720, 1993.
- Striegl, R.G., T.A. McConnaughey, D.C. Thorstenson, E.P. Weeks, and J.C. Woodward, Consumption of atmospheric methane by desert soils, *Nature*, 357, 145-147, 1992.
- Tate, C.M., and R.G. Striegl, Methane consumption and carbon dioxide emission in tallgrass prairie: Effects of biomass burning and conversion to agriculture, *Global Biogeochem. Cycles*, 7(4), 735-748, 1993.
- Topp, E., and R.S. Hanson, Metabolism of radiatively important trace gases by methane-oxidizing bacteria, in *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, edited by J.E. Rogers and W.B. Whitman, pp. 71-90. Am. Soc. for Microbiol., Washington, D. C., 1991.
- Torn, M.S., and J. Harte, Methane consumption by montane soils: Implications for positive and negative feedback with climatic change, *Biogeochemistry*, 32, 53-67, 1996.
- Valentine, D.W., E.A. Holland, and D.S. Schimmel, Ecosystem and physiological controls over methane production in northern wetlands, *J. Geophys. Res.*, 99(D1), 1563-1571, 1994.
- West, A.E., and S.K. Schmidt, Wetting stimulates atmospheric CH₄ oxidation by alpine soil, *FEMS Microbiol. Ecol.*, 25, 349-353, 1998.
- Whalen, S.C., and W.S. Reeburgh, A methane flux time series for tundra environments, *Global Biogeochem. Cycles*, 2(4), 399-409, 1988.
- Whiting, G. J., and J.P. Chanton, Plant-dependent CH₄ emission in a subarctic Canadian fen, *Global Biogeochem. Cycles*, 6(3), 225-231, 1992.
- Wickland, K.P., Controls of spatial and temporal variability of methane exchange in subalpine soils, M.A. thesis, Univ. of Colo., Boulder, 1997.
- Wickland, K.P., and R.G. Striegl, Measurement of soil carbon dioxide and methane concentrations and fluxes, and soil properties at four ages of jack pine forest in the Southern Study Area of the Boreal Ecosystem Atmosphere Study, Saskatchewan, Canada, 1993-95, *U.S. Geol. Surv. Open-File Rep. 97-49*, 73 pp., 1997.
- Winston, G.C., B.B. Stephens, E.T. Sundquist, J.P. Hardy, and R.E. Davis, Seasonal variability in CO₂ transport through snow in a boreal forest, in *Biogeochemistry of Seasonally Snow-Covered Catchments*, edited by K. Tonnessen, M.W. Williams, and M. Tranter, *IAHS Publ.*, 228, 61-69, 1995.
- Winston, G.C., E.T. Sundquist, B.B. Stephens, and S.E. Trumbore, Winter CO₂ fluxes in a boreal forest, *J. Geophys. Res.*, 102(D24), 28,795-28,804, 1997.
- Yavitt, J.B., G.E. Lang, and D.M. Downey, Potential methane production and methane oxidation rates in peatland ecosystems of the Appalachian Mountains, United States, *Global Biogeochem. Cycles*, 2(3), 253-268, 1988.

M.A. Mast and R.G. Striegl, U.S. Geological Survey, Denver, CO 80225.

S.K. Schmidt, Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309.

K.P. Wickland, U.S. Geological Survey, Boulder, CO 80303. (e-mail: kpwick@usgs.gov)

(Received April 21, 1998; revised August 12, 1998; accepted September 11, 1998.)