



Landscape patterns of CH₄ fluxes in an alpine tundra ecosystem

A. E. WEST¹, P. D. BROOKS², M. C. FISK³, L. K. SMITH⁴, E. A. HOLLAND⁵, C. H. JAEGER, III⁶, S. BABCOCK¹, R. S. LAI¹ & S. K. SCHMIDT¹

¹*E.P.O. Biology, University of Colorado, Boulder, CO 80309-0334, U.S.A.*; ²*USGS-WRD, 3215 Marine St., Boulder, CO 80303, U.S.A.*; ³*Department of Natural Resources, Cornell University, Ithaca, NY 14853, U.S.A.*; ⁴*CIRES, University of Colorado, Boulder, CO 80309-0216, U.S.A.*; ⁵*National Center for Atmospheric Research, PO Box 3000, Boulder, CO 80307-3000, U.S.A.*; ⁶*Department of Ecosystem Sciences, Policy and Management, 108 Hilgard Hall, University of California, Berkeley, CA 94720, U.S.A.*

Accepted 16 September 1998

Key words: alpine tundra, methane, trace gas

Abstract. We measured CH₄ fluxes from three major plant communities characteristic of alpine tundra in the Colorado Front Range. Plant communities in this ecosystem are determined by soil moisture regimes induced by winter snowpack distribution. Spatial patterns of CH₄ flux during the snow-free season corresponded roughly with these plant communities. In *Carex*-dominated meadows, which receive the most moisture from snowmelt, net CH₄ production occurred. However, CH₄ production in one *Carex* site (seasonal mean = +8.45 mg CH₄ m⁻² d⁻¹) was significantly larger than in the other *Carex* sites (seasonal means = -0.06 and +0.05 mg CH₄ m⁻² d⁻¹). This high CH₄ flux may have resulted from shallower snowpack during the winter. In *Acomastylis* meadows, which have an intermediate moisture regime, CH₄ oxidation dominated (seasonal mean = -0.43 mg CH₄ m⁻² d⁻¹). In the windswept *Kobresia* meadow plant community, which receive the least amount of moisture from snowmelt, only CH₄ oxidation was observed (seasonal mean = -0.77 mg CH₄ m⁻² d⁻¹). Methane fluxes correlated with a different set of environmental factors within each plant community. In the *Carex* plant community, CH₄ emission was limited by soil temperature. In the *Acomastylis* meadows, CH₄ oxidation rates correlated positively with soil temperature and negatively with soil moisture. In the *Kobresia* community, CH₄ oxidation was stimulated by precipitation. Thus, both snow-free season CH₄ fluxes and the controls on those CH₄ fluxes were related to the plant communities determined by winter snowpack.

Introduction

Methane is a greenhouse gas, which could contribute more to global warming than CO₂ (Lashof and Ahuja 1990; Rodhe 1990). Concentrations of CH₄ are rising but the exact cause is unclear (Cicerone & Oremland 1988; Fung et

al. 1991; Dlugokencky et al. 1994). Therefore, more precise estimates of the various sources and sinks of CH₄ are required.

One source of uncertainty in the global CH₄ budget is the relative importance of soils as sources and sinks of atmospheric CH₄. Estimates of soils as a global CH₄ sink range from 9.0 to and 55.9 Tg per year (Dörr et al. 1993; Prather et al. 1995; Potter et al. 1996). This range is large compared to the 30 Tg excess of CH₄ sources over sinks which historically has been accumulating in the atmosphere every year. The range of estimates for soil CH₄ production, such as in wetlands and rice fields is even larger, ranging from 85 to 300 Tg per year (Prather et al. 1995). In order to better assess the role of soil CH₄ fluxes in the global CH₄ budget, recent work has focused on investigating landscape patterns of CH₄ fluxes and environmental controls on CH₄ fluxes.

The alpine tundra of Niwot Ridge in the Colorado front range is well suited for studying spatial patterns of CH₄ fluxes, because of pronounced gradients of soil moisture which are likely to influence CH₄ flux. Variation in soil moisture regimes results from spatial variation of snowpack accumulation in this ecosystem. When the winter snowpack melts during spring thaw, it becomes the major source of soil moisture. However, this moisture is not distributed evenly. High winds during the winter cause snow to be swept away from exposed areas and to accumulate in other areas. Furthermore, drainage patterns cause meltwater to bypass some areas and to flow through others throughout the growing season. Thus, a wide range of soil microclimates can be found in close proximity to each other.

Discrete plant communities arise as a result of the divergent microclimates on Niwot Ridge (Walker et al. 1993). In areas which receive snowmelt throughout much of the growing season, plant communities are dominated by *Carex scopulorum*. In wind-blown areas where little snow accumulates, plant communities are dominated by *Kobresia myosuroides*. Between the two extremes, plant communities are dominated by *Acomastylis rossii*. As one moves from *Carex* through *Acomastylis* to *Kobresia* meadows, plant productivity, soil organic matter, and microbial activity decrease (Fisk et al. 1998). Also, the environmental factors limiting ecosystem processes shift from low soil temperatures to lack of water availability (Fisk & Schmidt 1995).

The objectives of this study were to measure CH₄ fluxes on Niwot Ridge during the snow-free season. Our sampling regime was designed to capture the spatial and temporal patterns of CH₄ fluxes associated with the natural plant communities in this system. Previous studies of alpine systems have measured CH₄ fluxes during the snowpack season (Sommerfeld et al. 1993) or were of limited scale and did not address the environmental controls important to landscape scale CH₄ flux in these systems (Neff et al. 1994). Therefore,



Figure 1. Location of the three original sites on Niwot Ridge. North is to the viewer's right. Niwot Ridge crosses from the center to the lower right corner. Arrows point to sites SS, LT, and NS as described in the text.

we measured CH_4 fluxes and soil moisture, temperature, and soil nitrogen throughout two growing seasons in *Carex*, *Acomastylis*, and *Kobresia* plant communities.

Materials and methods

Study sites

This study was conducted on Niwot Ridge, a U. N. Educational Scientific and Cultural Organization Biosphere Reserve and a National Science Foundation sponsored Long-Term Ecological Research (LTER) program, located near the University of Colorado Mountain Research Station in the Colorado Front Range.

Three sites of similar elevation (ca. 3500 m) but differing in slope and aspect were selected (Figure 1). One site is situated in the saddle of Niwot Ridge, which is where most ecological studies for the LTER program are

conducted. A second site is on the slope south of the saddle site, and a third site is on the slope north of the saddle site. The three sites are abbreviated as LT, SS, and NS for "LTER", "south slope", and "north slope", respectively. In each of these 3 sites, we chose 3 plots representing the 3 major plant communities of the alpine tundra for a total of nine plots. These plots were chosen because they have been used for extensive long-term monitoring of biogeochemical processes, and are described in more detail elsewhere (Fisk & Schmidt 1995; Fisk et al. 1998). Plots dominated by *Kobresia myosuroides*, *Acomastylis rossii*, and *Carex scopulorum* are referred to as *Kobresia*, *Acomastylis*, and *Carex* meadows respectively, and are abbreviated as K, A, and C. These three plant community types are described in more detail in May and Webber (1982) and Fisk et al. (1998). Abbreviations such as C-NS (*Carex* meadow plot of the north slope) and K-SS (*Kobresia* meadow plot of the south slope) are used to refer to individual plots.

Upon initiation of our measurements, we found that C-LT differed from the other *Carex* meadow plots in that snowmelt flowed over the soil surface throughout the season and CH₄ fluxes were strikingly higher. In 1993 measurements were made at a fourth wet meadow plot which was hydrologically more similar to the SS and NS *Carex* plots. This plot is the same as the control "wet meadow" described in Neff et al. (1994), and is abbreviated as C-NF. Fluxes from this plot were also more similar to C-SS and C-NS. Because the plots C-SS, C-NS, and C-NF were more similar to each other than to C-LT, we refer to these plots as "non-C-LT" *Carex* plots. We made measurements at C-NF only from June 10 to July 20, 1993, so the full seasonal pattern was not determined in this plot.

Field measurements

Methane fluxes were measured at each plot approximately every 2 weeks during 1992 (June 8 to September 23). In order to confirm spatial and temporal patterns noted during 1992, and in order to obtain data on CH₄ fluxes during snowmelt, CH₄ fluxes were selectively sampled in 1993 (June 1 to August 18). In the winter of 1992–93, more snow than average accumulated on Niwot Ridge (Figure 2). This deeper snowpack of 1993 also melted later, causing the snow-free season to begin later in 1993 than in 1992.

In the spring of 1992 and 1993, at least two weeks prior to initiation of CH₄ flux measurements, the collars of four static chambers (Matson et al. 1992) were installed in each plot. Collars consisted of PVC rings (15 cm tall × 25 cm diameter) which extended 5 to 10 cm into the soil. Vegetation extended well above the rims of the collars and was not substantially shaded by them. In C-LT, where surface drainage flowed throughout most of the season, the chamber collars were mounted on tussocks of vegetation

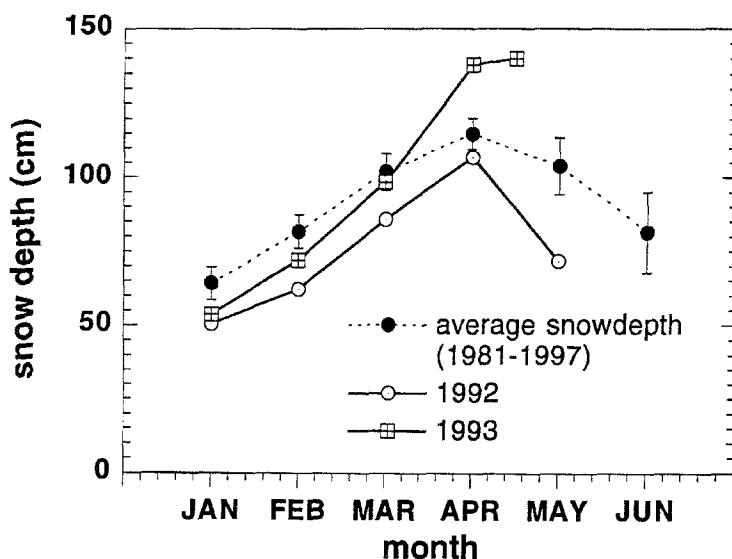


Figure 2. Snowpack depth recorded on Niwot Ridge in April of 1992 and 1993 compared to average snowpack depth.

which sat above the surface drainage. The chambers consisted of detachable acrylonitrile-butadiene-styrene (ABS) plastic covers that fitted over the collars. Each ABS cover was fitted with a septum for sampling and a pinhole port to equalize pressure during sampling.

On each sampling date, chambers were closed with the septa removed in order to avoid pressurizing the chamber. Septa were then replaced and duplicate gas samples were removed through the septa with 10-cc gas-tight glass syringes equipped with three-way stopcocks. Gas samples were collected every 30 to 45 minutes from approximately 9:30 am to 11:30 am. The long sampling period increased sensitivity, and Dise (1996) found that long sampling intervals had no significant effect on CH_4 flux calculations. However, in several instances when we were measuring CH_4 consumption, nonlinear points at the end of the sampling period had to be removed before CH_4 flux calculation. The linear change in CH_4 concentrations were corrected for temperature and pressure and used to calculate rates of CH_4 exchange with the atmosphere ($\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$). When regressions were not significant at $\alpha = 0.05$, CH_4 fluxes were assumed to be zero. The minimum detectable flux for a given static chamber was approximately $0.04 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$. The rates reported here are the averages of four chambers per plot. Gas samples were analyzed on a Hewlett Packard 5890A gas chromatograph using a flame ionization detector (FID) detector at 400°C . Variability of repeated

injections of a 1751.8 ppb CH₄ standard calibrated by the National Center for Atmospheric Research (NCAR) was less than ± 10 ppb.

Soil temperature, moisture, NH₄⁺ and NO₃⁻ were also measured. A soil temperature profile (recorded at depths of 1, 5, 10, and 15 cm) was taken next to each of the four bases using a thermistor. A composited soil sample (10 cm depth) was returned to the laboratory and sieved (2 mm) for determination of NH₄⁺, NO₃⁻ and gravimetric moisture content. Ammonium and NO₃⁻ were extracted from soil subsamples by shaking for 1 hour in 2 M KCl (volume:soil weight = 5:1), equilibrating for 12 h, and filtering using an extractor (Centurion, Inc.). These soil N determinations were made for 70 of the 113 CH₄ flux measurements. Extracts were analyzed for NH₄⁺ and NO₃⁻ using a Flow Injection Analyzer (Lachat, Milwaukee, WI). Gravimetric moisture content was determined on sub-samples dried to a constant weight at 60 °C.

Water-filled pore space (WFPS) was estimated as g H₂O per cm³ of saturated soil (H₂O_{sat}), assuming that H₂O has a density of 1 g per cm³ and that at saturation all pore space is filled with water. WFPS was estimated as %WFPS = (H₂O/H₂O_{sat})*100. This method does not make assumptions about particle density, making it better for the highly organic soils characteristic of these sites.

To estimate the H₂O_{sat} in each plot, four replicate intact cores (3 cm diameter) were taken from within 3 meters of the static chamber collars of each plot where vegetation closely resembled the vegetation inside the bases. Surface vegetation was removed and cores were sealed with paraffin on one end and deionized water was added slowly to the other end until the cores were saturated. Cores were weighed immediately and then dried to a constant weight at 60 °C. The H₂O of saturated soil was then calculated as the difference between the saturated weight and the oven-dried weight of the soil cores. Because of the variability of soils, it is possible for an individual %WFPS value to exceed 100%. This occurred in 2 *Carex* and 10 *Acomastylis* measurements of %WFPS.

The effects of recent precipitation on CH₄ fluxes were determined by codifying precipitation data which were collected as part of the LTER project. For each date on which CH₄ fluxes were measured, recent precipitation was quantified with the following variables: DSP = “days since precipitation” or the number of days since a precipitation event of 1 mm or more, MRP = “most recent precipitation” or the size of the most recent precipitation event (in millimeters), and QRP = “quantity of recent precipitation” or the amount of precipitation (in millimeters) which occurred in the 2 days prior to the sampling date.

The effects of recent rainfall events on *Kobresia* meadow CH₄ fluxes were further investigated by intensively sampling K-NS from July 14 to July 27,

1992. An 11 mm rainfall event on July 19 was supplemented with an additional 20 mm of deionized water on July 20, 1992 in experimental chamber collars. Prior to these water-additions, the most recent precipitation event larger than 5 mm had occurred on June 25, 1992 (7 mm). Methane fluxes and soil moisture levels were measured 6 days before and then 0.5, 24, and 48 hours and 5 days following the 20 mm water application.

To further investigate the high CH₄ emission from C-LT, composited soil samples (to 10 cm depth) were collected from C-LT and C-NS within 2 weeks of when soils became snow-free (June 26 and July 7, 1996, respectively). These soil samples were then incubated at 22 °C in mason jars equipped with septa from which samples of the jar headspace could be taken. Jar headspace was either equilibrated with room air to make the headspace aerobic, or flushed with industrial grade nitrogen gas to make the headspace anaerobic. Anaerobic conditions were confirmed with methylene blue anaerobic indicator strips. Headspace samples were taken regularly to assess CH₄ production and oxidation under aerobic and anaerobic conditions. Incubations lasted until steady linear increase or decrease of CH₄ concentrations could be confirmed, or up to 50 hours, whichever came first.

Statistical analyses

Data for soil moisture, soil temperature, and soil N, and the four replicate CH₄ flux measurements of each plot were analyzed using SAS (version 6.09, 1992) PROC REG. The importance of correlations with environmental factors was tested by removing the point most responsible for any significant relationships. If the relationship was no longer statistically significant, such a correlation was then classified as “weak”. The method of Judd and McClelland (1989) was used to determine whether surface or deep soil temperatures correlated better with CH₄ fluxes in the *Acomastylis* meadows. In this method, two mathematical models describing the data are compared with each other, and the SSE's of the two models are used to calculate r^2 , F^* , and a p -value.

Results

Landscape patterns

Spatial patterns of CH₄ fluxes corresponded roughly with the soil moisture and temperature regimes imposed by winter snowpack (Table 1). In the *Carex* meadows where more water was available from snowmelt, CH₄ fluxes were more likely to be positive. In the *Acomastylis* plant communities, which have intermediate moisture regime, CH₄ fluxes were predominately negative (seasonal mean = $-0.43 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) but some zero fluxes also occurred. In

Table 1. CH₄ fluxes and abiotic variables for individual plots within each plant community type. Values are means of all data from 1992 and 1993 in order to include full extent of seasonal trends.

Community and site	CH ₄ flux		min	mean (STD) H ₂ O ^a	mean %WFPS	mean at 15 cm	mean (STD) %SOM	mean NH ₄ ⁺ ^b	mean NO ₃ ⁻ ^b
	mean	max							
KOBRESIA MEADOWS									
SS	-0.63	-0.29	-0.87	36.46 (4.2)	62.2	5.65	19.68 (3.79)	10.1	0.6
LT	-0.86	-0.46	-1.22	60.37 (11.5)	62.1	4.35	29.56 (4.84)	14.2	1.0
NS	-0.80	-0.38	-1.25	42.17 (11.7)	52.2	5.33	26.56 (3.16)	14.6	1.2
ACOMASTYLIS MEADOWS									
SS	-0.72	0.0	-1.38	48.42 (19.5)	82.9	4.49	22.28 (5.62)	18.6	1.2
LT	-0.31	0.0	-0.84	91.57 (21.4)	80.9	3.91	41.54 (9.03)	22.2	1.3
NS	-0.33	-0.08	-0.84	69.36 (19.8)	82.2	3.48	25.67 (8.28)	12.5	0.6
CAREX MEADOWS									
SS	-0.06	+0.01	-0.22	167.20 (39.2)	73.3	3.00	47.4 (4.56)	13.9	0.4
LT	+8.45	+26.40	+1.30	136.28 (33.5)	70.9	2.66	32.41 (12.82)	12.9	0.8
NS	+0.05	+0.42	-0.25	100.52 (36.3)	59.0	3.60	31.36 (15.17)	14.3	1.1
NF ^c	+0.10	+0.30	0	NA	NA	3.59	NA	NA	NA

ABBREVIATIONS USED: SS – south slope, LT – LTER or saddle site, NS – north slope, NF – site used in Neff et al., 1994, NA – data not available. %WFPS – % water-filled porespace. %SOM – % soil organic matter. STD – Standard deviation. SUPPERSCRIPTS: ^ag H₂O (100 g d.w.)⁻¹, ^bug (g d.w.)⁻¹, ^cData from the NF *Carex* site were collected from June 10 to July 20, 1993, and may overestimate CH₄ emission.

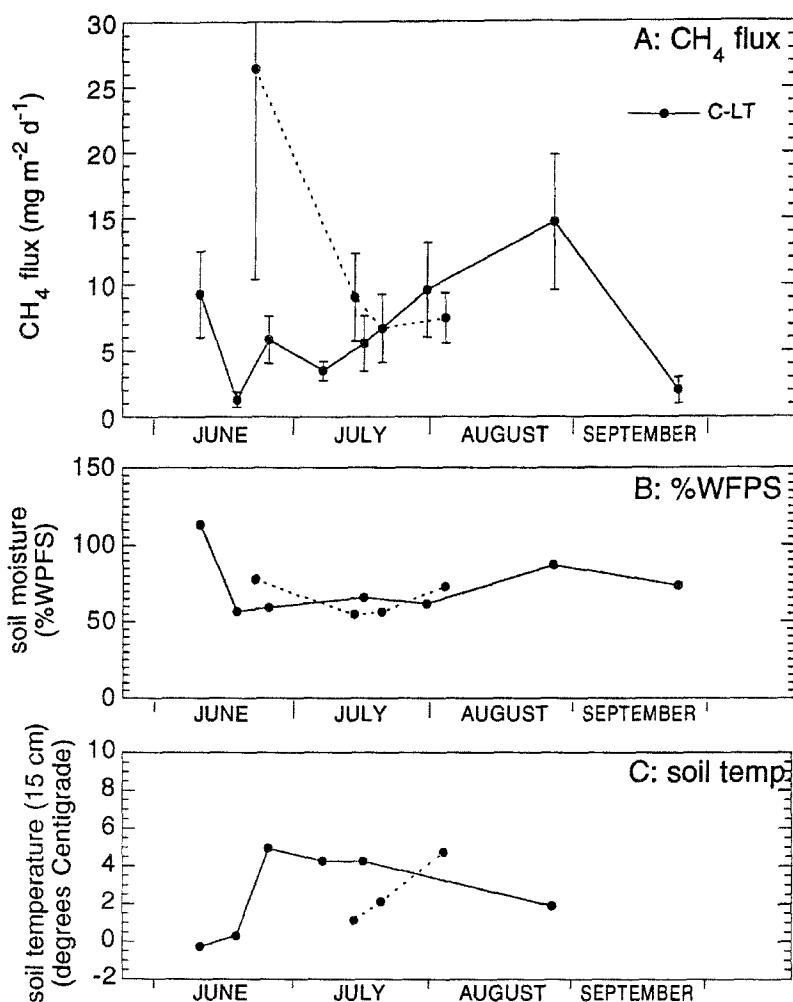


Figure 3. Seasonal patterns of CH₄ fluxes (A), soil moisture (B), and soil temperature (C) in the C-LT *Carex* meadow. Solid lines: 1992; dotted lines: 1993. Error bars show standard error.

the windswept *Kobresia* meadows, which receive the least amount of water from snowpack, only CH₄ oxidation occurred (seasonal mean = $-0.77 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$).

In the saddle *Carex* plot (C-LT), high amounts of CH₄ (seasonal mean = $+8.45 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) were emitted compared to the other *Carex* plots. In the other *Carex* meadows, seasonally averaged CH₄ fluxes were of small magnitude (seasonal means = -0.06 and $+0.05 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$, for C-SS and C-NS, respectively). In C-LT, snowmelt flowed over the soil surface throughout the growing season, but this surface drainage did not result in significantly higher moistures of the tussock soil where the chambers were

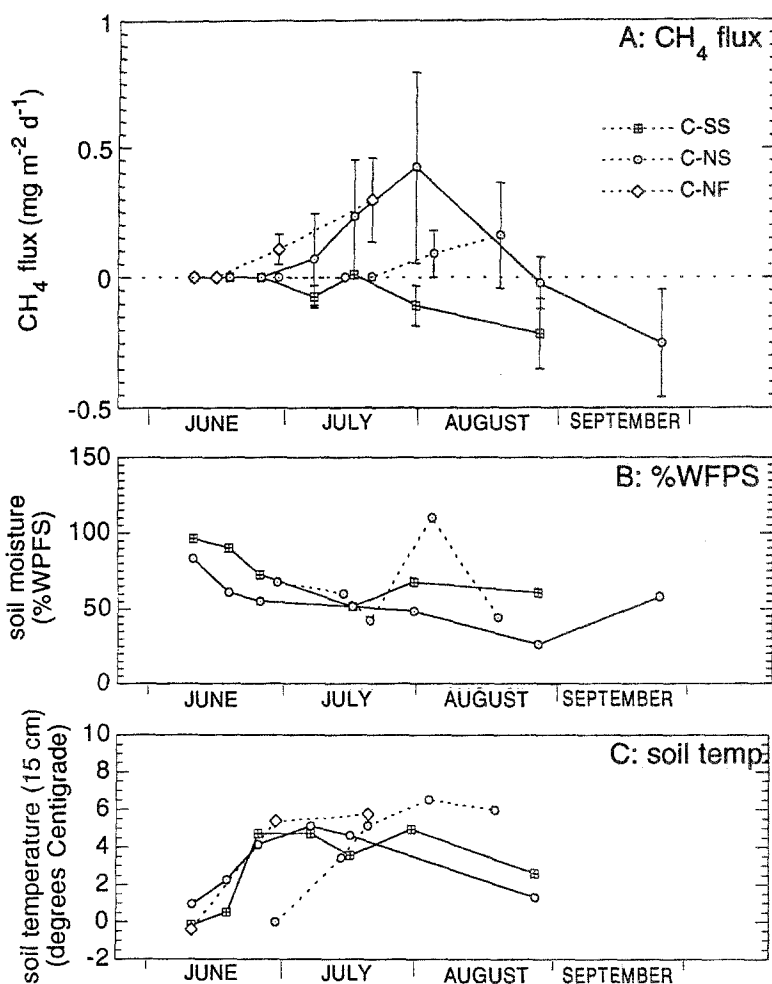


Figure 4. Seasonal patterns of CH₄ fluxes (A), soil moisture (B), and soil temperature (C) in the non-C-LT *Carex* meadows. Solid lines: 1992; dotted lines: 1993. Error bars show standard error.

installed (Table 1). In 1993 measurements were made of a fourth wet meadow plot (C-NF). Methane emissions from this plot were more similar to the C-SS and C-NS *Carex* plots (Table 1).

As soils dried and warmed during the growing season, a distinctive temporal pattern of CH₄ fluxes was observed in each plant community (Figures 3 to 6). In the LT *Carex* meadow site (Figure 3), CH₄ was emitted throughout the snow-free season, but the highest C-LT CH₄ emission occurred on the sampling date which was soonest after this site became snow free (June 22, 1993). This CH₄ emission was nearly twice as large as the next highest CH₄

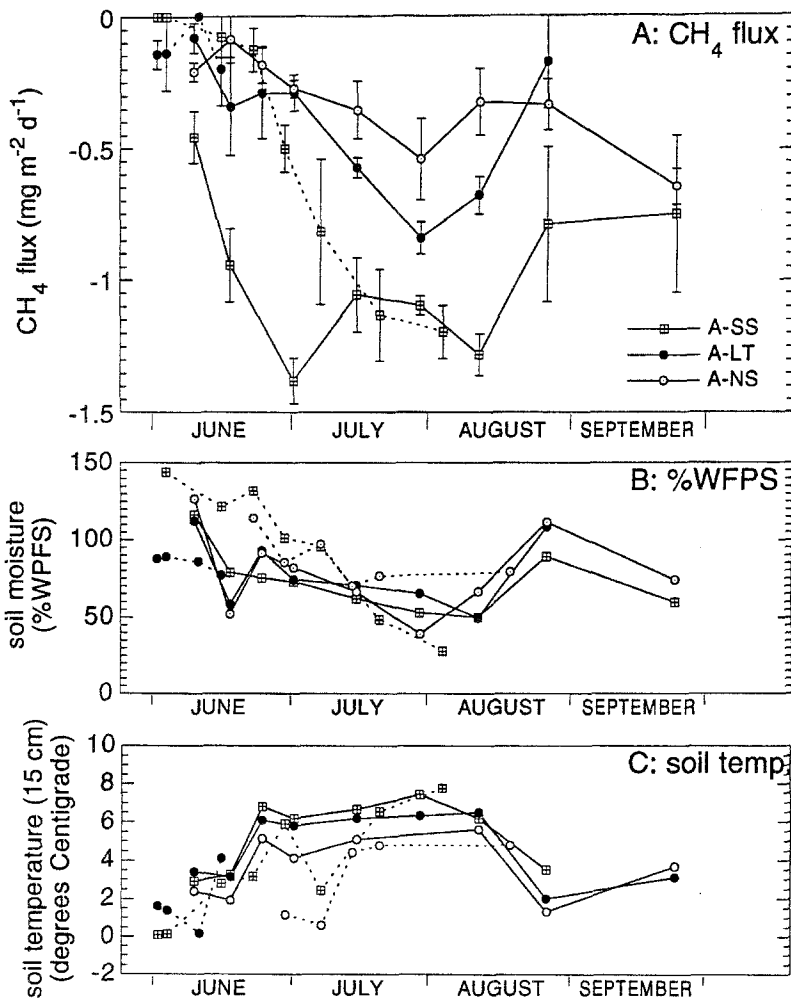


Figure 5. Seasonal patterns of CH₄ fluxes (A), soil moisture (B), and soil temperature (C) in *Acomastylis* meadows. Solid lines: 1992; dotted lines: 1993. Error bars show standard error.

flux and 3 times larger than the average CH₄ flux from C-LT. In the other *Carex* meadow sites (Figure 4), CH₄ fluxes were zero for 1 to 3 weeks after plots became snow-free. In the middle of the season, some CH₄ emissions were observed, followed by significant CH₄ oxidation. In the *Acomastylis* meadows (Figure 5), CH₄ oxidation rates were near 0 mg CH₄ m⁻² d⁻¹ in the beginning of the snow-free season. In the driest *Acomastylis* plot (A-SS), CH₄ oxidation rates then increased to exceed -1 mg CH₄ m⁻² d⁻¹. In the other *Acomastylis* plots, CH₄ oxidation rates also increased, but exceeded -0.7 mg CH₄ m⁻² d⁻¹ on only one date. In the *Kobresia* meadows (Figure 6), CH₄ oxidation rates increased from near -0.5 mg CH₄ m⁻² d⁻¹ in early June

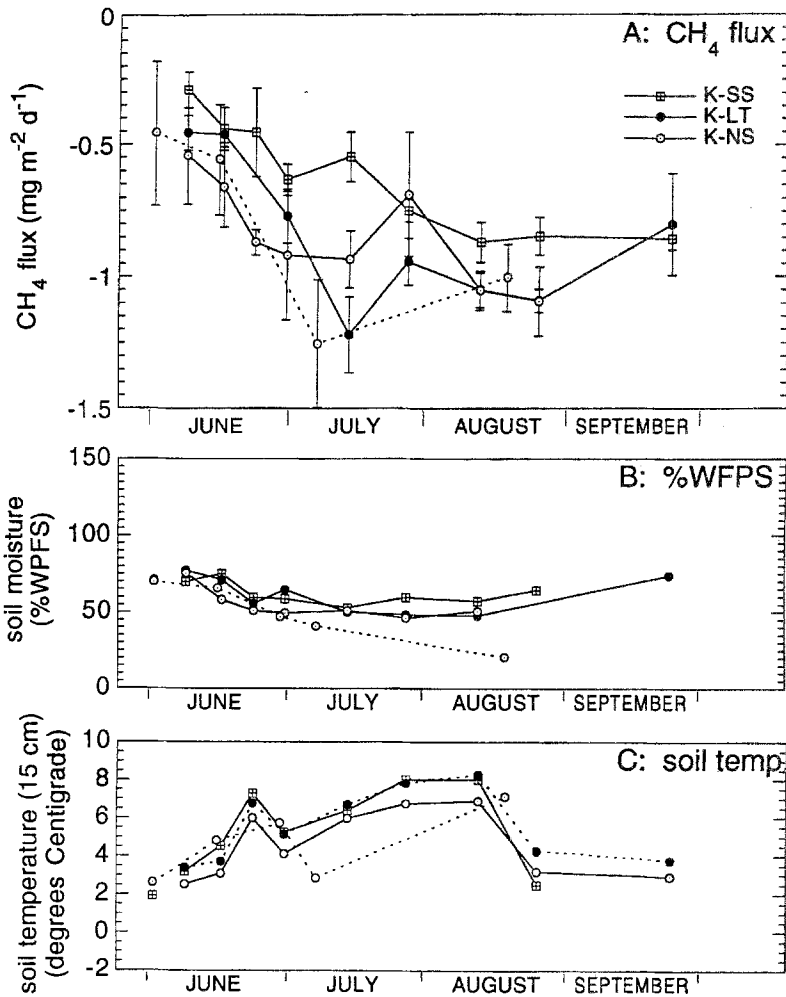


Figure 6. Seasonal patterns of CH₄ fluxes (A), soil moisture (B), and soil temperature (C) in *Kobresia* meadows. Solid lines: 1992; dotted lines: 1993. Error bars show standard error.

to near $-1 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ throughout the rest of the season. In each plot where data were available for both years of the study (C-NS, A-SS, and K-NS), the seasonal pattern for the second year (1993) was delayed (Figures 4 to 6). This delay was more pronounced in the *Carex* and *Acomastylis* meadows than in the *Kobresia* meadows.

Environmental factors

Methane fluxes correlated with a different set of factors in each plant community (Table 2). Soil nitrogen (extractable NH_4^+ and NO_3^-) was not a good

Table 2. Correlation coefficients (r) for regressions between the major controlling environmental factors and CH_4 fluxes in the four plant community types. Where $p > 0.10$, correlation coefficients are replaced with “—”.

	soil temperature				soil moisture		precipitation		
	CM15	CM10	CM5	CM1	H ₂ O	%WFPS	DSP	MRP	QRP
non-C-LT <i>Carex</i>	+0.40	+0.44 ^a	+0.50 ^a	+0.40	—	—	—	—	—
<i>Acomastylis</i>	-0.69 ^d	-0.61 ^d	-0.55 ^c	-0.47 ^b	+0.76 ^d	+0.60 ^d	—	—	—
<i>Kobresia</i>	—	—	—	—	—	+0.59 ^c	+0.50 ^b	-0.40 ^a	-0.48 ^b

ABBREVIATIONS: CM15, CM10, CM5, CM1 – soil temperature at 15, 10, 5, and 1 cm depth, respectively. H₂O – gravimetric moisture content (g H₂O (100 g d.w.)⁻¹). %WFPS – % water-filled pore space. DSP – “days since precipitation”; MRP – size of “most recent precipitation” (mm); QRP – “quantity of recent precipitation” (mm).

SUPERSSCRIPTS: ^a $p < 0.05$, ^b $p < 0.01$, ^c $p < 0.001$, ^d $p < 0.0001$.

Table 3. Methane production in composited soil samples from C-LT and C-NS under aerobic and anaerobic conditions.

soil type	CH ₄ production (pmol (g d.w.) ⁻¹ hr ⁻¹)	
	aerobic incubation	anaerobic incubation
C-LT	652.363 (±395)	3074.49 (±493)
C-NS	0	0

predictor of CH_4 fluxes in any of the plant communities. Soil temperature was important only in the *Carex* and *Acomastylis* plots, while soil moisture was important only in the *Acomastylis* and *Kobresia* plots.

In the non-C-LT *Carex* plots, soil temperature was most important. Positive CH_4 emissions occurred only after soils had warmed to 7, 5, 4, and 3 °C at 1, 5, 10, and 15 cm depth, respectively. Methane fluxes correlated positively with soil temperatures (Table 4, Model #1). Our data did not indicate more CH_4 emission from wetter *Carex* soils. In C-SS, CH_4 emission was observed only on the day of lowest soil moisture. In C-NS in both 1992 and 1993, CH_4 emissions increased as soil moisture decreased.

No environmental factor measured could account for the large CH_4 fluxes observed in the saddle *Carex* plot (C-LT) relative to the other *Carex* plots. Methane fluxes in C-LT correlated only weakly with surface soil temperatures (1 cm depth) and with soil NH_4^+ . In order to rule out transport of CH_4 through plants or from deeper soil layers, we carried out laboratory incubations to

Table 4. Models relating CH₄ fluxes to abiotic variables, plant community type and site. Regressions are grouped by plant community type in order of per cent error explained (r^2). All variables are in terms of mg CH₄ m⁻² day⁻¹ per unit of variable.

<i>CAREX</i> (non-C-LT) PLANT COMMUNITY:		
Model#	r^2	$p <$
1: CH ₄ flux = $-0.0801 + 0.0209^a$ CM5	0.25	0.05
<i>ACOMASTYLIS</i> PLANT COMMUNITY:		
Model#	r^2	$p <$
2: CH ₄ flux = $-0.8141^c + 0.0085^b$ H ₂ O -0.0669^d CM15	0.68	0.0001
<i>KOBRESIA</i> MEADOW PLANT COMMUNITY:		
Model#	r^2	$p <$
3: CH ₄ flux = $-1.3392^d + 0.0111^b$ %WFPS -0.0155^a QRP	0.45	0.0006
4: CH ₄ flux = $-0.2026^d + 0.0493^c$ H ₂ O _{sat} -0.0171^c H ₂ O	0.46	0.0004
5: CH ₄ flux = $-0.0467 - 0.0154^d$ H ₂ O _{sat} $+0.0128^c$ H ₂ O -0.0203^b QRP	0.62	0.0001
6: CH ₄ flux = $-0.2026 - 0.0156^c$ H ₂ O _{sat} $+0.0133^c$ H ₂ O $+0.0493^b$ DSP -0.0171^a MRP	0.71	0.0001

ABBREVIATIONS USED: DSP: days since precipitation; MRP: size of most recent precipitation (mm); QRP: quantity of precipitation in the previous 2 days; H₂O – gravimetric moisture content, %WFPS – per cent water-filled pore space, H₂O_{sat} – gravimetric moisture content at which soil is saturated.

SUPERSSCRIPTS: ^a $p < 0.05$, ^b $p < 0.01$, ^c $p < 0.001$, ^d $p < 0.0001$.

measure CH₄ production potential of the top 10 cm of soil from C-LT and C-NS (Table 3). The soils for this determination were collected within two weeks after these sites became snow-free, at the time when C-NS field CH₄ fluxes were zero. The pattern of CH₄ production from these soils in laboratory incubations paralleled the pattern of field CH₄ fluxes in these two sites. We also compared aerobic and anaerobic incubation of these soils to see if the lack of CH₄ emission at C-NS was due to a preponderance of oxidation at this site. Whether under aerobic or anaerobic conditions, C-LT soils immediately produced CH₄ at substantial rates, but soils from C-NS did not produce any CH₄ (Table 3).

In the *Acomastylis* meadows, CH₄ oxidation correlated positively with soil temperature (Table 2) and negatively with soil moisture (Table 2, Figure 7). Gravimetric soil moisture correlated with CH₄ oxidation better than %WFPS. Soil temperatures at 15 cm depth correlated better than soil temperatures closer to the surface. Soil moisture and temperature taken together accounted for 63% of the variation in *Acomastylis* meadow CH₄ fluxes (Table 4, Model #2), with moisture accounting for most of the variation. Methane oxidation rates were highest in the driest *Acomastylis* plot (A-SS).

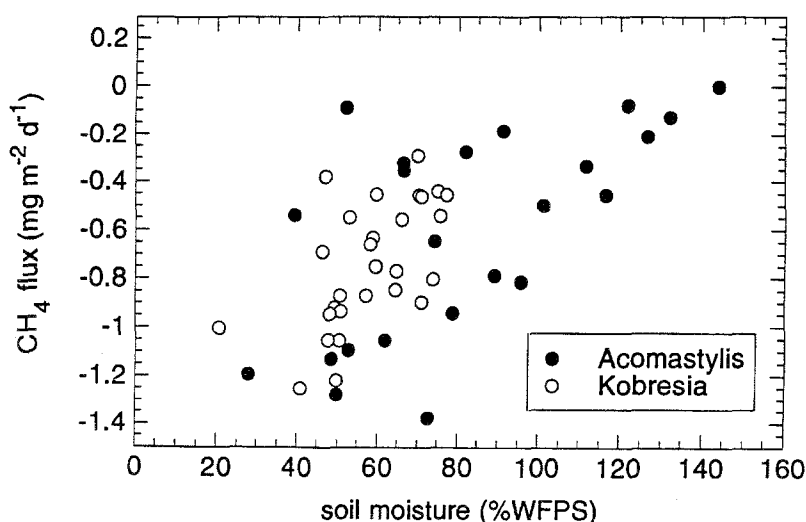


Figure 7. The relationship between soil moisture (%WFPS) and CH_4 fluxes in the *Kobresia* and *Acomastylis* meadows. Closed circles: *Acomastylis* meadow fluxes; open circles: *Kobresia* meadow fluxes.

In the windswept *Kobresia* community, CH_4 oxidation correlated with all the variables constructed to represent recent precipitation (Table 2). Methane oxidation rates were higher with more recent precipitation and with larger precipitation events. *Kobresia* meadow CH_4 fluxes also tended to be higher in drier soils, but only if soil saturation capacity was accounted for, either as %WFPS (Table 2) or as part of a multiple regression (Table 4, Model #4). Methane oxidation was highest in the wetter two *Kobresia* meadows (K-NS and K-LT). Combining soil saturation capacity, soil moisture, and the precipitation variables explained up to 71% of the variation in *Kobresia* meadow fluxes (Table 4, Models #3, 4, and 6). Intensive sampling of K-NS before and after a large water addition in the middle of a summer dry spell yielded similar results. On July 20, 1992, water additions increased soil moisture in watered bases at K-NS to 51% H_2O , and CH_4 oxidation rates were higher than any other *Kobresia* meadow measurement in 1992 or 1993 (Figure 8). Twenty-four hours later, K-NS soils dried below 40% H_2O , and CH_4 oxidation rates also decreased from -1.35 to $-0.61 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$.

Discussion

In the alpine tundra of the Colorado Front Range, snowpack determines soil moisture and temperature regimes which lead to variation in a number of biological processes. These include plant community type (Walker et al.

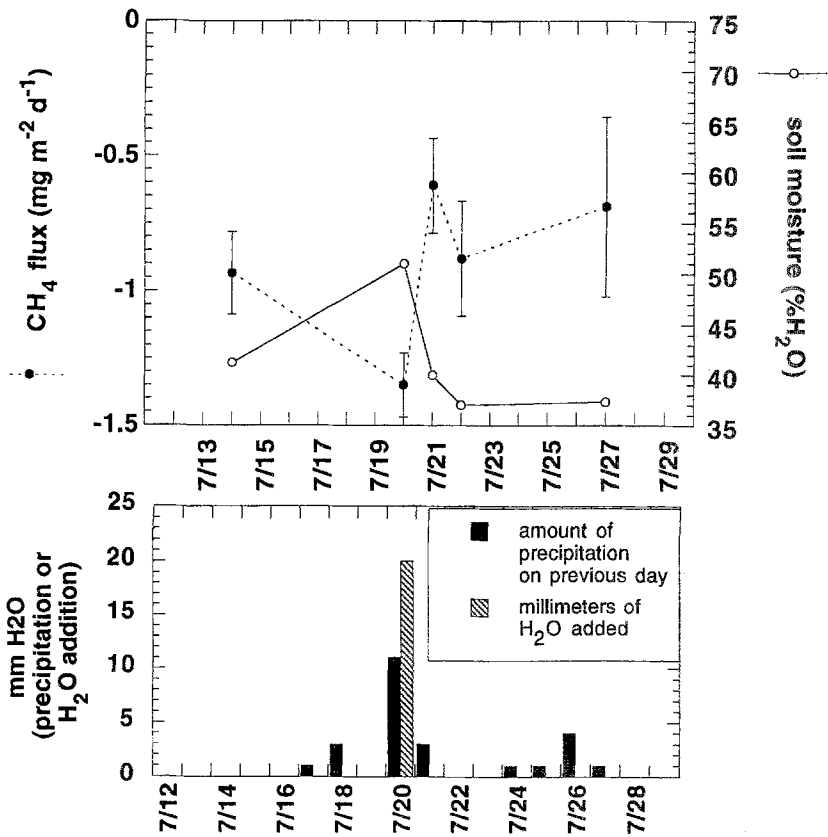


Figure 8. Methane oxidation rates, soil moisture, and water additions in K-NS, before and after a water-addition experiment.

1993), primary production (Fisk et al. 1998), and microbial processes (Fisk & Schmidt 1995; Brooks et al. 1997, 1998). Our results demonstrate that snowpack-induced moisture regime also leads to variation in CH₄ fluxes during the snow-free season. Moving from *Carex* to *Acomastylis* to *Kobresia* meadows, soils become drier, and seasonally averaged CH₄ fluxes become more negative. These results parallel previous findings that drier soils tend to consume more CH₄, and more CH₄ tends to be emitted from wetter soils (Mosier et al. 1993; Conrad 1995; MacDonald et al. 1996; Moosavi et al. 1996).

Environmental controls on CH₄ fluxes also corresponded with snowpack-induced moisture regime. The influence of soil moisture could be confirmed only in the two drier plant communities (*Acomastylis* and *Kobresia*). In the *Acomastylis* meadows, CH₄ oxidation appeared to be diffusion-limited (Striegl 1993), especially above 80% WFPS (Figure 7) where maximum CH₄

oxidation rates decline with greater %WFPS. In the *Kobresia* meadows, CH₄ oxidation was stimulated by water additions, indicating limitation by lack of moisture availability. These results were confirmed using incubations of the top 10 cm of soil from *Kobresia* meadows (West & Schmidt 1998). Soil temperature influenced CH₄ fluxes only in the two wetter plant communities (*Carex* and *Acomastylis*). In the *Carex* meadows, where soil moisture was ample, CH₄ fluxes correlated only with soil temperature. In the non-C-LT *Carex* meadows, CH₄ emission did not begin until after soils warmed to 5 °C. This is consistent with a temperature threshold for methane production. Alternatively, this could have resulted from temperature effects on plant phenology, but this is unlikely because sieved soil displays a similar temperature response (S.K. Schmidt, unpublished data).

These controls on CH₄ fluxes parallel the controls on other ecosystem processes in this alpine tundra ecosystem. For example, soil N processes are moisture-limited in the *Kobresia* meadows, but temperature-limited in the *Carex* and *Acomastylis* meadows (Fisk & Schmidt 1995). The controls on CH₄ fluxes in this ecosystem also parallel the controls on CH₄ fluxes in other ecosystems. Where CH₄ emission dominates, temperature is often an important controlling factor (Dunfield et al. 1993; Frolking et al. 1994; Mikkilä et al. 1995; Moosavi et al. 1996; Whalen & Reeburgh 1996; Granberg et al. 1997). In systems with intermediate moisture regimes, CH₄ oxidation is usually controlled by soil moisture as a result of diffusion-limitation (Adamsen & King 1993; Keller & Reiners 1994; Dunfield et al. 1995; Sitaula et al. 1995; Whalen & Reeburgh 1996), but sometimes soil temperature is also important (Crill et al. 1994; Peterjohn et al. 1994; Castro et al. 1995; Torn & Harte 1996; Granberg et al. 1997; Priemé & Christensen 1997). Finally, in systems where moisture is limiting, CH₄ oxidation can be stimulated by wetting (Striegl et al. 1992; Torn & Harte 1996).

In addition to the relationship between patterns of CH₄ fluxes and plant communities, our data demonstrate substantial spatial variability in CH₄ fluxes which are not associated with plant community. For example, within the CH₄-consuming plant communities (*Acomastylis* and *Kobresia*), maximum CH₄ oxidation occurred at an intermediate moisture availability. Previous studies have similarly demonstrated that microbial consumption of atmospheric CH₄ occurs at intermediate soil moistures (Gulledge 1996; Schnell & King 1996; Torn & Harte 1996). The SS site of our study dries out more quickly after snowmelt than the other sites, probably because it receives more solar radiation due to its southeastern exposure. Thus, the highest *Acomastylis* CH₄ oxidation rates were found in A-SS, but K-SS had the lowest *Kobresia* CH₄ oxidation rates (Table 1).

Another source of variation in CH₄ fluxes not associated with plant community was the high CH₄ emission in the saddle *Carex* plot (C-LT) relative to the other *Carex* plots. These high CH₄ fluxes could also not be explained in terms of the environmental factors that we measured. These high fluxes were also not explainable by higher plant production in C-LT (M.C. Fisk, personal communication). At similar moistures and temperatures, the *Carex* meadow of the saddle site emitted over 100 times more CH₄ than the other *Carex* plots. In other systems where large amounts of CH₄ are emitted, CH₄ flux is often controlled by the level of the water table (Whalen & Reeburgh 1990a; Granberg et al. 1997; Liblik et al. 1997) or by differential diffusion through plants (Schimel 1995). However, the patterns of CH₄ emission from the sieved soils (Table 3) suggest that neither explanation applies to this alpine tundra. Soils collected from the upper 10 cm of C-LT produced CH₄ proportional to C-LT field fluxes, indicating instead that the high CH₄ fluxes result from higher methanogenic activity of C-LT soils.

A possible explanation for the greater methanogenic activity of C-LT soils is shallower snow depth or less consistent snowpack during the winter. Snow greater than a certain depth acts as an insulator, allowing soils to thaw and mineralize labile C over the winter (Brooks et al. 1997, 1998), but snowpack does not accumulate to as great a depth on the more exposed saddle of Niwot Ridge (C-LT) as it does in the sloped sites (C-SS, C-NS, and C-NF). With less snow cover, C-LT soils remain frozen through much of the winter, and this may preserve methanogenic C sources for CH₄ production upon thawing.

Yearly variation in the timing of snowmelt controlled the temporal patterns of CH₄ fluxes from all the plant communities. The 1993 snowpack was larger and melted later than the 1992 snowpack (Figure 2). As a result, soil CH₄ fluxes and soil temperatures reached maximum levels 2 to 6 weeks later in 1993 than in 1992. This delay was more pronounced in the *Carex* meadows than in the *Acomastylis* meadows, and in the *Acomastylis* meadows than in the *Kobresia* meadows (Figures 3 to 6). Such yearly variations in snowpack have also been shown to control plant production (Walker et al. 1993; Fisk et al. 1998), winter trace gas fluxes (Brooks et al. 1997), and other soil microbial processes (Brooks et al. 1998).

The CH₄ fluxes that we report for this alpine tundra system are small in comparison to those reported for arctic tundra (Whalen & Reeburgh 1990b; Whalen & Reeburgh 1992; Adamsen & King 1993; Christensen 1993) but large in comparison to those previously reported for alpine tundra. With the exception of the C-LT plot, our rates are similar in both magnitude and seasonal pattern to those reported previously for Niwot Ridge (Neff et al. 1994). In contrast, our rates exceeded the -0.2 to +6.3 mg CH₄ m⁻² d⁻¹ range reported for alpine tundra by Whalen and Reeburgh (1990). Also, the

rates we report are considerably larger than the -0.15 to $+0.014$ $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ reported for snow-covered alpine sites by Sommerfeld et al. (1993). The wider range of CH_4 consumption and emission that we report suggests a more important role of alpine tundra soils in the global CH_4 budget. Alpine tundra covers roughly 10.5 million km^2 (Archibold 1995). Assuming a four-month snow-free season and that the fluxes reported here are typical of alpine tundra around the world, the annual contribution of alpine tundra to the global CH_4 budget could range from -1 to $+10$ Tg CH_4 .

Considering the relative abundance of the major plant communities in alpine tundra could provide a more precise estimate of global CH_4 fluxes. On Niwot Ridge, the CH_4 -consuming plant communities (*Kobresia* and *Acomastylis*) dominate, covering approximately 70% of the LTER saddle area, while wetter areas such as *Carex* meadows cover only 15% (Walker et al. 1993). Data from Neff et al. (1994) suggest that the non-C-LT pattern of CH_4 fluxes, with low CH_4 emissions and late-season CH_4 consumption, are more typical of *Carex* meadows. The seasonal average of these non-C-LT *Carex* plots were near zero. Therefore, the Colorado Rocky Mountain alpine tundra represented by Niwot Ridge may act as a CH_4 sink. In two Wyoming alpine sites, CH_4 consumption was also dominant, even under snowpack (Sommerfeld et al. 1993). However, if CH_4 hotspots such as C-LT covered as little as 5% of the area of Niwot Ridge, their CH_4 emission would negate all CH_4 consumption by *Acomastylis* and *Kobresia* communities. Therefore, a satisfactory estimate of the global contribution would require more information on the relative abundance of hotspots such as C-LT, which cannot be predicted by plant community type alone.

The strong relationship between snowpack and CH_4 fluxes in this study implies that changes in the contribution of alpine tundra to the global CH_4 budget in response to global change scenarios would be complex. For example, increases in summer precipitation would be likely to increase CH_4 consumption in *Kobresia* meadows but decrease CH_4 consumption in *Acomastylis* meadows. Yearly variations in winter snowpack accumulation could alter the soil C pools left for snow-free season CH_4 production. The timing of snowmelt would influence the date of maximum CH_4 production in *Carex* meadows. Longer-term shifts in the distribution of snowpack would have more pronounced effects on CH_4 fluxes, because changes in soil moisture regimes would alter plant community distribution (Walker et al. 1993) and therefore snow-free season CH_4 fluxes. For example, long-term increases in snow accumulation would lead to increased CH_4 production as CH_4 -consuming *Acomastylis* and *Kobresia* meadows shifted towards CH_4 -producing *Carex* communities.

In summary, we measured the spatial and temporal patterns of CH₄ fluxes from alpine tundra during the snow-free season. We further identified the environmental controls on CH₄ fluxes in this system. Both CH₄ fluxes and controls were related to the plant communities determined by winter snow-pack accumulation. Methane emissions from typical *Carex* meadows are small compared to the CH₄-consuming activity of *Acomastylis*, and *Kobresia* meadows. However, hotspots of CH₄ emission occur, as seen in plot C-LT of this study. Therefore, using plant community type to scale alpine tundra CH₄ fluxes to regional or landscape levels may not adequately capture the natural variability in CH₄ sources and sinks.

Acknowledgements

This research was supported by grant R81-9448 from the Environmental Protection Agency National Center for Environmental Research and Quality Assurance. Support was also received from the Biosphere/Atmosphere Research Training Grant (NSF BIR 94 13218) and NSF sponsorship of the National Center for Atmospheric Research. Logistical support was provided by the Niwot Ridge Long-Term Ecological Research project (NSF DEB 9211776) and the Mountain Research Station (BIR 9115097).

References

- Adamsen APS & King GM (1993) Methane consumption in temperate and subarctic forest soils: Rates, vertical zonation, and responses to water and nitrogen. *Appl. Environ. Microbiol.* 59: 485–490
- Archibald OW (1995) *Ecology of World Vegetation*. Chapman & Hall, London
- Brooks PD, Schmidt SK & Williams MW (1997) Winter production of CO₂ and N₂O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110: 403–413
- Brooks PD, Williams MW & Schmidt SK (1998). Soil inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochem.* 43: 1–15
- Castro MS, Steudler PA, Melillo JM, Aber JD & Bowden RD (1995) Factors controlling atmospheric methane consumption by temperate forest soils. *Global Biogeochem. Cycles* 9: 1–10
- Christensen TR (1993) Methane emission from arctic tundra. *Biogeochem.* 21: 117–139
- Cicerone RJ & Oremland RS (1988). Biogeochemical aspects of atmospheric methane. *Global Biogeochem. Cycles* 2: 299–327
- Conrad R (1995) Soil microbial processes involved in production and consumption of atmospheric trace gases. In: Jones JG (Ed) *Advances in Microbial Ecology* (pp 207–250). Plenum Press, New York
- Crill PM, Martikainen PJ, Nykänen H & Silvola J (1994) Temperature and N fertilization effects on methane oxidation in a drained peatland soil. *Soil Biol. Biochem.* 26: 1331–1339

- Dise NB (1996) Methane emission from Minnesota peatlands: spatial and seasonal variability. *Global Biogeochem. Cycles* 7: 123–142
- Dlugokencky EJ, Steele LP, Lang PM & Masarie KA (1994) The growth rate and distribution of atmospheric methane. *J. Geophys. Res.* 99: 17021–17043
- Dörr H, Katruf L & Levin I (1993) Soil texture parameterization of the methane uptake in aerated soils. *Chemosphere* 26: 697–713
- Dunfield P, Knowles R, Dumont R & Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biol. Biochem.* 25: 321–326
- Dunfield PF, Topp E, Archambault C & Knowles R (1995) Effect of nitrogen fertilizers and moisture content on CH₄ and N₂O fluxes in a humisol: measurements in the field and intact soil cores. *Biogeochem.* 29: 199–222
- Fisk MC, Schmidt SK & Seastedt TR (1998) Topographic patterns of above- and below-ground production and nitrogen cycling in alpine tundra. *Ecology* 79: 2253–2266
- Fisk MC & Schmidt SK (1995) Nitrogen mineralization and microbial biomass nitrogen dynamics in three alpine tundra communities. *Soil Sci. Soc. Am. J.* 59: 1036–1043
- Frolking S & Crill P (1994) Climate controls on temporal variability of methane flux from a poor fen in southeastern new Hampshire: Measurement and modeling. *Global Biogeochem. Cycles* 8: 385–397
- Fung I, John J, Lerner J, Matthews E, Prather M, Steele LP & Fraser PJ (1991) Three-dimensional model synthesis of the global methane cycle. *J. Geophys. Res.* 96: 13033–13065
- Granberg G, Mikkilä C, Sundh I, Svensson BH & Nilsson M (1997) Sources of spatial variation in methane emission from mires in northern Sweden: a mechanistic approach in statistical modeling. *Global Biogeochem. Cycles* 11: 135–150
- Gulledge J (1996) Doctoral Thesis. Soil Consumption of Atmospheric Methane: Importance of Microbial Physiology and Diversity. University of Alaska, Fairbanks, Alaska
- Judd CM & McClelland GH (1989) *Data Analysis*. Harcourt Brace Jovanovich, Inc., Orlando, FL
- Keller M & Reiners WA (1994) Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biochemical Cycles* 8: 399–409
- Lashof DA & Ahuja DR (1990) Relative contributions of greenhouse gas emissions to global warming. *Nature* 344: 529–531
- Liblik LK, Moore TR, Bubier JL & Robinson SD (1997) Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, Northwest Territories, Canada. *Global Biogeochem. Cycles* 11: 485–494
- MacDonald JA, Skiba U, Sheppard LJ, Hargreaves KJ, Smith KA & Fowler D (1996) Soil environmental variables affecting the flux of methane from a range of forest, moorland and agricultural soils. *Biogeochem.* 34: 113–132
- Matson PA, Gower ST, Volkman C, Billow C & Grier CC (1992) Soil nitrogen cycling and nitrous oxide flux in a Rocky Mountain Douglas-fir forest: effects of fertilization, irrigation and carbon addition. *Biogeochem.* 18: 101–111
- May DE and Webber PJ (1982) Spatial and temporal variation of vegetation and its productivity on Niwot Ridge, Colorado. In: Halfpenny JC (Ed) *Ecological Studies in the Colorado Alpine*, a Festschrift for John W. Marr. Occasional paper number 37 (pp 35–62). Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, U.S.A.

- Mikkilä C, Sundh I, Svensson BH & Nilsson M (1995) Diurnal variation in methane emission in relation to the water table, soil temperature, climate, and vegetation cover in a Swedish acid mire. *Biogeochem.* 28: 93–114
- Moosavi SC, Crill PM, Pullman ER, Funk DW & Peterson KM (1996) Controls on CH₄ flux from an Alaskan boreal wetland. *Global Biogeochem. Cycles* 10: 287–296
- Mosier AR, Klemetsson LK, Sommerfeld RA & Musselman RC (1993) Methane and nitrous oxide flux in a Wyoming subalpine meadow. *Global Biogeochem. Cycles* 7: 771–784
- Neff JC, Bowman WD, Holland EA, Fisk MC & Schmidt SK (1994) Fluxes of nitrous oxide and methane from nitrogen amended soils in the Colorado Alpine. *Biogeochem.* 27: 23–33
- Peterjohn WT, Melillo JM, Steudler PA, Newkirk KM, Bowles FP & Aber JD (1994) Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications* 4: 617–625
- Potter CS, Davidson EA & Verchot LV (1996) Estimation of global biogeochemical controls and seasonality in soil methane consumption. *Chemosphere* 32: 2219–2246
- Prather M, Derwent R, Ehhalt D, Fraser P, Sanhueza E & Zhou X (1995) Other Trace Gases and Atmospheric Chemistry. In: Houghton JT, Meira Filho LG, Bruce J, Lee H, Callander BA, Haites E, Harris N & Maskell K (Eds) *Climate Change 1994, Radiative Forcing of Climate Change and An Evaluation of the IPCC IS92 Emission Scenarios* (pp 73–126). Cambridge University Press, Cambridge, U.K.
- Priemé A & Christensen S (1997) Seasonal and spatial variation of methane oxidation in a Danish spruce forest. *Soil Biol. Biochem.* 29: 1165–1172
- Rodhe H (1990) A comparison of the contribution of various gases to the greenhouse effect. *Science* 248: 1217–1219
- Schimel JP (1995) Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. *Biogeochem.* 28: 183–200
- Schnell S & King GM (1996) Responses of methanotrophic activity in soils and cultures to water stress. *Appl. Environ. Microbiol.* 62: 3203–3209
- Sitaula BK, Bakken LR & Abrahamsen G (1995) CH₄ uptake by temperate forest soil: effect of N input and soil acidification. *Soil Biol. Biochem.* 27: 871–880
- Sommerfeld RA, Mosier AR & Musselman RC (1993) CO₂, CH₄, and N₂O flux through Wyoming snowpack and implications for global budgets. *Nature* 361: 140–142
- Striegl RG (1993) Diffusional limits to the consumption of atmospheric methane by soils. *Chemosphere* 26: 715–720
- Striegl RG, McConnaughey TA, Thorstenson DC, Weeks EP & Woodward JC (1992) Consumption of atmospheric methane by desert soils. *Nature* 357: 145–147
- Torn MS & Harte J (1996) Methane consumption by montane soils: implications for positive and negative feedback with climatic change. *Biogeochem.* 32: 53–67
- Walker DA, Halfpenny JC, Walker MD & Wessman CA (1993) Long-term studies of snow-vegetation interactions. *BioScience* 43: 287–301
- West AE & Schmidt SK (1998) Wetting stimulates atmospheric CH₄ oxidation by alpine soil. *FEMS Microbiology Ecology* 24: 349–353
- Whalen SC & Reeburgh WS (1990a) A methane flux transect along the trans-Alaska pipeline haul road. *Tellus* 42B: 237–249
- Whalen SC & Reeburgh WS (1990b) Consumption of atmospheric methane by tundra soils. *Nature* 346: 160–162
- Whalen SC & Reeburgh WS (1992) Interannual variations in tundra methane emission: a 4-year time series at fixed sites. *Global Biogeochem. Cycles* 6: 139–150
- Whalen SC & Reeburgh WS (1996) Moisture and temperature sensitivity of CH₄ oxidation in boreal soils. *Soil Biol. Biochem.* 28: 1271–1281