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METHANE CONSUMPTION AND EMISSION BY TAIGA

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Abstract. Taiga or boreal forest environments are a poorly understood component of the global CH_4 budget. Results from a 1-year study of CH_4 fluxes at a range of representative floodplain and upland taiga sites in the Bonanza Creek long term ecological research area show that soil consumption of atmospheric CH_4 was the dominant process. Methane emission occurred only sporadically in the earliest successional stages in the floodplain system; all other floodplain and upland sites were net CH_4 consumers. Our results suggest that upland and floodplain taiga soils are an atmospheric CH_4 sink of up to 0.8 Tg yr^{-1}. Point-source bogs and fens are the only important CH_4-emitting sites in taiga.

INTRODUCTION

Recent observations of increasing atmospheric CH_4 concentration [Rasmussen and Khalil, 1984; Steele et al., 1987; Blake and Rowland, 1989] have stimulated a reexamination of controls on the global CH_4 budget [Cicerone and Oremland, 1988]. High-latitude terrestrial environments are of particular interest because of their large stored soil carbon contents [Post et al., 1982]. This carbon is believed to have accumulated since the last glacial maximum [Adams et al., 1990] and continues to accumulate in taiga and coastal plain tundra environments [Billings, 1987]. There is concern that regional warming and changes in precipitation might mobilize this reservoir and make it available for biogeochemical conversion into products like CH_4 and CO_2. The possible mobilization and release of these radiatively active gases is generally viewed as capable of causing a positive climate feedback [Khalil and Rasmussen, 1989].

Tundra and boreal forest environments account for approximately equal amounts (13% and 14%, respectively) of the Earth's terrestrial soil carbon [Post et al. 1982]. Boreal forest is a general term describing the mixed deciduous-coniferous forest biome located between tundra and temperate forest. Taiga is an equivalent term used by Soviet and Alaskan workers. The taiga is one of the Earth's largest single circum-global forest units, covering some 11.1×10^{12} m^2 [Billings, 1987] and ranging in latitude from 70°N in Scandinavia and central Siberia to 45°N in eastern Siberia [Kimmins and Wein, 1986]. Tundra environments have recently received attention as a CH_4 source [Sebacher et al., 1986; Whalen and Reeburgh, 1988], but we are aware of only one estimate of CH_4 emission by taiga [Whalen and Reeburgh, 1990a].

The goal of this study was to obtain systematic CH_4 flux data from a range of representative taiga sites to determine the source strength of taiga in the global CH_4 budget. This paper presents CH_4 flux measurements obtained during the first year of a continuing study.

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METHODS

Sites

Our study was conducted at sites in the Bonanza Creek Experimental Forest (BCEF), a 5000-ha research area located 20 km west of the University of Alaska Fairbanks campus (Figure 1). The BCEF was established in 1963 through a 50-year lease by the U. S. Forest Service from the State of Alaska. Results from research performed within BCEF are summarized by Van Cleve et al. [1986]. The 1983 Rosie Creek Fire burned some 3500 ha and involved approximately half of the south-facing uplands in the BCEF [Juday and Dyrness, 1985]. A long term ecological research (LTER) program was initiated within BCEF in 1987. The activities of the Bonanza Creek LTER program focus on two successional sequences: primary succession on a river floodplain and secondary succession in an upland region following fire. This focus has led to establishment of a range of representative and well-understood sites where ancillary data are collected continuously; the BCEF LTER thus provides an ideal area for a study of taiga trace gas fluxes.

Van Cleve et al. [1991] summarize the state factors controlling taiga forest succession. The floodplain succession is controlled by river erosion and deposition and begins with bare sandbars. These are populated with grasses and shrubs and the soils are frequently salt affected (gypsum and calcite) as a result of evaporation of soil pore water following capillary rise. Fluvial deposition of silt and sand during high river stages leads to development of terraces, which are populated by alder and willow. This stage is followed by development of balsam poplar stands with an understory of white spruce. The longer-lived evergreen spruce overtops the poplar, and an insulating feather moss layer develops. Shading by the evergreen forest and insulation provided by the moss surface lead to development of permafrost. The climax in this successional sequence is a black spruce community, which develops into a bog. Soil pH decreases, and soil carbon and nitrogen increase during the

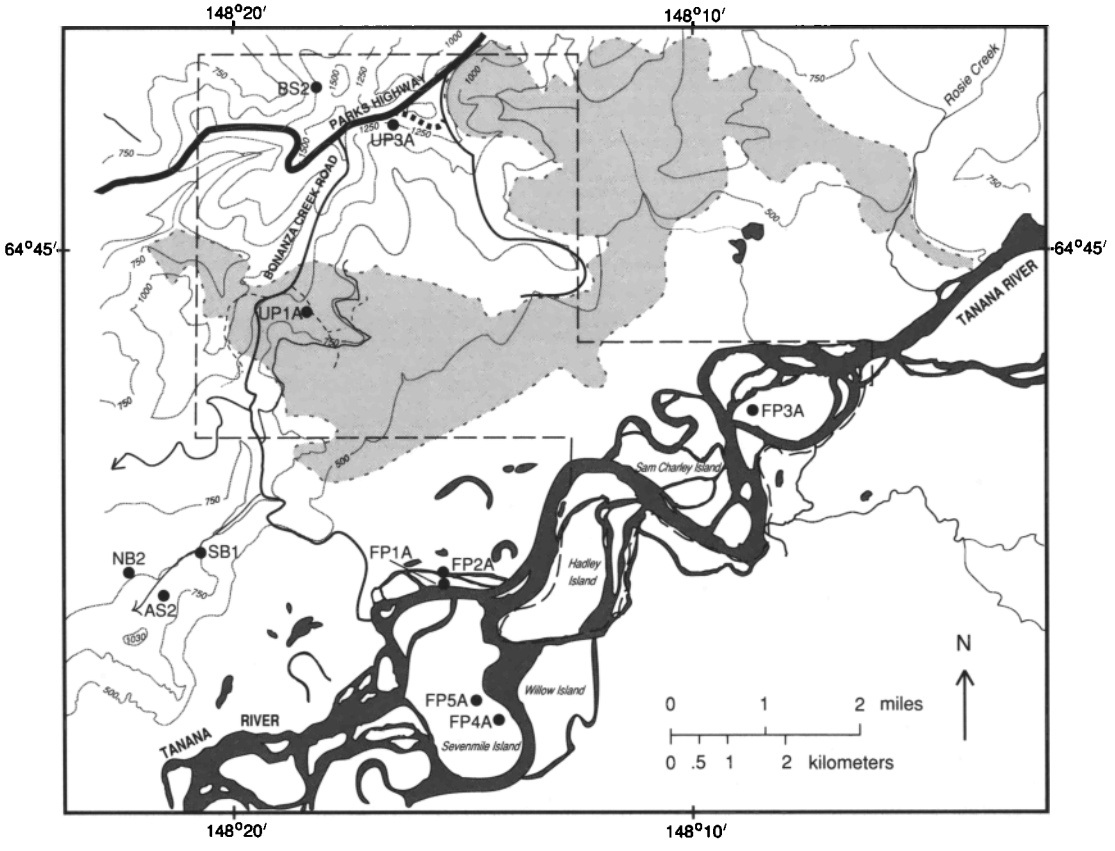

Fig. 1. Site locations, Bonanza Creek Experimental Forest, Alaska. Hatched area shows extent of 1983 Rosie Creek Fire.

succession. River erosion or fire resets the successional sequence.

The upland successional sequence is fire-dominated, and progresses on micaceous loess soils through herb-shrub, hardwood, and evergreen conifer stages, all governed by longevity and overtopping. North-facing slopes receive much less radiation and are dominated by black spruce and permafrost.

The sites at which we measured CH_4 fluxes are representative of each stage in the floodplain and upland successional sequences, so they cover the range of conditions encountered in taiga. Our flux chambers were permanently deployed in the vegetation control site adjacent the primary LTER sites. A variety of data are collected at these sites, including incident radiation, air and soil temperatures, precipitation, and water table depth. Complete vegetation and soil descriptions are available for each site. Table 1, which is largely adapted from Van Cleve et al. [1991], summarizes the sites involved in this study and contains information on the biota, soils, and disturbance history at similar sites.

Flux Measurements

Determinations of net CH_4 flux were made using a static chamber technique [Whalen and Reeburgh, 1988]. Each chamber consists of a skirted aluminum base, which is permanently seated in the soil, and lucite vertical sections and lids that utilize a water-filled channel for a seal. Flux chamber bases were permanently deployed in or near the 15 m x 15 m vegetation control plot within each of the floodplain and upland sites (Table 1) during September 1989. Bases were deployed in triplicate at all floodplain sites and at upland site UP3A. Bases at site UP1A were deployed in duplicate in areas where ground cover was predominantly *Calamagrostis* (bluestem) or *Equisetum* (horsetail). Experimental plots (also 15 m x 15 m) adjacent all other upland sites (AS2, SB1, NB2 and BS2) have been fertilized (1:1 mixture of urea and NH_4SO_4) twice per year since 1988 at rates of 5 and 20 g N m^{-2} yr^{-1}. The low-N treatment represents a doubling of the natural N input; the high-N treatment was intended to overwhelm microbiological contributions (F. S. Chapin, personal communication, 1991). Two chamber bases were deployed in the vegetation control and low-N plots within these sites to assess the effect of N fertilization on CH_4 flux.

Methane flux measurements were made weekly at each upland and floodplain site from late May through September 1990. Syringe samples were collected from each chamber over a 0.75-hour time course and were analyzed for CH_4 in the laboratory by flame ionization detection gas chromatography. Our CH_4 standards are relatable to National Bureau of Standards standards. The net CH_4 flux was calculated from a least squares fit of concentration change versus time within the chamber. Details are given by Whalen and Reeburgh [1988]. The minimum detectable flux depended on chamber area:volume ratios, but was usually ±0.2 mg CH_4 m^{-2} d^{-1}. Flux values below the detection limit are reported as zero.

Additional Measurements

A soil temperature profile was measured adjacent to one chamber at each site with a portable multithermistor probe (2-cm intervals), and the mean soil temperature to 15 cm was calculated. Soil moisture (w/w, oven-dried at 105°C) [Black, 1965] was determined on 2.8 cm diameter x 10 cm soil cores collected 1 m from each chamber. Soil organic content (w/w; loss on ignition at 550°C of oven-dried sample) and pH [Black, 1965] were measured on similar cores collected from each control plot in late September, 1990. These data are summarized in Table 2.

Soil CH_4 depth distributions were measured at upland sites NB2, SB1, BS2 and UP3A on samples obtained by inserting a steel tube probe to known soil depths and pumping soil gas into Tedlar sample bags [Born et al., 1990] with a battery-powered diaphragm pump. The bags were sampled and analyzed for CH_4 in the laboratory.

Methane consumption thresholds and capacities were studied at the above four sites using chambers with ambient and amended atmospheres. The ambient atmosphere experiments involved allowing chambers with free air atmospheres (~1.7 ppm CH_4) to "run down" with periodic sampling over a 24 hour period. The amended atmosphere experiments involved adjusting initial chamber atmospheres to concentrations of ~20 ppm CH_4 and sampling over a 24 hour period.

Methane fluxes were often below the limit of detection. We report the median and interquartile range (IQR; range of central 50% of data) of the CH_4 flux data as measures of central value and variability. This procedure is recommended by Helsel [1990] for analysis of censored (i.e., many values below detection limit) data. Nonparametric statistics [Conover, 1980; Zar, 1984] are used because of the large number of values below the detection limit and because no single data transformation consistently homogenized variances. Statistical analyses were

TABLE 1. Characteristics of Interior Alaska Taiga Sites

Site	Principal Vegetation	Soil Properties							Biomass[a]	Annual Production[a,e]	Time Since Disturbance[a]
		Aspect[a]	Texture[a]	Terrace Level[b] m	Heat[a,c] DD	pH	Organic Content[d] %	Permafrost?	kg m^{-2}	g m^{-2}	years
					Floodplain Sites						
FP1A	sandbar, willow	level	sand	1.8-2.2	1600	7.1	2	-	0.2-0.6	200-300	0-5
FP2A	alder-poplar	level	sand	1.1-2.6	696	6.5	21	-	1.0-6.4	290-350	5-30
FP3A	poplar-spruce	level	silt-sand	2.3-3.0	150-1300	6.5	30	-	1.0 -6.4	390-350	30-130
FP4A	white spruce	level	silt-sand	3.2-3.8	800-1140	6.1	35	±	14.6-22.7	331-540	100-200
FP5A	black spruce	level	silt-sand	4.0-4.5	40-760	5.3	45	+	1.6-10.9	57-148	130-250+
					Upland Sites						
UP1A	burn site, herb	south	silt	-	1150-1200	7.5	9	-	0.02-.2	5-20	0-8
AS2	aspen	south	silt	-	970-1400	5.6	18	-	4.6-17.5	346-760	30-130
SB1	birch	south	silt	-	970-1400	5.2	19	-	4.6-17.5	346-760	30-130
UP3A	white spruce	south	silt	-	875-1120	5.9	16	-	23.2	353	100-250+
NB2	birch	north	silt	-	1000	5.6	22	+	4.6-17.5	343-760	30-80
BS2	black spruce	north	silt	-	500-800	4.5	37	+	5.3-11.3	101-160	80-250+

[a] From Van Cleve et al. [1991]. Observations from sites similar to those in this study.
[b] Elevation above winter low river level. Mean annual river level range is 1.5 m. Historical extreme is 6 m. (L. A. Viereck, personal communication, 1991)
[c] Degree-days above 0°C at 10 cm depth (May to September).
[d] Surface 10 cm of soil.
[e] Aboveground.

TABLE 2. Summary Statistics for 1990 CH_4 Flux, Soil Temperature, and Soil Moisture in Bonanza Creek Long Term Ecological Research Sites

Site	CH_4 Flux, mg m^{-2} d^{-1}						Soil Temperature, °C				Soil Moisture, %w/w			
	n(BDL)[a]	Maximum	Minimum	Median	IQR[b] 25%ile	IQR[b] 75%ile	n	Maximum	Minimum	Mean(SEM)[c]	n	Maximum	Minimum	Mean(SEM)[c]
Floodplain Sites														
FP1A	48 (25)	8.37	0	0	0	1.85	16	21.8	6.2	15.7 (1.2)	33	52	20	37 (1)
FP2A	48 (42)	1.85	-0.35	0	0	0	16	14.3	4.3	10.5 (0.7)	33	108	32	66 (4)
FP3A	42 (27)	-0.22	-0.75	0	-0.31	0	14	14.9	3.3	11.1 (0.9)	30	159	32	72 (5)
FP4A	45 (9)	0	-1.01	-0.34	-0.43	-0.24	15	16.0	5.5	11.9 (0.8)	33	93	18	51 (3)
FP5A	45 (24)	0	-0.95	0	-0.37	0	15	21.9	1.4	12.2 (1.4)	32	180	7	88 (7)
Total	228 (127)	8.37	-1.01	0	-0.31	0	76	21.9	1.4	12.3 (0.5)	161	180	7	63 (2)
Upland Sites														
UP1A	76 (73)	0	-0.98	0	0	0	19	17.7	5.5	12.5 (0.9)	60	220	34	74 (5)
AS2	76 (10)	0	-0.77	-0.43	-0.51	-0.28	19	20.8	6.1	12.9 (0.9)	60	220	34	74 (5)
SB1	76 (42)	0	-0.52	0	0	-0.33	19	18.3	5.0	11.7 (0.9)	59	218	16	56 (4)
NB2	76 (26)	0	-0.55	-0.26	0	-0.34	19	16.1	3.2	10.6 (0.8)	60	256	20	15 (5)
UP3A	55 (3)	0	-0.79	-0.40	-0.52	-0.30	19	13.8	2.7	9.4 (0.7)	45	231	29	75 (6)
BS2	76 (6)	0	-1.81	-0.56	-0.67	-0.47	19	14.7	2.9	8.9 (0.9)	60	389	19	152 (10)
Total	435 (160)	0	-1.81	-0.29	0	-0.47	114	20.8	2.7	11.0 (0.4)	344	389	12	76 (3)
All Sites														
Total	663 (287)	8.37	-1.81	-0.23	-0.42	0	190	21.9	1.4	11.5 (0.3)	505	389	7	72 (2)

[a] BDL, number of flux measurements below detection limit; these measurements are reported as zero.
[b] IQR, interquartile range, central 50% of data.
[c] SEM, standard error of mean.

performed at a significance level of a=0.05 in all cases.

RESULTS

Fluxes from the floodplain sites and upland sites are are presented in Figures 2 and 3, respectively. Table 2 gives summary statistics for the CH_4 flux measurements. Both positive (net CH_4 emission) and negative (net CH_4 consumption) fluxes were observed. Fluxes varied from -1.81 to 8.37 mg CH_4 m^{-2} d^{-1}, with a median of -0.23 mg CH_4 m^{-2} d^{-1} for the entire data set. Overall, CH_4 fluxes were low, with 43% of the observations below the detection limit.

No seasonal signal for CH_4 flux was evident in the floodplain sites, but there were clear differences in fluxes among sites (Figure 2). A transition from CH_4 production to consumption with advancing plant community succession is evident in Figure 2. Methane emission was frequently observed in the earliest stage of succession (sandbar, Figure 2a), and

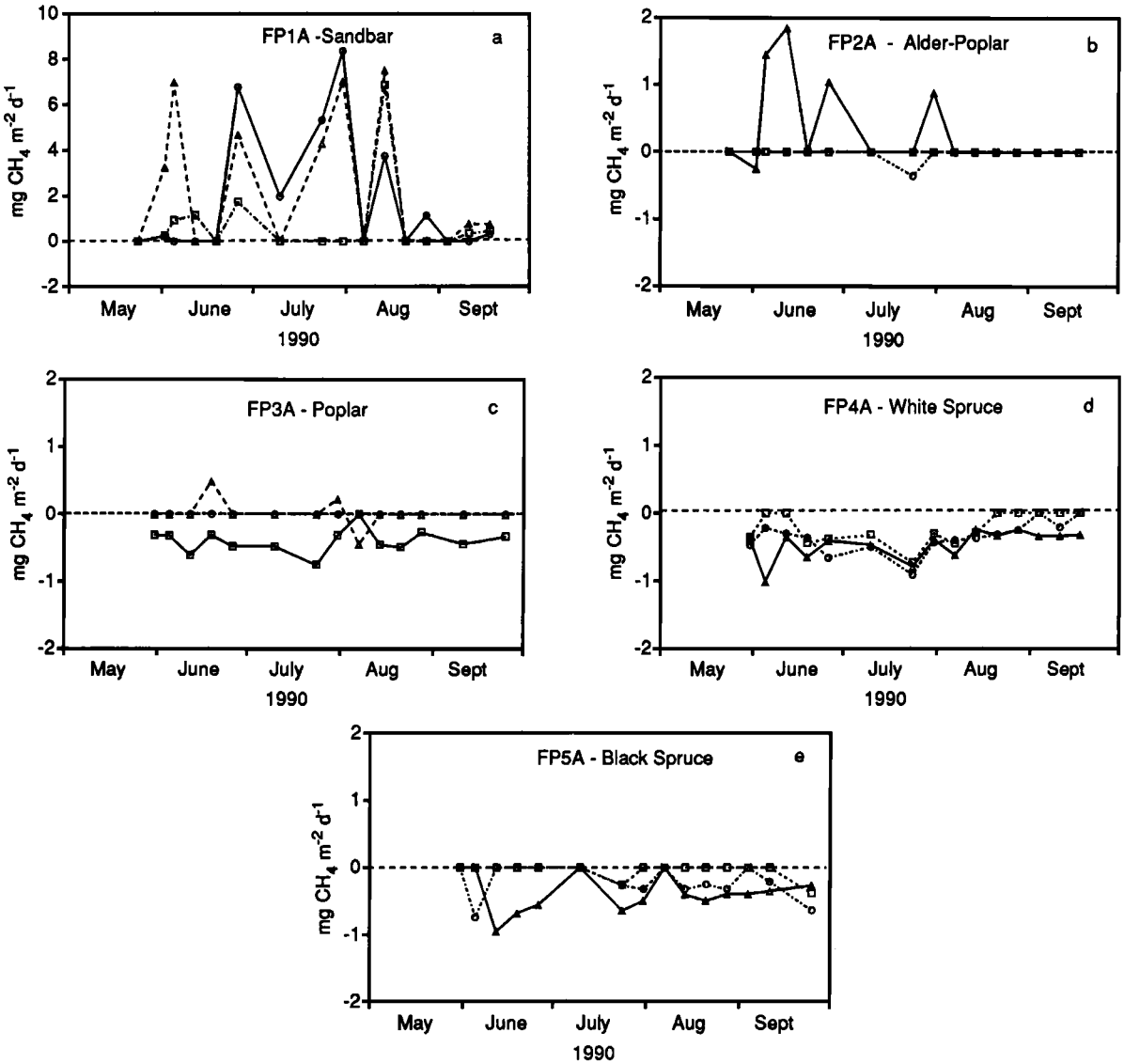

Fig. 2. Methane fluxes (mg m^{-2} d^{-1}) from Bonanza Creek Experimental Forest floodplain sites, May 24 to September 25, 1990. (a) FP1A, sandbar (note that flux scale differs from other sites). (b) FP2A, alder to poplar. (c) FP3A, poplar with spruce understory. (d) FP4A, white spruce. (e) FP5A, black spruce.

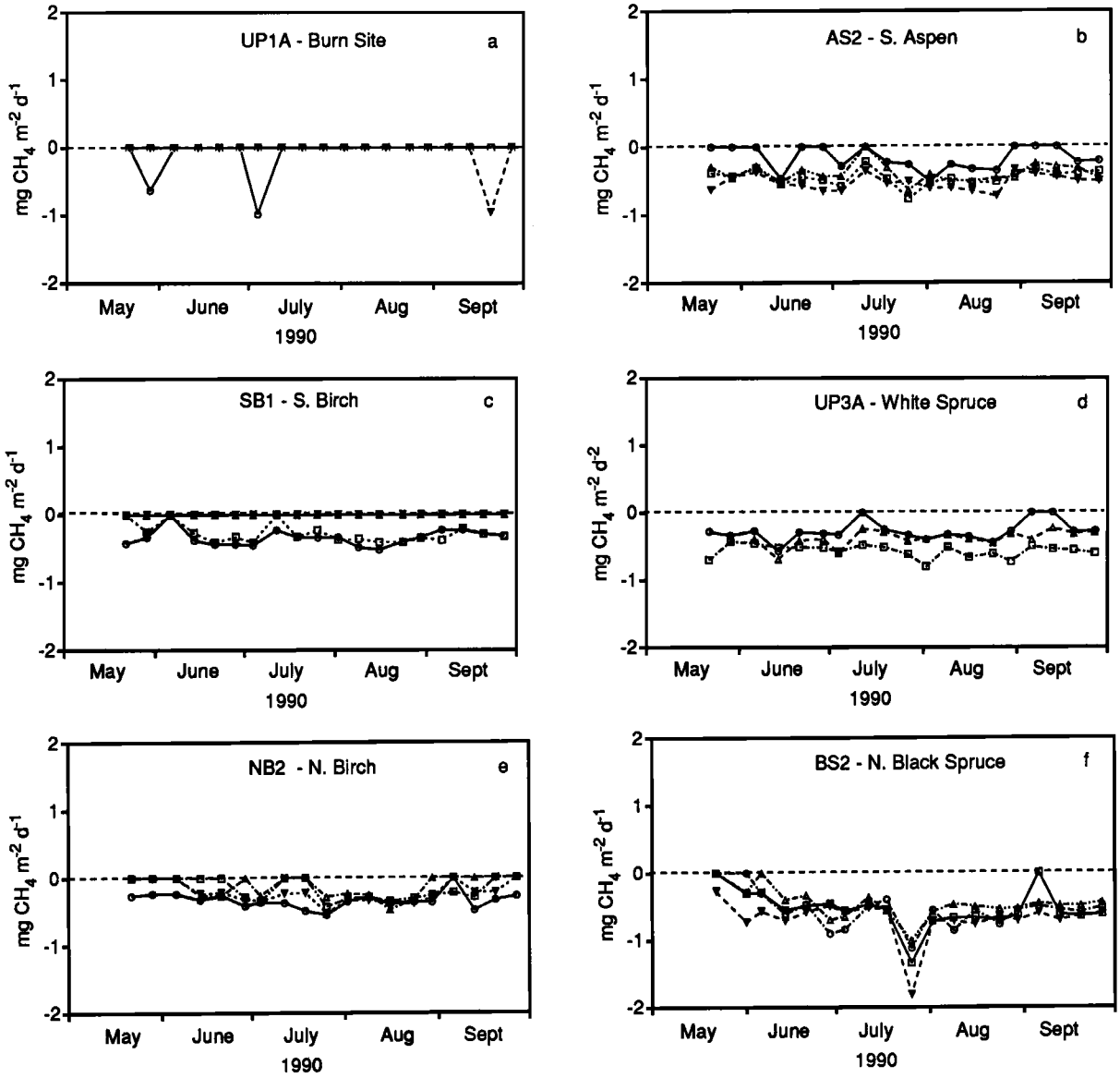

Fig. 3. Methane fluxes (mg m^{-2} d^{-1}) from Bonanza Creek Experimental Forest upland sites, May 22 - September 27, 1990. Data from the N-fertilized plots at sites AS2, SB1, NB2, and BS2 are plotted as triangles. (a) UP1A, burn site (*Calamagrostis*, triangles; *Equisetum*, open symbols). (b) AS2, aspen. (c) SB1, birch. (d) UP3A, white spruce. (e) NB2, north birch. (f) BS2, north black spruce.

sporadically seen in middle stages of succession (alder-poplar, Figure 2b; poplar, Figure 2c). The magnitude and frequency of emission decreased along the succession for these sites with some stations showing consumption as well as emission, depending on date. The late stages of succession, white spruce (Figure 2d) and black spruce (Figure 2e) showed only CH_4 consumption when fluxes were detectable. Differences in CH_4 flux among sites were statistically significant (Kruskal-Wallis one-way analysis of variance or ANOVA). A posteriori analysis by Dunn's nonparametric multiple comparison clearly showed that the sandbar site (Figure 4a) had the highest CH_4 flux (data ranked lowest to highest, i.e., greatest rate of consumption to greatest rate of emission). The remaining data showed three sets of overlapping similarities (Figure 4a). The mean ranks follow an order that shows the

(a) Floodplain

Site	FP4A	FP5A	FP3A	FP2A	FP1A
n	45	45	42	48	48
Mean Rank	57.4	89.9	104.4	139.9	174.6

(b) Upland

Site	BS2	UP3A	SB1	AS2	NB2	UP1A
n	38	55	38	38	38	76
Mean rank	60.8	95.8	128.9	129.8	152.9	223.2

Fig. 4. Multiple comparisons of ranked methane flux measurements for BCEF (a) floodplain and (b) upland sites by Dunn's nonparametric procedure. Mean ranks for the site types are arranged in increasing order. Sites underscored by the same line have no significant differences; sites not underscored by the same line show significantly different fluxes.

transition from CH_4 emission to consumption with increasing ecosystem maturity. There is no difference in CH_4 consumption between white spruce (FP4A) and black spruce (FP5A) or between black spruce and poplar (FP3A), but consumption is greater in white spruce than in poplar and in black spruce than in the alder-poplar (FP2A) stand.

Methane emission was never observed at the upland sites (Figure 3; Table 2). As in the floodplain sites, there was no clear seasonal signal for CH_4 flux. The earliest successional stage (burn site, Figure 3a) showed the smallest flux, with only 4% (3 of 76) of the flux determinations above the detectable level. The later successional stages, white spruce (Figure 3d) and black spruce (Figure 3f), exhibited higher rates of CH_4 consumption than the middle stages of succession (aspen, Figure 3b; and birch, Figures 3c and 3e). Differences in CH_4 flux at control stations among sites were significant (ANOVA), and multiple comparison of fluxes (Dunn's test) suggests that consumption increases with advancing plant community succession (Figure 4b). A significant increase in CH_4 consumption rate was observed at black spruce (BS2) relative to the burn site (UP1A). The CH_4 consumption rate at all other sites could not be clearly classified. However, ranks and overlapping similarities together indicated that white spruce (UP3A) was most closely related to black spruce (late successional stage) and north birch (NB2) was most closely related to other mid-successional (south birch, SB1 and aspen, AS2) sites. The lack of a significant difference in CH_4 consumption between south birch and north birch (Figure 4b) indicates that aspect had no influence on CH_4 flux for this plant community. Net CH_4 fluxes were significantly lower (i.e., higher rate of CH_4 consumption) in the upland sites than in the floodplain sites when the entire data were pooled (Mann-Whitney U test).

The soil pH at the study sites ranged from slightly basic to acidic (Table 1). The highest values of pH were observed in the first stage of succession (FP1A, UP1A), and the lowest values were found at the black spruce sites in both the floodplain (FP5A) and upland (BS2) areas. The soil organic content varied from 2 to 45% and from 9 to 37% in the floodplain and upland sites, respectively (Table 1), with the lowest value for each sequence occurring in the first successional stage.

The soil temperature during the observation period

varied from about 2° to 21° C in both the floodplain and upland sites (Table 2). Means varied from 10.5° to 15.7 °C for floodplain sites and from 8.9 to 12.9 °C for upland sites. The mean soil moisture content showed a higher range for upland sites (112%) than for floodplain sites (51%), due to the high mean soil moisture at BS2 (Table 2). The effect of soil temperature and moisture on CH_4 flux at each site was assessed by correlation analysis (Table 3). Correlations were not statistically significant in many cases. However, statistically significant data show three trends. First, CH_4 flux is negatively correlated with soil temperature, indicating that soil CH_4 consumption (negative flux) increases with increasing temperature. Second, CH_4 flux is positively correlated with soil moisture at sites showing no CH_4 emission (Figures 2 and 3), indicating that CH_4 consumption decreased with increasing soil moisture. Third, increasing CH_4 emission is correlated with decreasing soil moisture at the only site showing CH_4 emission and no consumption (FP1A, sandbar).

Nitrogen fertilization had no consistent effect on CH_4 flux in the upland sites. Neither station within the fertilized plot at SB1 (Figure 3c) showed detectable CH_4 consumption during the entire field season. Comparison of N-fertilized and control plots within other upland sites (Mann-Whitney *U* test) showed significantly increased consumption in the fertilized plot at AS2 (Figure 3b) and no difference between plots at BS2 (Figure 3f) and NB2 (Figure 3e).

The CH_4 concentration in soil atmospheres decreased rapidly with increasing depth at upland sites NB2, SB1, BS2, and UP3A. Figure 5a shows results from NB2, which are typical of the other sites. Methane was essentially depleted below a depth of 40 cm, and concentrations between 40 to 60 cm were consistently at or below the detection limit.

Soils at upland sites showed a low threshold and high capacity for CH_4 consumption. Methane concentrations in unamended chambers at NB2, SB1, BS2, and UP3A decreased to a threshold value varying from below the limit of detection (0.1 ppm) to 0.87 ppm over 24 hours; results from NB2 are shown in Figure 5b. Methane concentrations in

TABLE 3. Kendall's Rank Correlation Coefficient τ for Correlations Between CH_4 Flux and Soil Temperature and Moisture

	Kendall's τ				
	Soil Temperature	Soil Moisture			
Site	Station 1	Station 1	Station 2	Station 3	Station 4
FP1A			-0.59	-0.52	-
FP2A					-
FP3A					-
FP4A	-0.43	0.53	0.49		-
FP5A				0.63	-
UP1A					
AS2	-0.57	0.70	0.62	0.39	0.79
SB1	-0.38	0.47			
NB2	-0.60	0.46			
UP3A			0.46	0.41	-
BS2					

The number of observations at a station for each τ varied as follows: Floodplain temperature, 14-16; Floodplain moisture, 10-11; Upland temperature, 19; Upland moisture, 15. Stations 1 and 2 are within the control plot at upland sites; stations 3 and 4 are within the adjacent N-fertilized plot. Only statistically significant correlations are reported. A dash (-) indicates no data; a blank indicates no significant correlation.

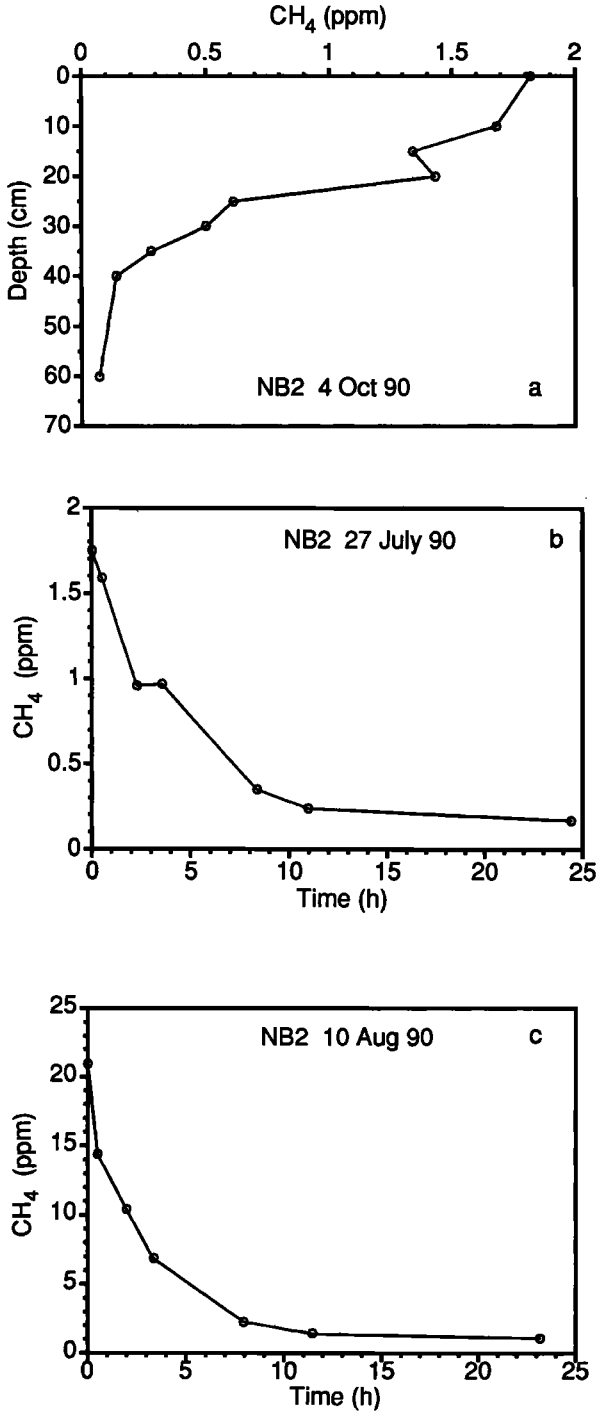

Fig. 5. Methane depth distribution and consumption at site NB2. (a) Depth distribution, October 4, 1990. (b) Chamber methane concentration vs. time with ambient (~1.7 ppm) initial atmosphere, July 27, 1990. (c) Chamber methane concentration vs. time with amended (~20 ppm) initial atmosphere, August 10, 1990.

chambers with atmospheres amended to ~20 ppm decreased to values varying from below the detection limit to 1.08 ppm within 24 hours. Figure 5c shows results from an amendment experiment at NB2.

DISCUSSION

Results of this study clearly indicate that well-drained taiga soils are a CH_4 sink. Seasonal studies have also reported net CH_4 consumption for other undisturbed, moist forest soils. Temperate deciduous and evergreen forests showed mean fluxes of -4.15 and -3.51 mg CH_4 m^{-2} d^{-1} [Steudler et al.,1990], and tropical forest soils had average fluxes of -0.14 [Keller et al.,1986], -0.57 (dry season) [Goreau and de Mello, 1988] and -0.8 [Keller et al., 1990] mg CH_4 m^{-2} d^{-1}. Our median flux of -0.23 mg CH_4 m^{-2} d^{-1} is closest to the lower mean reported for tropical soils.

The significant difference in CH_4 flux between floodplain and upland sites may be related to drainage and water table level. Early successional stages at floodplain sites (lowest terrace elevations, Table 1) showed episodic CH_4 emission (Figure 2a to 2c) following heavy rains. Sites at higher floodplain terrace elevations (late successional stages) and all upland sites consumed CH_4 or had fluxes below the detection limit. Soils in the floodplain and upland sites also differed; floodplain soils were a sandy or silty alluvium, while the upland soils consisted of a micaceous loess [Van Cleve et al., 1991].

Nitrogen fertilization had no influence on CH_4 consumption at our upland taiga sites but resulted in significantly lower CH_4 consumption rates in temperate hardwood and softwood forests [Steudler et al., 1990]. The studies differed in form of N added, relative N loading, and frequency of application, so their results are not directly comparable.

Soil CH_4 profiles (Figure 5a) strongly suggest that soils at deciduous and coniferous upland sites are well aerated at least to 60 cm. The organic horizon in these soils is generally limited to depths less than 20 cm. Thus it is likely that methanogenesis is nonexistent or confined to anaerobic microzones [Smith and Arah, 1985] and the important biological process influencing the soil CH_4 distribution is oxidation. Keller et al. [1990] and Born et al. [1990] found similar depth distributions for CH_4 in moist soils from tropical and temperate forests, which also suggests CH_4 consumption only. Yavitt et al. [1990] report CH_4 oxidation in the upper 0 to 20 cm

and production below 20 cm in CH_4 profiles for temperate mesophytic and spruce forest soils. Collectively, these data indicate that forest soils support a community of methanotrophs or other CH_4-oxidizing bacteria (e.g. nitrifiers [Bedard and Knowles, 1989]) whose CH_4 source is largely atmospheric.

Our taiga sites showed no strong seasonal signal for CH_4 consumption (Figures 2 and 3). Keller et al. [1983] found no seasonal trend in CH_4 consumption in soils of a temperate hardwood forest, and no seasonal variations are evident in the May through October record at other temperate hardwood sites [Steudler et al., 1990]. These reports are consistent with our observation that the atmosphere is the major CH_4 source for microbial oxidation in many forest soils. The moist surface zone of microbial activity can be expected to thaw and warm quickly in the spring. In contrast, the gradual thawing and warming of saturated, biologically active tundra soils underlain by permafrost results in a pronounced seasonal signal for CH_4 emission [Whalen and Reeburgh, 1988].

The low threshold and high capacity for CH_4 oxidation shown in the CH_4 amendment experiment (Figure 5c) is in agreement with our previous observations on end-member CH_4 oxidizing environments, namely well-drained subarctic tundra [Whalen and Reeburgh, 1990b] and the surface soil of a retired landfill [Whalen et al.,1990]. These results indicate the presence of a ubiquitous bacterial community capable of rapidly oxidizing CH_4 at concentrations well above and below atmospheric levels. These results also suggest that the rates of CH_4 consumption reported above for forest soils are governed by physical soil conditions (morphology, porosity, moisture content, and temperature) that regulate CH_4 diffusion to microbes, rather than intrinsic biological factors. Further support for physical control of CH_4 consumption by forest soils is shown in Table 3; increased CH_4 consumption (negative flux) was correlated with increasing soil temperature and decreasing soil moisture when significant values of τ were found for sites that showed CH_4 consumption only. It is likely that soil moisture content exerts the greatest physical influence on CH_4 oxidation rates in forest and other soils. We demonstrated experimentally that CH_4 oxidation rates in moist soils from a retired landfill were reduced nearly ten fold when saturated with water [Whalen et al., 1990], and Steudler et al. [1990] reported significant decreases in rates of CH_4 consumption by temperate forest soils under conditions of increased moisture.

The increase in CH_4 consumption with increasing ecosystem maturity (Figures 2 and 3) also points to physical control of the CH_4 consumption rate. As the taiga matures, mineral soil becomes covered with decaying organic matter and a thick carpet of feather moss [Van Cleve et al., 1991]. We observed the highest rates of CH_4 oxidation and gas diffusion in experiments involving both chambers and soil cores from mossy environments [Whalen and Reeburgh 1990b; also unpublished data, 1990], and attribute them to rapid gas phase diffusion in the pillowy, moist surface matrix.

Taiga has been considered a net CH_4 source [Sebacher et al., 1986; Matthews and Fung, 1987] of ~15 Tg yr^{-1} [Whalen and Reeburgh, 1990a], largely because of high rates of CH_4 emission from point sources (bogs and fens) [Crill et al., 1988; Harriss et al., 1985; Moore et al., 1990; Moore and Knowles, 1990] distributed throughout this environment. Using the overall flux results from this study (IQR of 0.0 to -0.42 mg CH_4 m^{-2} d^{-1}, Table 2), an active period of 150 days, and a global taiga coverage of 11.1×10^6 km^2, we estimate that upland and floodplain taiga have a CH_4 sink strength of 0 - 0.8 Tg yr^{-1}. This is smaller than the previous boreal forest soil consumption estimates of -1 to -15 Tg yr^{-1} [Born et al., 1990] and -0.3 to -5.1 Tg CH_4 yr^{-1} [Steudler et al., 1990], which were based on fewer data. Resolving the contributions of point sources within taiga environments will require a high resolution data base for the global extent of each site type.

The results from this study extend beyond establishing a firmly based estimate for CH_4 consumption by taiga. The data clearly show quantitative consumption of atmospheric CH_4 by moist taiga soils and support control of oxidation by physical processes. Recent studies have indicated that moist soils in both natural and managed ecosystems are net CH_4 sinks (summarized by Steudler et al. [1990] and Born et al. [1990]) and suggest CH_4 consumption equivalent to 1 to 11% of the 540 Tg CH_4 yr^{-1} emitted to the atmosphere from all sources [Cicerone and Oremland, 1988]. Consumption of atmospheric CH_4 by these ecosystems could provide a significant negative feedback to increases in atmospheric CH_4. Changes in soil physical characteristics resulting from temperature and precipitation changes are likely to influence rates of CH_4 consumption. Water table and temperature manipulation experiments (1 to 10 m^2 scale) are an approach to understanding these relationships.

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REFERENCES

Adams, J. M., H. Faure, L. Faure-Denard, J. M. McGlade, and F. I. Woodward, Increases in terrestrial carbon storage from the last glacial maximum to the present, *Nature, 348,* 711-714, 1990.

Bedard, C., and R. Knowles, Physiology, biochemistry and specific inhibitors of CH_4, NH_4^+ and CO oxidation by methylotrophs and nitrifiers, *Microbiol. Rev., 53,* 68-84, 1989.

Billings, W. D., Carbon balance of Alaskan tundra and taiga ecosystems: past, present and future, *Quat. Sci. Rev., 6,* 165-177, 1987.

Black, C.A., (Ed.), *Methods of Soil Analysis,* parts 1 and 2, American Society of Agronomy, Madison, Wis., 1965.

Blake, D. R., and F. S. Rowland, Continuing worldwide increase in tropospheric methane, 1978-1987, *Science, 239,* 1129-1131, 1989.

Born, M., H. Dörr, and I. Levin, Methane consumption in aerated soils of the temperate zone, *Tellus, Ser. B, 42,* 2-8, 1990.

Cicerone, R. J., and R. S. Oremland, Biogeochemical aspects of atmospheric methane, *Global Biogeochem. Cycles, 2,* 299-327, 1988.

Conover, W.J., *Practical Nonparametric Statistics,* John Wiley, New York, 1980.

Crill, P. M., K. B. Bartlett, R. C. Harriss, E. Gorham, E. S. Verry, D. I. Sebacher, L. Mazdar, and W. Sanner , Methane flux from Minnesota peatlands, *Global Biogeochem. Cycles, 2,* 371-384, 1988.

Goreau, T. J., and W. Z. de Mello, Tropical deforestation: Some effects on atmospheric chemistry, *Ambio, 17,* 275-281, 1988.

Helsel, D.R., Less than obvious: Statistical treatment of data below the detection limit, *Environ. Sci. Technol., 24,* 1766-1774, 1990.

Juday, G. P., and C. T. Dyrness (Eds.), Early results of the Rosie Creek Fire Research Project 1984, Misc. Publ. 85-2, 46 pp., Sch. of Agric. and Land Resour. Manage., Univ. of Alaska Fairbanks, 1985.

Keller, M., T. J. Goreau, S. C. Wofsy, W. A. Kaplan, and M. B. McElroy, Production of nitrous oxide and consumption of methane by forest soils, *Geophys. Res. Lett., 10,* 1156-1159, 1983.

Keller, M., W. A. Kaplan, and S. C. Wofsy, Emissions of N_2O, CH_4, and CO_2 from tropical forest soils, *J. Geophys. Res., 91*(D11), 11,791-11,802, 1986.

Keller, M., M. E. Mitre, and R. F. Stallard, Consumption of atmospheric methane in soils of central Panama: Effects of agricultural development, *Global Biogeochem. Cycles, 4,* 21-27, 1990.

Khalil, M. A. K. and R. A. Rasmussen, Climate-induced feedbacks for global cycles of methane and nitrous oxide, *Tellus, Ser. B, 41,* 554-559, 1989.

Kimmins, J. P., and R. W. Wein, Introduction, in *Forest Ecosystems in the Alaska Taiga,* edited by K. Van Cleve et al., pp. 3-8, Springer-Verlag, New York, 1986.

Harriss, R. C., E. Gorham, D. I. Sebacher, K. B. Bartlett, and P. A. Flebbe, Methane flux from northern peatlands, *Nature, 315,* 652-654, 1985.

Matthews, E., and I. Fung, Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources, *Global Biogeochem. Cycles, 1,* 61-86, 1987.

Moore, T. R., and R. Knowles, Methane emissions from fen, bog and swamp peatlands in Quebec, *Biogeochemistry, 11,* 45-61, 1990.

Moore, T., N. Roulet, and R. Knowles, Spatial and temporal variations of methane flux from subarctic/northern boreal fens, *Global Biogeochem. Cycles, 4,* 29-46, 1990.

Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger, Soil carbon pools and world life zones, *Nature, 298,* 156-159, 1982.

Rasmussen, R. A., and M. A. K. Khalil, Atmospheric methane in the recent and ancient atmospheres: Concentrations, trends and the interhemispheric gradient, *J. Geophys. Res., 89*(D7), 11,599-11,605, 1984.

Sebacher, D. I., R. C. Harriss, K. B. Bartlett, S. M. Sebacher, and S. S. Grice, Atmospheric methane sources: Alaskan tundra, an alpine fen and a subarctic boreal marsh, *Tellus, Ser. B, 38,* 1-10, 1986.

Smith, K. A., and J. R. M. Arah, Anaerobic microenvironments in soil and the occurrence of anaerobic bacteria, in *Microbial Communities in Soil*, FEMS Symp. 33, edited by V. Jensen et al., pp. 247-261, Elsevier, New York, 1985

Steele, L. P., P. J. Fraser, R. A. Rasmussen, M. A. K. Khalil, T. J. Conway, A. J. Crawford, R. H. Gammon, K A. Masarie, and K. W. Thoning, The global distribution of methane in the troposphere, *J. Atmos. Chem., 5*, 125-171, 1987.

Steudler, P. A., R. D. Bowden, J. M. Melillo, and J. D. Aber, Influence of nitrogen fertilization on methane uptake in temperate forest soils, *Nature, 341*, 314-316, 1990.

Van Cleve, K., F. S. Chapin III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, (Eds.), *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*, 230 pp., Springer-Verlag, New York, 1986.

Van Cleve, K., F. S. Chapin III, C. T. Dyrness, and L. A. Viereck, Element cycling in taiga forests: state-factor control, *BioScience, 41*(2), 78-88, 1991.

Whalen, S. C., and W. S. Reeburgh, A methane flux time series for tundra environments, *Global Biogeochem. Cycles, 2*, 399-409, 1988.

Whalen, S. C. and W. S. Reeburgh, A methane flux transect along the trans-Alaska pipeline haul road, *Tellus, Ser. B, 42*, 237-249, 1990a.

Whalen, S. C., and W. S. Reeburgh, Consumption of atmospheric methane by tundra soils, *Nature, 346*, 160-162, 1990b.

Whalen, S. C., W. S. Reeburgh, and K. A. Sandbeck, Rapid methane oxidation in a landfill cover soil, *Appl. Environ. Microbiol., 56*, 3405-3411, 1990.

Yavitt, J. B., D. M. Downey, G. E. Lang, and A. J. Sextone, Methane consumption in two temperate forest soils, *Biogeochemistry, 9*, 39-92, 1990.

Zar, J.H. *Biostatistical Analysis*, Prentice Hall, Englewood Cliffs, N.J., 1984.

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