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Plant transport and methane production as controls on methane flux from arctic wet meadow tundra

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Abstract. The roles of plant transport and CH_4 production in controlling CH_4 flux from wet meadow tundra communities were investigated. Plant transport was the dominant pathway of CH_4 flux from this ecosystem. Most CH_4 production (measured with *in situ* anaerobic incubations) occurred well below the water table, and C supply (estimated by anaerobic CO_2 production) was the best single predictor of CH_4 production rates. Plant transport of CH_4 was controlled both by CH_4 supply and the plant species. *Eriophorum angustifolium* transported substantially more CH_4 than did *Carex aquatilis*, due to differences in size and structure of the two species. The composition of the plant community was a greater control on CH_4 flux from the site than either water table height (which varied only slightly) or CH_4 production rates, indicating the importance of species-specific plant dynamics in controlling CH_4 flux from arctic wetlands.

Introduction

Most studies have indicated that high latitude wetlands are an important source of atmospheric CH_4, with fluxes from tundra of approximately 35 Tg/y; this is between 5% and 10% of the global total (Fung et al. 1991; Whalen & Reeburgh 1990; Roulet et al. 1994). Most of this flux is from sedge-dominated wet meadows (Whalen & Reeburgh 1988). Plant CH_4 transport, which effectively bypasses the aerobic zone of CH_4 oxidation, is an important process in CH_4 emissions from wetland ecosystems, including the tundra (Whalen & Reeburgh 1988; Schütz et al. 1991; Chanton & Dacey 1991; Morrisey & Livingston 1992; Chanton et al. 1992; Whiting & Chanton 1992). Plant species- or growth form-specific differences in transport rates may be an important control on CH_4 fluxes (Sebacher et al. 1985).

Transport, however, is but one way in which plants affect CH_4 dynamics (Schimel et al. 1993). Plants supply C to the soil methanogenic community both through production of soil organic matter and as fresh exudates and residues. Fresh plant material may be an important CH_4 precursor even in an organic matter-rich peat soil (Schütz et al. 1991; Whiting & Chanton 1992).

Strong correlations between net primary productivity and system-level CH_4 fluxes across a wide range of ecosystems highlights the importance of plant C inputs (Aselmann & Crutzen 1989; Whiting & Chanton 1993). A complete understanding of wetland CH_4 emissions therefore requires understanding how the different plant species in a wetland ecosystem affect both CH_4 production and CH_4 transport to determine the overall system-level effect on CH_4 flux.

This work examined the controls on CH_4 flux from an arctic wet meadow community. There were three goals: 1) determine how much of the CH_4 efflux was directly plant mediated, 2) determine whether total CH_4 efflux was controlled primarily by the CH_4 production rate or by plant transport kinetics and 3) determine how the different dominant sedge species affected these processes. The controls on CH_4 efflux were considered on both the individual plant tiller level and the plot level because the controls on CH_4 flux at these scales differed.

Methods

Site description

The research was done in a wet meadow community at the Toolik Lake Long Term Ecological Research (LTER) site on the North Slope of the Brooks Range in Alaska (68°38′ N, 149°38′ W)., The plant community was dominated by the sedges *Eriophorum angustifolium* and *Carex aquatilis*, with smaller amounts of *E. scheuchzeri*. Patches (up to ten meters across) were often dominated by a single species, though *E. scheuchzeri* rarely dominated the community and is more of an 'understory' species. Peak aboveground plant biomass averaged 185 $g \cdot m^{-2}$, ranging between 130 and 260 $g \cdot m^{-2}$, tiller density of *E. angustifolium* + *C. aquatilis* averaged 380/m^2. *E. scheuchzeri* averaged 100/m^2 but was very patchy. *E. angustifolium* had an average tiller mass of 1.05 g, tiller diameter of 7.9 mm, and total leaf area of 88 mm^2/plant (measured in late July 1991). It is a large sedge with a low root/shoot ratio, its roots are unbranched and are produced annually. *C. aquatilis* had an average tiller mass of 0.64 g, tiller diameter of 3.8 mm and leaf area of 43 mm^2/plant. It produces extremely large rhizomes and has a large root/shoot ratio with a mix of coarse perennial roots and fine, branching roots. The smallest plant in the study area was *E. scheuchzeri*, with an average tiller mass of 0.09 g and a diameter of 1.7 mm (leaf areas were not measured). The soils were peats overlying permafrost. There was a layer of stones at approximately 20 cm depth. The soils were generally saturated to the soil surface, though the actual

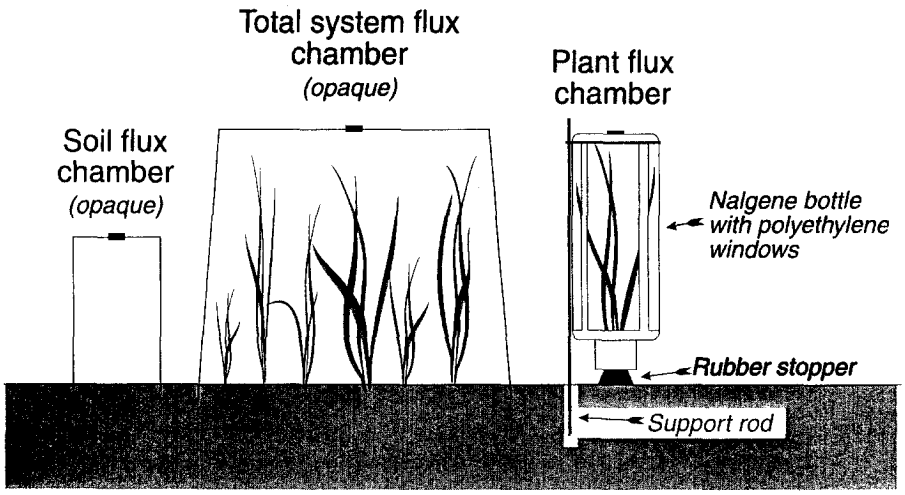

Fig. 1. Design of the different flux chambers.

water table depth ranged between 3 and 8 cm below the soil surface. Soil pH ranged between 6.3 and 7.2.

Gas fluxes

In order to sample across the range of natural variations, while ensuring that sets of measurements within plots were representative of each other, measurements were done in 3 m × 1.5 m plots distributed along a 0.5 km stretch of the shore of Toolik lake. Boardwalks were established to minimize site disturbance during sampling. Experiments were done 19–21 July 1991, 27–28 June 1992, 17–21 July 1993, and 7–8 August 1993. The sampling designs in 1991/92 and 1993 were slightly different. In 1991/92 one system-flux chamber was used per plot and the plant and soil fluxes measured closely around that to try to make all the measurements representative of that flux. In 1993 three system-flux chambers were used per plot.

Total ecosystem CH_4 flux was measured by placing chambers (29 cm diameter by 25 cm tall) approximately 2 cm into the saturated soil, just far enough to make a seal (Fig. 1). These were sampled every 10 minutes over 30 minutes. Next, the plants were collected, identified, tiller diameters measured and their biomass determined after drying at 60 °C. Flux from the soil surface was measured by placing a small chamber (a cut-off 500 ml Nalgene bottle fitted with a septum) between plants. The chambers were supported by a rod driven into the soil to limit disturbance while taking measurements.

Methane fluxes from plants were determined with chambers fitted around individual tillers of either *E. angustifolium* or *C. aquatilis* (Fig. 1). Three tillers of each species were used in each plot. Chambers were made from 1 L wide-mouth Nalgene bottles with large windows cut out of the sides and covered with clear polyethylene; a septum was put in the jar bottom for sampling. A hole was drilled in the lid to hold a rubber stopper. A rubber stopper with a hole drilled out and slit down the side was wrapped around the base of an individual tiller and seated on the soil. The chamber was then placed over the plant and onto the rubber stopper, sealing the system. To support the chamber a rod was driven into the soil before the chamber was placed over the plant. Gas samples (5 mL) were taken every 10 minutes for 30 minutes. In all measurements CH_4 concentrations increased linearly. After flux measurements, each plant was removed from the ground and its diameter at the tiller base, leaf area (in 1991 only), and dry mass were measured. Tiller cross-sectional area was calculated from the diameter measurement by assuming the tiller was cylindrical.

Gas samples were taken in individual syringes which were closed with a valve. They were returned to the lab and analyzed within 6 h. Samples were analyzed with a gas chromatograph equipped with a thermal conductivity detector (for CO_2) plumbed in series with a flame ionization detector (for CH_4).

Clipping experiments

Plant CH_4 flux was measured as above. Then the chamber was removed and the leaves were cut off with a razor between the blades and sheaths of the outermost leaves. This is the point at which the leaves open out from the tiller base and become green, and left approximately 5 cm standing. The chamber was then resealed and the flux measured again. This provided an estimate of the leaf resistance to CH_4 flux. Next, to determine whether the leaf blades, rather than pores on the leaf bases, were the pathway of CH_4 efflux from the plants, the chambers were opened and petroleum jelly was applied to the cut ends of the plants to block gas efflux. The chambers were then closed and the flux measured again.

Pore water CH_4 concentrations

In the 1993 samplings, immediately after a flux measurement was made on a tiller but before it was harvested, the pore water directly underneath the tiller was sampled at 5 cm and 15 cm depths. Using a syringe fitted with a valve and a 15 cm long, 18 gauge side-port needle, pore water (5–10 mL) was drawn and the valve was closed. The pore water sample was then transferred to a

previously evacuated serum bottle (70 mL). The bottle was shaken to extract CH_4, vented briefly to bring the headspace pressure up to atmospheric and the headspace analyzed for CH_4 concentration as described above. The bottles were weighted to determine the exact volume of pore water sampled.

Production rates of CO_2 and CH_4

Immediately after the tiller was harvested, a soil core (6.8 cm diameter) was taken where the plant had been. The cores were taken down to the stone layer, which was generally at approximately 20 cm. Each core was sectioned into the top 10 cm and the remaining depth, and the sections were placed intact into 1 L jars Mason Jars (Ball Inc.) fitted with septa. The jars were purged with N_2 for 20 minutes to make them anaerobic and let sit for approximately 30 minutes to allow dissolved gases to equilibrate with the headspace. The headspace was then sampled by syringe, and the jars were replaced in the ground for incubation. All the jars were placed into the soil until the jar tops were just below the soil surface (0–10 cm depth); it was impractical to try to place the core sections at the same depth they came from. Thus all the jar incubations within a plot were at the same temperature. The jars were sampled again 24 hours after being placed in the ground. Headspace gases were analyzed for CO_2 and CH_4 concentrations as described above. There were 6 measurements of pore water concentrations and CH_4 production potentials at each depth in each plot, 3 under *E. angustifolium* and 3 under *C. aquatilis*.

Calculations and statistics

Total plant flux on an areal basis (mg $C \cdot m^{-2} d^{-1}$) was calculated by multiplying the average flux for each species in the plot by the number of tillers of each species in the chamber. Plant CH_4 fluxes were measured simultaneously with the system-flux chamber measurements. *E. scheuchzeri* was not measured directly but was assumed to transport, on average, the same amount of CH_4 per unit tiller cross-sectional area as *E. angustifolium*. I used cross sectional area to scale CH_4 tiller fluxes because flux through *E. angustifolium* correlated better with cross sectional area than with tiller mass. The estimated flux due to *E. scheuchzeri* was always a small component of the total and this was unlikely to change based on the estimation method.

The balance of CH_4 production and flux was calculated for each of the six study plots examined in 1993. Production was calculated as the sum of production in both depth increments and extrapolated to a mg $C \cdot m^{-2} d^{-1}$ basis. Total flux was estimated by the system-flux chambers.

Clipping and sealing effects were determined by paired *t*-test of the treatment against the non-clipped control. The effects of the different plant species

Table 1. Methane fluxes and plant CH_4 transport in wet meadow tundra. In 1991/92 total flux was measured by one chamber per plot, in 1993 total flux was measured by three chambers per plot. Except where noted in the community composition column, *E. scheuchzeri* biomass was insignificant and the remaining biomass was *E. angustifolium*. Error ranges are standard errors.

Sampling date	Community composition *C. aquatilis as % of total biomass*	Total flux	Bare soil	Estimated plant transport[1]	% Plant transport[2]
		(mg C $m^{-2}d^{-1}$)			
July 1991	0	150.3	-1.0 ± 0.9	94.3	63–100
July 1991	100	10.5	0.1 ± 0.3	5.8	55–99
July 1991	26 (60)[3]	65.6	0.6 ± 0.2	66.1	99–100
July 1991	88	75.8	0.4 ± 0.9	61.8	81–99
July 1992	0	27.7	8.0 ± 6.6[4]	10.5	38–71
July 1992	50 (50)	20.6	8.0 ± 6.6[4]	14.6	63–68
July 1992	70	16.7	8.0 ± 6.6[4]	10.3	52–62
July 1993	36	119.1 ± 13.1	N.D.[5]	57.1	48
July 1993	52	65.9 ± 22.2	N.D.	67.9	103
July 1993	47 (20)	65.5 ± 20.6	N.D.	24.3	37
July 1993	82	21.1 ± 3.9	N.D.	18.1	86
August 1993	3	102.6 ± 19.5	N.D.	107.4	70–150
August 1993	25	47.4 ± 8.6	N.D.	45.4	80–130

[1] Total plant flux was estimated by multiplying the average flux for each species by the number of tillers in the chamber. *E. scheuchzeri* was assumed to transport the same amount of CH_4 per unit tiller cross-sectional area as *E. angustifolium*

[2] The range was estimated both from direct plant flux measurements and from the flux unaccounted for the total flux minus the soil flux.

[3] Percent biomass as *E. scheuchzeri.*

[4] In 1992, soil flux measurements were not associated with individual total flux chambers.

[5] Not Determined.

on CH_4 transport, pore water concentrations, and production rates were determined by 2-way ANOVA with species and plot as the independent variables. The effect of plant community composition across sampling was determined by MANOVA with sampling date as a categorical variable and % of total biomass as *Carex* in the plot as a covariate (Systat, Inc. 1992).

Results

Ecosystem CH_4 fluxes

Methane emissions from wet meadow tundra were variable both spatially and temporally (Table 1). The highest rate (150 mg CH_4-C·$m^{-2}d^{-1}$) and the lowest (10.5 mg CH_4-C·$m^{-2}d^{-1}$) occurred on the same day within 100 m of each other. Within plots, however, the coefficients of variation averaged only 36%. The lowest rates generally occurred in 1992, but these were early in the season. Flux generally increases over the season as the active layer thickens and soil temperatures increase (Whalen & Reeburgh 1988).

Methane fluxes were strongly controlled by the composition of the plant community, with greater fluxes associated with *E. angustifolium* domination. Methane flux correlated with species composition measured as % total biomass as *C. aquatilis* with an $r^2 = 0.68$ ($p = 0.014$). Species composition was a stronger predictor of CH_4 flux than either water table depth or total aboveground plant biomass, neither of which correlated with flux ($r^2 < 0.3$, $p > 0.45$).

Plant-mediated flux

The estimated CH_4 flux through plants always accounted for at least 37% of the total CH_4 flux to the atmosphere and averaged approximately 75% of total flux (Table 1). In some plots, plant transport could account for the entire measured CH_4 flux. With the exception of occasional hot spots of soil efflux (1 measurement in 20), very little CH_4 was released from the soil surface (< 5 mg C·$m^{-2}d^{-1}$).

Flux through individual plant tillers

Methane flux through individual tillers of *E. angustifolium* was significantly greater than flux through *C. aquatilis* ($p < 0.05$), even in sites where they co-existed. In the 1993 measurements, flux through *C. aquatilis* correlated significantly with tiller mass (Table 2), but not with tiller cross-sectional area, which is consistent with 1991 and 1992 measurements (data not shown). Flux through *E. angustifolium* didn't correlate with either measure of plant size in the 1993 sampling though in 1991 samplings there was a weak correlation with tiller cross-sectional area ($r^2 = 0.25$, $p < 0.1$).

For each species, there was a significant correlation between CH_4 flux and CH_4 pore water concentration, and for *C. aquatilis*, with production rate as well (Table 2). Flux through tillers of both species correlated better with CH_4 concentration and production rate in the surface than in the deep layer.

Table 2. Correlation between flux through individual tillers of *C. aquatilis* and *E. angustifolium* and different plant parameters and aspects of soil CH_4 supply in the July 1993 sampling. Significant levels of correlations: * <0.1, ** <0.05, *** <0.01, **** <0.005. 12 plants of each species were measured across 4 plots.

	C. aquatilis	*E. angustifolium*
	Tiller flux ($\mu g\ C \cdot h^{-1}$)	
	4.98	9.53
	Correlation coefficients	
	r^2	r^2
Plant characteristics		
Tiller cross-sectional area	0.07	0.06
Tiller mass	0.54****	0.07
Soil CH_4		
Surface layer		
Pore water	0.79****	0.33*
Production rate	0.35**	0.24
Deep layer		
Pore water	0.48**	0.08
Production rate	0.22	0.11

Table 3. Effect on CH_4 flux of clipping plants and of sealing the clipped ends. All values are shown relative to the specific control plant. ns means that the treatment effect was not significant ($p > 0.1$); * indicates the effect was significant at $p = 0.05$. Measurements were done in June 1992. 6 plants of each species were measured; ranges are standard errors.

	% of flux in control plants	
Species	Clipped	Sealed
E. angustifolium	106 ± 22^{ns}	35 ± 9*
C. aquatilis	159 ± 16*	36 ± 13*

Clipping the leaf blades significantly increased flux in *C. aquatilis* (Table 3), but not in *E. angustifolium*. Sealing the cut ends with Vaseline greatly reduced CH_4 flux in both species (Table 3), suggesting that leaves were the dominant pathway of CH_4 efflux in both plant species. Morrissey et al. (1993) came to a similar conclusion for *Carex*, but in most other wetland

plants, including *Oryza* (rice), *Pontedaria*, and *Sagittaria*, the main path of CH_4 efflux is micropores on the leaf sheath or petiole (Nouchi et al. 1990; Harden & Chanton 1994).

Soil carbon dynamics

Both CH_4 production rates and pore water concentrations varied significantly between plots ($p < 0.01$; Table 4), but the variation within plots was less. Pore water concentration coefficients of variation (C.V.) averaged 92% and 66% in the surface and deep layers respectively (Table 4). Methane production rates in the surface layer varied between plots from 0.2 μg $C \cdot g^{-1} d^{-1}$ to 14.0 μg $C \cdot g^{-1} d^{-1}$, and in the deep layer from 2.9 μg $C \cdot g^{-1} d^{-1}$ to 21.6 μg $C \cdot g^{-1} d^{-1}$. Again, within-plot variation was lower than between-plot variation (average within-plot C.V. were 85% and 73% for the surface and deep layers respectively). There was no significant association between any measure of soil CH_4 supply and the plant species dominating a plot (Table 5).

Methane production rates and pore water concentrations increased significantly with depth (Tables 4, 5). Methane concentration in the surface pore water averaged only 20% of the concentration in the deep layer. Methane production rate (per gram soil) in the surface layer averaged 58% of that in the deep layer, though this varied from 2% to 180% on individual cores. Due to greater soil bulk density at depth, however, production in the surface layer (per m^2) averaged only 25% of the production at depth.

There were significant correlations between all measures of CH_4 dynamics at both depths across plots. Production rates and pore water concentrations within a layer correlated with $r^2 = 0.31$ and 0.39 for the surface and deep measurements respectively ($p < 0.001$ in both cases). Pore water concentration in the surface and deep layers correlated with each other with $r^2 = 0.38$ ($p < 0.001$); production rate in the surface and deep layers correlated with each other with $r^2 = 0.14$ ($p = 0.03$). Thus, both pore water CH_4 concentration and production rate are indicators of CH_4 supply.

Carbon dioxide production rates were an estimate of total microbial activity, as CO_2 is a major product of most forms of anaerobic metabolism. Under controlled conditions with an undisturbed microbial community, CO_2 production rate is therefore an index of soil organic matter quality. Since the incubations were anaerobic, root respiration was not a component of CO_2 production, though carbon released from roots damaged by the coring could have contributed to microbial respiration. The CO_2 production rates were less variables than CH_4 production rates, though there were still significant differences between plots. The CO_2 production rates in the surface layer averaged 240 μg $C \cdot g^{-1} d^{-1}$ (plot averages ranged from 135 μg $C \cdot g^{-1} d^{-1}$ to 414 $\mu g \cdot g^{-1} d^{-1}$), while in the deep layer, the average was 137 μg $C \cdot g^{-1} d^{-1}$

Table 4. Methane pore water concentrations, methane production rates, methane flux and unaccounted for flux in the six plots sampled in 1993. Plots 1 through 4 were sampled in July 1993, while plots 5 and 6 were sampled in early August 1993. Error ranges are standard errors of the 6 replicate samples taken in each plot.

Plot	CH_4 pore water concentration at 5 cm depth mg C/L	CH_4 pore water concentration at 15 cm depth mg C/L	CH_4 production rate Surface	CH_4 production rate Deep	CH_4 production rate Total	CH_4 flux rate	Difference
					mg $C \cdot m^{-2} d^{-1}$		
1	0.27 ± 0.10	1.45 ± 0.49	6.6 ± 3.4	47.4 ± 7.5	54.0 ± 8.1	119.1 ± 13.0	−65.1
2	1.00 ± 0.13	2.24 ± 0.17	34.8 ± 9.9	102.6 ± 15.0	137.4 ± 8.3	65.9 ± 22.0	71.5
3	0.09 ± 0.02	0.93 ± 0.28	48.2 ± 12.0	53.9 ± 11.0	102.1 ± 18.0	65.6 ± 20.0	−36.5
4	0.04 ± 0.02	0.26 ± 0.10	0.3 ± 0.1	9.7 ± 5.0	10.0 ± 5.1	21.1 ± 3.9	−11.1
5	0.08 ± 0.03	1.63 ± 0.29	2.0 ± 1.0	27.0 ± 10.0	29.0 ± 11.0	102.6 ± 19.0	−73.6
6	0.16 ± 0.11	0.69 ± 0.23	0.8 ± 0.2	15.6 ± 5.7	16.3 ± 5.8	47.4 ± 8.6	−31.1

Table 5. Plant effects on CH_4 dynamics in arctic wet meadow tundra. Data are averages of 12 plants of each species across the 4 plots sampled in July 1993.

Species	Tiller flux $\mu g\ C \cdot h^{-1}$	Average pore water CH_4 concentration *Surface* mg C/L	Average pore water CH_4 concentration *Deep* mg C/L	CH_4 production potential *Surface* $\mu g\ C \cdot g^{-2} d^{-1}$	CH_4 production potential *Deep* $\mu g\ C \cdot g^{-2} g^{-1}$
E. angustifolium	9.5 ± 1.5	0.31 ± 0.11	1.23 ± 0.27	7.5 ± 2.2	11.4 ± 2.3
C. aquatilis	5.0 ± 1.8	0.40 ± 0.15	1.21 ± 0.33	7.9 ± 2.8	11.2 ± 2.8
$p =$ [1]	0.008	0.27	0.94	0.89	0.93

[1] Significance of species effect.

(ranging from 73 $\mu g \cdot g^{-1} d^{-1}$ to 192 $\mu g \cdot g^{-1} d^{-1}$). The average within-plot C.V. were 51% and 35% for the surface and deep layers respectively.

The CO_2 production rate in the surface layer averaged 175% of the rate in the deep layer (significantly different at $p = 0.001$). There was, however, no correlation between CO_2 production in the surface and deep layers ($r^2 = 0.04$, $p = 0.25$).

There were strong indications that *C. aquatilis* domination increased CO_2 production rates in the surface layer. Carbon dioxide production (per m^2) correlated with the percent biomass of *C. aquatilis* in a plot ($r^2 = 0.83$, $p = 0.012$) over both 1993 samplings. In the July sampling CO_2 production per gram soil correlated with percent *C. aquatilis* ($r^2 = 0.98$, $p = 0.01$), but including the August samples in this analysis reduced the r^2 to 0.39 ($p = 0.19$).

Methane production correlation with CO_2 production in the deep layer ($r^2 = 0.27$, $p = 0.001$) but not in the surface layer ($r^2 = 0.01$). The average ratio of CO_2/CH_4 produced in the surface layer (518) was significantly higher ($p = 0.001$) than in the deep layer (68), though median values were only 128 and 15 for the surface and deep layers, respectively due to some very large values. In both layers, the minimum CO_2/CH_4 ratio was between 5 and 6. There were no significant effects of plant species on the CO_2/CH_4 ratio.

Discussion

Ecosystem CH_4 fluxes

The greatest fluxes from arctic tundra are from wet, sedge-dominated meadows (Whalen & Reeburgh 1990; Nadelhoffer et al. 1993). The flux rates I measured were comparable to those other studies. Fluxes from wet meadow sites have often been characterized as extremely variable, but the greatest variation I observed was between discrete, identifiable patches, rather than being purely random microsite variability. Within individual patches, variability in CH_4 production rates, pore water concentrations, and flux rates was relatively low. Patches were defined primarily by the composition of the plant community, rather than total plant biomass, water table height or other environmental parameters.

The association of flux rates with identifiable patches should be useful in spatial modeling of CH_4 fluxes, scaling from individual plots to larger areas (Burke et al. 1991) and in predicting response of wet meadow tundra to changing conditions and plant distribution. Temporally, CH_4 fluxes varied such that samplings made just a few weeks apart in 1993 had different fluxes and associations of flux with measured controlling factors.

Most other studies evaluating the role of plants on CH_4 flux have found that biomass or productivity are good predictors of CH_4 flux either across a wide range of systems (Whiting & Chanton 1993) or within a single species (Schütz et al. 1989; Sass et al. 1990; Whiting et al. 1991; Whiting & Chanton 1992). Sebacher et al. (1985) found large differences in transport capacity between aquatic plant growth forms (e.g. species with soft root epidermal layers and extensive aerenchyma vs. species with hard epidermal layers and less developed aerenchyma), but did not carefully examine differences within growth form. My study was done at a tighter scale of plant differences than Sebacher et al. (1985) and of space than Whiting & Chanton (1993). I found that even within an area with a uniform growth form and productivity, species differences caused significant differences in CH_4 flux. Plots dominated by *E. angustifolium* effluxed more CH_4 than those dominated by *C. aquatilis*, and these differences were not due to differences in plant biomass.

Water table height was probably not a major factor in this study as it never dropped below 8 cm. Water table height is a critical control on CH_4 flux (Moore & Roulet 1993; Funk et al. 1994), but it generally must drop to 10–20 cm below the soil surface to significantly decrease flux.

The balance of production vs. flux was variable among the different plots (Table 4). Some plots had higher CH_4 production than flux, suggesting substantial CH_4 oxidation in either the rhizosphere (Gerard & Chanton 1993) or the surface soil. Most of the plots, however, had greater flux than total CH_4 production. These data suggest that either dissolved CH_4 was outgassing, there was CH_4 present in gas bubbles that was not measured, or that that substantial CH_4 production occurred deeper in the soil profile. Total dissolved CH_4 storage in the top 20 cm averaged 130 mg $C \cdot m^{-2}$, while the unaccounted-for flux (flux – production) ranged from 11 to 70 mg $C \cdot m^{-2} d^{-1}$. These data therefore cannot determine the source of the excess flux.

The very small fluxes from the soil surface indicate that either CH_4 diffusion out of the soil was slow, or that CH_4 was oxidized in the aerobic surface soil. The CH_4 balance data (Table 4), do not suggest the high rates of CH_4 oxidation that occur in some wetland systems (e.g. 90% of the CH_4 produced; Schütz et al. 1991). Limited diffusion combined with moderate levels of total oxidation probably explain the low flux from the soil surface. Field work using methyl fluoride to inhibit CH_4 oxidation at a similar site also suggests relatively limited oxidation (<25% of production; S. Moosavi & P. M. Crill pers. comm.). Since plant community composition did not appear to affect CH_4 production (Table 5), but did control CH_4 flux, community composition may be an important control on CH_4 oxidation and the balance of production to oxidation as well.

Soil carbon dynamics

The interactions of plant community, soil horizon, soil carbon dynamics, and CH_4 production were complex. Carbon dioxide production decreased with depth, while CH_4 production increased; these patterns suggest different C substrates in the two layers and different controls on CH_4 production. In the surface soil, fresh plant material was likely to be a major C source. Rooting density is high in the surface layer, particularly for *C. aquatilis* (Shaver & Billings 1975), and so root C inputs should be substantial. The relationship between *C. aquatilis* domination of a site and CO_2 production in the surface soil is consistent with the importance of plant inputs for C dynamics in this layer. In the surface layer, there was no relationship between CO_2 and CH_4 production, indicating that redox, the absence of methanogenic bacteria, or some other factor (probably related to soil aeration) was a greater proximate control on total CH_4 production than C availability in short-term incubations.

In the deep layer, where roughly 85% of the CH_4 was produced, C availability was an important control on CH_4 production as indicated by the relationship between CO_2 and CH_4 production. In this layer, soil organic matter (SOM) may be an important C source for methanogenesis. The lower rate of CO_2 production per gram soil in the deep layer relative to the surface indicated a lower average organic matter quality in the deep layer, suggesting greater importance of soil organic matter relative to fresh root inputs in soil C dynamics. Production of CO_2 showed no relationship to the dominant plant community, which also suggests less direct root influence at depth. In a lab study, CO_2 and CH_4 production by these soils did not significantly decrease even after several months anaerobic incubation at 15 °C, indicating the presence of a large pool of decomposable soil organic matter (E. A. Holland & J. P. Schimel, data not shown).

The relationship between CO_2 and CH_4 production in the deep layer also suggests that redox was consistently low and other factors were relatively constant; otherwise redox differences would have masked the effects of C supply. Dissolved CH_4 storage in the deep layer was only great enough to account for approximately 2 days CH_4 flux, suggesting relatively rapid CH_4 diffusion out of this zone.

The suggestion that SOM may be an important CH_4 source is at odds with several other studies that have indicated fresh plant material (either the current or previous year's production) as the dominant CH_4 source (Whiting et al. 1991; Whiting & Chanton 1992; Whiting & Chanton 1993). One difference between this study and those done in lower latitudes, is that peat quality at depth (where low redox allows significant CH_4 production) is generally higher in high-latitude systems than in warmer climates (Wieder & Starr

1994). Thus, SOM may be a more important CH_4 source in the arctic than in lower latitudes.

Flux through individual plant tillers

Most of the CH_4 efflux occurred through plant tillers. Similarly, several other studies in arctic tundra suggested that plant transport accounted for 90% of the total CH_4 efflux (Torn & Chapin 1992; Morrisey & Livingston 1992; Whiting & Chanton 1992).

The amount of CH_4 transported by a plant tiller may depend on three processes: the CH_4 supply to the roots, the rate at which CH_4 is transported into the root air spaces (aerenchyma), and the rate at which CH_4 can move through, and out of the plant (Schütz et al. 1991; Chanton & Dacey 1991). All three processes controlled CH_4 flux in this site, though on different spatial scales and to differing degrees between species.

The two plant species had different transport kinetics, as indicated by the greater flux through *E. angustifolium* even though the roots were exposed to the same bulk soil CH_4 supply (Table 5). For each species there were significant correlations of flux with some measure of CH_4 supply, thus, CH_4 supply was an important control of plant transport, though apparently more immediately so for *C. aquatilis*.

Methane efflux appeared to occur through the leaf blades in both species, though clipping increased flux only in *C. aquatilis*. Thus, transport through leaves and stomata was a rate-limiting step for CH_4 transport in *C. aquatilis*, but not for *E. angustifolium*. In *E. angustifolium* the rate-limiting step was probably transfer between the rhizosphere and the aerenchyma, as is common among most other plant species (Armstrong 1979; Chanton & Dacey 1991). The different transport controls in *C. aquatilis* and *E. angustifolium* may be related to plant architecture rather than to any physiological differences between the species. *E. angustifolium* is larger than *C. aquatilis* (1.7 times greater tiller mass and 2.5 times greater tiller cross-sectional area). *E. angustifolium* also has a low root/shoot ratio and unbranched roots, while *C. aquatilis*, has a high root/shoot ratio and extensively branched roots (Shaver & Billings 1975).

Conclusions

Methane dynamics in the arctic wet meadow tundra are controlled by several factors that interact to produce complex spatial patterns. Soil organic matter quality, plant community distribution, and water table depth may all play major roles in controlling CH_4 production and flux in wetland systems. The

relative importance of these factors may vary independently and on different spatial scales. Within individual patches, defined by the intersections of these factors, the variability in CH_4 dynamics was relatively limited.

My results suggested that soil organic matter was an important C source for CH_4 production and that SOM quality was an important control on CH_4 production. While this is consistent with some other experimental and modeling work (Valentine et al. 1994), it disagrees with studies indicating fresh plant material as the source of CH_4 (Whiting & Chanton 1992). Regardless, total CH_4 production was not a good predictor of actual flux. Flux was controlled primarily by the composition of the plant community and its ability to transport CH_4. The controls on CH_4 flux through *E. angustifolium* and *C. aquatilis* differed, apparently due to differences in plant size, architecture, and inherent transport capacity. These results indicate that to understand and predict CH_4 flux from arctic wet meadow tundra, the composition of the plant community needs to be considered. Additionally plant species shifts resulting from disturbance, development, or climate change could substantially affect the total CH_4 flux from the ecosystem, beyond any direct effects from changing CH_4 production.

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