Biogeochemistry **41:** 215–235, 1998.

Response of tundra CH_4 and CO_2 flux to manipulation of temperature and vegetation

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Accepted 6 October 1997

Key words: arctic, carbon dioxide, climate change, methane, plant transport, species composition

Abstract. We conducted plant species removals, air temperature manipulations, and vegetation and soil transplants in Alaskan wet-meadow and tussock tundra communities to determine the relative importance of vegetation type and environmental variables in controlling ecosystem methane (CH_4) and carbon dioxide (CO_2) flux. Plastic greenhouses placed over wet-meadow tundra increased air temperature, soil temperature, and soil moisture, but did not affect CH_4 or CO_2 flux (measured in the dark). By contrast, removal of sedges in the wet meadow significantly decreased flux of CH_4, while moss removal tended to increase CH_4 emissions. At 15 cm depth, pore-water CH_4 concentrations were higher in sedge-removal than in control plots, suggesting that sedges contribute to CH_4 emissions by transporting CH_4 from anaerobic soil to the atmosphere, rather than by promoting methanogenesis. In reciprocal-ecosystem transplants between the wet-meadow and tussock tundra communities, CH_4 and CO_2 emissions were higher overall in the wet-meadow site, but were unrelated to transplant origin. Methane flux was correlated with local variation in soil temperature, thaw depth, and water-table depth, but the relative importance of these factors varied through the season. Our results suggest that future changes in CH_4 and CO_2 flux in response to climatic change will be more strongly mediated by large-scale changes in vegetation and soil parameters than by direct temperature effects.

Introduction

Northern wetland and tundra communities currently contribute an estimated 6–8% of global CH_4 emissions (Steele et al. 1987; Cicerone & Oremland 1988; Reeburgh & Whalen 1990), although some studies suggest that dry tundra soils may be a sink for atmospheric CH_4 (Whalen & Reeburgh 1990a; Bartlett et al. 1992; Whalen et al. 1992; Whalen et al. 1996). Although arctic tundra soils have been accumulating carbon at an estimated rate of 0.1–0.3 Pg (10^{15} g) per year (Chapin et al. 1980; Billings 1987), recent work suggests that climate change has already caused the carbon balance to shift, and arctic tundra has become a source of atmospheric CO_2 (Oechel et al. 1993; Oechel et al. 1995; Zimov et al. 1996).

Global climate models predict that a doubling of the atmospheric CO_2 concentration will increase surface temperatures by 3–5 °C at high northern latitudes (IPCC 1995). This warming is expected to result in permafrost erosion, resulting in a thicker active layer and warmer, drier surface soils (Billings et al. 1983; Maxwell 1992; IPCC 1995). Vegetation zones and species composition of plant communities will likely shift in response to changes in environment (Chapin et al. 1995), as they have in the past (Prentice & Fung 1990; Hu et al. 1995). In order to predict how carbon trace-gas flux in the Arctic will respond to climate change, we must understand the relative importance of environment and vegetation type in controlling the carbon cycle.

Methane flux is highly variable at spatial scales ranging from a meter to several kilometers, and the environmental and biological controls on this variability are poorly understood. Arctic and sub-arctic methane emissions have been correlated with soil temperature, water-table depth, peat chemistry, and vascular plant biomass (Whalen & Reeburgh 1988; Bartlett et al. 1992; Whalen & Reeburgh 1992; Christensen 1993; Torn & Chapin 1993; Rouse et al. 1995), although these correlations are often site-specific and do not persist across a range of topography and vegetation types (Whalen & Reeburgh 1988; Whalen & Reeburgh 1992; Christensen 1993; Bubier et al. 1995; Christensen et al. 1995; Rouse et al. 1995).

As much as 90–98% of the CH_4 efflux from flooded sites is associated with vascular plants (Seiler et al. 1984; Morrissey & Livingston 1992; Whiting & Chanton 1992; Torn & Chapin III 1993; Schimel 1995). Vascular plants may influence CH_4 flux by determining the amount and quality of organic substrate available to methanogens (Happell & Chanton 1993; Whiting & Chanton 1993), by providing oxygen to methanotrophic bacteria in the rhizosphere (Epp & Chanton 1993; Denier Van Der Gon & Neue 1996), or by transporting CH_4 from the soil to the atmosphere along gas exchange pathways that aerate the roots (Sebacher et al. 1985; Chanton et al. 1992; Schimel 1995; Shannon et al. 1996). While CH_4 may be oxidized in the aerobic rhizospere, vascular transport bypasses aerobic surface soils, where as much as 55% of CH_4 traveling by diffusion may be consumed by oxidative methanogenesis (Whalen et al. 1996). Even in waterlogged sites, mosses that form the surface layer have high CH_4 oxidation potentials (Vecherskaya et al. 1993) and may be an important sink for soil and atmospheric CH_4.

Carbon dioxide efflux (respiration) from tundra systems is controlled by thaw depth, water table depth, soil temperature, soil moisture, and substrate quality (Billings et al. 1982; Nadelhoffer et al. 1991; Oberbauer et al. 1992; Funk et al. 1994; Tenhunen et al. 1995; Oberbauer et al. 1996). Although the active soil volume as defined by thaw depth and water table depth is the primary control over CO_2 efflux (Oberbauer et al. 1992; Oberbauer et al. 1996), predicted changes in soil temperature and moisture may increase decomposition and root-respiration rates, contributing to ecosystem CO_2 efflux (Billings et al. 1982; Oberbauer et al. 1991). Alternatively, changes in nutrient availability or vegetation composition might result in higher rates of ecosystem productivity and increased carbon storage (Shaver et al. 1992; Smith & Shugart 1993).

We compared temperature and vegetation manipulations and measured differences between vegetation types to determine the relative importance of these parameters in controlling CH_4 and CO_2 flux in two arctic tundra communities. Vegetation composition was manipulated both by species removal and by reciprocal transplants of vegetation-soil microcosms between plant community types.

Site description

The study was conducted in wet-meadow and tussock-tundra communities at the Long-Term Ecological Research (LTER) site at Toolik Lake, Alaska (68°38′ N, 149°34′ W, elevation 760 m), in the northern foothills of the Brooks Range. We conducted plant species-removal and temperature manipulations in a wet meadow adjacent to the inlet stream on the southwest shore of Toolik Lake. The wet-meadow site is typical of poorly drained lowlands in northern Alaska (Shaver & Chapin III 1991) and is dominated by two sedges, *Eriophorum angustifolium* and *Carex aquatilis*. A 0–5 cm mat of moss (*Drepanocladus* spp.) mixed with vascular plant litter overlies organic peat soil with a silt layer at 15 cm and permafrost at about 40–60 cm depth. The water table ranges seasonally from 5 cm above to 10 cm below the moss surface.

We conducted reciprocal transplants of vegetation and soil between the wet meadow and a tussock-tundra site on a north-facing slope above the wet meadow site. The tussock-tundra site is typical of upland tundra on the North Slope and is characterized by gently rolling topography, with an organic mat of variable thickness (0–20 cm) overlying silty to gravely soils and permafrost (Shaver & Chapin III 1991). Tussocks of *Eriophorum vaginatum* are surrounded by intertussock moss mats composed of *Sphagnum* spp. in waterlogged areas and *Hylocomium* spp. in more elevated sites (Whalen & Reeburgh 1988). Our experimental plots were established in the *Hylocomium* communities, which also contained vascular plants such as *Vaccinium vitis-idea*, *Ledum palustre*, *Carex bigelowii*, and small individuals of *Betula nana*. Nomenclature follows Hultén (1968).

Methods

Experimental plots

To determine the effects of plant species and increased air temperature on CH_4 and CO_2 flux, we established 70 1-m^2 plots in the wet meadow in July, 1993. Elevated boardwalks allowed access to the plots with minimal disturbance. Treatments consisted of fully factorial species-removal × temperature manipulations. Species removal treatments were (1) moss removal, in which the *Drepanocladus* mat was removed; (2) sedge removal, in which sedge shoots were pulled out from the shoot base, removing all above-ground parts and many of the rhizomes and coarse (aerenchymatous) roots; and (3) control, in which we disturbed the soil by digging our fingers into the surface as in the removal plots, but left the vegetation intact. Plants that regenerated from rhizomes left in the soil were weeded from the plots monthly, at least 24 hours before measuring gas flux. Temperature treatments were (1) ambient, with no manipulation; and (2) greenhouse, in which plastic greenhouses were placed over the plots. The greenhouses were constructed with wooden A-frames (150×150 cm) supporting walls of 0.15 mm thick, UV-resistant polyethylene sheets (Hobbie 1996). The greenhouses were placed on the plots each spring following snow-melt and removed each autumn. An opening in the top allowed air circulation, and was intended to minimize effects on CO_2 concentration and relative humidity in the greenhouses. Plots were arranged in a randomized block design with ten replicate blocks. Five additional replicates of both temperature treatments (no species removals) were established for destructive soil sampling and for measurement of environmental variables ("soil plots").

In 1993, we established a complete reciprocal transplant of cores containing tundra vegetation and the underlying organic soil in the wet-meadow and tussock-tundra sites. This design allowed comparison of effects due to site of origin, site of transplant, and their interaction. Cores of vegetation and underlying peat (20 cm diameter × 20 cm depth) were slid into permanent sleeves made of polyvinyl chloride (PVC) and placed in the ground. Cores from the wet-meadow site contained representative vegetation from that site, as described above. Tussock-tundra cores were taken from intertussock *Hylocomium* moss mats, similar to Whalen & Reeburgh's (1988) moss (M) sites. In the wet-meadow site, cores from both the wet-meadow and tussock-tundra sites were planted in each of 10 blocks. All blocks were roughly (within 2 m) equidistant from the lake, except Block 10, which was about 5 m further upslope. In the tussock-tundra site, cores were more widely distributed in ten blocks over the 1000-m^2 area from which the tussock-tundra moss mats had been collected.

Short-term species-removal treatments were also established in plots similar to the transplant cores, in order to measure the immediate response of CH_4 and CO_2 flux to vegetation removal. In order to isolate a known soil volume and provide a base for the flux chambers, PVC sleeves were inserted into pre-cut grooves in intact wet meadow vegetation and allowed to equilibrate for 24 hours. Methane and CO_2 flux were measured immediately after vegetation removal in each of the three treatments (control, moss removal, and sedge removal; $n = 5$).

Environmental variables

In the wet-meadow ambient and greenhouse soil plots, we measured air temperature at 40 cm height and soil temperature at 5, 10, and 20 cm depth from the moss-mat surface, using copper-constantan thermocouples ($n = 3$); photosynthetically active radiation (PAR) with photodiodes (Hamamatsu) individually calibrated to a LI-COR LI-190SA quantum sensor ($n = 3$); and relative humidity (RH) with a Campbell HMP35C Temperature/RH probe ($n = 1$). Measurements were recorded each minute by a Campbell CR10 data logger, from which hourly and daily means were calculated.

On each sampling date, soil temperature and thaw depth were measured immediately following gas sampling in each species-removal/greenhouse plot and in the reciprocal-ecosystem transplant cores. Soil temperature was measured using a Barnant 115 thermometer with a J-type thermocouple probe inserted to 10 cm depth from the surface of the moss mat. Thaw depth was measured from the moss surface by inserting a steel rod into the peat until it hit permafrost. In the wet-meadow site, water-table depth was measured in 2 cm diameter wells just outside each species-removal and greenhouse plot. Soil moisture was measured gravimetrically from samples taken at 5–10 cm depth in the soil plots in the wet-meadow site.

Methane and carbon dioxide flux measurements

Methane and CO_2 flux were measured during the 1994 and 1995 growing seasons, using the static-chamber technique (Whalen & Reeburgh 1988; Whalen & Reeburgh 1990b; Dise 1992; Christensen 1993; Torn & Chapin III 1993). Measurements were carried out on four sampling dates in the long-term species-removal plots, three dates in the reciprocal ecosystem transplants, and one date in the short-term species-removal plots.

The chambers used in the long-term species-removal plots consisted of a 1×1×0.25 m plexiglas chamber fitted with a capillary bleed for pressure equilibration and two fans for air circulation. The chamber was clamped to a moveable stainless-steel base (1×1×0.3 m) that was sunk beneath the water table in pre-cut grooves in the peat 20–30 minutes before sampling. Weather stripping and clamps provided a seal between the chamber and the base. Chambers were wrapped with aluminum foil to reduce solar heating. For the transplant and short-term species-removal cores, chambers were constructed from the same PVC pipe used for the core sleeves, with a plastic top and joint sleeve attached with silicone caulking. The plastic sleeves of the cores acted as permanent chamber bases, eliminating the disturbance associated with base insertion. The joint sleeve of the chambers fit tightly over the bases, and the seal was reinforced with weather stripping and rock weights.

For the first set of measurements, the chamber sampling ports were Swaglok O-seals with rubber septa, and gas samples were drawn into 10 ml glass syringes through needles fastened with epoxy cement (Whalen & Reeburgh 1988). After the June, 1994, sampling date, the chambers were fitted with three-way stopcock ports attached to a 10 cm length of nalgene tubing, which extended into the chamber. This apparatus was attached to the chamber top with a tubing connector, and the joints were sealed with silicone caulking. Syringe needles were replaced with three-way stopcocks that locked onto the sampling ports.

Four 8 ml gas samples were taken in duplicate at 10 minute intervals in the wet-meadow site and at 15 minute intervals in the tussock-tundra site, with T_0 at one minute following chamber placement (Whalen & Reeburgh 1988). Syringes were flushed several times with ambient air and three times with chamber air before samples were drawn. Samples were analyzed within 12 h on a gas chromatograph equipped with a flame ionization detector (FID) for CH_4 and thermal conductivity detector (TCD) for CO_2. Only one set of the duplicate samples was analyzed, unless problems such as leaky syringes, bad integrations, or strange peaks made a sample unreliable.

Concentrations of CH_4 and CO_2 were calculated from integrated peak areas based on a three- or four-point standard curve. Flux was calculated from the change in CH_4 or CO_2 concentration over time and chamber headspace volume, corrected for air temperature and pressure.

Pore-water methane measurements

In 1994, pore-water CH_4 concentration was measured in five replicates of the species-removal plots (ambient temperature only) in June, in all 10 replicates of all six treatments in July, and in 10 replicates of the species-removal treatments (ambient temperature only) in August. Pore-water was extracted at four depths (0–1 cm, 5 cm, 10 cm and 15–20 cm, measured from the moss mat surface) in order to establish a depth profile of CH_4 concentrations. Ten ml samples were drawn through a 5 mm diameter stainless steel tube into 30 ml plastic syringes. The tubing system was flushed with an 8–10 ml aliquot of water from each depth before taking a sample. Methane was extracted from the water by adding a 10 ml headspace of N_2 gas to the syringe and shaking vigorously for two minutes. Headspace gas was then transferred to another syringe prior to injection into the gas chromatograph. Pore-water concentrations were calculated from the partial pressure of CH_4 in the headspace before and after equilibration with the water sample. Diffusive CH_4 flux was calculated from the concentration gradient in the surface 5 cm, using Fick's Law and the diffusion coefficient for CH_4 in water (1.62×10^{-5} $cm^2\ s^{-1}$ at 20 °C; (Jähne et al. 1987).

Data analysis

Environmental variables were analyzed by two-factor analysis of variance (ANOVA) when compared among two-factor treatments and by Student's *t*-test when compared between single-factor treatments. Methane and CO_2 flux data were analyzed by two-factor analysis of covariance (ANCOVA), with soil temperature, thaw depth, and water-table depth as covariates. Pore-water CH_4 and CO_2 concentration data were analyzed by ANOVA. Homogeneity of variance was tested by Cochran's test for data sets with similar sample sizes, and by Bartlett's test when sample sizes were substantially different. ANCOVA was also qualified by a test for interaction between the treatments and covariates. In cases where variances were not homogeneous, data were analyzed by Kruskal-Wallis non-parametric two-factor analysis of variance (KW; Zar 1984), and correlation with environmental variables was determined by multiple regressions. Where noted, data were log-transformed prior to analysis.

Results

Species removal and greenhouse treatments

The greenhouse treatment did not significantly alter CH_4 flux or its response to the species-removal treatments ($p > 0.05$; Figure 1), despite significantly altering the environment in the wet-meadow site (Table 1). Across the season, air temperature increased by 4.2 °C in the greenhouse plots, and soil temperature increased by 2.0 °C at 5 cm depth, and by 1.5 °C at 10 cm depth. However, soil temperatures measured at 10 cm depth at the time of sampling did not differ between treatments on any of the sampling dates (data not shown). The greenhouses reduced mean PAR by 35%, maximum PAR by 28%, and RH by about 5%. Soil moisture, measured on each sampling date and averaged over the season, was 24% higher in the surface 5 cm and 16% higher at 5–10 cm

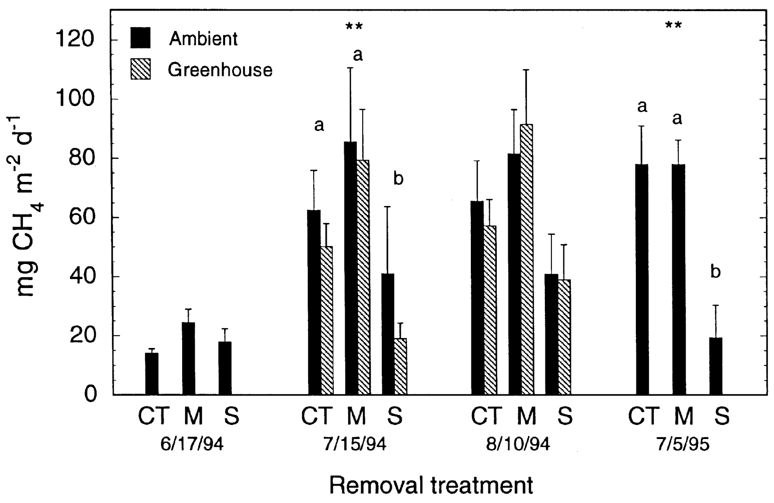

Figure 1. Methane flux in long-term species-removal and greenhouse plots in wet-meadow tundra. CT = control, M = moss removal, S = sedge removal. Data are means ±SE, $n = 10$ plots (ANCOVA, ** indicates $p = 0.01$ for overall effect of species removal). Different letters within a date indicate statistically significant differences among species-removal treatments (Tukey HSD, $p = 0.05$).

depth in the greenhouse plots. Water table depth and permafrost thaw depth did not differ between treatments.

Methane flux differed significantly among species-removal treatments on all dates except June, 1994 (ANCOVA, $p < 0.01$; Figure 1) and July, 1994, when there was a significant interaction between removal treatment and water table (test for interactions, $p = 0.03$; Figure 2). Sedge-removal plots had significantly lower CH_4 flux than the control and moss-removal plots, suggesting a role of sedges in CH_4 production and/or transport from anaerobic sediments to the atmosphere. Relative to the control, long-term sedge removal reduced CH_4 flux by about 35–50% in 1994, and by 75% in July, 1995 (Tukey HSD, $p < 0.05$). In measurements taken immediately following vegetation removal, CH_4 flux was about 60% lower after sedge removal (Tukey HSD, $p = 0.01$; Figure 3).

In contrast, moss removal increased CH_4 flux relative to the control (Figure 1), although this difference was not statistically significant. Over the course of the 1994 season, moss-removal CH_4 flux was 25–73% higher than the control flux (Tukey HSD, $p > 0.1$). In 1995, CH_4 flux was identical in the control and moss-removal plots.

In analyses of covariance, soil temperature, thaw depth, and water table depth were significantly correlated with CH_4 flux in 1994, although their relative importance varied over the three sampling dates. Methane flux increased

Table 1. Greenhouse effects on environmental variables in the wet-meadow site (1994 only). PAR = photosynthetically active radiation, RH = relative humidity, SM = soil moisture, H_20 = water table depth. Data are seasonal means of daily means, daily maxima, and daily minima (±SE), except thaw depth, SM, and H_2O, which were measured on the sampling dates only (paired *t*-test of daily values; † $p <$ 0.1, * $p < 0.05$, *** $p < 0.001$).

		Ambient			Greenhouse		
	n	Mean	Max	Min	Mean	Max	Min
Air temp (°C)	4	13.1 (0.2)	21.7 (0.8)	5.4 (0.2)	17.3 (0.4)***	33.0 (1.7)***	6.4 (0.2)***
Soil temp (°C)							
5 cm depth	4	10.6 (0.6)	16.1 (2.1)	6.8 (0.5)	12.6 (0.5)***	20.7 (1.0)***	7.5 (0.1)***
10 cm depth	3	8.1 (0.4)	11.6 (0.5)	6.0 (0.3)	9.6 (0.0)***	13.0 (0.1)***	7.3 (0.0)***
20 cm depth	3	4.8 (0.4)	7.3 (0.3)	3.2 (0.3)	5.7 (0.2)***	8.5 (0.2)***	4.1 (0.2)***
PAR (μmol m^{-2} d^{-1})	3	460.7 (26.7)	1843.4 (43.0)	–	299.4 (13.0)***	1326.6 (92.2)***	–
RH (%)	1	69.3	–	–	66.1	–	–
Thaw (cm)	10	44.5 (0.8)	55.7	30.7	45.6 (0.9)	57.0	31.5
SM (% dry mass)							
5 cm depth	5	855 (46)	1097	662	1066 (86)*	1744	842
10 cm depth	5	908 (52)	1227	719	1052 (46)†	1263	860
H_20 table (cm)	10	−3.1 (0.5)	3.0	−7.3	−4.2 (0.5)	0.5	−10.0

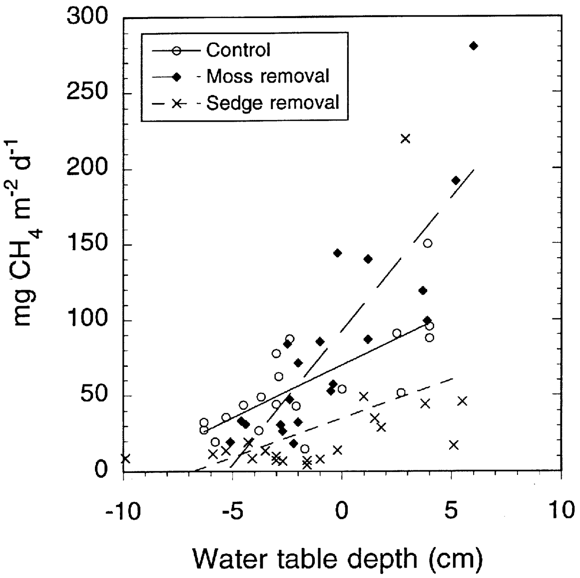

Figure 2. Interaction between water table depth and species-removal treatment in the wet-meadow species-removal and greenhouse plots on 7/11/94 (test for interactions, $p = 0.03$).

with soil temperature in July (ANCOVA, slope = 3.31, $p < 0.05$) and August (ANCOVA, slope = 22.01, $p < 0.01$; Figure 4). Thaw depth had a significant positive association with CH_4 flux in July (ANCOVA, slope = 7.97, $p < 0.001$), but was not correlated with CH_4 emissions in August, when permafrost had receded below the active organic horizon. Methane flux was related to water table depth in August, with the highest emission rates occurring in flooded plots (ANCOVA, slope = 3.66, $p < 0.05$). In July, there was a significant interaction between water table and species removal treatment, with the moss-removal plots having a more pronounced positive response to elevated water table than the control and sedge-removal plots (test for interactions, $p < 0.05$; Figure 2).

Depth profiles of pore-water CH_4 concentrations, measured in 1994 (Figure 5), suggested that the lower CH_4 emissions observed in the sedge-removal plots (Figure 1) were the result of slower transport from the soil to the atmosphere, rather than reduced methanogenesis. Removal treatment had a significant effect on pore-water CH_4 concentration on all three sampling dates (ANCOVA, $p < 0.001$). Pore-water CH_4 concentration was higher in the sedge-removal treatment than in the control- or moss-removal plots in July and August, 1994 (Tukey HSD, $p < 0.01$). Calculated diffusive CH_4 flux contributed significantly more to total CH_4 flux in the sedge-removal plots in July (Tukey HSD, $p < 0.001$; Figure 6).

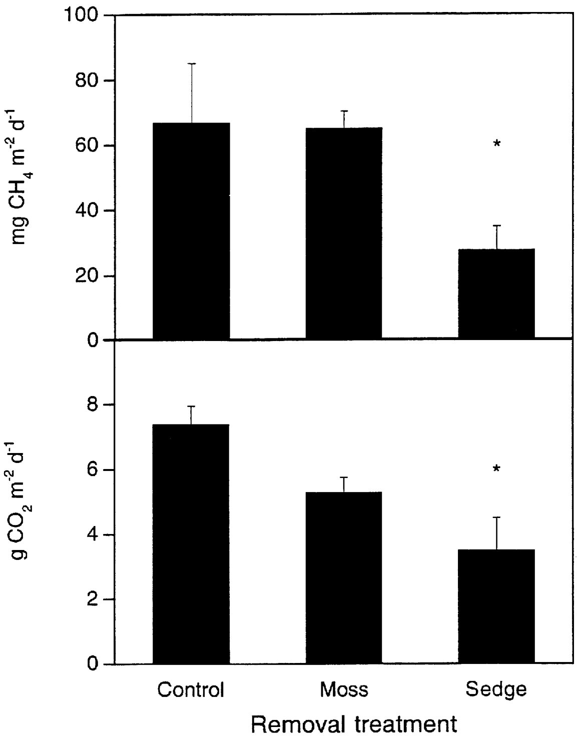

Figure 3. Methane and CO_2 flux in short-term species-removal plots in wet-meadow tundra. Data are means ±SE, $n = 5$ plots, * indicates statistically significant differences among species-removal treatments (Tukey HSD, $p = 0.05$).

In 1994, species-removal and greenhouse treatments had no effect on ecosystem CO_2 flux in the dark (ANCOVA, $p > 0.1$; Figure 7), but in 1995, CO_2 flux was significantly lower in the sedge removals, relative to the control and moss-removal plots (Tukey HSD, $p < 0.01$). Similarly, CO_2 flux was reduced by about 50% when measured immediately following sedge removal (Tukey HSD, $p < 0.05$; Figure 3). Carbon dioxide flux was not significantly correlated with any of the environmental variables measured. Pore-water CO_2 concentration (measured in August only; data not shown) did not differ among treatments.

Reciprocal ecosystem transplants

Environmental variables measured in the transplant gardens differed more between sites than between vegetation cores within a site (Figure 8). During the 1994 season, soil temperature (10 cm depth) averaged 1.6 °C higher in the wet-meadow than in the tussock-tundra control cores (ANOVA, $p < 0.001$).

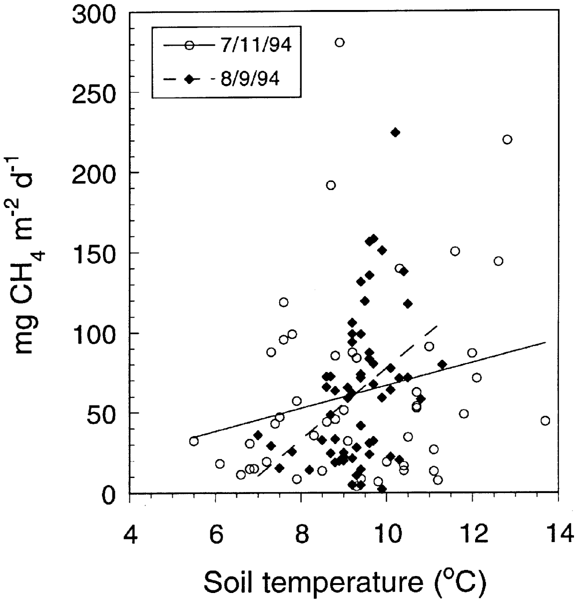

Figure 4. Relationship between soil temperature at 10 cm depth and CH_4 flux in all plots on 7/11/94 (ANCOVA, slope = 3.31, $p < 0.05$) and 8/9/94 (ANCOVA, slope = 22.01, $p < 0.01$).

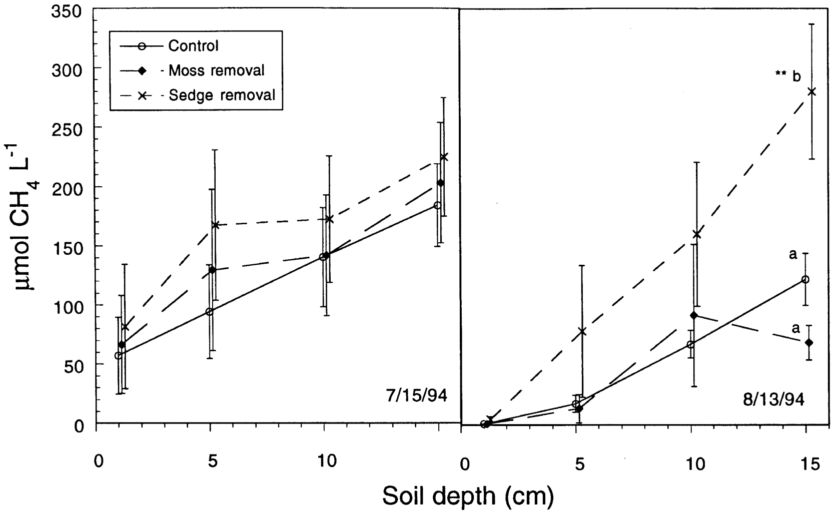

Figure 5. Depth profiles (measured from the surface of the moss mat) of pore-water CH_4 concentration in the long-term species-removal plots on 7/15/94 and 8/13/94. Data are means ±SE, $n = 10$ plots (ANCOVA, ** indicates $p = 0.01$ for overall effect of species removal). Different letters within a depth indicate statistically significant differences among species-removal treatments (Tukey HSD, $p = 0.05$).

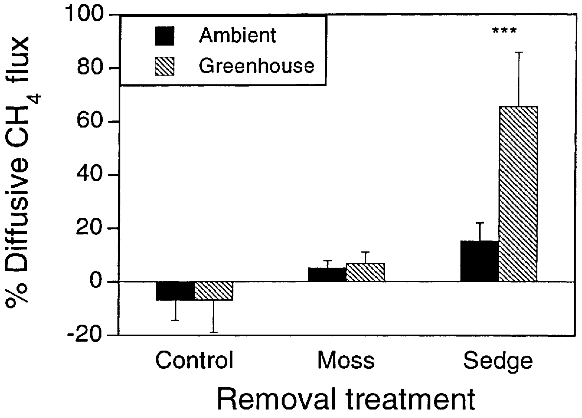

Figure 6. Calculated diffusive CH_4 flux as a percentage of total measured CH_4 flux in the long-term species-removal plots on 7/15/94. Data are means ±SE, $n = 10$ plots, *** indicates statistically significant differences among species-removal treatments (Tukey HSD, $p = 0.001$). Negative values result from an inversion of the CH_4 concentration gradient in the surface 5 cm.

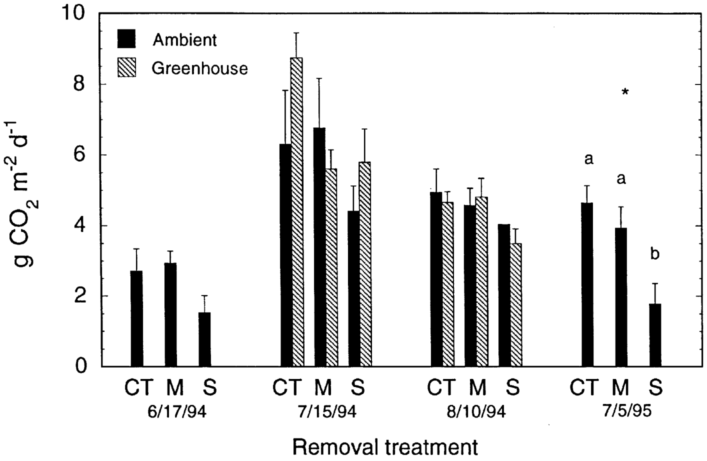

Figure 7. CO_2 flux in the long-term species-removal and greenhouse plots. CT = control, M = moss removal, S = sedge removal. Data are means ±SE, $n = 10$ plots (ANCOVA, * indicates $p = 0.05$ for overall effect of species removal). Different letters within a date indicate statistically significant differences among species-removal treatments (Tukey HSD, $p = 0.01$).

Depth to permafrost averaged 6.0 cm greater in the wet-meadow controls (ANOVA, $p < 0.001$). Transplant origin significantly affected only August thaw depth, which was greater in the wet-meadow vegetation cores at both sites (ANOVA, $p < 0.05$).

Similarly, CH_4 flux was affected primarily by site, with higher fluxes occurring in the wet meadow than in the upland tussock tundra (KW,

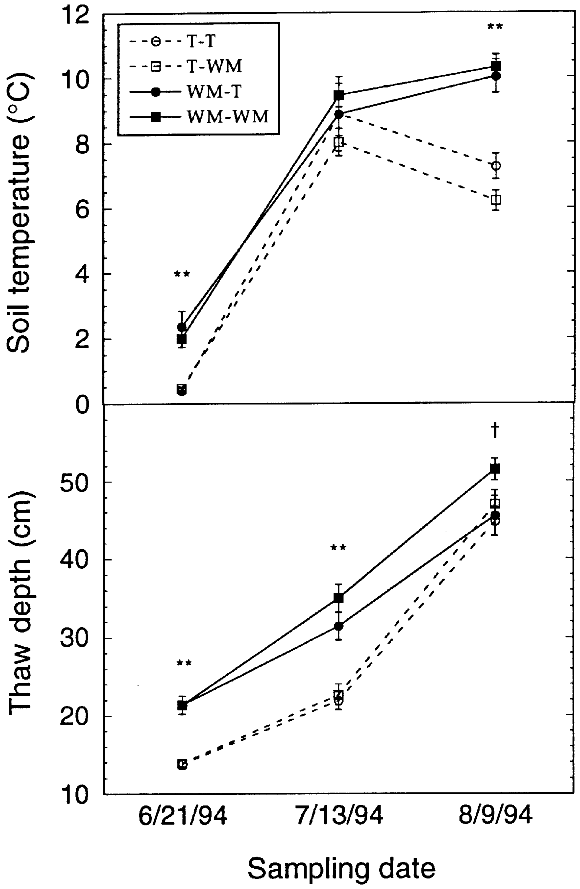

Figure 8. Environmental variables in the reciprocal ecosystem transplant cores. T-T = tussock site, tussock origin; T-WM = tussock site, wet meadow origin; WM-T = wet meadow site, tussock origin; WM-WM = wet meadow site, wet meadow origin. Data are means ±SE, n = 10 plots (ANCOVA, ** indicates $p < 0.001$ for site differences; † indicates $p < 0.05$ for origin difference).

$p < 0.001$; Figure 9). Methane emissions in the transplant cores were not correlated with measured environmental variables, except in July, when CH_4 flux was positively correlated with thaw depth ($r^2 = 0.54$, $p = 0.004$; data not shown). However, the differences in soil temperature and thaw depth between the wet meadow and tussock sites were greater than the variation within each site. This or a difference in water table depth may have accounted for the greater CH_4 flux in the wet meadow site.

Fluxes of CH_4 from cores originating from the two sites were not statistically different. In the wet meadow site, the wet-meadow control cores tended to have higher CH_4 flux than the tussock-tundra transplant cores in June and

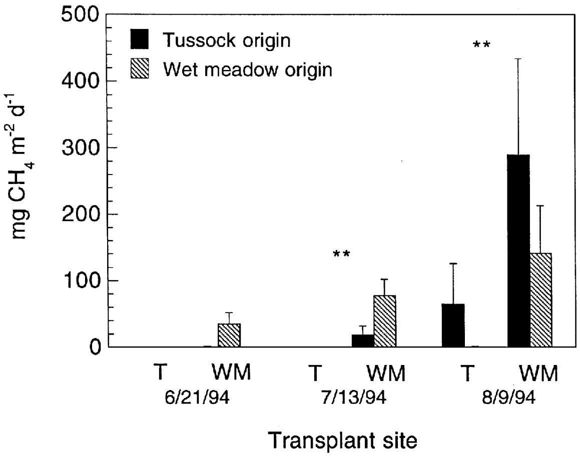

Figure 9. Methane flux in the tussock-tundra and wet-meadow reciprocal ecosystem-transplant cores. T = tussock site, WM = wet meadow site. Data are means ±SE, n = 10 cores (KW, ** indicates p = 0.01 for site differences).

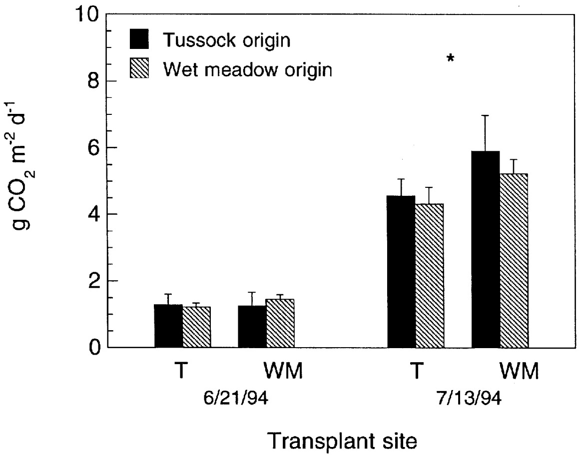

Figure 10. CO_2 flux in the tussock-tundra and wet-meadow reciprocal ecosystem-transplant cores. T = tussock site, WM = wet meadow site. Data are means ±SE, n = 10 cores (KW, * indicates p = 0.05 for site differences).

July. In contrast, August CH_4 flux tended to be higher in the tussock-tundra cores than in the wet-meadow cores at both sites.

CO_2 flux did not differ between treatments in June, but was significantly higher in the wet meadow site in July (log-transformed ANCOVA, p = 0.02; Figure 10). We did not measure CO_2 flux in the transplant cores in August.

Discussion

Species-removal and greenhouse treatments

Growth form composition was more important than temperature in controlling CH_4 flux in our wet-meadow tundra site. Sedge removal reduced CH_4 flux by as much as 60% and moss removal tended to increase CH_4 flux, while plastic greenhouses that significantly increased air and soil temperatures failed to influence CH_4 emissions.

By removing above- and below-ground plant parts, we were able to determine that sedges have a net positive effect on CH_4 emissions in wet-meadow tundra. Interruption of the gas transport pathway that aerates the roots and rhizomes of sedges is the most likely explanation for the initial decline in CH_4 flux in the sedge-removal plots, as suggested by a greater contribution of diffusive flux to total flux in the absence of sedges. It seems less likely that sedge removal reduced CH_4 flux by reducing the availability of substrate for methanogenesis because this would have caused a decline in pore-water CH_4 concentration, rather than the observed increase. The higher concentration of pore-water CH_4 at 15 cm depth in the sedge-removal plots is a logical consequence of the elimination of sedge-mediated transport of CH_4 to the atmosphere, although a decrease in rhizospheric CH_4 oxidation following the disruption of root aeration could also have contributed to higher pore-water CH_4 concentrations. The more pronounced reduction in CH_4 flux in the second season of measurements suggests that changes in substrate availability contributed to reduced CH_4 flux following prolonged sedge removal. However, the short-term removal plots exhibited a similar reduction in CH_4 flux immediately following sedge removal.

The decline in CH_4 flux we measured over the two years of long-term sedge removal was smaller than the 90% decline in flux that was previously measured immediately after sedge removal in the same site (Torn & Chapin III 1993). However, our measurements of CH_4 flux immediately following sedge removal were within the range of our long-term measurements. The soil disturbance associated with the removal of below-ground parts may account for the difference between our measurements and those of Torn and Chapin, who clipped above-ground parts without disturbing the soil surface.

The trend toward higher CH_4 emissions in the moss-removal plots is consistent with previous work that has found high rates of CH_4 oxidation in the moss layer (Vecherskaya et al. 1993) and surface (Whalen & Reeburgh 1990a; Whalen et al. 1996) of tundra soils. If photosynthesis continues when the moss mat is submerged, it may provide a source of oxygen for methanotroph activity in intermittently-flooded systems. The pore-water CH_4 concentration profiles indicate that the subsurface CH_4 production and oxidation balance was not altered by moss removal, suggesting that the trend toward higher fluxes and the July interaction with water table reflect changes in surface CH_4 oxidation, rather than production.

The initial lack of a response of ecosystem respiration in the dark to vegetation manipulations suggests that soil and root respiration, which dominate seasonal patterns of CO_2 flux in wet-meadow tundra (Oberbauer et al. 1992; Oberbauer et al. 1996), were not affected by species removal in the first season of measurements. The large quantities of labile organic matter in wet-meadow soils (Billings 1987) may have supported similar rates of microbial respiration in all plots, and remaining below-ground plant parts may have continued to respire following the removal of above-ground parts. However, the lower CO_2 flux measured in the sedge-removal plots in 1995 suggests that prolonged removal affected below-ground respiration by reducing carbon inputs.

The correlations of CH_4 flux with soil temperature, thaw depth, and water table depth were consistent with other studies that have found these parameters to be related to local variability in CH_4 flux (Bartlett et al. 1992; Morrissey & Livingston 1992; Whalen & Reeburgh 1992; Torn & Chapin III 1993). Given these correlations, the failure of CH_4 flux to respond to the higher soil temperatures in the greenhouse treatment may reflect counteracting effects of temperature on both CH_4 production and consumption or a stronger influence of water table (Whalen & Reeburgh 1992; Funk et al. 1994) or thaw depth (Whalen & Reeburgh 1992; Funk et al. 1994), which were not altered by temperature manipulations. If the permafrost erosion predicted by global change models results in a lower water table, soil temperature may become a more important control over CH_4 production and oxidation in drier surface soils.

Water table is also one of the primary environmental variables limiting CO_2 flux in tundra (Oberbauer et al. 1992; Tenhunen et al. 1995) and other peatland soils (Moore & Knowles 1989; Funk et al. 1994). Soil temperature controls variation in CO_2 flux within the range defined by water table (Oberbauer et al. 1992; Tenhunen et al. 1995; Oberbauer et al. 1996) Although seasonal soil temperatures and soil moisture differed between the temperature treatments, diel soil temperatures, water table depth, and soil moisture did not differ between treatments on the sampling dates, which may account for the failure of the greenhouse treatment to alter dark respiration in our plots.

Reciprocal ecosystem transplants

Differences in substrate quality and vegetation type undoubtedly influence variation in microbial activity among Arctic communities (Whalen & Reeburgh 1992; Oberbauer et al. 1996), but the results of our measurements in the reciprocal ecosystem transplants suggest that these parameters are secondary to site-level differences in environment.

Although CH_4 flux was not generally correlated with local environmental variability in the transplant cores, between-site differences in environment, especially water table, probably contributed to the higher CH_4 emissions in the wet meadow site. This conclusion is supported by the July correlation between CH_4 flux and thaw depth and the coincidence of higher CH_4 flux with warmer, wetter soils and deeper thaw in the wet meadow site, as compared to the tussock tundra site.

Similarly, our transplant results suggest site-of-origin differences in substrate quality and vegetation type were not important in controlling ecosystem respiration in the dark. Although CO_2 flux was not highly sensitive to local environmental variability in our plots, the higher CO_2 efflux measured in the wet-meadow site in July suggests that CO_2 flux does respond to site-level differences in soil parameters.

Conclusion

Our results suggest that vegetation composition will mediate the response of Arctic CH_4 and CO_2 flux to predicted global warming. Many investigations of carbon dynamics in the context of global change have focused on the direct effects of environmental changes, such as air and soil temperature and soil moisture, without considering changes in plant community composition. However, recent findings suggest that indirect effects of climate change, such as changes in litter quality and vegetation composition, will have equally important consequences for arctic carbon dynamics. In field experiments simulating climate change in arctic tundra, Chapin et al. (1995) found that short-term physiological responses of individual plant species were moderated at the ecosystem level by changes in species composition. Schimel (1995) demonstrated that the species composition of the vascular plant community in wet meadow tundra was an important control over ecosystem CH_4 emissions, due to differences in CH_4 transport efficiency among species. We found that, on a local scale, vegetation composition had a greater effect on CH_4 and CO_2 emissions than direct manipulation of air and soil temperature. Thus, we suggest that vegetation effects on CH_4 emissions are large enough that they must be included in future scenarios of ecosystem responses and feedbacks to global change.

Acknowledgements

We thank Georgia Murray for technical assistance and for providing the June and August pore-water data; Laurie Tucker, Ian Moore and Hailin Zhong for their hard work in the field; and Peter Vitousek and Chris Field for their helpful review of the manuscript. This research was supported by National Aeronautics and Space Administration grant #NAGW-3769 and National Science Foundation OPP grant #9318532.

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