Controls on Soil Carbon Dioxide and Methane Fluxes in a Variety of Taiga Forest Stands in Interior Alaska

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ABSTRACT

CO_2 and CH_4 fluxes were monitored over 4 years in a range of taiga forests along the Tanana River in interior Alaska. Floodplain alder and white spruce sites and upland birch/aspen and white spruce sites were examined. Each site had control, fertilized, and sawdust amended plots; flux measurements began during the second treatment year. CO_2 emissions decreased with successional age across the sites (alder, birch/aspen, and white spruce, in order of succession) regardless of landscape position. Although CO_2 fluxes showed an exponential relationship with soil temperature, the response of CO_2 production to moisture fit an asymptotic model. Of the manipulations, only N fertilization had an effect on CO_2 flux, decreasing flux in the floodplain sites but increasing it in the birch/aspen site. Landscape position was the best predictor of CH_4 flux. The two upland sites consumed CH_4 at similar rates (approx-imately 0.5 mg C m^{-2} d^{-1}), whereas the floodplain sites had lower consumption rates (0–0.3 mg C m^{-2} d^{-1}). N fertilization and sawdust both inhibited CH_4 consumption in the upland birch/aspen and floodplain spruce sites but not in the upland spruce site. The biological processes driving CO_2 fluxes were sensitive to temperature, moisture, and vegetation, whereas CH_4 fluxes were sensitive primarily to landscape position and biogeochemical disturbances. Hence, climate change effects on C-gas flux in taiga forest soils will depend on the relationship between soil temperature and moisture and the concomitant changes in soil nutrient pools and cycles.

Key words: CO_2 flux; CH_4 consumption; taiga; climate.

INTRODUCTION

Over ecological time scales (years to centuries), atmospheric CO_2 concentrations are controlled primarily by the balance of biotic uptake and release of CO_2 (Schimel and others 1995). The biota has the potential to affect global climate by controlling CO_2 concentrations and may drive both positive feedbacks (through enhanced decomposition with in-creased temperature) and negative feedbacks (through enhanced plant uptake with increased CO_2; Shaver and others 1992). There are two components to C cycling that are important in terms of controlling CO_2 cycling: the rate of C turnover and the amount of C stored in an ecosystem. Over the short term, the fast C turnover in tropical systems may dominate changes in global C cycling (McGuire and others 1995). Ultimately, however, northern tundra and taiga (boreal forest and wet-land) ecosystems are likely to be more important in driving changes in atmospheric CO_2 because of

their large C pools (approximately 40% of global soil C; McGuire and others 1995). These large C stores are of particular concern as components of a positive climate feedback because warming is predicted to be greatest in the north. The IPCC predicts a best estimate of global average warming of 2.5°C over the next century (Kattenberg and others 1996), whereas warming predictions for the boreal region average closer to 4°C (Moore 1996).

The taiga covers 12 million km^2 (Leith 1975) and contains roughly 18% of global soil C (McGuire and others 1995). It is a diverse biome, including a wide climatic range, from the cold, wet peatlands of Hudson Bay to the warm, dry aspen forests of interior Alaska. Even within a single watershed, the taiga can encompass great variation; for example, young, closed-canopy, dry birch and aspen stands often occur adjacent to mature, wet, open-canopy black spruce muskeg underlain by permafrost. The vegetation mosaic within a region is controlled by landscape structure (for example, upland vs river floodplain) and disturbance, particularly fire (upland) and fluvial dynamics (floodplain), which are the dominant factors in taiga ecology (Dyrness and others 1986). Much of the taiga experiences warm, dry, continental climates during the growing season; water stress is a common constraint on tree growth in interior Alaska (Jacoby and D'Arrigo 1995).

Models generally predict that the future climate of the taiga will have warmer summers, but the predictions for precipitation and soil moisture vary (Kattenberg and others 1996). It therefore is not surprising that predictions for changes in boreal C dynamics also vary. For example, models of aboveground biomass in various taiga sites range from tripling in a world with twice as much CO_2 (UKMO model for Northern Quebec; Smith and others 1992) to complete elimination (for example, UKMO and GFDL for Alaska; Smith and others 1992). Predictions of changes in soil organic matter range from −43% to +80% (Pastor and Post 1988). Because much of the variability in the models stems from soil moisture, any study that examines the C balance of taiga ecosystems should pay particular attention to soil moisture dynamics and the interactions of temperature and moisture to provide information that will enhance modeling efforts.

Atmospheric CH_4 concentration also is controlled by feedbacks between the biota and the climate system. Methane has several roles in atmospheric chemistry and physics, particularly as a greenhouse gas (Schimel and others 1996). Unsaturated taiga soils are generally CH_4 sinks (Whalen and others 1992), and the strength of the sink is affected by soil

moisture both through restricting CH_4 diffusion as well as regulating biological CH_4 consumption (Castro and others 1994; Gulledge and Schimel 1998). Temperature, on the other hand, appears to be a less important control on CH_4 consumption from the atmosphere (Whalen and Reeburgh 1996; Castro and others 1994).

In this study, we (a) measured soil CO_2 and CH_4 fluxes in a variety of Alaskan taiga forests, (b) evaluated the relationships among soil temperature, moisture, and gas flux in the different sites, and (c) evaluated the effects of nitrogen manipulations on gas fluxes. N availability can affect both soil microbial and root respiration (Söderstöm and others 1983; Hendricks and others 1993; Vance and Chapin 2000), both of which should be important components of total belowground respiration (Ruess and others 1996). Added NH_4^+ also inhibits CH_4 consumption in many ecosystems (Gulledge and others 1997).

We studied four taiga ecosystems at various times over a 4-year period. Three of the 4 years provided striking contrasts in weather patterns. By analyzing how CO_2 and CH_4 fluxes in the various sites responded to changes in temperature and soil moisture across contrasting years, we were able to make predictions about how gas fluxes in taiga soils may respond to different climate change scenarios.

MATERIALS AND METHODS

Study Sites

We studied four sites that are part of the Bonanza Creek Long Term Ecological Research (LTER) study, approximately 20 km southwest of Fairbanks, Alaska, USA (64°45′N, 148°18′W). Two sites (birch/aspen and white spruce) were in an upland, fire-dominated successional sequence, and the others (alder and white spruce) were in a floodplain succession along the Tanana River. The upland sites were on south-facing slopes at 400–450-m elevation and are on well-drained soils with a silty, micaceous loess parent material. The floodplain sites experience episodic flooding, resulting in a layering of organic and mineral horizons. The floodplain alder site is the youngest (approximately 20 years) followed by upland birch/aspen (approximately 85 years), upland white spruce (approximately 220 years), and floodplain white spruce (approximately 250 years). The vegetation and successional development of these sites have been described elsewhere (Van Cleve and others 1991; Viereck and others 1993a).

The summer climate of these sites can be sepa-

Table 1. Characteristics of Study Sites and Manipulation Treatments

Site	Stand Age (Years)	Soil Temperature[a] (1993, 1994)	Litter Characteristics			C and N Manipulations in Treated Plots	
			Lignin (%)	N (%)	Lignin/N	NH_4NO_3 Added (g/m²)	Sawdust Added (kg/m²)
Floodplain							
Alder	30–40	10.2, 8.6	27	1.2	22.5	6.67	5.0
White spruce	110–175	8.2, 7.8	21	0.6	35.0	4.23	0.7
Upland							
Birch/aspen	45–75	10.3, 8.7	19	0.6	31.7	17.14	3.58
White spruce	150–200	8.8, 7.4	23	0.5	46.0	14.29	3.2

[a]*Average daily soil temperature at 5 cm averaged over the period from May 1 to September 30. Data from the LTER climate database.*

rated into three main periods after snowmelt around the end of April (Yarie and others 1990; Viereck and others 1993b; US Weather Service data for Fairbanks). May is usually cool and dry (average air temperature of 9°C with 15 mm of rain). June and July are generally the hottest months of the year and are moderately dry (average temperature of 15–16°C with rainfall of 35–45 mm per month). August and September are cooler and wetter (average August temperature of 13°C and more than 50 mm of rain).

In each site, there is a set of long-term manipulation plots, including N fertilizer, sawdust, and, in the upland birch/aspen site, drought. The plots are 10×15 m in the alder and birch/aspen plots and 15×15 m in the white spruce plots. Fertilization levels were calculated to approximate the net annual mineralization, presumably doubling available N in the site. NH_4NO_3 was applied by dry broadcast each June, beginning in 1990. Sawdust amendment was intended to adjust the C:N ratio of the forest floor to 50 and was applied once in 1989. To simulate summer drought in the birch/aspen stand, a 10×15–m rain shelter was set up each spring and taken down each fall beginning in 1990. Hence, the only precipitation this plot received was snowfall, which comprises approximately 35% of total annual precipitation (269 mm; Viereck and others 1993b). The sites and manipulations are described in Table 1 and in more detail by Yarie and Van Cleve (1996).

Rather than focusing on quantifying the gas fluxes across the taiga landscape, this study focused on characterizing the process controls on fluxes within specific sites. We felt it was important to examine a diversity of communities to understand the relationships between plant community, landscape position, climatic parameters, and C-gas

fluxes. Hence, we chose to study one site in each ecosystem type intensively rather than attempting to replicate sites across the landscape. Although this approach does not stringently test the generality of our results for a given ecosystem type, previous work suggests that gas fluxes and their major ecological controls are generally consistent among sites with similar vegetation (Whalen and others 1991; Ruess and others 1996). Thus, although the site selection for this study may be considered to involve a case of "simple pseudoreplication" (Heffner and others 1996) for the purpose of estimating gas fluxes from different communities across the landscape, we feel the approach is valid for evaluating the process controls in different taiga communities.

The study ran from 1991 to 1994, but not all sites were sampled in all years. Measurements in the alder site were discontinued after 1992 because it had little CH_4 flux. Upland white spruce was added in 1993 to provide juxtaposition to the floodplain white spruce site, allowing plant community and landscape position to be compared as controls on C-gas flux. Measurements were discontinued in the floodplain white spruce after 1993 due to loss of personnel. All sites were examined for at least 2 years, and the floodplain spruce and upland birch/aspen sites each were examined in 3 consecutive years.

Measurements

Flux Rates. Flux rates were measured using permanently deployed static flux chambers similar to those of Whalen and Reeburgh (1988). Aluminum bases were placed in the forest floor by cutting them in several centimeters below the mineral soil surface to form a seal. The bases had a trough that was filled with water to make a seal with removable Plexiglas lids. The lids were fitted with rubber septa

for syringe sampling and were covered with aluminum foil to make them opaque and eliminate CO_2 fixation by plants in the chamber during measurements. Because feather mosses or *Equisetum* spp. often grew in the chambers, CO_2 fluxes represent the sum of belowground respiration (root plus microbial) and aboveground plant respiration. Three replicate chambers were placed randomly in the each of the control and treatment plots.

We measured gas fluxes approximately biweekly through the growing season (in 1992, we measured fluxes weekly in the birch/aspen site). The chamber headspace was sampled by syringe immediately after sealing and at 15-minute intervals for 45 minutes. Gas samples were taken with 10-mL glass syringes and stored in the sealed syringes for 1–3 days until analysis. Tests indicated no change in the concentrations of CO_2 or CH_4 during storage. Samples were analyzed using a Shimadzu GC-14A gas chromatograph (Shimadzu Corp. Kyoto, Japan) with a stainless steel Porapak-N column (2 m, 3.2 mm outer diameter, 40°C) with thermal conductivity (for CO_2) and flame ionization (for CH_4) detectors plumbed in series.

Ancillary Measurements. Starting in 1992, soil and air temperature and soil moisture measurements were made whenever flux measurements were taken. We measured soil temperatures at depths of 5 cm and 15 cm from the forest floor surface adjacent to each chamber and air temperature in each site during chamber sampling. Forest floor moisture was determined from two fresh samples taken adjacent to the control plot. These were returned to the lab and moisture content was determined by oven drying at 70°C overnight. We measured moisture on forest floor samples because this is where the highest concentrations of labile organic matter and fine roots are found, and thus where the bulk of activity should occur.

Calculations and Statistics. Flux rates from individual chambers were calculated using linear regression of concentration versus time. Slopes were typically linear ($R^2 > 0.9$). Higher flux rates sometimes resulted in a decrease in the slope over time, in which case we excluded the last data point to approximate initial rates. Occasional anomalous measurements gave low concentrations, indicating syringe leakage, and were excluded. No fluxes were calculated from fewer than three points. Treatment effects on flux rates within sites were determined for each year and for all the years combined by two-way repeated measures analysis of variance (ANOVA) by using ranked data from a single year or all years combined. Data were ranked to amelio-

rate nonnormality and unequal variances (Conover and Iman 1981).

Effects of temperature and moisture across sites were analyzed by nonlinear regression in Systat for Windows 7.0 (SPSS Inc., Chicago, IL, USA). We modeled temperature as an exponential function (Davidson and others 1998).

Temperature-only model: $flux = \alpha e^{\beta T}$,

where T is soil temperature, α is the flux rate at 0°C, and β is a temperature response coefficient; both are estimated by the software. This model will be referred to as the T-O model. We tested the model by using temperature at both 5 cm and 15 cm. The 5-cm values consistently gave much higher R^2 values, which is consistent with the greatest activity occurring in the forest floor, and so all the analyses presented here use the 5-cm temperature.

To determine whether moisture had a significant effect on respiration rates, we compared the R^2 values determined from the T-O analysis to those from models that incorporated moisture effects. We tested three different functional moisture responses.

Linear model: $flux = \alpha e^{(\beta T)} * (\times \cdot M)$

Quadratic model: $flux = \alpha e^{(\beta T)} - (M - \delta)^2$

Asymptote model: $flux = \alpha e^{(\beta T)} * (M/(M + \varepsilon))$.

In these models, α, β, and T are the same as in the T-O model, whereas M is soil moisture (g H_2O/g dry soil), and χ, δ, and ε are different moisture response constants. The quadratic model assumes an optimum moisture (represented by δ) that allows maximal activity. The asymptote model assumes that as moisture increases, respiration asymptotically approaches some maximum rate (as allowed by other factors such as temperature), but that moisture does not directly alter the biota's temperature sensitivity. The asymptote model shows a kinetic saturation response with increasing moisture, and ε represents the moisture at which the respiration rate is half the maximum. Thus, a low value indicates a drought-adapted soil community. This model structure is comparable to the Monod model used to model resource limited microbial growth (Bottomley 1998).

The calculations for the linear model routinely failed to converge on a solution, indicating that this model structure could not adequately describe respiration. The quadratic model is plausible, because moisture saturation is known to reduce respiration in some sites (Linn and Doran 1984), and the model

gave R^2 values only slightly lower than the asymptote model. However, less than 4% of the data points were above the estimated "optimum," and these wet samples did not respire less than samples at the optimum moisture. Therefore, we judged it inappropriate to use a model that forced a decline in rates when there was no evidence for such a decline in the data. The asymptote model had neither of the problems encountered with the linear and quadratic models and gave the highest R^2 values without requiring additional parameters. However, for several individual site/year combinations this model estimated ε values that were negative or greater than soil water holding capacity. In these cases, we ran the model with a minimum allowed ε value of 0.1 and a maximum of 2.5 (these soils have a water holding capacity of roughly 5 g H_2O/g soil, so 2.5 is a realistic estimate for the maximum possible half-saturation constant). Using these limits gave overall fits that were not significantly different (at α = 0.05) from the original estimates and did not substantially alter β estimates. For CH_4 fluxes, we modeled moisture by using a linear function because the main effect of moisture in these systems is to affect diffusion, in which case a linear function is the most reasonable because moisture contents never approached saturation.

Values of Q_{10} (relative increase in flux rate for a 10°C increase in temperature) for soil respiration were calculated from the temperature response as:

$$Q_{10} = e^{10\beta}$$

using β values from the asymptote model. The error range on Q_{10} estimates was determined by recalculating the Q_{10} with β + 1 standard error (SE) and β − 1 SE, in which SEs of the parameter estimate were provided by Systat. For estimating Q_{10} within individual years, we used the asymptote model to minimize interference from variations in moisture.

RESULTS

Floodplain Alder

CO_2 Fluxes.   The alder site had high CO_2 fluxes, averaging 3.44 (±0.37) g CO_2-C m^{-2}d^{-1} across the 2 years the site was sampled. There was a seasonal pattern, with low rates early and late in the season (Figure 1). This seasonality was associated with strong correlations of CO_2 flux with both temperature and moisture. For example, the decrease in respiration in mid-July 1992 was associated with a dry period, whereas the very strong decrease in September was associated with dropping temperature. The Q_{10} determined by the asymptote model

from the 1992 data was 1.9 and the moisture half-saturation constant (ε) was 0.97 (Table 2). Adding the moisture effects in the asymptote model increased the overall model R^2 from 0.25 to 0.51. Sawdust had no significant effect on CO_2 emissions in the alder site (Figure 2). N fertilization inhibited respiration by 37% over 1991 ($P = 0.045$) but had no effect in 1992 ($P = 0.63$).

CH_4 Fluxes.   There was very little CH_4 flux in the alder site in either year of sampling (average 2-year flux rate = −0.002 mg CH_4-C m^{-2}d^{-1}). In 1991 there was occasional net CH_4 production, but the rates were low (maximum of 0.6 mg CH_4-C m^{-2}d^{-1}), compared with those seen in wetlands. In 1992, there were relatively consistent, but low rates of CH_4 consumption, except on July 14, 1992 when flux was −0.67 mg CH_4-C m^{-2}d^{-1}; this was comparable to rates commonly seen in other sites. There was no significant seasonal pattern to CH_4 fluxes, and no clear environmental control over them. Moisture showed a weak correlation with CH_4 consumption in 1992 ($R^2 = 0.43$, $P = 0.11$). Sawdust apparently prevented CH_4 production in 1991 (Figure 2, $P = 0.05$) but had no effect on CH_4 fluxes in 1992. In 1992, when there was some consumption, it was inhibited by N fertilization ($P = 0.045$).

Floodplain White Spruce

CO_2 Fluxes.   The fluxes of CO_2 in the floodplain spruce site were relatively low, averaging 1.57 (±0.19) g CO_2-C m^{-2}d^{-1} across all years of sampling. There was limited seasonality to CO_2 fluxes (Figure 1). Very early and very late in the season, fluxes were generally low, but during the rest of the year there was little clear variation. The exception was the extremely high flux measured on July 14, 1992 (4.5 g CO_2-C m^{-2} d^{-1}), which was associated with a soil temperature of 17°C, the hottest recorded that year.

Across years, both temperature and moisture influenced respiration (Table 2). In 1992, there was a strong response of CO_2 flux to soil temperature, with an estimated Q_{10} of 11.7 (range 6.3–24; $R^2 = 0.82$), but no apparent moisture response. In 1993, there was a much weaker temperature response ($Q_{10} = 1.65$; $R^2 = 0.37$; Figure 3). The temperatures were consistently warmer in 1993 than in 1992 (soil temperature >18°C for over 1 month with air temperatures >20°C for 2 months), but the average flux rates were lower in 1993 than in 1992 ($P = 0.004$) and almost five times lower than would be predicted from the temperature response curve developed in 1992. In 1993, both sawdust and fertilization reduced respiration (relative inhi-
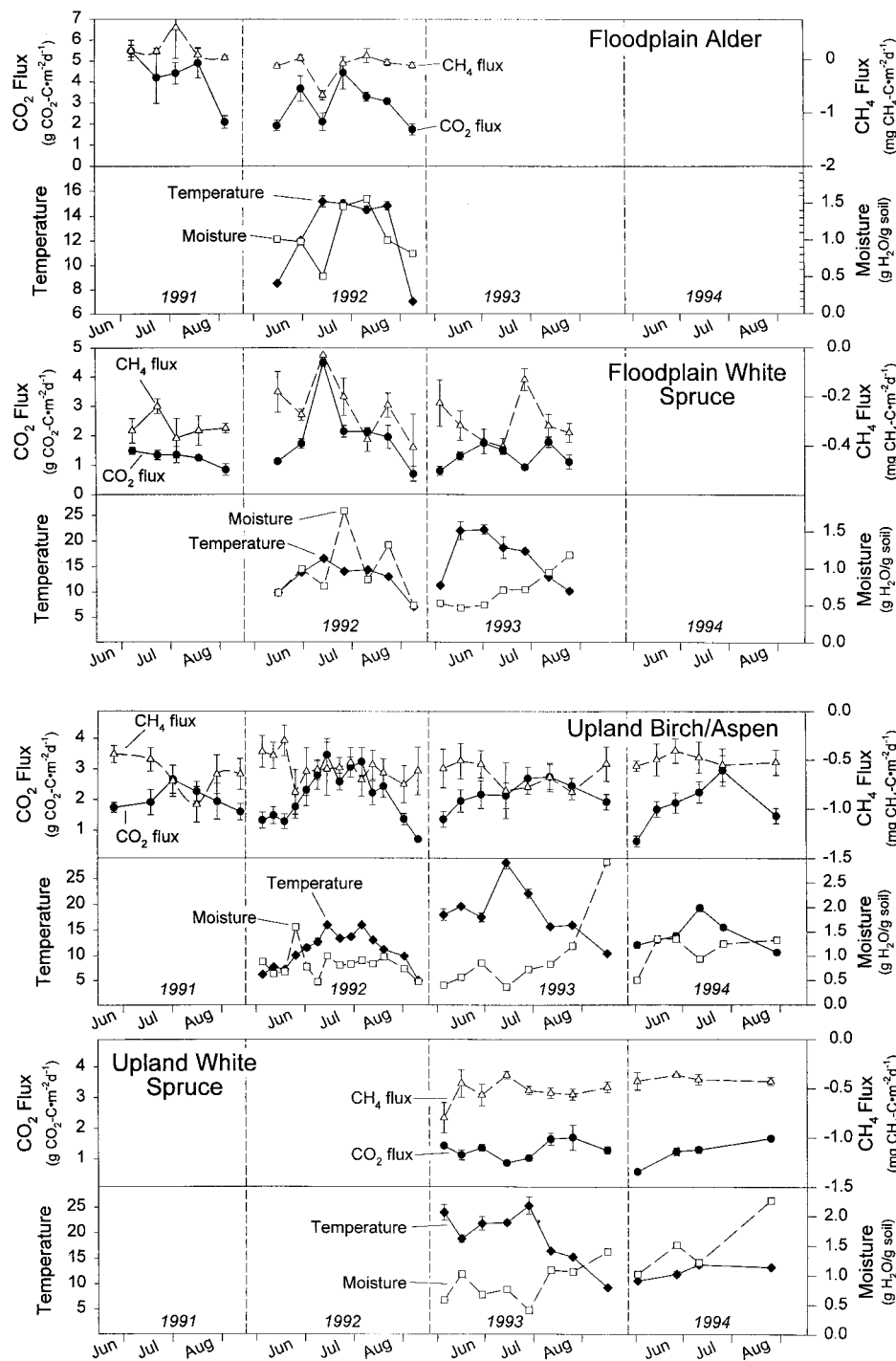
Figure 1. Patterns of CO_2 and CH_4 flux, forest floor soil moisture, and soil temperature (at 5-cm depth) in the control plots of the four study sites across the 4 years in which measurements were taken.

bitions of 24% and 21%, $P = 0.016$ and 0.048, respectively). These effects were not observed in 1992.

CH₄ Fluxes. The floodplain spruce consistently consumed CH_4, with an average consumption rate of 0.29 ($\pm$0.02) mg CH_4-C m^{-2}d^{-1} (Figure 1). Flux rates were consistent across time both within and between years, with the exception of

two dates that gave particularly low fluxes (July 14, 1992 when soil temperature was unusually high, and July 27, 1993). We did not observe any significant correlations with either soil moisture or soil temperature. Both N fertilization and sawdust caused significant inhibition of CH_4 flux (61% and 68% inhibition, respectively; $P < 0.001$ for both; Figure 2).

Table 2.   Model Results from the Temperature-Only and Asymptote Models for Each Site

Site	Temperature-only model		Asymptote model			
	β (Q_{10})	R^2	α	β (Q_{10})	ε	R^2
Floodplain						
Alder (1992 only)	0.063 (1.9)	0.25	1.21	0.062 (1.9)	0.97	0.51
White spruce (1992–93)	0.026 (1.3)	0.07	0.67	0.047 (1.6)	1.0	0.25
Upland						
Birch/aspen (1992–94)	0.024 (1.3)	0.12	1.13	0.037 (1.5)	0.37	0.23
White spruce (1993–94)	−0.002 (0.98)	<0.01	0.7	0.036 (1.4)	1.2	0.18

All measurements across the years available for each site were included to develop these parameters. Note that the β values from cross-year analyses are lower than those developed from periods when moisture was not limiting CO_2 flux.
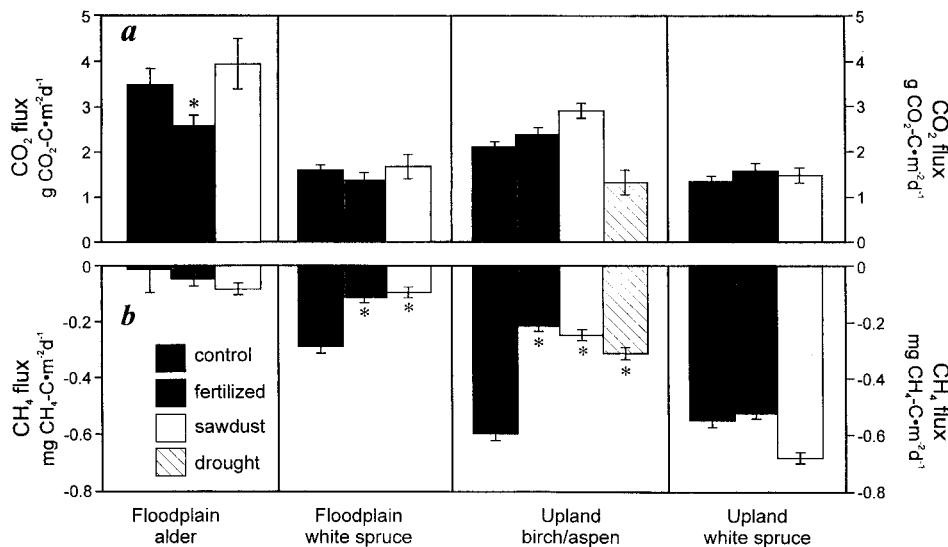

Figure 2. Averages of CO_2 (a) and CH_4 (b) flux rates across all 4 years in the control and treatment plots.

Upland Birch/Aspen

CO_2 Fluxes. CO_2 fluxes averaged 2.07 ($\pm$0.12) g CO_2-C m^{-2}d^{-1} over the 4 years sampled and showed a strong seasonal cycle, with the highest rates in midseason (Figure 1). Across all years, the overall temperature response had a Q_{10} of only 1.45 ($R^2 = 0.23$) and a moisture half-saturation constant (ε) of 0.37 g H_2O/g dry soil. The low overall Q_{10}, however, masked strong variation among years. Both 1992 and 1994 respiration showed strong responses to temperature (Figure 3), with a Q_{10} in 1992 of 2.9 ($R^2 = 0.66$) and in 1994 of 2.0 ($R^2 = 0.38$). In 1993, however, there was only a very weak response to temperature ($Q_{10} = 1.4$; $R^2 = 0.19$), and fluxes were lower than would be predicted based on other years. This is the same interannual pattern observed in the floodplain white spruce site described above. At the extreme, when soil temperature was 29°C, the CO_2 flux was roughly 20% of what would be predicted from temperature response curves from 1992 and 1994.

There were some indications that N manipulations and drought affected CO_2 flux. Over the 4 years of sampling, the mean respiration rate was 39% higher in the sawdust-amended plot than in the control plot (Figure 2). This difference was not statistically significant overall ($P > 0.1$), but it was significant in 1992 ($P = 0.01$) and 1993 ($P = 0.02$) and borderline in 1991 ($P = 0.12$) and 1994 ($P = 0.11$). Overall, fertilization significantly increased CO_2 flux by 13% ($P = 0.04$), but all the increase occurred during 1991 and the first half of 1992 (through July), during which period flux rates were 30% higher in the fertilized plot than in the control (significant at $P < 0.01$). After that, average flux in the fertilized plot was 98% of the control flux. In the drought treatment, the mean rate was 38% lower than in the control, but the decrease could not be demonstrated statistically ($P > 0.1$).

CH_4 Fluxes. Methane consumption averaged 0.58 mg ($\pm$0.03) CH_4-C m^{-2}d^{-1} over the 4 years of
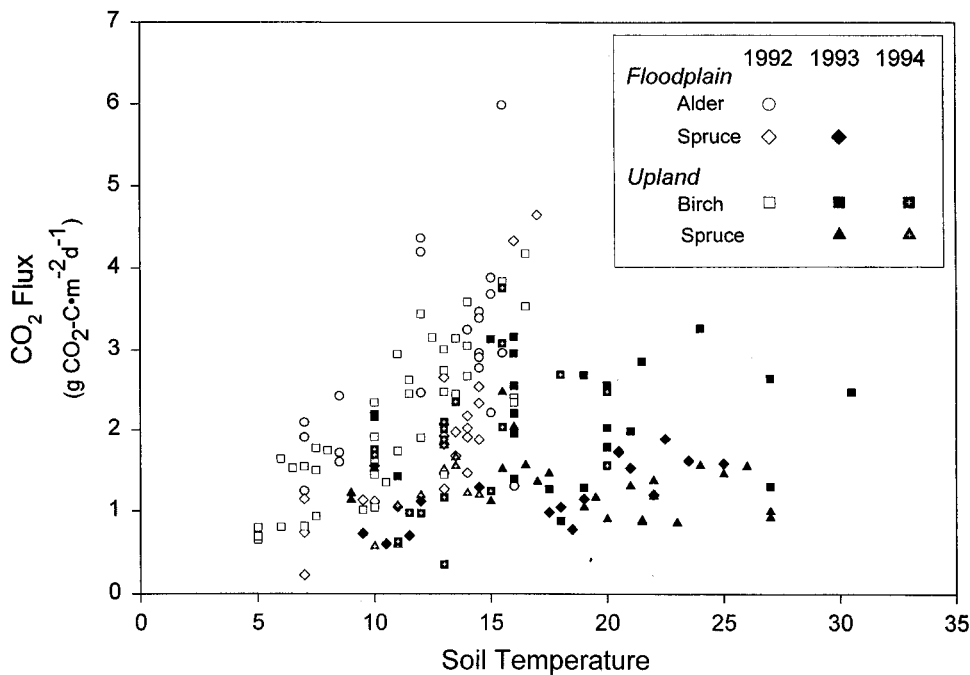
Figure 3. Temperature response of respiration. Temperature is the temperature at 5-cm forest floor depth. Each data point represents one flux measurement.

sampling (Figure 1). In 1992, there was a weak positive correlation with moisture (R^2 = 0.23, P = 0.08). In 1993, there was a negative correlation with moisture for much of the season, though this was not statistically significant overall ($P >$ 0.1). In 1994, there was no correlation between CH_4 consumption and moisture. Thus, there was little correlation between CH_4 flux and moisture overall. No correlation between CH_4 consumption and soil temperature was observed (R^2 = 0.14, P = 0.19). Over the duration of the study, fertilization, sawdust, and drought significantly inhibited CH_4 consumption by 64%, 59%, and 48%, respectively ($P <$ 0.05; Figure 2).

Upland White Spruce

CO_2 Fluxes. Average CO_2 fluxes were lower in this site than in the other three sites (1.31 ± 0.08 g CO_2-C m^{-2}d^{-1}; Figure 1) but were most similar to fluxes in the floodplain white spruce site. Using the data from both years of sampling, we found that Q_{10} was 1.4, and the moisture half-saturation constant (ε) was 1.2, although the overall R^2 of the model was only 0.18 (Table 2). In 1993, there was a weak temperature response of Q_{10} = 1.1 (R^2 = 0.07; Figure 3). In 1994, there was a strong positive response (Q_{10} = 3.4; range 1.2–9.0; R^2 = 0.82). There was no discernible relationship between CO_2 flux and soil moisture in 1993, whereas in 1994, incorporating moisture improved the model R^2 from 0.49 for the T-O model to 0.82 in the asymp-

tote model. There were no significant treatment effects on CO_2 fluxes. There appeared to be some enhancement by fertilization in the first half of 1993 (30% increase, P = 0.08), paralleling the enhancement of CO_2 flux in the first year and a half of measurements in the birch/aspen stand.

CH_4 Fluxes. The average CH_4 consumption rate in this site was 0.50 (±0.03) mg CH_4-C m^{-2}d^{-1} (Figure 1). This was slightly lower than the upland birch/aspen site (P = 0.02) and substantially higher than the floodplain white spruce site ($P <$ 0.001; Figure 2). There was no seasonal pattern to CH_4 fluxes (Figure 1), and there were no correlations with soil moisture or temperature. There were no overall significant effects of either fertilizer or sawdust (Figure 2). Sawdust did, however, significantly enhance CH_4 consumption by 41% in 1993 (P = 0.002), particularly late in the season (data not shown).

DISCUSSION

Climatic Patterns

Of the years we studied, 1992 was the closest to the 30-year average summer climate for the Fairbanks area with an average monthly air temperature 1.0°C higher than the long-term average and 0.11 cm/month less rain than average. The rest of 1992, however, was unusual, with an exceptionally late spring (snow in mid-May) and a very early winter
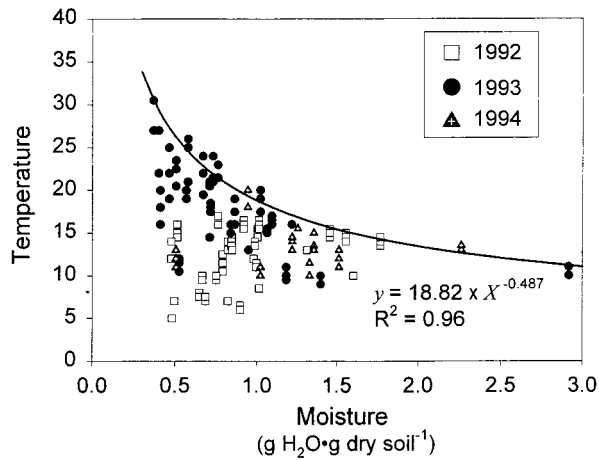
Figure 4. Soil temperature versus soil moisture across the soils sampled. The boundary curve shown was fit to the points representing the highest soil temperature in each interval of 0.1 g H_2O/g soil.

(snow in mid-September). The following year (1993) was hot and dry with summer temperatures 1.4°C above the long-term average and with 0.85 cm/month less rain. 1994 was intermediate, with a dry, hot period in mid-summer and cool, moist periods early and late in the season. Average temperature was 1.2°C above normal, whereas rainfall was 0.17 cm/month below average. The soil temperature (5-cm depth) and moisture values, as well as CO_2 and CH_4 fluxes from the control plots are shown in Figure 1.

By analyzing processes across this range of climatic conditions, it is possible to evaluate the effects of climate on process dynamics and predict likely effects of climate change on those processes (Whalen and Reeburgh 1988). Historically, there has been an inverse correlation between air temperature and rainfall in interior Alaska. If this pattern holds into a warmer future, then we would expect that the interior of Alaska would become warmer and drier, as predicted by Manabe and others (1992). Under this scenario, 1993 would likely provide a good model for future gas flux dynamics in interior Alaska. If, however, the climate becomes warmer and wetter, as predicted by other general circulation models (Kattenberg and others 1996; Gordon and O'Farrell 1997), 1993 would be a poor model. Under this scenario, we would need to extrapolate based on the results from 1992 and 1994 when soils were moister.

Although there was no overall correlation between soil temperature and moisture across all sites and years ($R^2 = 0.07$; Figure 4), soil temperature appeared to be constrained by soil moisture, such

that soil could only be very warm if it was very dry. The curve in Figure 4 describes the upper boundary of the soil moisture–temperature data cloud. Any value below the boundary is possible (for example, soils can be cold and wet at snowmelt, or cold and dry in the fall), but there may be climatological and physical constraints that make this line the limit of soil temperature at any given soil moisture. The limit on surface (5-cm depth) soil temperature is determined primarily by the temperature of rainwater and evaporative heat loss. Summer rain in interior Alaska is cool, and consequently soils are cool after a rainfall. When the weather gets hot and dry, latent heat loss limits how hot the soils can get. As long as soils are moist, evaporation can be rapid, cooling the soil. As soils dry, evaporation slows and more energy goes into heating the soil. The boundary on the soil moisture–temperature relationship is determined by soil texture and soil water content–water potential relationships (Hillel 1980). A fine-textured soil potentially could reach a higher temperature at a given water content than a coarse-textured soil; at a given water content, the fine textured soil has a lower water potential and so requires more energy to evaporate water. Given the uniform texture of the soils in this study, it is not surprising to see a uniform relationship across the sites. One question is whether the boundary on the soil moisture–temperature graph would change if the Alaskan climate warmed. If a warmer climate entailed hotter or longer sunny periods alternating with cool rainy periods, then the curve would be unchanged. Soils would merely spend more time at the hot, dry end of the graph. The boundary would only change if warming occurred during the wet periods. In this case, the right limb of the curve would rise to reflect higher rainwater temperatures. In dry periods, however, the thermodynamic properties of the soil should prevail, and the boundary on the left limb of the curve likely would not change. Thus, we believe that this boundary on the relationship between soil temperature and moisture would remain similar to that in Figure 4 under the likely climate change scenarios forecast for interior Alaska. Hence, this relationship may be useful for incorporating temperature–moisture relationships into ecosystem models of soil CO_2 flux.

Comparison of Sites and Environmental Control of Flux Rates

Assuming a 135-day growing season, we would estimate growing season CO_2 fluxes of 464, 212, 279, and 177 g CO_2-C m^{-2}y^{-1} for floodplain alder, floodplain spruce, upland birch/aspen, and upland spruce, respectively. Ruess and others (1996) mea-

sured soil respiration in these same sites (over different years than our measurements) by collecting CO_2 on soda lime in 24-hour biweekly measurements. Compared with their results, our flux estimates are lower for the white spruce sites, higher for the alder site, and similar for the birch/aspen stand. These differences may result from the inherent errors of the soda lime technique, which overestimates fluxes below 2.4 g CO_2-C m^{-2}d^{-1} (slightly higher than our estimate for the birch/aspen site), and underestimates fluxes above that value (Jensen and others 1996).

CO_2 flux was related to the successional age of the site, with the greatest fluxes in the early successional alder stand, intermediate in the midsuccessional birch/aspen stand, and lowest in the late successional white spruce stands (Figures 1 and 2). This pattern also is seen in the α values from the asymptote model (equal to the moisture-unlimited respiration rate at 0°C; Table 2), which are also highest for alder, intermediate for birch/aspen, and lowest for spruce. Interestingly, the CO_2 fluxes and their response to temperature in the two white spruce sites were similar, suggesting a unity of control over CO_2 fluxes between the sites: that is, the composition of the plant community was a more important control on CO_2 flux than the landscape position.

The pattern of decreasing CO_2 flux from alder and birch/aspen to white spruce parallels the moisture-unlimited temperature sensitivity of flux. Our estimates of the moisture-unlimited Q_{10} was lowest for alder (1.9), moderate for birch/aspen (2.8), and highest for the white spruce sites (3.4–12). We evaluated this using the wettest year available for a site (1994 for upland spruce, 1992 for the other sites), because when moisture is colimiting, estimated Q_{10} values are reduced (Davidson and others 1998). We saw this effect in two ways. First, adding moisture corrections in the models (that is, going from the T-O to the aymptote model) increased estimated Q_{10} values. Second, Q_{10} values were always higher in wet years than dry, even in the asymptote model that tried to account for moisture effects.

The reasons for these trends across sites are unclear and hard to decipher from our results. Not only is CO_2 flux a combined result of root respiration, rhizosphere respiration, litter and root decomposition, and soil organic matter turnover, but a number of possible controlling factors covary with CO_2 fluxes. For example, temperature, aboveground production, litterfall, litter quality, and forest floor turnover rate all vary in parallel along the alder to spruce gradient (Table 1;

Flanagan and Van Cleve 1983; Ruess and others 1996).

One important factor that may drive differences in CO_2 flux along the successional gradient is the contribution of roots to total soil respiration. Root + rhizosphere respiration appears to be more temperature sensitive than bulk soil microbial respiration (Boone and others 1998), and thus the greater the fraction of respiration from roots, the greater the Q_{10} is likely to be (Boone and others 1998). However, a large root contribution seems unlikely to explain the high Q_{10} values in the spruce stands. First, root biomass and production are lower in the white spruce stands than either the alder or the birch/aspen stands (Ruess and others 1996). Second, if you assume steady state conditions, then root production should equal root + rhizosphere respiration as analyzed by Boone and others (1998), and litterfall should equal bulk soil respiration. Given those assumptions, then the higher the ratio of root production to litterfall, the higher the overall Q_{10} for CO_2 flux should be. However, the ratio of fine root production to litterfall was actually higher in upland birch than upland spruce (Ruess and others 1996), which is the opposite pattern than that observed for Q_{10}. Thus, the high Q_{10} values in spruce may be more reflective of microbial respiration, perhaps following the pattern that colder soils exhibit higher Q_{10} values for microbial respiration than do warmer soils (Kirschbaum 1995). Alternatively, this would follow soil organic matter quality patterns. The temperature sensitivity of biochemical processes depends on the activation energy of the rate-limiting step, and it is likely that recalcitrant substrates have higher activation energy for their decomposition. Thus, one might expect greater temperature sensitivity of microbial respiration in soils with lower-quality soil organic matter.

The interaction effect of moisture on the apparent Q_{10} for CO_2 flux across years also may result from a shifting balance of root/rhizosphere and bulk soil respiration between moist and dry years. Plants are generally more sensitive to moisture limitation than soil microbes (Larcher 1995), and root/rhizosphere respiration appears to be more temperature sensitive than bulk soil microbial respiration (Boone and others 1998). Thus, one might expect that in wet years, root processes may more strongly drive CO_2 flux, producing a high overall Q_{10}, whereas in drier years bulk soil microbial activities may be more important, leading to a lower overall Q_{10} for soil CO_2 flux. Without direct studies on root and microbial temperature and moisture responses, however, it is impossible to make solid conclusions

about the differing temperature responses across sites or across years from our data alone.

Soil moisture was significant in controlling CO_2 fluxes, though it rarely explained much of the variation in respiration rates. The average R^2 (average of the across-year site-based values) for the T-O model was only 0.11, whereas adding moisture effects in the asymptote model increased the average R^2 to 0.29. A general linear model (site as category, temperature, and moisture as covariates) also showed that temperature and moisture were significantly correlated to CO_2 flux ($P < 0.001$ for each). Most models of soil moisture effects on microbial respiration assume a reduction as soils become saturated (Linn and Doran 1984). However, in semiarid areas, a saturation-kinetics response is common within the naturally occurring range of soil moisture (Parton and others 1987), as we observed in this study. The water-holding capacities of forest floor samples from these sites are in the range of 3–5 g H_2O/g dry soil, and the optimum moistures estimated by the quadratic model were 1.5–1.9. Thus, these soils never approached saturation (Figure 1). When analyzing individual sites and years, moisture effects on CO_2 flux were not always apparent. For example, in the upland birch/aspen stand in 1992, R^2 values for the T-O and asymptote models were identical (0.67). This is easily explained by a saturation-kinetics response: when soil moisture remains above the half-saturation value (ε), sufficient water is available, and variation in moisture becomes unimportant in affecting overall CO_2 flux, whereas other factors, such as temperature, explain the variation in CO_2 fluxes. In the birch/aspen site in 1992, the lowest soil moisture recorded was 0.48 g H_2O/g dry soil, which is still above the ε value for the birch/aspen site (0.37). The low ε value in the birch/aspen site suggests that it is relatively drought tolerant. In the other sites, ε values were close to 1 g H_2O/g dry soil, suggesting that those sites may be less drought tolerant. CO_2 emission rates during drought stress (soil temperature at 5-cm depth >17°C; Figure 3) were substantially higher in the birch/aspen site than the others, also suggesting greater drought tolerance in this site.

The changing balance between temperature and moisture effects accounts for the different patterns of respiration between 1992, 1993, and 1994. Whereas moisture was always adequate in 1992, and CO_2 production generally fit an exponential function on temperature, in 1993 drought limited CO_2 flux and temperature explained very little of the variation in CO_2 fluxes. In 1994, there were suggestions of both patterns. The hottest days were

dry, and the CO_2 fluxes were lower than would be predicted by the temperature response curves (Figure 3). Interestingly, whereas exponential relationships between CO_2 flux and temperature often held for temperatures below 17°C (Figure 3), flux rates at soil temperatures greater than 17°C were low and showed no relationship to temperature. This shift likely results from the relationship between maximum soil temperature and soil moisture discussed above. At a soil temperature of 17°C, the maximum soil moisture possible according to Figure 4 is approximately 1.2 g H_2O/g dry soil, which is very close to the ε values for most of the sites. Given the Alaskan climate and the properties of the soils in our sites, it is difficult for them to reach 17°C without becoming moisture limited.

The parameters in Table 2 represent the best fits of our data to the asymptote model across a range of climatic conditions. However, these parameters are not likely to be accurate for any given year, because the temperature response parameters (β) are underestimated for conditions when moisture is not limiting. Thus, in modeling on a large scale, integrating across a wide range of temperature and moisture conditions, these parameters should provide an adequate description of CO_2 flux dynamics. However, for modeling at a finer scale, a model that handles the shifting temperature response with moisture limitation may work better. Such a model may require more mechanistic detail on the various factors that actually drive CO_2 fluxes.

The timing of rainfall is critical for predicting CO_2 fluxes under altered climate, yet rainfall patterns are handled poorly by climate models. If a warmer climate scenario resembled 1993, with a hot dry early summer, then total soil CO_2 flux would be relatively small and would be much lower than would be predicted based on temperature response curves derived from cooler, moister years, such as 1992 and 1994. These conditions also could lead to stand replacement through increased fire or tree death from drought or insect attack, further changing biogeochemical relationships. If increased rainfall occurred in June and July, however, CO_2 flux would respond strongly to the elevated temperature; the high CO_2 fluxes of mid-July 1992 would then be an indication of the likely fluxes. Assuming a Q_{10} response, total CO_2 release from taiga soils under a 3°C warming would increase by 20%–25% in the midsuccessional stands and as much as 100% in the white spruce stands.

CO_2 Fluxes–Treatment Effects

Both floodplain sites showed evidence of reduced soil respiration due to N additions, though not ap-

parently in all years. There are several possible mechanisms for N inhibition of CO_2 flux like this. First, when whole root systems are fertilized, some plants reduce their belowground C allocation (Gower and Vitousek 1989; Gower and others 1992; Reynolds and D'Antonio 1996). This would reduce both root and rhizosphere microbial respiration. Lignolytic activity in a number of fungi (though not all) is inhibited by high concentrations of NH_4^+ (Kaal and others 1993), and reducing lignin degradation would reduce CO_2 fluxes from decomposers. Additionally, condensation of N-rich compounds with phenolics can make soil organic matter more recalcitrant, also reducing microbial respiration (Haider and others 1975). Finally, addition of NH_4^+ salts can inhibit microbial activity (Gulledge and others 1997). Which mechanism(s) accounts for the respiration reduction is unclear. Interestingly, neither upland site showed any evidence of respiration inhibition by N additions; rather, there were indications of the opposite. It is unclear why the upland and floodplain sites showed different responses to N additions. It may have to do with the interactions with other resources, such as water or P. Sawdust had no overall significant effects on CO_2 fluxes. Although sawdust is a potential C source to soil microorganisms, its substrate quality may be too low for it to have a large impact on respiration rates.

Methane Fluxes

In general, CH_4 consumption showed little response to climatic factors. With rare exception, fluxes varied within a narrow range in a given site, and there was no consistent correlation with either temperature or moisture. Considering that CH_4 consumption is controlled largely by CH_4 diffusion into the soil (Dörr and others 1993; Schimel and others 1993; Striegl 1993), one might expect a relationship with moisture. The lack of such a relationship likely results from the fact that these soils occur in a semiarid climate and are rarely saturated, and that the CH_4 oxidizers in these soils are relatively insensitive to drought (Gulledge and Schimel 1998).

The CH_4 consumption rates were associated with landscape position, with higher rates in upland sites than in floodplain sites. Alder, with the lowest elevation, was the only site that emitted CH_4 to the atmosphere, and only once in 2 years did it exhibit substantial CH_4 consumption. The floodplain white spruce, which is on a higher river terrace than the alder stand, consumed CH_4 consistently but at a lower rate than either of the upland sites. This difference between upland and wetland may have resulted from differences in soil moisture. Although

we did not detect significant differences in forest floor moisture, moisture in the underlying mineral soil may be more important for controlling CH_4 consumption rates because the zone of maximum activity lies 10–20 cm deep in the mineral horizons (Gulledge and others 1997). In 1996, Billings and others (1998) observed significantly more moisture in the mineral soil of the floodplain spruce site than in the upland birch/aspen site. Thus, elevated moisture in the floodplain soils may restrict diffusion of CH_4 into the soil and cause lower rates of atmospheric CH_4 consumption.

Methane consumption showed no consistent responses to any of the manipulation treatments across sites. Nitrogen fertilization inhibited CH_4 consumption in the upland birch/aspen and floodplain spruce sites, but not in the upland white spruce site (Figure 2). Differing effects of N fertilization across sites are commonly observed but poorly understood. Gulledge and others (1997) and Gulledge and Schimel (1998) showed that the atmospheric CH_4 oxidizers in the upland birch/aspen and spruce sites exhibit distinct physiological responses to NH_4^+ fertilization, CH_4 supply, elevated salt concentrations, and water stress. They concluded that the different responses of atmospheric CH_4 consumption to NH_4^+ fertilization resulted from the presence of physiologically distinct CH_4 oxidizers in the two soils. The distribution of these populations does not appear to be related strictly to landscape position because one upland site and one floodplain site showed inhibition. It also did not seem related to plant community because the two spruce sites are similar in plant community composition, climate, and CO_2 fluxes, but only one of them showed inhibition of CH_4 consumption. Being able to predict which sites will show N inhibition is important if we are to model the large-scale effects of N cycling on CH_4 consumption.

Sawdust strongly inhibited CH_4 consumption in the birch/aspen and floodplain spruce sites. These are the same sites that were inhibited by N fertilization, suggesting that the mechanism of inhibition by sawdust also may be linked to the microbial population differences among sites. The specific mechanism, however, remains unclear.

CONCLUSIONS

Large-scale controls on soil trace gas fluxes differed for CO_2 and CH_4. Whereas CO_2 emission rates varied with climate and successional age, CH_4 consumption rates were more responsive to landscape position and N manipulations. This difference between the two gases is probably because CO_2 fluxes

respond to root respiration, substrate quality, and nutrient availability, whereas net CH_4 consumption is driven by soil diffusion characteristics and physiological and population-level changes in a small set of soil microorganisms representing a narrow range of physiologies (Schimel 1995; Schimel and Gulledge 1998). The flux of CO_2 showed an exponential response to temperature, with differing Q_{10} values among sites, but the moisture response was best estimated by a saturation response. Thus, when soil moisture remained above about 0.5–1 g H_2O/g soil (depending on the site), variations in soil moisture did not appear to influence respiration. This work allows us to draw several conclusions about the effects of climate change on CH_4 and CO_2 fluxes. First, CH_4 consumption rates in the taiga are unlikely to change substantially with climate change because CH_4 flux was insensitive to the climatic variation we observed. CO_2 fluxes, however, are likely to respond strongly, though in different directions, depending on how climate change occurs. A warmer, wetter climate could cause CO_2 fluxes from the taiga soil to increase substantially from current levels. If past climatic relationships hold, however, the taiga will become warmer and drier, in which case soil CO_2 fluxes are likely to become uncoupled from temperature and decline due to drought stress.

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