Global Change Biology (1998) **4**, 597–605

Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce–fir forest soil in Maine, USA

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Abstract

The effect of soil warming on CO_2 and CH_4 flux from a spruce–fir forest soil was evaluated at the Howland Integrated Forest Study site in Maine, USA from 1993 to 1995. Elevated soil temperatures (~5 °C) were maintained during the snow-free season (May – November) in replicated 15 × 15-m plots using electric cables buried 1–2 cm below the soil surface; replicated unheated plots served as the control. CO_2 evolution from the soil surface and soil air CO_2 concentrations both showed clear seasonal trends and significant ($P < 0.0001$) positive exponential relationships with soil temperature. Soil warming caused a 25–40% increase in CO_2 flux from the heated plots compared to the controls. No significant differences were observed between heated and control plot soil air CO_2 concentrations which we attribute to rapid equilibration with the atmosphere in the O horizon and minimal treatment effects in the B horizon. Methane fluxes were highly variable and showed no consistent trends with treatment.

Keywords: carbon dioxide, climate change, forest soils, methane, soil respiration, soil warming

Received 16 June 1997; revised version received 22 September and accepted 26 September 1997

Introduction

Tropospheric concentrations of CO_2 and other trace gases have been increasing since the beginning of the industrial revolution, with an even more rapid increase over the last 50 years (Houghton *et al.* 1990; Denmead 1991; Keeling & Whorf 1992). It is expected that this increase in 'greenhouse' gases will raise mean global air temperature by 2–5 °C or more in the next 50–100 years, with a greater warming occurring in the higher latitudes than at the equator (Bolin *et al.* 1986; Hansen *et al.* 1988; IPCC 1990). Warmer air temperatures would likely result in warmer soil temperatures which could, in turn, enhance the mineralization of soil organic matter, with consequent increases in the flux of C from the soil to the atmosphere providing a positive feedback to climate change.

The efflux of C from soils to the atmosphere occurs primarily in the form of CO_2, and is the result of 'soil respiration'. Soil respiration represents the combined respiration of roots and soil micro and macro-biota. The magnitude of this flux is estimated to range between ≈ 68 Pg C y^{-1} (Raich & Schlesinger 1992) to 100 Pg C y^{-1} (Musselman & Fox 1991). This makes soil respiration one of the major pathways of C flux in the global C cycle, second only to gross primary productivity, which is estimated to range between 100 and 120 Pg C y^{-1} (Houghton & Woodwell 1989). Even a small increase in soil respiration could rival the annual input of CO_2 from tropical deforestation, land-use changes, or fossil fuel combustion which is estimated to be ≈ 7 Pg C y^{-1} (Lal *et al.* 1995). Production and consumption of CH_4 also plays a significant role in the global C cycle. Although the total flux of CH_4 is smaller than that of CO_2 [estimated at 500–540 Tg C y^{-1} by Fung *et al.* (1991)], CH_4 has the ability to trap 32 times as much thermal radiation as CO_2 on a molar basis (Bouwman 1990), and thus may play a significant role in shaping future climates.

Numerous studies have highlighted the temperature-dependence of soil respiration (for recent reviews see Raich & Nadelhoffer 1989; Raich & Schlesinger 1992; Raich & Potter 1995; Kirschbaum 1995) with flux rates generally increasing with increasing temperature. Although CH_4 dynamics are more variable, studies have shown increasing CH_4 uptake (i.e. oxidation) in response to increases in temperature (Crill *et al.* 1988, Born *et al.*

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1990; Crill 1991; Peterjohn *et al.* 1994; Johnson *et al.* 1996). For both CO_2 and CH_4, these studies have typically consisted of either field observations under ambient conditions or controlled greenhouse or laboratory manipulations of microcosms. Few studies to date have attempted to study temperature effects using *in situ* temperature manipulations. Such manipulations can provide a powerful tool to test predictive relationships between soil C flux and soil temperature under field conditions, and to scale-up results from laboratory experiments to larger, more relevant ecological units.

We describe here the results of a soil warming experiment designed to investigate the effects of a 5 °C increase in soil temperature on soil respiration and CH_4 uptake in a low elevation spruce–fir forest soil in Maine, USA.

Site description, experimental design, and methods

Study site

The study site is located in a low elevation (60 m) spruce–fir forest in east-central Maine (45°10′ N, 68°40′ W), adjacent to the Howland Integrated Forest Study (HIFS) site. The vegetation is dominated by red spruce (*Picea rubens* Sarg.) (≈ 50% of live basal area), with occasional codominant white pine (*Pinus strobus* L., ≈ 22%) and eastern hemlock (*Tsuga canadensis* Carr., 13%). Stand age is uneven (45–130 years), which reflects a logging history of single tree selection. Little or no understorey vegetation is present. Soils at the site are classified as Aquic Haplorthods developed from an underlying layer of dense basal till. Drainage ranges from well drained to poorly drained, with classic pit and mound microtopography. The climate is continental with mean temperature between 5 and 6 °C and mean precipitation slightly more than 100 cm y^{-1} (Lautzenheizer 1972).

Experimental design

Three 15 × 15-m plots were established in each of two locations (separated by ≈ 300 m) at the study site in the spring and summer of 1992. One warming treatment (5 °C above ambient) and two controls (an undisturbed 'control' with no disturbance from cable installation and a 'cabled control' in which subsurface cables were installed but not heated) were assigned to one plot in each location in a randomized complete block design, with location as the blocking factor. Cable installation was completed by July of 1992 and treatments were initiated in May of 1993, providing a 10 month equilibrium period to minimize disturbance effects. Plots were heated from mid-May through early November for 1993, 1994 and 1995.

A buried cable method was used to experimentally increase soil temperatures in the heated plots. In this method, heat resistance cables (Smith-Gates Easy Heat) were installed 1–2 cm below the O horizon soil surface at 20 cm intervals in each of the heated plots. After cable installation, six stations were established systematically in each plot in an approximate 'H' pattern for temperature and moisture measurements. All stations were located within an inner 12 × 12-m area within each 15 × 15-m plot to avoid edge effects. 'Temperature control' thermistors, connected directly to a Campbell CR-10^{TM} datalogger, were installed at a depth of 7 cm in the O horizon midway between cables at each of these six stations. The datalogger read temperatures from all O horizon thermistors and calculated mean plot temperatures at 10 minute intervals. If the mean temperature in a heated plot was less than 5 °C above the mean temperature in the adjacent control plot, then the datalogger would turn the heating cables on for that plot; conversely, if the mean temperature in the heated plot was 5 °C or greater than the mean temperature in the adjacent control plot, then the datalogger would turn off the heating cables. Cabled control plot temperatures were recorded for comparison.

Field and laboratory methods

In addition to the 'temperature control' thermistors, soil temperature was monitored at each of the six stations at four depths (O horizon, and 10-, 25-, and 50-cm below the surface of the B horizon). Thermistors from two depth profiles per plot were connected to the datalogger for automatic recording of soil temperature at four hour intervals throughout the field season (May through November). Thermistor readings from the other four depth profiles per plot were recorded manually on a weekly basis.

Soil moisture tensions were measured at each of the six stations per plot at two depths (10- and 25-cm below the surface of the B horizon) using Watermark® 200x soil moisture probes. Probes from two depth profiles per plot were connected to the datalogger and recording intervals were identical to those for soil temperature measurements. Soil moisture readings from the other four depth profiles per plot were recorded manually on a weekly basis. Gravimetric soil moisture for the O-horizon and top 10-cm of the B horizon was also determined at six week intervals from 10 soil cores per horizon per plot, and was expressed on a percentage dry mass basis.

Soil CO_2 and CH_4 fluxes were measured at three week intervals at three of the six stations per plot using a static chamber technique (modified from Steudler *et al.* 1989). In this method, permanent 18 cm diameter bases were inserted at each of the three stations per plot to a depth of ≈ 2 cm in the O horizon, and kept clear of vegetation for the duration of the study. For measurement of trace gas flux, PVC chambers were connected to the bases using a tongue-in-groove system with additional 1 kg weights on top of the chambers to ensure an air-tight seal. Gas samples were withdrawn from the chambers using a 10-mL gas-tight syringe; stored in evacuated glass tubes (Vacutainers®, Becton-Dickinson, Rutherford, NJ) which were cleaned by filling and emptying with CO_2-free He gas; and then analysed for CO_2 by thermal conductivity on a Gow-Mac Model 380 dual column gas chromatograph, and for CH_4 by flame ionization on a Gow-Mac 750P chromatograph (1994 and 1995 only). Initially, gas samples were withdrawn at time 0, 15, 30, and 60 min to assess the linearity of the flux rates. Given the approximate linearity of the flux measurements, the 15 and 30 minute samples were eliminated so that all chambers could be sampled in the same approximate hour and a half, thereby avoiding expected artifacts due to diurnal variation. Net flux was then calculated as the difference between the initial and final gas concentrations. During the first year, gas fluxes were measured at three times during a 24-h period (06.00, 12.00, 18.00 hours). Because no significant differences were observed between the sampling times, gas flux was only measured at 12:00 hours for the second and third years. On two dates (10–11 July 1995 and 28–29 September 1995), flux was measured at 3 h intervals over a 24-h period to evaluate diurnal patterns. For comparison, CO_2 evolution was also measured at three stations per plot by the sodalime technique as described by Edwards (1982). These measurements were initiated in June of 1994 and continued for the duration of the study.

We measured soil air CO_2 concentrations to evaluate trends in soil respiration with soil depth. Soil air CO_2 concentrations were measured at each of four depths (O horizon and 10-, 25- and 50-cm below the surface of the B horizon) at three of the six sampling stations per plot at three week intervals (typically within 24 h of the CO_2 measurements) throughout the field season following a protocol described by Erikson *et al.* (1990). Soil air access tubes consisted of polycarbonate tubes with perforated ends and a septum at the top were inserted into the soil to the appropriate depth. Gas samples were collected using a 10-mL gas-tight syringe, stored in Vacutainers, and analysed by the same method described for CO_2 evolution.

The percentage change in a response variable was calculated as:

$$100 \times [(\text{heated} - \text{control})/\text{control}].$$

Statistical analysis

Differences in CO_2 evolution, soil air CO_2 concentrations, CH_4 flux, temperature and moisture between treatments were determined using a *t*-test. Regression analyses and correlation analyses were used to investigate relationships between CO_2, CH_4, temperature and moisture. Statistical analyses for CO_2 evolution and soil air CO_2 concentrations were performed on natural logarithm (CO_2) transformations; statistical analyses for CH_4 flux were performed on natural logarithm (CH_4 + 200). Seasons were defined as spring (May–June), summer (July–August), and fall (September–November). All statistical analyses were performed on the Statistical Analysis System at the 0.05 level of significance unless otherwise noted (SAS 1985).

Results and discussion

Evaluation of treatment

The buried cable method used in this study was highly effective at maintaining surface soil temperatures at ~4–5 °C above ambient (Fig. 1). This temperature differential was maintained to a depth of 30–50 cm from the mineral soil surface resulting in a treatment involving the whole soil, well below the rooting depth (Fig. 2). Overall, no significant disturbance effects were observed for any of the measured parameters. We attribute this to the minimum impact involved in the cable installation and to the 10 month equilibration period between cable installation and the initiation of the study. Thus, results from the control and cabled control plots are pooled for this discussion.

Soil moisture

All three summers were relatively dry years when compared with the previous six years of data at the HIFS (Fernandez, unpubl. data). B horizon soil moisture tension was inversely related to throughfall volume, with peak moisture tensions typically occurring in early September when throughfall volumes were lowest. Although soil moisture tensions were significantly correlated to soil temperature over the range of 0–25 °C (Pearson correlation coefficient = 0.34; $P < 0.0001$), no significant treatment or depth trends were observed due to the high spatial variability in these measurements. Gravimetric soil moisture, on the other hand, showed significant effects for both depth and treatment, i.e. gravimetric soil moisture was significantly higher ($P < 0.0001$) in the O horizon relative to the upper B horizon (195 vs. 44%, respectively), and gravimetric soil moisture was significantly lower ($P < 0.0001$) in the O horizon in the heated plots relative to the control plots (mean 177 vs. 205%, respectively). Similar reductions in soil moisture in response to thermal manipulations have been reported by Peterjohn *et al.* (1994), Hantschel *et al.* (1995), Harte *et al.* (1995), and Pajari (1995). No significant differences

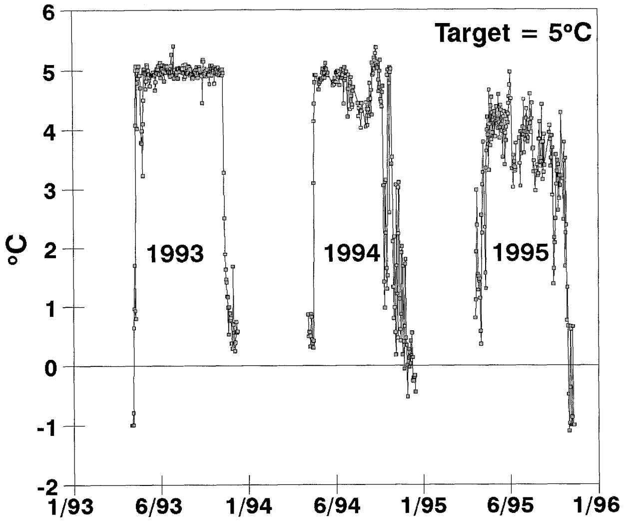

Fig. 1 Daily 0:00 h temperature deltas (calculated as the mean temperature in the heated plots minus the mean temperature in the control plots) for the Howland Integrated Forest Study site warming plots for 1993–95.

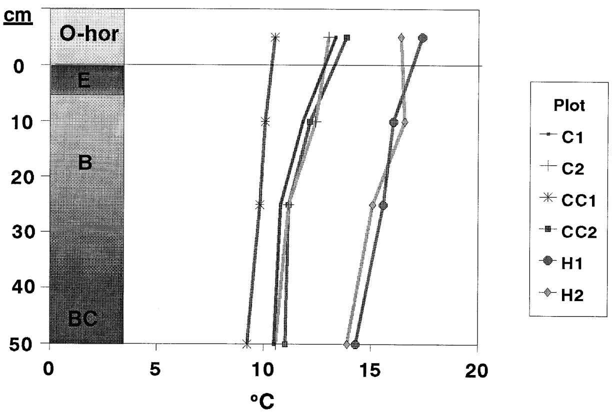

Fig. 2 Mean soil temperatures with depth for the heated ('H1' and 'H2'), control ('C1' and 'C2') and cable control ('CC1' and 'CC2') plots during the snow-free months (May through November) at the Howland Integrated Forest Study site for 1993–95.

between treatments were observed in gravimetric soil moisture in the B horizon.

CO_2 flux

Soil respiration rates, measured by the chamber method, ranged from 0.02 to 0.43 g CO_2 m^{-2} h^{-1}, with a mean (± SD) for all plots of 0.13 ± 0.05 g CO_2 m^{-2} h^{-1}. If we assume winter respiration rates of 0.04 g CO_2 m^{-2} h^{-1} (based on late fall and early spring measured values), then we can estimate an annual flux of 219 g CO_2-C m^{-2} y^{-1}. This is somewhat lower than annual respiration rates estimated from data reported by Simmons *et al.* (1996) for red maple-dominated sites distributed across a climatic gradient in Maine (mean 285 g CO_2-C m^{-2} y^{-1}), and considerably lower than the mean values reported by Raich & Schlesinger (1992) for 16 boreal forests (mean 322 g CO_2-C m^{-2} y^{-1}) and for 23 temperate coniferous forests (mean 681 g CO_2-C m^{-2} y^{-1}).

Soil respiration rates, measured by the soda-lime method, ranged from 0.13 to 0.55 g CO_2 m^{-2} h^{-1}, with a mean (± SD) for all plots of 0.28 ± 0.09 g CO_2 m^{-2} h^{-1}, or about twice that measured using the chamber method. If we again assume winter respiration rates of 0.04 g CO_2 m^{-2} h^{-1}, the estimated annual flux of CO_2 is 427 g CO_2-C m^{-2} y^{-1}, which is somewhat higher than the mean value reported by Raich & Schlesinger (1992) for boreal forests but lower than the mean value reported for temperate coniferous forests, as one might expect. Diel patterns of soil respiration were studied for 24-h sampling periods on two occasions to determine if diel variation explained the differences between CO_2 evolution rates measured by the soda-lime technique vs. the chamber method. Figure 3 shows that diel variation was minimal at this site and failed to explain the discrepancy. Although the reasons for this discrepancy are unknown, it is not altogether unexpected. Previous studies have shown large differences between soil respiration method techniques, with the static chamber method often underestimating soil respiration relative to the soda-lime ('alkali trap') method (Jensen *et al.* 1996) or the dynamic chamber method (Rochette *et al.* 1992).

Seasonal patterns were similar for both methods (Fig. 4). In 1993, soil respiration closely tracked soil temperature, while in 1994 and 1995, soil respiration showed more variable patterns, with mid-season declines coinciding with periods of higher moisture stress. Linear regression using temperature as the independent variable explained from 28% (soda-lime) to 35% (chamber method) of the variation in soil CO_2 efflux (Table 1). No significant relationships were observed between CO_2 flux and soil moisture, due in part to the high variability in soil moisture tensions. These seasonal patterns are comparable to those reported at other forest sites (Edwards & Harris 1977; de Jong *et al.* 1979; Toland & Zak 1994).

Raising surface soil temperatures by ~5 °C resulted in a 25% (chamber method) to 40% (soda-lime method) increase in measured rates of soil respiration ($P < 0.05$; Table 2), or an increased field season flux of 42–138 g CO_2-C m^{-2} y^{-1} from the soil to the atmosphere. These results are consistent with (a) the 19–27% increase in litter decay rates observed for red maple and red spruce litter during the initial 6–30-months of decay at this site (Rustad & Fernandez, in press), reflecting greater microbial activity and associated respiration, and (b) the 48% increase in O horizon fine root mass from root ingrowth cores reported after the first field season (Rustad

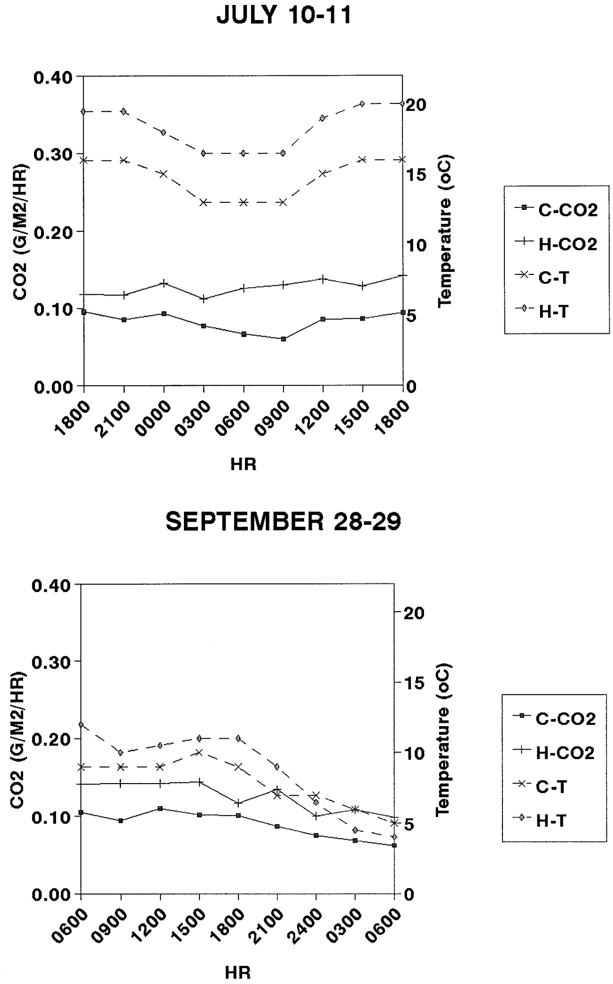

Fig. 3 Diurnal trends in CO_2 evolution and soil temperature for the heated ('H') and control ('C') plots in at the Howland Integrated Forest Study site for two dates in 1995.

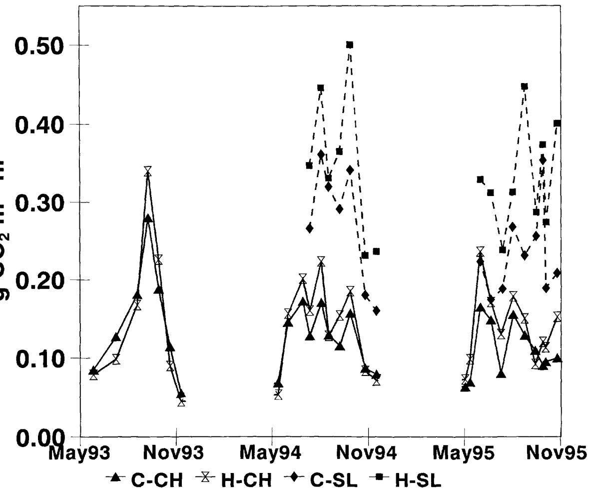

Fig. 4 Seasonal trends in CO_2 evolution for the heated plots (n = 6 for each date) and control plots (n = 12 for each date) at the Howland Integrated Forest Study site from 1993 to 1995. 'C-CH' refers to control plots, chamber method; 'H-CH' to heated plots,chamber method; 'C-SL' refers to control plots, soda-lime method; 'H-SL' to heated plots, soda-lime method;

et al. 1995) which would result in a net increase of root respiration. Similar increases in soil respiration due to elevated soil temperature *in situ* have been reported by Peterjohn *et al.* (1993) for a northern hardwood forest at Woods Hole, Massachusetts, Peterjohn *et al.* (1994) for a northern hardwood forest at the Harvard Forest in Petersham, Massachusetts, & Shaver *et al.* (1998) for wet sedge tundra in northern Alaska. The magnitude of the response at these different sites varies, likely reflecting differences in substrate quality, mean annual temperature, and soil moisture. Peterjohn *et al.* (1994) also suggested that the large efflux of CO_2 in response to elevated temperatures at the Harvard Forest may in effect be transitory, representing a depletion of a labile C pool. Once the labile C pools are gone, temperature effects may be less dramatic. This may also explain, in part, the relatively smaller increase in soil CO_2 efflux with a 5 °C increase in soil temperature observed at the Howland site (+ 25–40%) compared to the Harvard Forest site (+ 76%), i.e. the Howland site likely had a smaller pool of labile C. These site differences highlight the need to be cautious in extrapolating temperature effects on soil respiration across sites and over time.

Soil air CO_2 concentrations

Soil air CO_2 concentrations increased significantly with depth in all plots, with a three year mean (± SD) for all plots of 0.21 ± 0.09% in the O horizon, 0.34 ± 0.14% at the 10-cm increment, 0.48 ± 0.19 at the 25-cm increment, and 0.54 ± 0.22 at the 50-cm increment. Seasonally, soil air CO_2 concentrations showed a bimodal pattern for 1993 and 1994, with peak concentrations occurring in mid-summer and then again in early fall (Fig. 5). In 1995, an additional peak and trough occurred in early summer in response to an unusually dry early July. Mean soil air CO_2 concentrations and seasonal patterns observed at the Howland site were similar to those reported previously by Son *et al.* (1992) for the same site and by Fernandez & Kosian (1987) for a nearby red spruce site at Tunk Mountain, ME.

Linear regression, using temperature as the independent variable, explained from 6% (O horizon) to 16% (10-cm depth) of the variation in soil air CO_2 concentrations, whereas linear regression using moisture as the independent variable explained 3% or less of the variation at the 10- and 25-cm depths (Table 1). In general, r^2's for the relationship between soil air CO_2 concentrations and temperature were greater in the spring (r^2 = 0.33–0.64; $P < 0.0001$) and fall (r^2 = 0.24–0.44; $P < 0.05$) when soil

Table 1 Y-intercept, slope, r^2, and $P > F$ of temperature and moisture response curves of CO_2 evolution, soil air CO_2 concentrations and CH_4 evolution at the Howland Integrated Forest Study Site, Maine

Increment	Intercept	Slope	r^2	$P > F$
CO_2 evolution				
Chamber method				
temperature	– 2.96	0.062	0.35	0.0001
moisture	—	—	—	—
Soda-lime method				
temperature	– 1.88	0.038	0.28	0.0001
moisture	—	—	—	—
Soil air CO_2 concentrations				
O Horizon				
temperature	– 1.91	0.024	0.06	0.0001
moisture	—	—	—	—
10-cm				
temperature	– 1.68	0.045	0.16	0.0001
moisture	– 1.20	0.001	0.008	0.0460
25-cm				
temperature	– 1.21	0.035	0.11	0.0001
moisture	– 0.88	0.002	0.03	0.0006
50-cm				
temperature	– 1.07	0.037	0.07	0.0001
moisture	—	—	—	—
CH_4 evolution				
temperature	—	—	—	—
moisture	– 3.18	– 0.05	0.01	0.0440

Table 2 Mean (± SD) CO_2 evolution, soil air CO_2 concentrations, and CH_4 flux for control and heated plots at the Howland Integrated Forest Study site, Maine. Lower case letters following means indicate significant differences between the treatments at the 0.05 level

Parameter	Control	Heated
CO_2 evolution (g m^{-2} h^{-1})		
Chamber method	0.12 (0.04)a	0.15 (0.05)b
Soda-lime method	0.25 (0.07)a	0.35 (0.09)b
Soil air CO_2 (% CO_2)		
O horizon	0.22 (0.08)	0.20 (0.10)
10-cm	0.35 (0.15)	0.34 (0.12)
25-cm	0.50 (0.18)a	0.43 (0.20)b
50-cm	0.54 (0.18)	0.53 (0.28)
CH_4 flux (ug m^{-2} h^{-1})	– 4.2 (17)	– 6.2 (27)

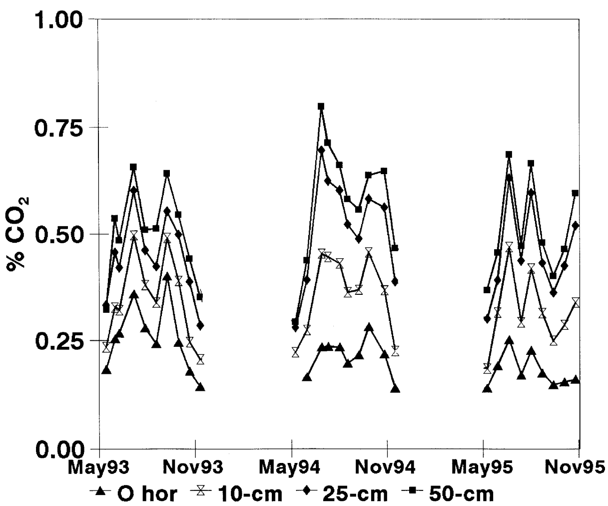

Fig. 5 Seasonal trends in soil air CO_2 concentrations with depth at the Howland Integrated Forest Study site from 1993 to 1995.

moisture was not limiting compared to the summer (r^2 = 0.004–0.04; nonsignificant), when soil moisture tensions were highest. Combining temperature and moisture as independent variables did little to improve the regression. The combination of temperature, moisture, station, and date explained 74–76% of the variation in soil air CO_2 concentrations for all depth increments. This suggests that the low r^2s between soil air CO_2 concentrations and temperature and moisture are due, in part, to seasonal and interstation differences in quantity and quality of organic matter, soil moisture, microclimate, and diffusivity.

Despite the significant positive relationship between soil air CO_2 concentrations and soil temperature over the range of 0–25 °C, the 3–5 °C increase in soil temperature induced by the treatments (Fig. 2) was generally not sufficient to significantly raise soil air CO_2 concentrations in the heated plots compared with the controls (Table 2).

In fact, contrary to expectation, soil air CO_2 concentrations were significantly lower ($P < 0.05$) in the heated plots compared to the controls at the 25-cm depth, despite the higher soil temperatures. We attribute this to higher CO_2 concentrations at several of the control stations, perhaps due to localized pockets of available labile substrates. Inter-station variability was generally high, and may have masked subtler differences in soil air CO_2 concentrations attributable to temperature alone. We also hypothesize that much of the soil respiration in these coniferous forest ecosystems occurs in the organic horizons, where both roots and labile organic materials are most abundant. The rapid diffusion of CO_2 from the soil to the atmosphere in these highly porous surface materials may, however, preclude our ability to detect significant differences between heated and control plot O horizon soil air CO_2 concentrations. The lack of treatment effects on soil air CO_2 concentrations at the 10-, 25-, and 50-cm depths, where both roots and soil organic matter are less prevalent, is logical.

CH_4 flux

Methane fluxes ranged from – 127 μg CH_4 m^{-2} h^{-1} (uptake) to 144 μg CH_4 m^{-2} h^{-1} (production), indicating that both methanotrophs (CH_4 oxidizing bacteria) and methanogens (CH_4 producing bacteria) were present in the soil microbial community at this site. Overall, oxidative processes dominated over production, with a mean flux rate (± SD) of – 4.8 ± 21.1 μg CH_4 m^{-2} h^{-1}. This compares to a mean rate of – 5 μg CH_4 m^{-2} h^{-1} for a hardwood forest soil in West Virginia (Yavitt *et al.* 1990), – 10 μg CH_4 m^{-2} h^{-1} for a northern hardwood soil in the Adirondack Mountains, New York (Yavitt *et al.* 1995), and – 12 (Keller *et al.* 1993), – 68 (Crill 1991), and – 173 μg CH_4 m^{-2} h^{-1} (Steudler *et al.* 1989) for northern hardwood soils in New Hampshire.

Overall, no clear seasonal trends were apparent for CH_4 flux (Fig. 6). Linear regression analysis indicated a weak relationship between CH_4 flux and soil moisture tensions, and no relationship between CH_4 flux and temperature (Table 1).

Over the two year period, no significant treatment effects were observed for CH_4 flux (Table 2). This is expected because mean CH_4 uptake was numerically greater in the control plots (– 5.8 ± 16 μg CH_4 m^{-2} h^{-1}) compared to the heated plots (– 3.6 ± 32 μg CH_4 m^{-2} h^{-1}) in 1994, but mean CH_4 uptake was significantly greater ($P < 0.03$) in the heated plots (– 8.4 ± 22.4 μg CH_4 m^{-2} h^{-1}) compared to the control plots (– 2.4 ± 18.1 μg CH_4 m^{-2} h^{-1}) in 1995. Clearly, longer-term studies are needed to understand relationships between CH_4 flux, temperature, moisture, and other factors.

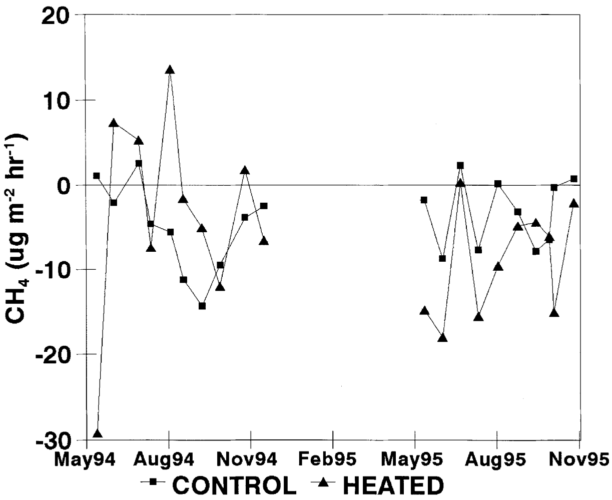

Fig. 6 Seasonal trends in CH_4 flux for the heated plots ($n = 6$ for each date) and the control plots ($n = 12$ for each date) at the Howland Integrated Forest Study site from 1993 to 1995.

Conclusions

Results from this study indicate that raising surface soil temperatures by ~5 °C could significantly increase soil respiration by 25–40%. Assuming a mean respiration rate for the temperate coniferous forest biome of 681 g C m^2 y^{-1} (Raich & Schlesinger 1992) and an estimated area for this biome of 508 × 10^6 ha (Houghton 1995), a 25% increase in soil respiration could release an additional 3.5 Pg of C to the atmosphere from this biome alone, or approximately half that released by tropical rainforest deforestation, land-use changes, and fossil fuel combustion. The effect of this same increase in temperature on CH_4 dynamics is less clear, although data from the second year of this study as well as data from Peterjohn *et al.* (1994) suggest that an increased uptake of CH_4 from forest soils may compensate, in part, for the increased efflux of CO_2. A net increase in photosynthesis, due either to longer growing seasons or to elevated atmospheric CO_2 concentrations, may also offset this increase in soil respiration. The ability of these forest soils to sustain increased rates of soil respiration is also questionable. Indeed, Peterjohn *et al.* (1994) suggest that the large increase in soil respiration in response to increased temperature at the Harvard Forest was only temporary, reflecting the depletion of a labile C pool. We suggest this is highly plausible, and that immediate changes in soil respiration due to warming are the result of the loss of labile C, whereas changes over longer time steps will ultimately reflect stages of altered litter quality and potentially forest species composition. Longer-term studies, particularly those that simultaneously assess moisture and substrate-related variables, will be important for ultimately determining the response of soil respiration to increases in soil temperature.

Acknowledgements

The authors would like to thank Dr Frank Bowles for his help with the technical design of this project, and Holly Hikel and Steve Scaturro for their invaluable assistance in the field. Funding for this study was provided by the U.S. Forest Service (Coop. Agree. #23–640) and the U.S.D.A. – C.S.R.S. (92–37101–7978).

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