Soil warming in a northern hardwood forest: trace gas fluxes and leaf litter decomposition

Patrick J. McHale, Myron J. Mitchell, and Francis P. Bowles

Abstract: The response of trace gas fluxes (CO_2, CH_4, and N_2O) and litter decomposition to increased soil temperature was evaluated in a northern hardwood forest. Four experimental plots (10 × 10 m) had heating cables installed within the forest floor. Temperatures at 5 cm were increased 2.5, 5.0, or 7.5°C in individual heated plots during the field season in 1993 and 1994. The fourth plot was a cabled, nonheated reference. Trace gas fluxes were monitored using closed chambers. Soil moisture was monitored using tensiometers and time domain reflectometry. Changes in leaf litter decomposition were quantified using litter bags for American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) litter. Fluxes of CO_2 increased exponentially with increased soil temperatures within treatments and were higher in heated plots than in the reference plot. Temperature coefficients (Q_{10}) and mass remaining of American beech leaf litter decreased with the level of heating, suggesting a nonlinear microbial response to elevated temperatures. Soil water content exhibited the most influence on CH_4 and N_2O flux in the second season. The experimental manipulations showed the importance of evaluating the influence of soil temperature coupled with effects of N and moisture availability.

Résumé : L'effet d'une augmentation de la température du sol sur le flux des gaz présents en très petites quantités (CO_2, CH_4 et N_2O) et sur la décomposition de la litière a été évalué dans une forêt feuillue nordique. Des câbles chauffants ont été installés dans le parterre forestier de quatre parcelles expérimentales (10 × 10 m). La température à 5 cm a été augmentée de 2,5, 5,0 et 7,5°C dans différentes parcelles pendant les saisons d'été de 1993 et 1994. La quatrième parcelle, où se trouvait un câble chauffant non utilisé, a servi de témoin. Le flux des gaz présents en très petites quantités a été suivi dans des chambres fermées. L'humidité du sol a été suivie à l'aide de tensiomètres et de la réflectométrie dans le domaine temporel. Les variations dans la décomposition de la litière de feuilles ont été quantifiées à l'aide de sacs à litière dans le cas de la litière de hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) et d'érable à sucre (*Acer saccharum* Marsh.). Le flux de CO_2 a augmenté de façon exponentielle avec l'augmentation de la température du sol dans les parcelles traitées et il était plus élevé dans les parcelles chauffées que dans la parcelle témoin. Les coefficients de température (Q_{10}) et la masse résiduelle de litière de feuilles de hêtre à grandes feuilles ont diminué en fonction de la température, suggérant une réponse microbienne non linéaire à des températures élevées. Le contenu en eau du sol avait le plus d'effet sur le flux de CH_4 et de N_2O au cours de la deuxième saison. Ces manipulations expérimentales montrent l'importance d'évaluer l'influence de la température du sol couplée aux effets de la disponibilité en eau et en N.

[Traduit par la Rédaction]

Introduction

The temperature of forest soils is a major variable influencing a wide range of biogeochemical processes, such as decomposition rates and other microbially mediated transformations (Bonan and Van Cleve 1991; MacDonald et al. 1995). There has been increasing concern regarding how future increases in soil temperature, induced by global warming, will affect soil processes. To address these concerns, field manipulations of soil temperature have been conducted in northeastern U.S. temperate forest ecosystems (Peterjohn et al. 1994; McHale et al. 1996; Rustad et al. 1996), and similar experiments have been initiated in Europe (Beerling and Woodward 1994).

Climatic variables such as soil temperature and soil moisture have an important influence on a wide range of plant and soil processes including soil respiration (Anderson 1973). Forests cover approximately 4.1×10^9 ha of the earth's land area and contain 1146 Pg of C, of which two thirds are contained in soils (Dixon et al. 1994). Northern forests account for about one half of the C in global forest ecosystems. Given that soils contain the largest pool of C in terrestrial ecosystems, combined with substantial C fluxes between the terrestrial and atmospheric pools, small changes in soil temperature and moisture could lead to a substantial increase in atmospheric CO_2 concentrations (Anderson 1992). Based on general circulation model predictions, it is anticipated that the greatest effects of global warming will be experienced in northern latitudes (Houghton and Woodwell 1989). Higher soil temperatures in northern forest and tundra ecosystems may lead to enhanced decomposition and N mineralization rates of soil organic matter (Bonan and

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Van Cleve 1991), resulting in increased NO_3^- levels in soil leachate and greater flux of CO_2 and N gases from soils to the atmosphere (Peterjohn et al. 1994) that could produce a positive feedback to climate change in the future. In addition, CH_4 is generally taken up by northern forest soils (Whalen et al. 1992). However, if N availability is increased due to enhanced mineralization, CH_4 uptake rates may decline (Steudler et al. 1989).

The objectives of this study were to examine how increasing soil temperature in a northern hardwood soil would effect trace gas fluxes (CO_2, CH_4, and N_2O) and leaf litter decomposition.

Methods

Site description

The research site was located at 530 m elevation within the Anna and Archer Huntington Wildlife Forest (HF), located in the central Adirondack mountains (43°59′N, 74°14′W) near Newcomb, New York. The location of the study site within the HF was selected for accessibility to a road and electrical power, which was required for heating the plots. The overstory was dominated by American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britt.). Soils at the HF are of glacial origin and are generally less than 1 m deep, over a bedrock of gneiss. Soils were coarse-loamy, mixed frigid, Typic Haplorthods in the Becket–Mundal association (Somers 1986). Mollitor and Raynal (1982) reported that the soil profile at a nearby site at the HF contained an Oi horizon (0–8 cm depth), an Oe horizon (8–10 cm depth), and an Oa horizon (10–13 cm depth). Soil profiles at our site were similar, with a mean O horizon depth of 12.5 cm. The mean annual temperature at the HF was 4.4°C. The growing season and dormant season mean temperatures were 14.3 and –2.8°C, respectively. Average mean precipitation was 101 cm·year^{-1} (NOAA 1980). The biogeochemistry of the HF has been well characterized by previous studies (David et al. 1982; Mollitor and Raynal 1982; Shepard et al. 1989).

Experimental design

Heating cables were installed in four experimental plots (10 × 10 m), which included a cabled, nonheated reference plot and three plots in which the forest floor temperature was increased during the growing season by 2.5, 5.0, and 7.5°C above ambient conditions to represent a temperature gradient. Heating cables were installed at 5 cm depth within the forest floor in all plots. Heat treatments were only conducted during the snow-free season because we did not want to produce artifacts that would have occurred due to artificial early melting of the snowpack. The assignment of treatment was done randomly. Larger plot size with no treatment replication was chosen versus smaller plot size in order to eliminate edge effects and to minimize the high costs of installation. Thirteen heating cables (Smith-Gates Easy Heat®) were buried at 5 cm depth within the forest floor of each plot, with 20-cm spacing between adjacent cable lengths. A single cable spanned a plot four times, was 43.3 m long, had a total resistance of 95.6 Ω, drew 2.4 A, and consumed 576 W when supplied with 240 V AC. The heating cables were installed approximately 1 year prior to the start of experimental soil heating to minimize any effects associated with cable installation (McHale et al. 1996). In each plot, there were six permanent data collection points for trace gas and lysimeter collections to reduce disturbance due to repeated sampling. A thermistor at each of these points recorded the soil temperature at 5 cm depth and the mean plot temperature was calculated as the mean of these six values.

Soil heating control

The cabled reference plot served as the mean ambient 5-cm soil temperature used by the heating control system for comparison with the 5-cm soil temperatures of all heated plots. A Campbell Scientific, Inc.® datalogger was used to read and record all temperature thermistors every 10 min and calculate the mean 5-cm temperature for each plot. If the temperature difference (Δ) between a heated plot and ambient was less than the assigned Δ, electric power was applied until Δ was greater than the designated temperatures (i.e., 2.5, 5.0, or 7.5°C).

Field methods

Trace gas fluxes

Fluxes of CO_2, CH_4, and N_2O between the soil and the atmosphere were quantified from air samples collected from closed chambers. Each chamber was a polyvinyl chloride (PVC), open-bottomed, cylindrical dome that completely enclosed an average soil area of 0.06 m^2. The volumes of chambers varied slightly, with an average of 5.1 L. The thick walls (2 cm) and white color of all chambers as well as collection of samples beneath the forest canopy minimized any heating within chambers due to solar radiation during the period of gas collection. Permanent "collars" to minimize gas leakage at the soil–chamber interface were not employed, as in other studies (Steudler et al. 1989; Bowden et al. 1990), but leakage was found to be minimal due to the mass (1.3 kg) of the chambers themselves. The chambers were not permanent structures within the plots and were removed following sample collection.

Each chamber was equipped with a 3.5-cm hole in which a rubber stopper was inserted. A 20-mL nylon syringe (SESI®) fitted with a three-way luer-lock valve (Pharmaseal, Inc.®) and a needle was used for sampling gas through the stopper. The syringe plunger was slowly drawn in and out three times, and a 20-mL sample was taken on the fourth time to insure sample heterogeneity. To avoid any contamination of the gas sample, a rubber band was placed around the top of the syringe body and the plunger top to keep the syringe contents pressurized until sample analyses within 3–4 days after sampling. Using these same methods, Richey (1994) reported no changes in gas concentrations for up to 9 days.

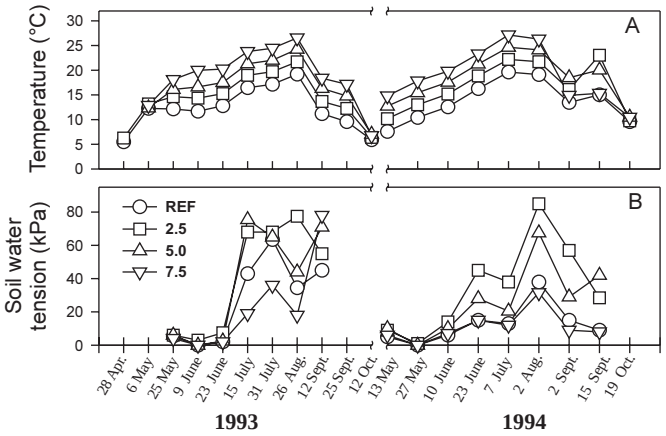
Gas samples were generally collected twice per month throughout the 1993 and 1994 field seasons (approximately May–September) and once in October. Samples were taken from five and six points per plot in 1993 and 1994, respectively. Samples were always collected from the same locations within each plot. Chambers were placed on the forest floor and an initial sample taken. Following a 30-min incubation period, the chambers were resampled. Soil and air temperatures were recorded once during the 30-min incubation time.

Litter bags

American beech and sugar maple (*Acer saccharum* Marsh.) leaf litter was collected and air-dried during autumn 1992. Fiberglass mesh (1 mm) litter bags were constructed by cutting a 30 × 15 cm piece of mesh, folding it into a 15 × 15 cm square, and sewing two of the three open sides to produce a bag. Approximately 1 week prior to installation in the field, 4 g of leaf litter (either American beech or sugar maple) was placed inside each bag, and the third side was sewn to secure the contents. An aluminum tag with a unique identification number was attached to a yellow polypropylene string that was sewn to each bag. There were 72 litter bags for each species (18 per plot) for a total of 144 bags. The dry mass of each bag, including contents, was recorded as the pretreatment mass prior to field installation.

Eighteen litter bags per species were installed along a transect in each field plot in November 1992. Each bag was placed within the Oa horizon, with a flag inserted through the identification tag to mark its location and keep it in place. Litter bags were collected

Fig. 1. Temperature and moisture for experimental plots during 1993 and 1994. (A) Soil temperature (5 cm depth); (B) daily mean soil water tension at 15 cm depth (B horizon).



from plots during October in 1993 (1 year) and 1994 (2 years). Six bags per species were removed from each plot in 1993 and 12 bags per species were removed in 1994. Upon collection, bags were oven-dried until constant mass at 65°C. Percent mass remaining was calculated based on pretreatment litter masses compared with values after collection. Concentrations of C and N were determined using a Perkin-Elmer 2400 CHN Analyzer®.

Other environmental variables

Soil moisture was monitored using two different methods. Tensiometers were used to measure soil water tension during 1993 and 1994 field seasons, while time domain reflectometry (TDR) was used to measure soil water content during the 1994 field season only. Tensiometers were installed at 15 cm depth at two points in each plot in the spring (1993 and 1994), after aboveground temperatures were >0°C. Data were manually recorded once per day. Individual TDR measurements were taken at three or four permanently located points in each plot. These measurements were an integration over 0–30 cm soil depth. Soil water content was recorded continuously every 4 h using a datalogger.

Gas analyses

Trace gas concentrations

Air samples from closed chambers were analyzed for trace gases (CO_2, CH_4, and N_2O) using gas chromatography (GC). CO_2 was analyzed using a Varian model 3700 GC fitted with a thermal conductivity detector (TCD) and CTR-1 column. A Hewlett-Packard 5890 GC was used for both CH_4 and N_2O analyses. It was fitted with a flame ionization detector (FID) to analyze CH_4 using a Carbosieve column. The GC was also fitted with a ^{63}Ni electron capture detector (ECD) to analyze N_2O using a Porapak Q column.

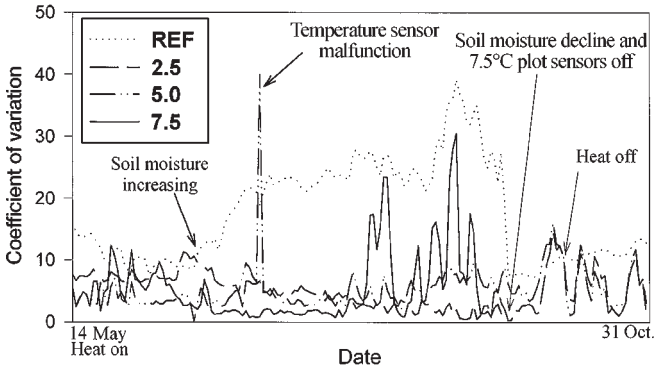
Trace gas flux calculations

Net trace gas fluxes were calculated as the rate of trace gas concentration change within the chamber over 30 min using the equation of Matthias et al. (1980):

$$[1] \qquad F = k\left(\frac{273}{T}\right)\left(\frac{V}{A}\right)\left(\frac{\Delta c}{\Delta t}\right)$$

where F is the rate of gas emission or uptake (e.g., kilograms of C or N per hectare per year), k is the unit conversion factor (micrograms per square centimetre per minute) (for calculation of flux as kilograms of C or N per hectare per year: 0.028 for CO_2 and CH_4 and 0.066 for N_2O), T is air temperature within the chamber (kelvins), V is volume of air within the chamber (cubic centimetres), A is the area of soil enclosed by the chamber (square centimetres), and $\Delta c/\Delta t$ is the rate of concentration change in air within the chamber (parts gas per billion (v/v) per minute). The rate of emission was calculated on an element basis (i.e., C or N) and converted to micrograms per square metre per hour.

Fig. 2. Daily horizontal variation (coefficient of variation) of temperature between two adjacent heating cables, one measurement per plot, in 1994.



Statistical analyses

Pearson's product moment correlation (Devore and Peck 1986) and least squares regression analyses were used to assess strength of the linear relationship between trace gas fluxes and environmental parameters including soil temperature and soil moisture. Multiple regression was used to examine the significance of temperature and soil moisture variables on trace gas fluxes. Means separation (Tukey HSD, $\alpha = 0.05$) (SAS Institute 1985) was used to detect differences in seasonal means between plots for trace gas fluxes using replicate measures within plots.

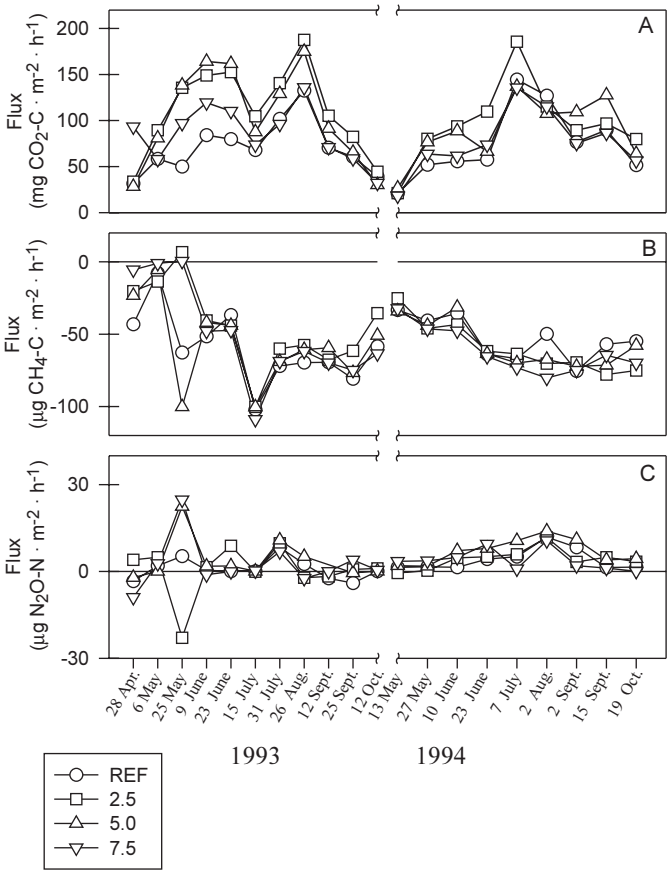
Results

Soil temperature manipulation

Mean soil temperature at 5 cm depth was elevated in heated plots, relative to the reference plot, from 19 May to 2 October 1993 and from 29 April to 30 September 1994 (Fig. 1A). Soil temperature data collection began on the first gas sampling date in both years, regardless of when the temperature treatments began. Intermittent electrical problems occurred in the 5.0 and 7.5°C plots from late August 1993 until heat treatments were terminated that year. The 7.5°C plot continued to experience intermittent electrical problems from early August through 10 September 1994. On this date, heating cables experienced an electrical short circuit that caused a small fire within the plot, and power to this plot was terminated.

Coefficient of variation for mean daily forest floor temperature (5 cm) decreased as level of heat treatment increased (Fig. 2). However, when the 7.5°C plot malfunctioned, marked increases in this variation were found due to failures in the heating cables in some portions of the plot. Even with these failures, the coefficient of variation in the 7.5°C plot was generally less than those in the reference plot.

Fig. 3. Trace gas flux measurements during 1993 and 1994. (A) CO_2 flux; (B) CH_4 flux; (C) N_2O flux. Vertical bars are standard errors.



Soil moisture

Soil water tension generally increased in all plots during June in both treatment years (Fig. 1B). At this depth, differences between plots were probably attributable to preexisting soil structural differences and less likely to temperature treatments. The reference and the 7.5°C plots typically had the lowest soil water tension in both treatment years and were notably similar during the 1994 treatment season.

CO_2

CO_2 flux was low in spring, increased and peaked in summer, and declined again in the fall during both 1993 and 1994 (Fig. 3A). Mean ambient CO_2 fluxes (reference plot) during the growing season (71 and 74 mg CO_2-C·m^{-2}·h^{-1} for 1993 and 1994, respectively) were in the same range as previously reported in other studies (Crill 1991; Bowden et al. 1993; Peterjohn et al. 1993; Rustad et al. 1996). CO_2 flux and soil temperature were positively correlated during both years while plots were heated (Table 1). CO_2 efflux and soil water tension did not exhibit any relationship in 1993, but were positively correlated in 1994 (Table 1). Likewise, CO_2 was negatively correlated with soil water content (measured in 1994 only). During both treatment seasons, mean seasonal CO_2 flux was highest in the 2.5°C plot, followed by the 5.0 and 7.5°C and reference plots, respectively (Table 2). Analysis of variance showed that plot means were statistically significantly different ($p < 0.05$); particularly, the 2.5 and 5.0°C plots were statistically higher than the reference plot in 1993. Only the 2.5°C plot was statistically greater than the reference plot in 1994.

When mean CO_2 fluxes per sampling date from all plots were combined ($n = 44$ for 1993, $n = 36$ for 1994), soil temperature explained 55 and 44% ($p = 0.0001$) of the variability of the logarithm of CO_2 flux for 1993 and 1994, respectively. CO_2 flux (all plots combined) increased exponentially with increasing soil temperature, with temperature coefficients (Q_{10}) of 1.9 and 2.8 for 1993 and 1994, respectively. Values of Q_{10} for individual plots decreased with increased heating ($Q_{10} \pm SE = 2.6 \pm 1.2$, 2.2 ± 1.2, 2.0 ± 1.2, and 1.9 ± 1.2 for the reference and 2.5, 5.0, and 7.5°C plots, respectively). Linear regressions between the logarithm of CO_2 flux and mean 5-cm soil temperature for individual plots (1993 and 1994 data combined) showed that this relationship was weaker with temperature treatment ($r^2 = 0.74$, 0.53, 0.45, and 0.48 for the reference and 2.5, 5.0, and 7.5°C plots, respectively). Linear multiple regression (LMR) analyses could account for 19% of the variability of the logarithm of CO_2 flux when the model included soil temperature and soil water tension for 1993 data with all plots combined. Alternatively, a LMR model that included soil temperature, soil water tension, and soil water content explained 55% of the variability of the logarithm of CO_2 flux for 1994 data. Including soil moisture did not significantly improve the fit of the model in either 1993 or 1994.

CH_4

Fluxes of CH_4 varied among plots and with time, ranging from an efflux of 7 µg CH_4-C·m^{-2}·h^{-1} to an uptake of 109 µg CH_4-C·m^{-2}·h^{-1} in 1993, with efflux occurring in spring only, when soils were nearly water saturated, and from 25 to 80 µg CH_4-C·m^{-2}·h^{-1} uptake in 1994. Mean CH_4 uptake in the reference plot was 60 µg CH_4-C·m^{-2}·h^{-1} in 1993 (May–October) and 52 µg CH_4-C·m^{-2}·h^{-1} in 1994. CH_4 uptake from experimental plots was generally lower in spring, increased and stabilized in summer, and was reduced again in October during 1993 (Fig. 3B). Uptake was highest in all plots on 15 July, during a dry period. During 1994, uptake was low in spring and then increased and remained relatively constant throughout the remainder of the measurement period. Seasonal patterns were similar for 1993 and 1994 in summer, but 1993 fluxes were more variable during spring, particularly on 25 May.

During 1993, CH_4 uptake was significantly correlated with soil temperature and soil water tension (Table 1). These same relationships were stronger in 1994. CH_4 uptake was also correlated with soil water content, which was monitored only during 1994. Soil heating did not markedly influence CH_4 uptake (Fig. 3B). Analysis of variance failed to show any significant differences among seasonal plot means (Table 2). Linear regression showed that soil temperature and CH_4 uptake were significantly related for all heated plots ($p < 0.05$) and that Q_{10} decreased as level of heat treatment increased (2.5°C = 1.37, 5.0°C = 1.34, 7.5°C = 1.30). Conversely, there was no relationship between temperature and CH_4 flux for the reference plot.

LMR showed that soil water tension was the primary influencing variable for CH_4 flux in 1993, but only accounted

Table 1. Results of correlation analyses between trace gas flux rates using the chamber method and environmental parameters for 1993 (n = 44) and 1994 (n = 36).

	Gas and year					
	CO_2		CH_4		N_2O	
Parameter	1993	1994	1993	1994	1993	1994
Soil temperature (5 cm)	0.69 (0.0001)	0.68 (0.0001)	0.32 (0.0173)	0.46 (0.0051)	ns	0.67 (0.0001)
Soil water content (0–30 cm integration)	nd	–0.59 (0.0010)	nd	–0.76 (0.0001)	nd	–0.77 (0.0001)
Soil water tension (15 cm)	ns	0.50 (0.0038)	0.41 (0.0177)	0.54 (0.0013)	ns	0.62 (0.0002)

Note: Data are Pearson's correlation coefficient, r, with p value in parentheses. nd, no data; ns, not significant.

Table 2. Mean seasonal trace gas fluxes.

	Gas and year					
Treatment	CO_2 (mg CO_2-C·m^{-2}·h^{-1})		CH_4 (µg CH_4-C·m^{-2}·h^{-1})		N_2O (µg N_2O-N·m^{-2}·h^{-1})	
level	1993	1994	1993	1994	1993	1994
Reference	70.6*c*	75.3*b*	59.5*a*	53.1*a*	0.83*a*	4.11*a*
2.5°C	111.4*a*	97.5*a*	44.9*a*	59.2*a*	0.37*a*	4.31*a*
5.0°C	104.8*ab*	89.9*ab*	57.4*a*	56.9*a*	3.99*a*	7.00*a*
7.5°C	85.9*bc*	76.6*ab*	49.9*a*	61.6*a*	2.42*a*	4.03*a*

Note: Statistically significant differences (p < 0.05) between values within a column determined by Tukey means separation test are indicated by different letters.

for 17% of the variability. Soil temperature did not significantly improve the fit of the model. In contrast, during 1994, water content was the important controlling variable, accounting for 58% of the variability of CH_4. Soil temperature and soil water tension did not significantly improve the fit of the model for 1994.

N_2O

Fluxes of N_2O varied among plots and over time from an uptake of 23 µg N_2O-N·m^{-2}·h^{-1} to an emission of 25 µg N_2O-N·m^{-2}·h^{-1} in 1993 and from an uptake of 1 µg N_2O-N·m^{-2}·h^{-1} to an emission of 14 µg N_2O-N·m^{-2}·h^{-1} in 1994. Mean N_2O flux in the reference plot was 1 µg N_2O-N·m^{-2}·h^{-1} in 1993 (May–October) and 4 µg N_2O-N·m^{-2}·h^{-1} in 1994. These two seasons showed very different N_2O flux patterns (Fig. 3C). Fluxes were low and highly variable in 1993, with N_2O uptake occurring on many dates. In 1994, a clearer temporal pattern existed, with fluxes being low in the spring, peaking in the summer, and declining in the fall. On only one occasion did a plot exhibit N_2O consumption during 1994.

N_2O flux failed to show any significant relationship with soil temperature or soil water tension during the 1993 field season (Table 1). In contrast, N_2O flux was significantly correlated with all environmental variables for 1994, exhibiting the strongest relationship with soil water content (negative correlation). Intraplot variability was reduced during 1994 compared with 1993 (Fig. 3C). Analysis of variance failed to show any significant differences among seasonal plot means (Table 2).

An LMR model including both soil temperature and soil water tension did not show any significant relationship with N_2O flux for 1993 data. For 1994 data, water content accounted for 60% of the variability of N_2O flux when LMR analyses were performed. Neither soil temperature nor soil water tension significantly improved the fit of the model for 1994.

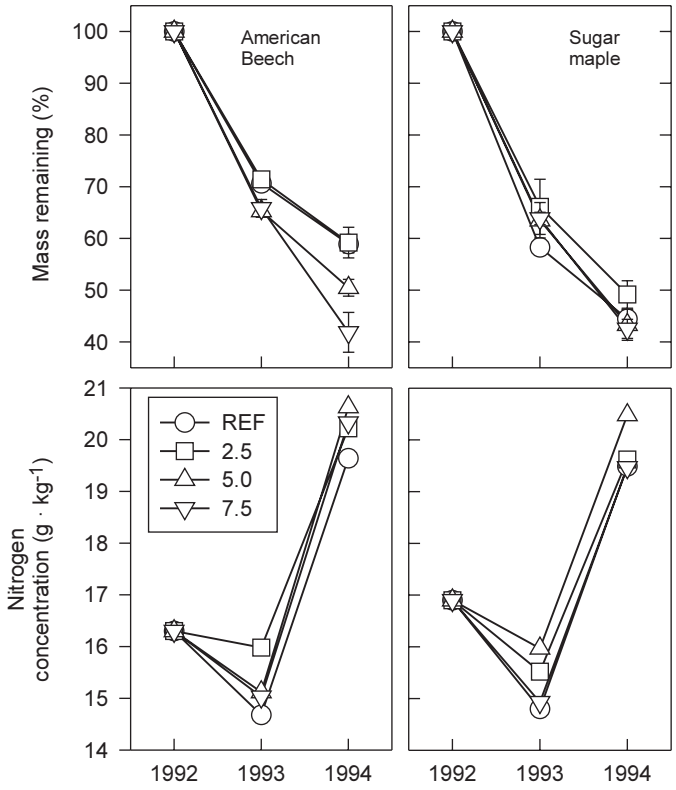
Litter bags

The percentage of litter mass remaining for American beech litter bags at 1 year since installation ranged from 65 to 71% and at 2 years from 42 to 59% (Fig. 4). The percentage of litter mass remaining for sugar maple litter bags at 1 year ranged from 58 to 64% and at 2 years from 42 to 49%. Percent mass remaining for American beech litter bags corresponded to level of heat treatment. At 1 year since installation, percent masses remaining in the 5.0 and 7.5°C plots were almost equal and less (p = 0.0001, n = 24) than in the reference and 2.5°C plots for which mean percent masses remaining were almost identical. At 2 years, percent mass remaining for American beech litter bags in the 7.5°C plot was significantly lower compared with the reference and 2.5°C plots (p = 0.0001, n = 48). Concentration of N decreased in both American beech and sugar maple leaf litter at 1 year following installation, and the reference plot exhibited the greatest decrease (Fig. 4). For American beech, the heated plots showed a greater decrease in N concentration as heating level increased. Sugar maple leaf litter exhibited the greatest N concentration decrease in the 7.5°C plot, followed by the 2.5 and 5.0°C plots. After 2 years, N concentrations in American beech and sugar maple litter bags exceeded initial concentrations (Fig. 4). For American beech leaf litter, the 5.0°C plot had the highest N concentration, followed by the 7.5 and 2.5°C and reference plots. For sugar maple leaf litter, the 5.0°C plot had the highest N concentration, followed by the 2.5°C, reference, and 7.5°C plots.

Discussion

Similar to other soil warming studies conducted in the northeastern United States (Peterjohn et al. 1994; Rustad

Fig. 4. Percent mass remaining and N concentration at 0, 1, and 2 years for American beech and sugar maple leaf litter.



et al. 1996), the present study examined the response of soil processes to temperatures. Unlike the other soil warming studies, which only manipulated soil temperature to 5°C above ambient, the present study used a range of temperature treatments (2.5, 5.0, and 7.5°C above ambient) to gain a better understanding of how an augmented range of soil temperatures affects soil processes.

Verification of flux measurement methods and potential errors

Previous work has shown that short incubations can reduce error associated with nonlinear gas concentration increases when incubations times are longer (Matthias et al. 1978, 1980; Jury et al. 1982; Raich et al. 1990). In similar studies (Steudler et al. 1989; Raich et al. 1990), the total incubation time of air within the sampling chambers was 30 min, with a sampling interval of 10 min. Likewise, we used a 30-min total incubation period, but air samples were collected only at 0 and 30 min, producing a 30-min collection interval. Therefore, the 30-min sampling interval in our study may have lead to an underestimation of gaseous fluxes, due to the possibility of nonlinear gas concentration increases. However, Rustad et. al. (1996) reported that the linearity of flux measurements in their study allowed for a 60-min sampling interval. Also, there may have been some gaseous loss from the chambers due to leakage at the edges of the chamber, since we did not use collars inserted into the forest floor, as others have done (Steudler et al. 1989; Bowden et al. 1990). Nevertheless, Richey (1994) found no such losses, since these chambers have thick walls and are relatively heavy.

The chamber flux estimates for our study were similar to those of other studies from temperate forests (Keller et al. 1983; Bowden et al. 1990, 1993; Crill 1991; Peterjohn et al. 1993; Rustad et al. 1996). In addition, we were primarily interested in the temperature response within our study site, with less focus on intersite comparisons or global estimates.

CO_2 flux and litter decomposition

It is well known that CO_2 efflux from soils is influenced by temperature (Witkamp 1966; Reiners 1968; Edwards 1975). Experiments on soil warming in northeastern U.S. temperate forests have provided quantitative results on these temperature effects. Rustad et al. (1996) showed that CO_2 efflux from the soil surface and CO_2 concentration in soil air both had a positive exponential relationship with soil temperature. Peterjohn et al. (1994) reported that linear regression explained 92% of the variability between temperature and CO_2 flux, with a Q_{10} of 2.5. Peterjohn et al. (1994) suggested that increased rates of CO_2 release may represent a short-term depletion of available C in the soil. The results of the present study also suggest the depletion of labile C in heated plots. Mean seasonal CO_2 fluxes in all heated plots were higher than in the reference plot for 1993 and 1994 (Table 2). Also, there was greater mass loss from American beech leaf litter with increased temperature (Fig. 4). In addition, Christ et al. (1997) reported that $CHCl_3$-labile C decreased with level of heat treatment for Oa horizon samples taken from our plots.

Mean seasonal plot fluxes failed to exhibit a pattern of a linear increase with augmented soil temperature among the treated plots (Table 2). One possible explanation is that heating the forest floor may have had a drying effect, limiting fine root respiration and microbial activity. Unfortunately, soil moisture levels were not monitored in the O horizon. Nevertheless, the pattern of mean seasonal flux in heated plots did parallel the pattern of soil water tension (Table 2; Fig. 1).

The reference and 7.5°C plots had very similar mean seasonal fluxes in 1994, but for much of that season, temperature could not be maintained in the 7.5°C plot. In contrast, the plot with the highest CO_2 flux was always (except once during heat treatments) either the 2.5 or 5.0°C plot, and the 7.5°C plot never had the highest mean CO_2 flux, even at the beginning of heat treatments. Additionally, leaf litter N concentrations exhibited similar patterns (Figs. 3 and 4). The highest N concentrations occurred in either the 2.5 or 5.0°C plot at 1 and 2 years since installation of the American beech and sugar maple leaf litter bags. The second highest N concentrations were found in either of the same two plots on three of four sampling events. The same plots (2.5 and 5.0°C) had the highest seasonal CO_2 fluxes in 1993 and 1994. Higher N concentrations in leaf litter suggest greater microbial mobilization (activity) in the 2.5 and 5.0°C heated plots. These results, coupled with declining Q_{10} values of CO_2 flux with increased heating, suggest a decreased microbial response to the augmented soil temperatures in our study.

CH_4 flux

Previous studies monitoring CH_4 flux in forested soils (Bowden et al. 1993; Peterjohn et al. 1994; Rustad et al.

1996) have reported values within the range of the current study. Peterjohn et al. (1994) found that soil heat treatments raised daily CH_4 uptake means significantly at HF, despite increased N availability. These researchers hypothesized that soil warming would enhance N mineralization and nitrification and thus reduce CH_4 uptake. However, Richey (1994) reported that N (NO_3^- and NH_4^+) additions at the HF resulted in greater CH_4 uptake rates compared with plots with no N additions. McHale et al. (1996) reported that soil warming did not result in increased concentrations of either NH_4^+ or NO_3^- at the HF, and thus, no effect due to increased N availability would be anticipated in the current study. As was found for CO_2, Q_{10} values for CH_4 flux decreased with increasing levels of soil warming (Q_{10} 2.5°C > Q_{10} 5.0°C > Q_{10} 7.5°C), suggesting a decreased microbial response to augmented soil temperature.

Crill (1991) suggested that the activity of CH_4-oxidizing bacteria will increase with temperature in spring until the supply of substrate for CH_4 becomes limiting, after which the uptake rates remain relatively constant. Seasonal patterns for our study, particularly in 1994, exhibited this pattern (Fig. 3B). The relationship between soil temperature and CH_4 flux (e.g., $r^2 = 0.46$ for 1994) was likely due to warmer temperatures coinciding with the drier soil, and indeed, temperature and soil water content were strongly related ($r^2 = 0.76$). Also, LMR analyses showed that soil water content was a major factor affecting CH_4 flux during our study. These results indicate the importance of porosity, and thus gas diffusivity, which would have been greatest in those periods with high temperature and low soil moisture. Other studies have reported that soil moisture had a stronger control on CH_4 uptake compared with soil temperature (Steudler et al. 1989; Born et al. 1990; Castro et al. 1993).

N_2O flux

Mean N_2O fluxes from the reference plot were 1 and 4 $\mu g \cdot m^{-2} \cdot h^{-1}$ during the 1993 and 1994 growing seasons, respectively. Richey (1994) monitored N_2O flux at the HF during the growing season in 1992 and 1993 and found fluxes of 11 and 3 $\mu g \cdot m^{-2} \cdot h^{-1}$, respectively. Bowden et al. (1990) found fluxes in hardwood plots at the HF to be lower at 0.27 $\mu g \cdot m^{-2} \cdot h^{-1}$. At the HF, Peterjohn et al. (1994) reported for a soil warming study that heated soils had low and highly variable N_2O fluxes. Peterjohn et al. (1994) also reported that soil temperature was not correlated with N_2O flux and heating the soil did not significantly influence fluxes. The variable nature of N_2O flux from forested soils was likely due to high spatial heterogeneity associated with these soils and the complexity of below-ground N cycling.

Conclusions

Soil warming had the most marked influence on CO_2 flux, with less response to CH_4 and N_2O fluxes. Soil moisture (water content) was the primary controlling variable for CH_4 and N_2O in 1994, and thus the role of this factor needs to be included in any evaluation of the effects of changing climate on the fluxes of these gases. Analyses of the effects of temperature on C fluxes also need to consider how changing C and N pools may lead to transient versus long-term enhancements of C losses from forest soils. Warming of soils may produce a pulse of CO_2 initially, but over time the response may be diminished as labile C is depleted. Alternatively, if there is a biomass buildup and subsequent increases of litter inputs to the forest floor in response to higher temperatures, elevated CO_2 emissions may contribute rising concentration of atmospheric CO_2 in the future.

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References

Anderson, J.M. 1973. Carbon dioxide evolution from two temperate, deciduous woodland soils. J. Appl. Ecol. **10**: 361–378.

Anderson, J.M. 1992. Responses of soils to climate change. Adv. Ecol. Res. **22**: 163–210.

Beerling, D.J., and Woodward, F.I. 1994. The climate change experiment (CLIMEX): phenology and gas exchange responses of boreal vegetation to global change. Global Ecol. Biogeogr. Lett. **4**: 17–26.

Bonan, G.B., and Van Cleve, K. 1991. Soil temperature, nitrogen mineralization, and carbon source–sink relationships in boreal forests. Can. J. For. Res. **22**: 629–639.

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

Bowden, R.D., Steudler, P.A., Mellilo, J.M., and Aber, J.D. 1990. Annual nitrous oxide fluxes from temperate forest soils in the northeastern United States. J. Geophys. Res. **95**: 13 997 – 14 005.

Bowden, R.D., Castro, M.S., Melillo, J.M., Steudler, P.A., and Aber, J.D. 1993. Fluxes of greenhouse gases between soils and the atmosphere in a forest following a simulated hurricane blowdown. Biogeochemistry, **21**: 61–71.

Castro, M.S., Steudler, P.A., Melillo, J.M., Aber, J.D., and Millham, S. 1993. Exchange of N_2O and CH_4 between the atmosphere and soils in spruce–fir forests in the northeastern United States. Biogeochemistry (Dordr.), **18**: 119–135.

Christ, M., David, M.B., McHale, P.J., McLaughlin, J.W., Mitchell, M.J., Rustad, L.E., and Fernandez, I.J. 1997. Microclimatic control of microbial C, N, and P pools in Spodosol Oa horizons. Can. J. For. Res. **27**: 1914–1921.

Crill, P. 1991. Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. Global Biogeochem. Cycles, **5**: 319–334.

David, M.B., Mitchell, M.J., and Nakas, J.P. 1982. Organic and inorganic sulfur constituents of a forest soil and their relationship to microbial activity. Soil Sci. Soc. Am. J. **46**: 847–852.

Devore, J., and Peck, R. 1986. Statistics: the exploration and analysis of data. West, New York.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science (Washington, D.C.), **263**: 185–190.

Edwards, N.T. 1975. Carbon cycling in a mixed deciduous forest floor. Ecology, **58**: 431–437.

Houghton, J.T., and Woodwell, G.M. 1989. Global climate change. Sci. Am. **260**: 36–44.

Jury, W.A., Letey, J., and Collins, T. 1982. Analysis of chamber methods used for measuring nitrous oxide production in the field. Soil Sci. Soc. Am. J. **46**: 250–256.

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

MacDonald, N.W., Zak, D.R., and Pregitzer, K.S. 1995. Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. Soil Sci. Soc. Am. J. **59**: 223–240.

Matthias, A.D., Yarger, D.N., and Weinbeck, R.S. 1978. A numerical evaluation of chamber methods for determining gas fluxes. Geophys. Res. Lett. **5**: 756–768.

Matthias, A.D., Blackmer, A.M., and Bremner, J.M. 1980. A simple chamber technique for field measurement of emissions of nitrous oxide from soils. J. Environ. Qual. **9**: 251–256.

McHale, P.J., Mitchell, M.J., Raynal, D.J., and Bowles, F.P. 1996. Increasing soil temperature in a northern hardwood forest: effects on elemental dynamics and primary productivity. *In* Proceedings: 1995 Meeting of the Northern Global Change Program, 14–16 March 1995, Pittsburgh, Pa. *Edited by* J. Hom, R. Birdsey, and K. O'Brian. U.S. For. Serv. Gen. Tech. Rep. NE-214. pp. 146–152.

Mollitor, A.V., and Raynal, D.J. 1982. Acid precipitation and ionic movements in Adirondack forest soils. Soil Sci. Soc. Am. J. **46**: 137–141.

NOAA. 1980. Climatological data — New York. Vol. 92. National Oceanic and Atmospheric Administration, Climatological Data and information Service, National Climatic Center. Asheville, N.C.

Peterjohn, W.T., Melillo, J.M., Bowles, F.P., and Steudler, P.A. 1993. Soil warming and trace gas fluxes: experimental design and preliminary flux results. Oecologia, **93**: 18–24.

Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.A., Bowles, F.P., and Aber, J.D. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecol. Appl. **4**: 617–625.

Raich, J.W., Bowden, R.D., and Steudler, P.A. 1990. Comparison of two static chamber techniques for determining carbon dioxide efflux from forest soils. Soil Sci. Soc. Am. J. **54**: 1754–1757.

Reiners, W.A. 1968. Carbon dioxide evolution from the floor of three Minnesota forests. Ecology, **49**: 471–483.

Richey, D.G. 1994. Nitrous oxide, methane and carbon dioxide flux between forest soils and the atmosphere and the effects of ammonium sulfate fertilization. M.S. thesis, Syracuse University, Syracuse, N.Y.

Rustad, L.E., Fernandez, I.J., and Arnold, S. 1996. Experimental soil warming effect on C, N, and major element cycling in a low elevation spruce–fir forest soil. *In* Proceedings: 1995 Meeting of the Northern Global Change Program, 14–16 March 1995, Pittsburgh, Pa. *Edited by* J. Hom, R. Birdsey, and K. O'Brian. U.S. For. Serv. Gen. Tech. Report, NE-214. pp. 132–139.

SAS Institute. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, N.C.

Shepard, J.P., Mitchell, M.J., Scott, T.J., Zhang, Y.M., and Raynal, D.J. 1989. Measurement of wet and dry deposition in a northern hardwood forest. Water Air Soil Pollut. **48**: 225–238.

Somers, R.C. 1986. Soil classification, genesis, morphology, and variability of soils found within the central Adirondack region of New York. Ph.D. dissertation, College of Environmental Science and Forestry, State University of New York, Syracuse, N.Y.

Steudler, P.A., Bowden, R.D., Melillo, J.M., and Aber, J.D. 1989. Influence of nitrogen fertilization on methane uptake in temperate forest soils. Nature (Lond.), **341**: 314–315.

Whalen, S.C., Reeburgh, W.S., and Barber, V.A. 1992. Oxidation of methane in boreal forest soils: a comparison of seven measures. Biogeochemistry, **16**: 181–211.

Witkamp, M. 1966. Rates of carbon dioxide evolution from the forest floor. Ecology, **47**: 492–494.