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RESPONSES OF TRACE GAS FLUXES AND N AVAILABILITY TO EXPERIMENTALLY ELEVATED SOIL TEMPERATURES[1]

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Abstract. We are conducting a field study to determine the long-term response of belowground processes to elevated soil temperatures in a mixed deciduous forest. We established 18 experimental plots and randomly assigned them to one of three treatments in six blocks. The treatments are: (1) heated plots in which the soil temperature is raised 5°C above ambient using buried heating cables; (2) disturbance control plots (cables but no heat); and (3) undisturbed control plots (no cables and no heat). In each plot we measured indexes of N availability, the concentration of N in soil solutions leaching below the rooting zone, and trace gas emissions (CO_2, N_2O, and CH_4). In this paper we present results from the first 6 mo of this study.

The daily average efflux of CO_2 increased exponentially with increasing soil temperature and decreased linearly with increasing soil moisture. A linear regression of temperature and the natural logarithm of CO_2 flux explained 92% of the variability. A linear regression of soil moisture and CO_2 flux could explain only 44% of the variability. The relationship between soil temperature and CO_2 flux is in good agreement with the Arrhenius equation. For these CO_2 flux data, the activation energy was 63 kJ/mol and the Q_{10} was 2.5.

The daily average uptake of CH_4 increased linearly with increasing soil temperatures and decreased linearly with increasing soil moisture. Linear regression could explain 46% of the variability in the relationship between temperature and CH_4 uptake and 49% of the variability in the relationship between soil moisture and CH_4 uptake.

We predicted the annual CO_2 flux from our study site in 1991 using two empirical relationships: the relationship between air temperature and soil temperature, and the relationship between soil temperature and CO_2 flux. We estimate that the annual CO_2-C flux in 1991 was 712 g/m² from unheated soil and 1250 g/m² from heated soil. By elevating the soil temperature 5°C above ambient, we estimate that an additional carbon flux of 538 $g \cdot m^{-2} \cdot yr^{-1}$ was released from the soil as CO_2.

Key words: CH_4 uptake; CO_2 flux; global change; global warming; N mineralization; N_2O flux; northern temperate forest; soil moisture; soil temperature; trace gases.

INTRODUCTION

Current models of climate change predict that the global mean annual temperature will increase ≈3°C during the next century (Houghton et al. 1992). One result of global warming may be changes in the rates of temperature-dependent soil processes such as decomposition (Swift et al. 1979), methane production and oxidation (Crill et al. 1988, Crill 1991), net N mineralization and nitrification (Focht and Verstraete 1977), denitrification (Malhi et al. 1990), and P availability (Van Cleve 1990). Thus, elevated soil temperatures, as a result of global warming, have the potential to dramatically alter local ecosystems.

Soil warming may also have global effects. For example, faster decomposition may significantly enhance global warming by increasing the release of CO_2 from soil (Schleser 1982, Jenkinson et al. 1991). However, the net feedback that results from the interaction of all ecosystem processes is unclear. For example, faster decomposition may increase the availability of N for plant growth and thereby decrease the net flux of CO_2 from ecosystems despite elevated soil respiration (McGuire et al. 1992, Rastetter et al. 1992, Shaver et al. 1992, Melillo et al., *in press*).

Past soil-warming experiments have shown dramatic results. These include: increased rootlet mortal-

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ity in a stand of yellow birch (Redmond 1955); reduced ecosystem C storage in cores of arctic tundra (Billings et al. 1982); increased inorganic N concentrations, P absorption, and plant growth in a wet sedge tundra (Chapin and Bloom 1976); increased yields and seedling growth in agricultural fields (Rykbost et al. 1975); and increased decomposition, nutrient availability, and foliar nutrient concentrations in an Alaskan black spruce forest (Van Cleve et al. 1990).

This paper reports results from the first 6 mo of an ongoing soil-warming experiment. The purpose of this experiment is to determine the response of belowground processes in a mixed deciduous forest to elevated soil temperatures, with a special emphasis on soil processes that could significantly alter ecosystem function, atmospheric chemistry, and global climate.

Methods

The study site

This study is being conducted in the Prospect Hill Tract of the Harvard Forest in central Massachusetts (42°30′ N, 72°10′ W). The research site consists of ≈1300 m^2 of an even-aged, mixed deciduous forest. Dominant tree species include paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), black oak (*Quercus velutina* Lam.), and striped maple (*Acer pensylvanicum* L.). Soils are mainly of the Gloucester series (fine loamy, mixed, mesic Typic Dystrochrept) with a surface pH of 3.83 and subsurface pH of 4.85. The average bulk density of the upper 15 cm is 0.64 g/cm^3. A distinct Ap horizon indicates past cultivation and historical records confirm that this old-field forest was established after abandonment at the turn of the century (D. F. Foster, Director of Harvard Forest, *personal communication*). There has been some cutting for firewood subsequent to abandonment. The climate is cool temperate and humid. The mean weekly air temperature varies from a high of ≈20°C in July to a low of ≈−6°C in January (Spurr 1957). Precipitation is distributed evenly throughout the year and annually averages ≈108 cm (Spurr 1957).

Experimental design and operation

At the research site we established 18 6 × 6 m plots in April 1991 (Fig. 1). The plots are grouped into six blocks and the three plots within a block were randomly assigned to one of three treatments. The treatments are: (1) heated plots in which the average soil temperature is elevated 5°C above ambient using buried heating cables; (2) disturbance control plots that are identical to heated plots except they receive no electrical power; and (3) undisturbed control plots that have been left in their natural state.

To warm a given plot, we buried four heating cables (Smith-Gates Easy Heat) at a depth of 10 cm in 6 m long rows spaced 20 cm apart. When supplied with 240 V alternating current, the heating cables have a power output of 13.6 W/m and produce a power density of ≈77 W/m^2. This method of warming soil has been previously evaluated and performs well under a variety of moisture and temperature conditions (Peterjohn et al. 1993).

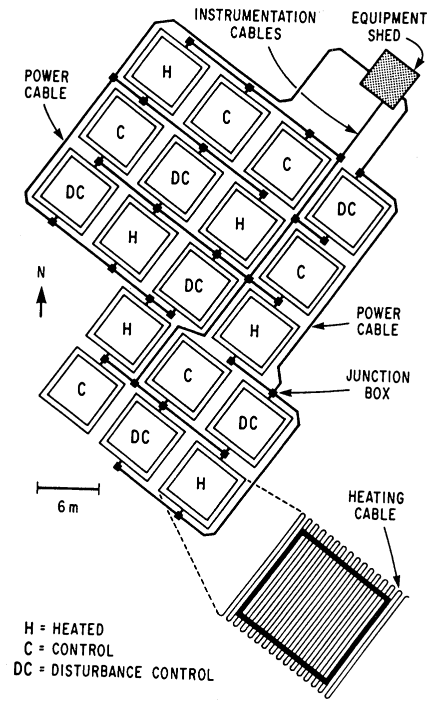

FIG. 1. Experimental design of the soil-warming experiment.

The heating system is controlled and monitored by a datalogger that is connected to 42 thermistors. Each heated plot contains five thermistors and each control plot (disturbed and undisturbed) contains one thermistor. All thermistors are placed in the soil at a depth of 5 cm. At 10-min intervals the datalogger calculates the average soil temperature in all undisturbed control plots and compares this value to the average soil temperature in each heated plot. If the difference in temperature between a particular heated plot and the undisturbed control plots is <5°C, then the datalogger closes a relay circuit and power is supplied to the heating cables in that plot. If the difference in temperature is ≥5°C, then the datalogger opens the circuit. In addition to soil temperature measurements, one thermistor measures air temperatures at a height of ≈2 m.

Field and laboratory methods

In a prototype soil-warming experiment (Peterjohn et al. 1993), we found that soil temperatures were consistently lower near the edges of a 6 × 6 m heated area. To avoid regions where the temperature is <5°C above ambient, all samples in the Harvard Forest experiment were taken from a 5 × 5 m experimental area that is nested within each 6 × 6 m plot.

We measured soil moisture, indexes of N availability, and trace gas fluxes (CO_2, CH_4, and N_2O) on two occasions every month. For a given month, nine plots (three blocks) were sampled on the first occasion and the remaining nine plots were sampled on the second. Thus, every plot was sampled once a month.

Net N mineralization and nitrification were measured for the forest floor and mineral soil using the buried bag technique (Eno 1960, Westermann and Crothers 1980, Pastor et al. 1984). Subsamples of two soil cores (6 cm in diameter and 13 cm deep) from each plot were extracted for 48 h with 2 mol/L KCl and the remaining soil was used to measure soil moisture gravimetrically. Soil cores adjacent to the initial cores were incubated in situ in polyethylene bags for 22–36 d before determining inorganic N concentrations and calculating the net change in extractable NH_4^+ and NO_3^-. Soil extracts were analyzed for NH_4^+ and NO_3^- using continuous flow colorimetry (Technicon Methods 780-86T and 782-86T). After sampling, all holes were filled with soil from outside the research site and identified to avoid resampling.

We measured the net flux of CO_2, CH_4, and N_2O between the soil and the atmosphere using previously published sampling and analytical techniques (Steudler et al. 1989, Bowden et al. 1990, Raich et al. 1990). Briefly, we made these measurements by placing static chambers over the surface of the soil for 30 min and sampling the headspace at 10-min intervals. The samples were analyzed for trace gas concentrations by gas chromatography and the changes in concentration were used to calculate net flux rates. On each sampling date, fluxes were measured in one chamber per plot at 0600, 1000, 1400, and 1800 h. Adjacent to each chamber, we also measured soil temperatures at depths of 2 and 4 cm. Throughout the experiment the locations of the chambers never changed.

In addition to the variables mentioned above, we also measured the concentration of inorganic N in water leaching below the rooting zone. Soil water samples were collected from one porous cup lysimeter per plot on two occasions every month. Lysimeters were placed at a depth of 50 cm and evacuated to 50 cm Hg, 24 h before sampling. All water samples were kept frozen until they could be analyzed for NH_4^+ and NO_3^-.

Statistical methods

For several variables a strong association between the mean and variance indicated heteroscedasticity. In addition, the approximate Wilk–Shapiro statistic (Shapiro and Francia 1972) and rankit plots (Sokal and Rohlf 1981) indicated that several variables were not normally distributed. Although the consequences of heteroscedasticity and nonnormality are not too serious (Sokal and Rohlf 1981), we subjected the data to both nonparametric and parametric statistical tests. Statistical significance for all tests was evaluated at the .05 level.

Soil warming began on 1 July 1991, but we measured soil temperature and trace gas emissions twice in June to confirm the absence of any preexisting differences among plots assigned to the various treatments. The June data were analyzed as a randomized complete block design using a two-way analysis of variance (ANOVA) followed by a Scheffé pairwise comparison of the means (Sokal and Rohlf 1981). The data were also subjected to a Friedman nonparametric two-way ANOVA (Gilbert 1987). For these tests, each sampling date in June was analyzed separately.

To test for significant treatment effects after soil warming began, the daily average values for each variable were paired spatially by blocks and temporally by sampling date. Paired data were then subjected to a paired *t* test to identify significant heating, disturbance, and heating + disturbance effects. A heating effect was defined as the difference between the daily average value for a heated plot and its paired, disturbance control plot. A disturbance effect was defined as the difference between the daily average value for a disturbance control plot and its paired, undisturbed control plot. A heating + disturbance effect was defined as the difference between the daily average value for a heated plot and its paired, undisturbed control plot. As a nonparametric alternative to the paired *t* test, we subjected the paired data to the sign test (Gilbert 1987).

Results

Preexisting "treatment" effects.—With one exception, there were no significant "treatment" effects for any variable measured before the experiment began (June 1991). The one exception was that soil temperatures measured at 4 cm were ≈2°C cooler in plots assigned to the heating treatment. This result, however, was significant for only one sampling date and only for the parametric test.

Soil temperature.—Heating successfully elevated soil temperatures 5°C above ambient soil temperatures (Fig. 2). In contrast, disturbing the soil had no detectable effect on daily average soil temperatures.

Soil moisture.—There were no significant heating or disturbance effects on soil moisture in the forest floor (Fig. 3A). Disturbing the soil also had no significant effect on soil moisture in the mineral soil. Heating, however, significantly reduced soil moisture in the mineral soil (Fig. 3B). There is a strong inverse relationship between soil temperature and moisture for both the forest floor and mineral soil ($R^2 = 0.55$, for mineral soil with one outlier removed).

Nutrient availability.—Heating consistently elevated the monthly average ammonium concentrations in both the forest floor and mineral soil, but the heating effect for the daily average concentrations was not statistically significant. Soil disturbance also tended to elevate the monthly average ammonium concentrations in both soil layers, but the disturbance effect for the daily averages was not significant. When combined, heating

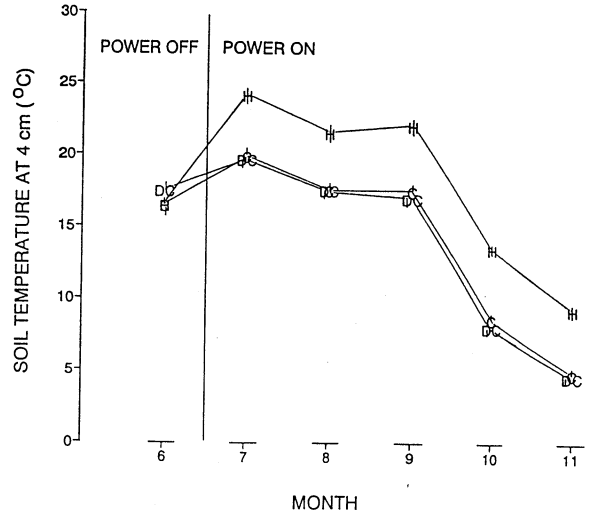

FIG. 2. Monthly average soil temperatures (mean ± 1 SE) measured in control (C), disturbance control (DC), and heated (H) plots during 1991.

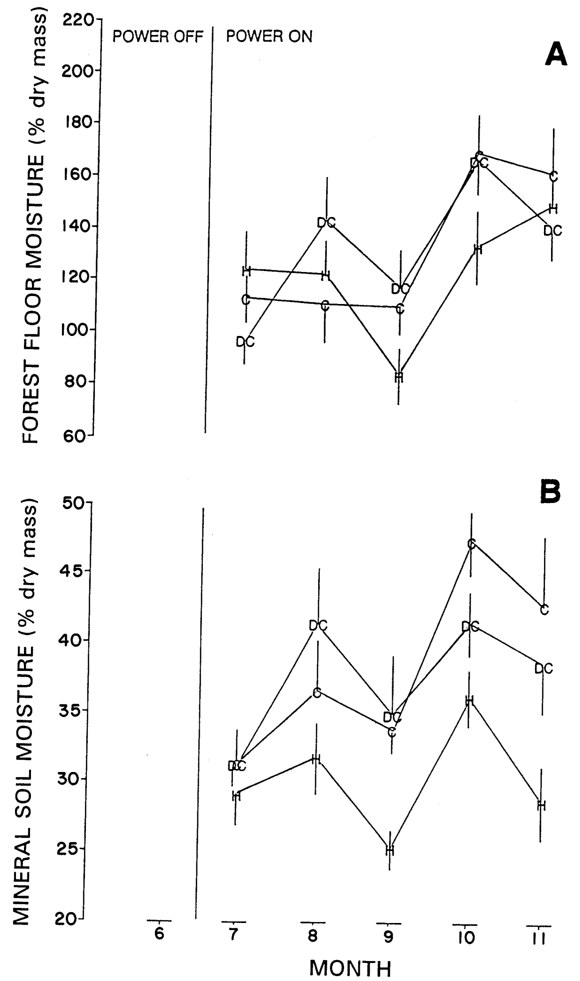

FIG. 3. Monthly average soil moistures (mean and 1 SE) measured in the forest floor (A) and mineral (B) soils during 1991. Data point symbols as in Fig. 2.

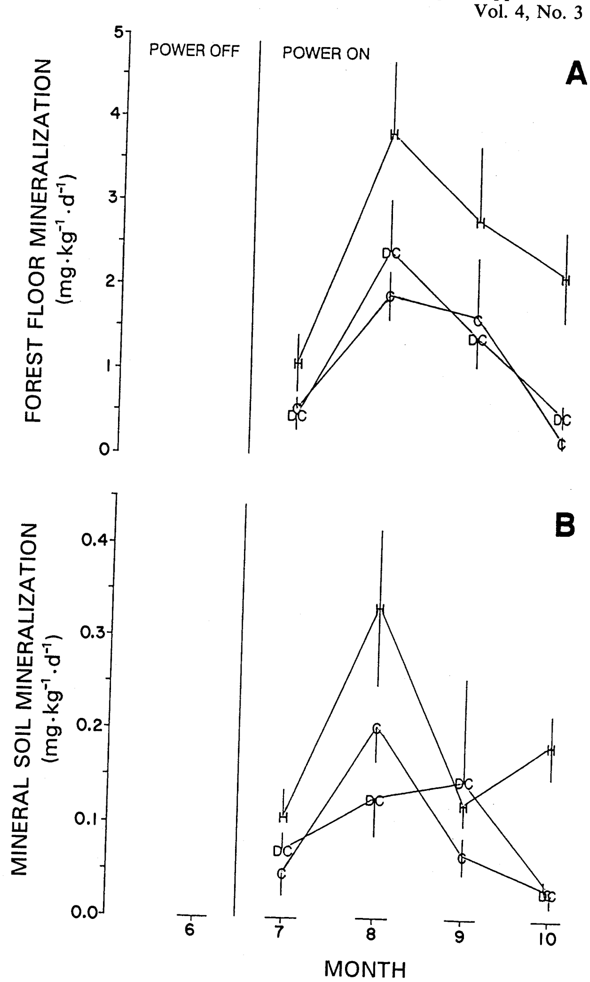

FIG. 4. Monthly average net N mineralizations (mean ± 1 SE) measured in the forest floor (A) and mineral (B) soils during 1991. Data point symbols as in Fig. 2.

and disturbing the soil elevated ammonium concentrations significantly in both soil layers. There were no significant effects on nitrate concentrations or availability; in fact, there was little extractable nitrate or net nitrification at any time during this study.

In both the forest floor and mineral soil, heating doubled the average net N mineralization rates (Fig. 4). In the forest floor, heating increased the average net N mineralization rates from 1.20 to 2.47 $mg \cdot kg^{-1} \cdot d^{-1}$. In the mineral soil, heating increased the averaged net N mineralization rates from 0.09 to 0.19 $mg \cdot kg^{-1} \cdot d^{-1}$. The heating effect on net mineralization was statistically significant, but the disturbance effect was not.

Soil water chemistry.—Of the 158 soil water samples collected from August through November, three contained measurable concentrations of nitrate (N content ranging from 0.18 to 0.57 mg/L) and 14 contained measurable concentrations of ammonium (N content ranging from 0.10 to 2.0 mg/L). The N detection limit for these analyses was 0.10 mg/L and all measurable concentrations of nitrate and ammonium occurred in

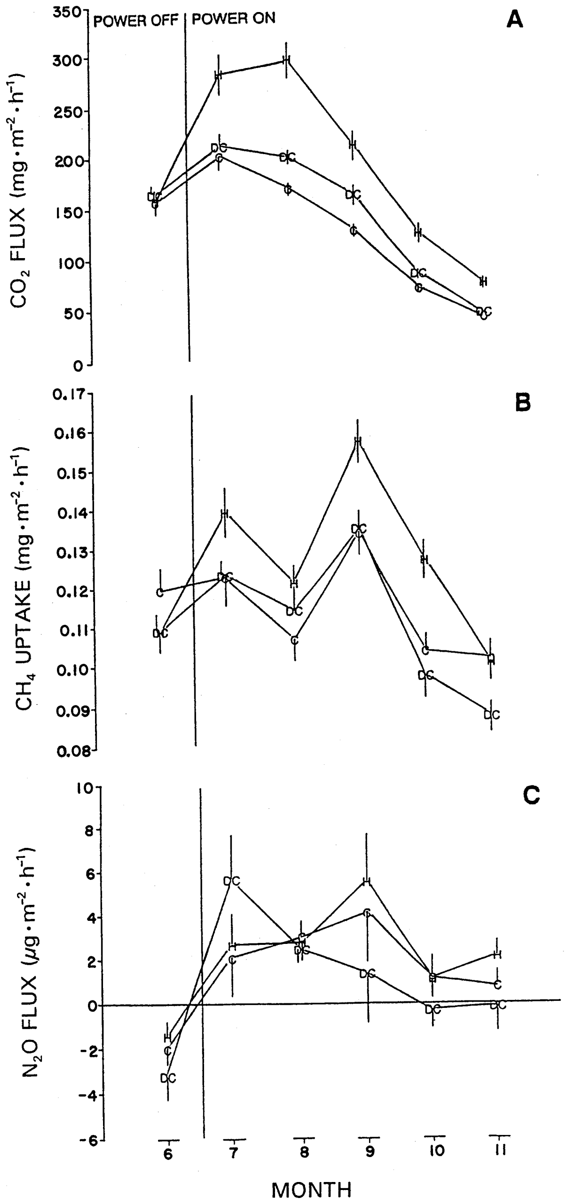

FIG. 5. Monthly average trace gas fluxes (mean ± 1 SE) from control, disturbance control, and heated plots during 1991. (A) CO_2 fluxes (as C). (B) CH_4 uptake (as C). (C) N_2O fluxes (as N). Data point symbols as in Fig. 2.

August and September. There were no apparent treatment effects.

CO_2 flux.—Both heating and disturbing the soil significantly increased the daily average CO_2 flux, but the heating effect was $\approx 3\times$ greater than the disturbance effect (Fig. 5A). The daily average efflux of CO_2 increased exponentially with increasing soil temperature (Fig. 6A) and decreased linearly with increasing soil moisture (Fig. 6B). Linear regression could explain 92% of the variability between temperature and the natural logarithm of CO_2 flux and 44% of the variability between soil moisture and CO_2 flux when one outlier was removed. Multiple linear regression could explain 94% of the variability in the natural logarithm of CO_2 flux, and soil moisture measurements significantly improved predictions once the effect of soil temperature had been modeled.

The exponential relationship between soil temperature and CO_2 flux is in good agreement with the Arrhenius equation. For these data the Q_{10} was 2.5 and the activation energy was 63 kJ/mol. This value for the activation energy is slightly higher than the range typical of enzyme catalysis (20.9–62.8 kJ/mol; Segel 1975).

CH_4 uptake.—Heating the soil elevated the average daily CH_4 uptake significantly, but disturbing the soil had no detectable effect (Fig. 5B). The daily average uptake of CH_4 increased linearly with increasing soil temperature (Fig. 7A) and decreased linearly with increasing soil moisture (Fig. 7B). Linear regression could

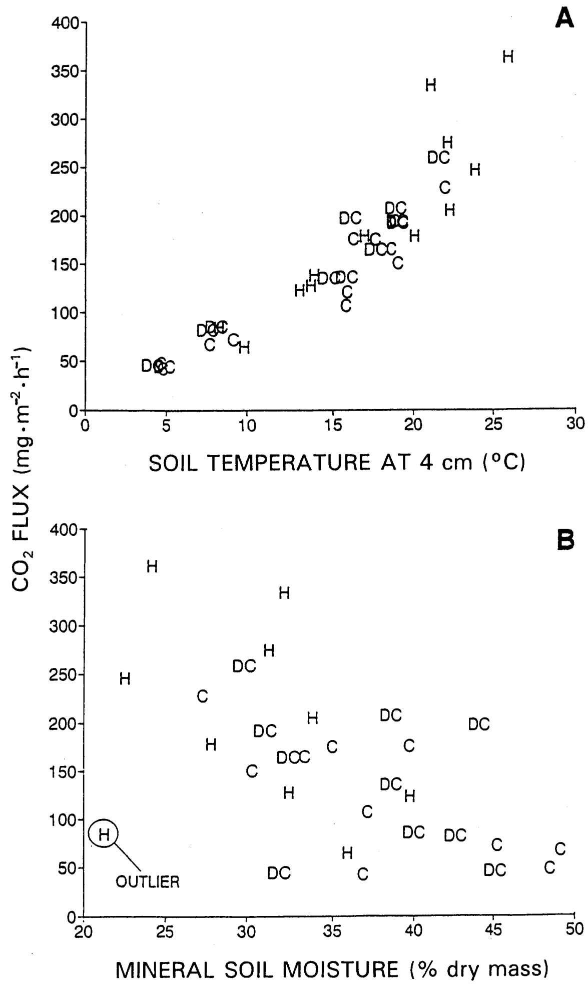

FIG. 6. Daily average CO_2 fluxes (as C) vs. (A) soil temperature (4 cm) and (B) mineral soil moistures during 1991. Data point symbols as in Fig. 2.

explain 46% of the variability between temperature and CH_4 uptake and 49% of the variability between soil moisture and CH_4 uptake when one outlier was removed. A logarithmic transformation of the CH_4 uptake values did not significantly improve these relationships. Multiple linear regression could explain 61% of the variability in CH_4 uptake, but soil moisture measurements did not significantly improve predictions of CH_4 uptake once the effect of soil temperature had been modeled. It should be noted, however, that the effect of soil moisture was nearly significant ($P = .0994$) and may have been weakened by the removal of seven cases that lacked corresponding soil moisture measurements.

N_2O flux.—The flux of N_2O from all treatments was low and relatively constant, and there were no significant heating or disturbance effects (Fig. 5C). The apparent absence of any nitrate and net nitrification in these soils may account for the low flux of N_2O. Only a weak relationship exists between the daily average flux of N_2O and both soil temperature and moisture. Linear regression could explain only 14% of the variability in the relationship between temperature and N_2O flux, and only 23% of the variability in the relationship between soil moisture and N_2O flux after one outlier was removed. Multiple linear regression could explain 28% of the variability in the flux measurements and did not significantly improve our predictions.

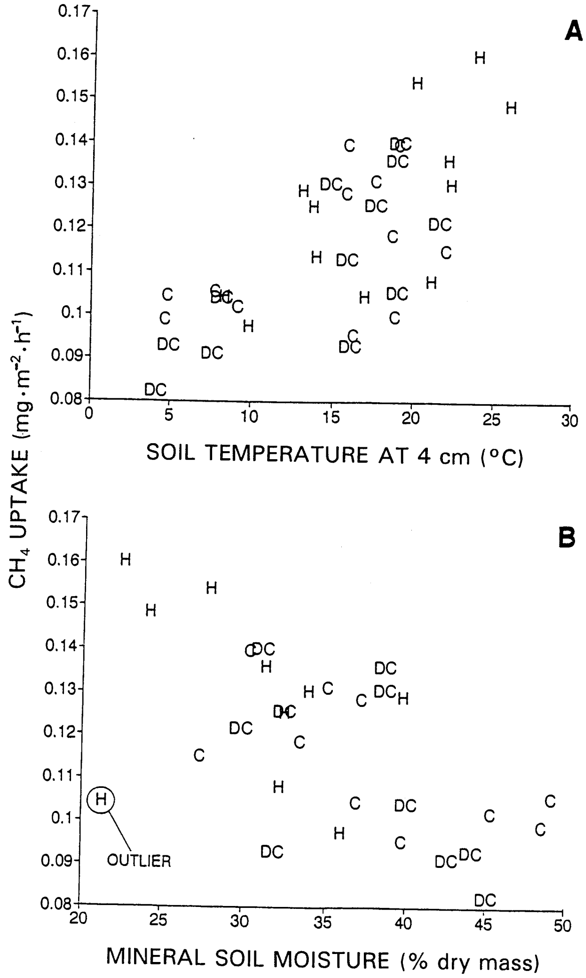

FIG. 7. Daily average CH_4 uptake (as C) vs. (A) soil temperature (4 cm) and (B) soil moistures during 1991. Data point symbols as in Fig. 2.

DISCUSSION

To understand how soil processes will respond to global warming, field measurements must be made at temperatures that are beyond the range of temperatures that normally occur at a given site. In the first 6 mo of this experiment, we measured soil processes at temperatures higher than any measured at the Harvard Forest during the previous 3 yr (Fig. 8). The responses of soil processes to these elevated temperatures were often distinct, but were not always anticipated.

We expected that soil warming would increase soil respiration and N availability, which would eventually lead to symptoms of N saturation. These symptoms include: (1) increased net N mineralization and net nitrification; (2) an increased flux of N_2O from the soil to the atmosphere; (3) increased concentrations of inorganic N in soil water; and (4) a decrease in CH_4 uptake due to enhanced N availability (Aber et al. 1989, Steudler et al. 1989).

During the first 6 mo of warming we observed the anticipated increase in soil respiration and net N mineralization. However, we have not detected any change in net nitrification, soil water N concentrations, or N_2O flux. In addition, CH_4 uptake increased rather than decreased in heated soil.

To put our results in a broader temporal context we predicted the annual CO_2 flux from our research site during 1991 by using air temperatures measured at the Harvard Forest weather station in conjunction with two empirical relationships: the relationship between air temperature and soil temperature (Fig. 9) and the relationship between soil temperature and CO_2 flux (Fig. 10). Our estimate for the annual carbon flux from unheated soil (as CO_2) is 712 g/m^2; the estimate for the heated plots, calculated by adding 5°C to the predicted soil temperature, is 1250 g/m^2. The actual measurements agree closely with predicted values for both unheated and heated soil ($R^2 = 0.885$ and 0.823, respectively). Thus, by elevating soil temperatures 5°C above ambient, we estimate that we induced an additional carbon release of 538 g·m^{-2}·yr^{-1} from the soil as CO_2. This increased release of CO_2 could be the result of increased microbial decomposition, increased root respiration, or a combination of both of these processes.

The exponential relationship we observed between soil temperature and CO_2 flux is consistent with data from other hardwood forests around the world (Fig. 10). If our soil-warming data are representative, then a global increase in soil temperature of 5°C would result in an additional carbon release of 1.9×10^{15} g/yr (as

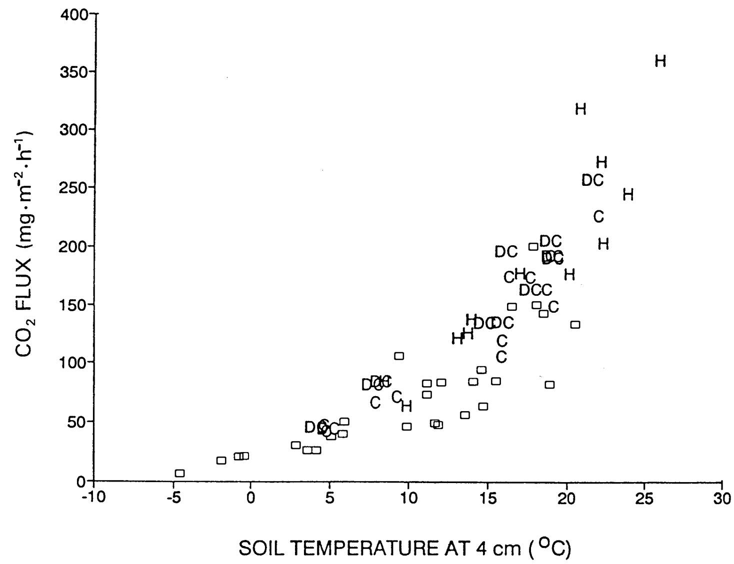

FIG. 8. Relationship between daily average CO_2 fluxes (measured as C) and soil temperature (4 cm depth). Letter data points are data from this study (see Fig. 2) and □ are data from 3 yr of research at a nearby hardwood forest (J. M. Melillo, *unpublished data*).

CO_2) from the soil surface to the atmosphere from the 3.6×10^{12} m^2 of temperate deciduous forest (Melillo et al., *in press*). Although this rate of CO_2 release is large, its effect on global climate is not clear for several reasons. First, the observed release of CO_2 may only represent a short-lived depletion of the labile C pool. Second, enhanced soil respiration may be offset by enhanced aboveground net primary productivity. Because our experiment "decoupled" below- and aboveground processes by warming only the soil, we cannot determine how global warming might affect the balance between photosynthesis and respiration for the entire ecosystem. Finally, other ecosystem interactions may occur. For example, if an increase in soil temperature is accompanied by enhanced N availability, then net primary production may increase faster than soil respiration and the entire ecosystem may store C rather than release it (McGuire et al. 1992, Rastetter et al. 1992, Shaver et al. 1992, Melillo et al., *in press*).

While our study cannot determine the impact of warmer soils on the global climate, we feel our experimental results will be useful in constraining ecosystem

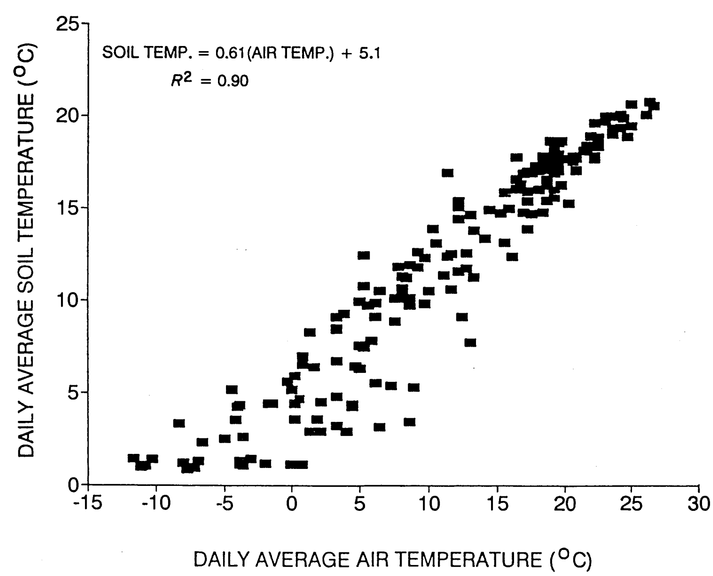

FIG. 9. Correlation between daily average air and soil (4 cm depth) temperatures. Air temperatures were measured at the NOAA weather station located at Harvard Forest. Soil temperatures were measured in the control plots of the soil-warming experiment.

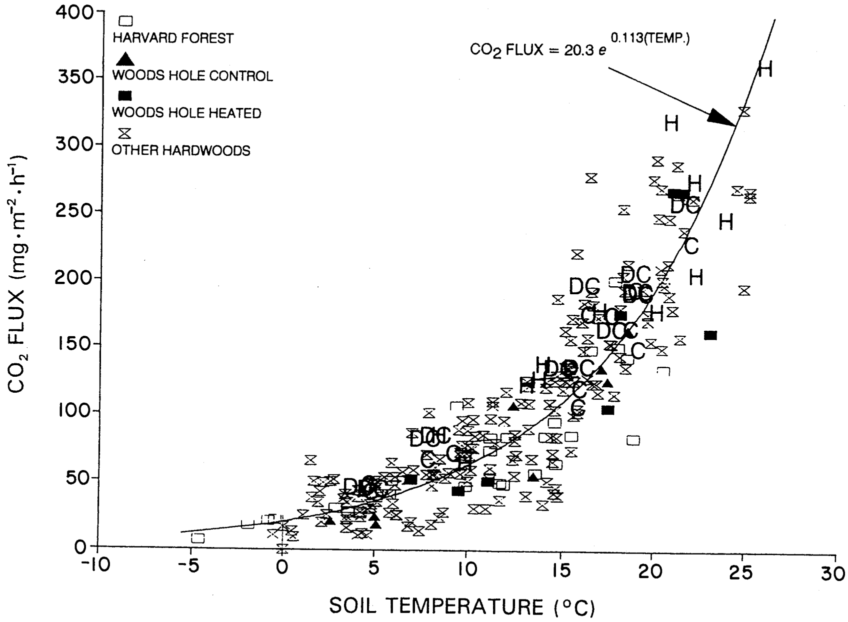

FIG. 10. Relationship between CO_2 flux (as C) and soil temperature for hardwood forests around the world. Letter data points as in Fig. 2 and Harvard Forest data as in Fig. 8. Darkened symbols are data from prototype soil-warming plots in Woods Hole, Massachusetts (Peterjohn et al. 1993). Values for other hardwood forests include data from: Minnesota (Reiners 1968); Tennessee (Edwards 1975); Missouri (Garrett and Cox 1973); United Kingdom (Anderson 1973); Italy (Virzo De Santo et al. 1976); and Japan (Nakane 1980).

models that are designed to explore this question (e.g., Rastetter et al. 1991).

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