Soil warming, carbon–nitrogen interactions, and forest carbon budgets

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Soil warming has the potential to alter both soil and plant processes that affect carbon storage in forest ecosystems. We have quantified these effects in a large, long-term (7-y) soil-warming study in a deciduous forest in New England. Soil warming has resulted in carbon losses from the soil and stimulated carbon gains in the woody tissue of trees. The warming-enhanced decay of soil organic matter also released enough additional inorganic nitrogen into the soil solution to support the observed increases in plant carbon storage. Although soil warming has resulted in a cumulative net loss of carbon from a New England forest relative to a control area over the 7-y study, the annual net losses generally decreased over time as plant carbon storage increased. In the seventh year, warming-induced soil carbon losses were almost totally compensated for by plant carbon gains in response to warming. We attribute the plant gains primarily to warming-induced increases in nitrogen availability. This study underscores the importance of incorporating carbon–nitrogen interactions in atmosphere–ocean–land earth system models to accurately simulate land feedbacks to the climate system.

climate system feedbacks | ecological stoichiometry | forest carbon budget | forest nitrogen budget | global climate change

The world's forests account for more than half of the organic carbon stored on land (1). Currently, forests of the temperate zone are actively accumulating carbon in large enough quantities to affect the global carbon budget (1, 2). A number of phenomena may be contributing to this enhanced carbon accumulation (3–8), including recovery from historical land use (e.g., abandoned agricultural land reverting to forested land), carbon dioxide (CO_2) fertilization of photosynthesis, increased nitrogen (N) deposition, and climate change.

In the future, climate change is likely to play a major role in the carbon balance of temperate forests and other land ecosystems, although the sign and magnitude of the resulting feedbacks to the climate system are uncertain (9, 10). The projected warming of between 1.1 °C and 6.4 °C over the next 100 y (11) could affect the carbon balance of terrestrial ecosystems by altering biogeochemical processes such as plant photosynthesis and microbial respiration (2, 12–14).

Soil warming experiments conducted in a variety of ecosystems, including forests, have shown short-term losses of soil carbon as CO_2 and acceleration of nitrogen cycling rates, leading to an increase in the availability of nitrogen to the vegetation (15–20). The principles of ecosystem stoichiometry (21–23) suggest that, in forest ecosystems, the redistribution of a relatively small amount of this newly available nitrogen from the soil to the trees could result in a substantial increase in carbon storage in woody tissues.

Until now, direct empirical evidence to evaluate the effects of soil warming on carbon budgets of forest ecosystems has been lacking. Determining ecosystem-level responses to warming is difficult for at least two reasons. First, a large area—hundreds of square meters—has to be heated in situ over a long enough time to capture the effects of warming on plant and soil carbon stocks at the forest-stand level. Second, evaluating belowground carbon-cycle responses to warming requires quantification of the relative contributions of microbial respiration and root respiration to total soil respiration, the flux commonly measured in soil-warming studies.

Here we report the changes in net carbon storage in trees and soil in a mixed hardwood forest ecosystem in central Massachusetts in response to a 5 °C increase in soil temperature. The study includes one large area (30 × 30 m) in which the soil was heated and an adjacent area (30 × 30 m) as a control. We present results after 8 y, including one pretreatment year followed by 7 y of soil warming. We quantified changes in plant carbon storage by using direct measurements of tree growth. To assess changes in soil carbon storage, we measured soil respiration, fine-root respiration, and fine-root biomass. We also measured changes in nitrogen availability in response to soil warming, as this ecosystem is nitrogen limited (24). This information has provided us with insights into the importance of carbon–nitrogen interactions in determining net carbon storage in forests in response to soil warming.

Results and Discussion

Soil warming has resulted in carbon losses from the soil and has stimulated carbon gains in the woody tissue of trees. Over the 7 y of treatment, the cumulative warming-induced net flux of carbon has been from the forest to the atmosphere, but the magnitude of the flux has diminished over time as a result of the increase in tree growth rate in the heated area.

Pretreatment measurements of carbon budget indexes showed the control and heated areas to be very similar. In 2002, the pretreatment year, tree carbon was 106 Mg·ha^{-1} in the control area and 109 Mg·ha^{-1} in the heated area. Woody increment was 1.73 Mg·C·ha^{-1} in the control area and 1.68 Mg·C·ha^{-1} in the heated area. Total soil respiration rates—the combination of root and microbial respiration—were 6.4·Mg·C ha^{-1} for control area and 5.8 Mg·C·ha^{-1} for the heated area (Fig. S1). During the 7-y treatment period, however, total soil respiration from the heated area was consistently higher than from the control area (Fig. 1).

We estimate that fine-root (<1 mm diameter) respiration averaged 26% of total soil respiration in the control area and 18% in the heated area over the 7 y of treatment (Fig. 1). These root respiration estimates reflect the effects of warming on both respiration rates per

Fig. 1. Total annual soil CO_2 efflux partitioned into soil organic matter loss, root respiration, and fine-root decomposition for the heated and control areas (in Mg·C·ha^{-1}).

unit of root mass and total root mass. Over the course of the study, soil warming has resulted in increased respiration rates per unit of root mass, whereas it has led to decreased fine-root mass.

Our estimate of the relative contribution of root respiration to total respiration in the control area falls between two earlier estimates made in unheated areas in other similarly structured deciduous stands at the Harvard Forest (18, 25). One of the studies, which used trenched plots to estimate the relative contributions of root and microbial respiration to total soil respiration, reported that root respiration accounted for about 20% of total soil respiration (18). Bowden et al. (25), also using a trenched-plot technique in a Harvard Forest deciduous stand that was not subject to warming, reported that root respiration accounted for 33% of total soil respiration. These Harvard Forest results are in the lower half of the range of the relative contribution of root respiration to total soil respiration reported in the literature. A review by Hansen et al. (26) shows that, globally, estimates of the contribution of root respiration to total soil respiration range widely—from 5 to 100%—depending on forest type, experimental setting, season, and time step of the analysis.

Fine-root respiration increased in the heated area relative to the control in the first 2 y of warming by an average of 19%. By the third year of heating, however, fine-root respiration in the control area surpassed that in the heated area by 9%, and this difference increased in magnitude in subsequent years due to a progressive decrease in fine-root biomass in the heated area (Table S1). We estimate that fine-root biomass in the top 10 cm of soil decreased by 62% in the heated area during the 7-y study. Other soil-warming studies in northern hardwood forests have shown similar dramatic decreases in fine-root biomass in response to warming (27, 28). The reduction of fine-root biomass with soil warming is consistent with current ideas that link carbon allocation in plants to the availability of nitrogen and other soil resources (29, 30). The logic is that, as nitrogen becomes more available with warming, trees do not have to allocate as much carbon resource belowground to acquire nitrogen, and so fine-root biomass decreases.

Microbial respiration associated with soil organic matter decay was the largest component of soil respiration in both the heated and the control areas during the pretreatment and treatment phases. By difference (total soil respiration minus root respiration), we estimate that, over the 7-y treatment period, microbial respiration accounted for 74% of the total respiration in the control area and 82% in the heated area (Fig. 1). We also estimate that, over this period, the warming-induced increase in microbial respiration resulted in a reduction of the total soil carbon pool to a depth of 60 cm by 14.7% relative to the control.

Carbon dioxide emissions from fine-root decay increased in the heated area each year with the growth of the fine-root detritus pool. The additional root litter decay in the heated area, however, was a small percentage (~1%) of total soil respiration.

Although soil warming caused a loss of carbon from the soil, it concurrently stimulated a gain of carbon in the vegetation (Fig. 2). The forest in the study area has been regrowing since a major, stand-replacing hurricane in 1938, which leveled most of the trees in both the control and the heated areas. Over the course of the study, carbon storage in the vegetation of the control area ranged between 1.7 and 3.6 Mg·C·ha^{-1}, with a mean for the 7 y of 2.2 Mg·C·ha^{-1}. For forest stands of similar age and composition in other parts of the Harvard Forest, Barford et al. (31) reported a biometrically determined carbon storage rate in the live vegetation of 1.7 Mt·C·ha^{-1} for the period 1993–2000.

The annual rate of carbon storage in the vegetation of the heated area was greater than in the control and ranged between 2.4 and 5.1 Mg·C·ha^{-1}, with a mean for the 7 y of 3.2 Mg·C·ha^{-1}. The rate of carbon storage in the vegetation increased over time. Compared with the control, the net annual ecosystem carbon balance resulting from warming shifted from a substantial carbon loss early in the experiment (2.0 Mg·C·ha^{-1}) to near zero (0.0 Mg·C·ha^{-1}) in year 7 (Fig. 3).

Integrated over the 7-y period, the warming-induced soil carbon losses have been greater than the warming-induced vegetation carbon gains. The cumulative carbon loss from the soil that was induced by warming over the 7 y of treatment was 13.0 Mg·C·ha^{-1}, and the warming-induced vegetation gain was 7.0 Mg·C·ha^{-1} (Fig. 4). Since the start of the experiment, the equivalent of 54% of the carbon released from soils in response to warming has been taken up and stored in trees in the heated area. Thus, although warming has resulted in a net positive feedback to the climate system, the magnitude of the feedback has been substantially dampened by the increase in storage of carbon in vegetation.

Increases in vegetation carbon storage in the heated area are likely due, for the most part, to the warming-induced increase in net nitrogen mineralization of about 27 kg·N·ha^{-1}·yr^{-1}. This represents a 45% increase relative to the nitrogen mineralization rate in the control area (Fig. 5).

We used the principles of ecosystem stoichiometry to explore whether or not the increase in net nitrogen mineralization in the heated area was large enough to support the measured increase in carbon storage in the trees growing there. When carbon is stored in plant tissues, a small amount of nitrogen is also stored, with the mass ratio of C:N specific to plant tissue type. In the

Fig. 2. (*A*) Annual vegetation carbon storage in the heated and control areas (in Mg·C ha^{-1}). (*B*) Annual vegetation in carbon storage delta (heated minus control) (in Mg·C·ha^{-1}).
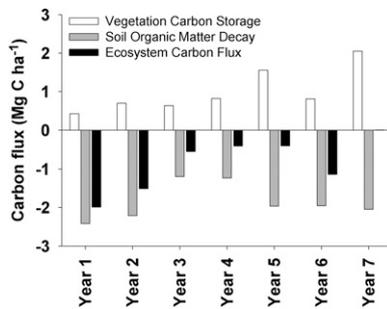
Fig. 3. The average annual effect of soil warming on the net carbon balance of the forest stand (ecosystem carbon flux) expressed as the difference between the warming-induced carbon loss from the soil (soil organic matter decay) and the gain in the above- and belowground perennial tissues of the canopy trees (vegetation carbon storage) (in $Mg \cdot C \cdot ha^{-1}$). These values are relative to the control area. Note that the ecosystem carbon flux value for year 7 is near $0 \; Mg \cdot C \cdot ha^{-1}$.

wood of deciduous trees at the Harvard Forest, the mass ratio of carbon stored per unit of nitrogen stored is ~300:1 (e.g., 32, 33). On the basis of this ratio, we estimate that the amount of nitrogen required to store $1,000 \; kg \cdot C \cdot ha^{-1} \cdot yr^{-1}$ in new woody growth resulting from warming is about $3.3 \; kg \cdot N \cdot ha^{-1} \cdot yr^{-1}$. This amount of nitrogen is about 12% of the additional $27 \; kg \cdot N \cdot ha^{-1} \cdot yr^{-1}$ made available to the trees growing in the heated area.

Our data show that most of the remaining $23.7 \; kg \cdot N \cdot ha^{-1}$ of the newly available nitrogen in the heated area has entered a rapidly cycling nitrogen pool that moves between the soil and vegetation. We have measured an annual average increase in nitrogen mass in the green canopy in the heated area relative to the control of $22.5 \; kg \cdot N \cdot ha^{-1}$, which accounts for almost all of this newly available nitrogen in the rapidly cycling pool. This accounting of the newly available nitrogen resulting from warming is consistent with our observations that there has been no evidence of nitrogen losses to groundwater or the atmosphere (as nitrous oxide) from either the heated or the control areas.

Although we think that most of the increased carbon storage in the trees is related to the warming-induced acceleration of the nitrogen cycle, we also observed a lengthening of the growing season with warming. Using a threshold number of 50% of the buds on the trees opening, we estimate that bud-break occurs
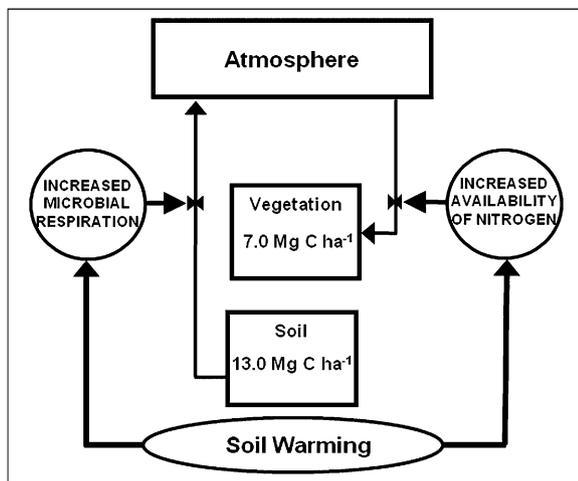
Fig. 4. The cumulative effect of soil warming on the carbon balance of the ecosystem after 7 y of warming in $Mg \cdot ha^{-1}$. Increases in growing season length may also contribute to vegetation carbon storage (not shown in this figure). These values are rounded to the nearest tenth of a Megagram (Mg).
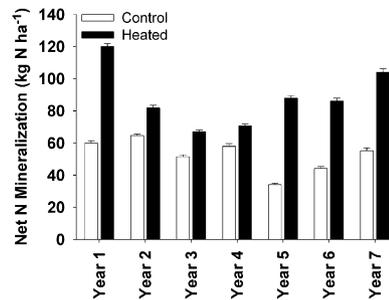
Fig. 5. Net nitrogen mineralization in the control and heated areas. Bars represent mean net nitrogen mineralization rates of subplots ($n = 10$) ± 1 SE in $kg \cdot N \cdot ha^{-1} \cdot yr^{-1}$.

between 4 and 7 d sooner in trees in the warmed area. This translates to a 3–4% increase in the mean growing season length of 161 d reported for deciduous stands at the Harvard Forest (34). A slightly longer growing season may be interacting with greater nitrogen availability to enhance plant productivity and carbon storage. However, as nitrogen is considered to be a major factor limiting plant growth in this system (24, 35), we attribute most of plant carbon gain to changes in the nitrogen cycle.

Although we believe that the warming of soils as the climate changes will affect carbon cycling in forest ecosystems by increasing nitrogen availability and lengthening the growing season, we recognize that the carbon balance of forest ecosystems in a changing climate will also depend on other factors that will change over the century (e.g., 36–38). For example, carbon storage in woody tissue will also be affected by changes in water availability, changes in the availability of other nutrients such as phosphorus, the effects of increased temperature on both plant photosynthesis and aboveground plant respiration, and the atmospheric concentration of CO_2. Reductions in soil moisture and the increased plant respiration associated with warming will tend to reduce carbon storage in mid-latitude forests, whereas moderate increases in soil moisture and increased concentrations of CO_2 will likely increase carbon storage in these systems, especially if nitrogen limitation is relieved.

It is important to recognize that the relief of nitrogen limitation by the redistribution of nitrogen from the soil to the vegetation has limits set by the size of the soil nitrogen pool and its accessibility to the microbial community. Results from individual field studies (39, 40) and meta-analyses (41, 42) support the argument that, for land ecosystems to sustain large, long-term carbon accumulations in response to rising atmospheric CO_2, nitrogen inputs will have to increase and/or nitrogen losses will have to decrease.

With model simulations, we have demonstrated the importance of including nitrogen in coupled atmosphere–ocean–land earth system models by comparing terrestrial carbon uptake in response to increased surface temperatures using two versions of our global biogeochemistry model, Terrestrial Ecosystem Model (the carbon only and coupled carbon–nitrogen versions), in the Massachusetts Institute of Technology's Integrated Global Systems Model framework (43). A change in terrestrial carbon uptake with increased surface temperatures was observed when nitrogen was included, leading to a net sequestration of carbon in the plant–soil system and a reduced CO_2 feedback to the climate system. Other research groups have obtained similar results when they incorporated their carbon–nitrogen models into atmosphere–ocean–land earth system models (44–46).

Conclusions

To date, the idea that warming-induced redistribution of nitrogen from soil to vegetation can alter the carbon budget of normally nitrogen-limited forest ecosystems has been an untested hypothesis (12, 23, 44–46). The results presented here provide empirical support for this concept and underscore the importance of in-

cluding both plant and soil carbon–nitrogen interactions in making projections of land carbon balance in a warmer world.

Materials and Methods

Site Description and Approach. The research site is an even-aged, mixed deciduous forest in central Massachusetts (42° 28′ N, 72° 10′ W). It is dominated by *Quercus rubra* and *Quercus velutina* (42% of basal area) and *Acer rubrum* (29%) with lesser components of *Fraxinus americana* (11%) and occurs on soils of the Canton series. As in an earlier, smaller (6 × 6 m) soil-warming study nearby (18), we used buried resistance cables to heat the soil. In large (30 × 30 m) heated and control (unheated) areas, we carried out a set of biogeochemical and plant phenology and growth measurements. The biogeochemical measurements include the emissions of CO_2 from the soil surface to the atmosphere, carbon accumulation in the vegetation, and in situ net nitrogen mineralization. For all of the stoichiometric analyses, we applied a pretreatment correction factor to differentiate between the effects of heating and preexisting microsite differences. The pretreatment correction factor adjusts the initial heated data to equal the control.

Historical records, stone walls, and soil horizon characteristics indicate that the area was used for either pastureland or low-intensity agriculture before 1908. White pines dominated the site by the early 1900s, but were destroyed in a hurricane in 1938. Blowdowns were salvaged and the area was left to recover and regrow naturally to its current state: a relatively young stand of mixed hardwoods. Soils are mainly of the Canton series (coarse-loamy over sandy or sandy-skeletal, mixed, semiactive, mesic Typic Dystrudepts) with a surface O horizon pH of 5.2 and subsurface mineral horizon pH of 5.5. The average bulk density is $0.37 \cdot g \cdot cm^{-3}$ in the organic layer and $0.78 \cdot g \cdot cm^{-3}$ in the mineral layer. The climate is cool, temperate, and humid. The mean weekly air temperature varies from a high of about 20 °C in July to a low of about −6 °C in January. Precipitation is distributed evenly throughout the year and annually averages about 108 cm.

During the summer and fall of 2001 about 5 km of heating cable was buried by hand to minimize disturbance in a 30- × 30-m area. Cables were buried at a 10-cm depth, spaced 20 cm apart. An adjacent 900-m^2 area was delineated to serve as the control area, with a 5-m buffer in between the two areas. Pretreatment biogeochemical data were collected during the 2002 growing season to compare the baseline biogeochemistry for the two large areas, control and treatment (*SI Text*; Figs. S1 and S2). This approach has been commonly used in large-scale ecosystem manipulations such as the Hubbard Brook Ecosystem Study (47). Results from an earlier soil-warming experiment confirmed that the soil disturbance associated with the installation of heating cables has had no effect on soil temperatures or soil respiration and only minor and variable impacts on soil moisture, net nitrogen mineralization (Fig. S3), and shrub growth (18).

When supplied with 240 volts of alternating current, the heating cables have a power output of 3.6 W$\cdot m^{-1}$ and produce a power density of about 77 W$\cdot m^{-2}$. There are 160 resistance heating cables, each of which is ~30 m long. A typical resistance per cable is 96 ohm. The heated area is monitored with 80 thermistors and 6 moisture probes, and the control plot has 12 thermistors and 6 moisture probes. Every minute heating cables are turned on and off automatically to maintain a 5 °C temperature differential between heated and control areas. This heating method works well under a variety of moisture and temperature conditions.

Heating commenced on the treated area in May 2003. For all analyses in the pretreatment and treatment periods, rates were calculated on the basis of "warming years," defined as consecutive 12-mo periods beginning in May 2002 (e.g., May 2002–April 2003).

Total Soil Respiration. The net flux of CO_2 was measured monthly from April through November in nine subplots in each of the heated and control areas. On each sampling date, fluxes were measured at early morning and afternoon intervals to capture low and high respiration rates. Although we did not measure CO_2 fluxes in the winter, we used a temperature model to extrapolate out data to daily fluxes. From 2002 to 2009, daily rates of soil respiration were modeled as:

$$F_{CO2} = \beta_0 e^{\beta_1 T}$$

where F_{CO2} is the rate of soil CO_2 efflux in mg$\cdot$C m$^{-2} \cdot$hr^{-1} and T is the soil temperature in degrees C measured at 4 cm. Soil temperature was measured adjacent to the gas sampling chambers at the time of sampling. β_0 and β_1 represent year- and treatment-specific parameters, which were calculated by linear regression analysis in SAS (version 9.1.3). The model was driven by measurements of soil temperature collected at 6-h intervals in each of the experimental areas from 2003 to June 2008 and hourly measurements from

then on. Hourly modeled values were then summed to determine annual CO_2 efflux values.

Root Biomass and Respiration. We used fine-root biomass and respiration data to assess the contribution of fine roots to total soil respiration in response to warming at the ecosystem level. Root biomass was measured in the organic and mineral soil horizons (0–10 cm depth) at Barre Woods from April through November 2008. Roots were extracted from soil cores taken from a subset of plots within each of the experimental areas and separated by size class (<1 mm and 1–3 mm diameter). Roots were then dried at 60 °C for 2 d and weighed. To assess the degree to which root respiration adjusts to warmer soil temperature regimes, specific root respiration rates (nmol$\cdot$ $CO_2 \cdot g^{-1} \cdot s^{-1}$) were measured from May through October in 2008 and in 2009. Specific respiration rates for fine roots (<1 mm) from control and heated areas were measured both at a common reference temperature of 18 °C and at the ambient soil temperature of the control or heated (5 °C) areas in each experiment. Roots were cut from the top 10 cm of soil, brushed free of soil, and immediately placed in a respiration cuvette where respiration rates were measured using an infrared gas analyzer. A Q10 value was determined for the heated and control areas for each month sampled on the basis of the reference and ambient temperatures (48).

Monthly fine-root respiration rates were calculated using the average monthly temperature on each area and the monthly Q10 values for the heated and control areas. We then calculated the daily fine-root respiration (g$\cdot$C$\cdot m^{-2}$) by multiplying the respiration rate by the fine-root biomass for each month sampled. We used the modeled daily soil respiration values to determine the percentage of total soil respiration accounted for by the roots. Analyses included fine roots less than 1 mm. Assuming that the percentage of total respiration accounted for by roots has remained stable in the control areas through time, we used a linear relationship to determine the change in root contribution to total respiration in the heated area through time. The average percentage of total respiration accounted for by roots in the heated and control areas was then applied to annual respiration values.

Root Carbon Inputs. We used fine-root biomass data from 2007 and 2008 in the heated and control areas to examine the root loss in the heated area through time, assuming that root biomass in the control area has remained stable through time and that the root biomass in the heated area in the pretreatment year equaled that in the control area in 2008. Root biomass estimates for the control area in 2007 were not significantly different from those measured in 2008. Over the course of the study, we estimated a 62% decrease in fine roots in the heated area relative to the control (Table S1). We used root carbon values from fine roots sampled in 2008 to estimate carbon input from roots to soil in response to warming. Carbon accounts for 46% of fine-root biomass.

Root Litter Decomposition. Using the estimates of root biomass loss in response to the warming calculated above, we determined the additional carbon pulse as a result of root litter decay in the heated area each year. The root detritus pool was calculated as the root litter from the previous year plus the pulse of new root biomass for the current year minus the root decomposition from the previous year. The root decomposition was calculated as:

$$\text{Root Litter Decomposition} = -k * Rp * H_{effect}$$

where $-k$ is a decay rate constant (49), Rp is the root detritus pool for that year, and H_{effect} is the proportional heating effect on total CO_2 efflux for that year (heated area respiration rate for given year/average control area respiration rate from 2002 to 2009).

Soil Organic Matter Decay. We combined the analyses above to estimate total soil organic matter decay as a result of warming. Soil organic matter decomposition was calculated as:

$$\text{SOM} = \text{Total Respiration} - \text{Root Respiration} - \text{Root Litter Decomposition}$$

with the components calculated as described in *Total Soil Respiration, Root Biomass and Respiration*, and *Root Litter Decomposition*. Changes in the soil carbon pool were calculated as:

$$\text{Soil C Pool}_{loss} = \text{SOM}_{loss} + \text{Root litter Decomposition}_{loss} - \text{Root C Inputs}_{gain}$$

with the components calculated as described above.

We calculated the percentage of the soil carbon pool that was lost over the study in the warmed area period using Gaudinski et al.'s (50) total carbon stock estimates at the Harvard Forest and our soil organic matter loss estimates (see above).

Vegetation Carbon Storage. Allometric equations were applied to monthly measurements of dendrometer bands on all trees >5 cm diameter at breast height to calculate changes in above- and belowground woody biomass carbon and vegetation carbon storage over time (51). Carbon inputs from the additional root litter in the heated area were subtracted from the woody biomass carbon delta for each year to account for the loss of fine-root mass due to warming.

Nitrogen Mineralization. Using the in situ buried bag incubation method, we measured the rates of net nitrogen mineralization and nitrification (18). Incubations were 5 wk in length from April to November and for 5 mo through the winter. Soils were separated into organic and mineral layers and sieved through a 5.6-mm screen to remove rocks and roots. The organic horizon had an average depth of 1.4 cm, and we analyzed the remaining 8.6 cm of mineral soil in the core. A subsample of the soil was weighed and dried at 105 °C for 24 h for soil moisture analyses. Approximately 10 grams

of the soil was placed in 100 mL of 2 M KCl, extracted for 36 h, and filtered. The extracts were analyzed for NO_3-N and NH_4-N using a Lachat QuikChem FIA+ 8000 Series Flow Injection Analyzer.

Statistical Methods. Hourly modeled total soil respiration values for each 5- × 5-m subplot (nine heated, nine control) were summed over the year and averaged to obtain estimates of total annual soil respiration for each treatment. Similarly, net nitrogen mineralization rates were averaged across the 10, 5- × 5-m subplots in the heated and control areas to obtain average annual rates. For both soil respiration and net nitrogen mineralization, annual average rates were compared between the heated and control areas using Friedman's test, a nonparametric repeated-measures analysis in SAS (v. 9.1.3).

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