Tree Physiology 16, 719–725

Fine root respiration in northern hardwood forests in relation to temperature and nitrogen availability

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Received December 11, 1995

Summary We examined fine-root (< 2.0 mm diameter) respiration throughout one growing season in four northern hardwood stands dominated by sugar maple (*Acer saccharum* Marsh.), located along soil temperature and nitrogen (N) availability gradients. In each stand, we fertilized three 50 × 50 m plots with 30 kg NO_3^--N ha^{-1} $year^{-1}$ and an additional three plots received no N and served as controls. We predicted that root respiration rates would increase with increasing soil temperature and N availability. We reasoned that respiration would be greater for trees using NO_3^- as an N source than for trees using NH_4^+ as an N source because of the greater carbon (C) costs associated with NO_3^- versus NH_4^+ uptake and assimilation.

Within stands, seasonal patterns of fine-root respiration rates followed temporal changes in soil temperature, ranging from a low of 2.1 μmol O_2 kg^{-1} s^{-1} at 6 °C to a high of 7.0 μmol O_2 kg^{-1} s^{-1} at 18 °C. Differences in respiration rates among stands at a given soil temperature were related to variability in total net N mineralized (48–90 μg N g^{-1}) throughout the growing season and associated changes in mean root tissue N concentration (1.18–1.36 mol N kg^{-1}). The hypothesized increases in respiration in response to NO_3^- fertilization were not observed. The best-fit model describing patterns within and among stands had root respiration rates increasing exponentially with soil temperature and increasing linearly with increasing tissue N concentration: $R = 1.347N\,e^{0.072T}$ ($r^2 = 0.63$, $P < 0.01$), where R is root respiration rate (μmol O_2 kg^{-1} s^{-1}), N is root tissue N concentration (mol N kg^{-1}), and T is soil temperature (°C). We conclude that, in northern hardwood forests dominated by sugar maple, root respiration is responsive to changes in both soil temperature and N availability, and that both factors should be considered in models of forest C dynamics.

Keywords: fine roots, N availability, root respiration, temperature, tissue N concentration.

Introduction

Global changes in temperature and atmospheric nitrogen (N) deposition have the potential to alter plant respiration significantly (Ryan 1991). Because respiration consumes a large proportion of the carbon (C) assimilated by trees (Edwards et al. 1990, Ryan et al. 1994), differential respiratory costs associated with climatic change could have important implications for forest C cycles. Of particular interest is the response of roots to climate change, because more than 50% of annual net primary productivity can be allocated below ground in many forest ecosystems (Fogel and Hunt 1979, Keyes and Grier 1981, Hendrick and Pregitzer 1993). Thus, understanding environmental controls on root respiration is important for the development of methods to quantify ecosystem-level C budgets. Furthermore, because worldwide CO_2 flux from root (and associated mycorrhizal) respiration is estimated to be about 18 Pg C $year^{-1}$, an order of magnitude larger than that produced by anthropogenic sources of CO_2 (Raich and Schlesinger 1992), understanding its control is also relevant to efforts to model global C budgets.

Experimental data on root respiration in relation to temperature (Lawrence and Oechel 1983, Sowell and Spomer 1986) or soil N availability (Ryan et al. 1996) are limited, but theoretical predictions and results from studies of aboveground tissues indicate that these factors are potentially important regulators of root respiration. The temperature dependence of all biochemical processes is widely recognized, and maintenance respiration in particular is known to increase exponentially with temperature (Amthor 1984, Johnson 1990). Changes in soil N availability could influence root respiration by several mechanisms. For example, an increase in the quantity of available N in soil will likely affect root respiration by increasing tissue N concentration and associated protein maintenance and construction costs. There is a strong relationship between tissue N content and maintenance costs in aboveground tissues (Merino et al. 1982, Waring et al. 1985, Irving and Silsbury 1987, Ryan 1991), and construction costs for all tissues are thought to increase with increasing protein concentration (Ryan 1991). If an increase in N availability results in higher N concentrations in root tissue, total root respiration will likely increase. Changes in the dominant form of N (i.e., NO_3^- versus NH_4^+) used by plants could affect respiration as a result of differential ion uptake or assimilation costs associated with these ions. Nitrate additions, if used preferentially by plants, could increase root respiration rates because this ion must be reduced before it is assimilated, whereas NH_4^+ can be assimi-

lated directly into biologically active plant compounds (Veen 1980, Johnson 1983). Respiration rates may also increase as a result of the greater costs of maintaining nitrate reductase, an enzyme with a short turnover time (Amthor 1984). However, if NO_3^- reduction occurs in the leaves, there may be little or no additional respiratory costs to roots associated with NO_3^- utilization (Smirnoff and Stewart 1985).

We determined the effects of soil temperature and N availability on fine-root (< 2.0 mm diameter) respiration rates by examining patterns of respiration in four northern hardwood stands that span gradients of temperature, soil N availability, and atmospheric N deposition. Experimental plots in each stand included control plots and plots fertilized with 30 kg NO_3^--N ha^{-1} $year^{-1}$. We hypothesized that root respiration will increase with increasing soil temperature and N availability. In addition, we reasoned that fine-root respiration rates will be greater for plants receiving NO_3^- additions than for plants in control plots.

Methods

Study sites

We previously located four northern hardwood stands (Figure 1), with similar overstory and soil properties (Table 1), that are distributed throughout the state of Michigan, USA (Burton et al. 1991). The stands occur along a 4 °C midsummer air temperature gradient, and atmospheric deposition of N increases from 6.8 to 11.8 kg N ha^{-1} $year^{-1}$ from the most northern to the most southern stand (Table 1). In each stand, we established six 30 × 30 m plots; three plots per stand served as controls and three plots received fertilizer applications equivalent to 30 kg N ha^{-1} $year^{-1}$ throughout the 1994 growing season. Dry, granular $NaNO_3$ (5 kg N ha^{-1}) was applied on six dates with a broadcast spreader. Plots were sampled at 5-week intervals from May 18 to November 8, 1994; sampling occurred at least one month following each NO_3^- application.

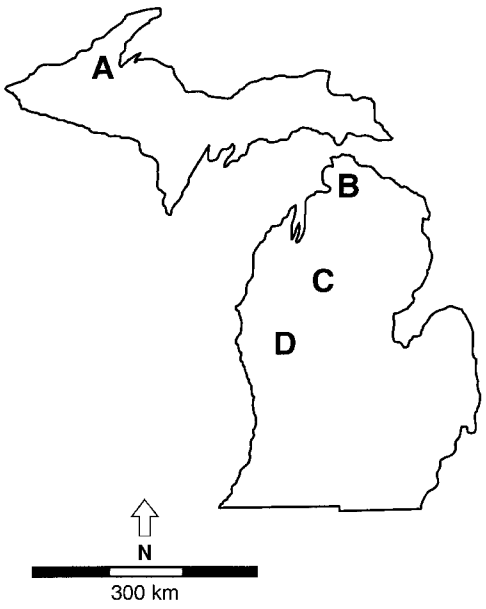

Figure 1. Locations of the four northern hardwood stands in Michigan, USA.

Table 1. Select stand characteristics of four northern hardwood stands in Michigan, USA.

	Stand			
	A	B	C	D
Overstory properties				
Total basal area (m^2 ha^{-1})	32.0	29.7	30.3	30.1
Sugar maple dominance (%)	86.0	87.0	83.0	75.0
Stand age	87	81	82	83
Soil properties[1]				
Silt + clay (%), A + E horizon	14.8	10.6	10.6	12.7
Organic C (%), A + E horizon	1.1	1.7	1.9	2.2
Temperature				
Mean annual air temp (°C)[2]	4.2	5.2	5.8	7.6
Atmospheric deposition (wet + dry)[3]				
NO_3^--N (kg ha^{-1} $year^{-1}$)	3.83	5.82	7.76	7.63
NH_4^+-N (kg ha^{-1} $year^{-1}$)	2.96	3.23	3.97	4.21

[1] Randlett et al. 1992.
[2] Thirty-year average, National Oceanic and Atmospheric Administration (1983).
[3] Three-year average, MacDonald et al. (1992).

Soil temperature, N mineralization and tissue N concentration

Soil temperature (15 cm depth) in each plot was determined by permanent, buried thermistors that recorded temperatures at 15-min intervals. Daily rates of net N mineralization were estimated *in situ* using buried bags (Eno 1960). On each sample date, three soil cores (5.4 cm diameter and 10 cm in depth, hereafter designated initial cores) were collected from random locations in each plot and transported on ice to a laboratory for processing. Soil cores consisted of both organic (O_e/O_a, 1–3 cm thick) and mineral horizons (A + E, > 7 cm thick). Additional soil cores were removed adjacent to the initial cores, placed in polyethylene bags, and incubated for five weeks in the field (hereafter designated incubated cores). After collection, all coarse fragments (> 2.0 mm diameter) and roots were removed from both the initial and incubated cores. Live, excised fine roots (< 2.0 mm diameter, most were < 0.5 mm) were removed from the initial cores, sorted by hand and composited on a plot basis for respiration measurements. Soil subsamples (10 g) were extracted with 20 ml of 2 M KCl and the filtrates were analyzed colorimetrically for NH_4^+-N and NO_3^--N with an Alpkem RFA 300 (Alpkem Corp., OR, USA). Oven dry weights (105 °C) were determined on 10-g subsamples. Net N mineralization (μg N g^{-1} day^{-1}) was calculated as the average increase in NH_4^+-N and NO_3^--N between initial and incubated soil cores. Tissue N concentration of fine roots was determined with a Carlo Erba elemental analyzer (Carlo Erba Model NA1500 Series II, Fisons Instruments, MA, USA).

Root respiration

Approximately 0.5 g fresh weight of excised roots was rinsed thoroughly in deionized water and wrapped in moistened tissue paper to prevent desiccation. We assumed that more than 75% of the roots in our soil cores were sugar maple (*Acer saccharum* Marsh.), based on the dominance of the species in the overstory (Table 1). Respiration rates of excised roots were measured over a 35-min period with a gas-phase, oxygen electrode (Model LD2-2, Hansatech Ltd., Norfolk, England); all measurements were completed within 3 h of collection. Circulating water baths were used to maintain roots at the average field temperature for each stand. Root respiration is reported here as O_2 consumption (μmol O_2 kg^{-1} dry weight s^{-1}); it can be converted to CO_2 evolved by multiplying by 0.8, the respiratory quotient (ratio of CO_2 evolved to O_2 consumed) as determined with an infrared gas analyzer (A.J. Burton and G.P. Zogg, unpublished data).

Qi et al. (1995) found that root respiration rates in Douglas-fir seedlings declined exponentially at elevated CO_2 concentrations and suggested that respiration measurements made at ambient CO_2 concentration may not accurately reflect *in situ* rates. Carbon dioxide concentrations within our sample cuvettes were greater than 3900 $\mu l\ l^{-1}$, which is an order of magnitude higher than that of ambient air (350 $\mu l\ l^{-1}$), and is also higher than the CO_2 concentrations in the upper 10 cm of soil in these stands (600–2000 $\mu l\ l^{-1}$; G.P. Zogg, unpublished data). An analysis of CO_2 effects on root respiration rates indicated that our reported respiration rates deviated by no more than 20% from those expected at actual soil concentrations (A.J. Burton and G.P. Zogg, unpublished data).

Statistical analyses

Differences in mean root respiration rates, net N mineralization and root tissue N concentration among sample dates, stands and treatments (fertilized versus control) were compared by analyses of variance and Fisher's protected least significant difference tests (Wilkinson 1990). Multiple linear regression was used to describe mean root respiration rates (date × stand × treatment) in relation to soil temperature, N mineralization and root tissue N concentration (Wilkinson 1990). Significance of all statistical tests was accepted at $\alpha = 0.05$.

Results

Soil temperature, N mineralization and tissue N concentration

Soil temperatures varied within stands, ranging from 6 °C in early spring and fall to 18 °C during mid-growing season (Figures 2a–d). In contrast, net N mineralization rates within stands were relatively constant throughout the year, although they decreased significantly in November ($P < 0.01$; Figures 2a–d). Root tissue N concentration displayed small seasonal variations, but it never changed by more than 25% (Figures 2e–h); however, during May and June, fine-root N concentrations were significantly greater than during other months of the growing season ($P < 0.01$; Figures 2e–h).

There were large differences among stands in net N mineralization and root tissue N concentration. However, values did not increase progressively from the most northern (A) to the most southern (D) stand as expected based on the background atmospheric N deposition gradient (Table 1). Soil N availability was greatest in stands B and C, where the total amount of N mineralized over the growing season was significantly greater than in stands A and D ($P < 0.01$; Figure 3a). Fine-root tissue N concentration averaged over the sampling dates was also significantly greater in stands B and C than in stands A and D ($P < 0.01$; Figure 3b), apparently reflecting differences in net N mineralization among stands (Figure 3). Nitrate fertilization had no influence ($P > 0.50$) on either net N mineralization or root tissue N concentration (Figures 2 and 3).

Root respiration

Root respiration rates within stands were typically highest in the middle of the growing season (Figure 4). For example, respiration rates in stands C and D were significantly higher during late July and late August–early September than at other times during the year (Figure 4; Table 2). Root respiration rates in stands A and B were also at or near their maximum on these dates, although values were not significantly different from values on other sample dates (Figure 4). Averaged over the sampling dates, the mean root respiration rate in stand A (3.43 μmol $O_2\ kg^{-1}\ s^{-1}$) was significantly lower (Table 2) than the rates in the other three stands (stand B = 4.53, stand C = 4.09, stand D = 4.07 μmol $O_2\ kg^{-1}\ s^{-1}$). Fertilization did not significantly influence fine-root respiration rates (Figure 4; Table 2).

Over the growing season, root respiration rates within individual stands increased exponentially with increasing soil temperature (Figure 5a; $r^2 = 0.59$, $P < 0.01$). Although the slopes did not differ among individual regression equations for each stand ($P > 0.48$), the intercepts for stands B and C were significantly greater than the intercepts for stands A and D ($P < 0.03$), indicating that, at a given soil temperature, root respiration rates were higher in stands B and C than in stands A and D (Figure 5a). Over the growing season, mean root respiration rates within stands were significantly but poorly correlated with net N mineralization (Figure 5b; $r^2 = 0.20$, $P < 0.01$); neither slopes nor intercepts differed among regression equations for each stand (Figure 5b). Although root respiration rates were not correlated with fine-root N concentration in individual stands, root tissue N concentration was a significant predictor of root respiration when data from all four stands were included in one regression model. The best-fit model accounted for 63% of the variation in fine-root respiration among sampling dates, stands and control and fertilized treatments: $R = 1.347N\ e^{0.072T}$ ($r^2 = 0.63$, $P < 0.01$), where R is root respiration rate in μmol $O_2\ kg^{-1}\ s^{-1}$, N is root tissue N concentration in mol N kg^{-1}, and T is temperature in °C. Soil temperature and net N mineralization could not be used in a single regression model because of multicolinearity.

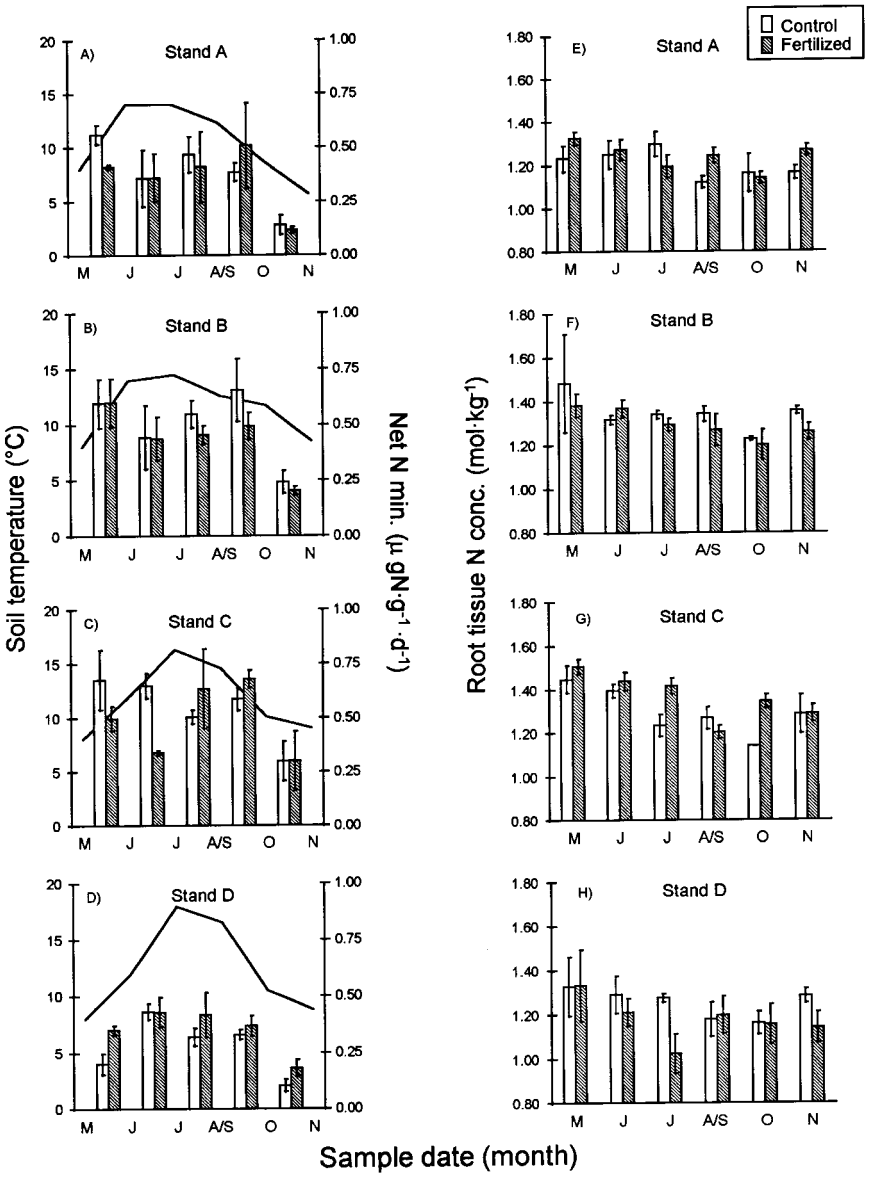

Figure 2. Seasonal patterns of temperature (A–D, solid line), net N mineralization (A–D, bars) and root tissue N concentration (E–H, bars) within the stands. Error bars indicate one SE of the mean.

Discussion

In northern hardwood forests dominated by sugar maple, root respiration is responsive to changes in both soil temperature and N availability. Soil temperature primarily controlled seasonal variation in root respiration within stands, whereas net N mineralization rates and associated root tissue N concentrations influenced the patterns of root respiration among geographically separate stands. Our respiration rates (4.0–5.8 nmol CO_2 g^{-1} s^{-1} at about 18 °C) are lower than those previously reported for sugar maple seedlings (10.0–20.5 nmol CO_2 g^{-1} s^{-1} mean respiration rate at about 20 °C; Walters et al. 1993, Reid and Strain 1994). Notwithstanding any temperature effects on root respiration, the higher rates in other studies may be the result of ontogenic effects (seedlings versus mature trees), differences in growth conditions (high nutrient conditions versus resource competition and possible N limitation) or overestimation associated with measurements made at low CO_2 concentration (Qi et al. 1994). It is unlikely that desiccation or carbohydrate depletion during processing or mechanical damage resulting from excising the roots influenced our results because there is no appreciable decline in root respiration rates within 6 h of sample collection (G.P. Zogg, unpublished data) and no difference in respiration rates between intact and severed roots (Walters et al. 1993). Furthermore, our values (2.4–5.1 nmol CO_2 g^{-1} s^{-1} at about 13 °C) are comparable to rates measured by Fahey and Hughes (1994) for root mats from mature forests dominated by sugar maple (5.2–8.0 nmol CO_2 g^{-1} s^{-1} at about 13 °C).

Over the growing season, root respiration rates within a given stand paralleled shifts in soil temperature and it is likely that soil temperature is the most important factor controlling temporal patterns within stands. Seasonal changes in root respiration rates within stands were also weakly correlated

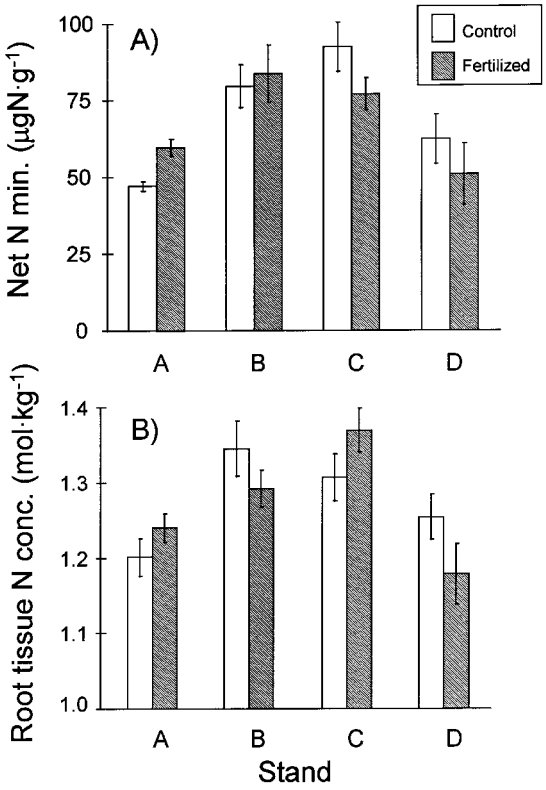

Figure 3. Total net N mineralized (A) and mean root tissue N concentration (B) among the stands for the period May 18 to November 11, 1994. Error bars indicate one SE of the mean.

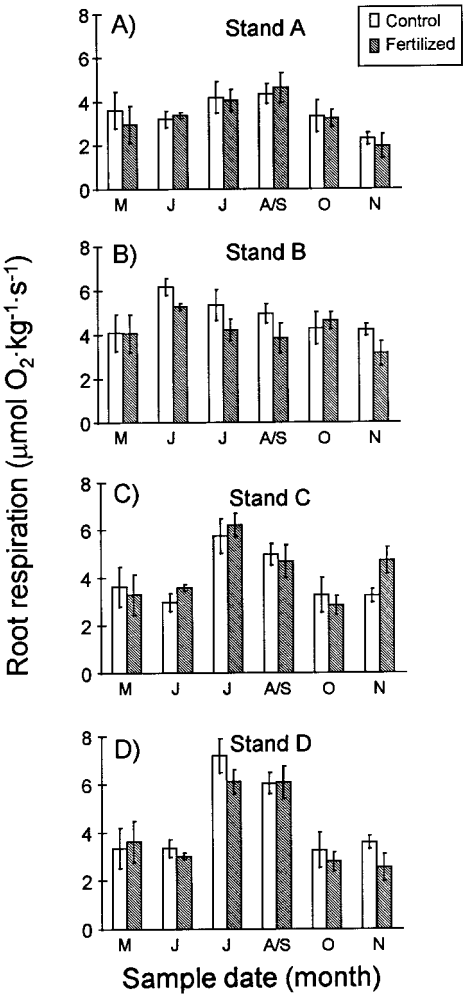

Figure 4. Seasonal patterns of root respiration within the stands (A–D). Error bars indicate one SE of the mean. Fisher's protected least significant difference for all pairwise comparisons is 0.67 μmol O_2 kg^{-1} s^{-1}.

with net N mineralization rates. However, the temperature-dependence of mineralization is widely recognized (Stanford et al. 1973, MacDonald et al. 1995) and these two variables were significantly correlated in our study, providing additional evidence that temperature was the most important factor influencing temporal variation in root respiration rates within a given stand. Root tissue N concentration had no significant influence over seasonal variation in respiration rates within stands. Although there is some evidence that tissue N concentration influences maintenance respiration rates of roots (Ryan et al. 1996), the relationship might not hold for total respiratory flux, as measured in this study, because of the differential response of the maintenance and construction components of respiration (Ryan 1991). We suggest that net N mineralization and root tissue N concentration had little influence on seasonal patterns of fine-root respiration in our study because they varied little over the growing season compared with the changes in soil temperature. Furthermore, the small variation in root tissue N concentration had little effect on root respiration rates within stands even when temperature effects were factored out by respiring roots at a uniform temperature (18 °C) on several sample dates (G.P. Zogg, unpublished data).

Nitrogen availability was, however, an important factor influencing root respiration rates among stands. We predicted that fine-root respiration rates on any given sample date would increase with increasing N deposition and soil temperature from the most northern to the most southern stand. Although root respiration rates at field temperatures were generally lowest in the most northern stand (A), rates in stands B and C were typically equivalent to or greater than rates in the most southern stand, D (Figure 4). Moreover, respiration rates at a given soil temperature were significantly higher in stands B and C

Table 2. Analysis of variance of the effects of sample date, stand location, and fertilization treatment on root respiration.

Source	df	MS	*F*-ratio	*P*
Date	5	18.57	15.98	0.01
Stand	3	7.83	6.73	0.01
Treatment	1	2.11	1.81	0.18
Date × Stand	15	4.01	3.45	0.01
Date × Treatment	5	0.10	0.08	0.99
Stand × Treatment	3	1.38	1.18	0.32
Date × Stand × Treatment	15	0.66	0.57	0.89

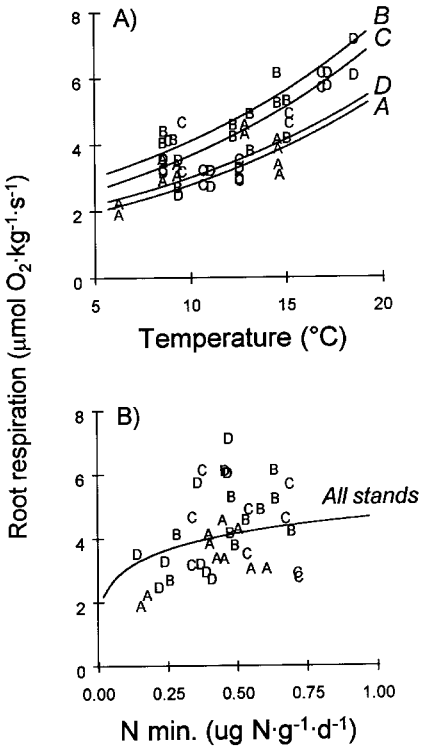

Figure 5. Root respiration within and among stands in relation to temperature (A) and net N mineralization (B). Letters in (A) and (B) refer to the stands. Equations for the temperature (T) response curves for root respiration (R) for each individual stand (pooled slopes) are: Stand A, $\ln(R) = 0.503 + 0.067T$; Stand B, $\ln(R) = 0.722 + 0.067T$; Stand C, $\ln(R) = 0.637 + 0.067T$; Stand D, $\ln(R) = 0.557 + 0.067T$. The relationship between respiration (R) and net N mineralization (N) for all stands combined is: $\ln(R) = 1.659 + 0.285 \ln(N)$.

than in stands A and D (Figure 5). We conclude, therefore, that differences in fine-root respiration rates among stands resulted from inherent differences in soil N availability among the stands rather than the underlying gradient of atmospheric N deposition or temperature. Nitrogen mineralization, root tissue N concentrations and root respiration rates were relatively high in stands B and C which occupy the middle portion of the gradient. It is likely that spatial variability in N mineralization (along the gradient) led to the differences in tissue N concentrations among roots from the four stands (Figure 3) and the resultant patterns of respiration. For example, tissue N concentration was a significant predictor of fine-root respiration when data from all four stands were included in a single multiple-regression model, suggesting that N concentration influences patterns among stands. Although temperature may be the most important factor controlling seasonal patterns of respiration within individual stands, relatively large differences among stands in N availability control spatial patterns of fine-root respiration across a broad geographic scale.

We postulated that the form of N used by plants will also influence respiration, as a result of the differential costs associated with NO_3^- versus NH_4^+ assimilation. However, we found that root respiration rates did not change in response to the NO_3^- additions. This result is consistent with our finding that fertilization did not influence tissue N concentration or nitrate reductase activity (Rothstein et al. 1996). The kinetics of NO_3^- uptake indicate that fine roots of sugar maple in both the control and fertilized plots had a low capacity to take up NO_3^- from soil solution (Rothstein et al. 1996). Although it is generally assumed that plants are an important sink for the atmospheric deposition of NO_3^- (Aber et al. 1989, Aber 1991), it appears that NO_3^- is of less importance than NH_4^+ in the N metabolism of these forests (Rothstein et al. 1996). However, the added NO_3^- may cycle through microbial biomass and ultimately re-enter soil solution as NH_4^+, thereby influencing respiratory rates over the long term by increasing total N availability (Aber et al. 1991).

In summary, we found that soil temperature and N availability are important regulators of fine-root respiration in sugar-maple-dominated forests spanning a broad geographic region. Soil temperature appeared to control temporal patterns of root respiration within stands, whereas net N mineralization rates and associated root tissue N concentrations had a stronger influence over spatial patterns of root respiration among stands. Because root respiration can consume a large proportion of the C assimilated by forest trees, these results have important implications for understanding forest C budgets and the response of forest ecosystems to environmental change. For example, it has been suggested that global warming has the potential to decrease net C uptake by plants, as a result of the different responses of photosynthesis and respiration of aboveground tissues to elevated temperatures (Woodwell 1987, McGuire et al. 1992). Greater respiratory costs for roots, associated with soil warming, could further decrease whole-plant net C gain. If root respiration rates also increase with increasing N availability, either because of the long-term effects of atmospheric N deposition or because of accelerated mineralization at higher temperatures, the C balance of forest trees may be further negatively affected. The net effect of an increase in belowground respiratory costs (per unit tissue) on whole-plant or ecosystem C balance can only be determined by further examining other factors that are sensitive to environmental change, such as the standing crop biomass of fine roots and the rates of aboveground C fixation. However, from our study, we conclude that soil temperature and N availability are important parameters that influence the respiration of fine roots and should be considered in forest C budget models describing the belowground response of plants to changing environmental conditions.

Acknowledgments

We thank the USDA Forest Service and the University of Michigan Biological Station for providing access to laboratory facilities. D.E. Rothstein, D. MacDonald, U. Govindarajulu, E. Stallman, A. Bean and W. Williams provided assistance in the field and laboratory. M.C. Fisk and D.L. Randlett provided helpful comments on an earlier draft of this paper. This research was funded by the U.S. National Science Foundation and the USDA Forest Service Northern Global Change Program.

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