

Temperature Effects on Kinetics of Microbial Respiration and Net Nitrogen and Sulfur Mineralization

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ABSTRACT

Global climate change may impact the cycling of C, N, and S in forest ecosystems because increased soil temperatures could alter rates of microbially mediated processes. We studied the effects of temperature on microbial respiration and net N and S mineralization in surface soils from four northern hardwood forests in the Great Lakes region. Soil samples were incubated in the laboratory at five temperatures (5, 10, 15, 20, and 25°C) for 32 wk. Headspace gas was analyzed for CO₂-C at 2-wk intervals, and soils were extracted to determine inorganic N and S. Cumulative respired C and mineralized N and S increased with temperature at all sites and were strongly related ($r^2 = 0.67$ to 0.90 , significant at $P = 0.001$) to an interaction between temperature and soil organic C. Production of respired C and mineralized N was closely fit by first-order kinetic models ($r^2 \geq 0.94$, $P = 0.001$), whereas mineralized S was best described by zero-order kinetics. Contrary to common assumptions, rate constants estimated from the first-order models were not consistently related to temperature, but apparent pool sizes of C and N were highly temperature dependent. Temperature effects on microbial respiration could not be accurately predicted using temperature-adjusted rate constants combined with a constant pool size of labile C. Results suggest that rates of microbial respiration and the mineralization of N and S may be related to a temperature-dependent constraint on microbial access to substrate pools. Simulation models should rely on a thorough understanding of the biological basis underlying microbially mediated C, N, and S transformations in soil.

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GLOBAL CLIMATIC CHANGE could have major impacts on C, N, and S cycling in forest ecosystems by increasing soil temperature (Jenkinson et al., 1991; Raich and Schlesinger, 1992). Because soil temperature exerts strong control over microbial activity (Nadelhoffer et al., 1991; Ellert and Bettany, 1992; Tate et al., 1993), accurate prediction of climatic effects on C, N, and S cycles depends on a clear understanding of the effects of temperature on the microbially mediated release of these constituents from soil organic matter. Although a few studies have examined the effects of temperature on in situ microbial respiration and N and S mineralization (Schlentner and Van Cleve, 1985; Foster, 1989), most studies have utilized laboratory incubations to examine the influence of temperature on these processes (Cassman and Munns, 1980; Addiscott, 1983; Marion and Black, 1987; Howard and Howard, 1993).

Kinetics of microbial respiration and net mineralization of N and S commonly have been described using a first-order rate equation [$y = a(1 - e^{-kt})$; Stanford and Smith, 1972; Paustian and Bonde, 1987; Ellert and Bettany, 1988; Zak et al., 1993]. The parameter a represents the pool size of labile substrate, and k is the rate constant for a particular process (Deans et al., 1986). Many studies have assumed that pool sizes are unaffected by incubation temperature and that rate constants predictably increase with rising temperature (Stanford et al., 1973; Campbell et al., 1981, 1984). Based on these

Abbreviations: HSD, honestly significant difference; Q_{10} = temperature coefficient; USGS, United States Geological Survey; resp, C respiration; Nmin, net N mineralization; Smin, net S mineralization. *, **, ***, Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

assumptions, the pool size is typically determined at high temperatures (35–40°C), and the rate constant is adjusted to other temperatures using Q_{10} or a similar factor (Marion et al., 1981; Parton et al., 1987; Paustian and Bonde, 1987; Cabrera and Kissel, 1988; Zak et al., 1993). Although this reasoning is intuitive, we are unaware of any study that has explicitly tested the assumptions of constant pool size and temperature-dependent rate constants in concert. Moreover, questions about the appropriate use of rate constants determined under different incubation conditions (Clark and Gilmour, 1983) and suggestions that temperature and pool size are related (Marion and Black, 1987; Ellert and Bettany, 1988, 1992) indicate that examination of the assumptions underlying the first-order kinetic model is warranted.

We investigated the effects of temperature on microbial respiration and on net mineralization of N and S in surface soils from northern hardwood forests in the Great Lakes region. The study sites span a geographic region where forests are expected to change dramatically during the next century as a direct result of global climate change (Pastor and Post, 1988). Objectives of our study were to: (i) determine if the temperature response and kinetics of microbial respiration and mineralization of N and S differ among sites, and (ii) examine the relationships among temperature, kinetic rate constants, and labile C, N, and S pools as estimated from the first-order kinetic model.

METHODS

We studied four forested sites that are distributed along a climatic gradient in the Great Lakes region (Fig. 1). Mean mid-March to mid-November soil temperatures increase from 10°C at Site A to 13°C at Site D; mean daily soil temperatures range from <5°C in early spring and late fall to >20°C in midsummer (N.W. MacDonald, 1994, unpublished data). These sites also are located along an atmospheric pollutant

deposition gradient, with mean annual wet + dry SO_4^{2-} -S deposition increasing from 5.0 kg ha⁻¹ at Site A to 9.7 kg ha⁻¹ at Site D (MacDonald et al., 1992; Fig. 1). All sites have overstories dominated by sugar maple (*Acer saccharum* Marshall) and soils classified as sandy, mixed, frigid Typic and Alfic Haplorthods. Although other factors also may affect soil properties and organic matter dynamics among sites, differences in climate and pollutant deposition are the major uncontrolled environmental factors.

In September 1992, we sampled the surface 10 cm of soil including Oa, A, and upper E horizons with 5.5-cm i.d. steel core samplers. We sampled a constant soil depth because genetic horizon development varied to some extent among sites (MacDonald et al., 1991; Randlett et al., 1992). We sampled three plots per site by taking eight randomly located cores per plot. Cores were taken within a 1-m radius of the random point to avoid downed logs, large roots, rocks, or disturbed areas. Cores were composited by plot, passed through a 2-mm sieve, and stored field moist at 5°C until the start of the experiment. Analyses to characterize major soil properties on a plot composite basis included texture (hydrometer), pH (1:1 soil/H₂O), and organic C (H₂SO₄-K₂Cr₂O₇ oxidation). Analytical methods followed were those documented by Page et al. (1982) and Klute (1986). Initial microbial biomass C and N were determined using the chloroform fumigation-incubation procedure (Jenkinson and Powlson, 1976; Voroney and Paul, 1984).

Microbial respiration and net mineralization of N and S were determined using the modified-microlysimeter technique of Zak et al. (1993). Thirty-gram soil samples were sealed in plastic filtration units (Falcon Model 7102, Becton Dickinson and Co., Cockeysville, MD), and the units were tested for leaks (Zak et al., 1993). Prior to the beginning of incubations, septa were removed and samples were extracted with 50 mL of 0.01 M CaCl₂ followed by 50 mL of a nutrient solution [0.002 M CaCl₂, 0.002 M MgCl₂, 0.005 M KCl, 0.005 M Ca(H₂PO₄)₂] to determine initial SO_4^{2-} , NO_3^- , and NH_4^+ concentrations. Leaching with 0.01 M CaCl₂ followed by nutrient solution closely follows the original methodology of Stanford and Smith (1972). The samples were brought to approximate field capacity (-0.05 MPa) using a hand-operated vacuum pump. Filtration units were flushed with five headspace volumes of CO₂-free air and then resealed with rubber septa.

Three samples from each site (one per plot composite) were independently incubated at 5, 10, 15, 20, and 25°C for 32 wk. Headspace gas from each filtration unit was analyzed for CO₂ at Weeks 1 and 2, and 2-wk intervals through Week 32. After each gas analysis, filtration units were flushed with CO₂-free air. Net increments of mineralized N and S were determined at Weeks 1, 2, 4, 8, 16, and 32 by extracting samples as described above. Gas samples (0.6 mL) were analyzed for CO₂ by gas chromatography (Zak et al., 1993). Soil extracts were analyzed for NH_4^+ by automated colorimetry and for NO_3^- and SO_4^{2-} by ion chromatography.

Product accumulation curves for microbial respiration were generated for each filtration unit and the data were fit to a first-order kinetic model [$y = a_{\text{resp}}(1 - e^{-k_{\text{resp}}t})$] using nonlinear least-squares regression (Wilkinson, 1989). Model parameters, where y is the cumulative amount of C respired at time t (weeks), provided estimates of the labile C pool (a_{resp} , milligrams C per kilogram) and the rate constant (k_{resp} , per week). Net N mineralization product accumulation curves were fit to a first-order model that included a constant [$y = c_{\text{Nmin}} + a_{\text{Nmin}}(1 - e^{-k_{\text{Nmin}}t})$] to account for initial amounts of inorganic N extracted from the soils. Product accumulation curves for net S mineralization were generally zero order; rates of S mineralization were compared using slopes (k_{Smin}) estimated by simple linear regression. For purposes of comparison with

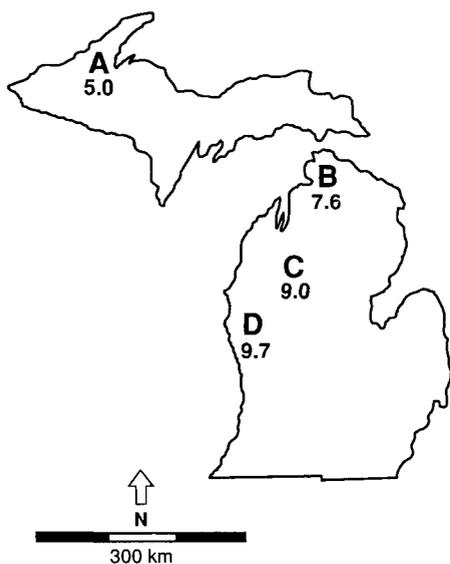


Fig. 1. Locations of northern hardwood forest research sites in the Great Lakes region. Numbers represent estimated mean annual wet + dry atmospheric SO_4^{2-} -S deposition in kilograms per hectare at the four study sites in the state of Michigan.

observed data, respired C rate constants (k_{resp}) determined at 25°C were adjusted to lower temperatures using the equation $k_2 = k_1 Q_{10}^{(25 - T_1)/10}$. Independent values of Q_{10} for each plot were estimated from Arrhenius plots of cumulative respired C data (Spain, 1982).

One-way analyses of variance for initial soil properties (texture, pH, organic C, and microbial C and N) were performed on the basis of plot composite data. Analyses of variance for all other variables were performed using a two-way analysis of variance with site and incubation temperature as factors. Analyses of variance were performed on untransformed data and mean separation was accomplished using Tukey's HSD test. Regression analyses relating observed cumulative respired C and net mineralized N and S to soil and environmental factors employed individual filtration unit response data ($n = 60$) as well as data determined at the site ($n = 4$) or plot ($n = 12$) level.

Analytical accuracy for CO₂-C analyses was assessed by comparing a certified CO₂ standard (2.01 ± 0.04% CO₂ in He, Scott Specialty Gases, Troy, MI) to gas standards prepared in the laboratory. Recovery percentage of the certified standard averaged 104%. Standard reference water samples supplied by the USGS also were periodically analyzed in the laboratory. Analytical accuracy determined by analysis of USGS samples in 1992 and 1993 was typically within ±10% of reference values for NH₄⁺ and NO₃⁻, ±5% for SO₄²⁻, and ±1% for pH. Quality control measures included 10% analytical replication, 13% replication of filtration units, and inclusion of filtration unit blanks at all incubation temperatures. Repeated-measurement errors for analytical replicates were <3% for all analyses except silt (6.3%), clay (14.1%), and organic C (13.6%). Repeated-measurement errors for replicate filtration units were 10.2% for cumulative microbial respiration, 4.2% for cumulative net N mineralization, and 34.1% for cumulative net S mineralization.

RESULTS AND DISCUSSION

Differences in soil pH among sites were relatively minor in terms of expected effects on microbial activity (Table 1). Similarly, differences in silt content were minor with respect to soil textural classification (sandy loam at Site A, loamy sand at other sites). Surface soil organic C significantly increased from Site A to Site D

Table 1. Characteristics of surface soils from four northern hardwood forests in the Great Lakes region.

| Property | Site A | Site B | Site C | Site D | P† |
|--|------------------|-----------------|----------------|----------------|-------|
| pH | 4.4ab‡ (0.1)§ | 4.7a (0.2) | 4.3b (0.1) | 4.3b (0.1) | 0.02 |
| Silt, % | 29.1a (11.9) | 11.0b (1.1) | 11.4b (0.6) | 9.6b (0.5) | 0.01 |
| Clay, % | 5.4 (1.5) | 3.7 (0.2) | 3.6 (0.3) | 3.8 (0.3) | 0.06 |
| Organic C, % | 1.1b (0.2) | 1.7a (0.3) | 1.9a (0.1) | 2.2a (0.2) | <0.01 |
| Microbial C, mg kg ⁻¹ | 213 (51) | 317 (34) | 415 (113) | 328 (127) | 0.13 |
| Microbial N, mg kg ⁻¹ | 62b (10) | 95ab (27) | 133a (9) | 92ab (12) | <0.01 |
| Extractable inorganic N, mg kg ⁻¹ | 8.3c (3.2) | 10.1bc (4.4) | 20.8a (4.5) | 13.2b (0.4) | <0.01 |
| Extractable inorganic S, mg kg ⁻¹ | 1.3c (0.2) | 2.2b (0.3) | 3.4a (0.4) | 3.4a (1.1) | <0.01 |

† Level of significance of analysis of variance.

‡ Means without common letters differ significantly at $P < 0.05$; lowercase letters compare individual soil property means among sites.

§ Standard deviations in parentheses.

largely as a result of increasing thickness of the A horizon from north to south. Contribution of the Oa to soil organic C was relatively constant across sites, as the total weight of organic horizons did not greatly differ among sites (MacDonald et al., 1991). Microbial biomass C and N tended to increase with soil organic C, but microbial N was greatest at Site C. Initial extractable inorganic N and S concentrations displayed significant site effects only (Table 2). Extractable N (NO₃⁻-N + NH₄⁺-N) varied among sites in a pattern similar to that of microbial N (Table 1). Extractable SO₄²⁻-S increased from Site A to Site D, corresponding to increases in organic C and atmospheric S deposition (Table 1).

Cumulative Microbial Respiration and Nitrogen and Sulfur Mineralization

Two-way analyses of variance revealed significant site, temperature, and site × temperature effects on cumulative (32 wk) microbial respiration, net N mineralization, and net S mineralization (Table 2). Temperature effects on cumulative respiration and mineralization were most pronounced in soils from the two most southerly sites (C and D), and differences among sites increased with incubation temperature (Fig. 2a, b, c). The magnitude of the microbial respiration response to temperature increased progressively from Site A to Site D as soil organic C increased (Fig. 2a; Table 1). This pattern was statistically explained using an interaction term (soil organic C × incubation temperature) as a single predictor variable ($r^2 = 0.90$ ***).

The overall pattern of cumulative net N mineralization (Fig. 2b) was not as strongly tied to increasing soil organic C. Greater net N mineralization at Site C was related to greater overall N availability at this site, as evidenced by higher N concentrations in organic layers, greater total N content in A+E horizons (MacDonald et al., 1991), and higher N concentrations in litter (Pregitzer et al., 1992). Similar relationships among mineralizable N, soil organic C, and soil total N were reported

Table 2. Analysis of variance results for effects of site (S) and incubation temperature (T) on kinetics of microbial respiration (resp) and N and S mineralization (Nmin and Smin) in northern hardwood forest surface soils.

| Variable† | Significance of F‡ | | | MSE (40)§ |
|-------------------|--------------------|----------------|------------|-----------|
| | Site(3) | Temperature(4) | S × T (12) | |
| Cumulative C | *** | *** | *** | 16254 |
| a_{resp} | *** | *** | *** | 43812 |
| k_{resp} | *** | NS | NS | 0.0001 |
| Cumulative N | *** | *** | * | 199 |
| a_{Nmin} | *** | *** | * | 2077 |
| K_{Nmin} | * | *** | * | 0.0002 |
| c_{Nmin} | *** | NS | NS | 16.3 |
| Extractable N | *** | NS | NS | 12.7 |
| Cumulative S | *** | *** | *** | 2.63 |
| k_{Smin} | *** | *** | *** | 0.0019 |
| c_{Smin} | *** | NS | NS | 0.536 |
| Extractable S | *** | NS | NS | 0.377 |

*, ***, Significant at $P < 0.05$ and 0.001, respectively; NS = not significant at $P \geq 0.05$.

† a = pool size of labile substrate; k = rate constant; c = constant.

‡ Source of variation: site, incubation temperature, and site × temperature interaction with degrees of freedom in parentheses.

§ Mean square error (MSE), with degrees of freedom in parentheses.

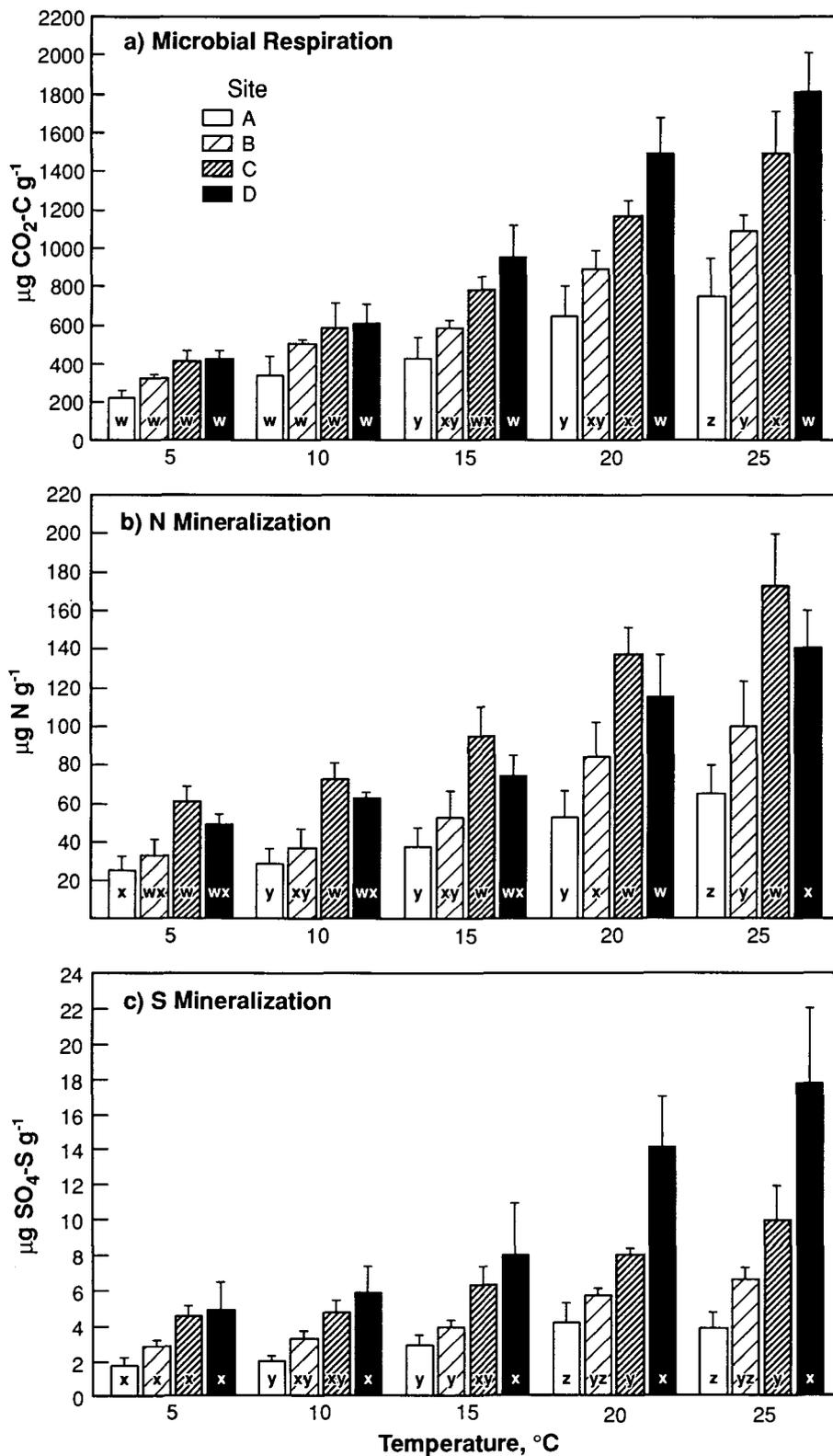


Fig. 2. Temperature effects on cumulative microbial respiration, net N mineralization, and net S mineralization in surface soils from four northern hardwood forests. Bars without common letters differ significantly at $P < 0.05$; w, x, y, z compare site means within a single incubation temperature. Error bars represent one standard deviation.

by Campbell et al. (1981). In our study, cumulative net N mineralization was statistically related to the organic C × temperature interaction term ($r^2 = 0.73^{***}$), with additional variability explained by microbial biomass N ($R^2 = 0.85^{***}$).

The pronounced site × temperature interaction for cumulative net S mineralization (Fig. 2c) also was consistent with an increasing temperature response with increasing soil organic C. This interaction was statistically related to the organic C × temperature interaction term ($r^2 = 0.67^{***}$), with additional variability explained by atmospheric S deposition rate ($R^2 = 0.74^{***}$). Similarly, net S mineralization was shown to be affected by previous fertilizer S inputs (Sakadevan et al., 1993), lending support to the contention that past history of atmospheric S deposition is likely to affect the magnitude of S mineralization and its response to increasing temperature.

In contrast to findings in arctic soils at 3 and 9°C (Nadelhoffer et al., 1991), we found that both C and N mineralization responded to an increase in temperature from 5 to 10°C. Increases in microbial respiration and net N mineralization as a result of a 5°C temperature increase often were equal to or greater than differences among sites at either temperature (Fig. 2a and 2b). Foster (1989) also reported that net N mineralization in the forest floor of a northern hardwood forest was particularly sensitive to temporal changes in average daily temperature.

The extent to which trends in surface soil organic C concentrations from Site A to Site D are generalizable to similar forest soils across this region is uncertain. Our conclusions are constrained by the fact that we sampled only the upper 10 cm of soil at four sites selected to be as ecologically similar as possible. Although previous regional studies found no strong geographic trends in organic C content in surface soils across the Upper Great Lake states (Franzmeier et al., 1985; Grigal and Ohmann, 1992), results of a more recent study (Kern, 1994) indicate that soil organic C contents to a depth of 1 m increase from south to north across the Upper Great Lakes region. Greater microbial response to temperature in soils higher in organic C suggests that regional variability

Table 3. Kinetic parameter estimates for microbial respiration (resp) in surface soils of four northern hardwood forests (k = rate constant; a = pool size of labile substrate).

| Temperature | Site A | Site B | Site C | Site D | Temperature mean |
|-------------|--|--------|---------|---------|------------------|
| °C | $k_{\text{resp}}, \text{wk}^{-1}$ | | | | |
| 5 | 0.056 | 0.061 | 0.059 | 0.053 | 0.057 |
| 10 | 0.064 | 0.061 | 0.061 | 0.053 | 0.060 |
| 15 | 0.061 | 0.066 | 0.056 | 0.050 | 0.059 |
| 20 | 0.067 | 0.074 | 0.068 | 0.048 | 0.064 |
| 25 | 0.079 | 0.067 | 0.058 | 0.041 | 0.061 |
| Site mean | 0.066a† | 0.066a | 0.061a | 0.049b | |
| | $a_{\text{resp}}, \text{mg C kg}^{-1}$ | | | | |
| 5 | 266.1 | 375.9 | 485.6 | 520.4 | 412.0z |
| 10 | 386.2 | 567.8 | 673.4 | 734.0 | 590.3yz |
| 15 | 490.5 | 646.8 | 910.1 | 1281.4 | 832.2y |
| 20 | 703.7 | 960.4 | 1278.7 | 1905.3 | 1212.0x |
| 25 | 778.5 | 1190.5 | 1766.1 | 2499.2 | 1558.6w |
| Site mean | 525.0d | 748.3c | 1022.8b | 1388.1a | |

† Means without common letters differ significantly at $P < 0.05$; w, x, y, z, compare temperature means; a, b, c, d compare site means.

Table 4. Kinetic parameter estimates for net N mineralization (N_{min}) in surface soils of four northern hardwood forests (k = rate constant; a = pool size of labile substrate; c = constant).

| Temperature | Site A | Site B | Site C | Site D | Temperature mean |
|-------------|---|---------|---------|---------|------------------|
| °C | $k_{N_{\text{min}}}, \text{wk}^{-1}$ | | | | |
| 5 | 0.056 | 0.054 | 0.064 | 0.043 | 0.054x† |
| 10 | 0.026 | 0.025 | 0.038 | 0.032 | 0.030y |
| 15 | 0.045 | 0.030 | 0.037 | 0.044 | 0.039xy |
| 20 | 0.057 | 0.041 | 0.039 | 0.036 | 0.043xy |
| 25 | 0.073 | 0.053 | 0.030 | 0.033 | 0.047x |
| Site mean | 0.051a | 0.040ab | 0.042ab | 0.038b | |
| | $a_{N_{\text{min}}}, \text{mg N kg}^{-1}$ | | | | |
| 5 | 20.1 | 26.8 | 42.9 | 45.2 | 33.8z |
| 10 | 38.9 | 45.5 | 70.8 | 74.7 | 57.5z |
| 15 | 37.0 | 73.1 | 100.7 | 86.0 | 74.2yz |
| 20 | 52.0 | 103.2 | 156.7 | 186.2 | 124.5xy |
| 25 | 61.0 | 123.9 | 289.3 | 196.3 | 167.6x |
| Site mean | 41.8c | 74.5bc | 132.1a | 117.7ab | |
| | $c_{N_{\text{min}}}, \text{mg N kg}^{-1}\ddagger$ | | | | |
| Site mean | 9.8c | 11.9c | 25.3a | 17.0b | |

† Means without common letters differ significantly at $P < 0.05$; a, b, c compare site means; x, y, z compare temperature means.

‡ Temperature and site × temperature effects not significant for $c_{N_{\text{min}}}$.

ity in soil organic C must be accounted for when attempting to predict the effects of soil warming on microbial respiration and S and N mineralization.

Site and Temperature Effects on Kinetic Parameters

All pool size (a) and rate (k) parameters, except for k_{resp} , were significantly related to site, temperature, and site × temperature interaction terms in the analysis of variance (Table 2). First-order microbial respiration and net N mineralization rate constants (Tables 3 and 4) decreased from Site A to Site D, being inversely proportional to initial soil organic C concentrations. Differences among sites in estimated C and N pool sizes (Tables 3 and 4) were related to underlying trends in soil organic C and N availability, as discussed above. Zero-order net S mineralization rates ($k_{S_{\text{min}}}$, Table 5) increased from Site A to Site D, corresponding to increasing soil organic C and extractable SO_4^{2-} -S concentrations. Labile S pool sizes could not be estimated because net S mineralization during the 32-wk experimental period did not conform to first-order kinetics.

Table 5. Zero-order rate and intercept estimates for net S mineralization (S_{min}) in surface soils of four northern hardwood forests (k = rate constant; c = constant).

| Temperature | Site A | Site B | Site C | Site D | Temperature mean |
|-------------|--|---------|--------|--------|------------------|
| °C | $k_{S_{\text{min}}}, \text{mg S kg}^{-1} \text{wk}^{-1}$ | | | | |
| 5 | 0.013 | 0.018 | 0.024 | 0.034 | 0.022z† |
| 10 | 0.018 | 0.028 | 0.032 | 0.062 | 0.035yz |
| 15 | 0.048 | 0.055 | 0.088 | 0.133 | 0.081y |
| 20 | 0.088 | 0.112 | 0.141 | 0.324 | 0.166x |
| 25 | 0.077 | 0.138 | 0.199 | 0.440 | 0.214x |
| Site mean | 0.049c | 0.070bc | 0.097b | 0.198a | |
| | $c_{S_{\text{min}}}, \text{mg S kg}^{-1}\ddagger$ | | | | |
| Site mean | 1.32c | 2.15b | 3.50a | 3.46a | |

† Means without common letters differ significantly at $P < 0.05$; a, b, c compare site means; x, y, z compare temperature means.

‡ Temperature and site × temperature effects not significant for $c_{S_{\text{min}}}$.

Respired CO_2 -C data from all sites and temperatures were closely fit by the first-order kinetic model ($r^2 > 0.98^{***}$). Rate constants (k_{resp}) independently estimated at each site-temperature combination were not significantly related to temperature (Tables 2 and 3). In contrast to the assumption of a constant, temperature-independent respirable C pool, estimates of pool size (a_{resp}) increased with temperature at all sites (Table 3). Respirable C pool size estimates that consistently increase with incubation temperature suggest that pool sizes are not constant, but may be temperature dependent to some degree. As noted by Ellert and Bettany (1992), apparent changes in pool sizes with increasing temperature may be related to shifts in the microbial community, changes in biochemical composition of the fraction mineralized, or changes in transport processes such as diffusion. Larger apparent pool sizes at higher temperatures also might be caused in part by lower microbial efficiency at higher temperatures.

A similar effect was apparent in rate constants (k_{Nmin}) and pool sizes (a_{Nmin}) determined by fitting the first-order kinetic model to net N mineralization data. Data again were closely fit by the model ($r^2 \geq 0.94^{***}$). Rate constants were not predictably related to temperature at any site, but estimated mineralizable N pools were strongly temperature dependent (Table 4). These results are directly contrary to reports of temperature-dependent rate constants from earlier studies (Stanford et al., 1973; Campbell et al., 1981). Time-zero intercept constants (c_{Nmin} , Table 4) estimated by nonlinear regression were unaffected by temperature (Table 2) and were similar to initial extractable soil N concentrations (Table 1).

In contrast to first-order rate constants determined for respired C and net N mineralization, zero-order rates estimated for net S mineralization (k_{Smin} , Table 5) increased with temperature at all sites. Rates were greatest and increased most dramatically at Site D, where organic C concentrations and atmospheric S deposition also were greatest. Time-zero intercept regression constants (c_{Smin} , Table 5) were not affected by temperature (Table 2) and closely approximated initial extractable S concentrations (Table 1). All net S mineralization accumulation curves displayed a brief (1–4 wk) initial lag phase followed by a relatively linear increase in net amounts of S mineralized. In spite of this initial lag, all regressions had $r^2 \geq 0.6^*$ and 53 of 60 had $r^2 > 0.8^{**}$. More rapid net mineralization at sites with surface soils higher in organic C and greater external S inputs suggests that response of S mineralization to temperature is affected by the degree to which S is microbially immobilized. The effect of immobilization on net S mineralization would be accentuated under experimental conditions where available SO_4^{2-} -S was being successively leached from the soil. Lags in net S mineralization (previously reported by Ellert and Bettany [1992]), zero-order kinetics (also reported by Tabatabai and Al-Khafaji [1980] and Foster [1989]), and sensitivity to history of external S inputs (e.g., Sakadevan et al., 1993) support previous observations that S mineralization, C respiration, and N mineralization are not strictly parallel metabolic processes (Kowalenko and Lowe, 1975).

Previous kinetic studies of temperature effects have commonly estimated rate constants by assuming the same pool size at all temperatures (e.g., Stanford et al., 1973; Campbell et al., 1981). This forced the rate constant to be temperature dependent by default, because the pool size was held constant. In our study, when C respiration and N mineralization models were fit assuming a constant pool size equal to that determined at 25°C, the predicted curves converged toward the single pool with time, and the estimated rate constants were temperature dependent as reported in previous studies. However, predicted curves only loosely approximated the observed data. In contrast, curves fit to observed data without assuming a constant pool size did not converge, consistent with temperature-dependent pool sizes. Net N mineralization curves presented by Campbell et al. (1981) also show little tendency to converge, but their reported temperature-dependent rate constants were derived using a single pool size determined at 40°C.

When we assumed a constant pool size (a_{resp} at 25°C) and adjusted the rate constant (k_{resp}) determined at 25°C to lower temperatures using estimated Q_{10} values (range = 1.8 to 2.4, mean = 2.0), predicted respired C accumulation curves deviated from the observed curves at all sites (Fig. 3a–3d). Predicted curves converged toward the assumed constant pool size with time, whereas the observed accumulation curves did not converge in this fashion. This pattern was consistent at all four sites, which differ in soil organic C concentrations, climatic conditions, atmospheric deposition rates, and may differ in composition of microbial communities. We noted a similar divergence between predicted and observed curves for net N mineralization. These results suggest that assumptions of constant pool sizes, temperature-dependent rate constants, and temperature adjustment of rate constants using Q_{10} may not be tenable. Similar conclusions with regard to pool sizes, rate constants, and use of Q_{10} were reached by Ellert and Bettany (1992). Because of the complexity of temperature effects on microbial respiration and net mineralization of N and S, alternate empirical methods of modeling these processes have been proposed elsewhere (e.g., Schlentner and Van Cleve, 1985; Marion and Black, 1987; Bonde and Lindberg, 1988; Ellert and Bettany, 1988). Ellert and Bettany (1992), however, were unable to identify a single best-fitting model that reliably described the time and temperature dependence of net N and S mineralization in a broad range of soils.

CONCLUSIONS

Microbial respiration and the net mineralization of N and S increased with temperature at all sites. Differences in temperature response among sites were primarily related to differences in initial soil organic C concentrations. Additional site-to-site variation in net mineralization of N and S were related to differences among sites in N availability and history of atmospheric S inputs. These results suggest that subtle changes in, and interaction among, climatic factors, soil organic matter pools,

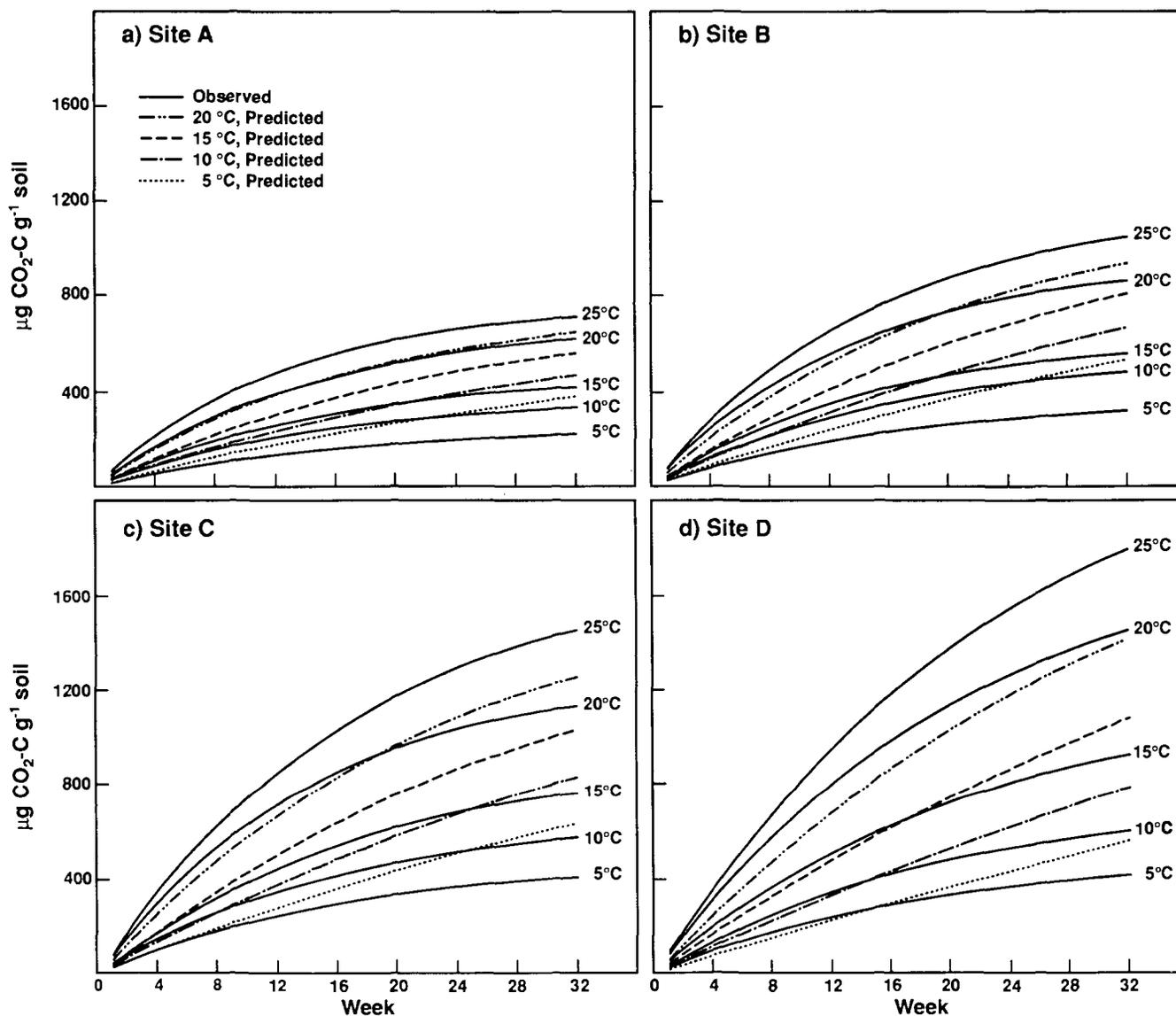


Fig. 3. Comparison of observed $\text{CO}_2\text{-C}$ accumulation curves with accumulation curves predicted assuming constant pool sizes (a_{resp} , 25°C) and temperature-adjusted rate constants (k_{resp}).

and pollutant deposition need to be considered when attempting to predict rates of microbial respiration and N and S mineralization in forest soils of the Great Lakes region.

Microbial respiration and net N mineralization data were closely fit by first-order kinetic models. Rate constants independently estimated for each site and temperature from these models were not consistently related to temperature. In contrast, estimates of labile C and N pools were strongly temperature dependent. Respired C accumulation curves predicted assuming a constant pool size and temperature-adjusted rate constants deviated from the observed data. These results suggest that the commonly accepted assumptions of constant pool sizes and temperature-dependent rate constants may not be tenable. Although alternate methods of modeling these processes have been proposed, the need to fully understand the underlying biology of microbially mediated C,

N, and S transformations in forest soils is of primary importance for the development of mechanistic and broadly applicable predictive models.

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