DIVISION S-7—FOREST & RANGE SOILS

Soil Warming and Carbon Loss from a Lake States Spodosol

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ABSTRACT

Elevated soil temperatures may increase C loss from soils by accelerating microbial respiration and dissolved organic C leaching. We evaluated the effect of elevated soil temperatures on C losses from a forest Spodosol by incubating soil cores from surface (Oa + A + E) and subsurface (Bhs) horizons at two seasonal temperature regimes. One regime simulated the normal course of soil temperatures in northern lower Michigan, and the other simulated soil temperatures representing an amount of warming that might occur under some global warming theory calculations. We measured the amounts of CO_2–C respired and dissolved organic C leached from the soil cores during a 33-wk period. Microbial respiration rates, after adjustment for variation in initial rates, were significantly increased by soil warming and were greater in surface than in subsurface horizons. Warming significantly increased cumulative C respired, with greater losses from surface soils (≥50 mg C g^{-1} C) as compared with subsurface soils (≤25 mg C g^{-1} C). Mean quantities of dissolved organic C leached, ranging from 2.3 to 3.2 mg C g^{-1} C, did not differ significantly by soil horizon or temperature regime. Increased microbial respiration in surface soil horizons was the process most responsive to soil warming in the Spodosol samples we examined. Whether this is a short-term effect that would disappear once pools of labile C are exhausted, or represents a long-term response to soil warming, remains uncertain.

SPODOSOLS, COMMON FOREST SOILS in northern latitudes, have high organic C contents in both surface and subsurface horizons, forming an important sink for C in temperate forests (Vance et al., 1986; Kern, 1994). Some global warming theories suggest that temperatures in Northern regions could warm substantially, raising questions about the stability of organic C in soils at these latitudes (Post et al., 1982; Nadelhoffer et al., 1991; Oechel, 1995) because temperature strongly affects microbial respiration in forest soils (Edwards, 1975; Hendrickson, 1985; Tate et al., 1993). Thus, soil warming has the potential to increase CO_2 fluxes from these soils, although those warming effects could be modified by changes in moisture regimes that might accompany other climatic changes. Under intermediate moisture conditions, though, temperature exerts a dominant influence on microbial respiration (e.g., Edwards, 1975; Schlentner and Van Cleve, 1985).

Concentrations of organic C in soil leachates also have been reported to be affected by temperature (James and Riha, 1987; Duffy and Schreiber, 1990), suggesting that losses of DOC from soils could increase as a result of soil warming. Dissolved organic C leaching from soils may ultimately return to the atmosphere as CO_2 lost from streams, lakes, or oceans (Kling et al., 1991). Depending on the above and below-ground responses of forests to elevated atmospheric CO_2 and warming (Curtis et al., 1994; Oechel et al., 1994; O'Neill, 1994), increased C fluxes from temperate forest soils could create a positive feedback to increasing atmospheric CO_2 concentrations (Jenkinson et al., 1991; Schimel et al., 1994; Kirschbaum, 1995).

Since 1987, we have been studying northern hardwood forests at several sites in the Great Lakes region (e.g., MacDonald et al., 1991; Pregitzer et al., 1992; Burton et al., 1993). Laboratory incubations of soils from these sites demonstrated that microbial respiration was highly responsive to increasing temperature (MacDonald et al., 1995). In addition, Zogg et al. (1997) found that the composition of microbial communities may change with increasing soil temperature in soils from these sites. Field investigations at these sites showed that fluxes of DOC from the forest floor also increased with soil temperatures (Liechty et al., 1995). If mean global air temperatures increase 1.5 to 4.5°C as a result of atmospheric CO_2 doubling (Houghton et al., 1992), it would be accompanied by increased soil temperatures. Assuming no major changes in soil moisture regimes, elevation of soil temperatures by 2 to 3°C during late spring, summer, and early fall should increase fluxes of both CO_2 and DOC from Lake States Spodosols.

Warming effects on the types of C losses from these soils, their relative magnitudes, and the contributions of surface and subsurface horizons to such losses remain largely undetermined. This paper reports our findings on the changes in C losses from a forest Spodosol as a result of increased temperature during a 33-wk laboratory study. Our objective was to determine the amounts of C lost by microbial respiration and DOC leaching, and to compare the contributions of surface and subsurface horizons to these losses.

METHODS

We obtained soil samples for this study from a site near Pellston, MI (45°33′ N, 84°52′ W), one of several northern hardwood sites we have studied previously (Randlett et al., 1992; MacDonald et al., 1995). This site is representative of extensive forest ecosystems in a geographic region that may experience significant warming if the global climate were to change, as some have predicted (Pastor and Post, 1988). The

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Abbreviations: PVC, polyvinyl chloride; Q_{10} = temperature coefficient; DOC, dissolved organic carbon.

overstory is dominated by sugar maple (*Acer saccharum* Marshall) and the soils are classified as sandy, mixed, frigid Typic and Alfic Haplorthods (MacDonald et al., 1991). At a depth of 15 cm, mean weekly soil temperatures range from <5°C in early spring and late fall to >15°C in midsummer (N.W. MacDonald, 1996, unpublished data).

On 21 April 1994, we collected 18 soil cores each from surface (Oa + A + E) and subsurface (Bhs) horizons. Cores were taken at random locations along a 50-m transect in a well-drained upland area within the stand. To collect the upper 10 cm of surface horizons, we first removed superficial organic layers (Oi + Oe), and then drove a pre-weighed, 13.8-cm long, 4.4-cm inside diameter PVC tube into the soil to a depth of 10 cm. The Oa and A horizons were minimally developed, absent in some locations and only 2 to 3 cm thick in others. The E horizon made up most of the weight and volume of surface-horizon cores. We took additional soil samples (composites of four cores each) immediately adjacent to the PVC tube using a standard split-tube soil sampler, sealed them in plastic bags, and placed them into a cooler. We then excavated around the PVC tube, removed the tube with its intact soil core, sealed the core in a plastic bag, and immediately placed the core into a cooler. The upper 10 cm of the subsurface Bhs horizon was sampled in the same way after excavating to the top of this horizon at each location (approximately 18 cm deep). We recorded soil temperature at each sampling location and depth using a portable temperature probe. On the day of sampling, mean surface soil temperatures were 3.0 ± 0.7°C and mean subsurface soil temperatures were 2.2 ± 0.2°C.

We sub-sampled the additional soil samples to determine moisture content, and air-dried the remainder at 25°C before sieving with a 2-mm sieve. We analyzed the air-dried samples for organic C using the Walkley-Black procedure (H_2SO_4–$K_2Cr_2O_7$ oxidation followed by titration with $FeSO_4$). Repeated-measurement error for this procedure calculated from analytical replicates was 8.6%. Two of the 18 soil cores taken from each sampling depth also were air-dried, composited, sieved, and then analyzed for pH (1:1 soil:water) and texture (hydrometer method). Analytical methods followed are documented in Klute (1986) and Page et al. (1982). Both surface and subsurface soils were acidic, coarse-textured, and had organic C concentrations with means around 10 g kg^{-1} (Table 1).

On return to the laboratory, we weighed the intact, field-moist soil cores and then stored them in a cold room at 5°C until the start of the experiment 1 wk later. We calculated oven-dry weight and organic C content of individual cores based on the organic C and moisture content of the samples taken adjacent to each core (Table 1). We covered the bottoms of each core with a Gelman A/E glass-fiber filter (Pall Gelman Sciences, Ann Arbor, MI) and secured it in place with polyethylene mesh fastened to the outside of the PVC tubes. Cores were incubated in glass canning jars with 1-cm diameter rubber septa fitted in their lids. Jars were individually tested with a pressure transducer to ensure that each was air tight (Zak et al., 1993). Jar volumes (975.6 ± 1.2 cm^3) were determined by filling jars with deionized water and calculating volumes based on weight and temperature of the water. Headspace volumes were calculated by subtracting estimates of soil core plus PVC tube volumes (based on weights and densities, 197.7 ± 2.2 cm^{-3}) from total jar volumes.

Table 1. Properties of soil cores taken from surface (Oa + A + E) and subsurface (Bhs) horizons of a northern hardwood forest Spodosol.

Property	Oa + A + E	Bhs
Organic C†, g kg^{-1}	10.2 ± 4.4	10.6 ± 2.8
Core weight, g	191.4 ± 15.8	216.4 ± 11.9
Organic C‡, g/core	1.9 ± 0.7	2.3 ± 0.6
pH§	3.78	4.05
Sand§, %	92.5	94.0
Silt§, %	5.7	2.4
Clay§, %	1.8	3.6

† Mean ± SD, based on analyses of 16 samples from each horizon.
‡ Mean ± SD, based on organic C analyses and intact core weights.
§ Means of replicate samples from a composite sample of two cores per horizon.

Incubation temperatures simulated two seasonal temperature regimes (Fig. 1). One followed the normal course of soil temperature at the study site; the other simulated soil temperatures that might occur at this site if the earth were to warm. Increases in soil temperatures under the warming scenario were based on measured differences between seasonal progressions of soil temperature at forest sites 180 km north and 220 km south of the study site (N.W. MacDonald, 1996, unpublished data). Mean March-to-November soil temperatures were 2.7°C higher at the more southerly site as compared with the more northerly site, approximating one prediction of the rise in global temperatures that would result from a doubling in atmospheric CO_2.

Eight cores from each soil depth were randomly assigned to each seasonal temperature regime, for a total of 32 cores in the experiment. Surface and subsurface cores were randomly assigned to incubation regimes independently, not as pairs based on original sampling location. Four jars containing empty PVC tubes fitted with glass-fiber filters and polyethylene screens served as blanks, with two blank jars assigned to each temperature regime. We measured the amounts of CO_2–C respired and collected leachates from cores at 16 2-wk intervals during a 33-wk period beginning on 27 April 1994. For the first and last sampling intervals, all cores were incubated at 5°C in a cold room. This temperature approximated early spring and late fall soil temperatures under both normal and warming scenarios. During all other sampling intervals, sets of cores were kept in separate incubators set at temperatures corresponding to the assigned seasonal temperature regime (Fig. 1). Chamber effects other than differences in temperature were assumed to be minimal.

At each sampling interval, headspace gas was analyzed for CO_2–C by gas chromatography as described by Zak et al. (1993) and MacDonald et al. (1995). Sample CO_2–C concentrations were adjusted by subtracting mean blank analytical values determined for each sampling interval. We then removed the cores from the incubation jars and leached them with 60

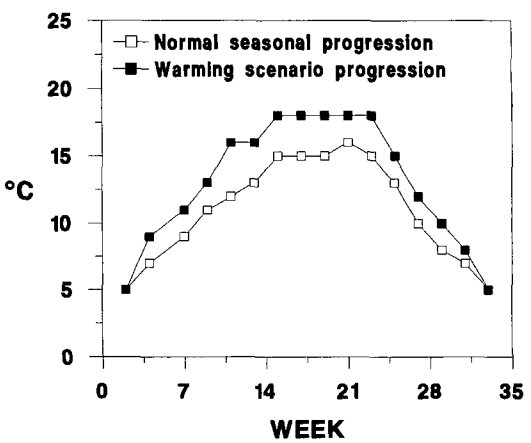

Fig. 1. Seasonal soil temperature regimes followed during the course of the incubation experiment. The normal progression represents current mean seasonal soil temperatures at the study site in northern lower Michigan, and a warmer soil temperature regime.

mL of simulated rain (including empty cores from blank jars). The amount of simulated rain approximated the mean 2-wk precipitation of 37.5 mm that falls at the study site between mid-April and mid-November (N.W. MacDonald, 1996, unpublished data). The ionic constituents of the simulated rain (0.51 mg L^{-1} NH_4^+, 0.04 mg L^{-1} K^+, 0.10 mg L^{-1} Mg^{2+}, 0.41 mg L^{-1} Ca^{2+}, 0.24 mg L^{-1} Na^+, 0.11 mg L^{-1} Cl^-, 1.55 mg L^{-1} SO_4^{2-}, 1.88 mg L^{-1} NO_3^-) also approximated precipitation chemistry at this site, as determined from National Atmospheric Deposition Program data (MacDonald et al., 1992). To collect leachate samples, we placed the cores in Büchner funnels fitted with glass-fiber filters (Gelman A/E) and applied vacuum until no additional leachate was collected (cores at approximate field capacity, −0.05 MPa). We then resealed the cores in the jars, and incubated them for another 2 wk at the desired temperature.

Leachate samples were acidified to pH 3.0 with H_2SO_4 and then stored at 5°C. Total volumes of leachings from each core were composited across four sequential sampling intervals into a preweighed 250-mL glass bottle, giving a total of four composite samples from each core for the entire experiment. After four collection intervals, composite leachate samples were weighed to estimate volume, mixed thoroughly, and a subsample was filtered through a 0.45-μm filter. These subsamples were sparged with N_2 prior to analysis for nonpurgeable organic C using a Shimadzu TOC-5000. Our DOC analyses were duplicated for all samples, with an average percent difference between duplicates of 3%. Sample DOC concentrations also were adjusted by subtracting mean blank analytical values.

Data were statistically analyzed using a two-way analysis of variance with temperature regime and soil horizon as factors and sampling interval (16 2-wk intervals for CO_2–C and four 8-wk intervals for DOC) as a repeated measure. Microbial respiration rates from the initial 2-wk interval, where all cores were incubated in a cold room at 5°C, were used as covariates in analyses of covariance for microbial respiration rate and cumulative respired C data. These initial respiration rates incorporated variability among cores related to abundance of labile C, microbial community composition and biomass, respiration of moribund roots, and soil physical and chemical properties. This variability was in addition to variability in total organic C already accounted for by expressing respiration rates and cumulative respired C on a g^{-1} soil C basis. Similar analyses of covariance were not possible for DOC data because initial leachings were not analyzed separately. Regressions relating microbial respiration rates to incubation temperatures were based on treatment means from each sampling interval (n = 8 intervals for each warming or cooling trend regression). Temperature coefficient (Q_{10}) values were calculated as the ratio between respiration rates (Hendrickson, 1985) predicted for 6 and 16°C using these regression equations.

Table 2. Repeated-measures analysis of variance and covariance results for effects of temperature regime, soil horizon, and sampling interval on CO_2–C respired and dissolved organic C leached from a northern hardwood forest Spodosol.

Source of variation	Microbial respiration rate†	Adjusted microbial respiration rate†	Dissolved organic C‡
	Probability of a greater F		
Temperature Regime (TR)	0.329	0.046	0.309
Soil Horizon (SH)	<0.001	<0.001	0.107
TR × SH	0.850	0.204	0.603
Covariate§	NA	<0.001	NA
MSE_a (df)¶	66 881 (28)	21 714 (27)	1 693 (28)
Sampling Interval (SI)	<0.001	<0.001	<0.001
TR × SI	<0.001	<0.001	0.199
SH × SI	<0.001	<0.001	0.102
TR × SH × SI	0.234	<0.001	0.986
Covariate × SI§	NA	<0.001	NA
MSE_b (df)¶	1 202 (420)	731 (378)	239 (84)

† Base units for microbial respiration rates in μg C g^{-1} C d^{-1}.
‡ Base units for cumulative dissolved organic C in μmol C g^{-1} C (8 wk)$^{-1}$.
§ Covariate = initial 2-wk respiration rate in μg C g^{-1} C d^{-1}, NA = not applicable (covariate not used in specified analysis).
¶ Appropriate mean square errors and (degrees of freedom) from analysis of variance or covariance.

RESULTS AND DISCUSSION

Microbial Respiration

Microbial respiration rates were significantly greater in surface than in subsurface horizons, with greater differences between horizons in the first two thirds of the incubation period (Table 2, Fig. 2a). Unadjusted mean microbial respiration rates tended to be greater in soils incubated at the warmer temperature regime (Fig. 2a), but differences were not significant (Table 2). Using microbial respiration rate for the initial 2-wk incubation period as a covariate, both temperature regime and soil horizon effects were significant (Table 2, Fig. 2b). After adjustment for the covariate, greatest temperature effects on microbial respiration rates were apparent for

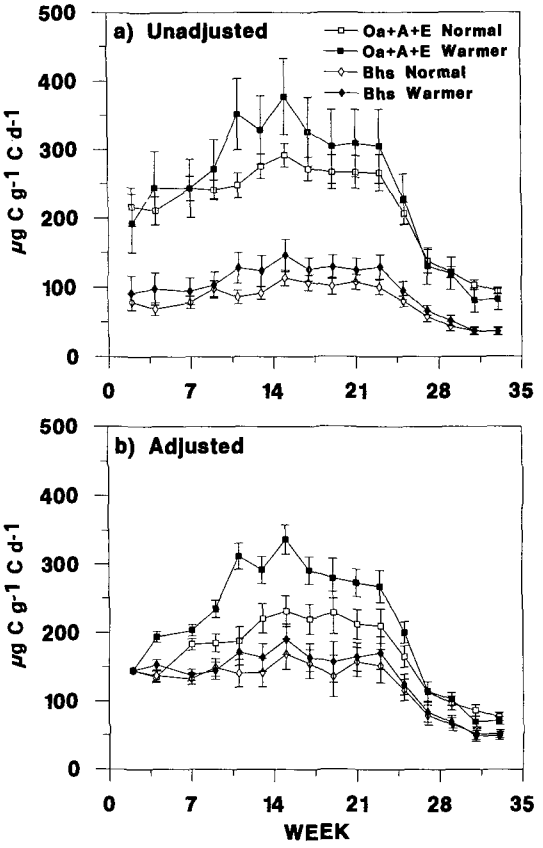

Fig. 2. (a) Unadjusted microbial respiration rates measured during the course of the incubation experiment, and (b) respiration rates adjusted using initial 2-wk respiration rates as a covariate. Incubations followed the current normal seasonal course of soil temperatures, and a warmer soil temperature regime projected by one theory of how much the globe would warm if atmospheric CO_2 were to double. Error bars represent standard errors of means.

surface soil during the warmest incubation periods (Week 10–25), with smaller temperature effects on subsurface soil during Week 10 to 25, and smaller differences between soil horizons from Week 25 on (Fig. 2b). At the end of the incubation period, cumulative C respired from surface horizon cores was 2.6 times greater than that respired from subsurface horizon cores (Table 3, Fig. 3a). While unadjusted cumulative respired C did not significantly differ between temperature regimes (Fig. 3a, Table 3), when microbial respiration rate for the initial 2-wk incubation period was used as a covariate, soil warming effects were significant (Table 3, Fig. 3b). Use of the covariate increased statistical sensitivity to temperature effects by substantially reducing error mean squares (Tables 2 and 3).

The seasonal progression of respiration rates, increasing during the warming phase, reaching a peak midway through the incubation period, and declining during the cooling phase (Fig. 2), closely followed the seasonal progression of CO_2 evolution from in situ forest soils measured at other sites (Edwards, 1975; Fernandez et al., 1993; Toland and Zak, 1994; Yavitt et al., 1995). Elevated microbial respiration rates in response to elevated seasonal soil temperature regimes also were consistent with greater rates of soil respiration from experimentally warmed field plots (Peterjohn et al., 1993; 1994). Laboratory incubation of cores differs from field conditions by causing physical soil disturbance and by severing root and mycorrhizal connections during core collection (Hendrickson and Robinson, 1984). Laboratory measurements on cores also reduce normal variations in soil water content and evaporation rates (Schlentner and Van Cleve, 1985; Kirschbaum, 1995). Our incubation experiment did not simulate either the input of DOC in throughfall (Qualls et al., 1991), or the seasonal pulses of C in the form of fresh leaf and root litter that normally occur in deciduous forest soils (Edwards, 1975; Holmes and Zak, 1994). We measured only the loss of CO_2–C from soil cores. Losses of CH_4 and other nonmethane volatile organic compounds may have occurred from the soils we incubated, but these losses are usually negligible in well-drained forest soils (Hanson and Hoffman, 1994; Yavitt et al., 1995).

Lower respiration rates and lesser cumulative amounts of respired C from subsurface (Bhs) than surface (Oa + A + E) cores were consistent with reports of lower microbial respiration in subsurface horizons of a Cryofluvent (Nadelhoffer et al., 1991) and in a Cryochrept and a Cryorthod rich in Al + Fe humus complexes (Tate, 1992). In undisturbed soils, temperature changes will be most pronounced in forest floor and surface mineral horizons (e.g. Oechel et al., 1995). This factor, together with the refractory nature of organic matter in Bhs horizons (Vance et al., 1986; Vance and David, 1989), suggest that Spodosol surface horizons will be more susceptible to rapidly increased losses of C via increased microbial respiration than underlying B horizons.

Microbial respiration rates declined rapidly after week 23 (Fig. 2a), corresponding to the onset of the cooling phase of the incubation (Fig. 1). This rapid decline in respiration rates appears to be a temperature-dependent response, as respiration rates had declined only gradually during the preceding 10-wk period when soil temperatures were relatively constant (Fig. 1 and 2a). When soils were incubated at a constant temperature for 21 d, Hendrickson and Robinson (1984) reported initial C mineralization rates double those of final rates, and attributed the declining rates to a progressive depletion of the labile C pool. While we did not see this type of obvious depletion response in our

Table 3. Analysis of variance and covariance results for effects of temperature regime and soil horizon on CO_2–C respired and dissolved organic C leached from a northern hardwood forest Spodosol.

Source of variation	Cumulative respired C†	Adjusted cumulative respired C†	Cumulative DOC‡
	Probability of a greater F		
Temperature Regime (TR)	0.343	0.047	0.309
Soil Horizon (SH)	<0.001	<0.001	0.107
TR × SH	0.868	0.207	0.603
Covariate§	NA	<0.001	NA
MSE (df)¶	2.26×10^8 (28)	0.66×10^8 (27)	6770 (28)

† Base units for cumulative respired C in $\mu g\ C\ g^{-1}\ C$.
‡ Base units for cumulative dissolved organic (DOC) in $\mu mol\ C\ g^{-1}\ C$.
§ Covariate = initial 2-wk respiration rate in $\mu g\ C\ g^{-1}\ C\ d^{-1}$, NA = not applicable (covariate not used in specified analysis).
¶ Appropriate mean square errors and (degrees of freedom) from analysis of variance or covariance.

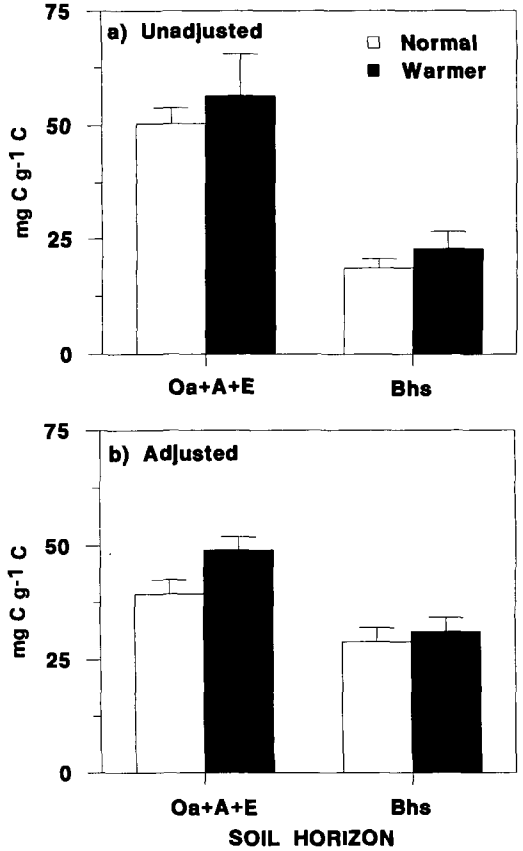

Fig. 3. (a) Unadjusted cumulative CO_2–C respired after 33-wk, and (b) cumulative CO_2–C respired adjusted using initial 2-wk respiration rates as a covariate. Incubations followed two seasonal temperature regimes as described in Fig. 2. Error bars represent standard errors of means.

study, such a depletion of the labile C pool may have accentuated the rapidly declining respiration rates noted toward the end of our experiment, especially as this period corresponds to the time during which an influx of fresh leaf and root litter would normally occur.

The seasonal progression of incubation temperatures had a warming period of rising temperatures during Weeks 1 to 17, and a cooling period of falling temperatures during Weeks 18 to 33 (Fig. 1). During both warming and cooling periods, microbial respiration rates were significantly correlated with incubation temperatures in both surface and subsurface soils and under both seasonal temperature regimes (Table 4). Edwards (1975), Schlentner and Van Cleve (1985), and Peterjohn et al. (1994) have reported similar relationships between CO_2 fluxes from forest soils and soil temperature. In our study, regression constants for the initial 17-wk warming period (respiration rates at 0°C) were consistently greater than regression constants for the final 16-wk cooling period (Table 4). This suggests abundant labile C at the start of the incubation, and less labile C at the end of the incubation. Regression coefficients and Q_{10} values were greater during the final 16-wk cooling period than during the initial 17-wk warming period (Table 4), consistent with microbial respiration rates falling more rapidly in response to cooling than they initially rose in response to warming (Fig. 2).

Previous research has not revealed this type of variability, as effects of temperature on microbial respiration have been determined from separate incubations at constant temperatures (e.g., MacDonald et al., 1995), based on only part of a seasonal soil temperature progression (e.g., Peterjohn et al., 1994), or based on data pooled across seasonal warming and cooling trends (e.g., Edwards, 1975; Toland and Zak, 1994). Values of Q_{10} calculated from constant-temperature incubations are commonly reported to be around 2 (Hendrickson, 1985; Zak et al., 1993), with higher Q_{10} values observed at temperatures below 20°C (Kirschbaum, 1995). Values of Q_{10} calculated from our study ranged from 1.4 to 1.6 during the warming period (Weeks 1–17), and from 2.9 to 3.6 during the cooling period (Weeks 18–33, Table 4).

Table 4. Regression equations showing relationships between microbial respiration rates (MRR) and incubation temperatures (IT) by soil horizon, warming or cooling trend, and seasonal temperature regime.

Horizon	Weeks†	Temperature regime	Regression equations‡	r^2§	Q_{10}¶
Oa+A+E	1–17	Normal	MRR = 203.9 + 0.355 (IT)²	0.88	1.4
Oa+A+E	1–17	Warming	MRR = 187.5 + 0.537 (IT)²	0.91	1.6
Oa+A+E	18–33	Normal	MRR = 65.4 + 0.844 (IT)²	0.98	2.9
Oa+A+E	18–33	Warming	MRR = 38.8 + 0.817 (IT)²	0.98	3.6
Bhs	1–17	Normal	MRR = 66.9 + 0.180 (IT)²	0.80	1.5
Bhs	1–17	Warming	MRR = 82.4 + 0.161 (IT)²	0.87	1.4
Bhs	18–33	Normal	MRR = 23.6 + 0.336 (IT)²	0.99	3.1
Bhs	18–33	Warming	MRR = 21.0 + 0.327 (IT)²	0.99	3.2

† Weeks within incubation experiment. Weeks 1–17 represent a trend of increasing incubation temperatures, Weeks 18–33 represent a trend of decreasing incubation temperatures.
‡ Microbial respiration rates (MRR) in $\mu g\ C\ g^{-1}\ C\ d^{-1}$, incubation temperatures (IT) in °C.
§ Coefficients of determination, all significant at $P < 0.005$.
¶ Temperature coefficients calculated from microbial respiration rates estimated at 6 and 16°C using regression equations.

Higher Q_{10} values during cooling as compared with warming periods suggest different microbial responses to changing temperature during the two time periods, not just a simple temperature effect on respiration rates. Interacting factors, including response to sampling disturbance (Hendrickson and Robinson, 1984), change in microbial community composition (Zogg et al., 1997), microbial metabolism of different substrate pools (MacDonald et al., 1995), and depletion or lack of replenishment of the labile C pool (Kirschbaum, 1995), may be involved.

Dissolved Organic Carbon Losses

Losses of DOC were less sensitive to soil horizon effects than were rates of microbial respiration. Both incremental and cumulative losses of DOC tended to be greater from surface soils than subsurface soils ($P = 0.11$, Tables 2 and 3, Fig. 4 and 5), consistent with a report of lower leaching of DOC from B horizons (Vance and David, 1989) and an observation of declining DOC concentrations with depth in Spodosols (Ross and Bartlett, 1996). While a trend toward increased leaching of DOC from soils incubated at warmer temperatures was noticeable (Fig. 4 and 5), soil temperature effects were not significant (Tables 2 and 3). Inability

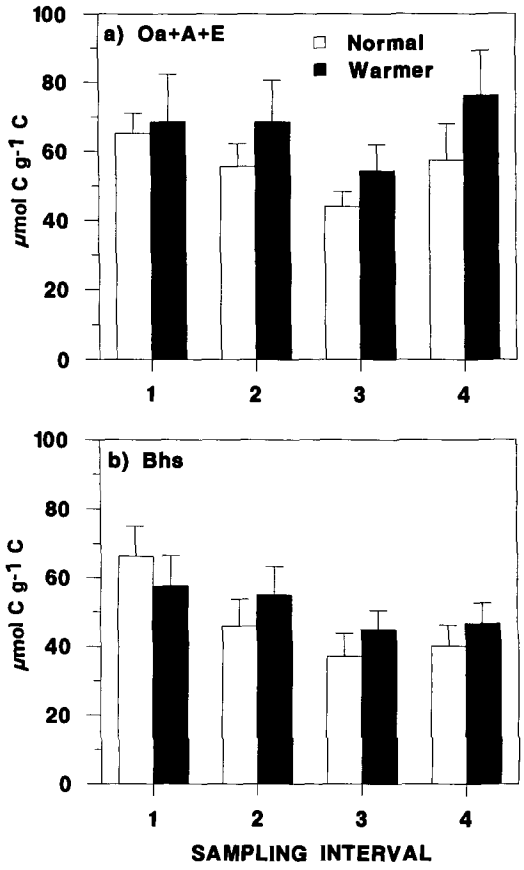

Fig. 4. Dissolved organic C leached from (a) surface and (b) subsurface cores during four sampling intervals (Week 1–9, 9–17, 18–25, 25–33) under two seasonal temperature regimes. Error bars represent standard errors of means.

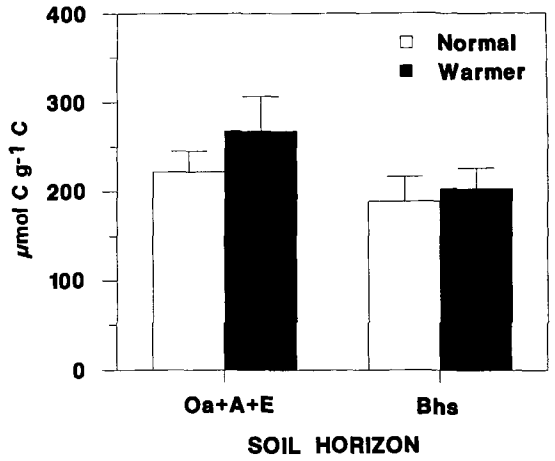

Fig. 5. Cumulative dissolved organic C leached from cores after 33-wk under two seasonal temperature regimes. Error bars represent standard errors of means.

to perform an analysis of covariance as we did with microbial respiration data precluded a more sensitive statistical analysis.

A variety of factors, including disturbance, drought, soil-solution chemistry, contact time between soil and solution, and temperature during this contact, have been shown to affect losses of DOC from forest soils (James and Riha, 1987; Vance and David, 1989; Duffy and Schreiber, 1990; Cronan et al., 1992). If losses of DOC from organic horizons of forest soils increase as a result of soil warming (Liechty et al., 1995), the ultimate sink for this mobilized soluble C would determine the effect on ecosystem and global C cycles. While most DOC is normally retained in the B horizons of Spodosols (Vance et al., 1986; Vance and David, 1989; Ross and Bartlett, 1996), soils may release quantities of organic C to aquatic systems when subsurface stormflow occurs (Boissier and Fontvieille, 1995). Increased fluxes of DOC from soils to aquatic systems could result in increased fluxes of C to the atmosphere (Kling et al., 1991), creating an indirect positive feedback to increasing atmospheric CO_2 concentrations.

In our study, we found no significant increase in leaching losses of DOC from surface or subsurface soils as a result of elevated soil temperatures (Tables 2 and 3; Fig. 4 and 5). Cumulative DOC losses (2.3 to 3.2 mg C g^{-1} C, Fig. 5) were small compared with cumulative C losses via microbial respiration (18.6 to 56.4 mg C g^{-1} C, Fig. 3a). According to Hendricks and White (1995), groundwater in the vicinity of the study site is not thought to be a significant source of DOC in local streams, with average riparian groundwater concentrations ranging from 2.5 to 7.9 mg C L^{-1}. This suggests that current fluxes of DOC from upland soils to aquatic systems in northern lower Michigan via groundwater are minimal. Our results suggest that, for the short term, elevated C losses from these Spodosols would more likely result from increased fluxes of CO_2 than from increased solution fluxes of DOC.

Under field conditions, increased fluxes of CO_2 to the atmosphere from forest soils in response to elevated soil temperatures are the result of increased decomposition, increased root respiration, or a combination of both (Edwards, 1975; Peterjohn et al., 1994). Such elevated CO_2 releases may only represent a short-lived depletion of the labile C pool, which could be offset by enhanced C inputs to soil from above and belowground production or changes in leaf and root litter chemistry, also in response to increases in atmospheric CO_2, air temperature, and N availability (Curtis et al., 1994; O'Neill, 1994; Peterjohn et al., 1994). Oechel et al. (1994), however, found that net ecosystem CO_2 fertilization effects were transient, with a tundra ecosystem exposed to elevated CO_2 going from a sink of C back to a source of C in 3 yr. Similarly, existing ecosystem models suggest that while increases in C inputs and widened detrital C:N ratios may reduce effects of warming on loss of soil C to some extent, a net loss of soil organic C as a result of soil warming is probable (Schimel et al., 1994; Kirschbaum, 1995).

Observed variation in soil organic C contents along the climatic gradient in the Great Lakes region provides additional clues to the likely effect of soil warming on soil C pools. In the Great Lakes region, quantities of organic C in the upper 1 m of soils decrease from north to south (Kern, 1994). This regional trend in organic C content is commonly accepted to be the result of the warmer climate at the southern end of the region. At specific northern hardwood forest sites that we have studied along the climatic gradient in the Great Lakes region, the amount of soil organic C to a depth of 75 cm decreases by a factor of 2.9 from north to south (493 Mg ha^{-1} to 169 Mg ha^{-1}, MacDonald et al., 1991), while total annual aboveground litterfall increases by a factor of 1.3 (4.3 Mg ha^{-1} to 5.4 Mg ha^{-1}, Burton et al., 1993). Mean annual air temperatures increase from 3.7°C at the most northerly site to 7.6°C at the most southerly site (Burton et al., 1993). These observations suggest that the likely response to soil warming in this region will be a gradual net loss of soil organic C, even though inputs of organic C from root and foliar litter may increase as temperatures and atmospheric CO_2 increase.

CONCLUSIONS

Microbial respiration rates were greater in surface than in subsurface soils from a northern hardwood forest Spodosol. Cumulative quantities of C respired from surface horizons were 2.6 times greater than from subsurface horizons. Microbial respiration rates, when adjusted for initial differences in respiration rates, were significantly increased by soil warming. Increases in microbial respiration rates and cumulative amounts of C respired in response to soil warming were greatest in surface soils, suggesting that these horizons may be most responsive to soil warming. While quantities of DOC leached from these soils displayed trends similar to those noted for microbial respiration, means did not differ significantly by soil horizon or temperature regime. These results suggest that rapid changes in C storage in northern hardwood forest soils in response to soil warming would most likely occur as a result of increased rates of microbial respiration and loss of CO_2 to the

atmosphere, and not through increased losses of dissolved organic C. The question if increases in microbial respiration represent a long-term response to soil warming cannot be addresssed adequately by short-term laboratory incubation studies. More conclusive answers will require long-term research to examine the interactive effects of climate and CO_2 on forest productivity, litter chemistry, microbial activity, and soil organic C storage.

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