EXPERIMENTAL WARMING SHOWS THAT DECOMPOSITION TEMPERATURE SENSITIVITY INCREASES WITH SOIL ORGANIC MATTER RECALCITRANCE

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Abstract. Soil C decomposition is sensitive to changes in temperature, and even small increases in temperature may prompt large releases of C from soils. But much of what we know about soil C responses to global change is based on short-term incubation data and model output that implicitly assumes soil C pools are composed of organic matter fractions with uniform temperature sensitivities. In contrast, kinetic theory based on chemical reactions suggests that older, more-resistant C fractions may be more temperature sensitive. Recent research on the subject is inconclusive, indicating that the temperature sensitivity of labile soil organic matter (OM) decomposition could either be greater than, less than, or equivalent to that of resistant soil OM. We incubated soils at constant temperature to deplete them of labile soil OM and then successively assessed the CO_2-C efflux in response to warming. We found that the decomposition response to experimental warming early during soil incubation (when more labile C remained) was less than that later when labile C was depleted. These results suggest that the temperature sensitivity of resistant soil OM pools is greater than that for labile soil OM and that global change-driven soil C losses may be greater than previously estimated.

Key words: decomposition; soil organic matter; temperature sensitivity.

INTRODUCTION

The sensitivity of chemical reactions to increased temperature is inversely proportional to reaction rate (Arrhenius 1889, Davidson and Janssens 2006), so it is reasonable to suspect that decomposition of soil organic matter (OM) will respond similarly, with greater temperature sensitivity for more decomposition-resistant soil OM compounds. But soil OM decomposition kinetics are also a function of soil OM-mineral interactions within the soil and spatial separation and isolation of soil OM from decomposing microbes (Sollins et al. 1996, von Lutzow et al. 2006, Ågren and Wetterstedt 2007). Temperature clearly increases the rate of decomposition (Kirschbaum 1995, Davidson et al. 2000), but it could also enhance the rate of protection from decomposition (Thornley and Cannel 2001). Most of our understanding of decomposition responses to temperature is based on the response of the more labile SOM substrates that contribute the bulk of respiration in field experiments or short-term incubation studies (Leifeld and Fuhrer 2005). Soil OM variation across sites and differing experimental approaches have likely led to results showing that labile soil OM decomposition

could be more, less, or equally sensitive to temperature than more resistant soil.

Several recent studies suggest that the temperature sensitivities of labile and more resistant soil OM may be similar. Short-term responses of $^{13}CO_2$ fluxes derived from younger vs. older soil OM (Conen et al. 2006), models fit to incubations conducted at different temperatures for a range of soils (Rey and Jarvis 2006), and field experimental data (Luo et al. 2001) all show that little or no difference in temperature sensitivity between labile and resistant soil OM. An incubation study in which the temperature sensitivity was successively evaluated as labile soil C was depleted, found no significant change in temperature sensitivity with decreasing soil OM lability (Fang et al. 2005).

Other investigations using different approaches suggest that resistant soil OM may be more sensitive to temperature than labile soil OM. When compounds of different lability were added to the soil (Fierer et al. 2005), the compounds that decomposed slowly were most responsive to increased temperature. Similarly, when physically separated soil OM components were incubated separately, the compounds that decomposed more slowly were more sensitive to increased temperature (Leifeld and Fuhrer 2005). Our previous work (Conant et al. 2008) employed a new computational method for assessing the temperature sensitivity of labile vs. more resistant OM applied to data from OM incubations (field and laboratory) at contrasting tem-

TABLE 1. Climatic characteristics (mean annual temperature [MAT] and precipitation [MAP]) of the two sites and edaphic characteristics for the cultivated and grassland management treatments at both sites.

Site and management	MAT (°C)	MAP (mm)	Duration of cultivation (yr)	Vegetation	Silt (%)	Clay (%)	Soil C (g C/100 g soil)†
Mandan, North Dakota	5	400					
Cultivated			21	wheat	48.5	34.3	2.80 ± 0.24
Grassland				northern mixed-grass prairie	49.2	29.7	3.24 ± 0.06
Vernon, Texas	17	665					
Cultivated			>30	wheat	43.1	42.3	1.02 ± 0.04
Grassland				southern mixed-grass prairie	52.0	30.9	1.12 ± 0.02

† Mean ± SE.

peratures. Results from new incubations, reanalysis of previously published data, and a long-term, cross-site, litter decomposition experiment all showed that the more resistant OM was more temperature sensitive (Conant et al. 2008).

This study describes an experimental test of the hypothesis that resistant soil OM is more sensitive to temperature than more labile soil OM. In the laboratory we created soils with varying soil OM lability by incubation for different durations at constant temperature. After incubatory labile soil OM depletion, samples were warmed and temperature sensitivity was assessed through changes in respiration rates. Whereas Conant et al. (2008) used a new computational approach for analyzing OM incubation data, here we describe an experimental approach to alter soil OM lability and then directly observe the temperature sensitivity of labile and more resistant soil OM. The approach used here is similar to that of Fang et al. (2005) and Koepf (1973), but in this study soil OM was depleted to a much greater extent and responses were observed over a longer period of time, thus depleting labile soil C to a greater degree.

Materials and Methods

Sample collection and preparation

Soil samples were collected from two sites: the Northern Great Plains Research Laboratory located near Mandan, North Dakota (hereafter ND; Black and Tanaka 1997) and the Waggoner Ranch in northern Texas, south of the town Vernon in Wilbarger County (33°50′ N, 99°02′ W; hereafter TX) (Martin et al. 2003). The climatic and edaphic characteristics of the native prairie grassland (GR) and cultivated (CU) treatments at both sites are described in Table 1.

Incubations

Samples for a given field treatment were thoroughly mixed and four laboratory replicate samples (80 g) were drawn and placed in plastic specimen cups. Soil moisture was brought to 60% water-filled pore space and the cups were enclosed in 1-quart (946-mL) canning jars. Moisture inside the jars was maintained with a small vial of water and water was added to all samples to return soil moisture content to initial soil moisture when soil moisture dropped by 5%.

Soil respiration rates were determined through periodic analysis of CO_2 concentration of headspace gas samples using a LI-COR 6525 (LI-COR, Lincoln, Nebraska, USA) infrared gas analyzer (IRGA). Respiration rates were sampled daily for the first 14 days, weekly for the next 14 days, monthly for the next 270 days, and every third month thereafter.

Depletion of labile soil C

To distinguish the response of labile vs. more recalcitrant soil C to increased temperature, we incubated soils for varying durations (60, 150, 300, and 450 days) to deplete the samples of labile soil C. Implicit in this approach is the assumption that changed lability is the dominant factor driving changes in the respiration rate under constant temperature and moisture conditions. Even though microbial biomass and microbial community composition are likely to change over the course of long-term incubation (Fang et al. 2005, Steinweg et al. 2008), the widely observed declines in respiration rates over time during incubation under constant temperature and moisture conditions are typically attributed to decreases in the lability of remaining soil C (Paul et al. 1998, Fang et al. 2005, Kirschbaum 2006). In order to minimize the influence of the amount of microbial biomass on responses to raised incubation temperatures and to maximize the influence of soil OM lability, we examined CO_2 responses over 60 days—after much of the most-labile soil C had been depleted—rather than over shorter response periods used in other studies (Fang et al. 2005, Fissore et al. 2007).

Warming treatments

Incubation-induced depletion of labile soil OM was followed by assessments of temperature sensitivity of the remaining SOM. Following incubation at one of three temperatures (4°, 15°, or 25°C), treatment samples were moved to incubators that were 10°C warmer (or 11°C in the case of the samples incubated initially at 4°C) and incubated for 60 more days. Control samples were incubated at one of the three constant temperatures over the entire course of the experiment. Data from the Texas soils incubated at a constant 25°C, which serve here as control data for samples subsequently warmed to 35°C,
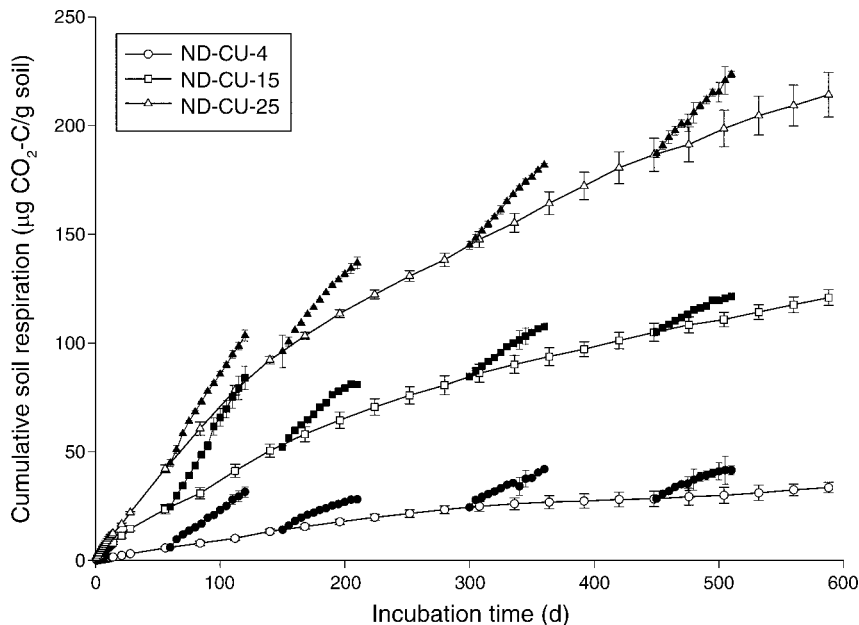
FIG. 1. Cumulative soil respiration (μg CO_2-C/g soil) over the course of soil incubation for the cultivated (CU) soil from Mandan, North Dakota (USA), at three temperatures (4°, 15°, and 25°C, respectively denoted ND-CU-4, ND-CU-15, ND-CU-25). Patterns of cumulative soil respiration and responses to increased temperature were similar in the other three soils. Error bars show $\pm$SE.

were previously reported in Conant et al. (2008). Respiration rates were monitored in all samples throughout the course of incubation, with measurement frequency varying as a function of respiration rates (every seven days the first month of incubation and every 28 days thereafter). Respiration rates were determined every five days for control and warmed samples following warming treatments. Temperature sensitivity of soil C decomposition (denoted Q_{10}) was calculated as the ratio of cumulative respiration of the warmed samples to that of the control samples over the 60 days. In the case of the samples incubated at 4°C and then 15°C, the 11°C temperature differential was corrected for by raising the calculated temperature sensitivity factor to 10/11.

Statistical analyses

Temperature sensitivities between the three initial incubation temperatures and between the four pre-incubation durations were compared using ANOVA and Scheffé's means comparison tests. Regression slope significances were used to asses the response of temperature sensitivity to soil C depletion within each of the three incubation temperatures. All statistical analyses were conducted using SAS/STAT (SAS Institute, Cary, North Carolina, USA) and differences were considered significant at $P < 0.05$.

RESULTS

Soil respiration in control (no temperature increase) soils

Cumulative soil respiration was significantly greater at warmer incubation temperatures for all four soils over

the duration of all incubations (Fig. 1). Respiration rates over the course of incubation were an average of 166% greater for soils incubated at 15°C compared with 4°C and 100% greater at 25°C compared with 15°C. Differences in respiration rates between temperatures were greatest during the early phases of incubation. A significantly larger percentage of total soil C was lost during incubation at warmer temperatures (Table 1). Cumulative CO_2-C loss normalized for soil C content was significantly greater for the Texas soils (nearly twice as large as the ND soil at each of the three temperatures). Within either site, native and cultivated soils did not respire significantly different proportions of soil C when normalized for soil C content (Table 2).

Respiration rates for all soils declined over the course of the incubation (Fig. 1). Cumulative (60 d) respiration for control samples declined by an average of 66% between days 60 and 450. Respiration rates for control samples declined significantly across successive treatment periods for all but three of the 64 soil–temperature pre-incubation combinations. The three exceptions, in which respiration of the control samples increased over time, all occurred at 4°C between the first (60 d) and second (150 d) timed-temperature increases (ND-GR, TX-CU, and TX-GR).

Respiration responses to warming

Soil respiration rates increased in response to experimental warming across all combinations of soil, initial temperature, and incubation duration prior to warming (Fig. 1; Appendix). The magnitude of the respiration response to warming (respiration for warmed samples

TABLE 2. Percentage of soil C (mean ± SE) lost over the course of 588 days of incubation at three constant temperatures.

	Percentage of soil C lost as CO_2-C during incubation (g CO_2-C respired/100 g soil C)		
Soil	4°C	15°C	25°C
ND-CU	1.24 ± 0.09	4.48 ± 0.13	7.94 ± 0.38
ND-GR	1.52 ± 0.20	4.53 ± 0.35	9.41 ± 0.79
TX-CU	2.85 ± 0.39	8.62 ± 0.20	15.61 ± 0.98
TX-GR	3.08 ± 0.67	9.60 ± 0.46	14.97 ± 1.10

Note: Key to abbreviations: ND, North Dakota; TX, Texas; CU, cultivated; and GR, grassland.

minus controls) tended to decline over time, with the response of samples warmed on day 60 an average of 43% greater than the response to samples warmed on day 450.

Following experimental warming, respiration rates for warmed samples declined over time by an average of 49%, but increased respiration rates relative to controls incubated at constant temperature were sustained for the full 60 days after warming in all but two cases (ND-CU-4 and ND-CU-15, day 150). Respiration rates declined during the course of the first two warming treatments (warming at day 60 and day 10) by an average of 39% whereas the declines for the third (warming at day 300; 62%) and fourth (warming at day 450; 59%) were greater. Respiration rates declined for control samples too, but those declines in respiration rates (average decline = 3%) were always significantly smaller than those observed for the warmed samples.
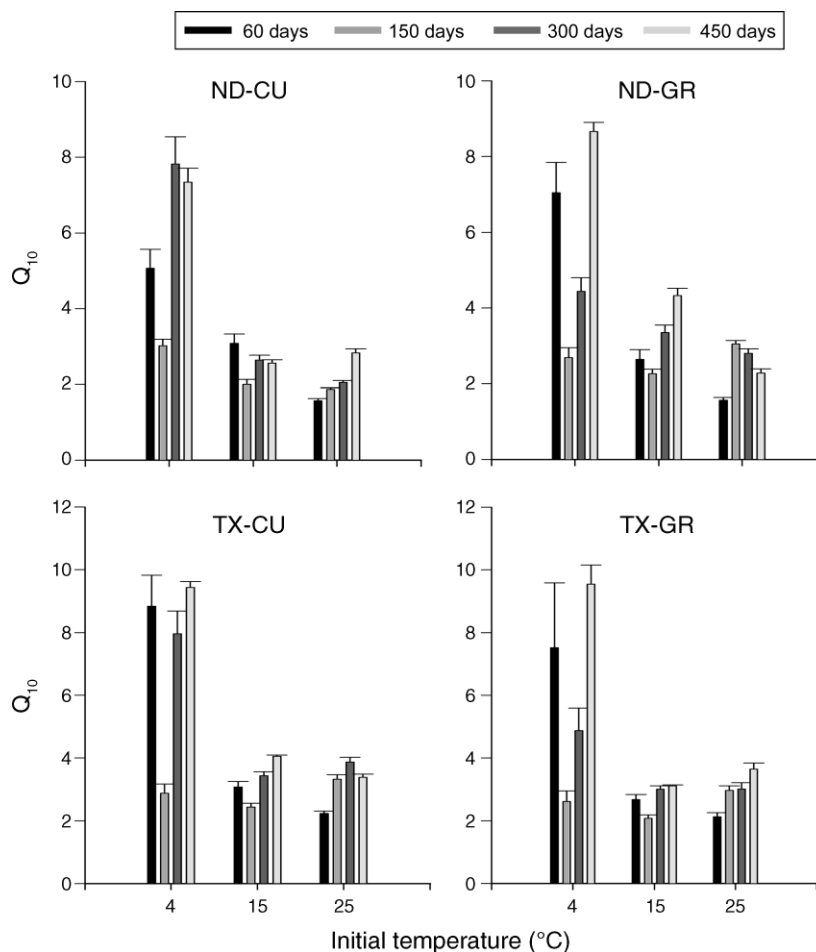

FIG. 2. Temperature sensitivities (Q_{10}) for grassland (GR) and cultivated (CU) soils from sites in North Dakota (ND) and Texas (TX) incubated at one of three initial temperatures (4°, 15°, and 25°C). The shade of gray of the bars indicates the incubation day at which the samples underwent warming treatments. Error bars show +SE.
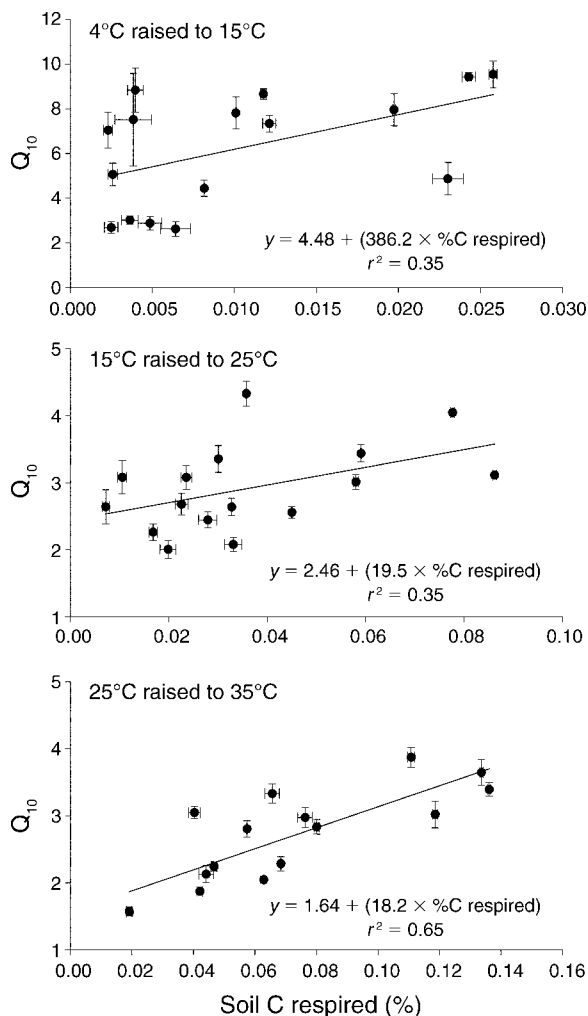
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FIG. 3. Temperature sensitivity (Q_{10}) vs. the percentage of soil C respired during incubation; each panel represents a different initial incubation temperature (4°, 15°, or 25°C). Error bars show ±SE.

Temperature sensitivities

Temperature sensitivity (Q_{10}) tended to be greater at the cooler initial incubation temperature, averaging 8.5, 3.2, and 2.9 for 4°, 15°, and 25°C, respectively (Fig. 2). At the coolest incubation temperature (4°C), the response to warming declined significantly between the first (day 60) and second (day 150) warming treatments, then increased significantly for the subsequent two warming treatments. The same general pattern was observed at 15°C. At 25°C, temperature sensitivity tended to increase over incubation time with the Q_{10} for the initial warming treatment (day 60) significantly less than that for the final warming treatment (day 450). With the exception of the warming treatment (day 60) at 4° and 15°C, across all temperatures Q_{10} tended to increase with duration of pre-incubation preceding the timed-temperature increases. Q_{10} values averaged across

the four soils increased by 74% between the first and last heating treatment at the warmest incubation temperature.

Within all three initial incubation temperatures as soil C became more depleted, the response to heating treatments increased significantly (Fig. 3). Average Q_{10} values were greatest at the cooler incubation temperature, but the least amount of C was lost during incubation at 4°C. While the absolute increase in Q_{10} with soil C loss was greatest at 4°C, the proportional increase between the estimated intercept (4.6) and the observation with the most soil C depletion (TX-GR; $Q_{10} = 9.6$) was smallest. The opposite was true at the warmest incubation temperature (1.6 intercept vs. 3.4 for TX-CU). When the regression lines from the three incubation temperatures are plotted together (not shown), the slope (i.e., the change in Q_{10} for a given degree of soil C depletion) at 4°C was significantly greater than that at either 15° or 25°C.

Discussion

Soil respiration was more sensitive to temperature in soils that were more OM depleted than soils that were less OM depleted. This was true when data were combined within each of the three incubation temperatures and it was also true within soil–temperature treatment combinations in most cases, with the initial (60 day) responses at 4° and 15°C being the most common exceptions. The overall pattern of our results is similar to the trend observed by Fang et al. (2005) when we considered only those observations from this study that fell within the range of soil C depletion observed in the Fang et al. (2005) (less than 6% of soil C lost during incubation). In such cases, the Q_{10} was greater for later heating treatments only about 56% of the time. In contrast, in cases in which more than 6% of soil C was lost, Q_{10} increased with depletion in 86% of cases. These results indicate that labile soil OM is less sensitive to temperature than more resistant soil OM and that observation of this difference is not evident until incubated soils lose a substantial portion of the more labile soil OM.

The tendency for greater Q_{10} values at cooler incubation temperatures is consistent with predictions from chemical thermodynamics (Davidson and Janssens 2006), but it is unclear why the 4° and 15°C responses to the initial (day 60) warming treatments were so much greater than the subsequent treatments (day 150). Not only was the magnitude of the responses to the initial treatments significantly greater than for subsequent treatments, but the cumulative amount of C respired after 120 days (60 at initial incubation temperature plus 60 at the warmer incubation temperature) occasionally exceeded cumulative respiration after 210 days (150 days incubation at the initial temperature plus 60 days at the warmer temperature). This was true for all four soils incubated initially at 4°C and one soil (TX-CU) incubated initially at 15°C, but the pattern of a greater
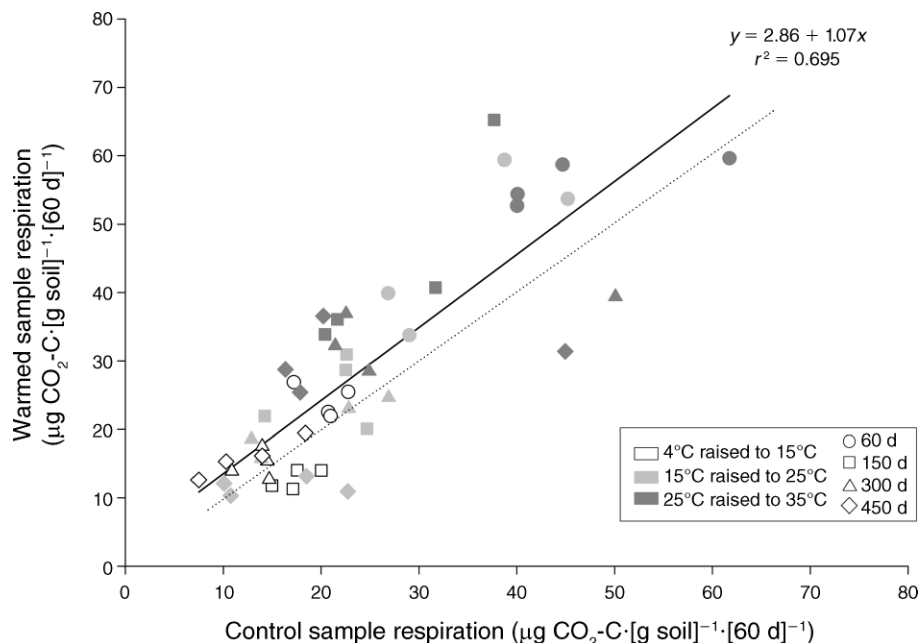
$y = 2.86 + 1.07x$
$r^2 = 0.695$

Legend:
□ 4°C raised to 15°C
▨ 15°C raised to 25°C
▪ 25°C raised to 35°C
○ 60 d
□ 150 d
△ 300 d
◇ 450 d

FIG. 4. Cumulative (60-d) soil respiration (μg CO_2-C/g soil) for samples that underwent warming treatments ("warmed sample respiration") and control samples that did not ("control sample respiration"). Each point represents a comparison of the amount of respiration for samples depleted of soil C to the same degree, but via incubation at one of two temperatures (e.g., 25°C for a "control" sample vs. 15°C for a "warmed" sample). Different shades and symbols indicate the initial incubation temperature and timing of the warming treatments.

Q_{10} for the initial warming treatment followed by a decline in Q_{10} for subsequent warming treatments was observed for the 4° and 15°C soils whether the magnitude of the respiration response declined or not.

Samples incubated at cooler temperatures and those undergoing earlier warming treatments contained a larger proportion of labile C compared to warmer incubation temperatures or later warming treatments. It is possible that greater availability of labile C led to a larger response early in the incubations at cooler temperatures. However, this would not explain why respiration over 120 days exceed those over 210 days when both included a warming treatment, because much of the labile C suspected to contribute to the observed Q_{10} patterns would still remain in the soil and susceptible to the heating treatment at 150 days. Moreover, these observations for cold soils early during incubation are inconsistent with the overall pattern of increasing temperature sensitivity with decreasing lability. Declines (Fang et al. 2005, Follett et al. 2007) and shifts (R. A. Drijber, R. T. Conant, J. Six, A. F. Plante, J. M. Steinweg, *unpublished manuscript*) in microbial community composition during long-term incubation have been documented in other studies, but we are aware of no studies that have assessed how long-term incubation influences the temperature response capability of soil microbial communities. If there were a large reduction in microbial biomass between the times two warming treatments were initiated, the latter response to

experimental warming would be more constrained by microbial biomass, potentially confounding findings of apparent temperature sensitivity in response to soil C lability. On the other hand, if declines in biomass or changes in microbial community composition limit responses to temperature, then the observed increase in temperature sensitivity with decreasing soil OM lability could be greater than that which we calculated.

Incubation of samples of the same soil at different temperatures eventually produced samples that had lost the same amount of soil C (i.e., soil C has been depleted the same amount), but through incubation at different temperatures. Following the warming treatments, soils depleted to the same degree (but via different incubation temperatures) were then incubated at the same temperature for 60 days. If temperature impacted labile and resistant soil C decomposition rates to the same degree, soil C depletion would be faster at warmer initial incubation temperatures, but the quality of soil C lost during incubation would not be impacted by initial incubation temperature. Also, respiration rates for "warmed" samples (i.e., those incubated at constant temperature and then incubated at a warmer temperature for 60 days) and "control" samples (i.e., control samples depleted of soil C to the same degree, but by incubation at constant temperature) should not differ. Our results show that after soil C was depleted to a given degree (i.e., a given amount of CO_2-C had been respired), respiration in "warmed" samples was strongly

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related to, but was slightly greater than, that in "control" samples (Fig. 4). If incubation-driven declines in microbial community size constrained soil respiration and response to warming treatments during the latter phases of incubation, we would see lower rates of respiration in the "warmed" samples since they had been incubated longer (143 days on average). Thus the observation that "warmed" samples respire at a higher rate after the same degree of soil C depletion suggest that the quality of the soil C remaining differs as a function of initial incubation temperature.

The results from this study are not inconsistent with field studies indicating acclimation to heating over the course of an experiment (Luo et al. 2001, Rustad et al. 2001, Melillo et al. 2002). If soil CO_2 efflux in field treatments is dominated by CO_2 derived from the most labile soil C, then depletion of this soil C pool could render observed responses derived from more slowly decomposing soil OM negligible (Gu et al. 2004, Kirschbaum 2004). In contrast to field warming experiments, our and other laboratory incubation investigations into warming impacts on decomposition undergo progressive depletion of labile soil OM. Our results imply that the acclimation response observed in field soil warming experiments is driven by depletion or labile soil OM rather than microbial acclimation.

Previous work has demonstrated the sensitivity of future atmospheric CO_2 concentrations to soil OM decomposition responses to temperature (Jones et al. 2003, 2005). While those responses are currently modeled in different ways and they all forecast response is a substantial net release of CO_2 from the soil (Friedlingstein et al. 2006), the same temperature sensitivity factors are typically applied equally for all soil C pools (Rodrigo et al. 1997, Friedlingstein et al. 2006). If, as our results suggest, the temperature sensitivity for a large pool of slowly-decomposing soil OM is greater than that observed in short-term studies of the small, labile soil OM, then the temperature-induced release of soil CO_2 from soils may be larger than suggested from current modeling work (Jones et al. 2005, Friedlingstein et al. 2006).

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APPENDIX

Mean cumulative respiration (μg CO_2-C/g soil) over successive 60-d periods for control sites incubated at constant temperature and soils that underwent incubation experimental warming after 60, 150, 300, and 450 days (*Ecological Archives* E089-134-A1).

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