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Sensitivity of organic matter decomposition to warming varies with its quality

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Abstract

The relationship between organic matter (OM) lability and temperature sensitivity is disputed, with recent observations suggesting that responses of relatively more resistant OM to increased temperature could be greater than, equivalent to, or less than responses of relatively more labile OM. This lack of clear understanding limits the ability to forecast carbon (C) cycle responses to temperature changes. Here, we derive a novel approach (denoted Q_{10-q}) that accounts for changes in OM quality during decomposition and use it to analyze data from three independent sources. Results from new laboratory soil incubations (labile $Q_{10-q} = 2.1 \pm 0.2$; more resistant $Q_{10-q} = 3.8 \pm 0.3$) and reanalysis of data from other soil incubations reported in the literature (labile $Q_{10-q} = 2.3$; more resistant $Q_{10-q} = 3.3$) demonstrate that temperature sensitivity of soil OM decomposition increases with decreasing soil OM lability. Analysis of data from a cross-site, field litter bag decomposition study (labile $Q_{10-q} = 3.3 \pm 0.2$; resistant $Q_{10-q} = 4.9 \pm 0.2$) shows that litter OM follows the same pattern, with greater temperature sensitivity for more resistant litter OM. Furthermore, the initial response of cultivated soils, presumably containing less labile soil OM ($Q_{10-q} = 2.4 \pm 0.3$) was greater than that for undisturbed grassland soils ($Q_{10-q} = 1.7 \pm 0.1$). Soil C losses estimated using this approach will differ from previous estimates as a function of the magnitude of the temperature increase and the proportion of whole soil OM comprised of compounds sensitive to temperature over that temperature range. It is likely that increased temperature has already prompted release of significant amounts of C to the atmosphere as CO_2. Our results indicate that future losses of litter and soil C may be even greater than previously supposed.

Keywords: decomposition, litter, soil carbon, temperature sensitivity

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Introduction

Organic matter (OM) decomposition is intrinsically sensitive to increased temperature (Davidson & Janssens, 2006; Kirschbaum, 2006). Therefore, the fate of the terrestrial carbon (C) sink under changing climate – whether it saturates, grows, or even reverses – hinges upon OM decomposition responses to temperature (Jones *et al*., 2003; Lenton & Huntingford, 2003). Yet, agreement has not been reached on how temperature sensitivity varies with the lability of OM substrates (Davidson & Janssens, 2006; Kirschbaum, 2006) and a consensus is critical to ensure that models of OM dynamics are properly constructed to forecast long-term CO_2 release from soils under changing climate. Basic thermodynamics predicts that biochemically complex substrates that normally resist decomposition will be more sensitive to increased temperature (Bosatta & Ågren, 1999; Ågren, 2000; Davidson & Janssens, 2006). Nevertheless, assessing labile vs. resistant OM temperature sensitivity is challenging because (a) environmental and edaphic variations confound cross-site and cross-soil comparisons (Davidson & Janssens, 2006), (b) several factors may contribute to temperature sensitivity of decomposition (Ågren & Wetterstedt, 2007),

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(c) the duration of temperature manipulation studies is typically much less than OM mean residence times, and (d) different interpretations of experimental data can lead to opposing conclusions (Liski *et al*., 1999, 2000; Ågren, 2000; Knorr *et al*., 2005; Fang *et al*., 2006). These challenges have fostered diverse approaches to investigating relationships between OM lability and temperature sensitivity. Results from previous research suggest that the temperature sensitivity of more resistant substrates may be greater than (Leifeld & Fuhrer, 2005; Fierer *et al*., 2005), equivalent to (Fang *et al*., 2005; Conen *et al*., 2006), or less than (Liski *et al*., 2000; Luo *et al*., 2001; Melillo *et al*., 2002; Rey & Jarvis, 2006) temperature sensitivity of more labile substrates.

Traditional means of expressing the temperature sensitivity of soil respiration (denoted as Q_{10}) represent the difference in respiration over a 10 °C interval measured during the same fixed period of incubation for both temperatures. A shortcoming of this approach is that the rate of respiration typically declines during incubation and the rate of this decline decreases with temperature, leading to temperature-induced differences in the amount and quality of soil C respired (Reichstein *et al*., 2000). Temperature sensitivity is thus confounded because temperature influences the OM source of respired CO_2. We have derived an approach that accounts for the fact that decomposition rates decline over time during controlled incubation (Paul *et al*., 2006), regardless of incubation temperature.

We determined the temperature responses by comparing the times required to respire a given amount of soil C at two different temperatures (e.g. t_{L-35}/t_{L-25} for more labile soil OM and t_{R-35}/t_{R-25} for more resistant soil OM; Fig. 1b). During incubation the lability of the remaining OM decreases as labile material is lost, thus it is possible to calculate the temperature sensitivity – which we denote using Q_{10-q} – for more labile OM decomposed during the early stages of incubation vs. that for relatively more resistant OM decomposed later in the incubation. This approach builds upon that taken by Rey & Jarvis (2006) and is conceptually similar to the assessment of temperature responses following incubation-induced depletion of labile OM (Fang *et al*., 2005), but it does not require timed experimental manipulations and can be used to reexamine published soil and litter decomposition data from longer-term, field and laboratory experiments.

We used this approach to (a) analyze data from a new temperature-controlled soil incubation study, (b) reassess temperature sensitivity for previously published studies of soil C decomposition, and (c) analyze temperature sensitivity of litter mass loss using data from a multiple-litter, cross-site decomposition experiment (LIDET – the Long-term Intersite Decomposition Experiment Team; Gholz *et al*., 2000). In cases for which the temperature differences were not 10 °C, we adjusted Q_{10-q} to estimate the impact on decomposition for a 10 °C difference. Such a response integrates the temperature sensitivity of the diverse reactions and substrates contributing to OM decomposition across a given range of temperatures. It is related, but not identical, to the energy of activation (Davidson & Janssens, 2006).

Materials and methods

Q_{10-q} calculations

We calculated Q_{10-q}s by carrying out comparisons following decomposition of given proportions of C or biomass originally present in the soil or litter. This approach contrasts with traditional analyses, which are often done at the end of a predetermined incubation period. Our method of analysis eliminates the problem of fixed incubation duration leading to comparison of different OM pools, which confounds characterization of temperature sensitivity (Reichstein *et al*., 2000, 2005; Leifeld & Fuhrer, 2005). More importantly, this approach enables comparison of the same fraction of OM across different incubation or site temperatures.

There are two assumptions implicit in using this approach. The first is that changes in decomposition rates during incubation are driven primarily by changes in the lability of the OM being decomposed. The second assumption is temperature impact on the sequence in which OM compounds are decomposed is small relative to the effect of temperature on decomposition rates, such that a given fraction of respired CO_2 (e.g. the first 1% respired) arises from decomposition of similar quality OM across different temperatures. Results from another soil incubation studies using methods like those described in this paper were used to assess these assumptions. We collected CO_2 and $^{13}CO_2$ flux data for Brazilian pasture soils incubated at 25 and 35 °C for 336 days. The pasture was converted from forest 33 years before samples were collected. Using the ^{13}C signatures of the C_4 pasture (−13‰) and C_3 forest (−28‰) vegetation, we partitioned the respiration source (i.e. old, C_3-derived vs. young, C_4-derived).

For this analysis, we used the frequency of observations and duration of incubations (in terms of mass or C lost) to dictate our data analyses. In conducting our analyses, the goal was to group our data into segments narrow enough to investigate responses of relatively labile OM during the early stages of incubation vs. those for relatively more resistant OM later during incubation, and yet wide enough to minimize undue influence by any single observation period. The width

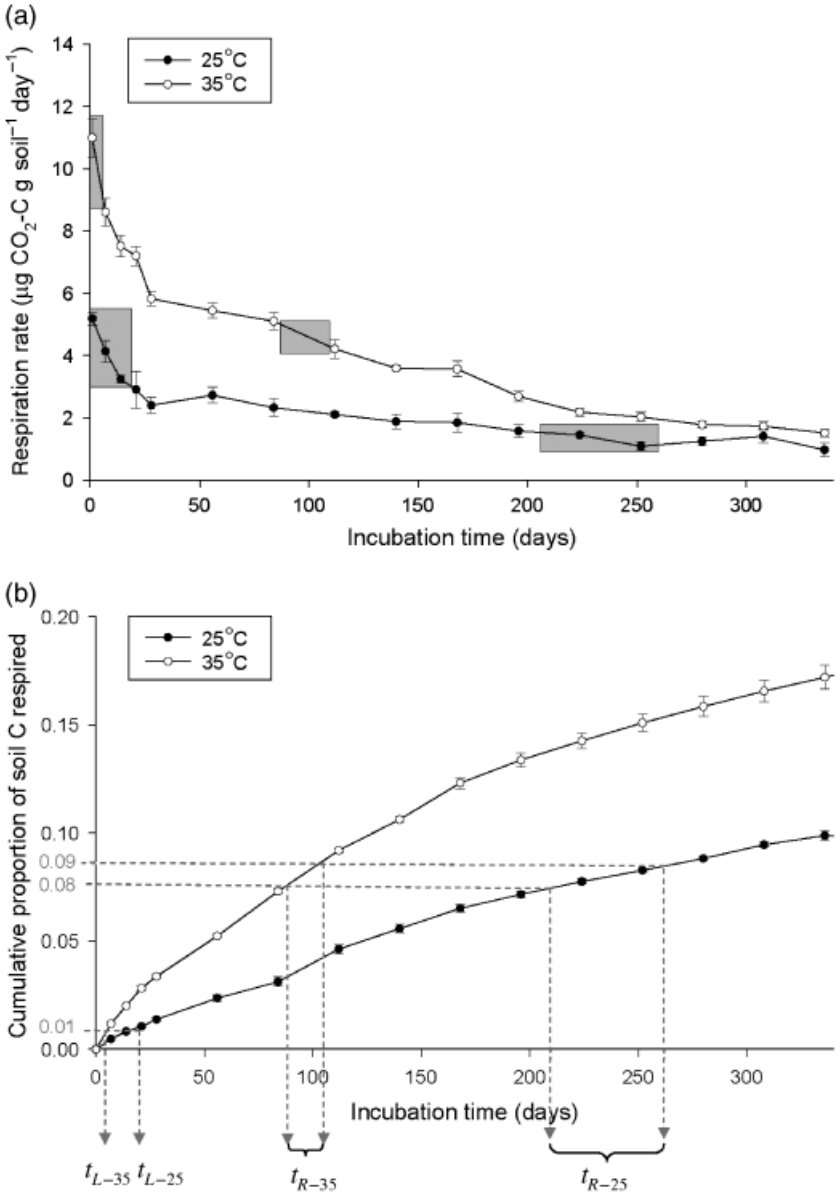

Fig. 1 Since decomposition rates decline over time as labile material is lost during incubation and the lability of the remaining organic matter (OM) decreases over time (a), comparing the time required to decompose a fixed amount of OM for a given soil or litter type enables calculation of temperature sensitivity of successively decomposed OM fractions and an evaluation of the temperature sensitivity of labile ($Q_{10-q} = t_{L-35}/t_{L-25}$) vs. more resistant ($Q_{10-q} = t_{R-35}/t_{R-25}$) OM fractions (b). In applying this method to data from new soil incubations, we defined the labile fraction as cumulative respired CO_2-C equivalent to 1% of initial soil C, and the resistant fraction as CO_2-C equivalent to an additional 1% of initial soil C respired after 8% of initial soil C had already been respired (illustrated by shaded areas).

of the bins for analysis of soil incubation data was 1% of initial soil C. None of the previously published soil incubation studies reported as much C respired as our incubations, and some studies reported substantially less. For litter analyses, we used 50% mass loss as the threshold to distinguish between early and late phase decomposition because the rates were much slower for decomposition of the second half of litter mass (an average of 18 times slower) and since setting the threshold at 50% resulted in several observations for both phases of decomposition.

New soil incubations

Four 80 g soil samples were drawn from 2 mm sieved, bulked, replicate soil samples (0–20 cm) collected from soil pits in cultivated and grassland plots near Akron, CO (40.15°N, 103.15°W) and Vernon, TX (33.9°N,

99.4°W). Samples were transferred into plastic containers, moistened to 60% water-filled pore space (determined by assuming mineral soil density of 2.65 g cm^{-3}), and incubated in 1 L glass jars at two temperatures (25 and 35 °C). Soil CO_2 efflux was measured using an infrared gas analyzer over 336 days of incubation. Samples were flushed with compressed air when CO_2 concentrations approached 50 000 ppm CO_2 and samples were remoistened to maintain soil moisture above 95% of original moisture. Soil C content was calculated from core-based bulk density measurements and dry combustion C concentrations. The Q_{10-q} values for the more labile portion of soil OM were determined by dividing the time taken to respire the first 1% of initial soil C at 25 °C by the time taken at 35 °C. Q_{10-q} values for the more resistant portion were determined using the time taken to respire one additional percent of initial soil C after 8% of initial soil C had already been respired (essentially the final 1% of initial soil C respired during the incubation at 25 °C for the cultivated Colorado soil), and dividing the time taken at 25 °C by time taken at 35 °C. All statistical tests comparing calculated Q_{10-q} values were two-tailed *t*-tests.

Previously published studies

Based on the citations within previously published reviews on temperature sensitivity, we identified six studies from three articles (Ross & Cairns, 1978; Blet-Charaudeau *et al*., 1990; Winkler *et al*., 1996) that contained information necessary to estimate soil Q_{10-q} responses (i.e. soil C content and continuous time-series incubation respiration data). We converted published data to cumulative CO_2 respired per amount of soil C lost and linearly interpolated time taken to respire the first 1% of initial soil C and the final 1% of initial soil C lost during the course of the incubation [e.g. 2.5–3.5% for Winkler *et al*. (1996), 4.5–5.5% for Blet-Charaudeau *et al*. (1990)]. For each of those studies, we used data from samples incubated only at the warmest two temperatures to maximize the proportional soil C loss over the course of the incubations. We calculated temperature sensitivities (Q_{10-q}s) by dividing time taken to respire a given fraction of soil C at the colder temperature (t_c) by time taken at the warmer temperature (t_w) and correcting for the actual incubation temperature differential ($T_w - T_c$)

$$Q_{10-q} = \left(\frac{t_c}{t_w}\right)^{\left(\frac{10}{(Tw-Tc)}\right)}. \quad (1)$$

LIDET analyses

We split LIDET (Gholz *et al*., 2000) decomposition data into two phases: the first phase comprised observations until 50% of litter mass was lost; the second phase comprised all subsequent observations. We derived decay constants for each phase of decomposition by fitting exponential decay models to observed decay rates for each of five leaf and three root litters. If data were insufficient to develop an exponential decay model during the first phase of decomposition (i.e. if fewer than two litter bags were harvested before 50% of the litter had been decomposed), we used a linear model to estimate initial decay rates (39 cases out of 85 litter-site combinations). Data were retained for cross-site analysis only if exponential model fit explained at least 75% of the observed variation in decay rates over time (>85% of all observations were retained). One leaf litter (*Drypetes glauca*) was excluded from this analysis because an average of less than half of mass remained at the time of the first litter bag harvest. One species of pine root litter (*Pinus resinosa*) of similar chemical composition was substituted for another (*Pinus elliotti*) at some sites and those pine litters were subsequently treated as if they were one litter type. We used only sites at which the five common leaf litters or three root litters were incubated. Sites were restricted to those for which moisture was deemed unlikely to limit decomposition for a significant portion of the year so that temperature was the main difference across the sites included for this analysis [actual : potential evaporatranspiration ratio >0.7; Juneau, AK; Hubbard Brook Experimental Forest, NH; Harvard Forest, MA; HJ Andrews Experimental Forest, OR; Olympic Peninsula, OR; Coweeta Long-term Experimental Research site, NC; Monte Verde, Costa Rica; University of Florida, FL; Luquillo Experimental Forest, Puerto Rico; Monte Verde, Costa Rica; Barro Colorado Island, Puerto Rico; see Gholz *et al*. (2000) and Table 1 for more information on sites used in this analysis]. Temperature sensitivities (Q_{10-q}s) were calculated by comparing slopes of regression lines between mean annual temperature of the sites and the log of the time taken to decompose 10% of litter mass during the first phase of decomposition vs. time taken to decompose an equivalent litter mass during the second phase of decomposition.

Results

After 336 days of incubation, at least 9% of initial soil C had been respired and decomposition rates had declined by an average of 83% across all eight of the soil-temperature combinations we incubated (Table 2; Fig. 1). Results from analyses of $^{13}CO_2$ evolution from Brazilian soils show that the source of CO_2 evolved either during the early or later phases of incubation was not significantly influenced by incubation temperature (Fig. 2). The proportion of CO_2 derived from younger

Table 1 Long-term Intersite Decomposition Experiment Team (LIDET) study sites included in this analysis

Site	Location	Vegetation type	Mean annual temperature (°C)	Mean annual precipitation (mm)	AET/PET
H. J. Andrews Experimental Forest; Oregon	44°14′N 122°11′W	Cool temperate coniferous forest	10	2500	0.78
Barro Colorado Island; Puerto Rico	9°11′N 79°51′W	Moist tropical forest	26	2614	1.0
Coweeta LTER site; North Carolina	35°N 83°301′W	Warm temperate hardwood forest	13	1800	0.87
Harvard Forest; Massachusetts	42°40′N 72°15′W	Cool temperate hardwood forest	7	1119	0.88
Hubbard Brook Experimental Forest; New Hampshire	43°56′N 71°45′W	Cool temperate hardwood forest	5	1300	0.88
Juneau, Alaska	58°N 134°W	Cool temperate conifer forest	4	1368	0.91
La Selva Biological Station; Costa Rica	10°N 83°W	Wet tropical forest	25	4000	0.96
Luquillo Experimental Forest; Puerto Rico	19°N 66°W	Wet tropical forest	23	3456	1.0
Monte Verde; Costa Rica	10°18′N 84°48′W	Tropical cloud forest	18	2300	0.93
Olympic Peninsula; Oregon	47°50′N 123°53′W	Cool temperate coniferous forest	10	3200	0.76
University of Florida	29°30′N 82°15′W	Warm temperate coniferous forest	21	1350	0.72

AET, actual evaporatranspiration; PET, potential evaporatranspiration.

Table 2 Soil incubation studies reanalyzed for this investigation

Study	Site/vegetation	Incubation temperatures (°C)	Incubation duration (days)	Soil C concentration (g 100 g soil^{-1})	% of soil C respired*	Q_{10}†	Q_{10-q} labile	Q_{10-q} resistant
This study	Texas; wheat	25 and 35	364	1.0	11.5	1.58	1.8 ± 0.1	3.9 ± 0.6
This study	Texas; grass	25 and 35	364	1.1	11.5	1.60	1.9 ± 0.1	3.8 ± 0.5
This study	Colorado; wheat	25 and 35	364	0.7	9.1	1.88	3.1 ± 0.4	3.8 ± 0.5
This study	Colorado; grass	25 and 35	364	1.2	12.9	1.78	1.7 ± 0.2	3.8 ± 0.6
Blet-Charaudeau *et al.* (1990)	Champagne Crayeuse region, France; wheat	19 and 28	50	1.8	5.5	1.8	2.2	4
	Champagne Crayeuse region, France; grass	19 and 28	50	3.8	5.5	1.4	1.2	2.8
Ross & Carins (1978)	Harihari, New Zealand/ grassland	20 and 24	45	2.5	6.7	3.2	2.9	5.7
	Tawhiti, New Zealand/ grassland			4.6	2.5	2.9	3.0	3.5
	Tima, New Zealand/ grassland			3.7	4.1	2.7	3.0	4.0
Winkler *et al.* (1996)	Duke forest, USA; forest	22 and 38	120	1.0	3.8	1.5	1.7	2.0

*At the cooler incubation temperature.
†Standard Q_{10} calculated using cumulative respiration at the warmer temperature divided by cumulative respiration at the cooler temperature.
C, carbon.

(C_4-derived) soil organic matter (SOM) declined over the course of the incubation, providing support for our first assumption, that changes in decomposition rates during incubation are driven primarily by changes in the lability of the OM being decomposed. The fact that this difference was greater than the difference induced

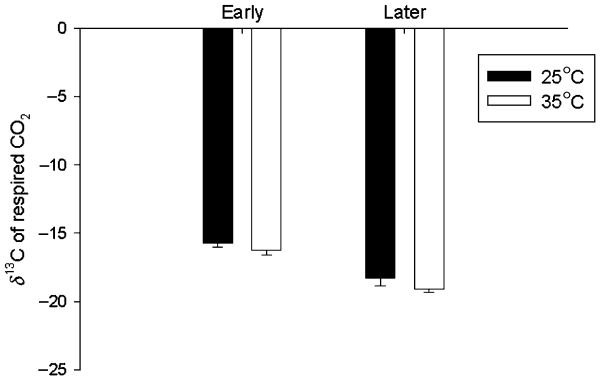

Fig. 2 ^{13}C signature of CO_2 evolved from Brazilian pasture soils incubated at 25 and 35 °C early during incubation (cumulative CO_2-C respiration equivalent to 2% of initial soil C; $P = 0.219$, $n = 3$) or later (respiration of the same mass of CO_2-C, but after the equivalent of 6% of initial soil C had already been respired; $P = 0.270$, $n = 3$). Error bars indicate standard errors estimated from four replicates.

by different incubation temperatures during either the early or later phases of incubation supports our second assumption, that temperature impact on the sequence in which OM compounds are decomposed is small relative to the effect of temperature on decomposition rates.

During the early phase of incubation, calculated Q_{10-q} values for both grassland and cultivated soils were near two (Fig. 3a). Over the course of incubation, Q_{10-q} values increased to more than three (Fig. 3a). The Q_{10-q} for CO_2 evolved from labile soil C early in the incubation for grassland soils ($Q_{10-q} = 1.7 \pm 0.1$; mean $\pm$ SEM; $n = 8$) was significantly less than for the CO_2 evolved from more resistant soil C respired later ($Q_{10-q} = 3.8 \pm 0.3$; average $\pm$ SEM; $n = 8$; $P = 0.003$). We found similar results for cultivated soils, with significantly smaller Q_{10}s for respiration of labile soil C ($Q_{10-q} = 2.4 \pm 0.3$; average $\pm$ SEM; $n = 8$) than for respiration of more resistant soil C ($Q_{10-q} = 3.8 \pm 0.3$; average $\pm$ SEM; $n = 8$; $P = 0.013$).

The Q_{10-q}s for labile soil C from previously published data (Ross & Cairns, 1978; Blet-Charaudeau *et al*., 1990; Winkler *et al*., 1996) (calculated in the same manner as for our incubations) were less than those for more resistant soil C for all six studies (Fig. 3b). The Q_{10-q} for respiration of labile soil C during the early periods of these incubations ranged from 1.2 to 3.0, and averaged 2.3, whereas Q_{10-q} of more resistant soil C ranged from 2.0 to 5.7 and averaged 3.6. Across the three

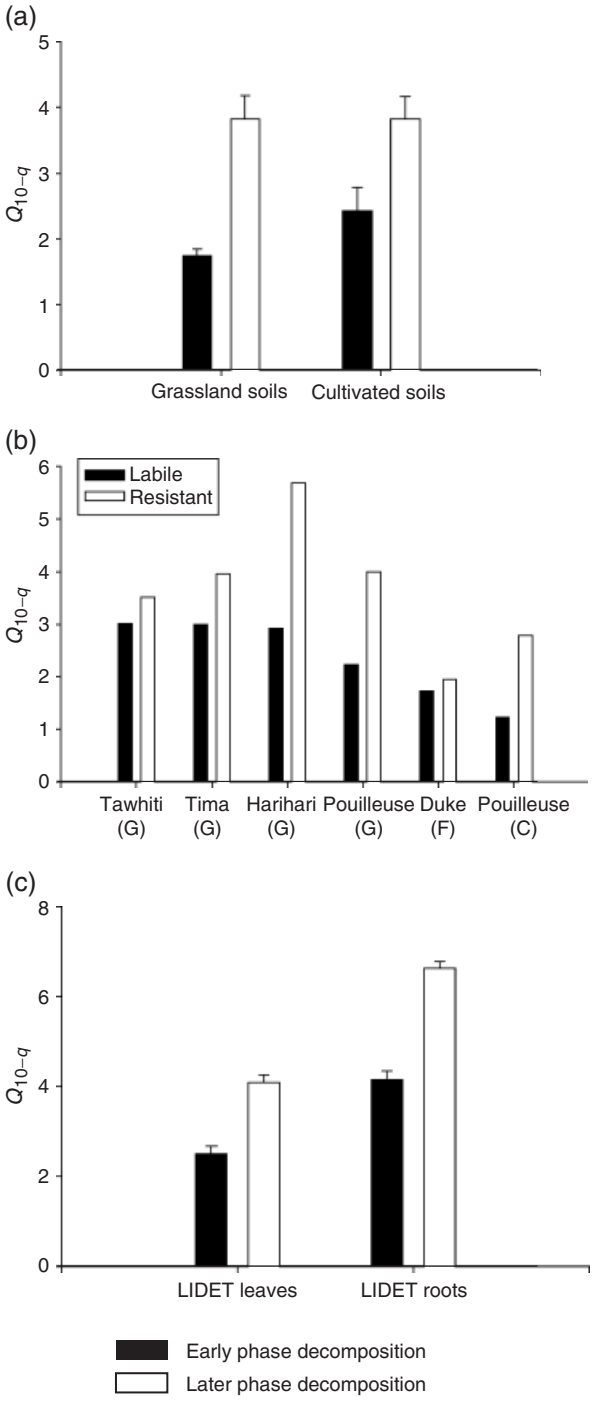

Fig. 3 Temperature sensitivities (Q_{10-q}s) of labile and resistant organic matter. (a) For native and cultivated soil C respired early during incubation (through loss of 1% of organic C initially present in soil) vs. those for C respired later (loss of equivalent C after 8% of soil C had been respired). (b) Q_{10-q}s for respiration of the first 1% of C respired vs. those for the final 1% of C respired during a variety of soil incubation studies. (c) Q_{10-q}s for the first (up to 50% mass lost) vs. the second phase of litter decomposition from the LIDET experiment. Soils were from grassland (G), forest (F), or cultivated (C) soils. All values are means; error bars represent 1 SEM. LIDET, Long-term Intersite Decomposition Experiment Team.

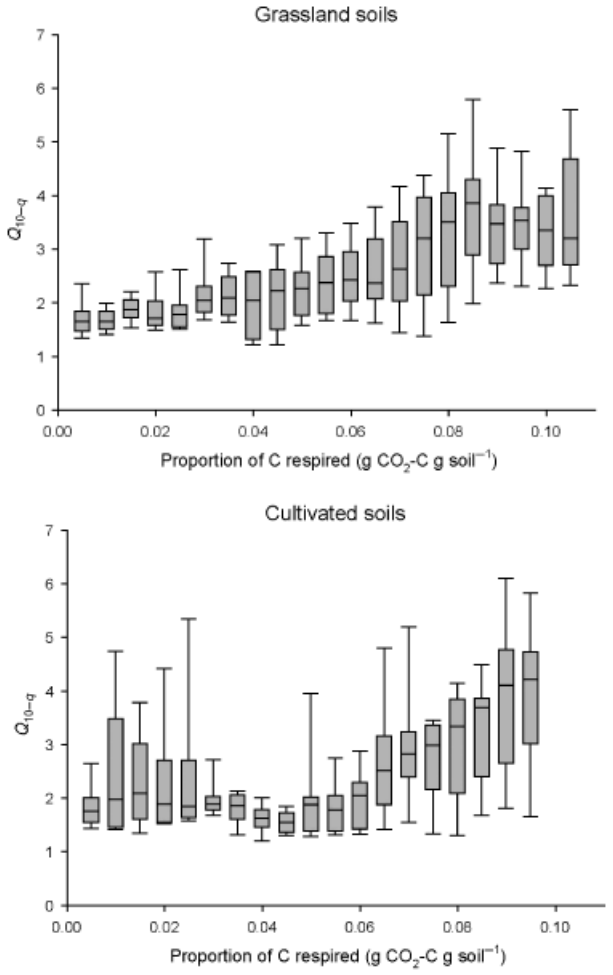

Fig. 4 Box and whisker plots for grassland and cultivated soils showing the median (solid horizontal line), 10th and 90th percentiles (whiskers), and the middle two quartiles (25th and 75th percentiles; box ends) for Q_{10-q} vs. proportion of soil carbon respired during incubation.

incubation experiments, the magnitude of the Q_{10-q} response (measured either as absolute difference, ratio, or proportional difference of labile Q_{10-q} vs. resistant Q_{10-q}) increased with increasing proportion of soil C lost during incubation (data not shown).

Results from analysis of LIDET data show that Q_{10-q}s for leaf and root decomposition were significantly less during early stages of decomposition than for later stages (Fig. 3c). Averaged across the five common LIDET leaf litter types, the Q_{10-q} for decomposition of labile OM (first 50% of litter mass; $Q_{10-q} = 2.5 \pm 0.2$) was significantly less than that for more resistant OM (based on the observations after the first 50% of litter mass was lost; $Q_{10-q} = 4.1 \pm 0.2$; averages $\pm$ SEM; $n = 52$; $P = 0.002$). The Q_{10-q}s were also significantly less for labile than for relatively more resistant OM proportions for LIDET root litters (4.1 ± 0.2 vs. 6.6 ± 0.2; average $\pm$ SEM; $n = 33$; $P < 0.001$).

For both grassland and cultivated soils, Q_{10-q} tended to increase during incubation as more soil C was respired (Fig. 4). Whereas, within the grassland soil, the increase began early during incubation and continued to increase throughout, there was considerable variation in Q_{10-q} values in the cultivated soil and Q_{10-q}s during earlier phases of incubation and Q_{10-q}s did not begin to increase until CO_2-C equivalent to about 6% of total soil C had been respired. Differences between initial Q_{10-q} (first 1% of soil C) and subsequent Q_{10-q} values were not significant until the equivalent of 6% (cultivated soils) and 4% (native grassland soils) of initial soil C had been respired.

Discussion

Our analyses of new soil C incubation data, data synthesized from previously published soil C incubation studies, and data from a large-scale litter decomposition experiment all concur that temperature sensitivity of relatively more resistant OM is greater than that of relatively more labile OM. Greater temperature sensitivities for more resistant OM within both soil and litter are consistent with expectations based on basic thermodynamics (Bosatta & Ågren, 1999; Davidson *et al*., 2006), suggesting that the response observed here is driven by a shift to decomposition of more biochemically resistant materials over time. In that respect our results agree with studies that have addressed the same topic using shifts in plant-derived ^{13}C signatures during incubation (Waldrop & Firestone, 2004; Vanhala *et al*., 2007), incubation of isolated soil C fractions (Leifeld & Fuhrer, 2005), and loss of resistant (^{13}C-depleted) C (Biasi *et al*., 2005). Our results seem to be in conflict with results based on $^{13}CO_2$ fluxes from short-term (a few hours to a few days) incubation results of Conen *et al*. (2006). However, it is generally accepted that collecting samples from the field, followed by laboratory preparation (e.g. sieving or rewetting) prompts the release of substantial amounts of soil C, even from those fractions that have persisted for decades or centuries under field conditions (Wynn *et al*., 2006). Such a short-term respiration pulse from soil C that is largely resistant to decomposition could lead to short-term results that contrast with longer-term responses. The study most similar to ours (Fang *et al*., 2005) produced similar trends – although nonsignificant results – but our approach enabled us to examine soil and litter that had undergone a greater degree of decomposition. Greater depletion of labile soil OM in our study relative to that of Fang *et al*. (2005), in which an average of 6% of soil C was respired during incuba-

tion, likely enabled detection of significant increases in temperature sensitivity with decreasing lability because temperature sensitivity in our incubations did not increase significantly until more than 4–6% of soil C had been respired.

Responses for both initial ($Q_{10-q} = 2.5 \pm 0.2$) and later phases ($Q_{10-q} = 4.1 \pm 0.2$) of decomposition averaged across all leaf litters from the LIDET experiment tended to be less than corresponding initial ($Q_{10-q} = 4.2 \pm 0.2$) and final ($Q_{10-q} = 6.6 \pm 0.2$) values averaged across root litters. This could reflect a bias in which the difference between air and soil temperature is greater for colder regions (Adair *et al*., 2007). It is interesting to note that we observed similar Q_{10-q} values in both the early ($Q_{10-q} = 2.1 \pm 0.2$ for soil and 2.5 ± 0.2 for leaf litter) and later stages of decomposition ($Q_{10-q} = 3.8 \pm 0.3$ for soil and 4.1 ± 0.2 for leaf litter) for soil OM and leaf litter OM, despite different study durations (336 days for soil vs. 10 years for litter), different temperature ranges (25–35 °C for soil vs. 4–26 °C MAT for litter), and, presumably, differences in initial and final OM quality.

Data on C_3- vs. C_4-derived CO_2 during incubation of the Brazilian soils show that the lability of the soil C being decomposed declined during incubation. This coincides with work from others that shows that the age of soil C decomposed becomes progressively older as incubation proceeds (Wynn *et al*., 2006). Other work has documented significant declines in microbial biomass over the course of long-term incubation (e.g. Follett *et al*., 2007), that could contribute to declines in soil respiration rates during long-term incubation. However, Follett *et al*. (2007) and Fang *et al*. (2005) conducted experiments in which the incubation temperature was raised following incubation for some length of time [500 days for Follett *et al*. (2007); approximately 10, 20, 30, 50, 60, and 105 days for Fang *et al*. (2005)]. In all cases, soil respiration rates increased significantly following the temperature increases, suggesting that a viable population of soil microbes remained active in the soil. Respiration pulses have also been observed in response to substrate additions – even after long-term incubation (600 days; M. Steinweg *et al*., unpublished data). Taken together, these observations indicate that during incubation – even after significant declines in microbial biomass-respiration rates are constrained by substrate availability and incubation temperature and that limitation by microbial populations seems unlikely. An additional treatment for the Brazilian soils was incubation at two different moisture contents. This enabled assessment of whether a factor that controls decomposition rates but that is not expected to vary with SOM quality would produce a similar pattern: the moisture response increases as decomposition progresses. There was no relationship between percent C respired and response to soil moisture for any of the four soil-incubation temperature combinations (data not shown), suggesting that results using our method do not indicate Q_{10-q} differences where none exist.

Cumulative soil C decomposition normalized per unit soil C in our incubations was much less for cultivated (9.9% and 11.7% of soil C lost over 336 days at 25 and 35 °C, respectively) than for native soils (17% and 20% soil C lost at 25 and 35 °C), suggesting that cultivated soils were depleted of labile C relative to grassland soils. The initial Q_{10-q} of cultivated, labile C-depleted soils (2.4 ± 0.3) was significantly greater ($P = 0.04$; $n = 8$) than that for undisturbed grassland soils (1.7 ± 0.1), yet there were no differences for Q_{10-q}s during later stages of the incubation (Q_{10-q}s for both $= 3.8 \pm 0.3$; $P = 0.99$; $n = 8$). These observations indicate that decomposition of the more labile grassland soil C is less sensitive to temperature than the less labile cultivated soil C. This result is consistent with data from the only other study for which comparable data are available (Blet-Charaudeau *et al*., 1990). Comparison of temperature sensitivity of cultivated and native soils complements our other results showing a negative relationship between lability and temperature sensitivity.

The Q_{10-q} values we calculated could underestimate the temperature sensitivity of the relatively more resistant soil OM to the extent that chemically labile soil OM continued to contribute to respiration during the later phases of incubation. This would make our approach more conservative. At the same time, even after 336 days of incubation the majority of SOM remained undecomposed in all of the soil studies. Therefore, our results do not reflect the temperature sensitivity of the most resistant SOM. If the undecomposed OM is more biochemically resistant to decomposition, its Q_{10-q} could be greater than the values we observed. Alternatively, if the remaining soil OM is protected from decomposition by mechanisms other than biochemical recalcitrance, such as physical protection within aggregates and chemical protection by sorption to minerals (Thornley & Cannel, 2001), and those protection mechanisms are insensitive to temperature, temperature sensitivity for the most resistant OM could be less than the values we observed. Low and relatively unchanging rates of respiration observed near the end of the incubation suggest that incubation for several additional years would be required to investigate the temperature sensitivity of the most stable soil OM.

To the extent that biochemical resistance is the factor driving increased temperature sensitivity with decreasing lability, soil C losses estimated using this approach will differ from estimates based on traditional Q_{10}

calculations. The size of the difference will be a function of the magnitude of the temperature increase and the proportion of whole soil OM comprised of compounds that become available over that temperature range. Field studies (Luo *et al*., 2001; Melillo *et al*., 2002) indicate that temperature responses persist for a limited time, but such results are not inconsistent with greater temperature sensitivity for more resistant soil OM (Kirschbaum, 2004). We are aware of no incubation studies that have illustrated acclimation. All else equal, soils with a larger proportion of biochemically recalcitrant soil OM and more resistant litter OM are likely to exhibit a larger response to a given temperature increase. The amount of biochemically recalcitrant OM in soils is poorly characterized (Paul *et al*., 2006), limiting our ability to forecast the effect of increased temperature on CO_2 release from soils. However, OM models typically do not differentiate temperature responses by OM lability (Burke *et al*., 2003; Friedlingstein *et al*., 2006). Therefore, greater sensitivity of OM turnover for relatively more resistant OM suggests that previous forecasts of C release with increased temperature may underestimate the ultimate respiratory response of OM decomposition to increased temperature.

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