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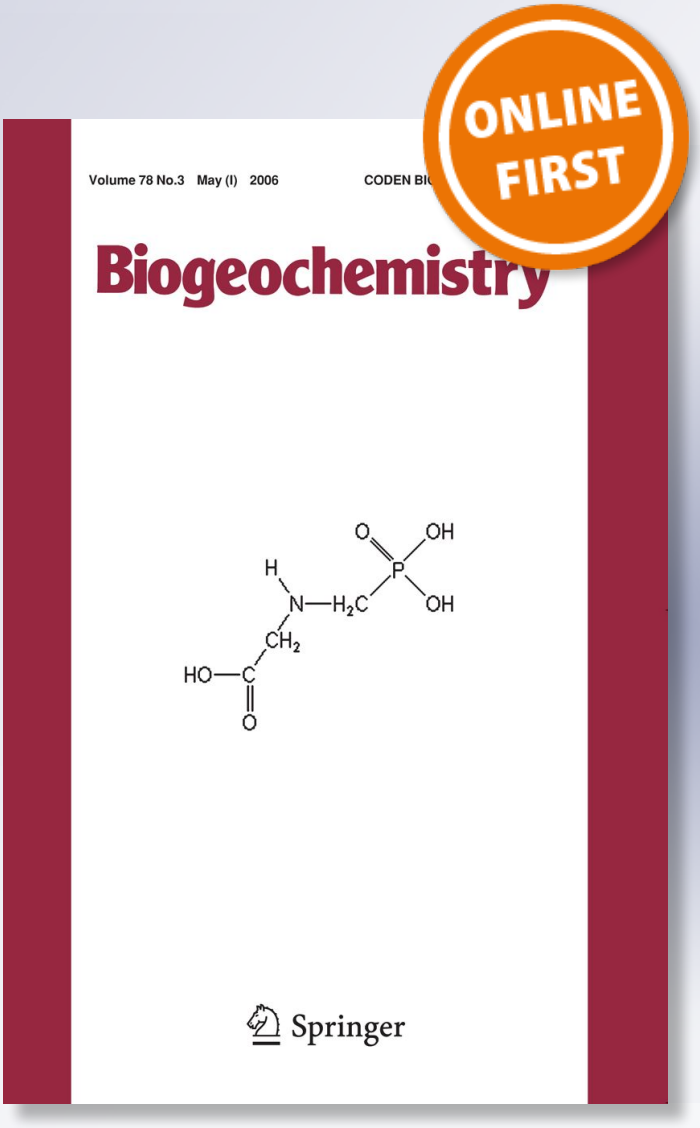

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Reduction of the temperature sensitivity of soil organic matter decomposition with sustained temperature increase

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Abstract The degree to which microbial communities adjust their decomposition of soil carbon over time in response to long-term increases in temperature is one of the key uncertainties in our modeling of the responses of terrestrial ecosystems to warming. To better understand changes in temperature sensitivity of soil microbial communities to long-term increases in soil temperature, we incubated 27 soils for one year with both short-term and long-term manipulations of temperature. In response to increasing temperature short-term from 20 to 30 °C, respiration rates increased more than threefold on average across soils. Yet, in response to long-term increases in temperature, respiration rates increased approximately half as much as they did to short-term increases in temperature. Short-term Q_{10} of recalcitrant C correlated positively with long-term Q_{10} measured between 10 and 20 °C, yet there was no relationship between short-term Q_{10} and long-term Q_{10} between 20 and 30 °C. In all, under laboratory conditions, it is clear that there is reduction in the temperature sensitivity of decomposition to long-term increases in temperature that disassociate short- and long-term responses of microbial decomposition to temperature. Determining the fate of soil organic matter to increased temperature will not only require further research on the controls and mechanisms of these patterns, but also require models to incorporate responses to both short-term and long-term increases in temperature.

Keywords Decomposition · Temperature · Acclimation · Soils · Carbon

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Introduction

Soil carbon (C) is the largest pool of terrestrial C and a key to understanding whether ecosystems will be a net source of C to the atmosphere in a warmer world. Short-term increases in temperature generally increase microbial decomposition of soil C. That said, the

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apparent temperature sensitivity of decomposition can be reduced by protection of soil organic matter or drought (Davidson and Janssens 2006), while other processes such as the thawing of frozen organic matter increasing the pool of carbon available for decomposition (Lee et al. 2010; Oquist et al. 2009; Schuur et al. 2009). However, short-term temperature dependence varies among soils and soil pools due to, among other factors, the biochemical recalcitrance of the organic matter being decomposed. With decomposition of the most biochemically recalcitrant organic matter showing the greatest relative sensitivity to temperature (Bol et al. 2003; Conant et al. 2008b; Craine et al. 2010; Fierer et al. 2005; Hartley and Ineson 2008; Karhu et al. 2010a), future increases in temperature could generate a positive feedback to global warming.

As the flux of carbon from soils is dominated by multiple processes, understanding how increases in temperature ultimately affect soil CO_2 flux and soil C storage requires understanding how increases in temperature affect component processes (Craine et al. 1998; Fang and Moncrieff 1999; Ryan and Law 2005). One of the keys to modeling future carbon cycling is to quantify the relationships between temperature and microbial decomposition of soil carbon (Anderson 1991; Fang and Moncrieff 2001; Lloyd and Taylor 1994; Singh et al. 2010; von Lützow and Kögel-Knabner 2009). Currently, most coupled climate-carbon cycle models assume a doubling of microbial decomposition for every 10 °C increase in temperature ($Q_{10} = 2$) (Friedlingstein et al. 2006), but there is little empirical basis for using this specific coefficient. Our inability to accurately parameterize temperature sensitivity generates a large uncertainty in predictions of future changes in soil C storage (Davidson et al. 2006). Although multiple approaches are possible for improving predictions of temperature sensitivity of microbial respiration such as including estimates of substrate supply rates (Davidson et al. 2006), models of soil C decomposition could be improved with coefficients of temperature sensitivity derived from short-term manipulations of temperature. However it is not known if the longer-term responses of decomposition to increases in temperature might parallel responses to short-term increases (Bradford et al. 2008; Karhu et al. 2010b).

There are two sets of mechanisms by which microbial decomposers might respond to higher temperature causing long-term and short-term temperature sensitivities to be disassociated (Singh et al. 2010). First, soil C pools can become depleted faster at higher temperatures, which would reduce the long-term response of microbial activity to increases in temperature. As a result, specific microbial activity or community biomass could decline with long-term increases in temperature as soil C pools are depleted, which does not constrain short-term temperature increases. At some time scales, increases in temperature can increase the size of the pool of available or labile C (Conant et al. 2008a; von Lützow and Kögel-Knabner 2009; Waldrop and Firestone 2004), which could ultimately lead to apparently greater temperature sensitivity on some time scales. Secondly, microbes or microbial communities could respond to increases in temperature which would alter long-term temperature sensitivity (Allison et al. 2010). These responses, which we'll refer to here generically as acclimation responses, could be manifested at the individual level or at the community level and might respond at a variety of time scales. Some factors such as reductions in utilization of alternative oxidation pathways or down-regulation of activity to minimize adenylate accumulation (Atkin and Tjoelker 2003; Joergensen and Raubuch 2003) would decrease temperature sensitivity. Other factors, such as expression of isoenzymes with higher temperature optima (Hochachka and Somero 2002) or shifts in microbial communities (Singh et al. 2010; Vanhala et al. 2011) could increase temperature sensitivity or at least constrain down-regulation of microbial activity via other mechanisms.

Laboratory incubations of soils at different temperatures allows for relatively direct assessment of the effects of increased temperature on soil C decomposition, but conclusions to date have been conflicting, generating hypotheses regarding the controls over and patterns of temperature sensitivity of microbial respiration. For example, Bradford et al. (2008) showed that actual and potential rates of soil C mineralization assayed ex situ were lower in soils that had been warmed in situ for more than 15 years compared to control soils, which suggests some sort of down-regulation of activity of the microbial community. The authors also concluded that the potential rate of respiration per unit microbial biomass was lower in warmed soils, which suggested physiological acclimation. Yet, it has been suggested that their data actually reveal a higher, not lower, respiration per unit

microbial mass with soil warming (Hartley et al. 2008b, but see Bradford et al. 2009). Wetterstedt et al. (2009) found that long-term Q_{10} of litter and SOM decomposition tended to be higher for substrates that were moved between two temperatures than for those that maintained at the same temperature, which also suggests microbial shifts in response to changes in temperature regimes.

In contrast to the evidence and assertions that the microbial community reduces its collective activity to increased temperatures Hartley et al. (2008a), concluded that microbial communities from arctic soils do not acclimate to changes in temperature. They found that temporarily lowering the temperature of a soil did not lead to greater rates of respiration upon recovery of the initial temperature as would be expected if microbes acclimated to reduced temperature by increasing their respiration. Conant et al. (2008b) also failed to find evidence of acclimation when comparing the temperature response of soils incubated at different temperatures but having respired equivalent amounts of C. In these cases, soils incubated at the warmer temperature subsequently respired more C than those at the lower temperature.

To better understand whether there are fundamental differences between short-term and longer-term responses to temperature increases, we conducted an experiment to test whether the temperature sensitivity of microbial decomposition of soil C differed consistently between short-term and longer-term increases in temperature. 27 North American soils, which differ greatly in their overall biochemical recalcitrance (Craine et al. 2010), were incubated over 1 year at 10, 20, and 30 °C. For these soils we were able to determine the temperature sensitivity of respiration for equivalent amounts of carbon over time, which could then be compared to the temperature sensitivity of microbial decomposition for the same soils with short-term manipulations of temperature (Craine et al. 2010). If microbial decomposers acclimate sensu lato to temperature, then temperature sensitivity would be greater for short-term increases in temperature than long-term manipulations of temperature. We further test whether the differences in short- and long-term responses of microbial communities to increases in temperature are associated with changes in the effective sizes of labile C pools or potential rates of microbial activity, which would potentially indicate different mechanisms underlying any shifts in temperature sensitivity.

Materials and methods

During the summer of 2008, soils were collected from 27 sites distributed across North America from Puerto Rico to Alaska. At each of the 27 sites, mineral soil was collected from the top 10 cm of the soil profile, generally restricted to the A horizon. Soils were then mailed to Kansas State University where they were passed through a 2 mm sieve and maintained at 5 °C for 10–60 days until incubations began. For each soil, we measured texture via the hydrometer method (Gee and Bauder 1979), C and N concentrations on a Leco CHN analyzer, water holding capacity (WHC) (Elliott et al. 1999), and pH in a 1:1 mixture of soil and water (Robertson et al. 1999). Climate data for each site was acquired from New et al. (2002).

To determine responses of temperature sensitivity to long-term differences in temperature, we adjusted four replicates of 20 g dry-equivalent soil to 35 % WHC and placed them in open 50 mL polyethylene centrifuge tubes. Two replicates were incubated at 20 °C, another at 10 °C and a fourth at 30 °C. Periodically, the 4 replicates for each soil were sealed with a cap in which was placed a rubber septum and incubated at their respective temperatures for 18–72 h. At the end of the incubation, 4 mL of air was removed from each tube, the gas injected in-line into an N_2 gas stream, and the peak heights measured with a Licor 6252 infra-red gas analyzer (LiCor, Lincoln, NE, USA). Via frequent 2-point calibrations using a standard gas (390 ± 1 ppm), peak heights were converted to CO_2 concentrations in the tubes. CO_2 concentrations were compared with CO_2 concentrations of empty tubes sealed at the beginning of the incubation to determine initial CO_2 concentrations in the vial in order to determine respiration rates, which were scaled relative to soil organic C. This process was repeated 15 times over 365 d (1, 15, 22, 29, 41, 55, 74, 102, 163, 197, 227, 260, 291, 337, and 365 d).

After 365 d of incubation, all four long-term replicates were then placed at 20 °C for 48 h. 400 mg of glucose was added to each soil, the tubes capped after 20 min of equilibration, and respiration rates were determined after 2–4 h. This substrate induced respiration (SIR) was used as an index of potential respiration rate of the microbial community (Fierer et al. 2003; Wardle and Ghani 1995).

To determine the sensitivity of microbial decomposition of soil C to these long-term differences in

temperature, we first determined cumulative respiration for each soil at each temperature with discrete integrations of respiration (Craine et al. 2007). A nonlinear curve was fit to the average cumulative respiration data over time of each combination of soil and temperature by parameterizing a two-pool model (Alvarez and Alvarez 2000) with nonlinear curve-fitting in JMP 8.0.1 (SAS Institute, Cary, NC, USA):

$$C_t = C_L \times \left(1 - e^{-kLt}\right) + k_R t \quad (1)$$

where C_t is the known cumulative amount of C respired at sampling time t, C_L is the size of the labile C pool, k_L is the exponential decay constant for the labile pool, and k_R is the linear mineralization rate of the more recalcitrant pool. This model assumes an exponential decay of the labile pool, a linear decay of the recalcitrant pool (constant decay rate), and was not constrained for C_t. For 22 of the 27 soils, parameters could be determined for all three temperatures (Auxiliary material). For these 22 soils, an average of 99 % of the variation in cumulative respiration for a soil could be explained with a two-pool model.

To determine the temperature sensitivity of SOC decomposition for soils, we compared the amount of time that was required to respire equivalent units of C at different temperatures. This approach is similar to the approach of Conant et al. (2008b), but allows for comparison of temperature sensitivity across the entire range of respired carbon rather than just at individual time points. Equation 1 was solved for time t (Eq. 2) and used to calculate the amount of time it took to respire each unit of C:

$$t(C_t) = \frac{-C_L k_L + C_t k_L + k_R W\left(\frac{C_L k_L e^{k_L (C_L - C_t)/k_R}}{k_R}\right)}{k_L k_R} \quad (2)$$

where W, represents Lambert's W, also known as the product logarithm. Lambert's W function, W(x), is the complex valued function that satisfies $W(x)e^{W(x)} = x$. The function allows us to solve equations that involve linear and exponential components with the functional form of $g(x)^{g(x)} = x$ since $g(x) = e^{W(\ln(x))}$. Equation (2) was solved to a precision of 1×10^{-12} using an iterative algorithm based on Halley's method (Corless et al. 1996). The ratio of time required to respire a unit of C at the lower temperature to higher temperature (20 vs. 30 °C, 10 vs. 20 °C) is the equivalent of the Q_{10} of microbial respiration for that unit of C.

Determination of the short-term response of microbial decomposition of SOC from the same soils was taken from Craine et al. (2010). In brief, the same 27 soils were incubated at 20 °C over 1 year with replicates periodically incubated for 24–72 h at 10, 15, 20, 25, and 30 °C with longer incubations at different temperatures as the experiment progressed. Activation energy of the short-term response to temperature was assessed with the Arrhenius equation, which was then transformed into Q_{10}′s between each temperature pairing of the long-term experiment.

Average long-term Q_{10}′s could be generated across the range of respired C and then compared to short-term Q_{10}′s in a continuous fashion, but the range of C respired over the 1-year incubation varied by over an order of magnitude. Hence, comparing the pattern of Q_{10}′s with increasing cumulative C respired would vary the number and identity of soils being compared, while comparing the patterns with increasing incubation time would not be comparing similar C quality for a given soil. As such, we conservatively compared Q_{10}′s categorically rather than continuously. Q_{10}′s were compared (a) over the entire incubation period and (b) for just recalcitrant C. First, at every time point Q_{10} was calculated for short-term temperature manipulations, Q_{10} from long-term temperature manipulations was calculated with the Lambert W function at an equivalent amount of C respired. These two Q_{10} parameters were compared with orthogonal regression and paired t tests. Second, to calculate the temperature sensitivity of recalcitrant carbon when incubated under different temperatures long-term, we calculated the ratio of k_r at different temperatures for each soil. To compare with the long-term Q_{10} of recalcitrant carbon, we calculated the average Q_{10} over the last 100 d of incubation of each soil based on respiration rates at 10 and 20 °C as well as 20 and 30 °C. Short-term Q_{10}′s for soils were relatively stable during this period (Craine et al. 2010) and provide the best basis of comparison of the response of recalcitrant C to short-term increases in temperature.

Comparison of pool sizes and rates between temperatures were accomplished with paired t tests and orthogonal regressions. To examine the broad patterns of pool parameters across temperatures and soils, we ran a principal component analysis with the nine parameters (C_L, k_L, and k_R at each of three temperatures). The first two axes were subsequently rotated with Varimax rotation to strengthen contrasts.

Table 1 Eigenvectors for rotated principal components analysis

	Axis 1[a]	Axis 2[b]
C_L10	0.59	0.01
C_L20	0.83	−0.21
C_L30	0.83	−0.25
k_L10	0.01	0.41
k_L20	−0.11	0.94
k_L30	0.01	0.90
k_R10	0.85	−0.03
k_R20	0.83	0.18
k_R30	0.93	0.09

[a] Axis 1 explained 45 % of the total variation in parameters, 4.0 times more than expected by chance

[b] Axis 2 explained 22.4 % of the total variation in parameters, 2.0 times more than expected by chance

All data were analyzed in JMP 8.0.1 (SAS Institute, Cary, NC, USA).

Results

Comparing C pool dynamics among temperatures and soil

C pool parameters provide basic descriptions of the dynamics of microbial decomposition and an index of how decomposition responded to changes in temperature. Among 27 soils, soils that had large labile carbon pools had recalcitrant organic matter that decomposed relatively fast, but the labile pool did not decompose faster or slower than soils with small labile pools. In analyzing the relationships among soil C pool parameters, soils that had high C_L at a given temperature also had a high k_R (Table 1). k_L was independent of C_L and k_R among soils and temperatures (Table 1).

Although labile carbon pool size and decomposition rates of the labile and recalcitrant carbon pools all consistently scaled across temperatures, increased long-term temperature generated a larger apparent labile C pool with both labile and recalcitrant C being decomposed faster (Fig. 1). Soils that had high C_L at 20 °C also had high C_L at 10 and 30 °C (Table 2). Likewise, soils that had high k_L or k_R at 20 °C also had high k_L or k_R at 10 and 30 °C. As temperature increased, the size of the labile pool increased while both labile and recalcitrant organic matter decomposed faster. C_L more than tripled from 10 to 30 °C (364.3, 707.5, 1209.2 μg g^{-1} for 10, 20, and 30 °C, respectively). Across the same temperature range, k_L increased 60 % (0.017, 0.023, and 0.028 h^{-1}, respectively) and k_R increased almost fourfold (1.32, 2.86, 5.19 μg g^{-1} h^{-1}, respectively).

Comparing temperature sensitivity among soils

With C pool parameters generated across soils and temperatures, long-term temperature sensitivity patterns could be generated over time. The sensitivity of microbial respiration to long-term differences in temperature early in the incubations was greater at low temperatures than high temperatures. Initially, for the 22 soils for which the two-pool model could be fit for all three temperatures, Q_{10} between 10 and 20 °C was 3.01 and peaked at 4.25 by the 350th μg C (Fig. 2). Between 20 and 30 °C, Q_{10} was initially 2.23 and peaked to 3.10 also by the 350th μg C. Q_{10} between the higher temperatures was consistently less than at the lower temperatures, averaging 28 % less over the first 1,000 μg g^{-1} C and 36 % less over the last 1,000 μg g^{-1} C.

Across the year-long incubation, Q_{10}′s derived from short-term manipulations of temperature were correlated with ($r = 0.49$) but on average were significantly higher than Q_{10}′s generated from long-term manipulations of temperature when compared at the same unit of carbon respired (geometric means: 3.31 vs. 2.76, respectively, $P < 0.001$; Fig. 3). Comparing Q_{10}′s for the C categorized as recalcitrant from the 2-pool model for 22 soils, Q_{10}′s compared for just recalcitrant C were greater for short-term manipulations of temperature when compared to long-term differences in temperature. Short-term Q_{10} of recalcitrant C averaged 3.63, compared to 3.09 for long-term Q_{10} between 10 and 20 °C, and 1.90 for long-term Q_{10} between 20 and 30 °C. The short-term Q_{10} of recalcitrant C correlated positively with long-term Q_{10} for 10 and 20 °C (Fig. 3; $r = 0.46$, $P = 0.03$). In contrast, there was no relationship between the Q_{10} derived from short-term manipulations of temperature and long-term manipulations at 20 and 30 °C ($P = 0.5$). There were no relationships between either long-term recalcitrant C Q_{10} (10–20 °C or 20–30 °C) and site climate or soil parameters such as soil pH, [C], or texture category ($P > 0.1$).

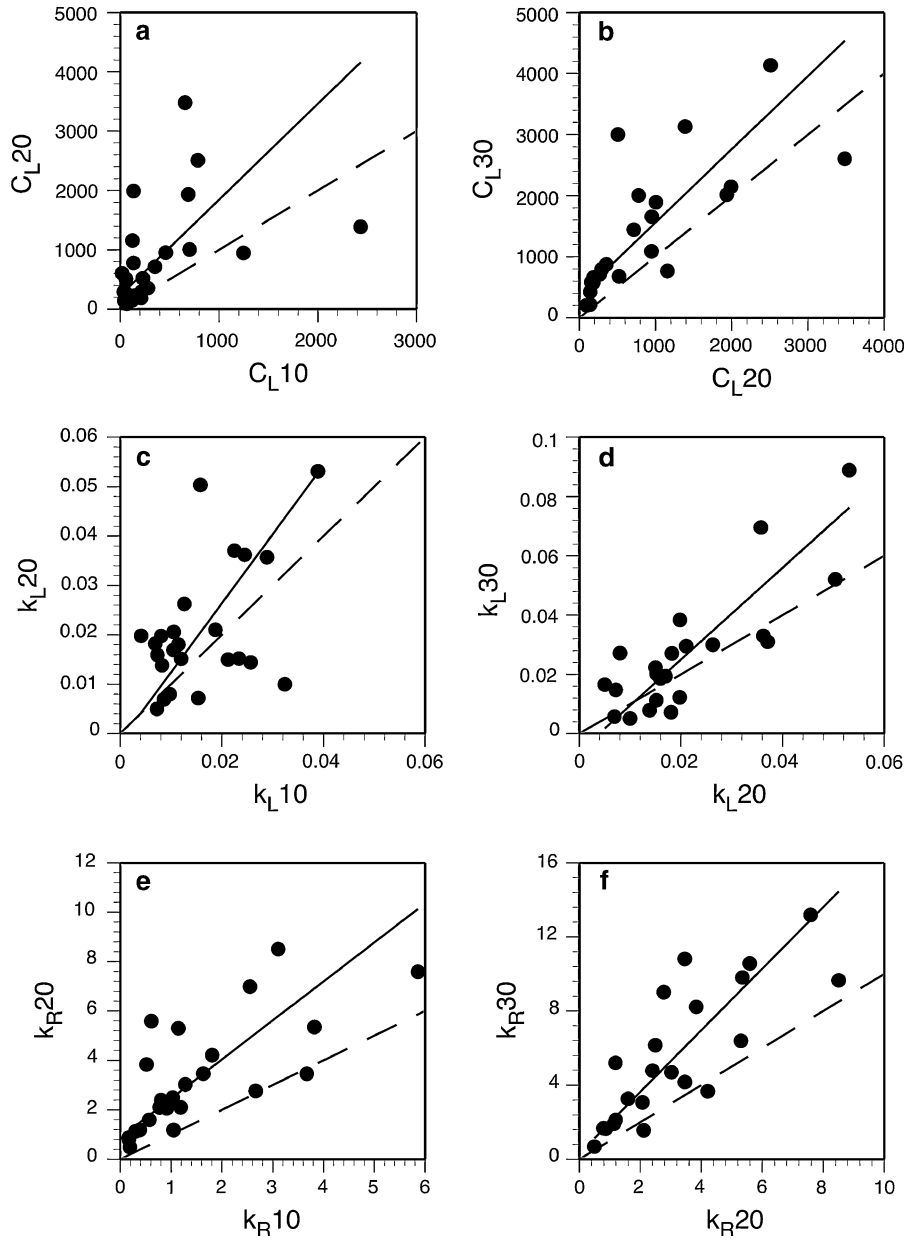

Fig. 1 Relationships among soil C pool parameters. *Solid lines* are orthogonal regressions. *Dashed lines* are 1:1. Units for C_L are μg C g^{-1}; k_L μg C g^{-1} h^{-1}; k_R is unitless

Potential respiration rates after one year

The lower Q_{10} with long-term manipulations of temperature compared to short-term manipulations was associated with a down-regulation of the active microbial biomass pool as determined by measuring standardized potential microbial activity under substrate-unlimited conditions. In general, for each temperature, soils that had higher unamended respiration rates had higher amounts of active microbial biomass (Fig. 4). Increasing temperature increased the rate of respiration of carbon and soils incubated at 30 °C still had the highest respiration rates at the end of one year. Yet, when compared at a common temperature, active microbial biomass levels decreased with long-term soil temperature. SIR_{20} declined by over 70 % from 10 to 30 °C (61.21 ± 5.57, 46.43 ± 4.93, 18.33 ± 5.03).

Table 2 Correlation coefficients between soil C pool parameters

	C_L20	C_L30	k_L10	k_L20	k_L30	k_R10	k_R20	k_R30
C_L10	**0.58**	**0.49**	**−0.32**	0.00	0.10	0.13	**0.62**	**0.72**
C_L20		**0.64**	−0.27	−0.20	0.07	**0.78**	**0.70**	**0.79**
C_L30			0.22	−0.19	−0.26	**0.66**	**0.86**	**0.61**
k_L10				**0.28**	0.18	0.10	0.13	−0.11
k_L20					**0.70**	−0.02	0.10	0.19
k_L30						0.01	0.02	0.28
k_R10							**0.70**	**0.61**
k_R20								**0.88**

Bold indicate significant at $P < 0.05$

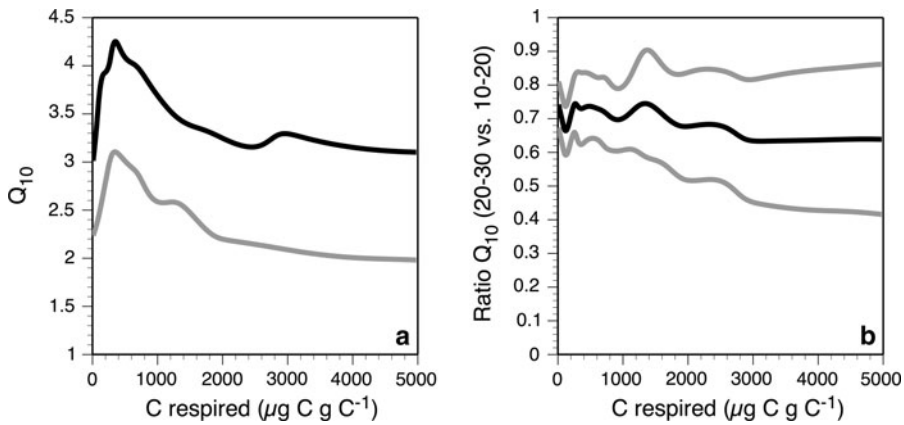

Fig. 2 Changes in Q_{10} in response to long-term increases in temperature among 22 soils compared for the same units of carbon respired. Shown are Q_{10}′s (± s.e.) between 10 and 20 °C (*black line*) and 20 and 30 °C (*gray line*). Calculations of Q_{10} were calculated out to 2,000 μg g^{-1} C for all 22 soils. The ratio of the Q_{10} at the higher temperature range and the lower temperature range (*black line* with 95 % C·I in *gray*) is shown in b

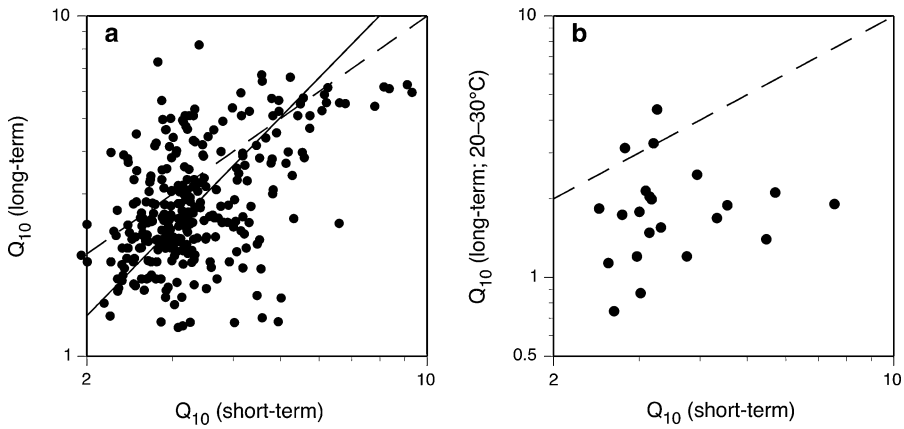

Fig. 3 Relationships between Q_{10} of C derived from short-term manipulations of temperature and Q_{10} derived from long-term manipulations of temperature **a** over the entire year-long incubation with long-term Q_{10} estimated at each time point from Lambert's equation and, **b** for recalcitrant C with long-term Q_{10} calculated from ratio of respiration rates between 30 and 20 °C over the last 100 d of incubation. *Solid lines* are orthogonal regression. *Dashed lines* are 1:1

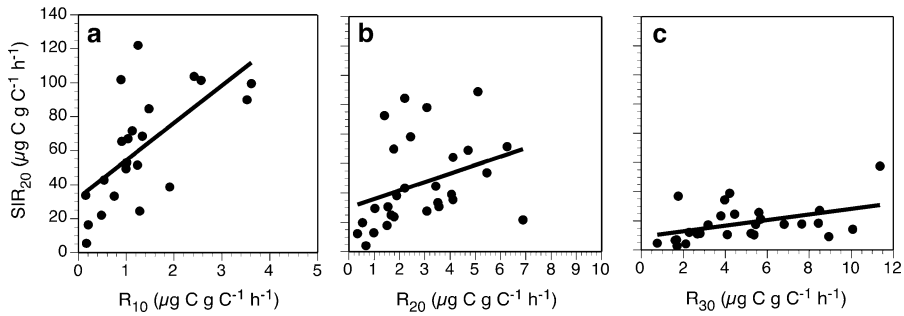

Fig. 4 Relationships between soil respiration rates at 10, 20 and 30 °C of soils incubated long-term at these temperatures and respiration rate of the same soils at 20 °C when provided glucose, i.e. substrate induced respiration

Discussion

In response to increasing temperature short-term for 20 to 30 °C, respiration rates increased more than threefold on average across soils. Yet, in response to long-term increases in temperature, respiration rates increased approximately half as much as they did to short-term increases in temperature. The lowered response to long-term temperature increases (determined from examining the ratios of k_R's at different temperatures) cannot be explained by substrate depletion since microbial respiration rates were compared at the same level of cumulative carbon reduction. Increasing temperatures long-term increased the apparent amount of available C, as has been observed before (Conant et al. 2008b; Haddix et al. 2011; Waldrop and Firestone 2004). If anything, greater availability of C with increased temperature would lead to increased, not reduced, temperature sensitivity of respiration with long-term temperature increases.

The pattern of reduced temperature sensitivity for the long-term temperature increases suggests some type of acclimation by the microbial community. These could include a reduction in the size of the microbial community, reduced enzymatic degradation potential, or reduced carbon use efficiency (Allison et al. 2010). The reduced size of the active microbial biomass pool (determined via SIR) at the end of the incubation under long-term versus short-term temperature increases (and greater SIR with long-term temperature reductions) suggest that long-term temperature increases reduce the metabolic potential of soil microbial communities. Yet, the SIR patterns are only a demonstration of change, not necessarily a mechanism for the observed acclimation, since we were not able to compare SIR for short- and long-term temperature manipulations holding cumulative C respired constant. As such, it is uncertain whether the reduced temperature sensitivity can be explained solely by a reduction in microbial biomass or a reduction in the potential activity of the biomass (Hartley et al. 2008b).

The most striking pattern observed was the collapse of Q_{10} for recalcitrant C with long-term increases. There was no relationship between short-term Q_{10} over the last 100 d and the Q_{10} of recalcitrant C warmed long-term. Between 20 and 30 °C, Q_{10} of recalcitrant C averaged just 1.9 compared to 3.6. Although some soils had a long-term Q_{10} that was the same or greater than the short-term Q_{10}, e.g. soil from Kellogg Biological Station (4.4 vs. 3.3), long-term temperature increases reduced the temperature sensitivity of decomposition compared to short-term temperature increases. For example, soils from the Florida Coastal Everglades exhibited a short-term Q_{10} of 7.6, but just 1.9 under long-term temperature increases. These results suggest that parameterizing ecosystem carbon models with a Q_{10} of 2.0 for microbial decomposition might not be unrealistic for a given temperature range if empirical responses to increased temperature follow the responses to long-term increases in temperature observed here.

Conclusions

In all, under isolated conditions, it is clear that there is a reduction in the temperature sensitivity of the microbial community to long-term versus short-term increases in temperature. Due to the ever-changing nature of soil temperatures, determining the fate of soil organic matter to increased temperature will require models that incorporate responses to both short-term and long-term increases in temperature. Still, more research is necessary to begin to match the results of field warming experiments with laboratory incubations.

For example, the rate of temperature sensitivity reduction is still unknown, which is an important factor in partitioning responses of decomposition to short-term and long-term temperature changes. In addition, whether the collapse of Q_{10} of recalcitrant C to ~ 2 with sustained temperature increases at relatively high temperatures represents an appropriate characterization of the temperature sensitivity of recalcitrant OM or might be biased by the lack of labile C inputs with ex situ incubations (Fontaine et al. 2007; Subke et al. 2004; Zhu and Cheng 2011) remains to be seen. The difference in temperature sensitivity reduction at different temperature ranges might suggest that the underlying processes are temperature-sensitive or increase with increasing organic matter recalcitrance, which makes model parameterization even more complex.

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