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REVIEW

Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward

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Abstract

The response of soil organic matter (OM) decomposition to increasing temperature is a critical aspect of ecosystem responses to global change. The impacts of climate warming on decomposition dynamics have not been resolved due to apparently contradictory results from field and lab experiments, most of which has focused on labile carbon with short turnover times. But the majority of total soil carbon stocks are comprised of organic carbon with turnover times of decades to centuries. Understanding the response of these carbon pools to climate change is essential for forecasting longer-term changes in soil carbon storage. Herein, we briefly synthesize information from recent studies that have been conducted using a wide variety of approaches. In our effort to understand research to-date, we derive a new conceptual model that explicitly identifies the processes controlling soil OM availability for decomposition and allows a more explicit description of the factors regulating OM decomposition under different circumstances. It explicitly defines resistance of soil OM to decomposition as being due either to its chemical conformation (*quality*) or its physico-chemical protection from decomposition. The former is embodied in the depolymerization process, the latter by adsorption/desorption and aggregate turnover. We hypothesize a strong role for variation in temperature sensitivity as a function of reaction rates for both. We conclude that important advances in understanding the temperature response of the processes that control substrate availability, depolymerization, microbial efficiency, and enzyme production will be needed to predict the fate of soil carbon stocks in a warmer world.

Keywords: decomposition, experiments, new conceptual model, review, soil carbon, temperature sensitivity

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Introduction

There is considerable uncertainty about whether or not ecosystem models can predict the response of carbon pools to warming (Friedlingstein *et al*., 2006). A useful heuristic for evaluating model predictions is to determine whether or not they are consistent with first principles, such as kinetic theory. Widely applied ecosystem models are largely consistent with kinetic theory describing chemical reactions (Arrhenius, 1889) in that when substrate availability and enzyme activity do not constrain reaction rates, decomposition rates increase with temperature (Burke *et al*., 2003; Davidson & Janssens, 2006; Friedlingstein *et al*., 2006). Some models are also consistent with a second component of kinetic theory, that increases in decomposition rates with warming temperatures should be greatest at cold temperatures (e.g., Del Grosso *et al*., 2005), which has been widely

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observed in field soil respiration (Lloyd & Taylor, 1994) and soil incubation experiments (Kirschbaum, 1995). When applied at regional and global scales, such models can reliably reproduce observed distributions of soil carbon stocks. The ability of models to reproduce patterns of soil carbon stocks across space does not necessarily mean they will accurately forecast global change-driven changes in soil carbon stocks (see Ågren & Bosatta, 2002; Ise & Moorcroft, 2006). The duration of most global change experiments is short relative to the mean residence time of slowly cycling soil OM pools, making forecasting changes in long mean residence time soil OM pools difficult. The third component of kinetic theory implies that decomposition reactions with high activation energies (i.e., slow rates) will experience greater proportional increases with increasing temperature than will those with low activation energy (i.e., fast rates). While this component of kinetic theory could inform our understanding of the longer-term response of decomposition to temperature, its applicability to soil OM decomposition remains uncertain (Davidson & Janssens, 2006; Von & Kögel-Knabner, 2009).

Much of the debate about the fate of soil carbon stocks in a warmer world, which we review below, centers on the third component of the kinetic theory. We believe that at least part of that debate arose because of incorrect assumptions and imprecise terminology. Because our article focuses on a better understanding of the factors regulating soil carbon decomposition, we believe that it is important to clarify these issues first. A common assumption in this debate is that an increased response in the *rate* of decomposition of less decomposable substrates will result in large soil carbon losses. Such a rate increase may or may not be important, depending on the decomposition rate before the temperature change. The decomposition rate of the least decomposable soil carbon may be kinetically very sensitive to temperature, but the decomposition rate may be so slow that little carbon would decompose no matter what the temperature.

The third component of kinetic theory lurks behind a series of controversies in the literature on this topic – advances followed by refutations and extensive debates. Based on soil carbon stock and ^{14}C data from across a latitudinal temperature gradient, Liski *et al.* (1999) concluded that the decomposition rate of old soil carbon responds little to temperature. Analysis by Ågren (2000) suggested that model construction influenced interpretation of observations, though the likelihood of that was questioned (Liski *et al.*, 2000). Giardina & Ryan (2000) showed that for both long-term (ca. 1 year) incubations and 5–50 year vegetation replacement cross-site studies, bulk soil carbon decomposition rates differed very little with mean annual temperature. However, representing responses of soil carbon to temperature as a single pool with a single temperature response may obscure a temperature response for some components of soil OM (Davidson *et al.*, 2000), and an increase in the proportion of slowly decomposing soil carbon with mean annual temperature could also have yielded a lack of a bulk temperature response across sites. Knorr *et al.* (2005) identified potential problems with making inferences based on results from short-term incubations at different temperatures: varying either soil carbon pool sizes or decomposability[1] with temperature can explain observed variation in CO_2 fluxes. Subsequent analyses using the same or similar data (Reichstein *et al.*, 2005a; Fang *et al.*, 2006; Kätterer *et al.*, 2008) confirm the challenges of using model fits to incubation data to draw conclusions about the response to temperature of slowly decomposing soil OM. Turnover time responses estimated from soils at steady state are much less responsive to temperature than turnover times estimated from incubating the same soils over short periods of time at different temperatures (Ågren & Bosatta, 2002).

The relationship between decomposability and response of the decomposition rate to temperature and the fate of soil carbon in a warmer world remain unresolved and have been addressed differently in leading climate-carbon models (Huntingford *et al.*, 2009). The unknowns in these two issues make predictions of feedbacks to atmospheric CO_2 concentrations from soil carbon uncertain (Zhou *et al.*, 2009; Janssens & Vicca, 2010). We argue that the debate should be refocused to examine how temperature affects the various factors controlling the decomposability of SOM. The use of the term 'temperature sensitivity'[2] also causes much confusion and misunderstanding, because it has been used to refer to the temperature response of bulk soil carbon, of individual components of soil carbon (e.g., active vs. slow vs. passive), and the kinetic response of the enzymes that depolymerize complex molecules to the simpler ones available for microbial uptake. It could also refer to the temperature response of substrate availability, aggregate protection, microbial enzyme production, microbial uptake or microbial metabolic efficiency. Similarly, definitions of 'acclimation' that are oriented toward either organisms or ecosystem can lead to con-

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[1] We use the term decomposability to signify differences in decomposition rates.

[2] We define temperature sensitivity as the rate of a process (i.e., decomposition, de-sorption, etc.) at one temperature relative to the rate at a control temperature. Q_{10} – the factor change in a response variable (often CO_2 flux) for a 10 °C change in temperature – is one example of a measure used to describe temperature sensitivity.

trasting definitions of response variables, and undermine clear discussion of results (see Hartley *et al.*, 2008; Bradford *et al.*, 2010). We suggest that future articles refer to the specific process – for example, the 'temperature sensitivity of enzyme kinetics' – and state specifically how they measure temperature sensitivity (e.g., Q_{10}, relative rates at an intermediate temperature, etc.).

Herein, we briefly review the recent literature on the relationship between the response of the decomposition rate to temperature and soil OM decomposability. We show the limitations of current approaches, and suggest other important factors that need to be considered to predict the response of soil carbon stocks to an increase in temperature. We then present a new conceptual framework intended to improve these predictions and guide wider-ranging efforts to understand temperature controls on decomposers and substrate availability. We discuss the implications of this conceptual model within the context of the broader literature on soil carbon decomposition and stabilization and temperature sensitivities of several processes involved in decomposition. From this knowledge base we distill a set of recommendations intended to guide future research.

Studies investigating the relationship between decomposability and the response of decomposition rate to temperature

Incubation studies

Most of the recent work investigating the relationship between decomposability and the response of decomposition rate to temperature has been based on laboratory incubations. Incubation experiments have isolated soil OM fractions with different mean residence times in the soil (Leifeld & Fuhrer, 2005; Feng & Simpson, 2008; Karhu *et al.*, 2010; Plante *et al.*, 2010) or litter (Malcolm *et al.*, 2009; Wetterstedt *et al.*, 2010), or have added compounds with varying decomposability (Fierer *et al.*, 2005; Gillabel *et al.*, 2010). Progressive enrichment of soil δ^{13}C (Biasi *et al.*, 2005; Rasmussen *et al.*, 2006) and ^{14}C (Dioumaeva *et al.*, 2002; Bol *et al.*, 2003) has been used to track changes in the response of decomposition rate to temperature over time, as has depletion of soil OM during incubation (Fang *et al.*, 2005; Reichstein *et al.*, 2005a; Koch *et al.*, 2007; Conant *et al.*, 2008b; Hartley & Ineson, 2008; Fissore *et al.*, 2009b; Craine *et al.*, 2010) and loss of newly derived soil carbon identified using changes in δ^{13}C associated with C_3/C_4 plant shifts (Waldrop & Firestone, 2004; Conen *et al.*, 2006; Haddix, 2007; Vanhala *et al.*, 2007). Two studies used depth as a surrogate for decomposability (Lomander *et al.*, 1998; Karhu *et al.*, 2010) and another related C : N ratio of the light fraction to the response of the whole soil to temperature (Schindlbacher *et al.*, 2010). Data from concurrent incubations at different temperatures have also been used to assess the effect of decomposability on the response of decomposition rate to temperature (Conant *et al.*, 2008a; Fissore *et al.*, 2008, 2009b; Gillabel *et al.*, 2010; Zimmermann *et al.*, 2010).

The majority of published incubation studies suggest that the decomposition rate of slowly decomposing soil carbon responds more to temperature than the decomposition rate of more rapidly decomposing soil carbon. All whole-soil incubation experiments that minimized the influence of the soil mineral matrix, and so minimized the influence of substrate availability, are consistent with the third component of kinetic theory (Coûteaux *et al.*, 2001, 2002; Fierer *et al.*, 2005; Reichstein *et al.*, 2005b; Conant *et al.*, 2008a; Feng & Simpson, 2008; Malcolm *et al.*, 2009; Gillabel *et al.*, 2010; Wetterstedt *et al.*, 2010). With the exception of one (Plante *et al.*, 2010), all experiments that evaluated the response of decomposition rate to temperature of different soil OM fractions found that those fractions that decomposed more slowly had decomposition rates that responded proportionally more to temperature than did the more readily decomposable substrates (Bol *et al.*, 2003; Biasi *et al.*, 2005; Leifeld & Fuhrer, 2005; Yuste *et al.*, 2007; Malcolm *et al.*, 2009; Karhu *et al.*, 2010; Plante *et al.*, 2010). Three (Waldrop & Firestone, 2004; Haddix, 2007; Vanhala *et al.*, 2007) out of four (Conen *et al.*, 2006) experiments that used plant-derived shifts in ^{13}C composition found that response of decomposition rate to temperature of old soil carbon was greater than that for newly derived soil carbon, though this approach is biased in favor of such results (Conant *et al.*, 2010).

In summary, when the influence of the mineral matrix is limited (when the decomposition of soil carbon compounds or fractions with varying rates of decomposition are isolated) those compounds or fractions that decompose more slowly have a greater decomposition-rate response to temperature. In contrast, incubation studies in which substrate availability potentially has a much greater effect on decomposition show mixed results with some showing that the decomposition rate of less decomposable carbon responds *less* to temperature than that of more decomposable carbon (Fig. 1).

Field studies

Data from long-term field warming experiments, like those in the tallgrass prairie of the Central Plains (Luo *et al.*, 2001), temperate deciduous forests at Harvard Forest (Melillo *et al.*, 2002), and the boreal forest at Flakaliden (Strömgren, 2001) suggest that increased rates of soil respiration observed in the first several years of warming do not persist. One explanation for

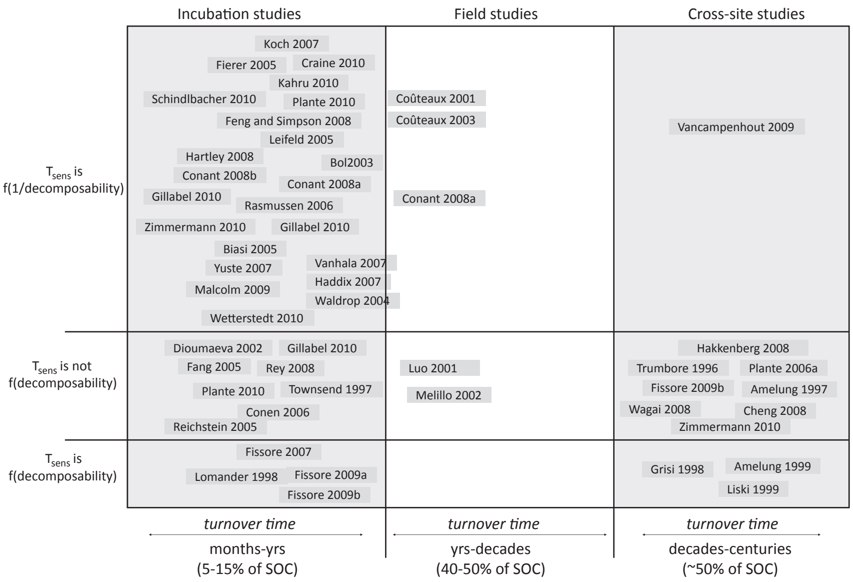


Fig. 1 The majority of incubation studies have found that decomposition rates of slowlydecomposing soil OM are more sensitive to temperature [i.e., T_{sens} = f(1/decomposability), as indicated on the *y*-axis], consistent with the predictions of basic thermodynamics. However, as shown by the range each two-headed arrow covers on the *x*-axis, incubation studies are necessarily confined to describing the responses of the most readily decomposable 5–15% of soil OM. Long-term, cross-site studies indicate the decomposition of the most slowly decomposing soil OM is relatively insensitive to temperature.

this is acclimation of decomposer organisms to the new temperature conditions (Luo *et al.*, 2001), but such observations can also be explained by loss of readily available substrate (Kirschbaum, 2004; Eliasson *et al.*, 2005). Bradford *et al.* (2008) found evidence for both mechanisms in the Harvard Forest study.

Interpretation of CO_2 efflux data from field warming experiments is complicated by warming-induced changes in belowground allocation, root respiration, and net primary production, all of which can affect commonly measured response variables, such as soil OM stocks and CO_2 flux, independently of the temperature effect (Subke & Bahn, 2010). The temporal and spatial heterogeneity of soil respiration may also prevent detection of statistically significant differences in the response to temperature of the decomposition rate of pools that turn over very slowly and contribute little to instantaneous flux. Yet, over long time scales, these small changes can be very significant (Kirschbaum, 2004). Three studies have examined relationship between decomposability and the response of decomposition rate to temperature in the field using long-term litter bag experiments (Coûteaux *et al.*, 2001, 2002; Conant *et al.*, 2008a).

The existing field studies are of limited value for discerning long-term response of soil carbon stocks, because (1) differences in belowground carbon inputs and the difficulty in isolating carbon with different decomposabilities makes them subject to different interpretations, and the implications of the results uncertain (Luo *et al.*, 2001; Melillo *et al.*, 2002; Kirschbaum, 2004; Eliasson *et al.*, 2005; Braakhekke & De, 2007; Bradford *et al.*, 2008) or (2) they focus only on litter (Coûteaux *et al.*, 2001, 2002; Conant *et al.*, 2008a).

Cross-site studies

If slowly-decomposing soil OM has a decomposition rate that responds more to temperature, then soils found in warmer locations should be relatively depleted in soil carbon that decomposes slowly, and vice versa. Testing this hypothesis requires that other factors that affect soil carbon decomposition and stabilization, such as precipitation, soil carbon input amount and quality, soil texture, mineralogy, etc., remain constant. Several field studies have examined how mean annual temperature affects soil carbon mean residence time (e.g., Trumbore *et al.*, 1996; Liski *et al.*, 1999; Fissore *et al.*, 2009a) and soil OM quality (e.g., Amelung *et al.*, 1997; Grisi *et al.*, 1998) and relative enrichment of soil OM compounds and fractions that resist decomposition (Trumbore *et al.*, 1996; Amelung *et al.*, 1997; Grisi *et al.*, 1998; Plante *et al.*, 2006; Cheng *et al.*, 2008; Hakkenberg *et al.*, 2008; Fissore *et al.*, 2009b; Sollins *et al.*, 2009; Vancampenhout *et al.*, 2009; Wagai *et al.*, 2009; Zimmermann *et al.*, 2010). Studies that have examined soil OM turnover and differential enrichment across temperature gradients have most often found no relationship (Trumbore *et al.*, 1996; Amelung *et al.*, 1997; Plante *et al.*, 2006; Cheng *et al.*, 2008; Hakkenberg *et al.*, 2008; Wagai *et al.*, 2008; Fissore *et al.*, 2009a; Zimmermann *et al.*, 2010). This may be because the 'other factors' listed above are nearly impossible to keep constant, so the temperature gradient is confounded with some other factor that affects soil OM decomposition or stabilization. These studies are qualitatively different than laboratory and field experiments because they are not active manipulations of conditions to examine the impacts of temperature (Ågren & Bosatta, 2002). Gradient studies are also different because the response variable is a change in temperature-driven equilibrium of soil OM mass or quality rather than CO_2 flux, shift in $^{13}CO_2$ signature, or loss of mass (as for field and laboratory experiments) driven by a change in reaction kinetics.

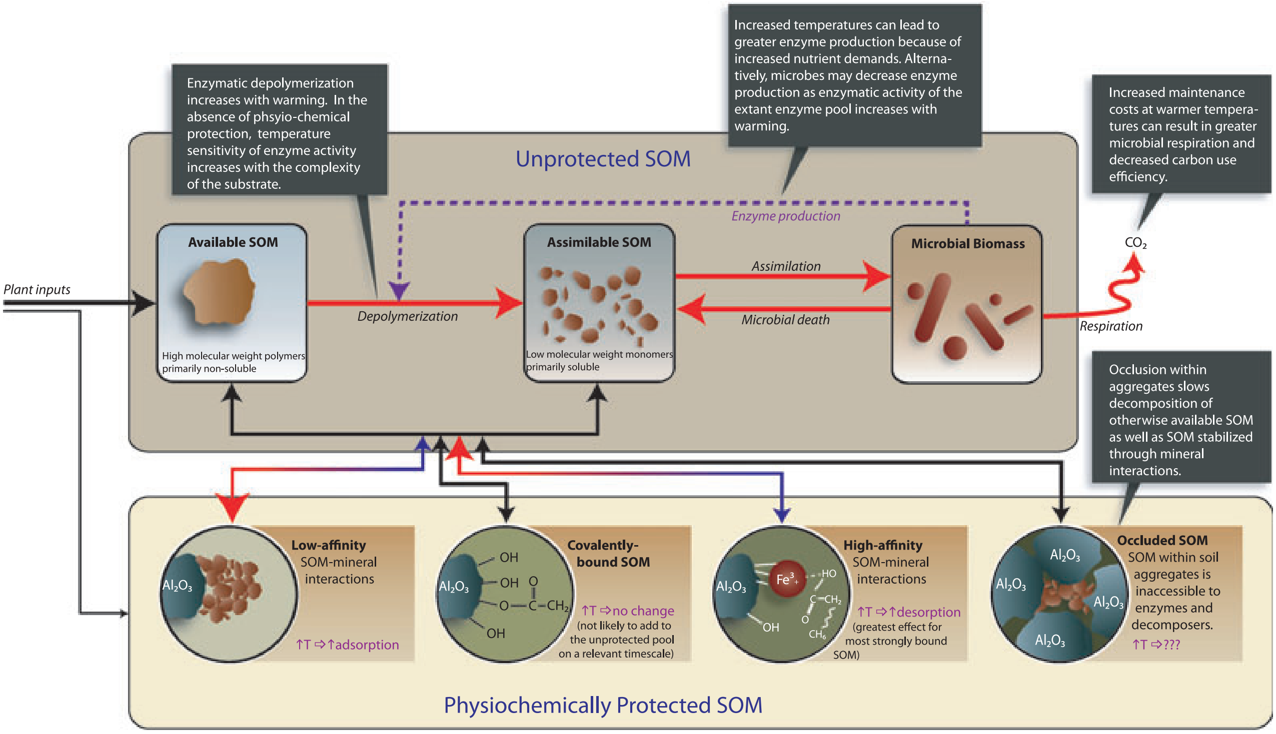
Synthesis of current state of knowledge

When substrate is available, the decomposition rate of less decomposable substrates appears to respond more to temperature than the decomposition rate of readily decomposable substrates. However, processes controlling substrate availability and the response of those processes to temperature as well as the intrinsic decomposition rate of the less decomposable compounds are also critically important (Kleber *et al.*, 2011). The dearth of studies examining the soil OM pool that takes decades to turn over (and which is likely to dominate responses to global change in the coming decades) is a major shortcoming of research to-date (see Fig. 1). Appropriate field experiments are difficult to implement and interpret while gradient studies are constrained by our limited ability to control for factors other than temperature. We believe that incubation studies have a limited utility to shed additional light on the issue of temperature controls on changes in soil carbon stocks, except to the extent that they help us understand temperature controls on the components of decomposition of available OM. Even very long-term incubations likely capture little information about decomposition of the larger soil OM pools that are of the greatest interest for understanding bulk soil carbon responses to warmer temperatures. We believe that *in situ* measurements of soil respiration in response to treatments or different temperatures will also contribute little to understanding soil carbon response to temperature. In the field, perhaps only 10% or less of soil respiration is derived from the decomposition of older soil carbon (Giardina *et al.*, 2004), yielding a very small signal to separate from the noise of respiration of recent material. Using respiration as a response variable to understand the dynamics of the slowly decomposing soil carbon pools is challenging (Subke & Bahn, 2010). In addition, the variable allocation of microbial carbon uptake into growth and respiration complicates the use of respiration as a proxy for decomposition rates.

A way forward through a new conceptual framework

Uncertainty and disagreement about how to interpret experimental results prompted Reichstein *et al.* (2005a) to suggest that new experimental approaches need to be formulated based on an ongoing dialog between modelers and experimentalists. We concur. A critical component for moving forward is to recognize the multi-component nature of the problem and the complications arising because of interactions, which sometimes even can be counteracting, between components. We believe that the shortcomings of past work are not just in the methods used, but in a more fundamental failure to clearly identify why some OM resists decomposition and to integrate that knowledge into experiments, as recently articulated by Kleber *et al.* (2011). We propose a new conceptual framework that we believe may help resolve some of the inconsistencies in observations and help guide future investigations (Fig. 2). Our framework distinguishes soil OM *available* for decomposition from that which can be *assimilated* into microbial biomass and also distinguishes the different steps of the decomposition process – depolymerization, uptake, and microbial catabolism – from the processes that make soil OM available for decomposition (adsorption/desorption and aggregate turnover). This conceptual model more explicitly identifies the processes controlling soil OM availability for decomposition and allows a more explicit description of the factors regulating OM decomposition under different circumstances. It explicitly defines resistance of soil OM to decomposition as being due either to its chemical conformation (*quality*) or its physico-chemical protection from decomposition. The former is embodied in the depolymerization process, the latter by adsorption/desorption and aggregate turnover. We hypothesize a strong role for variation in temperature sensitivity as a function of reaction rates for both.

Our conceptual model facilitates moving from general questions about the interaction between decomposability and the response of decomposition rates to temperature to more specific studies examining temperature controls on the processes affecting decomposition rates – whether due to protection by the soil matrix or because soil OM compounds are biochemically complex and of low quality, and therefore recalcitrant. The conceptual framework presented herein allows the question of the general temperature controls on decomposition to be supplanted with questions of the temperature dependence of specific mechanisms controlling



Enzymatic depolymerization increases with warming. In the absence of physio-chemical protection, temperature sensitivity of enzyme activity increases with the complexity of the substrate.

Increased temperatures can lead to greater enzyme production because of increased nutrient demands. Alternatively, microbes may decrease enzyme production as enzymatic activity of the extant enzyme pool increases with warming.

Increased maintenance costs at warmer temperatures can result in greater microbial respiration and decreased carbon use efficiency.

Occlusion within aggregates slows decomposition of otherwise available SOM as well as SOM stabilized through mineral interactions.

Fig. 2 A new conceptual model of decomposition illustrating organic matter pools and fluxes. Lines indicate OM fluxes, with the dashed line signifying the OM flux associated with enzyme production and its contribution to OM depolymerisation. Red arrows (and red arrowheads) indicate that rates accelerate with increasing temperature while those in blue indicatethat rates slow with warming temperatures. Black arrows are fluxes for which temperature controls are poorly understood (e.g., type of OM released from chemical protection) or beyond the scope of this review (plant inputs). Physical protection slows depolymerization of otherwise available SOM and exchange of chemically protected SOM, but its response to temperature is not well understood. Temperature response of chemical protection varies as a function of the type of binding (covalent bonds are effectively irreversible on short time-frames) and bonding affinity (temperature effects on diffusion processes dominate for low-affinity mineral-bound SOM while desorption dynamics dominate for high-affinity SOM). As physiochemically protected SOM becomes available for decomposition some may be assimilable, but we expect that most will require depolymerization before it can be assimilated by microbes.

carbon availability and decomposability. All of the results reviewed above integrate responses of multiple processes identified in our model. Even studies that minimized the influence of the mineral matrix, but used either CO_2 or depletion of substrate as response variables, integrate multiple processes, each of which could have an impact on the relationship between decomposability and temperature sensitivity.

Temperature controls on microbes and decomposition

Enzymatic depolymerization. One of the primary reasons for expecting OM decomposition to increase with short-term temperature rise is that the rate of enzyme-mediated reactions increases sharply with increasing temperature, especially in the low-temperature range (Davidson *et al.*, 2006; Kirschbaum, 2006; Lawrence *et al.*, 2009; Wallenstein *et al.*, 2009, 2010). When OM in soils is physically accessible, it is vulnerable to degradation by extracellular enzymes that are produced by soil microbes. Microbes can only assimilate soluble, low molecular weight compounds (i.e., *assimilable* carbon in Fig. 2), and thus need to break down, or depolymerize, most of the constituents of soil OM to access the nutrients and energy contained within. Extracellular enzymes degrade soil OM through hydrolytic or oxidative processes, producing assimilable dissolved OM that is rapidly incorporated by microbes. It has been suggested that the rate of dissolved OM production is the rate-limiting step in decomposition and respiration (Bengtson & Bengtsson, 2007), and that the enzymatic depolymerization of OM is also the rate-limiting step in N mineralization (Schimel & Bennett, 2004). As defined in our conceptual model, the depolymerization process is analogous to an enzyme-mediated chemical reaction, suggesting that those depolymerization reactions that happen more slowly (i.e., of the lowest quality soil OM) are likely to be the most temperature sensitive.

Rates of enzymatic depolymerization of available OM in soils are primarily determined by the frequency of substrate-enzyme interactions, which is a function of the concentration of enzymes and available OM within the soil matrix. The size of the enzyme pool is controlled both by microbial production of enzymes and the rate of enzyme turnover. Temperature affects both production and turnover of extracellular enzymes in soils (since turnover is partially due to protease activity), thus possibly indirectly affecting the relationship between decomposability and temperature sensitivity, as recently pointed out by Cusack *et al.* (2010). For example, since enzyme activity of the extant pool should increase with temperature, microbes may downregulate enzyme production, especially as substrate or other resources become limiting (Allison *et al.*, 2010a).

Several studies have demonstrated that the temperature sensitivity of extracellular enzymes changes seasonally (Fenner *et al.*, 2005; Trasar-Cepeda *et al.*, 2006; Koch *et al.*, 2007; Wallenstein *et al.*, 2009), consistent with trade-offs in enzyme binding abilities and catalytic rates (Hochachka & Somero, 2002; Angilletta, 2009). Some research suggests that thermal adaptation in enzyme function can affect whole-soil heterotrophic respiration (Bradford *et al.*, 2008, 2009, 2010). Aquatic research shows that individual microorganisms (Hochachka & Somero, 2002; Hahn & Pöckl, 2005) and microbial communities (Grzymski *et al.*, 2008) maintain isoenzymes with different temperature optima. The most parsimonious explanation for temperature-driven changes in microbial function (e.g., growth, OM mineralization) observed over a few weeks to years is that genotypes with different temperature optima change in abundance when the thermal regime is shifted (Barcenas-Moreno *et al.*, 2009; Bradford *et al.*, 2010).

Microbes, plants, and animals all exhibit well-established, evolutionary trade-offs that occur during adaptation of respiratory metabolism to ambient thermal regimes (Hochachka & Somero, 2002; Angilletta, 2009). At the physiological level, the most fundamental is the trade-off between the binding ability of an enzyme and its maximum catalytic rate (Hochachka & Somero, 2002; Angilletta, 2009). The trade-off between binding competence and catalytic rate arises because the function of an enzyme requires both an initial conformational change to bind the substrate(s) and then a second conformational change to release the product(s). The intermediate state – where the reaction is catalyzed – is rapid compared to the speed of these conformational changes to bind the substrate and release the product (for a detailed review of the biochemical basis for this trade-off, see Hochachka & Somero, 2002; Angilletta, 2009). A more flexible (and hence less stable) structure helps an enzyme change shape (i.e., conformation) faster during binding and release. Yet, this instability comes at a price: a flexible enzyme spends a greater proportion of its time in a conformation that prevents the binding of substrate (Fig. 3a), which lowers its substrate affinity. In general, an enzyme with greater conformational stability functions better at warmer temperatures, and an enzyme with lower conformational stability (i.e., greater flexibility) functions better at cooler temperatures (Fig. 3b). Microbial uptake, death, and respiration.

There is broad evidence that microbial substrate uptake, growth, and respiration are strongly regulated by temperature. Trade-offs in organism physiologies, such as temperature-driven changes in membrane composition (Hall *et al.*, 2010), contribute to thermal

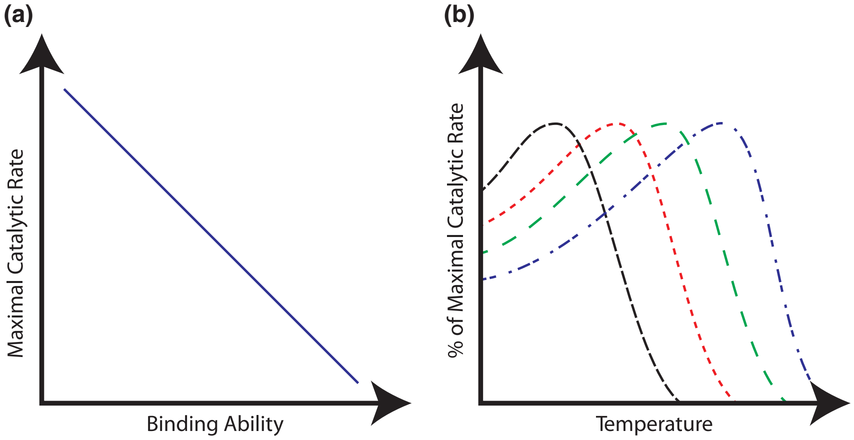


Fig. 3 (a) Representation of the negative relationship between enzyme-binding ability and catalytic rate as a result of the trade-off between enzyme conformational structures that maintain binding (as opposed to non-binding) states vs. higher reaction rates. (b) Idealized thermal sensitivities of the activities of respiratory enzymes resulting as a consequence of the trade-off shown in (a) [based on Angilletta (2009)], where the black curve is from the coolest environment and the dot-hatch blue curve from the warmest.

adaptation and have functional consequences for soil OM turnover (Bradford *et al*., 2008, 2010; Balser & Wixon, 2009; Barcenas-Moreno *et al*., 2009; Allison *et al*., 2010b). But assimilable OM is a relatively uniform available pool within our model, obviating biochemical resistance to decomposition as a factor capable of directly affecting microbial uptake, death, and respiration.

If the responses of anabolic vs. catabolic processes to increasing temperature are uncoupled, microbial biomass can grow or shrink with changes to microbial growth efficiency (MGE) – defined as the fraction of assimilated substrate that is allocated for biomass and enzyme production vs. that respired as CO_2. Soil OM models often include a static microbial efficiency parameter, but sensitivity analyses have shown that this is one of the parameters to which model output is most sensitive. For example, Hyvönen *et al.* (1998) showed that a difference of 5% in this parameter, when estimated from 2 year decomposition data, could change estimates of steady-state carbon stocks by more than a factor of two. Further, Allison *et al.* (2010b) demonstrated large losses of soil carbon across 30 years in a modeling study where MGE was fixed (i.e., non-responsive to temperature). Yet, when the MGE was permitted to decrease with increasing temperature they observed decreased microbial biomass, which led to lower extracellular enzyme production, reduced soil OM decomposition, lower CO_2 efflux, and slight increases in soil carbon stocks after 30 years. Wetterstedt & Ågren (2011) found that a decrease in MGE with increasing temperature was more important than differences in temperature response to substrates qualities when modeling a litter decomposition experiment. If correct, this mechanism could help explain the results from long-term soil warming studies where stimulation of soil respiration due to heating diminishes after a few years (e.g., Melillo *et al*., 2002).

There is dearth of measurements of MGE responses to temperature in soils. In those studies that have tested this (e.g., Van Ginkel *et al*., 1999; Devêvre & Horwath, 2000; Steinweg *et al*., 2008), or at least measured both respiration and growth (e.g., Pietikäinen *et al*., 2005), there is support for declining MGE with increasing temperature. The impact of temperature-driven changes in MGE on the relationship between decomposability and temperature sensitivity is complicated by the fact that MGE tends to be lower for low quality, recalcitrant substrates. Because use of low quality substrates may increase as temperatures rise, measured declines in MGE for the soil microbial biomass might be a direct consequence of temperature, or an indirect product of changing substrate use (Devêvre & Horwath, 2000). Such complexities drive the substantial controversy in freshwater and marine systems as to whether temperature or substrate availability explains decreasing bacterial growth efficiencies under warmer conditions (Del Giorgio & Cole, 1998; Rivkin & Legendre, 2001; López-Urrutia & Morán, 2007).

Temperature controls on substrate availability

Organic matter-mineral binding and physical occlusion of OM within soil aggregates both act to limit the availability of otherwise decomposable OM substrates (Tisdall & Oades, 1982; Sollins *et al*., 1996; Jastrow & Miller, 1997; Six *et al*., 2002; Gershenson *et al*., 2009). The turnover times of free, or bio-available, soil OM compounds can be orders of magnitude less than those for the same compounds found in association with soil minerals (Sørensen, 1972). Such physical isolation of reactants limits the utility of kinetic theory for understanding temperature dependence of decomposition (Davidson & Janssens, 2006; Ågren & Wetterstedt, 2007). But soil OM adsorption to mineral surfaces is also a chemical process, meaning that it too is subject to kinetic theory. Organic matter binds with mineral particles via covalent bonds and several types of non-covalent bonds, such as van der Waals forces, charge interactions, and hydrogen bonding (Mortland, 1970). Ten Hulscher & Cornelissen (1996) partitioned adsorption reactions into fast, high-affinity reactions regulated by equilibrium thermodynamics and slow, low-affinity reactions regulated by diffusion. We discuss temperature controls on each of these in turn.

Temperature effects on protection of soil OM within soil aggregates have not been studied in great depth. While aggregation clearly has an impact on studies assessing responses to temperature (Lomander *et al*., 1998), isolating the effects of temperature on aggregate formation and breakdown is experimentally challenging. Leifeld & Fuhrer (2005) found similar Q_{10} values for soil OM in different size classes (greater and less than 63 μm), while Plante *et al.* (2009) found response to temperature was not different for non-occluded vs. soil OM released on crushing of aggregates. These data are limited, but could indicate that aggregate turnover may be as responsive to temperature as decomposition and that decomposition of soil OM released from aggregates will respond similarly to decomposition of non-occluded soil OM.

Warmer temperatures favor desorption for high-affinity soil OM-mineral interactions. High-affinity sorption-desorption processes that do not involve significant atomic or molecular overlap (i.e., non-covalent bonding) can be understood as reversible equilibrium reactions (Pignatello, 2000). At constant temperature (and pressure), equilibrium between forward (i.e., adsorption) and reverse (i.e., desorption) reactions minimizes the Gibb's free (ΔG) energy of the system. The equilibrium constant (the amount of product divided by the amount of reactants; K) is thus a function of the difference in free energy between the non-sorbed and the sorbed states (Fig. 4). Adsorption is often an exothermic process and the energy of activation (E_a) for adsorption tends to be smaller than that for desorption (Hamaker & Thompson, 1972; Pignatello, 2000). Le Chatelier's principle states that for exothermic reactions, an increase in temperature decreases the equilibrium constant K (i.e., shift toward reactants), whereas in endothermic reactions a temperature increase shifts K toward products. Accordingly, an increase in temperature should increase the rate of desorption relative to adsorption, meaning that substrate availability (i.e., the non-sorbed fraction) should be greater at warmer temperatures. This is true for several types of soil OM-mineral adsorption reactions, including van der Waals forces, hydrogen bonding, ligand exchange, and dipole-dipole interactions, and sometimes for chemisorption (formation of covalent chemical bonds) (Ten Hulscher & Cornelissen, 1996). Several experimental studies suggest that desorption increases with increasing temperature (Table 1 and see literature review by Kalbitz *et al.* 2000).

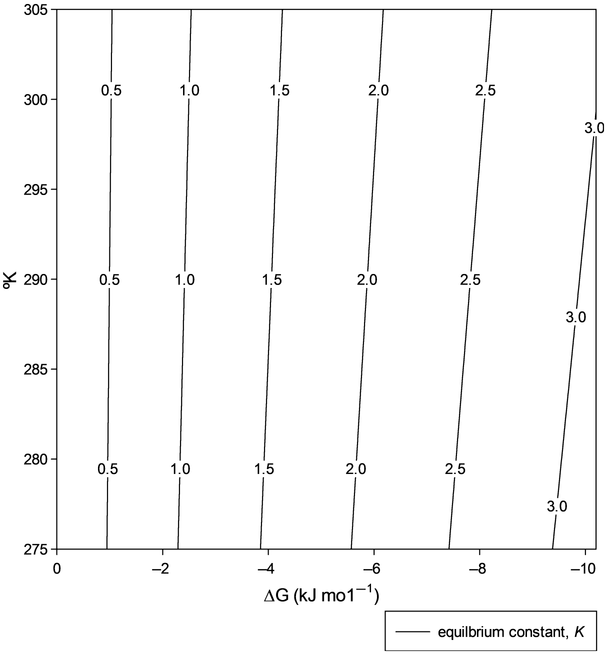


Fig. 4 Change in equilibrium constant K (values indicated along contours) as a function of temperature and ΔG. The influence of temperature on the balance between products and reactants (i.e., free and mineral-bound soil OM, respectively) varies most strongly as a function of temperature when reaction kinetics most strongly favour tight bonding.

For high-affinity reactions, desorption temperature sensitivity is related to bonding strength. The relative effect of temperature increases exponentially with ΔG, suggesting that the faster and stronger the adsorption, the greater is the absolute temperature effect (Fig. 4). Thus, temperature increases will have the largest desorptive effect on molecules that have the greatest affinity for soil mineral surfaces. This relationship is visualized in Fig. 4, which shows the change in K along a temperature gradient from −2 to 32°C for ΔG values representing a range of adsorption/desorption reactions. Steeper slopes for K in Fig. 4 illustrate that the effect of temperature on desorption is larger for reactions with more negative ΔG; i.e., compounds more tightly bound. Marschner & Bredow (2002) and Khairy *et al.* (1996a,b) have both observed that a rise in temperature moves the system toward a higher share of non-sorbed reactants, and temperature has a progressively larger effect as more energy is needed to desorb reaction partners. Temperature also increases diffusion and dissolution, both of which increase substrate availability to soil microbes and leaching losses of soil carbon (Xu & Saiers, 2010).

Warmer temperatures favor adsorption for low-affinity soil OM-mineral interactions. Slow adsorption processes describe soil OM-mineral interactions in which diffusion of soil OM into contact with soil minerals limits the rate of reaction (Ten Hulscher & Cornelissen, 1996). Soil OM diffusion can be limited by steric interference with bound soil OM. Such interference can be overcome via slow diffusion, breaking (and then possibly re-forming) existing soil OM-mineral bonds, or breaking OM-OM bonds (Cornelissen *et al.*, 1998; Pignatello, 2000; Ghosh *et al.*, 2001). Based on the thermodynamic relationships described for high-affinity reactions, as temperatures increase some of the existing bonds between soil OM and mineral particles will break. Breaking these bonds may open 'holes' in the OM surfaces on soil minerals that will enable new interactions between soil OM and minerals. Temperature-driven increases in desorption of high-affinity SOM increases opportunities for low-affinity SOM-mineral interactions. Thus, 'hole' creation is an exothermic process favoured by warmer temperatures and 'hole' occupation is an endothermic process (Ten Hulscher & Cornelissen, 1996). Adsorption involving very strong bonding, such as through ligand exchange, can have relatively large E_a for adsorption due to orbital rehybridization and displacement of other ligands (Pignatello, 2000). This suggests that the formation of tight

Table 1 Summary of data on temperature impacts on adsorption/desorption of soil OM

References	Study description	Response variable	Q_{10}
Kaiser *et al.* (2001)	Subsoil samples	Extractable organic C	1.2–1.3
Kaiser *et al.* (2001)	Subsoil samples	Adsorption coefficient	0.97–1.0
Christ & David (1996)	O_a-horizon of a spodosol	OM release	1.7–2.0
Gödde *et al.* (1996)	Forest floor	Organic C release	1.5–2.0
Khairy *et al.* (1996a,b)	Nucleobases on humic acid	Desorption coefficient	2.5 (averge of several observations)
Talhout & Engberts (2001)	benzamidine binding to trypsin	Negative reaction enthalpies	4.0*
Schmidt *et al.* (1990)	Adsorption of lysozyme onto alkylated silicon oxide surfaces	Desorption coefficient	>1
Gianfreda *et al.* (1995)	Tannic acid binding to Al and Fe	Desorption coefficient	1.5†
Moore & Dalva (2001)	Soil and plant tissues	Leached DOC	1.6

*Estimated from E_a of 92 kJ mol^{-1}.
†Estimated from E_a of 21–28 kJ mol^{-1}.

bonds for soil OM adsorption via ligand exchange could increase with temperature, contrary to the expectation for other bonds like van der Waals forces, charge interactions, and hydrogen bonding. Angove *et al.* (2006a,b) concluded that for two adsorbents commonly found in soil (Goethite and Kaolinite), adsorption of mellitic acid was accompanied by a strong increase in entropy. Increases in entropy can be important enough to offset the endothermic nature of some adsorption reactions, resulting in reactions that are spontaneous and endothermic. Indirect effects of warming, such as the disappearance of the water mantle surrounding dissolved solutes leads to increasing disorder, potentially driving endothermic desorption reactions (Ten Hulscher & Cornelissen, 1996). Several studies in the literature have observed endothermic adsorption (e.g., Elshafei *et al.*, 2009; Jia *et al.*, 2010).

Conclusions and recommendations

We have identified three component processes for which variation in rates could affect response to temperature: depolymerization of biochemically complex compounds; production and conformation of microbial enzyme production; and processes that limit the availability of soil OM (adsorption/desorption and aggregate turnover). Understanding the net effect of rising temperature on soils requires understanding all of these component processes and their interactions (e.g., Bosatta & Ågren, 1999). Studies that experimentally minimized the influence of soil OM availability generally found that processes that happened slowly exhibited greater responses to temperature, consistent with the third component of kinetic theory. These results indicate that either (1) depolymerization of lower quality substrates is more responsive to temperature, or (2) temperature-driven changes in enzyme activity are greater for enzymes that degrade low quality polymers. Our conceptual model indicates that new experiments that distinguish between these possibilities will help us understand temperature impacts on decomposition of available soil OM.

The challenge of understanding how temperature affects soil OM availability is compounded by limited knowledge of the contribution of different binding mechanisms to soil OM stabilization, their enthalpy and entropy constraints, their degrees of saturation (*sensu* Six *et al.*, 2002; Stewart *et al.*, 2007), and the characteristics of the soil OM that becomes available at warmer temperatures (Plante *et al.*, 2009; Kleber *et al.*, 2011).The discontinuous response surface relating temperature sensitivity to strength of soil OM-mineral bonds obviates the ability to explore temperature sensitivity using bulk responses of mineral-associated soil carbon fractions. The procedures most widely used to separate soil into meaningful fractions are not capable of distinguishing strong, high-affinity bonds from slowly forming bonds that fill 'holes' in mineral surface coatings. Both contribute to long-term stabilization of soil OM, yet the literature suggests that their responses to increased temperature will be opposite each other.

Studies investigating the relationship between decomposition rates and response to temperature have employed a variety of operational definitions of decomposability that are not uniformly tied to OM quality alone. Our review recognizes that decomposability of bulk soil OM is a function of several independent processes (Kleber, 2010). Different operational definitions of decomposability confound these processes and will not likely lead to the deeper understanding of temperature effects on less decomposable soil OM. The use of CO_2 as a response variable is inadequate because different components of the decomposition process affect rates of CO_2 flux from soil, masking the cause and effect of warming on decomposition rates.

Advances in understanding the processes that regulate substrate supply (adsorption/desorption and aggregate turnover) and their response to temperature are required to understand this question. Experiments on the influence of temperature on microbial efficiency and microbial enzyme production will be important to complete our understanding of controls over the decomposition of less decomposable substrates. Establishment of long-term, low-cost experiments (e.g., Sullivan & Welker, 2005) sustained over many years to monitor field-level responses of soil carbon stocks to experimental warming would constrain process-level studies. Finally, it is important to recognize that temperature as well as its indirect effects via soil moisture will alter plant production, partitioning of that carbon to roots and leaves and to litter, and litter quality, which were not addressed in this review. Temperature-driven changes in inputs, together with decomposition losses, will determine the fate of soil carbon in a warmer world; understanding those processes underlying these inputs and losses is the grand challenge.

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