

REVIEW

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

RICHARD T. CONANT*†, MICHAEL G. RYAN‡, GÖRAN I. ÅGREN§, HANNAH E. BIRGE*, ERIC A. DAVIDSON¶, PETER E. ELIASSON§, SARAH E. EVANS*, SERITA D. FREY||, CHRISTIAN P. GIARDINA**, FRANCESCA M. HOPKINS††, RIITTA HYVÖNEN§, MIKO U. F. KIRSCHBAUM‡‡, JOCELYN M. LAVALLEE*, JENS LEIFELD§§, WILLIAM J. PARTON*, JESSICA MEGAN STEINWEG*, MATTHEW D. WALLENSTEIN*, J. Å. MARTIN WETTERSTEDT§ and MARK A. BRADFORD¶¶

*Natural Resource Ecology Laboratory, Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523-1499, USA, †Institute for Sustainable Resources, Queensland University of Technology, Brisbane, QLD 4001, Australia, ‡Rocky Mountain Research Station, USDA Forest Service, Fort Collins, CO 80526, USA, §Department of Ecology, Swedish University of Agricultural Sciences, Uppsala 750 07, Sweden, ¶Woods Hole Research Center, Falmouth, MA 02540-1644, USA, ||Department of Natural Resources and Environment, the University of New Hampshire, Durham, NH 03824, USA, **Pacific SW Research Station, Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI 96785, USA, ††Department of Earth System Science, University of California, Irvine, CA 92697-3100, USA, ‡‡Landcare Research, Palmerston North 4442, New Zealand, §§Agroscope Reckenholz Tanikon, Air Pollution Climate Group, Zurich 8046, Switzerland, ¶¶School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

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

Received 4 October 2010; revised version received 14 June 2011 and accepted 20 June 2011

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 deter-

mine 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

Correspondence: Richard T. Conant, Natural Resource Ecology Laboratory, Department of Ecosystem Science and Sustainability, Colorado State University, Fort Collins, CO 80523-1499, USA, tel. + 1 (970) 491 1919, fax + 61 04 3596 2840, e-mail: conant@nrel.colostate.edu; richard.conant@qut.edu.au

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 decomposability¹ 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-

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

²We 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 $\delta^{13}\text{C}$ (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 $\delta^{13}\text{C}$ 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 (Strömberg, 2001) suggest that increased rates of soil respiration observed in the first several years of warming do not persist. One explanation for

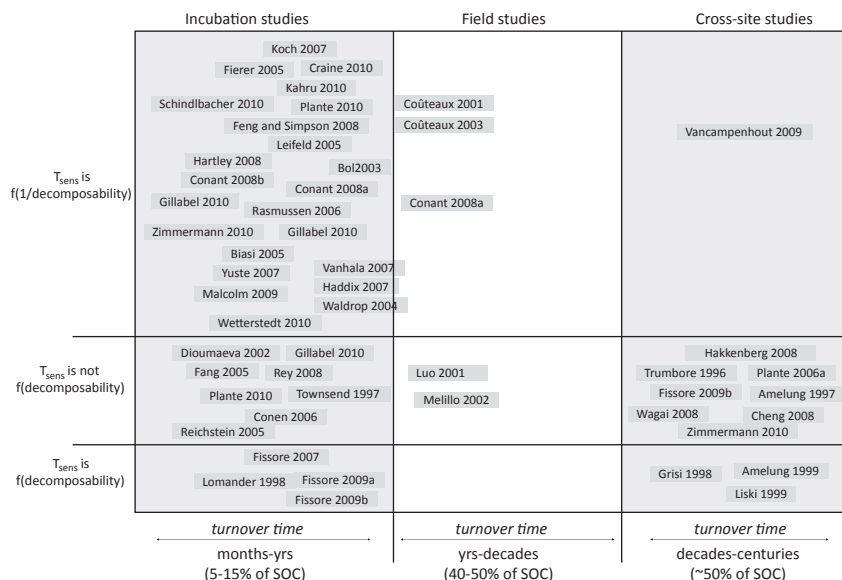


Fig. 1 The majority of incubation studies have found that decomposition rates of slowly decomposing soil OM are more sensitive to temperature [i.e., $T_{sens} = f(1/\text{decomposability})$], as indicated on the y -axis, consistent with the predictions of basic thermodynamics. However, as shown by the 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 CO₂ flux, shift in ¹³CO₂ 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

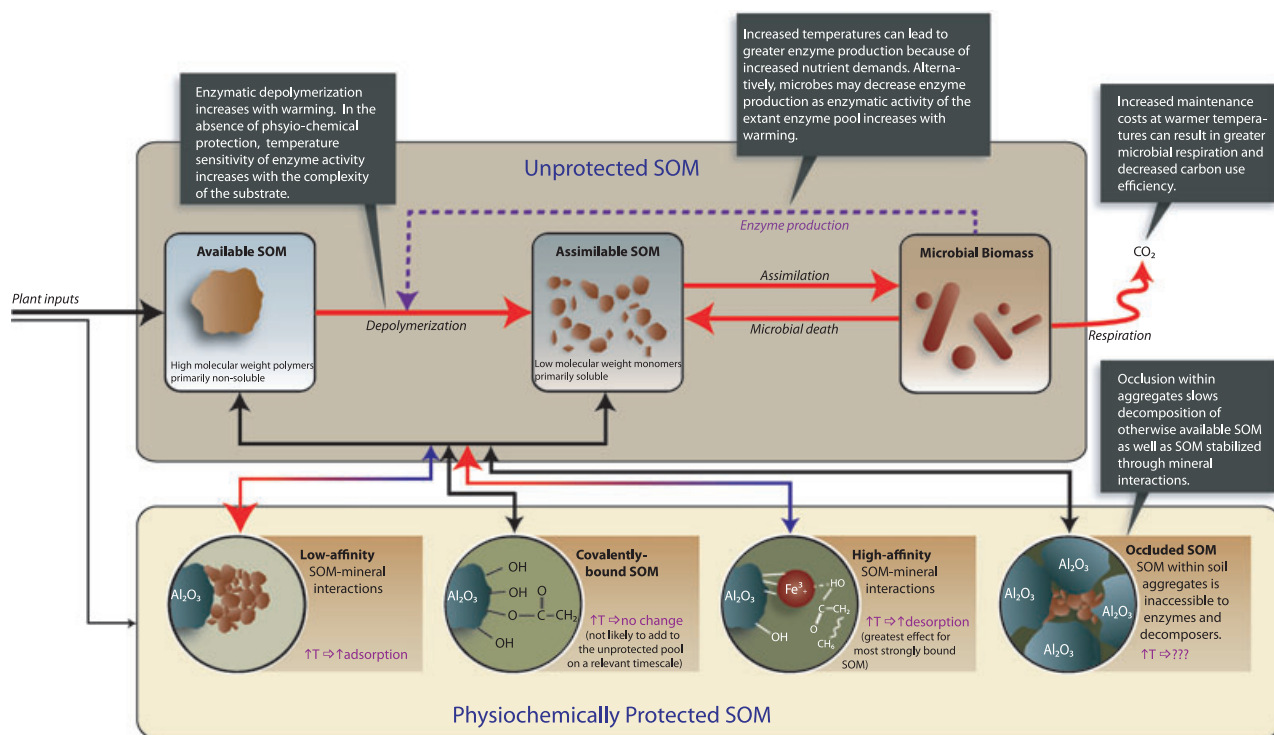


Fig. 2 A new conceptual model of decomposition illustrating organic matter pools and fluxes. Lines indicate OM fluxes, with the dashed line signifying the OM flux associated with enzyme production and its contribution to OM depolymerisation. Red arrows (and red arrowheads) indicate that rates accelerate with increasing temperature while those in blue indicate that 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 depolymerisation 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 depolymerisation 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 (Grzymiski *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 (Barceñas-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

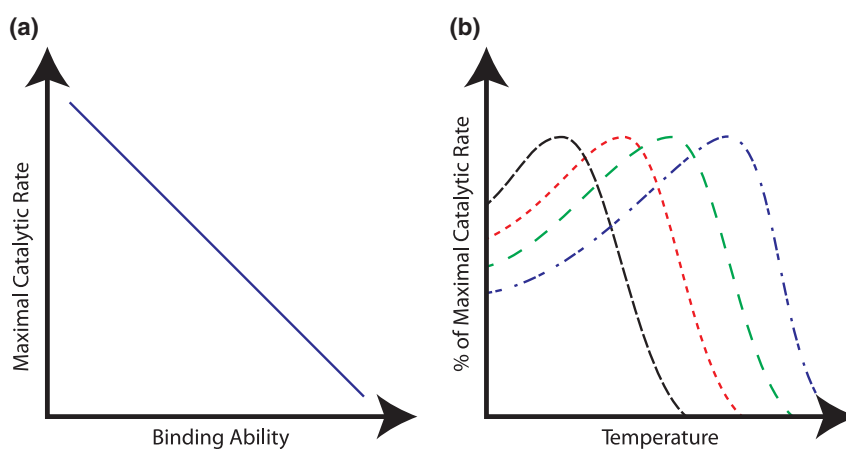


Fig. 3 (a) Representation of the negative relationship between enzyme-binding ability and catalytic rate as a result of the trade-off between enzyme conformational structures that maintain binding (as opposed to non-binding) states vs. higher reaction rates. (b) Idealized thermal sensitivities of the 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 & Wi-xon, 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 CO₂. 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 CO₂ 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 con-

troversy 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 Q₁₀ 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 Gibbs 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

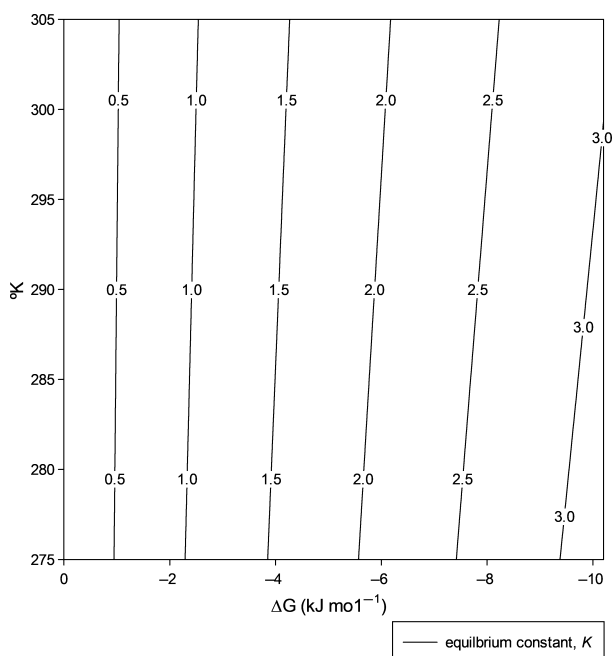


Fig. 4 Change in equilibrium constant K (values indicated along contours) as a function of temperature and ΔG . The influence of temperature on the balance between products and reactants (i.e., free and mineral-bound soil OM, respectively) varies most strongly as a function of temperature when reaction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

desorption increases with increasing temperature (Table 1 and see literature review by Kalbitz *et al.* 2000).

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 & Saier, 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 <i>et al.</i> (2001)	Subsoil samples	Extractable organic C	1.2–1.3
Kaiser <i>et al.</i> (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 <i>et al.</i> (1996)	Forest floor	Organic C release	1.5–2.0
Khairy <i>et al.</i> (1996a,b)	Nucleobases on humic acid	Desorption coefficient	2.5 (average of several observations)
Talhout & Engberts (2001)	benzamidine binding to trypsin	Negative reaction enthalpies	4.0*
Schmidt <i>et al.</i> (1990)	Adsorption of lysozyme onto alkylated silicon oxide surfaces	Desorption coefficient	>1
Gianfreda <i>et al.</i> (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 CO₂ as a response variable is inadequate because

different components of the decomposition process affect rates of CO₂ 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.

Acknowledgements

This article reflects ideas initially discussed at a one-day workshop following the 'Soil Organic Matter Dynamics: Land Use, Management and Global Changes' meeting held at Colorado Springs, CO in July 2009. We are grateful for the travel support provided to some of the authors of this work. The workshop was supported by NSF award 0842315 to Conant and US Department of Energy awards to Wallenstein (2008-35107-18655 and 3454-CSU-DOE-4157). We thank the three anonymous reviewers for their helpful comments on earlier versions of this manuscript.

References

- Ågren GI (2000) Temperature dependence of old soil organic matter. *Ambio*, **29**, 55–55.
- Ågren GI, Bosatta E (2002) Reconciling differences in predictions of temperature response of soil organic matter. *Soil Biology and Biochemistry*, **34**, 129–132.
- Ågren GI, Wetterstedt JÅM (2007) What determines the temperature response of soil organic matter decomposition? *Soil Biology and Biochemistry*, **39**, 1794–1798.
- Allison DD, Weintraub MN, Gartner TB, Waldrop MP (2010a) Evolutionary-economic principles as regulators of soil enzyme production and ecosystem function. In: *Soil Enzymology* (eds Shukla G, Varma A), pp. 229–243. New York, Springer-Verlag.
- Allison SD, Wallenstein MD, Bradford MA (2010b) Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, **3**, 336–340.
- Amelung W, Flach KW, Zech W (1997) Climatic effects on soil organic matter composition in the great plains. *Soil Science Society of America Journal*, **61**, 115–123.
- Angilletta MJ Jr (2009) *Thermal Adaptation. A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Angove MJ, Wells JD, Johnson BB (2006a) The influence of temperature on the adsorption of mellitic acid onto goethite. *Journal of Colloid and Interface Science*, **296**, 30–40.
- Angove MJ, Wells JD, Johnson BB (2006b) Influence of temperature on the adsorption of mellitic acid onto kaolinite. *Langmuir*, **22**, 4208–4214.
- Arrhenius SZ (1889) Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Säuren. *Zeitschrift für Physikalische Chemie*, **4**, 226–248.
- Balser TC, Wixon DL (2009) Investigating biological control over soil carbon temperature sensitivity. *Global Change Biology*, **15**, 2935–2949.
- Barcenas-Moreno G, Gomez-Brandon M, Rousk J, Baath E (2009) Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. *Global Change Biology*, **15**, 2950–2957.
- Bengtson P, Bengtsson G (2007) Rapid turnover of DOC in temperate forests accounts for increased CO₂ production at elevated temperatures. *Ecology Letters*, **10**, 783–790.
- Biasi C, Rusalimova O, Meyer H *et al.* (2005) Temperature-dependent shift from labile to recalcitrant carbon sources of arctic heterotrophs. *Rapid Communications in Mass Spectrometry*, **19**, 1401–1408.
- Bol R, Bolger T, Cully R, Little D (2003) Recalcitrant soil organic materials mineralize more efficiently at higher temperatures. *Journal of Plant Nutrition and Soil Science*, **166**, 300–307.
- Bosatta E, Ågren GI (1999) Soil organic matter quality interpreted thermodynamically. *Soil Biology and Biochemistry*, **31**, 1889–1891.
- Braakhekke WG, De Bruijn AMG (2007) Modelling decomposition of standard plant material along an altitudinal gradient: a re-analysis of data of Coûteaux *et al.* (2002). *Soil Biology and Biochemistry*, **39**, 99–105.
- Bradford MA, Davies CA, Frey SD *et al.* (2008) Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters*, **11**, 1316–1327.
- Bradford MA, Wallenstein MD, Allison SD *et al.* (2009) Decreased mass specific respiration under experimental warming is robust to the microbial biomass method employed. *Ecology Letters*, **12**, E15–E18.
- Bradford MA, Watts BW, Davies CA (2010) Thermal adaptation of heterotrophic soil respiration in laboratory microcosms. *Global Change Biology*, **16**, 1576–1588.
- Burke IC, Kaye JP, Bird SP, Hall SA, McCulley RL, Sommerville GL (2003) Evaluating and testing models of terrestrial biogeochemistry: the role of temperature in controlling decomposition. In: *Models in Ecosystem Science* (eds Canham CD, Cole JJ, Lauenroth WK), pp. 254–271. Princeton University Press, Princeton.
- Cheng CH, Lehmann J, Thies JE, Burton SD (2008) Stability of black carbon in soils across a climatic gradient. *Journal of Geophysical Research-Biogeosciences*, **113**, G02027.
- Christ MJ, David MB (1996) Dynamics of extractable organic carbon in Spodosol forest floors. *Soil Biology and Biochemistry*, **28**, 1171–1179.
- Conant RT, Drijber RA, Haddix ML *et al.* (2008a) Sensitivity of organic matter decomposition to warming varies with its quality. *Global Change Biology*, **14**, 868–877.
- Conant RT, Steinweg JM, Haddix ML, Paul EA, Plante AF, Six J (2008b) Experimental warming shows that decomposition temperature sensitivity increases with soil carbon recalcitrance. *Ecology*, **89**, 2384–2391.
- Conant RT, Haddix ML, Paustian K (2010) Partitioning soil carbon responses to warming: model-derived guidance for data interpretation. *Soil Biology and Biochemistry*, **42**, 2034–2036.
- Conen F, Leifeld J, Seth B, Alewell C (2006) Warming mobilises young and old soil carbon equally. *Biogeosciences*, **3**, 515–519.
- Cornelissen G, Van Noort PCM, Govers Haj (1998) Mechanism of slow desorption of organic compounds from sediments: a study using model sorbents. *Environmental Science and Technology*, **32**, 3124–3131.
- Coûteaux MM, Bottner P, Anderson JM *et al.* (2001) Decomposition of C-13-labelled standard plant material in a latitudinal transect of European coniferous forests: differential impact of climate on the decomposition of soil organic matter compartments. *Biogeochemistry*, **54**, 147–170.
- Coûteaux MM, Sarmiento L, Bottner P, Acevedo D, Thiery JM (2002) Decomposition of standard plant material along an altitudinal transect (65–3968 m) in the tropical Andes. *Soil Biology and Biochemistry*, **34**, 69–78.
- Craire JM, Fierer N, Mclauchlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience*, **3**, 854–857.
- Cusack DF, Torn MS, McDowell WH, Silver WL (2010) The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology*, **16**, 2555–2572.
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.
- Davidson EA, Trumbore SE, Amundson R (2000) Soil warming and organic carbon content. *Nature*, **408**, 789–790.
- Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q₁₀. *Global Change Biology*, **12**, 154–164.
- Del Giorgio PA, Cole JJ (1998) Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics*, **29**, 503–541.
- Del Grosso SJ, Parton WJ, Mosier AR, Holland EA, Pendall E, Schimel DS, Ojima DS (2005) Modeling soil CO₂ emissions from ecosystems. *Biogeochemistry*, **73**, 71–91.

- Devèvre OC, Horwath WR (2000) Decomposition of rice straw and microbial carbon use efficiency under different soil temperatures and moistures. *Soil Biology and Biochemistry*, **32**, 1773–1785.
- Dioumaeva I, Trumbore S, Schuur EaG, Goulden ML, Litvak M, Hirsch AI (2002) Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research-Atmospheres*, **108**, 1–12 art. no. 8222.
- Eliasson PE, Mcmurtrie RE, Pepper DA, Strömgren M, Linder S, Ågren GI (2005) The response of heterotrophic CO₂ flux to soil warming. *Global Change Biology*, **11**, 167–181.
- Elshafei GS, Nasr IN, Hassan ASM, Mohammad SGM (2009) Kinetics and thermodynamics of adsorption of cadusafos on soils. *Journal of Hazardous Materials*, **172**, 1608–1616.
- Fang C, Smith P, Moncrieff JB, Smith JU (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature*, **433**, 57–59.
- Fang C, Smith P, Smith JU (2006) Is resistant soil organic matter more sensitive to temperature than the labile organic matter? *Biogeosciences*, **3**, 65–68.
- Feng X, Simpson MJ (2008) Temperature responses of individual soil organic matter components. *Journal of Geophysical Research*, **113**, G03036.
- Fenner N, Freeman C, Reynolds B (2005) Observations of a seasonally shifting thermal optimum in peatland carbon-cycling processes; implications for the global carbon cycle and soil enzyme methodologies. *Soil Biology and Biochemistry*, **27**, 1814–1821.
- Fierer N, Craine JM, Mclauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. *Ecology*, **86**, 320–326.
- Fissore C, Giardina CP, Kolka RK *et al.* (2008) Temperature and vegetation effects on soil organic carbon quality along a forested mean annual temperature gradient in North America. *Global Change Biology*, **14**, 193–205.
- Fissore C, Giardina CP, Kolka RK, Trettin CC (2009a) Soil organic carbon quality in forested mineral wetlands at different mean annual temperature. *Soil Biology and Biochemistry*, **41**, 458–466.
- Fissore C, Giardina CP, Swanston CW, King GM, Kolka RK (2009b) Variable temperature sensitivity of soil organic carbon in North American forests. *Global Change Biology*, **15**, 2295–2310.
- Friedlingstein P, Cox P, Betts R *et al.* (2006) Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *Journal of Climate*, **19**, 3337–3353.
- Gershenson A, Bader NE, Cheng W (2009) Effects of substrate availability on the temperature sensitivity of soil organic matter decomposition. *Global Change Biology*, **15**, 176–183.
- Ghosh U, Talley JW, Luthy RG (2001) Particle-scale investigation of PAH desorption kinetics and thermodynamics from sediment. *Environmental Science and Technology*, **35**, 3468–3475.
- Gianfreda L, Decristofaro A, Rao MA, Violante A (1995) Kinetic-behavior of synthetic organo-complexes and organo-mineral-urease complexes. *Soil Science Society of America Journal*, **59**, 811–815.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.
- Giardina CP, Binkley D, Ryan MG, Fownes JH, Senock RS (2004) Belowground carbon cycling in a humid tropical forest decreases with fertilization. *Oecologia*, **139**, 545–550.
- Gillabel J, Cerbrian-Lopez B, Six J, Merckx R (2010) Experimental evidence for the attenuating effect of SOM protection on temperature sensitivity of SOM decomposition. *Global Change Biology*, **16**, 2789–2798.
- Gödde M, David MB, Christ MJ, Kaupenjohann M, Vance GF (1996) Carbon mobilization from the forest floor under red spruce in the northeastern USA. *Soil Biology and Biochemistry*, **28**, 1181–1189.
- Grisi B, Grace C, Brookes PC, Denedetti A, Dell'abate MT (1998) Temperature effects on organic matter and microbial biomass dynamics in temperate and tropical soils. *Soil Biology and Biochemistry*, **30**, 1309–1315.
- Grzymalski JJ, Murray AE, Campbell BJ *et al.* (2008) Metagenome analysis of an extreme microbial symbiosis reveals eurythermal adaptation and metabolic flexibility. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17516–17521.
- Haddix ML (2007) *Temperature Sensitivity of Soil Organic Matter Pools*. Colorado State University, Fort Collins, CO.
- Hahn HW, Pöckl M (2005) Ecotypes of planktonic actinobacteria with identical 16S rRNA genes adapted to thermal niches in temperate, subtropical, and tropical freshwater habitats. *Applied and Environmental Microbiology*, **71**, 766–773.
- Hakkenberg R, Churkina G, Rodeghiero M, Borner A, Steinhof A, Cescatti A (2008) Temperature sensitivity of the turnover times of soil organic matter in forests. *Ecological Applications*, **18**, 119–131.
- Hall EK, Singer GA, Kainz MJ, Lennon JT (2010) Evidence for a temperature acclimation mechanism in bacteria: an empirical test of a membrane-mediated trade-off. *Functional Ecology*, **24**, 898–908.
- Hamaker JW, Thompson JM (1972) Adsorption. In: *Organic Chemicals in the Soil Environment* (eds Goring CaI, Hamaker JW), pp. 49–143. Marcel Dekker, New York.
- Hartley IP, Ineson P (2008) Substrate quality and the temperature sensitivity of soil organic matter decomposition. *Soil Biology and Biochemistry*, **40**, 1567–1574.
- Hartley IP, Hopkins DW, Garnett MH, Sommerkorn M, Wookey PA (2008) Soil microbial respiration in arctic soil does not acclimate to temperature. *Ecology Letters*, **11**, 1092–1100.
- Hochachka PW, Somero GN (2002) *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford University Press, Oxford.
- Huntingford C, Lowe JA, Booth BBB, Jones CD, Harris GR, Gohar LK, Meir P (2009) Contributions of carbon cycle uncertainty to future climate projection spread. *Tellus Series B-Chemical and Physical Meteorology*, **61**, 355–360.
- Hyvönen R, Ågren GI, Bosatta E (1998) Predicting long-term soil carbon storage from short-term information. *Soil Science Society of America Journal*, **62**, 1000–1005.
- Ise T, Moorcroft PR (2006) The global-scale temperature and moisture dependencies of soil organic carbon decomposition: an analysis using a mechanistic decomposition model. *Biogeochemistry*, **80**, 217–231.
- Janssens IA, Vicca S (2010) Biogeochemistry: soil carbon breakdown. *Nature Geoscience*, **3**, 823–824.
- Jastrow JD, Miller RM (1997) Soil aggregate stabilization and carbon sequestration: feedbacks through organo-mineral associations. In: *Soil Processes and the Carbon Cycle* (eds Lal R, Kimble JM, Follett RF, Stewart BA), pp. 207–224. CRC Press, Boca Raton.
- Jia CX, You C, Pan G (2010) Effect of temperature on the sorption and desorption of perfluorooctane sulfonate on humic acid. *Journal of Environmental Sciences-China*, **22**, 355–361.
- Kaiser K, Kaupenjohann M, Zech W (2001) Sorption of dissolved organic carbon in soils: effects of soil sample storage, soil-to-solution ratio, and temperature. *Geoderma*, **99**, 317–328.
- Kalbitz K, Sloinger S, Park JH, Michalzik B, Matzner E (2000) Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Science*, **165**, 277–304.
- Karhu K, Fritze H, Tuomi M, Vanhala P, Spetz P, Kitunen V, Liski J (2010) Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. *Soil Biology and Biochemistry*, **42**, 72–82.
- Kätterer T, Andersson L, Andrén O, Persson J (2008) Long-term impact of chronosequential land use change on soil carbon stocks on a Swedish farm. *Nutrient Cycling in Agroecosystems*, **81**, 145–155.
- Khairy AH, Davies G, Ibrahim HZ, Ghabbour EA (1996a) Adsorption of aqueous nucleobases, nucleosides, and nucleotides on compost-derived humic acid. 1. Naturally occurring pyrimidines. *Journal of Physical Chemistry*, **100**, 2410–2416.
- Khairy AH, Davies G, Ibrahim HZ, Ghabbour EA (1996b) Adsorption of aqueous nucleobases, nucleosides, and nucleotides on compost-derived humic acid. 2. Naturally occurring purines. *Journal of Physical Chemistry*, **100**, 2417–2421.
- Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry*, **27**, 753–760.
- Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology*, **10**, 1870–1877.
- Kirschbaum MUF (2006) The temperature dependence of organic-matter decomposition – still a topic of debate. *Soil Biology and Biochemistry*, **38**, 2510–2518.
- Kleber M (2010) What is recalcitrant soil organic matter? *Environmental Chemistry*, **7**, 320–332.
- Kleber M, Nico PS, Plante A, Filley T, Kramer M, Swanston C, Sollins P (2011) Old and stable soil organic matter is not necessarily chemically recalcitrant: implications for modeling concepts and temperature sensitivity. *Global Change Biology*, **17**, 1097–1107.
- Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature*, **433**, 298–301.
- Koch O, Tschermo D, Kandeler E (2007) Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. *Global Biogeochemical Cycles*, **21**, GB4017.
- Lawrence CR, Neff JC, Schimel JP (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biology and Biochemistry*, **41**, 1923–1934.
- Leifeld J, Fuhrer J (2005) The temperature response of CO₂ production from bulk soils and soil fractions is related to soil organic matter quality. *Biogeochemistry*, **75**, 433–453.

- Liski J, Ilvesniemi H, Mäkelä A, Westman CJ (1999) CO₂ emissions from soil in response to climatic warming are overestimated – The decomposition of old soil organic matter is tolerant of temperature. *Ambio*, **28**, 171–174.
- Liski J, Ilvesniemi H, Mäkelä A, Westman CJ (2000) Temperature dependence of old soil organic matter. *Ambio*, **29**, 56–57.
- Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.
- Lomander A, Kätterer T, Andrén O (1998) Carbon dioxide evolution from top- and subsoil as affected by moisture and constant and fluctuating temperature. *Soil Biology and Biochemistry*, **30**, 2017–2022.
- López-Urrutia A, Morán XaG (2007) Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. *Ecology*, **88**, 817–822.
- Luo Y, Wan S, Hui D, Wallace L (2001) Acclimation of soil respiration to warming in a tall grass prairie. *Nature*, **613**, 622–625.
- Malcolm GM, Lopez-Gutierrez JC, Koide RT (2009) Temperature sensitivity of respiration differs among forest floor layers in a *Pinus resinosa* plantation. *Soil Biology and Biochemistry*, **41**, 1075–1079.
- Marschner B, Bredow A (2002) Temperature effects on release and ecologically relevant properties of dissolved organic carbon in sterilised and biologically active soil samples. *Soil Biology and Biochemistry*, **34**, 459–466.
- Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.
- Moore TR, Dalva M (2001) Some controls on the release of dissolved organic carbon by plant tissues and soils. *Soil Science*, **166**, 38–47.
- Mortland MM (1970) Clay-organic complexes and interactions. *Advances in Agronomy*, **22**, 75–117.
- Pietikäinen J, Pettersson M, Bååth E (2005) Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. *FEMS Microbiology Ecology*, **52**, 49–58.
- Pignatello JJ (2000) The measurement and interpretation of sorption and desorption rates for organic compounds in soil media. *Advances in Agronomy*, **69**, 1–73.
- Plante AF, Conant RT, Paul EA, Paustian K, Six J (2006) Acid hydrolysis of easily dispersed and microaggregate-derived and silt- and clay-sized fractions to isolate biologically resistant soil organic matter. *European Journal of Soil Science*, **57**, 456–467.
- Plante AF, Kougentakis A, Sen AM, Slominski C, Six J, Paul EA, Conant RT (2009) Does physical protection of soil organic matter attenuate temperature sensitivity? *Soil Science Society of America Journal*, **73**, 1168–1172.
- Plante AF, Carlson J, Greenwood R, Schuman J, Paul EA, Conant RT (2010) Decomposition temperature sensitivity of particulate and non-hydrolyzable soil organic matter. *Soil Biology and Biochemistry*, **42**, 1991–1996.
- Rasmussen C, Southard RJ, Horwath WR (2006) Mineral control of organic carbon mineralization in a range of temperate conifer forest soils. *Global Change Biology*, **12**, 834–847.
- Reichstein M, Kätterer T, Andrén O *et al.* (2005a) Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook. *Biogeosciences*, **2**, 317–321.
- Reichstein M, Subke J-A, Angeli AC, Tenhunen JD (2005b) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? *Global Change Biology*, **11**, 1754–1767.
- Rivkin RB, Legendre L (2001) Biogenic carbon cycling in the upper ocean: effects of microbial respiration. *Science*, **291**, 2398–2400.
- Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology*, **85**, 591–602.
- Schindlbacher A, De Gonzalo C, Díaz-Pinés E *et al.* (2010) Temperature sensitivity of forest soil organic matter decomposition along two elevation gradients. *Journal of Geophysical Research*, **115**, 1–10, doi: 10.1029/2009JG001191.
- Schmidt CF, Zimmermann RM, Gaub HE (1990) Multilayer adsorption of lysozyme on a hydrophobic substrate. *Biophysical Journal*, **57**, 577–588.
- Six J, Conant RT, Paul EA, Paustian K (2002) Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant and Soil*, **241**, 155–176.
- Sollins P, Homann P, Caldwell BK (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. *Geoderma*, **74**, 65–105.
- Sollins P, Kramer M, Swanston C *et al.* (2009) Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial- and mineral-controlled soil organic matter stabilization. *Biogeochemistry*, **96**, 209–231.
- Sørensen LH (1972) Stabilization of newly formed amino acid metabolites in soil by clay minerals. *Soil Science*, **114**, 5–11.
- Steinweg JM, Plante AF, Conant RT, Paul EA, Tanaka DL (2008) Patterns of substrate utilization during long-term incubations at different temperatures. *Soil Biology and Biochemistry*, **40**, 2722–2728.
- Stewart CE, Paustian K, Conant RT, Plante AF, Six J (2007) Soil carbon saturation: concept, evidence and evaluation. *Biogeochemistry*, **86**, 19–31.
- Strömberg M (2001) Soil-surface CO₂ flux and growth in a boreal Norway spruce stand. Effects of soil warming and nutrition. Unpublished PhD. Swedish University of Agricultural Sciences, Uppsala, 220 pp.
- Subke JA, Bahn M (2010) On the ‘temperature sensitivity’ of soil respiration: can we use the immeasurable to predict the unknown? *Soil Biology and Biochemistry*, **42**, 1653–1656.
- Sullivan PF, Welker JM (2005) Warming chambers stimulate early season growth of an arctic sedge: results of a minirhizotron field study. *Oecologia*, **142**, 616–626.
- Talhout R, Engberts JBFN (2001) Thermodynamic analysis of binding of p-substituted benzamides to trypsin. *European Journal of Biochemistry*, **268**, 1554–1560.
- Ten Hulscher TEM, Cornelissen G (1996) Effect of temperature on sorption equilibrium and sorption kinetics of organic micropollutants – a review. *Chemosphere*, **32**, 609–626.
- Tisdall JM, Oades JM (1982) Organic-matter and water-stable aggregates in soils. *Journal of Soil Science*, **33**, 141–163.
- Trasar-Cepeda C, Gil-Sotres F, Leiros MC (2006) Thermodynamic parameters of enzymes in grassland soils from Galicia, NW Spain. *Soil Biology and Biochemistry*, **39**, 311–319.
- Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, **272**, 393–396.
- Van Ginkel JH, Whitmore AP, Gorissen A (1999) *Lolium perenne* grasslands may function as a sink for atmospheric carbon dioxide. *Journal of Environmental Quality*, **28**, 1580–1584.
- Vancampenhout K, Wouters K, De Vos B, Buurman P, Swennen R, Deckers J (2009) Differences in chemical composition of soil organic matter in natural ecosystems from different climatic regions – A pyrolysis-GC/MS study. *Soil Biology and Biochemistry*, **41**, 568–579.
- Vanhala P, Karhu K, Tuomi M, Sonninen E, Jungner H, Fritze H, Liski J (2007) Old soil carbon is more temperature sensitive than the young in an agricultural field. *Soil Biology and Biochemistry*, **39**, 2967–2970.
- Von M, Kögel-Knabner I (2009) Temperature sensitivity of soil organic matter decomposition – what do we know? *Biology and Fertility of Soils*, **46**, 1–15.
- Wagai R, Mayer LM, Kitayama K, Knicker H (2008) Climate and parent material controls on organic matter storage in surface soils: a three-pool, density-separation approach. *Geoderma*, **147**, 23–33.
- Wagai R, Mayer LM, Kitayama K (2009) Nature of the ‘occluded’ low-density fraction in soil organic matter studies: a critical review. *Soil Science and Plant Nutrition*, **55**, 13–25.
- Waldrop MP, Firestone MK (2004) Altered utilization patterns of young and old C by microorganisms caused by temperature shifts and N additions. *Biogeochemistry*, **67**, 235–248.
- Wallenstein MD, McMahon SK, Schimel JP (2009) Seasonal variation in enzyme activities and temperature sensitivities in Arctic tundra soils. *Global Change Biology*, **15**, 1631–1639.
- Wallenstein MD, Steinweg JM, Ernakovich J, Allison S, Sinsabaugh RL (2010) Controls on the temperature sensitivity of soil enzymes: a key driver of in-situ enzyme activity rates. In: *Soil Enzymology* (eds Shukla G, Varma A), pp. 245–258. Springer, New York.
- Wetterstedt JÅM, Ågren GI (2011) Quality or decomposer efficiency – which is most important in the temperature response of litter decomposition? A modelling study using the GLUE methodology. *Biogeosciences*, **8**, 477–487.
- Wetterstedt JÅM, Persson T, Ågren GI (2010) Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. *Global Change Biology*, **16**, 1806–1819.
- Xu N, Saiers J (2010) Temperature and hydrologic controls on dissolved organic matter mobilization and transport within a forest topsoil. *Environmental Science and Technology*, **44**, 5423–5429.
- Yuste JC, Baldocchi DD, Gershenson A, Goldstein A, Misson LW, S. (2007) Microbial soil respiration and its dependency on carbon inputs, soil temperature, and moisture. *Global Change Biology*, **13**, 1–18.
- Zhou T, Shi PJ, Hui DF, Luo YQ (2009) Global pattern of temperature sensitivity of soil heterotrophic respiration (Q_{10}) and its implications for carbon-climate feedback. *Journal of Geophysical Research-Biogeosciences*, **114**, 9.
- Zimmermann M, Leifeld J, Conen F, Bird MI, Meir P (2011) Can composition and physical protection of soil organic matter explain soil respiration temperature sensitivity? *Biogeochemistry*, doi: 10.1007/s10533-010-9562-y (in press).