Biogeochemistry (2012) 108:1–15
DOI 10.1007/s10533-011-9596-9

SYNTHESIS AND EMERGING IDEAS

Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations

Carlos A. Sierra

Received: 2 November 2010 / Accepted: 6 March 2011 / Published online: 22 March 2011

Abstract Previous theoretical analyses based on Arrhenius kinetics and thermodynamics have shown that the temperature sensitivity of low-quality substrate is higher than that of high-quality substrate. Because soils store large amounts of low-quality carbon, understanding its response to increasing temperatures will help to predict the response of atmospheric CO_2 to climate change. However, empirical studies do not provide conclusive evidence to corroborate this theoretical argument. Although there are various possible reasons for this disagreement, the theory behind this argument has not been scrutinized carefully. Based on a simple mathematical analysis of the Arrhenius equation it is shown here that low-quality substrates are less temperature sensitive when analyzed in absolute rather than in relative terms, a result that may seem counterintuitive to previous theory. However, this is a paradox intrinsic to the Arrhenius equation and it is often ignored within the 'quality-temperature' debate. In fact, different measures commonly used to analyze the temperature sensitivity of different substrates can provide apparently different and contradictory results even though they are based on the same basic principles. Distinguishing between absolute and relative measures of sensitivity is essential for understanding the sensitivity of respiration to environmental change. An analysis of the available empirical evidence on this topic shows that most studies actually agree with the Arrhenius and thermodynamics theory, with less disagreement than previously thought. To address some of the issues identified here, a formal theoretical framework is proposed to study the sensitivity of respiration rates with respect to changes in multiple drivers of decomposition.

Keywords Quality-temperature hypothesis · Arrhenius kinetics · Soil respiration · Carbon cycle feedbacks · Organic matter quality

Introduction

The temperature sensitivity of soil organic matter decomposition is a highly debated topic due to its important implications for the global carbon cycle and feedbacks to the climate system (Davidson and Janssens 2006). An important aspect of this debate is the temperature sensitivity of non-labile or low-quality organic matter. Theoretical analyses agree that low-quality substrates would have higher sensitivities to temperature change (Bosatta and Ågren 1999; Davidson and Janssens 2006), which is now known as the 'quality-temperature' hypothesis, but empirical studies provide mixed results with no conclusive evidence to confirm this prediction (von

---

C. A. Sierra (✉)
Max-Planck-Institute for Biogeochemistry,
Hans-Knöll Str. 10, 07745 Jena, Germany
e-mail: csierra@bgc-jena.mpg.de

Lützow and Kögel-Knabner 2009). Some authors have tried to explain contradictory empirical results on the basis of the *intrinsic* vs. *apparent* temperature sensitivities of respiration (Davidson and Janssens 2006; Subke and Bahn 2010), pointing out important confounding factors that limit our ability to single out the direct effects of temperature on respiration. However, one important issue when trying to compare different studies looking at the temperature sensitivity of different qualities of organic matter is the variety of indices or measures used to evaluate this sensitivity. The most common measure of sensitivity in the literature is the temperature coefficient Q_{10}, but other authors have used other measures such as decomposition rates, mean residence times, activation energy, respiration rates, among others (Table 1). It is possible that some of the discrepancy among studies is due to the use of different measures of temperature sensitivity. Therefore, a careful theoretical analysis of these different measures would

Table 1 Summary of empirical studies in which the quality temperature hypothesis has been tested

Study	Measure of sensitivity	Agrees with Arrhenius theory?
1. Decomposition rates of stable SOM pools are not temperature sensitive within a temperature range 5–35°C		
Fang et al. (2005)	Q_{10}	No
Giardina and Ryan (2000)	τ	No
2. Decomposition of stable SOM pools have a higher temperature sensitivity than that of labile SOM pools		
Boddy et al. (2008)	k	No
Bol et al. (2003)	τ	Yes
Conant et al. (2008a)	Q_{10}	Yes
Conant et al. (2008b)	Q_{10}	Yes
Craine et al. (2010)	E	Yes
Curiel-Yuste et al. (2007)	Q_{10}	Yes/no
Hakkenberg et al. (2008)	τ	Yes
Hartley and Ineson (2008)	Q_{10}	Yes
Knorr et al. (2005)	$\ln \tau$	Yes
Koch et al. (2007)	Q_{10}	Yes
Koch et al. (2007)	$\left(\frac{1}{f}\frac{df}{dT}\right)$[a]	Yes
Larionova et al. (2007)	Q_{10}	Yes
Leifeld and Fuhrer (2005)	Q_{10}	Yes
Rey et al. (2008)	Q_{10}	Yes
Vanhala et al. (2007)	Q_{10}	Yes
3. Labile and resistant SOM pools respond similarly to changes in temperature		
Fang et al. (2005)	Q_{10}	Partially
Reichstein et al. (2005)	Q_{10}	Partially
Townsend et al. (1995)	τ, $\ln 2/k$	Partially
4. The decay rate of the labile SOM is very temperature-sensitive, but not the decay rate of stable SOM		
Bradford et al. (2008)	C, R	Yes
Eliasson et al. (2005)	R	Yes
Liski et al. (1999)	k, C, soil age	Yes
Luo et al. (2001)	Q_{10}	No
Melillo et al. (2002)	k	Yes
Trumbore et al. (1996)	τ	No

[a] f denotes enzyme activity

Studies organized according to von Lützow and Kögel-Knabner (2009) help to discern possible theoretical issues that could help to resolve some of the controversy associated with empirical studies.

This manuscript presents a theoretical analysis of the different measures commonly used to assess the temperature sensitivity of organic matter decomposition in empirical studies. The backbone of the analysis is the Arrhenius equation, which provides a solid theoretical framework for the study of temperature sensitivity with substrates of different qualities or levels of biochemical recalcitrance (Bosatta and Ågren (2009); Davidson and Janssens 2006). Due to this focus on the Arrhenius equation, the scope of the analysis is on the interactive effects of litter quality and temperature.

There are four main objectives that this manuscript attempts to achieve: (1) to show that different indices commonly used in the quality-temperature debate can produce different and contrasting answers. (2) To present the contrasting behavior between relative and absolute measures of temperature sensitivity and how these two levels of abstraction have created confusion regarding the temperature sensitivity of substrates with different qualities. (3) To show that there is less disagreement in this debate than what is currently thought and most of experimental studies can be explained within the context of the Arrhenius theory. (4) To present a formal conceptual framework for the study of the sensitivity of the decomposition process to multiple environmental factors. This last objective is an attempt to provide a mathematical framework to study the overall sensitivity of the decomposition process to other factors in addition to temperature and litter quality.

A mathematical analysis of the different measures of soil organic matter decomposition is presented in the "Temperature sensitivity of different measures of decomposition" section below to address objectives 1 and 2. "Comparing theoretical measures and empirical studies" section in combination with the "Discussion" section address objective 3, and "A general framework to study sensitivities to environmental change" section focuses on the last objective. For clarity, the main terms used in this analysis are defined below.

Terminology and notation

An important issue in the quality-temperature sensitivity debate is the lack of clear and consistent terminologies. For example, in the literature the terms 'temperature dependence' and 'temperature sensitivity' are treated almost indistinctively. To avoid confusion with previous terminology several distinctions are made in this manuscript. First, temperature dependence is defined here in the context of independent and dependent variables. A process is temperature dependent if temperature is an explanatory or independent variable in the mathematical representation of this process. For example, soil respiration R is temperature dependent if there is a function f for which temperature T is one of the independent variables in the model ($R = f(T, \ldots)$). This differs from temperature sensitivity, which is defined here as the rate of change of some measure X (respiration flux, decomposition rate, or turnover time) with respect to temperature while all other variables are held constant. Mathematically, this is equivalent to the partial derivative of X with respect to temperature $\partial X / \partial T$. Sensitivity expressed as partial derivatives is not a new concept and has been used in the past by other authors (e.g., Lloyd and Taylor 1994; e.g., Bosatta and Ågren 1999).

Similarly, absolute and relative sensitivity are treated explicitly here. The absolute sensitivity $\partial X / \partial T$ expresses the absolute change of the measure X for a given unit change in temperature, while the relative sensitivity $(1/X)\, \partial X / \partial T$ expresses this change relative to the actual value of the measure X. For example, the absolute sensitivity of decomposition rates measures the amount of change in the decomposition rate per unit change in temperature (units of time^{-1} K^{-1}), while the relative sensitivity measures this change as a proportion per unit change in temperature (units of K^{-1}).

This analysis will focus on four of the most common measures used to asses the temperature sensitivity of organic matter decomposition: respiration flux R, decomposition rate k, turnover time τ, and Q_{10}. The respiration flux R is the total amount of carbon released from the soil as carbon dioxide resulting from the activity of non-autotrophic organisms. It takes into account the total amount of carbon stored in the soil and how it is distributed among different pools with different qualities. The decomposition rate k is a constant that describes the exponential decrease of organic matter with time. The inverse of the decomposition rate is the turnover time τ. The temperature coefficient Q_{10} measures the proportional change of a biological or chemical system as a consequence of increasing the temperature by 10°C. Mathematical definitions of this terms and their sensitivities to temperature are provided below.

Organic matter quality in this study is defined only in a biochemical context. Since this study only focuses on Arrhenius kinetics, the quality of a substrate is measured here in terms of the activation energy; i.e. the amount of energy required for a chemical reaction to proceed. For the process of organic matter decomposition, the activation energy is inversely proportional to its quality, the higher the amount of energy required to breakdown a substrate the lower its quality. This definition is equivalent to that from Bosatta and Ågren (1999) based on thermodynamics: *quality is the number of enzymatic steps required to release as carbon dioxide a carbon atom from an organic compound*.

Temperature sensitivity of different measures of decomposition

Decomposition rates

It is commonly accepted that reaction rates (k) in the decomposition process follow the Arrhenius equation given by

$$k = A\exp\left(\frac{-E}{\Re T}\right), \tag{1}$$

where A is the pre-exponential factor and E the activation energy. Both are assumed independent of temperature. $\Re$ is the universal gas constant and T absolute temperature (K). By definition, Eq. 1 implies that a substrate of low-quality requires high amounts of energy (E) to be degraded, therefore its rate of decomposition (k) is slow. Activation energy is a measure of substrate quality, the higher the activation energy the lower the quality of the substrate, and as E increases $k \to 0$.

One formal definition to test the temperature sensitivity of decomposition is the partial derivative of the decomposition rate with respect to temperature

$$\begin{aligned}\frac{\partial k}{\partial T} &= \frac{EA}{\Re T^2}\exp\left(\frac{-E}{\Re T}\right), \\ &= k\frac{E}{\Re T^2}.\end{aligned} \tag{2}$$

Since all terms before the exponential are positive, the values of this derivative are always positive. This implies that as temperature increases the decomposition rate will always increase for constant values of the activation energy.

Another way to represent the temperature sensitivity of decomposition rates is in relative terms or logarithmic form

$$\frac{\partial \ln k}{\partial T} = \frac{E}{\Re T^2} = \frac{1}{k}\frac{\partial k}{\partial T}. \tag{3}$$

Absolute (Eq. 2) and relative (Eq. 3) sensitivities of decomposition rates produce different and apparently contradictory results (Fig. 1). While the relative sensitivity shows that low-quality substrates are more sensitive to changes in temperature, in absolute terms high-quality substrates are indeed more temperature sensitive. Low-quality substrates have low decomposition rates, and although they are more sensitive in relative terms, they are not in absolute values (Fig. 1).

Comparing the limiting behavior of these two sensitivities as the quality of the substrate decreases we find that

$$\lim_{E\to\infty}\frac{\partial k}{\partial T} = 0, \tag{4}$$

$$\lim_{E\to\infty}\frac{1}{k}\frac{\partial k}{\partial T} = \infty. \tag{5}$$

These limits show that as substrate quality decreases ($E \to \infty$) the absolute and the relative sensitivities of decomposition rates behave in opposite directions, with the absolute sensitivity exponentially decreasing towards zero and the relative sensitivity linearly increasing to infinity (Fig. 1).

An example can help us to understand these apparently contradictory behaviors. Suppose two different substrates are studied experimentally; substrate 1 has an activation energy of 50 kJ mol^{-1}, and substrate 2 an activation energy of 55 kJ mol^{-1}, which means that substrate 2 has lower quality than substrate 1. The experiment reveals that at 278K (5°C) substrate 1 decomposes at a rate $k_{5,\ 1} = 0.14$ year^{-1}, while substrate 2 decomposes at a rate $k_{5,\ 2} = 0.01$ year^{-1}. When temperature was increased by 10K the substrates decomposed at rates $k_{15,\ 1} = 0.30$ year^{-1} and $k_{15,\ 2} = 0.04$ year^{-1}, respectively. These results showed that a 10° increase in temperature increased the decomposition rate of substrate 1 by 0.16 year^{-1}, while the decomposition rate of substrate 2 only by 0.03 year^{-1}. For substrate

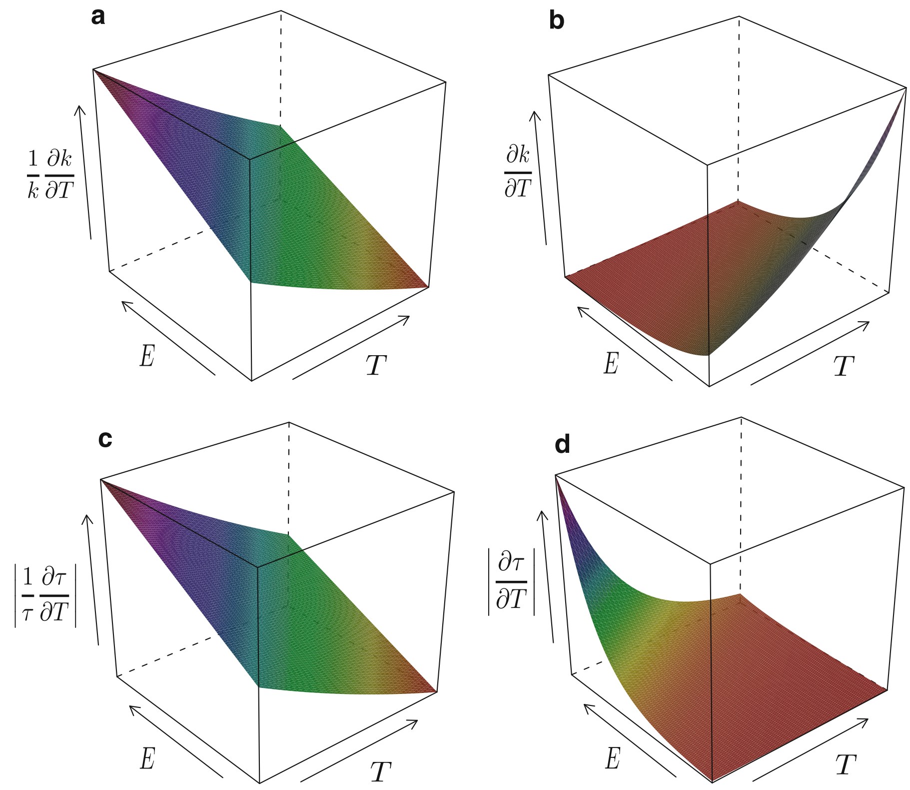

Fig. 1 Temperature sensitivity of decomposition rates *k* and turnover times τ as a function of temperature *T* and activation energy *E*. **a** Relative sensitivity of decomposition rates $(1/k)\ \partial k/\partial T$. **b** Absolute sensitivity of decomposition rates $\partial k/\ \partial T$. **c** Relative sensitivity of turnover times $(1/\tau)\ \partial\tau/\partial T$. **d** Absolute sensitivity of turnover times $\partial\tau/\partial T$. Values for the sensitivity of turnover times (**c**) and (**d**) were transformed to positive values for clarity. Low activation energy implies high quality substrate

1 this is equivalent to an increase of 0.016 year^{-1} for each Kelvin increased, and 0.003 $\text{year}^{-1}\text{K}^{-1}$ in the case of substrate 2. These last two values are analogous to the concept of the absolute sensitivity of decomposition rates depicted by Eq. 2. Alternatively one can calculate the temperature sensitivity relative to the decomposition rate at 278K. The experiment showed that the decomposition rate of substrate 1 increased by 11% for each degree increase in temperature while for substrate 2 it increased by 13% for the same degree increased. If the results were analyzed solely on the basis of the relative increase in decomposition rates one would conclude that substrate 2, which has lower quality, is more sensitive to decomposition. However, if the results were analyzed on the basis of the absolute sensitivity the opposite would be concluded. According to Arrhenius theory and the limits in Eqs. 4 and 5, these contradictory behaviors apply to any substrate under any given temperature.

Turnover times

The turnover time or mean residence time τ is defined as the inverse of the decomposition rate

$$\tau = \frac{1}{k} = \frac{\exp(E/\Re T)}{A}. \tag{6}$$

The absolute temperature sensitivity of the turnover time with respect to temperature is then

$$\begin{aligned}\frac{\partial\tau}{\partial T} &= \frac{-E}{A\Re T^2}\exp(E/\Re T),\\ &= \tau\frac{-E}{\Re T^2},\end{aligned} \tag{7}$$

and the relative sensitivity is

$$\frac{1}{\tau}\frac{\partial\tau}{\partial T} = \frac{\partial\ln\tau}{\partial T} = \frac{-E}{\Re T^2}. \tag{8}$$

Even though they have different signs, in relative terms the sensitivity of the turnover times and that of the decomposition rates produce similar behaviors (Fig. 1a, c); however, in absolute terms these two indices of sensitivity produce contrasting results (Fig. 1b, d). This discrepancy can be explained by the asymptotic behavior of the term $1/k$ for low values of the activation energy; i.e., $\lim_{k\to 0} \partial\tau/\partial T = +\infty$. This behavior, rather than a biophysical property, is a mathematical artifact introduced in the calculation of turnover times for substrates with decomposition rates very close to zero.

Q_{10}

A commonly used relative measure of temperature sensitivity is Q_{10}, the factor by which a reaction, or total soil respiration, changes as a consequence of a 10°C increase in temperature,

$$Q_{10} = \frac{K_{T+10}}{K_T}, \tag{9}$$

where K is either the decomposition rate k or the respiration rate R. Since it is a relative measure of the change in reaction rates, Q_{10} provides a measure of sensitivity similar to that of the relative sensitivities of decomposition rates and turnover times (Fig. 2). In qualitative terms, Q_{10} is an approximation to the term $E/\Re T^2$.

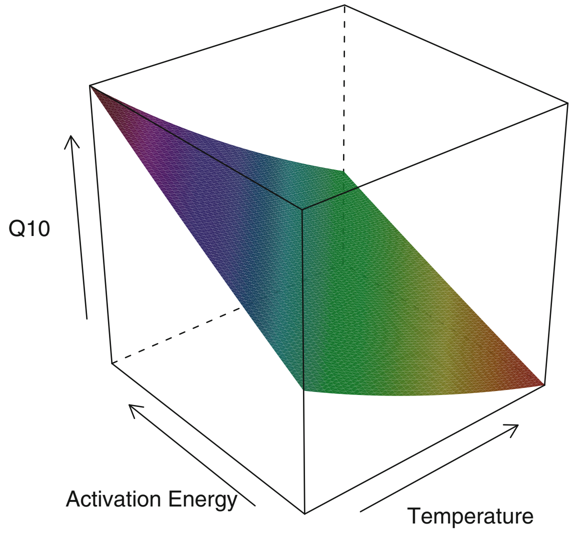

Fig. 2 Q_{10} calculated from the Arrhenius equation. Low activation energy implies high quality substrate

Temperature sensitivity of respiration

Sensitivity of respiration for a homogeneous substrate

The instantaneous release of carbon through respiration is commonly expressed as the product between the decomposition rate k and the amount of carbon available for decomposition C, therefore respiration equals $R = k\ C$ for a homogeneous substrate (Olson 1963). Then, absolute and relative sensitivities of respiration are

$$\frac{\partial R}{\partial T} = \frac{\partial k}{\partial T} C = k \frac{E}{\Re T^2} C, \tag{10}$$

and

$$\frac{1}{R}\frac{\partial R}{\partial T} = \frac{E}{\Re T^2}, \tag{11}$$

respectively. Notice that the relative sensitivity of respiration (Eq. 11) is identical to the relative sensitivity of reaction rates and can also be approximated with the Q_{10} function. The absolute sensitivity of respiration rates with respect to temperature (Eq. 10) is the product between the relative sensitivity of decomposition rates, the decomposition rate itself, and the amount of carbon available for decomposition. In contrast to other measures of sensitivity presented before, the absolute sensitivity of respiration is proportional to the size of the carbon pool. An important consequence of Eq. 10 is that respiration of low-quality substrates is less sensitive to temperature than that of high-quality substrates

$$\lim_{E\to\infty} \frac{\partial R}{\partial T} = 0. \tag{12}$$

Sensitivity of respiration for a heterogeneous substrate

Assuming constant inputs I of organic matter to the soil, one obtains the instantaneous rate of change of carbon for a homogeneous substrate as

$$\frac{dC}{dt} = I - kC. \tag{13}$$

We can partition a substrate into n quality classes i depending on the number of distinct substrates with homogenous activation energies as

$$\frac{dC_i}{dt} = I_i - k_i C_i, \tag{14}$$

with total respiration as $R = \sum_{i=1}^{n} k_i \, C_i$.

A substrate in this model can be composed by a higher proportion of high- than low-quality substrate, or conversely by more low- than high-quality substrate (Fig. 3, upper panels). This simple soil carbon model can be run to steady-state with a distribution of the initial amount of carbon in different qualities equal to the distribution of the litter inputs.

The results show that the amount of respiration tends to be dominated by carbon released from high quality substrates, even when the amount of carbon in the soil is predominantly of low qualities (Fig. 3, lower panels). The total amount of carbon at steady-state (Fig. 3, middle panels) does not differ significantly in the

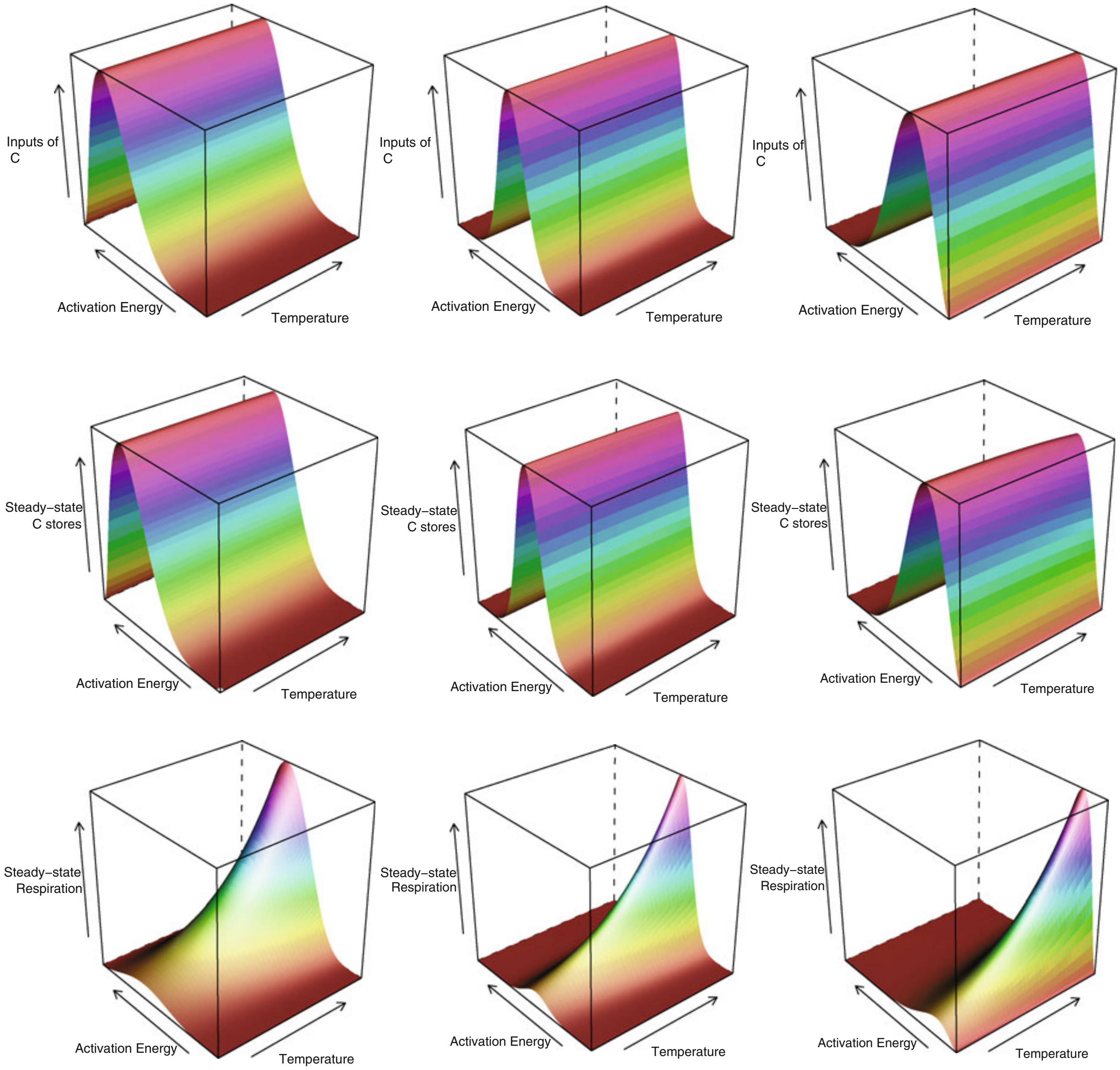

Fig. 3 Steady-state amounts of carbon and respiration predicted by the simple soil carbon model of Eq. 14. The *upper row* of figures show the inputs of carbon at each time step in the simulations for different assumptions of the distribution of carbon in different qualities. The *middle row* of figures shows the distribution of carbon at steady-state, while the *lower row* shows the distribution of the respiration fluxes at steady-state

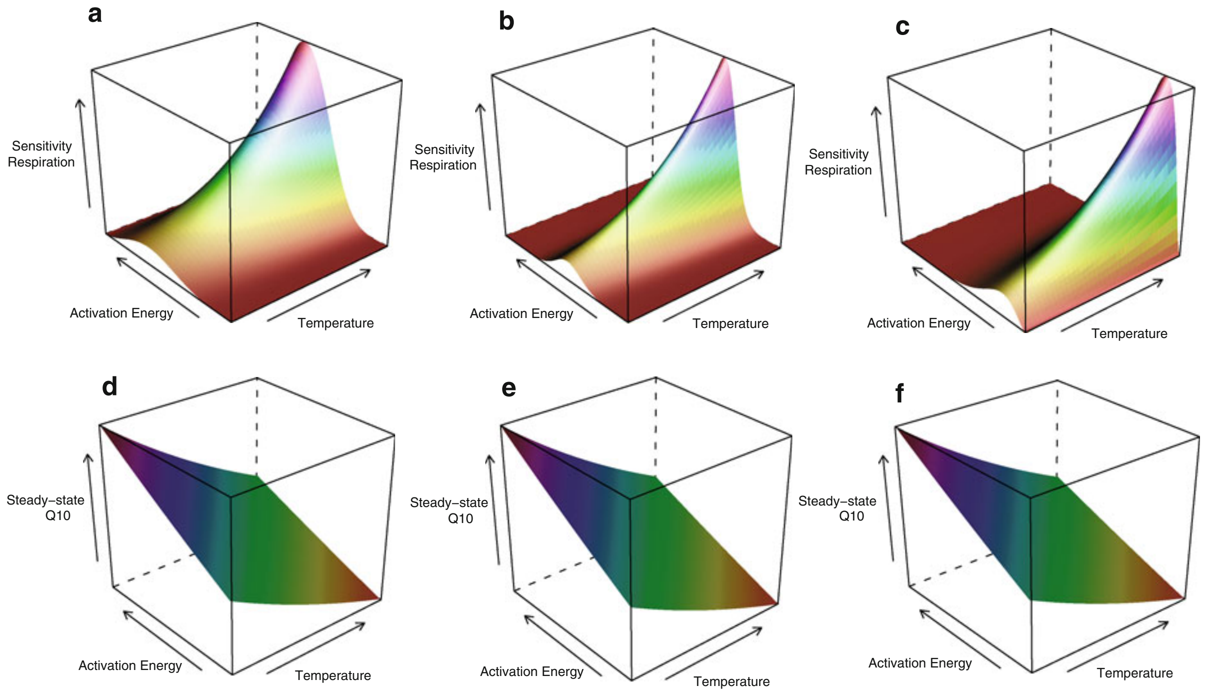

Fig. 4 Sensitivity of respiration for the simulations of Fig. 3 calculated as the absolute sensitivity of respiration rates $\partial R / \partial T$ shown in the *upper panels* (units of mass of C time^{-1} K^{-1}), and as Q_{10} shown in the lower panels (units of K^{-1})

distribution of quality from the distribution of the quality of the inputs. Only the amount of carbon in the higher qualities at high temperatures is lower in comparison with the carbon in the same qualities at lower temperatures, but this difference is actually hard to see in the figures. This suggests that at the scale of months, at which the model was run (100 days), differences in soil carbon pools due to temperature may be undetectable.

In terms of sensitivity, the Q_{10} for these respiration numbers shows that in relative terms the low quality substrate was more sensitive to temperature and similar in all cases. The Q_{10} shows what pools increase faster relative to reaction rates. However, the Q_{10} in this case fails to show what pools are respiring more and emit more carbon to the atmosphere, which can be better observed with the absolute sensitivity of respiration (Fig. 4).

Comparing theoretical measures and empirical studies

In a review of different empirical studies used to test the quality-temperature hypothesis, von Lützow and Kögel-Knabner (2009) organized these studies according to their main conclusion; these are: (1) decomposition rates of stable SOM pools are not temperature sensitive within a temperature range 5–35°C, (2) decomposition of stable SOM pools have a higher temperature sensitivity than that of labile SOM pools, (3) labile and resistance SOM respond similarly to changes in temperature, (4) the decay rate of the labile SOM is very temperature-sensitive, but not the decay rate of stable SOM. These studies are listed in Table 1 with the measure the authors of each study used to assess temperature sensitivity for different qualities. Studies evaluating changes in δ^{13}C were excluded from this table because their lack of a measure similar to decomposition rates, turnover times, or Q_{10}, and issues of uncertainty previously found in these types of studies (see Conen et al. 2008).

A review of the measures of temperature sensitivity used in previous studies reveals that a mix of relative and absolute sensitivity measures have been used by different authors (Table 1). Studies that have found low-quality, recalcitrant or stable organic matter more sensitive to temperature have predominantly used relative measures of sensitivity such as $Q_{10}, \ln \tau$, or activation energy E (used as a proxy for the relative sensitivity of decomposition rates). Turnover times τ have been also used as a measure of sensitivity, and although this is an absolute measure, it predicts higher sensitivities for low quality substrates because of the asymptotic behavior of this measure as $E \rightarrow \infty$ and $k \rightarrow 0$.

In contrast, studies predicting higher sensitivity for labile or high-quality substrates have predominantly used absolute measures of sensitivity such as changes in decomposition rates k, carbon pools C, and respiration fluxes R (Table 1).

The apparent disagreement between studies therefore, is not as dramatic as previously suggested. The majority (70%) of studies in Table 1 agree with the Arrhenius theory presented above in which low-quality substrates are more sensitivity in relative terms and high-quality substrates are more sensitive in absolute terms. There are however, some studies that apparently do not conform to the Arrhenius theory, but the behavior reported in some of those studies could partially be explained by specific combinations of temperature and substrate quality (E). The three-dimensional shapes of the different indices of sensitivity in Fig. 1 can be cut by many different planes in different directions according to different combination of T and E specific to each study. Some of these combinations can result in sensitivities with no trends. For example, sensitivities of turnover times at intermediate to high temperatures can be the same for low- and high-quality substrates (Fig. 1d). This behavior can partially explain the results found by Townsend et al. (1995). Similarly, for relative measures of sensitivity such as Q_{10} it is possible that a simultaneous change in E and T result in a horizontal displacement along the response plane. An experiment at which a temperature increase results in a depletion of labile substrates and an increase in low-quality substrate can provide undetectable changes in Q_{10}. This behavior can be observed in the same color-shaded areas in Fig. 2. This potential behavior of Q_{10} can partially explain the results found by Fang et al. (2005) and Reichstein et al. (2005). Although, these possibilities need a more rigorous test, they are indeed plausible within the theory provided by Arrhenius kinetics.

Discussion

Differences between theory and empirical studies

The theoretical argument that predicts higher sensitivity for low-quality substrates has not been analyzed in detail within the ‘quality-temperature’ debate. A careful reexamination of the theory in which this argument is based shows opposite and apparently contradictory behaviors among different measures of temperature sensitivity (Figs. 1, 4). In particular, to the question of what biochemical pools are more sensitive to temperature change, this analysis showed that absolute and relative measures of sensitivity provide contrasting answers. This is a paradoxical behavior embedded within the Arrhenius equation and it is based entirely on the theory of enzyme kinetics. It is a paradox because these two opposite behaviors lead to contradictory statements at two different levels of abstraction, the relative and the absolute level. The distinction between relative and absolute sensitivity therefore, is essential to understand the overall sensitivity of organic matter decomposition with respect to changes in temperature.

Differences between absolute and relative sensitivities have been described before, most notably in Davidson and Janssens (2006). However, the mathematical details pertaining to different decomposition measures have not been analyzed in detail. The different measures used in the literature to assess the temperature sensitivity of substrates of different quality combine absolute and relative sensitivities (Table 1) without much distinction among them for comparison purposes.

The terms relative and absolute sensitivity could be a source of confusion though. It is important to consider that in the context of this analysis, relative and absolute sensitivities are described in reference to the measure itself. For example, the relative sensitivity of the decomposition rate is relative to the decomposition rate itself and cannot be confused as if it were relative to the pool size. The only measure of sensitivity that is proportional to pool sizes is the absolute sensitivity of respiration rates, which is the product of the total amount of carbon, its decomposition rate, and the relative sensitivity of the decomposition rate (Eq. 10).

In addition to the distinction between absolute and relative sensitivity, it is important to emphasize differences in other measures of sensitivity such as changes in turnover times and Q_{10}. Turnover times can largely overestimate the sensitivity of the decomposition process for low-quality substrates because of the asymptotic behavior of the term $1/k$. For substrates that require high amounts of energy for decomposition, very small changes in E cause very large changes in turnover times simply as a result of having very small numbers in the denominator. In other words, the sensitivity of turnover times for low-quality substrates are dominated by the asymptotic behavior of the term $1/k$ and should be avoided for comparison purposes within this debate.

Although estimating Q_{10} values in decomposition or incubation experiments provide some useful information, they do not necessarily provide the information required to understand the overall temperature sensitivity of different substrates (e.g., Davidson et al. 2006, Fig. 4). In some situations using Q_{10} may have advantages because it provides the sensitivity of the reactions independent of the absolute rate or the amount of carbon available for decomposition. However, Q_{10} does not provide any information on what pools release more carbon from soil organic matter.

Despite all these differences in the behavior of different measures of temperature sensitivity there seems to be less disagreement among empirical studies and theory than previously thought. In the Arrhenius and thermodynamics theory of decomposition, low-quality or biochemically recalcitrant substrates are more temperature sensitive than labile substrates in relative terms, but less sensitivity in absolute terms. Therefore, studies that present these contradictory statements can be in agreement with Arrhenius kinetics and thermodynamics depending on the type of measure used to assess temperature sensitivity (Table 1). Even studies that show equal or no sensitivities for different pools can be consistent with this theory depending on the specific changes in temperature and activation energy intrinsic to the experimental conditions. For example, an incubation experiment in which an increase in temperature produces an increase in the activation energy of the substrate (depletion of the labile pool) can result in undetectable changes in Q_{10} (Fig. 2).

More on Q_{10}s

Although the temperature coefficient Q_{10} is conceptually well defined, there is in the literature a variety of functions used to calculate this coefficient (Table 2). These different functions can produce different estimates that may impose limitations for inter-comparisons, but perhaps more importantly, some of these functions introduce biases.

When calculated as in Eq. 9, Q_{10} is simply a ratio between two measurements of respiration. This is a convenient method for calculating Q_{10} under experimental conditions where temperature can be controlled in ranges of 10°. However, when temperature cannot be manipulated the only option to calculate Q_{10} is fitting a model to the observed data by least-squares regression. One such a model is a modification of the Van't Hoff equation

$$R = R_{ref} Q_{10}^{\frac{T - T_{ref}}{10}}, \tag{15}$$

where R_{ref} is a fixed amount of respiration at a reference temperature T_{ref}. Q_{10} and R_{ref} can be

Table 2 Examples of different equations used for calculating Q_{10} in different laboratory incubation studies

Study	Q_{10} equation	Terms
Fang et al. (2005)	$Q_{10} = \left(\frac{R}{a}\right)^{(10/T)}$	a: empirical coefficient
Fierer et al. (2005)	$Q_{10} = \exp\left(\frac{10}{T} \ln\left(\frac{R}{B}\right)\right)$	B: empirical coefficient
Leifeld and Fuhrer (2005)	$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10/(T_2 - T_1)}$	R_i: respiration at temperature T_i
Hartley and Ineson (2008)	$Q_{10} = \left(\frac{R}{kC}\right)^{10/(T - T_{ref})}$	T_{ref}: reference temperature
Conant et al. (2008a)	$Q_{10} = \left(\frac{t_c}{t_w}\right)^{10/(T_w - T_c)}$	t_c, t_w: time required to respire a given fraction at cold T_c and warm T_w temperatures, respectively
Wetterstedt et al. (2010)	$Q_{10} = R_{T+10}/R_T$	

calculated by least-squares regression with known values of R and T. Solving for Q_{10} one obtains

$$Q_{10} = \left(\frac{R}{R_{ref}}\right)^{\frac{10}{T-T_{ref}}}. \tag{16}$$

If temperature and respiration can be measured without experimental error and follow exactly the relationships in Eq. 15, Q_{10} would always be constant. However, this is never the case and the random behavior of T and R impose a random behavior on Q_{10} that is somehow predictable. In other words, given that Q_{10} can hardly behave as a universal constant in empirical studies it behaves according to the properties of random variables. In this context and in contrast with Eq. 9, Eq. 16 shows that Q_{10} is a function that depends on temperature, declines as temperature increases, and has asymptotic behavior at the temperature extremes,

$$\begin{aligned} \lim_{T\to\infty} Q_{10} &= 1, \\ \lim_{T\to T_{ref}} Q_{10} &= \infty, \end{aligned} \tag{17}$$

if $(R/R_{ref}) > 1$.

One important problem of using Eq. 15, is that it introduces an undesired behavior when analyzing the temperature sensitivity of organic matter decomposition for different temperature ranges. For example, taking random numbers of temperature and respiration and using Eq. 15 to calculate Q_{10} at fixed values of T_{ref} and R_{ref}, one obtains a behavior that could be attributed to certain biological process while in fact is the result of the mathematical formula used (Fig. 5a). This problem is specially important when combining different estimates of Q_{10} from the literature or from a set of experiments because in these cases Q_{10} is not a single constant derived from one single regression but a random variable estimated from multiple regressions.

A similar asymptotic behavior is obtained with randomly generated numbers to calculate Q_{10}s as in Fierer et al. (2005). In their study the authors found that temperature sensitivity decreases with an index of substrate quality, but given their formula to calculate Q_{10} it is also possible to obtain the same behavior with randomly generated numbers (Fig. 5b). In this case the asymptotic behavior is created by the term B in their formula, which causes that $Q_{10} \to \infty$ as $B \to 0$.

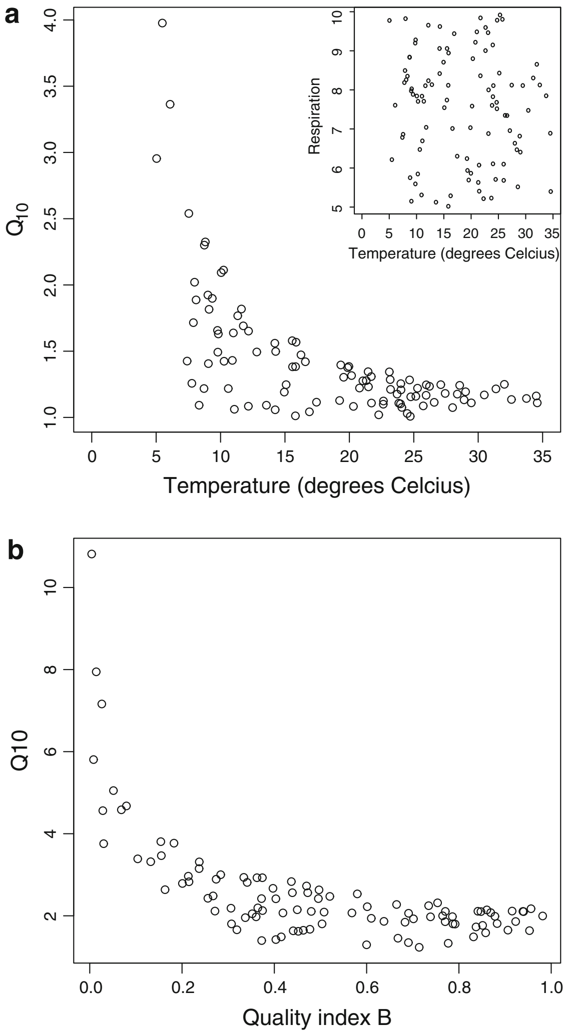

Fig. 5 **a** Temperature coefficient Q_{10} calculated with randomly generated respiration numbers assigned to random values of temperature (*inset*). Q_{10} calculated as $Q_{10} = \left(R/R_{ref}\right)^{\frac{10}{T-T_{ref}}}$, with $R_{ref} = 5$ and $T_{ref} = 1$. **b** Temperature coefficient Q_{10} calculated with randomly generated respiration numbers assigned to random values of the quality index B. Q_{10} calculated as $Q_{10} = \exp(10\ln(R/B)/T)$, as in Fierer et al. (2005). Please refer to Fig. 1 in that study for comparison of behaviors

The fact that these behaviors can be explained by mathematical artifacts does not necessarily invalidate the conclusions of some studies however. The results from Fierer et al. (2005) are consistent with the theory presented here and other empirical studies as well (Table 2). The main problem is the use of a measure to assess temperature sensitivity that is model dependent and therefore produces the intrinsic behavior expressed in the model.

In general, the temperature coefficient Q_{10} should be interpreted very carefully and comparisons among different values that use different formulas should be avoided whenever possible. On one hand, the Q_{10} only provides information on the relative sensitivity of decomposition and does not provide information on the pools that are responding more to temperature changes in absolute carbon values (Fig. 4). On the other hand, depending on the formula used to calculate Q_{10}, undesirable behaviors could be introduced that obfuscates the interpretation of empirical results.

A general framework to study sensitivities to environmental change

Measuring the temperature sensitivity of decomposition or respiration rates while maintaining all other factors constant is difficult if not impossible in experimental or observational studies (Subke and Bahn 2010). In fact, future temperature change will be correlated with changes in soil moisture, microbial community composition, and carbon supply to the soil, among other factors involved in the decomposition process. To tackle this research challenge, an appropriate theoretical framework would be to study the absolute change in respiration rates in the trajectory of change of the different factors involved in the decomposition process. The gradient of respiration ∇R is a convenient framework to study the sensitivity to these multiple factors. Formally, the definition of the gradient for a function that depends on multiple factors $R = f(X_1, X_2, \ldots, X_n)$ is

$$\nabla R = \left\langle \frac{\partial R}{\partial X_1}, \frac{\partial R}{\partial X_2}, \ldots, \frac{\partial R}{\partial X_n} \right\rangle. \tag{18}$$

If we were interested in calculating the sensitivity of respiration with respect to a specific change of different factors occurring simultaneously, the *directional derivative* of respiration in the direction $\mathbf{u}$ is given by

$$\nabla R \cdot \mathbf{u} = \frac{\partial R}{\partial X_1} u_1 + \frac{\partial R}{\partial X_2} u_2 + \cdots + \frac{\partial R}{\partial X_n} u_n, \tag{19}$$

where $\mathbf{u}$ is the unit vector (see example below).

Lets assume for example that we can represent respiration by three different variables: substrate quality in the form of activation energy E, soil temperature T and soil water content W as

$$R = A \exp\left(\frac{-E}{\Re T}\right) \frac{W}{W + \epsilon}; \tag{20}$$

where the term $(W/W + \epsilon)$ is a Michaelis-Menten-type coefficient that modifies the decomposition rate depending on the amount of moisture available (cf. Gulledge and Schimel 2000). The gradient in this case is given by

$$\begin{aligned} \nabla R &= \left\langle \frac{\partial R}{\partial E}, \frac{\partial R}{\partial T}, \frac{\partial R}{\partial W} \right\rangle, \\ \nabla R &= \left\langle R\frac{-1}{\Re T}, R\frac{E}{\Re T^2}, R\frac{\epsilon}{W(W+\epsilon)} \right\rangle. \end{aligned} \tag{21}$$

The usefulness of this equation is on predicting the sensitivity of respiration for a substrate of a given quality under specific conditions of temperature and moisture. If a substrate with activation energy $E = 50$ kJ mol^{-1} and $\epsilon = 10\%$ is under conditions of temperature $T = 300$K, and soil water content $W = 5\%$, its respiration would be $R_1 = 0.65$ g C m^{-2}d^{-1} according to this model, and its sensitivity to changes in quality, temperature, and moistures would be given by $\nabla R_1 = < -0.26, 0.04, 0.09 >$, in units of (g C m^{-2} d^{-1} kJ^{-1} mol, g C m^{-2} d^{-1} K^{-1}, g C m^{-2} d^{-1} %$^{-1}$); or $< -0.40, 0.07, 0.13 >$ as a proportion of the total amount of respiration in units of (kJ^{-1} mol, K^{-1}, %$^{-1}$). In contrast, the same substrate under conditions of temperature $T = 300$ K, and soil water content $W = 90$ %, has a respiration of $R_2 = 1.77$ g C m^{-2} d^{-1} and a sensitivity of $\nabla R_2 = < -0.71, 0.12, 0.02 >$ in (g C m^{-2} d^{-1} kJ^{-1} mol, g C m^{-2} d^{-1} K^{-1}, g C m^{-2} d^{-1} %$^{-1}$), or $< -0.40, 0.07, 0.01 >$ in (kJ^{-1} mol, K^{-1}, %$^{-1}$). We can see that in the two cases respiration is more sensitive to changes in activation energy per unit change in kJ mol^{-1}. However, in the first case the substrate under the given environmental conditions is more sensitive to changes in % soil water content than temperature per Kelvin, while in the second case the substrate is more sensitive to temperature. This example points out that sensitivities to different factors depend on the given conditions, so the sensitivity of respiration to one factor would be stronger under certain environmental conditions than in others. Notice that the value of the sensitivities depend on the choice of units, but this can be easily set for the specific problem under consideration.

Now, if we are interested in calculating the sensitivity of respiration when multiple factors change simultaneously, we can calculate this sensitivity as the directional derivative. First we need to calculate the unit vector **u** according to the projected change. If, for example we are interested in calculating the effect of decreasing substrate quality by 1 kJ mol^{-1}, increasing temperature by 3K, and reducing soil moisture by 10%, then the unit vector is given by

$$\mathbf{u} = \left\langle \frac{-1}{\sqrt{(-1)^2 + 3^2 + (-10)^2}}, \frac{3}{\sqrt{(-1)^2 + 3^2 + (-10)^2}}, \frac{-10}{\sqrt{(-1)^2 + 3^2 + (-10)^2}} \right\rangle. \tag{22}$$

For the function in this example, the directional derivative is given by

$$\nabla R \cdot \mathbf{u} = \frac{\partial R}{\partial E} u_1 + \frac{\partial R}{\partial T} u_2 + \frac{\partial R}{\partial W} u_3, \tag{23}$$

so, in the first case above,

$$\nabla R_1 \cdot \mathbf{u} = (-0.26)(-0.09) + (0.04)(0.29) + (0.09)(-0.95) = -0.5, \tag{24}$$

and for the second case,

$$\nabla R_2 \cdot \mathbf{u} = (-0.71)(-0.09) + (0.12)(0.29) + (0.02)(-0.95) = 0.10, \tag{25}$$

in g C m^{-2} d^{-1}. In the first case, the simultaneous change causes a 7% decrease in respiration rates while in the second case a 6% increase.

Within this general framework it is possible to study multiple factors in combination or in isolation. Since experiments to address a wide combination of different factors are perhaps unrealistic, this framework is useful to understand how certain combinations affect respiration rates under realistic scenarios of environmental change. In addition, this framework addresses more explicitly the concepts of intrinsic versus actual sensitivity. While the gradient can be viewed as the actual sensitivity, its components are the intrinsic sensitivities for each of the factors involved in the decomposition process.

Conclusions

The temperature sensitivity of organic matter decomposition has been assessed in the literature with different measures such as turnover times, decomposition rates, or the temperature coefficient Q_{10}. In this analysis it was found that these different measures can provide different and contrasting answers to the question of what are the more sensitive carbon pools or substrates to changes in temperature.

Within the theory of Arrhenius kinetics, low-quality or biochemically recalcitrant substrates are more sensitivity to changes in temperature when analyzed in terms of the relative sensitivity of decomposition rates and respiration fluxes. Conversely, high-quality or labile substrates are more sensitive to changes in temperature when analyzed in terms of the absolute sensitivity of decomposition and respiration rates. This paradox between absolute and relative sensitivities is of fundamental importance to understand the overall role of changes in temperature on the decomposition of organic matter of different qualities.

Previous empirical studies have used a mixture of relative and absolute measures of temperature sensitivity and synthesis on this topic have compared them indistinctively. In general, most studies using relative measures of temperature sensitivity have found the stable or recalcitrant pool to be more sensitive, while most studies looking at absolutes measures of temperature sensitivity have found the labile pool to be more sensitivity. These empirical findings are consistent with Arrhenius kinetics, which suggests that there is less disagreement on this topic than what is currently perceived.

The sensitivity of different substrates to temperature change is best studied using the absolute and relative sensitivities of decomposition in combination. Ultimately, it is the absolute amount of carbon released from soils what matters for the climate system. Similarly, the absolute amounts of carbon that can be mineralized from global soil carbon stocks are of ultimate importance and cannot be studied by looking at relative changes in decomposition rates alone, evaluated with measures such as Q_{10}.

In addition to temperature and litter quality, other physical and chemical factors not studied here can affect the sensitivity of organic matter decomposition. However, the overall sensitivity of the decomposition process to multiple factors can be studied formally using the concept of gradients from vector calculus. Within this framework it is possible to address explicitly the concepts of intrinsic and actual sensitivity of the decomposition process. Organic matter decomposition is probably more sensitive to temperature only in a limited set of circumstances and experiments testing multiple interacting factors can benefit from concepts such as the gradient or directional derivatives.

Acknowledgments This manuscript was possible thanks to the feedback and encouraging discussions with many individuals, among them S. Trumbore, M. Ryan, E. Davidson, and M. Reichstein. In addition, C. Phillips, S. Trumbore, M. Ryan, three anonymous reviewers, and the subject editor made important comments on previous versions of this manuscript. Financial support provided by the Max-Planck Gesellschaft.

References

Boddy E, Roberts P, Hill PW, Farrar J, Jones DL (2008) Turnover of low molecular weight dissolved organic C (DOC) and microbial C exhibit different temperature sensitivities in Arctic tundra soils. Soil Biol Biochem 40(7):1557–1566

Bol R, Bolger T, Cully R, Little D (2003) Recalcitrant soil organic materials mineralize more efficiently at higher temperatures. J Plant Nutr Soil Sci 166(3):300–307

Bosatta E, Ågren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biol Biochem 31: 1889–1891

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11(12):1316–1327

Conant RT, Drijber RA, Haddix ML, Parton WJ, Paul EA, Plante AF, Six J, Steinweg JM (2008a) Sensitivity of organic matter decomposition to warming varies with its quality. Glob Change Biol 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 organic matter recalcitrance. Ecology 89(9):2384–239

Conen F, Karhu K, Leifeld J, Seth B, Vanhala P, Liski J, Alewell C (2008) Temperature sensitivity of young and old soil carbon—same soil, slight differences in 13C natural abundance method, inconsistent results. Soil Biol Biochem 40(10):2703–2705

Craine JM, Fierer N, McLauchlan KK (2010) Widespread coupling between the rate and temperature sensitivity of organic matter decay. Nature Geosci 3(12):854–857

Curiel-Yuste J, Baldocchi DD, Gershenson A, Goldstein A, Misson L, Wong S (2007) Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Glob Change Biol 13(9):2018–2035

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. Glob Change Biol 12:154–164

Eliasson PE, McMurtrie RE, Pepper DA, Stromgren M, Linder S, Ågren GI (2005) The response of heterotrophic CO_2 flux to soil warming. Glob Change Biol 11:167–181

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

Fierer N, Craine JM, McLauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86:320–326

Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. Nature 404:858–861

Gulledge J, Schimel JP (2000) Controls on soil carbon dioxide and methane fluxes in a variety of taiga forest stands in interior Alaska. Ecosystems 3:269–282

Hakkenberg R, Churkina G, Rodeghiero M, Bürner A, Steinhof A, Cescatti A (2008) Temperature sensitivity of the turnover times of soil organic matter in forests. Ecol Appl 18(1):119–131

Hartley IP, Ineson P (2008) Substrate quality and the temperature sensitivity of soil organic matter decomposition. Soil Biol Biochem 40:1567–1574

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301

Koch O, Tscherko D, Kandeler E (2007) Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. Global Biogeochem Cycles 21(4):GB4017

Larionova AA, Yevdokimov IV, Bykhovets SS (2007) Temperature response of soil respiration is dependent on concentration of readily decomposable C. Biogeosciences 4(6):1073–1081

Leifeld J, Fuhrer J (2005) The temperature response of CO_2 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) CO_2 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

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. Funct Ecol 8:315–323

Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413(6856):622–625

Melillo JM, Steudler PA, Aber JD, Newkirk K, Lux H, Bowles FP, Catricala C, Magill A, Ahrens T, Morrisseau S (2002) Soil warming and carbon-cycle feedbacks to the climate system. Science 298(5601):2173–2176

Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

Reichstein M, Subke JA, Angeli AC, Tenhunen JD (2005) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time. Glob Change Biol 11(10):1754–1767

Rey A, Pegoraro E, Jarvis PG (2008) Carbon mineralization rates at different soil depths across a network of European forest sites (FORCAST). Eur J Soil Sci 59(6):1049–1062

Subke J-A, Bahn M (2010) On the 'temperature sensitivity' of soil respiration: can we use the immeasurable to predict the unknown. Soil Biol Biochem 42:1653–1656

Townsend AR, Vitousek PM, Trumbore SE (1995) Soil organic matter dynamics along gradients in temperature and land use on the Island of Hawaii. Ecology 76(3): 721–733

Trumbore SE, Chadwick OA, Amundson R (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. Science 272(5260): 393–396

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 Biol Biochem 39(11):2967–2970

von Lützow M, Kögel-Knabner I (2009) Temperature sensitivity of soil organic matter decomposition—what do we know. Biol Fert Soils 46:1–15

Wetterstedt JM, Persson T, Ågren GI (2010) Temperature sensitivity and substrate quality in soil organic matter decomposition: results of an incubation study with three substrates. Glob Change Biol 16:1806–1819