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What determines the temperature response of soil organic matter decomposition?

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Abstract

The temperature dependence of litter and soil organic matter (SOM) mineralisation is important because it determines how strong the feedback from the expected warmer climate may be on the atmospheric CO_2 concentration. We have used a simple, analytical model to investigated how three different mechanism (i) the rate at which decomposers take up substrate at their surface; (ii) the rate by which substrate diffuses up to the surface of the decomposer; and (iii) the rate at which substrate is made available in the environment interact to determine the temperature response. The mechanisms are characterised by activation energies; two for the uptake rate (i) and one for each of the other two (ii, iii). The model shows that the temperature dependence is the result of the number of processes that effectively contributes to the rate of mineralisation; this result should also be valid if other processes are included. Depending upon the relative magnitude of the four activation energies, the temperature response is mainly determined by one or two of the mechanisms. In a transition zone, where all activation energies are similar and the number of contributing processes changes, there can be either a sharp increase or a sharp decrease in the temperature response when activation energies change.

Keywords: Activation energy; Diffusion; Temperature sensitivity

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Introduction

The temperature dependence of litter and soil organic matter (SOM) mineralisation is important because it determines how strong the feedback from the expected warmer climate may be on the atmospheric CO_2 concentration. At the same time it is scientifically a controversial issue with no consensus (Davidson and Janssens, 2006; Kirschbaum, 2006). The temperature dependence is commonly described by a Q_{10} function but there are no biological reasons for choosing such a function rather than other functions with similar shapes. When empirical data are analysed in terms of Q_{10} functions, the Q_{10} value is not stable but decreases with temperature, which indicates that other functions should rather be chosen. One of the reasons for the difficulty in identifying the temperature response is that several mechanisms are involved, each with its own specific temperature response. For example, Thornley and Cannell (2001) showed that a temperature dependent adsorption reaction that stabilises organic matter can even increase soil carbon stores if temperature increases and Davidson et al. (2006) argued that the temperature dependences of the maximum enzyme activity and the affinity constant may cancel each other and result in weak temperature responses.

We will in this paper analyse the consequences of combining three different mechanisms that contribute to the temperature dependence of SOM mineralisation.

Theory

The use of organic matter by decomposers is determined by at least three independent mechanisms: (i) the rate at which decomposers take up substrate at their surface (μ); (ii) the rate by which substrate diffuses up to the surface of the decomposer (D); and (iii) the rate at which substrate is made available in the environment (S). All these three processes depend on temperature.

We will analyse the problem by looking at the diffusion of a substrate from an external surface to the surface of the decomposer. At the external surface we assume that the substrate is in equilibrium with a huge reservoir such that the substrate concentration at the external surface is constant and equal to S. The equilibrium between the reservoir and the concentration is, however, temperature dependent. At the surface of the decomposer, the rate of substrate assimilation is described by a Michaelis-Menten equation with temperature dependent maximal rate μ and half-saturation constant K. Let the concentration at a point $\vec{r}$ in the space between the external surface and the decomposer be $c(\vec{r})$. If the temperature dependent, but otherwise constant, diffusion coefficient is D, the general problem we have to solve is

$$\begin{aligned}
&\frac{\partial c(\vec{r})}{\partial t} = D\nabla^2 c(\vec{r}) \\
&c(a) = S \\
&F = D\hat{r}\bullet\nabla c(b) = \frac{\mu c(b)}{K + c(b)}
\end{aligned} \tag{1}$$

where $c(a)$ and $c(b)$ are the substrate concentrations on the external surface and the decomposer surface, respectively, $\hat{r}$ is a normal to the decomposer surface, and F the rate of assimilation of substrate. A summary of symbols used is given in Table 1.

Table 1.

Definition and default values of variables and parameters

Variable/ Parameter	Explanation	Default value
a	Distance to external surface	
b	Radius of decomposer	
A_μ	Activation energy for carbon uptake	5000 K
A_D	Activation energy for diffusion	5000 K
A_K	Activation energy for half-saturation of carbon uptake	5000 K
A_S	Activation energy for carbon release	5000 K
D	Diffusion coefficient	
D_0	Base value for diffusion coefficient	$1/273 \bullet 10^8$
F	Carbon flux into decomposer	
K	Half-saturation value for carbon uptake	
K_0	Base value for half-saturation value for carbon uptake	$4.71 \bullet 10^7$
L	Distance between decomposer and external surface, a - b	10
S	Rate of carbon release	
S_0	Base rate for carbon release	10^8
μ	Rate of carbon uptake	
μ_0	Base rate for carbon uptake	10^8

When not given, the units chosen are arbitrary, but values are chosen to give consistent magnitudes

The steady state solution to eqn (1) in planar geometry is

$$\begin{aligned} \frac{d^2c}{dx^2} &= 0 \\ \frac{dc}{dx} &= k_1 \\ c &= k_1x + k_2 \end{aligned} \tag{2}$$

where k_1 and k_2 are integration constants, which are determined from the boundary conditions at $x = a$ and $x = b$ ($L = a - b$). With the boundary conditions defined in eqn (1), we get

$$F = Dk_1 = \frac{1}{2}\left(\mu + D\frac{K+S}{L}\right) - \sqrt{\frac{1}{4}\left(\mu + D\frac{K+S}{L}\right)^2 - \frac{\mu DS}{L}} \tag{3}$$

The special cases when either of μ, D, S or K is small or large are of interest

$$F \approx \begin{cases} \dfrac{SD}{L}, \ \mu \text{ large} \\ \mu, \ S \text{ large} \\ \dfrac{\mu S}{K+S}, \ D \text{ large} \\ \dfrac{\mu S}{K}, \ K \text{ large} \end{cases} \qquad F \approx \begin{cases} \mu, \ \mu \text{ small} \\ \dfrac{\mu DS}{KD + \mu L}, \ S \text{ small} \\ \dfrac{SD}{L}, \ D \text{ small} \\ \dfrac{SD}{L}, \ K \text{ small} \end{cases} \tag{4}$$

Eqn (3) is also valid for a cylindrical geometry where the decomposer is a tube with radius *a* inside a tube of radius *b*, and for a spherical geometry where the decomposer is a sphere of radius *a* inside a sphere of radius *b* if the characteristic distance *L* is replaced as follows

$$\begin{aligned} &L \to b \ln \frac{a}{b} \quad \text{cylindrical geometry} \\ &L \to \frac{b}{a}(a-b) \quad \text{spherical geometry} \end{aligned} \tag{5}$$

We will now assume that the four rate determining parameters vary with temperature *T* as follows

$$\begin{aligned} \mu(T) &= \mu_0 e^{-A_\mu/T} \\ S(T) &= S_0 e^{-A_S/T} \\ D(T) &= T D_0 e^{-A_D/T} \\ K(T) &= K_0 e^{-A_K/T} \end{aligned} \tag{6}$$

The temperature dependence of $D(T)$ is taken from Jost (1960), whereas for the others we have assumed conventional Arrhenius temperature responses. We will for simplicity refer to the *A*'s as activation energies, rather than a more precise E $(=AR)$.

Typical values for D are 10^{-5} cm^{2}s^{-1}. We estimate L as follows. The length of living fungal hyphae can be 200 km dm^{-3} (Berg and McClaugherty, 2003). This gives an average radius of soil around the hyphae of $4{\cdot}10^{-6}$ dm, which should be a typical value for L. Concentrations of dissolved organic carbon ($\sim S$) can be 100 mg (C) L^{-1} (Fröberg, 2004). The flux of carbon to decomposers is of the order of $SD/L = 100{\cdot}10^{-6}{\cdot}10^{-7}{\cdot}3600{\cdot}24/4{\cdot}10^{-4}$ kg (C) d^{-1} = $0.2{\cdot}10^{-2}$ kg (C) d^{-1} in 1 dm^3 of soil. If the soil contains 30 % organic matter with a carbon concentration of 50 %, this flux of carbon corresponds to carbon loss rate of approximately 1 % d^{-1}, which is on the high side but of the right order of magnitude. According to Jost (1960, p 473) the temperature dependence for D in the system $C_2H_2Cl_4$-$C_2H_2Br_4$ corresponds to $A_D = 5756$ K, which in the temperature range of interest is close to $Q_{10} = 2$. We lack information allowing us to estimate the other parameters (μ_0, A_μ, S_0, A_S, K_0, and A_K) but we will choose them such that all three processes (uptake, diffusion, and release) have approximately the same magnitudes and the same temperature dependence. With the default parameters (Table 1), the Q_{10}'s at 288 K for the individual processes are 1.8 except for D with 1.9. With increasing activation energies, Q_{10}'s increase as a direct consequence of the formulation of temperature dependencies in equation (6). Since our focus is on the temperature response and we do not intend to predict absolute values of carbon fluxes but only to investigate the relative importance of different processes, it is the relative values of the parameters, except the activation energies, that matter. We have therefore chosen a set of default parameters (Table 1) that give approximately equal importance to the three processes and then investigated changes around these default values.

For simplicity we will express results as Q_{10} values, which we define as follows

$$Q_{10} = e^{10 \partial \ln F / \partial T} \tag{7}$$

Results

Fig. 1 shows the variation in carbon flux for each of the four activation energies. The flux responds to differences in activation energies such that increasing any of the activation energies A_μ, A_D, and A_S or decreasing A_K, places this process in control of the overall rate, and the rate decreases rapidly with increasing/decreasing activation energy.

The carbon flux, F, and the substrate concentration at the decomposer surface, $c(b)$, both increase smoothly with temperature, data not shown, as a consequence of all involved processes running faster at higher temperatures. The relative change in the two variables with temperature, Q_{10}, decreases on the other hand as a direct consequence of the Arrhenius functions, Fig. 2. Such a decrease in the temperature response (Q_{10}) of the carbon flux has often been observed (Kirschbaum, 2006).

The variation in temperature response with the activation energies is, however, more complex, Fig. 3. Increasing the activation energy for either D or S leads to a monotonous increase in Q_{10}; the increase is a sharp just below the common (default) activation energy. The slight difference between S and D depends on the extra temperature factor in D. The variation in Q_{10} when the activation energy for μ is changed is quite different. Increasing the activation energy from low values has almost no effect until the common activation energy is reached, where a sharp drops occurs. With further increases in the activation energy, Q_{10} starts to increase.

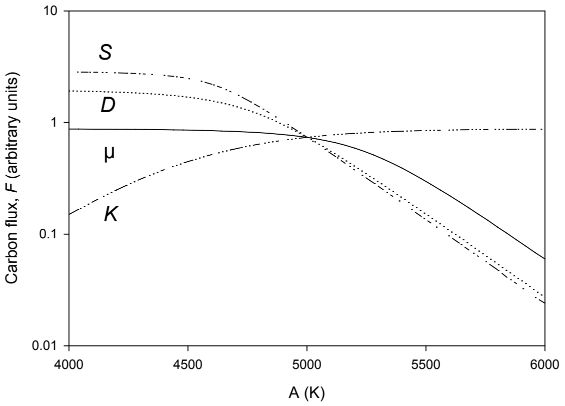

Fig. 1. The carbon flux at T = 288 K as a function of the activation energies A_μ, A_D, A_S, and A_K, respectivley. The activation energy is at the default value for the other three processes.

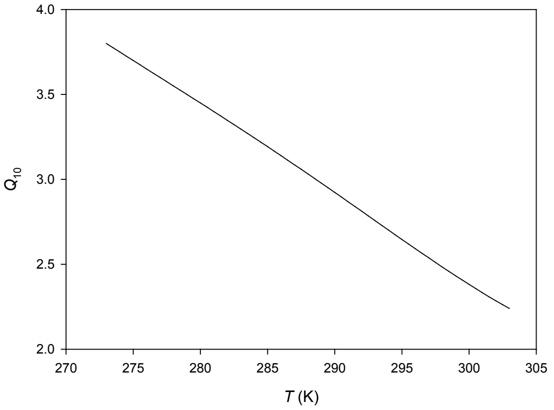

Fig. 2. Q_{10} as a function of temperature with default parameter values.

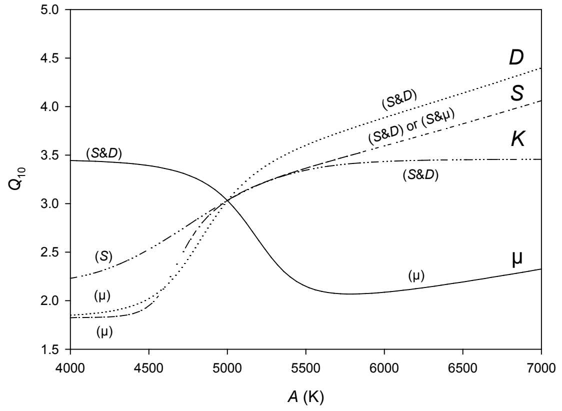

Fig. 3. Q_{10} at T = 288 K of the uptake of carbon (F) as a function of the activation energies A_μ, A_D, A_S, and A_K, respectively. The activation energy is at the default value for the other three processes. Within parentheses are shown the process(es) dominating the temperature response.

The different behaviours in the Q_{10} response to activation energy can be understood from eqn (4). Let us first note that Q_{10} of two processes that multiply each other is the product of the individual Q_{10}'s. At the default activation energy (5000 K), Q_{10} of the total system is 3.0, which is less than the product of any two of the individual processes (3.3 or 3.5 depending on whether D is one of the processes or not). The temperature response is, therefore, less than the combined effect of two individual processes. However, when we lower the activation energy from the default value for

μ (i.e. μ increases): the flux of carbon becomes controlled by transport (S and D) – two processes;

S (i.e. S increases): the supply at the decomposer surface will always be large and the flux is only determined by μ ($S >> K$) – one process;

D (i.e. D increases): the supply at the decomposer surface will always be large and the flux is determined by μ, but with some effect of S – one process;

K (i.e. K increases): the temperature dependencies of μ and K cancel out, but the temperature dependence of the supply at the decomposer surface remains and is controlled by S – one process.

When the activation energies are increased from the default value for

μ (i.e. μ decreases): there will always be a large supply at the decomposer surface and the rate is determined by μ alone – one process;

S (i.e. S decreases): there will be a shortage at the decomposer surface if D is small and the rate is determined by S in combination with D or if μ is small the rate will depend on the supply S and the uptake μ – two processes

D (i.e. D decreases): anything arriving at the decomposer surface will be taken up and D and S will in combination determine the rate – two processes;

K (i.e. K decreases): the uptake becomes independent of K and Q_{10} does not respond to any further changes in A_K but the level of uptake is determined by the combination of S and D.

The effects of changing the activation energy can therefore be interpreted in terms of the number of rate controlling processes. Going from low to high activation energies with *S* and *D* means going from conditions where only one process dominates the rate to conditions where two processes are important. Q_{10} is therefore initially low but at the transition from one to two controlling processes Q_{10} increases rapidly but beyond the transition Q_{10} still increases but at a slower pace following eqn (6). For μ the opposite occurs. At low activation energies, two processes are dominating, resulting in a high Q_{10} and with the transition to only one dominating process Q_{10} has to drop but beyond this transition Q_{10} increases with further increases in the activation energy as follows from eqn (6).

Discussion

It has not been the purpose of this paper to come up with the definite temperature response function for litter and SOM decomposition but rather to shed light on the reasons behind the variability in observed temperature responses. We have chosen to describe differences between systems in terms of four activation energies. It is clear that these activation energies can vary from one system to the other. Decomposer organisms vary between systems and it is likely that they behave differently, modifying the function μ. The quality of substrate interacts directly with temperature (Bosatta and Ågren, 1999; Fierer et al., 2006), which also will modify the function μ. S represents the combined effect of all processes producing dissolved organic carbon from SOM. Decomposition of organic matter by exoenzymes and root exudation contribute to *S* as well as interactions between organic matter and mineral complexes (adsorption/desorption), all of which will vary with temperature. The diffusion of substrates depends on a number of environmental factors such as soil water and physical structure, modifying the function *D*.

The relative magnitude of different processes clearly plays an important role in determining the temperature response and when moving between systems the limiting factor(s) can shift with non-trivial results. As Fig. 3 shows, the combined effect of several mechanisms can be so far from additive/multiplicative that even if Q_{10} increases with the activation energy for each process involved, increasing the activation energy for one of the processes can lead to a decrease in Q_{10} in the combined response. The carbon flux in the model has two components, the uptake at the decomposer surface and the supply of carbon to the decomposer surface. The uptake is controlled by two activation energies (A_μ and A_K) but the net effect of these two is always less than that of any one of them alone. When there is abundant substrate at the decomposer surface and the carbon flux is controlled by uptake there will, therefore, be at most one activation energy determining the temperature response. The supply of carbon to the decomposer surface, on the other hand, depends on both the rate of diffusion and the rate at which carbon is released in the environment. These two processes will in general reinforce each other and hence give a stronger temperature response.

With this model there will never be a situation without temperature response ($Q_{10} \approx 1$) as discussed by e.g. Davidson et al. (2006), because the temperature response of two functions (μ and *K*) cancel out. For such a cancellation *K* must be large relative to *S*, otherwise the temperature dependence of *K* does not matter. But when *K* is large, the temperature dependence of the supply, *S*, is still there. Experimental identification of which processes might contribute to the temperature response would therefore be valuable in order to make experiments comparable. This is not a simple question as experimentally varying potential factors does not always produce expected effects, Reichstein et al. (2005).

Our approach has by necessity involved simplifications. The release of substrate from a surface at a fixed distance from the decomposer is one such simplification. A more detailed description could include exoenzymes diffusing away from the decomposer and releasing substrate in the entire volume surrounding the decomposer. The description of the diffusion process is also simplified for such a complex media as soil and could include adsorption-desorption as components. A warmer soil might mean less soil water with a reduced diffusion rate and hence a temperature response opposite of the one in eqn (6) but such effects are not included in our model. Uptake of substrate by decomposers is probably also more complex than described here. However, already with the simple model used here the combined effect of three independent temperature responses produces non-trivial results and emphasises the need to ensure that experimental conditions are, indeed, comparable. Or as Kirschbaum (2006) writes in his Citation classic, “It is likely that this lack of consensus is largely due to different studies referring to different experimental conditions where confounding factors play a greater or lesser role.”

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