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Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlook

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Abstract. Knorr et al. (2005) concluded that soil organic carbon pools with longer turnover times are more sensitive to temperature. We show that this conclusion is equivocal, largely dependent on their specific selection of data and does not persist when the data set of Kätterer et al. (1998) is analysed in a more appropriate way. Further, we analyse how statistical properties of the model parameters may interfere with correlative analyses that relate the Q_{10} of soil respiration with the basal rate, where the latter is taken as a proxy for soil organic matter quality. We demonstrate that negative parameter correlations between Q_{10}-values and base respiration rates are statistically expected and not necessarily provide evidence for a higher temperature sensitivity of low quality soil organic matter. Consequently, we propose it is premature to conclude that stable soil carbon is more sensitive to temperature than labile carbon.

1 Introduction

The temperature sensitivity of soil carbon decomposition is a key factor determining the response of the terrestrial carbon balance to climatic change as most recently shown in coupled global carbon climate-vegetation model studies (e.g., Jones et al., 2003). Consequently, temperature sensitivity of soil respiration and soil organic matter decomposition has received a lot of attention (e.g., Lloyd and Taylor, 1994; Davidson et al., 1998; Kätterer et al., 1998; Luo et al., 2001; Reichstein et al., 2003; Sandermann et al., 2003). In particular the questions have arisen, whether the temperature sensitivity differs between labile and stable soil carbon pools (Liski et al., 1999; Ågren, 2000; Davidson et al., 2000; Giardina and Ryan, 2000) and whether soil organisms acclimate to higher temperatures (e.g., Luo et al., 2001).

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2 Analysis and discussion of results found by Knorr et al. (2005)

Recently, Knorr et al. (2005) demonstrated that neither acclimation to higher temperature, nor temperature insensitivity of stable soil organic carbon decomposition is necessary to explain recent results from soil warming and incubation experiments (Giardina and Ryan, 2000; Luo et al., 2001). We agree with Knorr et al. (2005) that these findings can be more convincingly explained by the intrinsic dynamics of soil carbon pools with substantially different decomposition rates as implemented in most global carbon cycle models (cf. also Reichstein et al., 2000; Kirschbaum, 2004). Hence, the hypothesis of increased soil organic matter decomposition inducing a positive carbon cycle feedback in response to global warming cannot be rejected.

Knorr et al. (2005) also conclude from their study that the decomposition of stable soil organic matter is even more sensitive to increases in temperature than that of labile pools, thereby exerting an even stronger positive feedback to global warming than assumed by current carbon cycle models. We do not agree with this conclusion, since we propose that it is largely contingent on the subset of the incubation review data from Kätterer et al. (1998) chosen for the analysis. A significant positive correlation between the activation energy (Ea) in the Arrhenius-equation (which determines the temperature sensitivity) and the log-transformed apparent turnover time of the sample appears when studies with incubation times of less than 100 days are excluded (Fig. 1, red crosses and red line). However, if all data from Kätterer et al. (1998) are retained, no significant correlation remains (Fig. 1, diamonds and black line). Short-term soil incubation studies are

Table 1. The effect of the random error standard deviation (σ_ε) on the statistical properties of the parameter estimates of the Q_{10} model as found by the Monte-Carlo analysis. See text for details.

σ_ε	Percentiles for Q_{10}		Percentiles for base respiration		Linear correlation Q_{10} and base respiration
[μg C g^{-1} soil h^{-1}]	–	–	[μg C g^{-1} soil h^{-1}]		–
	5%	95%	5%	95%	
0.125	2.43	2.72	0.080	0.108	−0.99
0.25	2.41	2.98	0.068	0.112	−0.96
0.5	2.03	3.30	0.049	0.176	−0.94

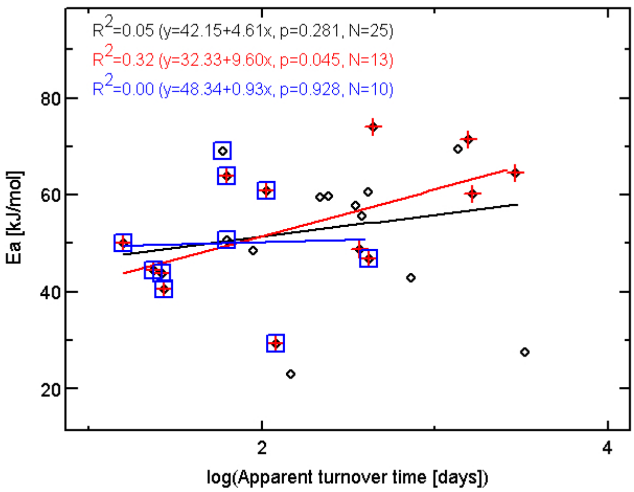

Fig. 1. Correlations between activation energy (Ea) and turnover time using data from Kätterer et al. (1998). Black diamonds and black regression line reflect all data in Kätterer et al. (1998). Red crosses and red regression line represent studies with incubation time over 100 days (as in Knorr et al., 2005). Blue squares and regression lines represent all studies where incubation time was at least as long as the apparent half-life of the sample. Coefficients of determination (R^2), the regression equation, the significance level (p) and the number of the studies included (N) are given at the top in the respective colour.

less reliable for parameter estimations when turnover is slow. Hence, in our view it is more appropriate to exclude incubation studies according to a criterion relating incubation time to apparent turnover time of the sample. Excluding all soil incubation studies that lasted less than 69% of the apparent turnover time, i.e. less than the apparent half-life, leads to no correlation at all (Fig. 1, blue squares and line).

Moreover, analysing the original data with a two-compartment decomposition model, where the rate constants of the labile and stable pool are allowed to vary independently with temperature, yields a small reverse difference between the temperature sensitivity of the stable and labile pools, the activation energy being 47.3±0.9 kJ/mol for the labile and 44.5±0.6 kJ/mol for the stable pools, respectively.

In general, studies where parameters are estimated from experimental data and a posteriori correlated against each other (e.g., Fierer et al., 2005), should be interpreted with care, taking into account the expected statistical correlations of model parameters (e.g., Draper and Smith, 1981) that do not necessarily have an ecological meaning. We demonstrate this here using a Monte-Carlo approach, where we create simulated data sets by adding normal random errors (representing experimental noise) to a deterministic temperature (T_{soil}) response of soil respiration (R_{soil}) described by $R_{soil}=B\times Q_{10}^{0.1\times T_{soil}}$ (B=0.1 μg C g^{-1} soil h^{-1}; Q_{10}=2.5; T_{soil} range 10–30°C). These settings are similar to the data recently presented by Fierer et al. (2005). In this way, we produced each 100 data set realizations with random error standard deviations (σ_ε) of 0.125, 0.25 and 0.5 μg C g^{-1} soil h^{-1}, respectively (cf. Fig. 2a). Subsequently, for each data set the parameters B and Q_{10} were estimated by a non-linear least squares algorithm (nlinlsq in PV-WAVE 7.0; Visual Numerics Inc, 1993). Figure 2b shows the resulting parameter distribution for σ_ε=0.25 μg C g^{-1} soil h^{-1}, yielding Q_{10}-values between 2.3 and 3.2, which are strongly correlated with the basal respiration rate parameter B. This correlation is merely an effect of the statistical model properties (Draper and Smith, 1981), since the constructed data set originates from a simple Q_{10} response with simulated noise. While the negative correlation between the parameters is high, with all magnitudes of the experimental error (σ_ε), it is evident that with decreasing experimental error the range of Q_{10}-values declines (Table 1), which is in agreement with statistical theory, i.e. lower data uncertainties result in lower standard errors of parameters. Hence, it should be checked to which extent the results by Fierer et al. (2005) are affected by such statistical correlation, or – stated differently – if the correlations found by them are significantly higher than those expected from the statistical effect shown here.

Well-designed studies are necessary to test hypotheses regarding how soil carbon pool properties and their temperature sensitivities are related. Recent laboratory experiments indicate very similar responses of labile and more stable soil organic matter to temperature (Fang et al., 2005; Reichstein et al., 2005). However, due to their short duration, these studies can only differentiate between pools with very short and moderate turnover times, while no information on the behaviour of very old, resistant and or physically protected soil organic matter fractions can be obtained. Moreover, by definition, short-term studies, where high-frequency temperature oscillations are imposed (Fang et al., 2005; Reichstein et al., 2005) are not designed for detecting any possible acclimation effects. On the other hand, longer-term studies might create very unnatural conditions in the incubated soil samples since no fresh carbon input enters the soil (unlike in the ecosystem). This factor may induce microbial starvation and associated modifications of microbial assimilation efficiency, and may affect the respiratory quotient (ratio of CO_2 production and O_2 consumption) (Persson et al., 2000), cause accumulation of metabolic by-products (e.g., Kirschbaum, 1995), and change the microbial community structure. The latter has been clearly shown in situ in a girdling experiment, where the soil organismic community changed severely during one year of no supply of photosynthates (Schulze et al., 2004). Moreover, while the apparent acclimation of respiration observed during warming experiments can be favourably explained just by the dynamics of soil organic matter pools without real acclimation (Reichstein et al., 2000; Kirschbaum, 2004; Knorr et al., 2005), it cannot be doubted that acclimation does occur in biological systems as e.g. recently reviewed for plants (Atkin et al., 2005) and studied for fungi (Lange and Green, 2005). However the importance of these effects at the ecosystem level in the context of global warming remains unclear. Until these issues are more completely resolved, we have to live with more uncertainty with respect to the temperature sensitivity of soil organic matter decomposition than the Knorr et al. (2005) study seems to convey.

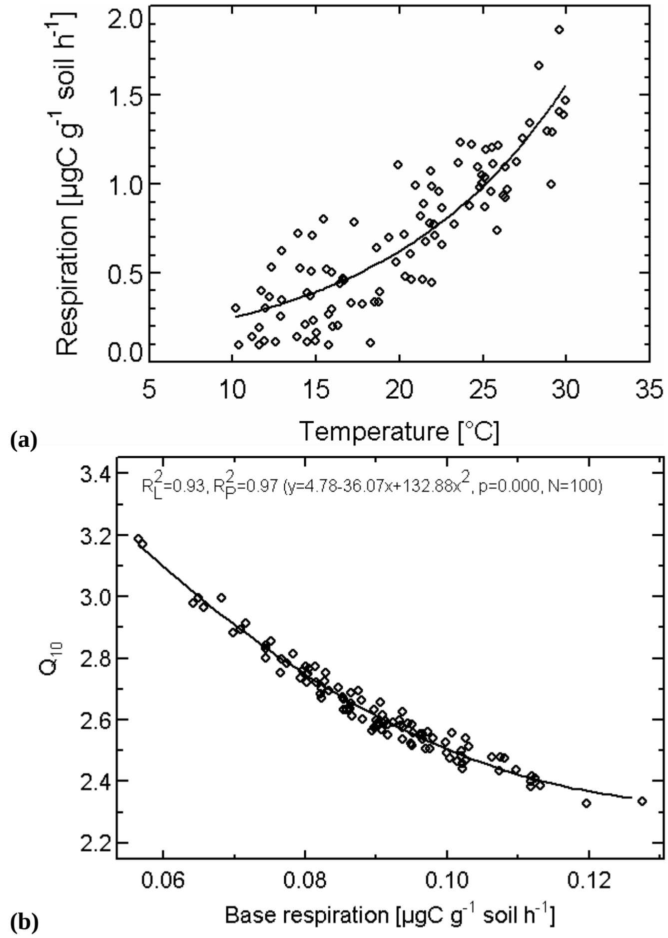

Fig. 2. (a) One single realisation of the data set in the Monte-Carlo analysis. This data set (symbols) was created by adding a normally distributed random error with a standard deviation of 0.25 μg C g^{-1} soil h^{-1} to the function $R_{\mathrm{soil}}=B\times Q_{10}^{0.1\times T_{\mathrm{soil}}}$ (B=0.1 μg C g^{-1} soil h^{-1}; Q_{10}=2.5). One hundred of those realizations were constructed, and for each realization the parameters B and Q_{10} estimated by non-linear regression. Panel **(b)** shows the distribution of the parameters after this procedure. A 2nd order polynomical regression line is added, and the linear (R_L^2) and polynomial (R_P^2) coefficients of determination, the polynomial regression equation, the significance (p) and the number of data points (N) are indicated at the top.

3 Conclusion and perspectives

Based on our analysis, we believe that it is premature to conclude that stable soil organic matter is more sensitive to temperature than labile organic matter. Although it is reasonable from a theoretical point of view that low quality substrates with long turnover times may have stronger temperature dependence than high quality substrates (Bosatta and Agren, 1999), the implementation of this assumption in global carbon models is currently not justified by empirical evidence. It seems that current experimental and modelling approaches cannot unequivocally answer this question of temperature sensitivity in relation to organic matter quality. We need to overcome two major types of obstacles that hampered fundamental breakthroughs in the past:

1. Although being dynamical, including up to several soil organic matter pools, most soil organic matter pools largely remain (semi-) empirical in the sense that the different pools are conceptual or abstract and not clearly related to measurable quantities. Thus, model evaluations are often possible only against total soil organic matter dynamics or total soil efflux, but these bulk quantities then do not contain enough information to falsify or parameterize these models (problem of model identification and equifinality). Model identification is also complicated a) by the fact that observed signals (e.g. of total efflux) are influenced by various confounding factors not considered in most models (e.g. CO_2 dissolution and dissociation in the soil solution, microbial dynamics) and b) by the problem that information with respect to older soil organic matter pools is limited in the

bulk fluxes, since most of the short-term efflux comes from the labile fraction as pointed out most recently by Leifeld (2005). Hence, if models attempt to describe the dynamics of more observable quantities like biophysical components (particle size or density distributions), biochemical components (substrates) or biological components (e.g. microbial biomass), more opportunities for model identification and falsification would arise. Moreover, instead of re-iterating various forms of pool models, model development should attempt to describe the underlying processes of soil organic matter stabilization and destabilization (substrate recalcitrance, substrate-mineral-soil physico-chemical interactions, sterical substrate accessibility, cf. Sollins et al., 1996). In a pure scientific sense, it is important to a priori formulate and derive concrete distinguishable hypotheses via the models that are then experimentally testable.

2. While more concrete and testable modelling approaches are certainly desirable, it has to be mentioned that lacking appropriate experimental methodology to produce high-precision, unbiased and generally applicable data has also been limiting the respective model development. For example estimates of microbial biomass still remain somewhat semi-quantitative and absolute numbers are hardly to compare between different soil types and soil textures. However, a lot of progress has been made, e.g. with respect to soil organic matter fractionation techniques and isotopic characterisation of the soil organic matter (e.g. Biasi et al., 2005; Leifeld and Fuhrer, 2005). Combinations of respiratory flux observations, organic matter fractionation and isotopic chararacterisation of both SOM fractions and CO_2 efflux should be able to impose a multiple constraint on soil organic models as outlined under point 1). A limitation of fractionation approaches of course is their destructive nature, which hampers the transferability of results to in-situ conditions. Hence, minimal-disturbance and in-situ experiments must be undertaken in parallel; the development of continuous parallel flux and isotopic measurements offers a lot of prospect for this. In the context of the temperature sensitivity of soil organic matter pools one could for instance imagine an experiment where magnitude and "^{14}C-age (or in C3/C4 transitional systems ^{13}C-age)" of the efflux are monitored continuously while a controlled temperature regime is imposed onto the soil. Under the hypothesis that older pools have a different temperature sensitivity than younger pools, a change of the carbon-age of the efflux at higher temperatures should be expected together with an increase of the total flux magnitude. Corollary to the previous paragraph on the modelling it is desirable to pursue experiments that can enlighten us with respect to the various mechanisms of stabilization. Examples are given in Leifeld (2005) and include the study of temperature dependence of enzyme and/or substrate specific reactions, sterilised versus biologically active soils, and absorption-desorption dynamics.

In summary, there is need for an ongoing dialogue between modellers and experimentalists to trigger a co-evolution of modelling and experimental approaches. In this context, the temperature sensitivity of different soil carbon pools merits particularly high-priority scientific experimental and theoretical dedication, in order to overcome the uncertainties that the Knorr et al. (2005) unfortunately could only apparently reduce.

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