**Temperature control of decomposition rate - a critical review using literature data analysed with different models**

**Contrôle par la température du degré de décomposition – Revue critique en utilisant divers modèles et les données de la littérature**

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**Introduction**

The strong correlation between soil respiration and temperature has been quantified for many soils under different conditions (for reviews see Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Kirschbaum, 1995). However, there is no consensus on the form of the relationship between decomposition and temperature. Besides the \( Q_{10} \) relationship, several other functions have been used to describe temperature responses. However, a comparison between studies where different approaches were used is possible. Problems arise when comparing studies where different methods had been used to estimate these functions. The fact that sometimes accumulated values of, e.g., \( \text{CO}_2 \) emission have been used and sometimes rates have been used in the studies is probably a minor problem. However, initial rates (Winkler et al., 1996), rates observed during different time periods at different incubation temperatures (Ross and Cairns, 1978), or rate constants as estimated by different models and using different fitting algorithms (e.g. Blet-Charaudeau et al., 1990; Updegraff et al., 1995; Thierron and Laudelout, 1996; Lomander et al., submitted) have been used to estimate temperature responses, which makes a direct comparison difficult to interpret.

The objective of the work presented here was to estimate the functional relationship between temperature and decomposition rates using a novel modelling approach. The literature was reviewed and a data set was compiled from data given in figures and tables. This data set was analysed using dynamic one-component and two-component models.
**Material and methods**

*Data sources*

The literature was reviewed regarding laboratory incubation studies where C mineralization was measured in laboratory incubations. The selection criteria were:
- the same substrate was incubated at least at two different temperatures, and
- time series were available and were comprised of at least four measurements for each substrate and temperature.

To avoid too heavy dependence on a single study, we included only three experiments (low, medium and high decomposition rates) from references where more than three experiments were presented (Azmal et al., 1996a,b). We excluded also experiments where decomposition rates were decreasing with temperature (Pöhhacker and Zech, 1995; E- and B-horizon, Winkler, 1996) or where temperature did not affect C-mineralization (Varnero et al., 1987; Pöhhacker and Zech, 1995). An overview of the resulting data set is given in Table 1.

*Data analysis*

The data were scaled to a common unit. A first-order one-component model and a parallel first order two-component model were used for the analysis of CO\textsubscript{2}-C evolution rates (\(C_{\text{flux}}\): mg (g substrate\(^{-1}\) day\(^{-1}\)) or cumulative CO\textsubscript{2}-C evolution (\(C_{\text{cum}}\): mg g substrate\(^{-1}\)):

\[
C_{\text{flux}} = \alpha C_0 k_1 e^{-k_1 t} + (1-\alpha) C_0 k_2 e^{-k_2 t}; \quad 0 \leq \alpha \leq 1
\]

\[
C_{\text{cum}} = \alpha C_0 (1 - e^{-k_1 t}) + (1-\alpha) C_0 (1 - e^{-k_2 t}); \quad 0 \leq \alpha \leq 1
\]

where \(C_0\) is the initial amount of total carbon in the substrate and \(\alpha C_0\) and \((1-\alpha)C_0\) are the initial amounts of carbon in the two respective pools in the two-component model, and \(k_1\) and \(k_2\) are the corresponding rate constants. In the one-component model: \(\alpha=1\), and thus only one pool remains. If both rates and cumulative C-evolution were available, we analysed the rates to avoid statistical problems concerning autocorrelated residuals (Hess and Schmidt, 1995).

The models were fitted to the time series for the highest incubation temperature (\(T_{\text{max}}\)) in each experiment by optimising values for \(\alpha\), \(k_1\) and \(k_2\) simultaneously, using an algorithm for non-linear least squares (Ralston and Jennrich, 1979). Thereafter, the model was fitted to the time series for the remaining incubation temperatures of the corresponding experiment. For all these temperatures below \(T_{\text{max}}\), the value for \(\alpha\) was given the same value as estimated for \(T_{\text{max}}\) and the ratio between \(k_1\) and \(k_2\) (as estimated for \(T_{\text{max}}\)) was also fixed, i.e., temperature was assumed to affect \(k_1\) and \(k_2\) equally:

\[
k_1 = r k_{1_{\text{max}}}
\]

\[
k_2 = r k_{2_{\text{max}}}
\]

where \(r\) is the temperature response factor and \(k_{1_{\text{max}}}\) and \(k_{2_{\text{max}}}\) are the rate constants at \(T_{\text{max}}\).

The next step was to describe the dependence of these response factors on temperature for each experiment. We tested four functions \(r(T)\), all with one free parameter apart from the reference temperature (\(T_{\text{ref}}\)), i.e., the temperature at which \(r\) equals unity:

1) An Arrhenius-type function

\[
r(T) = e^{-\frac{T_{\text{ref}}}{R} \left[ \frac{1}{T_{\text{ref}} + 273.15} - \frac{1}{T + 273.15} \right]}\]

\[(3)\]
where \( R \) is the universal gas constant (8.314 J mol\(^{-1}\) K\(^{-1}\)) and \( E \) is the activation energy (J mol\(^{-1}\)).

2) A two-parameter function proposed by Lloyd and Taylor (1994)

\[
r(T) = e^{\frac{E_o}{T_{ref} + 273.15 - T - 273.15 - T_o}}
\]

(4)

where \( E_o \) and \( T_o \) are parameters. Here, we used the value for \( E_o \) (=35.41°C) proposed by Lloyd and Taylor (1994).

3) The \( Q_{10} \) function

\[
r(T) = Q_{10}^{T - T_{ref}}
\]

(5)

4) A function proposed by Ratkowsky et al. (1982)

\[
r(T) = \frac{(T - T_{min})^2}{(T_{ref} - T_{min})^2}
\]

(6)

where \( T_{min} \) is the value of \( T \) at which C-evolution equals zero.

After fitting these functions to the \( r \)-factors for each experiment (\( T_{ref} = T_{max} \)), we normalized these functions for a common reference temperature, \( T_{ref} \), and recalculated the \( r \)-factors for each experiment and function (cf. Andrén and Paustian, 1987). Thereafter, we fitted the corresponding four functions to these normalized \( r \)-factors (as estimated using the same functions) for the whole data set. \( R^2 \), the coefficient of determination, adjusted for the number of parameters, as calculated by linear regression was used as a measure for goodness of fit between C-evolution measurements and model output; \( R^2 \) as calculated by non-linear regression was used as a measure of goodness of fit between \( r(T) \) and \( r \)-factors.

**Results and discussion**

The two-component model could describe the dynamics of the 25 experiments much more adequately than the one-component model. The agreement between all modelled and measured values (all temperatures) of each experiment resulted in much higher \( R^2 \)-values for the two-component model than for the one-component model (Table 1). All three simultaneously estimated parameters (\( \alpha \), \( k_1 \) and \( k_2 \)) were highly correlated. This implies that changes in one are compensated by changes in the other two parameters without greatly affecting the fit of the model. For example, reducing \( \alpha \) by 50% of the optimized value affected the resulting \( r \)-factors in average by less than 5%. The strong correlation between the parameters makes it difficult to interpret each of them separately, although this has been tried (Updegraff et al., 1995).

All four tested temperature response functions could be fit well to the response factors of each experiment (\( R^2 \)-values were generally high; not shown). However, the estimated parameter values varied greatly between experiments (Table 1). The choice of reference temperature (\( T_{ref} \)) when rescaling the \( r \)-factors from \( T_{max} \) to the common \( T_{ref} \) influenced the resulting total response function (not shown). The \( R^2 \)-value was highest (=0.96) for all four tested response functions when 30°C was chosen as the reference temperature. The estimated parameter values for \( E \), \( E_o \), \( Q_{10} \) and \( T_{min} \), were 54.2, 233, 2.06 and -3.78, respectively (with \( T_{ref} \) =30°C and \( T_{max} \) =40°C).

The fit of the response functions to \( r \)-factors deriving from the one-component model was much poorer (Table 1) and the response was generally less concave than that of the
two-compartment model, i.e., \( r \)-factors increased less with temperature than they did for the two-component model.

The assumption made in the two-compartment model that \( k_1 \) and \( k_2 \) are equally affected by temperature was tested. These two parameters were estimated independently for each incubation temperature and experiment, whereafter the response functions (Eqs. 3-6) were fitted to the \( r \)-factors according to the procedure described above, but for \( k_1 \) and \( k_2 \) separately. The resulting response functions as estimated for \( k_1 \) and \( k_2 \) were similar to each other and to those for their combined response (i.e. when \( k_1 \) and \( k_2 \) were equally affected by temperature).

A \( Q_{10} \) value of 2 as used in many model applications is probably an adequate value when modelling the effect of temperatures between about 5 and 35°C on decomposition, at least when simulating ecosystem responses at larger scales. However, for individual substrates, \( Q_{10} \) values may deviate greatly from 2.

To model temperature responses above 35°C, bell-shaped functions—which consider that responses are decreasing above an optimum temperature—should be used (cf. Kirschbaum, 1995). Constant values for \( E \) and \( Q_{10} \) at lower temperature intervals are theoretically unreasonable, since both \( E \) and \( Q_{10} \) approach infinity when \( r(T) \) approaches zero. Thus, for temperature below 5°C, functions not based on \( Q_{10} \) are probably more adequate. The models proposed by Ratkowsky et al. (1982) and Lloyd and Taylor (1994) may be good candidates. However, due to the paucity of data from low-temperature incubations (Table 1), this suggestion is only tentative, and more experimental work is called for.

References
Ralston ML, Jennrich RI (1979) DUD, a derivative-free algorithm for non-linear least squares. Technometrics 1:7-14
Waksman SA, Gerretsen FC (1931) Influence of temperature and moisture upon the nature and extent of decomposition of plant residues by microorganisms. Ecology 12:33-60

Keywords : carbon evolution, decomposition, model, Q10, temperature effects, soil respiration
Mots clés : évolution du carbone, décomposition, modélisation, Q10, effet de la température, respiration du sol
Table 1. Short description of the experiments included in the data set and rate constants as estimated by fitting a one-component ($k$) and a two-component ($\alpha$, $k_1$, and $k_2$) decomposition model to C evolution rates or cumulative C evolution (cum.) from the experiment with the highest incubation temperature. The corresponding goodness of fit, $R_{1\text{adj}}^2$ and $R_{2\text{adj}}^2$, respectively, were determined by linear regression (modelled vs. measured values). Parameter values determining the four temperature response functions (eqs. 3-6) refer to the two-component model and were estimated by non-linear regression. When the carbon concentration (C%) was given in the references, the dimension of the rate constants was relative to substrate mass (mg C g substrate$^{-1}$); otherwise (C%=100) the rates were relative to the C mass (mg C g substrate C$^{-1}$).

<table>
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<th>Data source</th>
<th>Substrate</th>
<th>Incubation temperatures (°C)</th>
<th>Days</th>
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<th>$k$ ($\times 10^{-4}$)</th>
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<th>$\alpha$ ($\times 10^{-3}$)</th>
<th>$k_1$ ($\times 10^2$)</th>
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