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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., 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_2-C evolution rates (C_{flux}; mg (g substrate)$^{-1}$ day^{-1}) or cumulative CO_2-C evolution (C_{cum}; mg g substrate^{-1}):

$$C_{flux} = \alpha C_0 k_1 e^{-k_1 t} + (1-\alpha) C_0 k_2 e^{-k_2 t}\,; \qquad 0 \le \alpha \le 1 \qquad \text{(1a)}$$

$$C_{cum} = \alpha C_0 \left(1 - e^{-k_1 t}\right) + (1-\alpha) C_0 \left(1 - e^{-k_2 t}\right); \qquad 0 \le \alpha \le 1 \qquad \text{(1b)}$$

where C_0 is the initial amount of total carbon in the substrate and αC_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_{max}) in each experiment by optimising values for α, 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_{max}, the value for α was given the same value as estimated for T_{max} and the ratio between k_1 and k_2 (as estimated for T_{max}) was also fixed, i.e., temperature was assumed to affect k_1 and k_2 equally:

$$k_1 = r k_{1\max} \qquad \text{(2a)}$$

$$k_2 = r k_{2\max} \qquad \text{(2b)}$$

where r is the temperature response factor and k_{1max} and k_{2max} are the rate constants at T_{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_{ref}), i.e., the temperature at which r equals unity:

1) An Arrhenius-type function

$$r(T) = e^{\left[\frac{E}{R}\left(\frac{1}{T_{ref}+273.15} - \frac{1}{T+273.15}\right)\right]} \qquad \text{(3)}$$

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)

$$r(T) = e^{E_0\left(\frac{1}{T_{ref}+273.15-T_o}-\frac{1}{T+273.15-T_0}\right)} \tag{4}$$

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

$$r(T) = Q_{10}^{\frac{T-T_{ref}}{10}} \tag{5}$$

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

$$r(T) = \frac{\left(T - T_{\min}\right)^2}{\left(T_{ref} - T_{\min}\right)^2} \tag{6}$$

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_{adj}^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_{adj}^2-values for the two-component model than for the one-component model (Table 1).

All three simultaneously estimated parameters (α, 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 α 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.

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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 (α, 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_{1adj}^2 and R_{2adj}^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}).

Data source	Substrate	Incubation temperatures (°C)	Days	C %	k ($\times10^{-4}$)	R_{1adj}^2	α ($\times10^{-3}$)	k_1 ($\times10^{-2}$)	k_2 ($\times10^{-4}$)	R_{2adj}^2	E	T_o	Q_{10}	T_{min}
Winkler et al. 1996	A-horizon	4, 15, 22, 38	120	1.0	11.1	0.54	13.7	15.3	6.49	0.92	48.7	231	1.92	-5.55
Honeycutt et al. 1988	Soil and sludge	5, 10, 15, 20, 25, 30	77	34.6	4.12	0.03	19.1	13.7	0.342	0.92	55.6	232	2.15	-4.65
Ross & Cairns 1978	Topsoil	5, 10, 15, 20, 24	45	4.6	7.70	0.80	2.07	189	7.32	0.97	59.5	230	2.33	-6.39
Ross & Cairns 1978	Topsoil	5, 10, 15, 20, 24	45	2.5	23.2	0.49	35.2	8.10	13.1	0.95	59.9	230	2.34	-6.59
Waksman & Gerretsen 1931	Oat straw	7, 27, 37	273	100	46.5	0.93	620	1.33	0.00	0.98	29.4	211	1.48	-22.7
Waksman & Gerretsen 1931	Oat straw	7, 27, 37	273	100	106	0.82	497	7.18	19.4	0.97	40.5	225	1.72	-9.93
Waksman & Gerretsen 1931	Oat straw	7, 27, 37	273	100	163	0.88	609	6.04	18.6	0.99	43.9	227	1.80	-7.47
M. Reichstein, unpublished	Organic layer	5, 15, 25	104	43.5	1.84	0.99	1.67	11.0	1.61	1.00	64.6	233	2.50	-5.16
M. Reichstein, unpublished	A-horizon	5, 15, 25	104	6.13	3.12	0.97	9.01	4.98	1.94	1.00	71.5	236	2.75	-2.90
Pöhhacker & Zech 1995	L-Layer	5, 12, 22, 32	50	100	11.4	0.86	370	0.62	2.40	0.93	60.6	229	2.40	-8.28
Blet-Charaudeau et al. 1990	Topsoil	2, 10, 19 ,28	56	1.8	2.57	0.95	3.72	15.9	1.43	0.99	69.6	237	2.64	-1.39
Blet-Charaudeau et al. 1990	Topsoil	10, 19, 28	56	7.4	0.94	0.98	0.82	28.4	0.69	0.99	27.7	204	1.47	-30.9
Roper 1985	Topsoil + straw	15, 20, 25, 30, 35, 40	105	50	6.93	0.67	21.6	37.7	12.5	0.94	60.8	243	2.19	+6.28
Roper 1985	Straw + soil	15, 20, 25, 30, 35, 40	300	50	53.4	0.29	26.0	54.7	16.9	0.82	63.9	244	2.28	+6.21
Azmal et al. 1996b	Topsoil	25, 35	56	2.2	6.76	0.98	7.88	11.4	4.83	0.99	42.9	229	1.75	-5.81
Azmal et al. 1996b	Topsoil + rice straw	25, 35	11	2.4	15.9	0.96	30.3	19.9	8.14	0.99	23.0	202	1.35	-36.6
Azmal et al. 1996b	Topsoil + *Azolla*	25, 35	9	2.4	20.7	0.90	48.9	21.5	7.90	0.99	48.5	233	1.89	-1.77
De Neve 1996	Topsoil + cauliflower	5.5, 10, 16	300	100	255	0.81	523	11.9	25.3	0.99	50.1	220	2.10	-15.9
Azmal et al. 1996a	Topsoil	15, 25, 35	56	2.2	7.83	0.98	2.20	98.7	7.27	0.99	57.8	237	2.16	+0.17
Azmal et al. 1996a	Topsoil + rice straw	15, 25, 35	56	2.4	17.9	0.91	25.3	62.5	11.3	0.99	69.2	243	2.51	+5.19
Azmal et al. 1996a	Topsoil +*Sesbania*	15, 25, 35	56	2.4	22.6	0.85	42.5	35.2	11.3	0.98	50.7	233	1.96	-2.36
Jansson 1958	Topsoil	25, 35	720	2.56	5.33	0.91	13.3	15.9	2.80	1.00	46.8	226	1.91	-9.11
Jansson 1958	Topsoil + straw	25, 35	720	2.97	17.6	0.85	85.7	49.0	2.80	0.98	44.4	224	1.84	-10.8
Lomander et al. (submitted)	Topsoil	0.3, 5, 15, 25	300	2.37	16.3	0.87	51.8	2.30	11.6	0.95	74.1	236	2.88	-2.48
Lomander et al. (submitted)	Subsoil	15, 25	300	1.3	4.70	0.73	17.7	1.40	3.68	0.75	60.3	233	2.33	-4.05