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## Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different models

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**Abstract** The literature was reviewed regarding laboratory incubation studies where C mineralization was measured. Experiments were selected in which the same substrate was incubated at least at two different temperatures and where time-series were available with at least four measurements for each substrate and temperature. A first-order one-component model and a parallel first-order two-component model were fitted to the CO<sub>2</sub>-C evolution data in each experiment using a least-squares procedure. After normalising for a reference temperature, the temperature coefficient ( $Q_{10}$ ) function and three other temperature response functions were fitted to the estimated rate constants. The two-component model could describe the dynamics of the 25 experiments much more adequately than the one-component model (higher R<sup>2</sup>, adjusted for the number of parameters), even when the rate constants for both were assumed to be equally affected by temperature. The goodness-of-fit did not differ between the temperature response models, but was affected by the choice of the reference temperature. For the whole data set, a  $Q_{10}$  of 2 was found to be adequate for describing the temperature dependence of decomposition in the intermediate temperature range (about 5–35 °C). However, for individual experiments,  $Q_{10}$  values deviated greatly from 2. At least at temperatures below 5 °C, functions not based on  $Q_{10}$  are probably more adequate. However, due to the paucity of data from low-temperature incubations, this conclusion is only tentative, and more experimental work is called for.

**Key words** Carbon evolution · Decomposition · Modelling · Temperature coefficient ( $Q_{10}$ ) · Temperature effects

### Introduction

It has been hypothesized that the positive response to increases in temperature is higher for decomposition than for primary productivity (Woodwell 1978; Jenkinson et al. 1991; Schimel et al. 1994; Kirschbaum 1995). Temperature increases are expected due to the emission of greenhouse gases (e.g. Houghton et al. 1990) and may provide a positive feed-back in the global C cycle due to decreases in soil C stocks.

The basic theory of decomposition kinetics has been well described by several authors (Bunnell and Tait 1974; Swift et al. 1979). The strong correlation between soil respiration and temperature was noted by Lundegårdh (1927) and has been quantified for many soils under different conditions (for reviews see: Singh and Gupta 1977; 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. In many decomposition studies, the temperature coefficient  $Q_{10}$  relationship (van't Hoff 1898) is used to describe the dependence of decomposition on temperature. Kirschbaum (1995) reviewed 20 different data sources and compiled reported  $Q_{10}$  values regarding C mineralization. Fitting the  $Q_{10}$  function to this data set resulted in high  $Q_{10}$  values at low temperatures, decreasing from about 8 at 0 °C to about 2.5 at 20 °C.

Besides the  $Q_{10}$  relationship, several other functions have been used to describe temperature responses: linear functions (e.g. Witkamp 1966; Froment 1972; Gupta and Singh 1981), power functions (e.g. Kucera and Kirkham 1971), Arrhenius-type functions (e.g. Howard and Howard 1979; Lloyd and Taylor 1994), S-shaped functions (e.g. De Neve 1996) and the heat sum concept (e.g. Andrén and Paustian 1987; Honeycutt et al. 1988)

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which corresponds to  $Q_{10}$  values exponentially decreasing with temperature. These functions can easily be converted into each other by changing parameters into temperature-dependent variables. Thus, a comparison between studies where different approaches were used is possible. However, problems arise when making a comparison, since experimental procedures and their analyses vary. The fact that sometimes accumulated values were used and sometimes rates were 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 algorithms to fit the data (e.g. Blet-Charaudeau et al. 1990; Updegraff et al. 1995; Thierron and Laudelout 1996; Lomander et al. 1998) have been used to estimate temperature responses.

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

## Materials and methods

### Data sources

The literature was reviewed regarding laboratory incubation studies where C mineralization was measured. The selection criteria were:

1. The same substrate was incubated at least at two different temperatures.

2. Time-series were available and comprised at least four measurements for each substrate and temperature.

From the resulting data set, several experiments were excluded:

1. Azmal et al. (1996a) presented results for eight different substrates. To avoid depending too heavily on a single study, we included only three substrates (low, medium and high decomposition rates).

2. Since only monotonously increasing response functions were considered, two substrates were excluded from one reference (E and B horizon; Winkler 1996) where decomposition rates decreased with temperature, and one substrate was excluded from Pöhhacker and Zech (1995), where temperature did not affect C mineralization (in a humic mineral horizon). The highest temperature (32°C) was also excluded for another substrate (beach litter) presented by Pöhhacker and Zech (1995), since CO<sub>2</sub> evolution was higher at 22°C than at 32°C.

Data from experiments where incubation temperatures exceeded 40°C were also excluded (Roper 1985).

One reference was excluded, where temperatures (10–60°C) had almost no effect on C mineralization in a Mediterranean soil (Varnero et al. 1987). 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<sub>2</sub>-C evolution rates ( $C_{flux}$ ; mg g<sup>-1</sup> substrate day<sup>-1</sup>) or cumulative CO<sub>2</sub>-C evolution ( $C_{cum}$ ; mg g<sup>-1</sup> substrate):

**Table 1** Short description of the experiments included in the data set and rate constants ( $k$ ) 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 ( $C_{cum}$ ) from the experiment with the highest incubation temperature. The corresponding goodness of fit,  $R^2_{adj}$  and  $R^2_{ind}$ , 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 C concentration (C%) was given in the references, the dimension of the rate constants was relative to substrate mass (mg C g<sup>-1</sup> substrate); otherwise (C% = 100) the rates were relative to the C mass (mg C g<sup>-1</sup> substrate C)

ID	Data source	Vegetation and soil	Substrate	Incubation temperatures (°C)	Days	Data type	C%	$k$ ( $\times 10^{-4}$ )	$R^2_{adj}$	$\alpha$ ( $\times 10^{-3}$ )	$k_1$ ( $\times 10^{-3}$ )	$k_2$ ( $\times 10^{-3}$ )	$R^2_{ind}$	$E$	$T_0$	$Q_{10}$	$T_{min}$
1	Winkler et al. (1996)	Mixed forest, Ultisol	A-horizon	4, 15, 22, 38	120	rates	1.0	11.1	0.54	13.7	15.3	6.49	0.92	48.7	231	1.92	-5.55
2	Honeycutt et al. (1988)	Agriculture	Soil and sludge	5, 10, 15, 20, 25, 30	77	cum.	34.6	4.12	0.03	19.1	13.7	0.342	0.92	55.6	232	2.15	-4.65
3	Ross and Cairns (1978)	Tussock grassland, silt loam	Topsoil	5, 10, 15, 20, 24	45	rates	4.6	7.70	0.80	2.07	189	7.32	0.97	59.5	230	2.33	-6.39
4	Ross and Cairns (1978)	Tussock grassland, loamy sand	Topsoil	5, 10, 15, 20, 24	45	rates	2.5	23.2	0.49	35.2	8.10	13.1	0.95	59.9	230	2.34	-6.59
5	Waksman and Gerretsen (1931)	Straw, dry, nutrients	Oat straw	7, 27, 37	273	cum.	100	46.5	0.93	620	0.00	0.00	0.98	29.4	211	1.48	-22.7
6	Waksman and Gerretsen (1931)	Straw, dry, nutrients added	Oat straw	7, 27, 37	273	cum.	100	106	0.82	497	7.18	19.4	0.97	40.5	225	1.72	-9.93
7	Waksman and Gerretsen (1931)	Straw, moist, nutrients added	Oat straw	7, 27, 37	273	cum.	100	163	0.88	609	6.04	18.6	0.99	43.9	227	1.80	-7.47
8	Reichstein (unpublished)	Heath, podzol	Organic layer	5, 15, 25	104	cum.	43.5	1.84	0.99	1.67	11.0	1.61	1.00	64.6	233	2.50	-5.16
9	Reichstein (unpublished)	Subalpine herbs and grass, podzol	A-horizon	5, 15, 25	104	cum.	6.13	3.12	0.97	9.01	4.98	1.94	1.00	71.5	236	2.75	-5.90
10	Pöhhacker and Zech (1995)	Deciduous, forest, brown earth	L-layer	5, 12, 22, 32	50	rates	100	11.4	0.86	370	0.62	2.40	0.93	60.6	229	2.40	-8.28
11	Blet-Charaudeau et al. (1990)	Wheat field, Rendoll	Topsoil	2, 10, 19, 28	56	cum.	1.8	2.57	0.95	3.72	15.9	1.43	0.99	69.6	237	2.64	-1.39
12	Blet-Charaudeau et al. (1990)	Native grassland, Rendoll	Topsoil	10, 19, 28, 30, 35, 40	56	cum.	7.4	0.94	0.98	0.82	28.4	0.69	0.99	27.7	204	1.47	-30.9
13	Roper (1985)	Wheat field, clay	Topsoil + straw	15, 20, 25, 30, 35, 40	105	rates	50	6.93	0.67	21.6	37.7	12.5	0.94	60.8	243	2.19	+6.28
14	Roper (1985)	Wheat field, loamy sand	Soil + straw	15, 20, 25, 30, 35, 40	300	rates	50	53.4	0.29	26.0	54.7	16.9	0.82	63.9	244	2.28	+6.21
15	Azmal et al. (1996b)	Upland field, loamy sand	Topsoil	25, 35	56	cum.	2.2	6.76	0.98	7.88	11.4	4.83	0.99	42.9	202	1.75	-5.81
16	Azmal et al. (1996b)	Upland field, clay loam	Topsoil + rice straw	25, 35	11	cum.	2.4	15.9	0.96	30.3	19.9	8.14	0.99	23.0	209	1.35	-36.6
17	Azmal et al. (1996b)	Upland field, clay loam	Topsoil + Azolla	25, 35	9	cum.	2.4	20.7	0.90	48.9	21.5	7.90	0.99	48.5	233	1.89	-1.77
18	De Neve (1996)	Chicory field, loamy sand	Topsoil + cauliflower	5.5, 10, 16	300	cum.	100	255	0.81	523	11.9	25.3	0.99	50.1	220	2.10	-15.9
19	Azmal et al. (1996a)	Upland field, clay loam	Topsoil	15, 25, 35	56	cum.	2.2	7.83	0.98	2.20	98.7	7.27	0.99	57.8	237	2.16	+0.17
20	Azmal et al. (1996a)	Upland field, clay loam	Topsoil + rice straw	15, 25, 35	56	cum.	2.4	17.9	0.91	25.3	62.5	11.3	0.99	69.2	243	2.51	+5.19
21	Azmal et al. (1996a)	Upland field, clay loam	Topsoil + Sesbania	15, 25, 35	56	cum.	2.4	22.6	0.85	42.5	35.2	11.3	0.98	50.7	233	1.96	+2.36
22	Jansson (1958)	Upland field, clay loam	Topsoil	25, 35	720	cum.	2.56	5.33	0.91	13.3	15.9	2.80	1.00	46.8	226	1.91	-9.11
23	Jansson (1958)	Agriculture	Topsoil + straw	25, 35	720	cum.	2.97	17.6	0.85	85.7	49.0	2.80	0.98	44.4	224	1.84	-10.8
24	Lomander et al. (1998)	Arable field, heavy clay	Topsoil	0.3, 5, 15, 25	300	rates	2.37	16.3	0.87	51.8	2.30	11.6	0.95	74.1	236	2.88	-2.48
25	Lomander et al. (1998)	Arable field, heavy clay	Subsoil	15, 25	300	rates	1.3	4.70	0.73	17.7	1.40	3.68	0.75	60.3	233	2.33	-4.05

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

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

where  $C_0$  is the initial amount of total C in the substrate and  $\alpha C_0$  and  $(1-\alpha)C_0$  are the initial amounts of C 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  $C_{flux}$  and  $C_{cum}$  were available, we analyzed 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  $\alpha$ ,  $k_1$  and  $k_2$  simultaneously, by 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 temperatures below  $T_{max}$ , the value for  $\alpha$  was the same as that 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:

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

$$k_2 = r k_{2max} \quad (2a)$$

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 (cf. Andr n and Paustian 1987). We tested four  $r(T)$  functions, 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

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

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

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

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

where  $E_o$  and  $T_o$  are parameters used to fit the data (Lloyd and Taylor 1994). Here, we used the value for  $E_o$  ( $=35.41 \text{ }^\circ\text{C}$ ) proposed by Lloyd and Taylor (1994).

3. The exponential  $Q_{10}$  function

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

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

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

where  $T_{min}$  is a hypothetical value at which  $C_{flux}$  equals zero.

By fitting these functions to the  $r$  factors for each experiment ( $T_{ref} = T_{max}$ ), we obtained a set of 25 parameter values normalized for  $T_{max}$ . Since  $T_{max}$  differed (ranging from 16 to  $40 \text{ }^\circ\text{C}$ ) between the experiments, we had to normalize these functions for a common  $T_{ref}$  to estimate a common parameter value for each response function (Eqs. 3–6) representing all experiments. Thus, we recalculated the  $r$  factors as estimated for each experiment and function and fitted the corresponding four functions to these normalized  $r$  factors (as estimated using the same functions) for the whole data set.  $R^2_{adj}$ , 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  $C_{cum}$  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  $R^2_{adj}$  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, on average by less than 5%. The strong correlation between the parameters hardly makes it possible to interpret each of them separately as Updegraff et al. (1995) did.

All four tested temperature response functions fitted well to the response factors of each experiment ( $R^2_{adj}$  values were generally high; not shown). However, the estimated parameter values varied greatly between experiments. For example, the estimated  $Q_{10}$  values varied between 1.35 and 2.88 in the 25 experiments (Table 1).

The choice of  $T_{ref}$  when rescaling the  $r$  factors from  $T_{max}$  to the common  $T_{ref}$ , influenced the resulting total response function (Table 2). The  $R^2$  value was highest ( $=0.96$ ) for all four tested response functions when  $30 \text{ }^\circ\text{C}$  was chosen as  $T_{ref}$  (Table 2). For example, for

**Table 2** Parameter values for  $E$  (Eq. 3),  $T_o$  (Eq. 4),  $Q_{10}$  (Eq. 5),  $T_{min}$  (Eq. 6), as estimated for the whole data set at different reference ( $T_{ref}$ ) and maximum ( $T_{max}$ ) temperatures.  $R^2$  indicates

$T_{ref}$	$T_{max}$	$E$	$R^2$	$T_o$	$R^2$	$Q_{10}$	$R^2$	$T_{min}$	$R^2$
10	40	54.1	0.74	237	0.57	2.04	0.75	+3.54	0.36
20	40	53.6	0.89	236	0.85	2.02	0.89	+0.50	0.82
30	40	54.2	0.96	233	0.96	2.06	0.96	-3.78	0.96
40	40	52.7	0.91	231	0.92	2.05	0.90	-5.17	0.93
10	30	54.8	0.79	235	0.59	2.10	0.78	+2.07	0.28
20	30	53.6	0.95	233	0.92	2.07	0.95	-2.81	0.89
30	30	54.8	0.93	231	0.93	2.13	0.93	-5.25	0.92

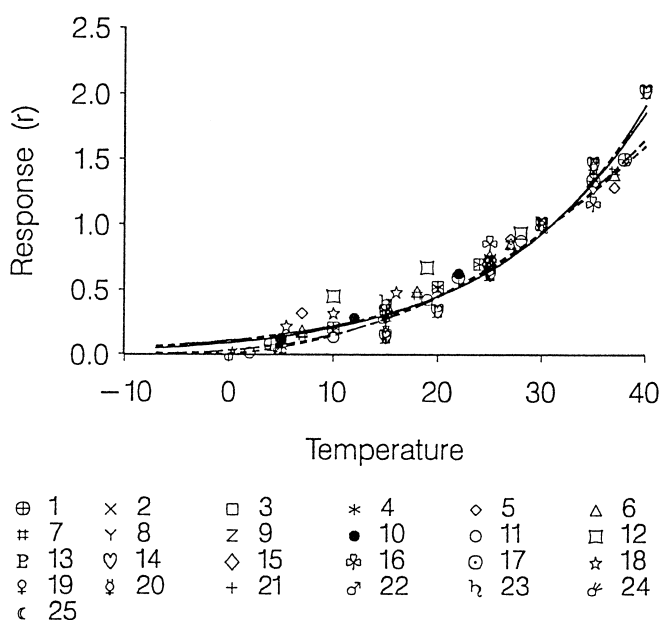
goodness-of-fit between the two-component model and temperature response factors according to non-linear regression

$T_{ref}=10^{\circ}\text{C}$ , the  $R^2$  values were as low as 0.36 for the "Ratkowsky model" (Table 2). We also tested the sensitivity of the response functions when excluding high incubation temperatures uncommon under field conditions (Table 2). When excluding temperatures above  $30^{\circ}\text{C}$  from the data set, the  $R^2$  values decreased when  $T_{ref}$  was equal to  $30^{\circ}\text{C}$ .

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. For the one-component model, the values for  $E$ ,  $E_o$ ,  $Q_{10}$  and  $T_{min}$ , were 32.5, 213, 1.56 and  $-21.8$ , respectively, and the corresponding  $R^2$  values were 0.80, 0.87, 0.79 and 0.87 (with  $T_{ref}=30^{\circ}\text{C}$  and  $T_{max}=40^{\circ}\text{C}$ ) i.e. lower than for the two-component model (Table 2).

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, whereupon 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. For ten experiments the optimized values for  $k_2$  became negative for one or several temperatures. In these cases  $k_2$  was set to "missing" for the whole experiment. 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). For  $k_1$ , the estimated parameters  $E$  ( $R^2$ ),  $E_o$  ( $R^2$ ),  $Q_{10}$  ( $R^2$ )  $T_{min}$  ( $R^2$ ) were 47.3 (0.89), 228 (0.89), 1.89 (0.89) and  $-7.99$  (0.87), respectively. Corresponding values for  $k_2$  ( $R^2$ ) were 44.5 (0.60), 226 (0.85), 1.85 (0.59) and  $-4.80$  (0.86). Consequently, the assumption that  $k_1$  and  $k_2$  were equally affected by temperature seems to be reasonable.

The goodness-of-fit did not differ between the temperature response models in the intermediate temperature range (about  $5\text{--}35^{\circ}\text{C}$ ). 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  $5^{\circ}\text{C}$  and  $35^{\circ}\text{C}$  on decomposition, at least when simulating ecosystem responses at larger scales. However, for individual substrates,  $Q_{10}$  values may deviate greatly from 2. Possibly, this variation in  $Q_{10}$  values is due to temperature optima which can differ in time and space between organism communities. For example, lignin decomposers may have another temperature dependence than other functional groups of decomposers. It is also possible that soil organism communities in cold climates are adapted to these, and thus will show comparatively high activities at low temperatures (e.g. Kirschbaum 1995). Hidden interactions of temperature response with other factors (e.g. soil moisture, salt concentration or  $\text{O}_2$  oxygen partial pressure) during the incubations may also have caused variation in  $Q_{10}$  values.



**Fig. 1** The dependence of the first-order decomposition rates  $k_1$  and  $k_2$  on temperature. Lines denote four tested temperature response ( $r$ ) models with parameter values given in Table 2: Eq. 3 — Eq. 4 - - - Eq. 5 - - - Eq. 6 - - -. The reference temperature is  $30^{\circ}\text{C}$ . Symbols are  $r$ -factors (see text) as normalized for the reference temperature using Eq. 6. Numbers in the legend correspond to those given under "ID" in Table 1

In the data set analyzed here, only two or three experiments included temperatures above  $35^{\circ}\text{C}$  or below  $5^{\circ}\text{C}$ . Although  $R^2_{adj}$  values for the four temperature response models were similar, the models diverged considerably above and below these temperatures (Fig. 1). Probably, the models proposed by Ratkowsky et al. (1982) and Lloyd and Taylor (1994) are more adequate for the lower temperature range and possibly for the whole temperature range examined here. To model temperature responses above  $35^{\circ}\text{C}$ , bell-shaped functions – which consider that responses decrease above an optimum temperature – should be used (cf. Kirschbaum 1995). Constant values for  $E$  and  $Q_{10}$  at lower temperature intervals are also theoretically unreasonable since both  $E$  and  $Q_{10}$  approach infinity when  $r(T)$  approaches zero. Thus, under natural conditions where temperatures are close to  $0^{\circ}\text{C}$  during longer time periods, e.g. at high elevation or latitude, functions not based on  $Q_{10}$  are probably more adequate. However, due to the paucity of data from low-temperature incubations, this conclusion is only tentative, and more experimental work is called for.

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