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Quality or decomposer efficiency – which is most important for the temperature response of litter decomposition? A modelling study using the GLUE methodology

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Abstract

Effects of temperature history on litter decomposition was evaluated with the Q-model calibrated to a needle litter incubation experiment and using the GLUE modelling framework. The needle litter incubation was a full factorial design with initial and final temperatures 5, 15 and 25°C. Samples going to a different second temperature were moved when approximately 12% carbon had respired. We used four variations of the Q-model; the combination of *one* or *two* initial litter quality values and *fixed* or *temperature-dependent* decomposer efficiency. The model was calibrated to the constant temperature subset of the data. Evaluated against the subset containing temperature shifts, gave good results, except just after the change in temperature where the model predicted less than measured. Using *one* or *two* initial litter quality values and *fixed* decomposer efficiency had little effect on litter quality and respiration during the final incubation temperature. When the decomposer efficiency was allowed to vary with temperature, the best predictions had decomposer efficiency values that decreased between 5 to 15°C and did not change between 15 and 25°C. Having *flexible* decomposer efficiency resulted in substantial differences in litter quality between the three temperatures at the end of the initial incubation. This resulted in that samples at the same final temperature, subjected to different initial temperatures, decomposed at significantly different rates. The result suggests that it might be important to consider other factors than the variation in temperature sensitivity with quality when evaluating effects of temperature changes on soil organic matter stability.

Keywords: carbon use efficiency, carbon utilization efficiency, substrate use efficiency, CUE, SUE, temperature, quality, GLUE, Q-model

Introduction

In view of the expected future climatic change (Solomon, 2007), the temperature dependence of decomposition of litter and soil organic matter (SOM) has since long attracted much interest. A strong positive temperature dependence of decomposition would create a strong positive climatic feedback (Anderson, 1992). Both in laboratory incubations and field studies, temperature history and not only current temperature has been shown to affect respiration rates, such that SOM with different temperature histories will cause different decomposition rates at the same temperature. These effects can be short or long term, and be the result of factors like substrate depletion, changes in decomposer community composition and abundance, and differential quality change (Kirchbaum, 2006). That differential quality change should be the main mechanism responsible for temperature sensitivity has been challenged, because there are several other processes involved, also affected by temperature (Davidson & Janssens, 2006; Ågren & Wetterstedt, 2007). It is thus even more of interest to also consider the temperature dependence of the other factors regulating decomposition. Decomposer community composition and decomposer biomass are two important factors that may be affected by temperature. Furthermore, it has been demonstrated (Devêvre & Horwáth, 2000; Steinweg *et al.*, 2008) that the efficiency of decomposers decreases with temperature, probably as a result of higher maintenance costs.

Most models, *e.g.* Century (Parton *et al.*, 1987), G'Day (Comins & McMurtrie, 1993), RothC (Coleman & Jenkinson, 1995), Q (Ågren & Bosatta, 1998), dealing with soil organic carbon (SOC) conform to the same generic structure (Fig. 1). SOC can be described as a continuous spectrum of carbon of different quality (the curve), or as belonging to different pools (the three bars). There are three main processes that drive change in SOC quantity and quality: (i) A decomposer community feeding on SOC at some rate (*growth rate*). (ii) When doing so, part of the carbon they use is respired as carbon dioxide and part remains as SOC; we call the fraction remaining efficiency (*decomposer efficiency*). (iii) The fraction remaining undergoes changes in quality. We call this transfer between pools *dispersion*. On average SOC increases in recalcitrance/decreases in quality with time.

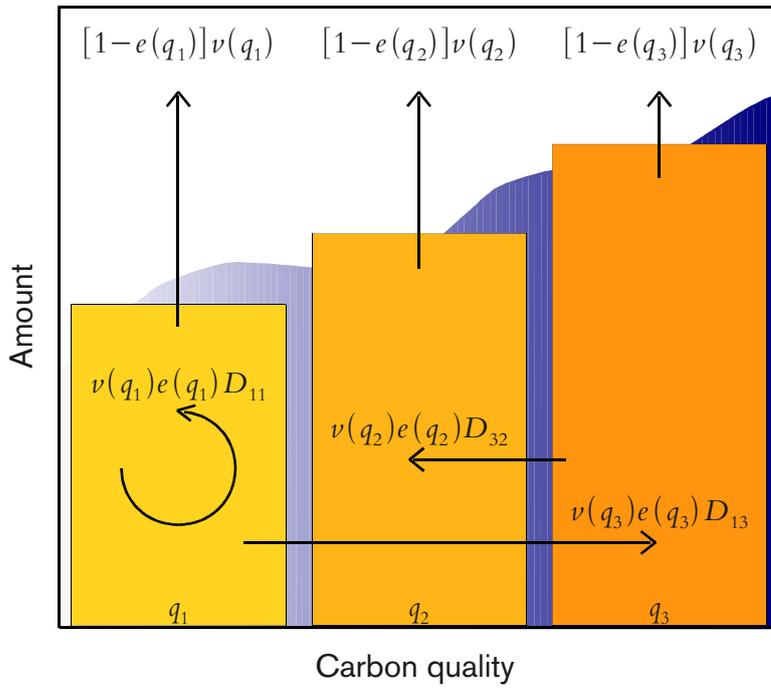


Figure 1. Generic model of soil organic matter decomposition. Soil carbon can be regarded as belonging to a distribution of quality values, continuous (the curve) or discrete/as pools (the three bars along the x-axis). Respiration (CO_2 loss) from different quality values/pools is indicated by arrows pointing upwards, its quantity shown by the formula. Three quality dependent factors determine how quality changes with time. [1] The rate of use, $v(q)$, of the substrate by the decomposer community. [2] The partitioning of used carbon between respiration, $1 - e(q)$, and remaining, $e(q)$. [3] The transformations of quality of the carbon not respired between or within qualities/pools (*dispersion function*, D_{ij}). For simplicity, only three of the six possible transformations are shown in the figure. $v(q_2)e(q_2)D_{22}$, $v(q_3)e(q_3)D_{33}$, and $v(q_2)e(q_2)D_{12}$ are missing.

To address the question of how the factors quality and decomposer efficiency affect the temperature response we choose to use the Q-model (Ågren & Bosatta, 1998; Bosatta & Ågren, 2003) because the fate of carbon and the decomposition processes are relatively easy to follow in it. Data from a recently published temperature variation experiment (Wetterstedt *et al.*, 2009) is used, both for calibration and evaluation. We will use the model to explore the consequences of having *one* or *two* initial litter qualities in combination with *fixed* or *flexible* (with regard to temperature) decomposer efficiency.

We have chosen to use the GLUE (Generalised Likelihood Uncertainty Estimation, Beven 2006) framework for model calibration and evaluation. GLUE can be used as a modelling protocol and is well suited to give uncertainty estimations in model output. It also provides criteria for complete model rejection, *i.e.* if the model fails to predict empirical data well enough, the model structure needs to be changed.

Materials and methods

The Q-model

The Q-model describes litter or SOC as consisting of a continuous spectrum of carbon qualities as opposed to being partitioned into a small number of discrete pools (*cf.* Parton *et al.*, 1987). The Q-model has certain advantages over such discrete models. Firstly, there are analytical solutions, making it easier to understand and explain model behaviour. Approximate solutions, which are similar in their behaviour, are also available (Bosatta & Ågren, 2003). The approximate solutions are much less computationally demanding and are therefore preferred when doing large model runs, for example during calibration. They substitute the complete distribution of litter qualities in the exact solution with one average quality. There are also fewer parameters and the model formulation enforces consistency between them. Parameters estimated with the approximate solution can also be used in the exact solution, possibly with some slight recalibration.

Fig. 1 illustrates two different ways of looking at organic matter; as a continuous quality spectrum, illustrated by the area under the curve, and as different pools shown by the three bars. In the model, fresh litter is characterised by having most material at high quality; with time the quality spectra shifts more and more towards low quality. In the model, growth rate of the decomposers depends on carbon quality and temperature. Decomposer efficiency will be set to be either temperature independent (*fixed*) or temperature dependent (*flexible*). In this application all other processes are assumed to be temperature independent. Table 1 shows the parameters used in the model. When running the model with *two* initial litter quality values, the two q_0 will be selected from behavioural models (see below) and chosen to be somewhat separated. The reason for using *two* initial q_0 values in this experiment is to explore the effect of how the different temperature sensitivity of different q_0 values translates into a differential quality evolution.

The model was run with four different combinations of conditions: *one* or *two* initial quality values in combination with *fixed* or *flexible* decomposer efficiency. When using two initial litter quality values, the initial amount of substrate was partitioned equally between q_{0-1} and q_{0-2} .

Table 1. List of parameters. Parameter values are those corresponding to the highest LM. Range is the range used during calibration. Sampling was done uniformly for all parameters but u_0 which was sampled from a log-distribution. With two initial quality values, q_{0-1} and q_{0-2} , were set to fixed, their values picked out of values obtained running the model with one initial quality. Fixed and Flex. in the table heading refer to fixed or flexible e_0 . Initial parameter range was greater to find suitable parameter space.

	One q_0		Two q_0		Comment	
	Range	Fixed	Flex.	Fixed		Flex.
q_0	1.5-4.5	2.50	2.15	-	-	Initial litter quality (unit-less)
q_{0-1}	fixed	-	-	1.80	1.80	1 st initial litter quality in the two q_0 version
q_{0-2}	fixed	-	-	2.50	2.50	2 nd initial litter quality in the two q_0 version
ΔG^0 #		127	93	127	99.5	Gibbs' free energy (J)
e_0	0.15-0.40	0.377	-	0.220	-	Decomposer efficiency in the fixed version (unit-less)
e_{0-5}	- : -	-	0.369	-	0.393	e_0 at 5°C in the flexible version
e_{0-15}	- : -	-	0.327	-	0.336	e_0 at 15°C --- : ---
e_{0-25}	- : -	-	0.321	-	0.330	e_0 at 25°C --- : ---
u_0	10^7 - 10^9	7.63×10^8	2.46×10^7	6.57×10^8	1.21×10^7	Decomposer growth rate regulating parameter ($\text{g C (g C)}^{-1}\text{d}^{-1}$)
η_{12}	0.1-0.45	0.120	0.199	0.0663	0.0476	Rate of quality decrease, approximate solution (unit-less)
Q_{10}	1.4-4.0					Only used to create plausible parameter range for ΔG^0

#For ΔG^0 the range is $q_0 R \frac{T_5 T_{15}}{10} [-\log [Q_{10\max}] \dots -\log [Q_{10\min}]]$.

Observational data

We have chosen to use the spruce (*Picea abies*) needle litter data from the temperature experiment by Wetterstedt *et al.* (2009) (See Fig. 2 and 3). The data consists of time series of respiration rates from four replicates at different temperatures. In some time series the samples have been shifted from one temperature to another when approximately 12% of the initial carbon had been respired. We will write temperature combinations as initial

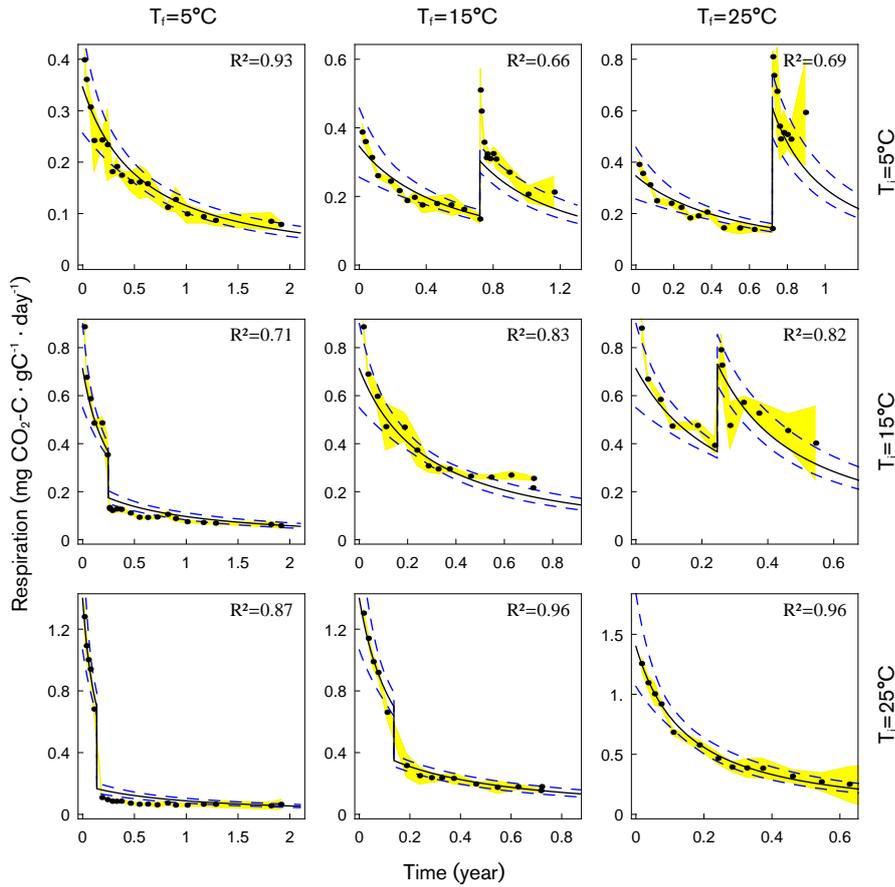


Figure 2. Model predictions of respiration rates for the *one* initial quality, *fixed* decomposer efficiency model and observed respiration rates for all combinations of initial (T_i) and final (T_f) temperatures (5, 15, and 25°C). Weighted ensemble run predictions are shown (solid black line) with max/min curves (blue dashed lines) for the behavioural parameter sets. The yellow fields show the 95% error bounds around measured data points (dots). Least square R^2 values are shown in the top right corner of each sub-graph.

temperature+final temperature, *e.g.* 5+15°C, meaning that the sample was first exposed to 5 and then 15°C. The data used for calibration were from needles stored at three temperatures without shifts in temperature (5+5°C, 19 data points; 15+15°C, 14 data points; and 25+25°C, 16 data points). To reduce the variability in data between measurement points, we used a running mean of three consecutive points to smooth the curve (except first and last point that were averaged from two points). We also normalised the

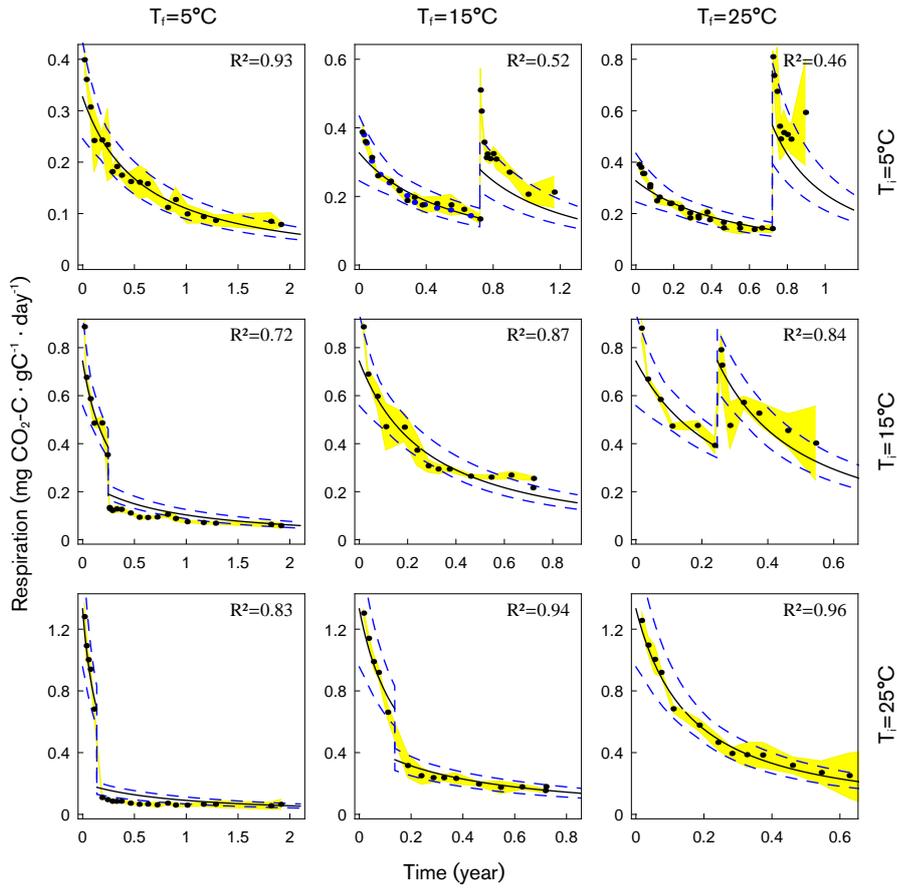


Figure 3. Model predictions of respiration rates for the *one* initial quality, *flexible* decomposer efficiency model and observed respiration rates for all combinations of initial (T_i) and final (T_f) temperatures (5, 15, and 25°C). Weighted ensemble run predictions are shown (solid black line) with max/min curves (blue dashed lines) for the behavioural parameter sets. The yellow fields show the 95% error bounds around measured data points (dots). Least square R^2 values are shown in the top right corner of each sub-graph.

standard deviation at each measurement point by averaging the coefficient of variation over the whole measurement period for each temperature, *i.e.*

$$Var(\bar{O}_i) = \bar{O}_i \sum_i \frac{Var(\bar{O}_i)}{\bar{O}_i} / n ,$$

where n is the number of points in the measurement series. These steps were taken to obtain a more robust calibration process. When the calibrated

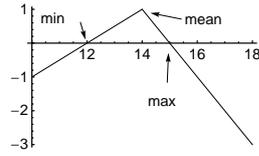
models are evaluated using the least square method, R^2 are with respect to non-smoothed data (Fig. 2 and 3).

GLUE

The GLUE methodology introduced by Beven & Binley (1992) is a framework for calibrating and using models in predictions. It includes criteria and methods for model rejection and sensitivity analysis of model parameters. A ‘model’ in GLUE terminology is the combination of the ‘model structure’, *e.g.* the Q-model as opposed to some other model, and the parameter values used to run the model. A ‘behavioural model’ is a model that can simulate real data “good enough”. It follows that a non-behavioural model should not be used to forecast data; instead, it would need better parametrisation or a change in model structure. In this text we will however use the term ‘model’ meaning ‘model structure’. The use of GLUE includes the following steps (Beven, 2009):

1. Likelihood measure

Decide on an informal (or formal) likelihood measure or measures (LM) for use in evaluating each model run, including the rejection criteria, which for a non-behavioural model run will be given a likelihood of zero. Ideally this should be done before running the model, taking into account possible input and observational errors: Since calibration data contain means as well as standard deviations, we used a triangular shaped likelihood measure:

$$l(M, O_{min}, O_{mean}, O_{max}) = \begin{cases} \frac{M - O_{min}}{O_{mean} - O_{min}} & M \leq O_{mean} \\ \frac{O_{max} - M}{O_{max} - O_{mean}} & M > O_{mean} \end{cases}$$


If model output equals the average measured value (O_{mean}) the function returns 1, at ± 1.96 standard deviations (O_{max} , O_{min}) zero, and negative values when model output deviates more from the observed mean value. These values were summed for each temperature and divided by the number of observed values, $n_{O,T}$, and then averaged over the three temperatures

$$L(M(\Theta), O) = \sum_{T=5,15,25^{\circ}\text{C}} \left(\sum_{O_T} \frac{l(M_{O,T}, O_{min,T}, O_{mean,T}, O_{max,T})}{n_{O,T}} \right) / 3 .$$

Θ stands for the parameter set used. This likelihood measure takes variability in the observed data into account and is less influenced by outliers than the least square method. Ideally, the model with the parameters in question, should predict all observed data points within their 95% error bounds; *i.e.* for all $l(M, O_{min}, O_{mean}, O_{max}) \geq 0$ observations.

2. Model parameters

Decide which model parameters and input variables are to be considered uncertain: All model parameters were considered uncertain (Table 1).

3. Parameter distributions

Decide on prior distributions from which the uncertain parameters and variables can be sampled: We have chosen uniform initial distributions for all parameters except u_0 , for which a logarithmic one was used (Table 1). To further narrow the sampling space, initial sample runs were made to localise parts of the parameter space that were more likely to generate good fits.

4. Random realisations of the model

Decide on a method of generating random realisations of models consistent with the assumptions in steps 1 and 2: Twenty thousand parameter sets were drawn from uniform distributions for all parameters except u_0 , which was drawn from a log-distribution, (Table 1) and used as initial points in the Simulated annealing algorithm (Mathematica 7.01.0 Ubuntu/Linux) resulting in one ‘optimum’ set of parameters. This set together with its resulting likelihood value was stored and the procedure repeated 28 000 times. Calibration was made simultaneously against samples that had been kept at 5+5°C, 15+15°C and 25+25°C.

Dotty plots

There exists a number of methods to assess sensitivity in non-linear models. The method most often used within the GLUE-framework is to make a scatter-plot/dotty plot of each parameter (on the x-axis) versus the likelihood measure (y-axis). From the resulting swarm of points, one can find trends showing for example that certain parameters are present in only a short interval of the initially sampled points, whereas others have a uniform density along the x-axis. If only a small segment of the initially sampled parameter space is found among the behavioural model runs, restricting that parameter to a smaller range will probably improve the number of behavioural model runs. If behavioural runs, on the contrary, are

equally distributed along the parameter axis, extending the parameter range might disclose/unravel areas of the parameter space which is more likely to result in behavioural parameters.

Using the models

Behavioural parameter sets are used in ensemble runs to generate a mean output value and likely error bounds. An ensemble run is when running the same model with many parameter sets (as is the case in this article) or running different models to obtain a distribution of results. The likelihood measure, LM, or any other performance measure, can then be used to create a weighted mean from the different outputs. Error bounds can be generated from the *max* and *min* from the model runs, or at any preferred significance level obtained from a cumulative density curve. In this article we will simply use *max* and *min* of the selected models as bounds.

Results

One initial quality, fixed decomposer efficiency

With *one* initial quality (q_0) and *fixed* decomposer efficiency (e_0) the generated parameter sets were more or less evenly distributed over the whole parameter set. The exception was u_0 with higher values more likely resulting in a high LM, indicating that the upper boundary for u_0 might have been too small (data not shown). The even distribution of other parameters means that the model is rather insensitive to the parameters within the range used.

Ideally, all of modelled points should have been within the error bounds of the calibration data but that was not the case. Therefore, we decided to use all parameter sets with positive LM in the ensemble model runs. We then got 257 parameter sets that were behavioural. The best fit yielded a LM of 0.243, and was within boundaries at 37 out of 48 data points in the calibration set (Fig. 2).

When validated against experiments with a shift in temperature, the model follows the data well during the initial temperature phase; this is not surprising because it was calibrated on similar data (Fig. 2). During the final temperature incubation after a temperature increase, the model underestimates the increase in respiration during the first days when going from 5 to 15 or 25°C. When shifting downwards in temperature the model predicts initially slightly higher values than observed.

When looking at how the model behaved qualitatively with regard to temperature history, temperature history has negligible effect on current respiration rates (Fig. 4). The respiration at the final temperature after the shift for the 5+25°C treatment is the same as the respiration after 12% C loss in the 25+25°C treatment (orange and blue lines). The same holds for the 25+5°C and 5+5°C treatment.

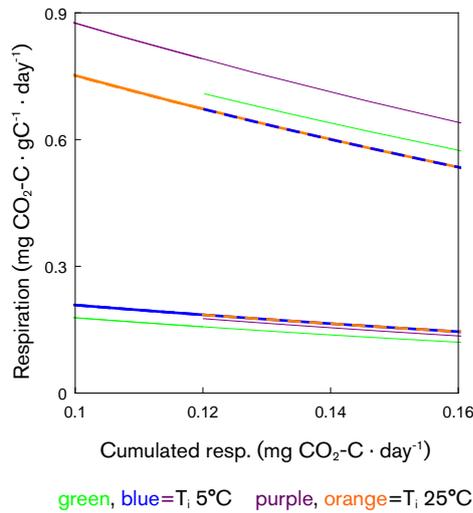


Figure 4. Respiration rates as a function of carbon loss as predicted by the *flexible* and *fixed* decomposer efficiency models, samples being at constant temperature or shifted between 5 and 25°C at 12% respired carbon. Solid orange line: *Fixed* model prediction for samples starting at 25°C and ending at either 5 or 25°C. Solid and broken blue line: *Fixed* model prediction for samples starting at 5°C and ending at either 5 or 25°C. Solid purple line: *Flexible* model prediction for samples starting at 25°C and ending at either 5 or 25°C. Solid green line: *Flexible* model prediction for samples starting at 5°C and ending at either 5 or 25°C. With *fixed* e_0 initial temperature has no effect on respiration rates after the shift in temperature.

One initial quality, flexible decomposer efficiency

With *one* initial quality (q_0) and *flexible* decomposer efficiency (e_0) there are few points at the extremes of the x-axis for q_0 , meaning that high and low q_0 where unlikely to give good fits. u_0 , ΔG^0 and e_0 values are fairly evenly distributed (Fig. 5). However, the best fits for the different e_0 parameters are more to the centre. η_{12} is somewhat skewed towards the lower end of the spectrum.

The best fit yielded a LM of 0.284, and was within boundaries at 37 out of 48 points (Fig. 3). 33 sets were found behavioural, *i.e.* with LM>0.

The model with *flexible* decomposer efficiency fitted the data slightly better than the *fixed* decomposer efficiency version when validated against the experiment with temperature shifts, as well as bracketing more of the data points due to the wider uncertainty bounds (Fig. 3). However, when going down in temperature, the model seems to over-shoot slightly, at least

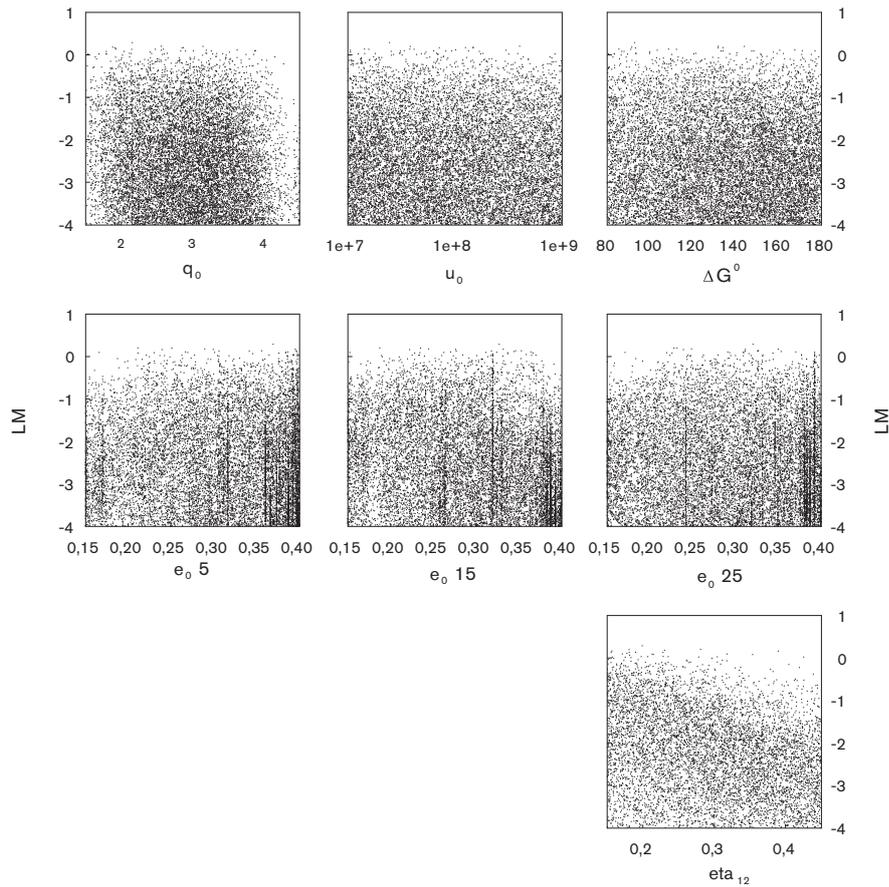


Figure 5. Dotty plots for the *one* initial quality, *flexible* decomposer efficiency. Each dot represent one model run. The likelihood measure, LM, or ‘goodness of fit’, is plotted against parameter values. The x-scales show range allowed for the different parameters. Parameter sets resulting in a $LM > 0$ where used in ensemble simulation runs.

initially ($15+5^{\circ}\text{C}$, $25+5^{\circ}\text{C}$). When going up ($5+25^{\circ}\text{C}$ and possibly $15+25^{\circ}\text{C}$) the model still misses the initial respiratory peak.

To look for trends in how e_0 varied with temperature we did additional simulations with the *one* q_0 *flexible* e_0 model, obtaining a total 160 behavioural parameter sets, $LM > 0$. Decomposer efficiency was plotted in pairs, *i.e.* $(e_{0-5}, e_{0-15})_i$, $(e_{0-15}, e_{0-25})_i$ and $(e_{0-5}, e_{0-25})_i$ (Fig. 6). The plots show that the e_0 values are highly correlated. For the interval between 5 and 15°C (left), average e_0 decreased by 0.03 units, and then increased with 0.02

(middle), resulting in an overall decrease of 0.01 from 5 to 25°C (right). Selecting only the top 10 sets (green lines and dots, LM 0.25 – 0.31) resulted in a decrease in e_0 with 0.03 units from 5 to 15°C, and keeping constant between 15 and 25°C.

With temperature dependent decomposer efficiency, respiration responded strongly to temperature history (Fig. 4). For example, the sample incubated at 25°C respired substantially more than the one first incubated at 5°C when both were at 25°C (top green vs. top purple). Similarly, the sample initially at 25°C respired more than the one initially at 5°C when both were at 5°C (bottom green vs. bottom purple).

Two initial qualities, fixed and flexible decomposer efficiency

In the model runs with two initial qualities, the contribution (both at time 0 and at 12% carbon loss) of the lower quality (q_{0-1}) to respiration is 1/4700 and 1/2700 of the respiration of the higher quality (q_{0-2}) at 5°C and 25°C, respectively. Therefore the model behaved qualitatively the same as with a single initial quality but with different ‘optimal’ parameters.

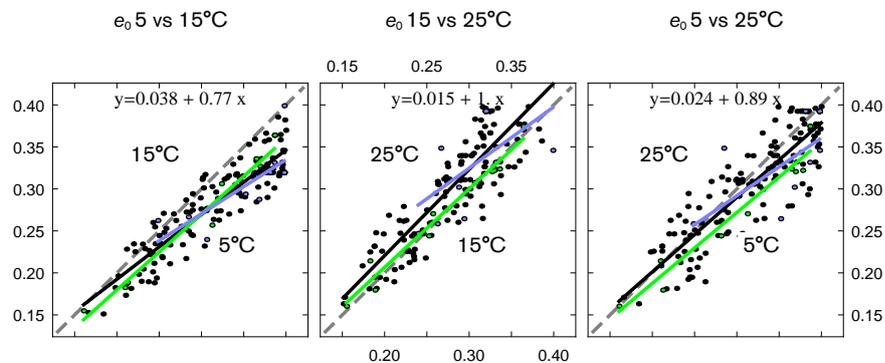


Figure 6. Correlations between efficiencies at 5, 15, and 25°C from behavioural parameter sets in the one initial quality, flexible decomposer efficiency model. Solid line: Linear regression of data. Broken line: 1:1 line. Green line: Linear regression to the top 10 parameter sets. Blue line: bottom 10.

Discussion

Model behaviour

The calibration data showed considerable variation in the variability between days. Also, respiration did not decrease monotonically as expected. From the Wetterstedt *et al.* (2009) study it is not clear whether the variability in the data comes from short time biological variation or related to measurement errors. We had, however, to relax the condition that, for each behavioural parameter set, predictions should be within error bounds for all points in each temperature series. Despite that, calibration to the constant temperature subsets worked well with R^2 values in the range of 0.83–0.96. However, even though the ensemble runs mostly covered all calibration points, at 5 and 15°C the data shows a more concave pattern than what the model can predict (Fig. 2 and 3 at 5+5°C, 15+15°C). When the model is validated against the temperature shift experiments, experiments tend to respond more strongly just at the temperature shift than the model.

Choice of likelihood measure (LM)

Our choice of likelihood measure, LM, is subjective. Ultimately, the objective should be to acquire parameters “useful in model prediction” (Beven 2009, p 124), and the LM should be chosen to help in doing so. One way of interpreting “useful in model prediction” is that the model should be able to bracket our observations, which it did in most of the cases (Figs. 2 and 3). Since the objective of this paper is to highlight the effect of efficiency and quality coupled to temperature, the likelihood measure used is of lesser importance; see Beven (2009, pp 165) for further discussion of choice of likelihood measure.

Mechanisms for temperature history to influence current respiration

One or several initial qualities

We have considered two main ways in which temperature history can affect current respiration rates. The first is that different qualities have different temperature dependency, which should lead to a difference in quality composition at different temperatures but equal carbon loss (for a more detailed discussion, see Wetterstedt *et al.*, 2009). However, with our choice

of *two* different initial quality values ($q_{0-1}=1.80$, $q_{0-2}=2.50$), the lower quality decomposed at only about 1/4700 (@5°C) and 1/2700 (@25°C) of the rate of the higher one. Together with the relatively small difference in temperature sensitivity between the two q_0 values (fixed two q_0 model: $Q_{10-1}=2.9$, $Q_{10-2}=2.1$; flexible two q_0 model: $Q_{10-1}=2.9$, $Q_{10-2}=2.3$) this did not translate into a sufficiently large difference in quality evolution between the temperatures, because it is effectively only the highest quality that decomposes. Selecting a larger q_{0-1} resulted in more use of the lower quality, but at the expense of a smaller difference in Q_{10} between the two qualities. By letting q_{0-1} vary and keeping q_{0-2} fixed, we found that $q_{0-1}=2.25$ yielded the biggest quality difference after initial incubation at 5 and 15°C respectively, until 12% carbon was lost (Fig. 7). The difference between the two initial temperature treatments in average quality was then only 4.10×10^{-5} . The difference in respiration was also very small (0.35%) when both samples were at 15°C. As a consequence, the use of *two* initial quality values instead of *one* made no difference; the curves for *two* initial qualities cannot be distinguished from the one initial quality curves in Fig. 4.

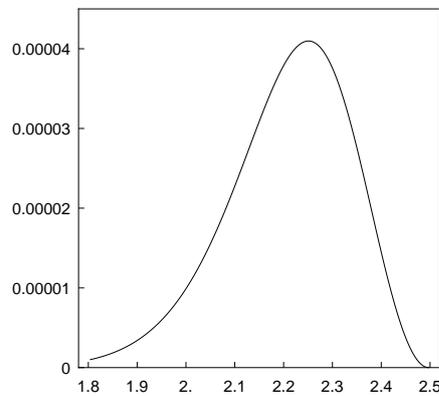


Figure 7. Test of the effect of choice of initial qualities on respiration rates. The higher quality (q_{0-2}) is fixed at 2.50 whereas the lower (q_{0-1}) has been varied along the x-axis. The y-axis shows the difference between samples incubated at 5 and 15°C in quality after 12% carbon loss. At the maximum, the difference in respiration is 0.35% when both placed at 15°C.

Fixed or flexible decomposer efficiency

The second mechanism, varying decomposer efficiency (e_0) with temperature, resulted in a clear effect on quality distribution and thus temperature sensitivity and respiration rates (Fig. 5 and 8). The reason for

this is two-fold. Most importantly, with higher efficiency, when carbon is taken from the initial quality, a smaller part is lost by respiration and a larger part is converted into lower qualities. Thus, to obtain the same mass loss more of the initial quality has to be processed. In addition, the dispersed carbon will for the same reason persist for longer which means that yet more initial carbon need to be processed before reaching the same cumulative respiration as at the lower decomposer efficiency.

The *flexible* model predicts the rapid decrease at the beginning of the experiment as well as experimental data after the shift in temperature better. Having a temperature dependent e_0 also leads to a model that simulates differences in respiration rates at the same final temperature from samples of different initial incubation temperature (Fig. 5). Surprisingly, having *flexible* decomposer efficiency resulted in fewer behavioural parameter sets. This is surprising because it adds two extra parameters which should increase the possibility of finding better fits. It seems however that the two extra parameters decreased the probability of finding good parameter sets and because the calibration was run with the same number of trial parameter sets, fewer behavioural parameter sets were obtained.

The behaviour of e_0 points in the direction that decomposer efficiency might decrease with increasing temperature. This could be one of the explanations to why respiration is so strongly correlated to temperature. However, we need to keep in mind that even though we may perceive e_0 in the same way, effectively, it can still be difficult to compare e_0 between different models, between models and experiment, or indeed, between different experiments (*cf.* Devèvre & Horwáth, 2000; Steinweg *et al.*, 2008). In experiments e_0 is not measured directly and a number of more or less explicit assumptions are introduced when calculating e_0 from measurable quantities such as consumed substrate and respiration; such assumptions may or may not distort the relation between conceptual and observed values. In models, we also simplify the system; simplifications that differ between models.

Other temperature effects

The model has difficulty in reproducing experimental data directly after temperature shifts, when respiration is either underestimated or overestimated after upward and downwards shifts respectively. These deviations between predictions and observations are similar to those observed when comparing respiration rates obtained at constant temperatures to temperature shifts in the study by Wetterstedt *et al.* (2009).

We propose that these deviations over a few days represent transient adjustments in decomposer properties to new conditions. It remains an open question how important such transients may be under field conditions where temperatures are changing continuously, albeit less rapidly than in the experimental study.

It should also be born in mind that the temperature response we find in e_0 depends on the assumptions we have made about the temperature dependence of the other factors. For example, we are assuming that the dispersion function is temperature independent although the rate of decomposition is highly sensitive to the strength of dispersion, efficiency likewise (Hyvönen *et al.* 1998). This is a simplifying assumption but we are not aware of any experiments demonstrating temperature sensitivity of dispersion. Likewise, although there are theoretical arguments for the temperature dependence of the rate of carbon utilisation (Bosatta & Ågren, 1999), it has not been tested rigorously experimentally.

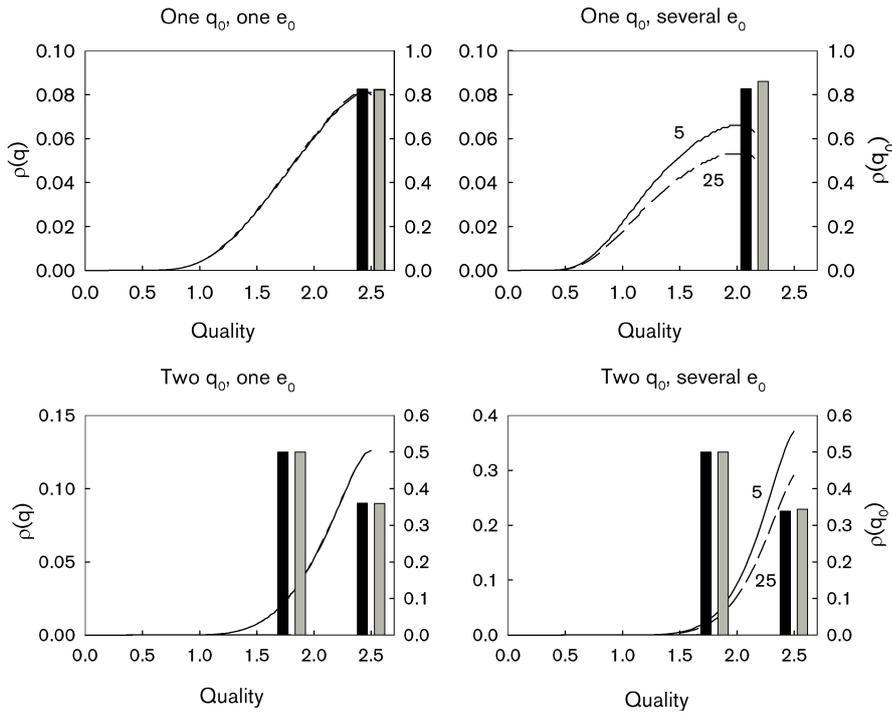


Figure 8. Distributions of qualities for combinations of *one* or *two* initial quality values and *fixed* or *flexible* decomposer efficiency (e_0) when 12% carbon has been lost for sample incubated at 5 or 25°C. Solid lines and black bars are for samples at 5°C. Dashed lines and grey bars are for samples at 25°C. The bars have been shifted slightly leftward and rightward from their value to visually separate them. Bars show the amount of carbon that has not been used by decomposers so far (remaining at the initial qualities). The lines show the distributions of carbon that the decomposers have converted into new qualities. With flexible decomposer efficiency, more carbon has been converted (lines) and less remains at the initial quality (bar). With two initial qualities the losses have essentially only occurred from the highest quality.

Conclusion

In this study, a temperature sensitive decomposer efficiency was shown to have a much stronger influence on quality differentiation, and thus respiration, than the temperature sensitivity of utilisation of different qualities. The difficulties in capturing changes in respiration rates at rapid temperature changes should caution us about extrapolating short term effects to longer time periods (*cf.* Wetterstedt *et al.*, 2009); understanding the rate at which a microbial community can adjust requires more investigation. Our results also show that it is necessary to consider other processes than those directly coupled to the rate of substrate utilisation more carefully.

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