Decomposition of Soil Organic Matter

Experimental and Modelling Studies of the Importance of Temperature and Quality

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Decomposition of Soil Organic Matter. Experimental and Modelling Studies of the Importance of Temperature and Quality

Abstract

The climate is changing and with it the capacity of soils to store carbon in all likelihood, since there is strong evidence that decomposition increases with increasing temperature. The soil contains about twice as much carbon as the atmosphere, so decreasing soil carbon will increase atmospheric CO_2 concentrations proportionally more, further contributing to temperature increase.

Different types of soil carbon may respond differently to climate change. A central theory in explaining temperature sensitivity is the activation energy concept *sensu* Arrhenius. Applied to soil organic matter (SOM) it suggests that low quality SOM will respond more strongly to increased temperature than high quality SOM. Much of the carbon in soil is old and believed to be of low quality.

This thesis examines the effects of temperature and SOM quality, separately and in combination. A model of decomposition as three processes in series resulted in unexpected temperature sensitivity, which may explain why the temperature sensitivity is so variable in the literature. A subsequent incubation experiment with different types of organic matter subjected to combinations of different initial and final temperatures showed that the temperature sensitivity increased with time, in agreement with existing theory. In contrast, the effects of past temperatures on present respiration were different than expected. When the decomposition experiment was modelled using the Q-model, decomposer efficiency decreased with temperature, greatly affecting the SOM quality decrease and indirectly affecting temperature sensitivity. Other results presented in the thesis showed that high quality SOM can be stored for hundreds of years and still be made available to decomposers simply by subjecting the soil to drying/wetting cycles.

The results presented in this thesis have theoretical and experimental implications and indicate that *quality* might be less important than previously believed in terms of SOM susceptibility to increasing temperatures. The other processes involved need further attention.

Keywords: quality, temperature-quality hypothesis, Q-model, decomposition, SOM, GLUE, Q_{10}, temperature response, Arrhenius, Michaelis-Menten

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Ågren GI, Wetterstedt JÅM. 2007. What determines the temperature response of soil organic matter decomposition? *Soil Biology & Biochemistry* 39:1794–1798.

II Wetterstedt JÅM, Persson T, Ågren GI. 2009. Temperature sensitivity and substrate quality in soil organic matter decomposition – results of an incubation study with three substrates. *Global Change Biology* (in press).

III Wetterstedt JÅM, Ågren GI. Quality or decomposer efficiency – which is most important for the temperature response of litter decomposition? A model analysis using the GLUE methodology (manuscript).

IV Schimel JP, Wetterstedt JÅM, Holden PA, Trumbore SE. Drying/rewetting cycles mobilize old C from deep soils from a California annual grassland (manuscript).

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Abbreviations and Definitions

DOC	dissolved organic carbon
DIC	dissolved in-organic carbon
POC	particulate organic carbon
SOM	soil organic matter
OC	organic carbon, mostly referring to carbon in OM or SOM
OM	organic matter
Q_{10}	difference in a process (*e.g.* respiration) with 10°C temperature difference
activation energy	energy barrier that must be exceeded for a reaction to occur
autotrophic	coming from plants
heterotrophic	coming from organism needing external energy input, *i.e.* decomposers
respiration	release of CO_2 as a result of biological metabolic activity
substrate	OM in the sense of being a target for enzymes or ingestion by decomposers
litter	organic matter coming mainly from plants. Thus termed as long as its plant origins are still recognisable.

1 Theory of theory

1.1 Models

1.1.1 We all use models

We all use models, in their widest sense, in our daily lives to help us make decisions. For example, we may use the sun and time of day to work out which way is north or south. Although we will not get an exact direction, the information obtained will probably be enough to decide on a street – but we would not venture on a sailing trip to a small island in the middle of the Atlantic with just the sun to lead our way. Our model in this case might be: the sun rises in the east, sets in the west and stands in the south at midday. Those in the Northern hemisphere would say that this model is correct, but someone raised close to the equator or in the southern hemisphere would say it is wrong. This highlights the fact that because it is a simplification, a model always has its field of validity, or use. Having a more complex model for how to calculate directions from the sun, for example by knowing day of the year, position on the globe and angle above the horizon, would be of no use if we did not have the initial information, or the other way around.

The studies described in this thesis centred around a ‘concept’ of decomposition called the Q-model (Ågren & Bosatta, 1998). The Q-model exists both as a computer model, *i.e.* a computer programme, and as a theory, *i.e.* an abstract description of reality and how it is constituted. There are of course many other ‘theories’, models and descriptions about decomposition. These are discussed below in terms of *theory driven* (theoretical) and *data driven* (empirical) model development. Another way of differentiating them is the difference between how we *understand* and what we *observe*.

1.1.2 Theory driven

A good example of a theory driven model is the Q-model (as a theory). Decomposition in the Q-model is described in terms of carbon atoms (as an abstraction), having a quality feature changing over time. In this approach, a model becomes more well founded if it can be based on established (physical) principles. The outcome is usually a mathematically formulated theory, which can be turned into a computer model. It is important to keep in mind what assumptions were made in the underlying theory, determining the applicability of, and the limitations imposed on, the model.

1.1.3 Data driven

The other approach to model development is data driven. Here, the data collected are fed directly into the model, or turned into correlations and simple functions, which are used as building blocks. Connection of the building blocks still needs theoretical insights but can be of a more qualitative nature, since the quantitative part has already been accounted for by measurements. The reason for using these kinds of models is the appreciation that the system under study is complex, with so many interacting processes and mechanisms that it is impossible to derive the behaviour of the system from underlying or *first principles*. Such models may need extensive calibration and a high degree of ‘craftsmanship’ to use. Examples include the Century model (Parton *et al.*, 1987) and its derivatives.

1.1.4 The pool approach to decomposition

In reality, placing a model in one of the two categories described above might not be the correct option, because most models contain components from both categories, and because other types of categorisation may be equally meaningful. In the Century and similar models, SOM is modelled as belonging to different pools (an abstract container) having different turn-over times. During decomposition, SOM is transferred to pools with longer and longer turn-over times, loosing carbon as *e.g.* respiration on its way. The virtue of the pool approach does not lie in being the most accurate description possible of the decomposition processes, but rather in providing a kind of *ad hoc* theory proven to work well in generating realistic figures. Furthermore, since pools are not directly measurable, they need to be inferred within the framework of the model, probably rendering parameter values site and model specific (see discussion on incommensurability, Beven 2009). As a theory for *understanding* decomposition the pool concept is weak, but has proven very useful in data driven modelling, which is not a contradiction. The pool approach to SOM and that used in the Q-model (described later) are two contrasting and illustrating examples of SOM description in terms of decomposability and turn-over in models.

2 The papers

2.1 Introduction

The first task in the work of this thesis was to assess how ‘old’ (interpreted as low quality, see below) soil organic matter (SOM) would react to increasing temperature due to climate change. There are claims that old SOM is more temperature sensitive than young (Bosatta & Ågren, 1999). However, the experimental evidence has pointed in opposing directions (Giardina & Ryan, 2000; Reichstein *et al.*, 2000; Vanhala *et al.*, 2007; Conant *et al.*, 2008), although the reasons behind the differences between experiments have been debated (Kirschbaum, 2006). From a theoretical point of view, the reason that some SOM carbon is old could be because it is difficult to decompose as a result of having a high activation energy (Arrhenius, 1889). Since the activation energy determines the temperature sensitivity, old SOM would presumably be more temperature sensitive than young. A key question here of course is whether age is a good measure of quality.

The importance of the temperature sensitivity of old SOM becomes clearer against the background of the global carbon budget. Globally, soil (1550 Pg) contains about twice as much carbon as the atmosphere (760 Pg) (Lal, 2004) and there are large annual fluxes between the soil and the atmosphere. Soil carbon stocks are increased by plant litter input and decreased through decomposer respiration and water mediated losses of *e.g.* DOC, POC, and PIC. It is expected that soil respiration will increase faster than plant production with increasing temperature (Anderson, 1992), leading to less soil carbon, further increasing the atmospheric CO_2 concentration and thus creating a positive feedback.

In the work described in this thesis, the focus is on the factors regulating the decomposition processes but not including other processes regulating soil carbon, such as plant input or leaching of DOC, which were intentionally omitted. However, the studies are discussed in a broader context in an example at the end of the thesis.

The question of decomposition of organic matter is approached here in the context of temperature and quality (Ågren & Bosatta, 1998; Bosatta & Ågren, 1999). *Paper I* studies the effect of temperature on decomposition without taking quality directly into consideration. *Papers II* and *III* consider the combined effect, as well as other temperature related processes. *Paper IV* deals solely with SOM quality.

2.2 Decomposition

Decomposition is the process by which organic matter in (or on top of) the soil is converted into progressively smaller pieces and eventually inorganic compounds. Organic matter contains carbon and hydrogen as well as a number of other elements such as oxygen, nitrogen, phosphorus *etc.*, and can originate from plants or animals. The major input into the soil is from plants, in the form of aboveground litter, *i.e.* leaf litter, twigs and stems, or belowground material, *i.e.* root litter, exudates and mycorrhizal hyphae. There are both abiotic and biotic processes involved in decomposition. Abiotic processes include mechanic forces acting on the litter, caused by *e.g.* freezing/thawing and drying/wetting cycles. Part of the effect of bioturbation, *e.g.* by earthworms, is also mechanical. Light, *i.e.* UV photooxidation, plays an important part by having both direct and indirect effects on litter and OM (as well as DOC, DIC, POC, SOM) in terrestrial and marine ecosystems (Austin & Vivanco, 2006; Zepp *et al.*, 2007).

Bacterial and fungal decomposers are responsible for more than 95% of the biotic part of OM decomposition (Persson *et al.*, 1980). Decomposers rely on water as a medium for transport of substrate (Marschner & Kalbitz, 2003). To break down macromolecules into pieces small enough for ingestion, decomposers produce exoenzymes that diffuse through the water films to the substrate. Different kinds of litter require different types of enzymes to break them down. For example, degradation of lignin, an abundant structural part of wood, requires special lignolytic enzymes (Jennings & Lysek, 1999).

Soil organic matter can be protected from decomposition in a number of ways. It can be *physically protected* in the interior of soil aggregates, inaccessible to exoenzymes and decomposers and where oxygen levels may be lower. Organic matter can also be *chemically protected* by adsorption onto mineral surfaces. In addition, there is also the chemical structure of the organic molecules themselves that makes them more or less easy to decompose. For example cellulose, which has a very regular structure, is easy to split into its subunits, whereas irregular humic substances offer less accessible attack points for enzymes. In deep soils, where decomposers may be scarce, larger scale spatial separation can also slow down decomposition.

Temperature affects decomposition in a number of ways (Fig. 2). Litter fragmentation can increase with freezing/thawing cycles. The speed at which exoenzymes break down larger molecules is temperature dependent, in principle described by the Arrhenius equation. Adsorption/desorption reactions are also temperature sensitive. Water is needed as a means of transportation of enzymes to the substrate and substrate to decomposers and the diffusion that regulates this is temperature dependent. Water is also needed for transporting oxygen and oxygen solubility decreases with temperature. When water freezes, transport is shut down. However, not all soil water freezes at 0°C, explaining why soil (heterotrophic) respiration can continue even when temperatures reach some degrees below zero (Öquist *et al.*, 2009). The decomposers themselves also change with temperature, *e.g.* altering cell membrane fatty acid composition. Decomposer community composition may also change. Other types of exoenzymes are produced, and the lifetime of the enzymes depends on temperature.

Decomposers use organic matter as a source of metabolic (*e.g.* carbohydrate) energy and as a source of nutrients. Previous studies have shown that decomposer carbon use efficiency decreases with temperature (Steinweg *et al.*, 2008).

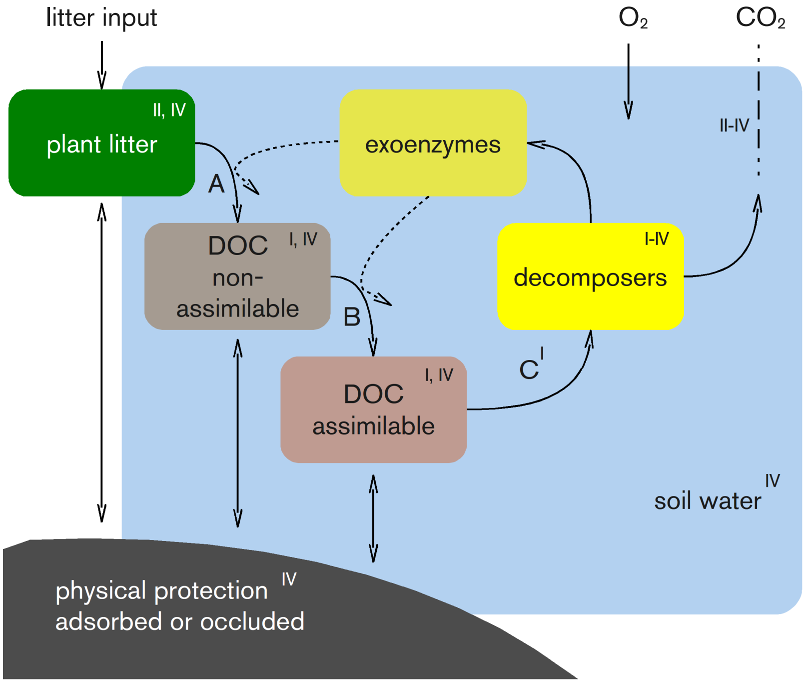

Figure 1. Illustration of temperature dependent decomposition sub-processes. Solid arrows represent mass flow, dashed arrows illustrate effects on other processes. Roman numerals indicate the paper (*I-IV*) in which the different processes are investigated. Plant litter enters the soil (top left) and becomes gradually more fragmented. Exoenzymes break down the litter into small and dissolvable fractions (DOC) or directly assimilable products (arrow not drawn). Soil particles (bottom left) can inhibit decomposition through physical protection and adsorption. Water mediates diffusion of DOC, enzymes, oxygen and CO_2. Decomposer community composition changes with temperature, as does the fatty acid composition of individual decomposers. The activity and community composition of decomposers affect the release of exoenzymes, which in turn are affected by temperature in that breakdown of enzymes is temperature dependent. Decomposers also produce different enzymes with temperature.

2.2.1 What is quality?

The term quality should be interpreted from the point of view of a decomposer. Litter and organic matter need to provide decomposers with both energy and nutrients, and high quality substrates lead to high decomposer growth rates. In this sense, it is the composition of plant litter that determines its quality.

This short definition of quality is intuitively appealing but raises a number of questions:

1. Since the decomposition of some organic molecules, such as lignin, requires special enzymes that are only produced by some decomposers, does quality depend on the composition of the decomposer community?
2. How should the changes litter undergoes over time be dealt with, and how do these affect decomposer growth and thus quality. Is quality something purely instantaneous, or should it be defined as integrated over time?
3. Since the substrate can interact with mineral particles, do such interactions modify quality?
4. How should the quality definition incorporate the temperature sensitivity observed in many studies (*cfr.* Bosatta & Ågren, 1999)?
5. Are there definitions of quality that lead to easily and reliably measurable quantities (*cfr.* Bruun *et al.*, 2010)?
6. If decomposers grow faster/slower on a mixture of substrates (priming, *cfr.* Kuzyakov *et al.*, 2000), how is this related to quality?

Whatever the definition chosen, it should be useful as a theoretical tool or in making empirical predictions. It is also preferable if the definition is 'stable' under the influence of *e.g.* factors 1) and 3).

2.2.2 Quality in the Q-model

The Q-model offers a well developed and formalised framework for interpretation of quality. The theory suggests that quality is related to the number of enzymatic steps required for a carbon atom to be metabolised (and released) by a decomposer (Bosatta & Ågren, 1999). This way of looking at quality involves the concept of activation energy, thereby connecting quality and temperature. Temperature sensitivity becomes inherent in the theory.

Since each carbon atom is viewed as having a certain quality, a number of particles (a soil sample) will have carbon atoms of varying quality described by a quality spectrum (Fig. 1). From a theoretical perspective, quality can thus be viewed at the *individual* carbon atom level, hereafter denoted with the superscript I. It can also be viewed as the *average* of many carbon atoms, denoted with the superscript A. Without A and I, quality is used in the text in its more general sense. When decomposition takes place, some carbon is lost as respiration and the rest undergoes a change in quality. That change is referred to as dispersion ($D_{i,j}$), going from the quality^{I} i to quality^{I} j.

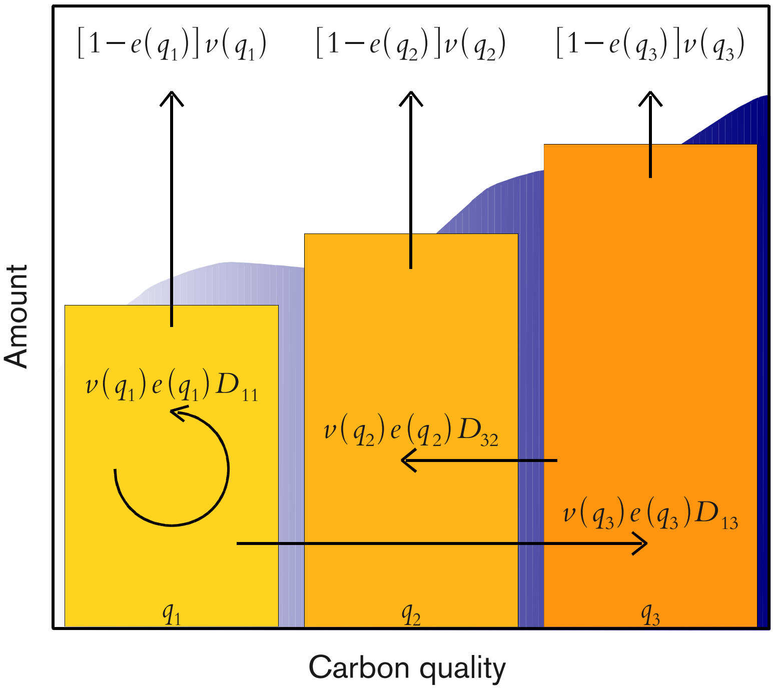

Figure 2. Generic model of soil organic matter decomposition. Soil carbon can be regarded as belonging to a distribution of quality values, continuous (the curve) or discrete/as pools (the three bars along the x-axis). Respiration (CO_2 loss) from different quality values/pools is indicated by arrows 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.

2.2.3 The temperature-quality hypothesis

A feature of describing organic matter decomposition by a temperature function that is non-linear, *i.e.* the Arrhenius function, and coupled to quality$^{\mathrm{I}}$ and where temperature has a diminishing impact with higher temperature is that organic matter of different quality$^{\mathrm{I}}$ will decompose at different rates. In addition, the proportion of decomposition for OM of differing quality$^{\mathrm{I}}$ will vary with temperature. This means that two samples of the same substrate, having lost the same amount of carbon at different temperatures, will differ in the distribution of carbon quality$^{\mathrm{I}}$. If placed at the same temperature, the sample coming from the higher temperature will have more high quality[I] carbon relative to low quality[I] than the sample coming from the low temperature. Therefore, samples coming from the high temperature should have a higher respiration rate than those coming from the low temperature (when at the same second temperature). This hypothesis was termed the temperature-quality hypothesis in *Paper II.*

2.2.4 Description of temperature sensitivity and Q_{10}

Ideally, the temperature sensitivity of a rate $F(T)$ would be calculated as

$$\frac{1}{F(T)}\frac{\partial F(T)}{\partial T}=\frac{\partial \ln F(T)}{\partial T} \quad .$$

In practice, however, temperature sensitivity is estimated by taking the ratio of the rate at two different temperatures. When these are 10 K apart Q_{10} becomes:

$$Q_{10}=\frac{F(T+10)}{F(T)} \quad .$$

In the special case of a rate that depends exponentially on temperature ($F_0 e^{\alpha T}$) Q_{10} is independent of temperature:

$$Q_{10}=\frac{F_0 e^{\alpha(T+10)}}{F_0 e^{\alpha T}}=e^{10\alpha} \quad .$$

All other functions describing the temperature dependence of a rate lead to Q_{10} values that change with temperature. The choice of reference temperature is therefore normally important.

2.2.5 The Arrhenius function

The Arrhenius function (Arrhenius, 1889) is generally used to describe how the reaction rate constant (k) of a single chemical reaction depends on temperature (T) as follows:

$$k=A e^{\frac{-E_A}{RT}}$$

An effect of this description is that the Q_{10} value of processes defined by the Arrhenius function does not stay constant with temperature. The resulting k of a series of reactions where certain steps also take place in parallel is difficult to determine or to derive from theory.

In this thesis, *Papers I* and *III* are modelling papers, whereas *Papers II* and *IV* are empirical studies.

2.3 Paper I

In P*aper I* a theoretical description of decomposition was formulated, focusing on three processes expected to contribute to the temperature dependence:

i The rate of substrate (derived from SOM) uptake by a decomposer across its outer surface (μ, K).
ii The diffusion of substrate to the decomposer from the surrounding soil (D).
iii The rate at which substrate becomes available in the soil (S).

Substrate becoming available (iii) can be viewed as the combined effect of exoenzymes acting on the substrate together with any processes that make more substrate available and accessible to the enzyme.

These three processes were then formulated in mathematical terms using physical laws. When describing carbon uptake, decomposers were modelled as spheres and cylinders for bacteria and fungal hyphae respectively. The model included four activation energies (A) for the three processes: substrate availability (A_S), diffusion to the decomposer (A_D), maximum uptake rate (A_μ) and the half-saturation constant for uptake (A_K). For simplicity the activation energy was expressed as an equivalent temperature ($A = RT$).

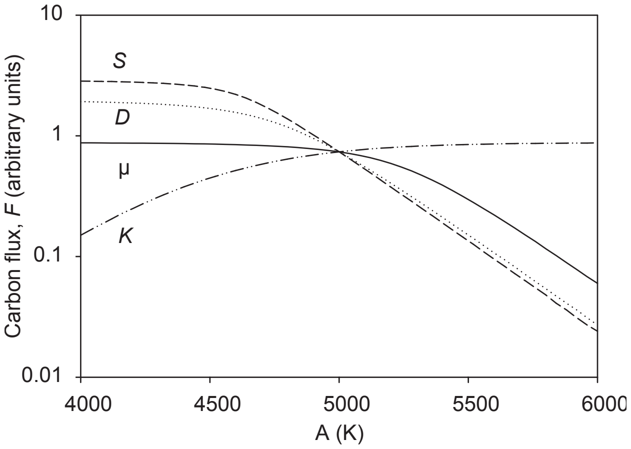

Figure 3. Respiration (carbon flux) at T 288 K as a function of the activation energies A_{μ}, A_D, A_S, and A_K, respectively. The activation energy is the common default value for the other three processes.

When the activation energies A_D, A_{μ}, A_S were increased one at a time, with the others kept constant, the carbon flux to the decomposers decreased smoothly. Increasing A_K increased the carbon flux (Fig. 3). The temperature sensitivity, expressed as Q_{10}, showed a different pattern (Fig. 4). When A_D, A_S, or A_K were increased the temperature sensitivity increased up to a point (5000 K) at which the activation energies were similar, where the temperature sensitivity changed rapidly. With increasing A_{μ} the temperature sensitivity decreased, again rapidly around the common activation energy (5000 K), thereafter increasing more slowly. In most cases the temperature sensitivity was determined by a combination of two of the processes, for example substrate release and diffusion or substrate release and uptake kinetics. The results were the same regardless of whether uptake was by (idealised) bacteria or fungi.

This model, a simplification as always, shows that the potential exists for complex responses to temperature as a result of several interacting temperature dependent processes.

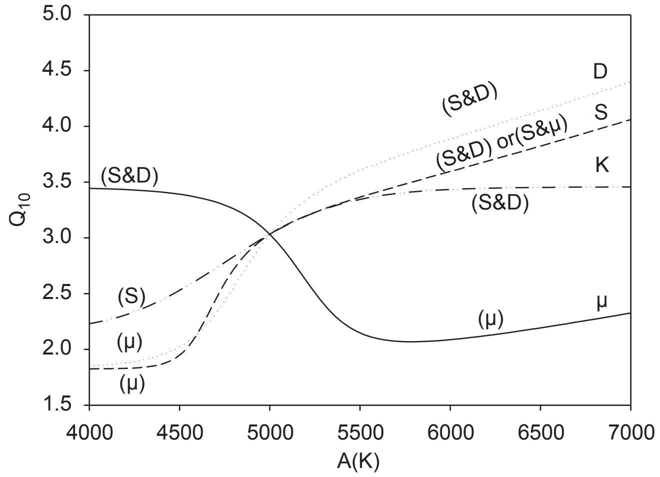

Figure 4. Q_{10} T=288 K of carbon uptake (F) as a function of the activation energies A_μ, A_D, A_S, and A_K, respectively. The activation energy is the common default value for the other three processes. Abbreviations in brackets show the process(es) dominating the temperature response.

2.4 Paper II

Paper II describes an incubation experiment with humus, straw and spruce needles. The substrates were first incubated (Fig. 5b, c) at 5, 15, or 25°C (initial temperature) and then moved to one of the same three temperatures (final temperature) in a full factorial design. According to the temperature-quality hypothesis described above, two samples of the same substrate that have decomposed to the same degree of carbon loss but at different temperatures will differ in their carbon quality$^{\mathrm{I}}$ distribution, *i.e.* when placed at the same final temperature, the sample coming from the higher initial temperature will have higher overall carbon quality$^{\mathrm{A}}$ (and thus higher respiration rate) than the sample coming from the lower initial temperature.

This experimental design enabled different hypotheses about temperature and quality to be tested. Apart from the fundamental question of whether past (initial) temperature affects future (final temperature) respiration through the temperature-quality hypothesis, the consequences of different ways of calculating Q_{10} could also be compared. Q_{10} can either be estimated from samples at constant but different temperatures at the same level of carbon loss, or by comparing the respiration rates of the same sample before and after a temperature change (between initial and final temperature). The latter assumes that the carbon lost between the measurements is negligible.

Figure 5. (*a*) shows jars used in *Paper IV*. The top end of the protrusion was fitted to evacuated flasks at gas sampling. (*b*) and (*c*) show incubation jars containing Norway spruce needles used in *Paper II*. (*b*) shows how the jar was stored between measurement occasions. In the bottom of the depression there is a small hole, enabling gas exchange whilst preventing too rapid water loss. Photos by the author.

Needle samples treated with initial incubation temperature 25°C respired the least at all final temperatures, while those initially incubated at 5 and 15°C respired more or less the same. Both these results were unexpected. Humus and straw (although the latter with considerable scatter) behaved differently in that samples for which the final incubation was at the same temperature as the initial incubation respired faster than those that had experienced a change in temperature. This could be an example of home temperature advantage. Therefore, these results do not support the temperature-quality hypothesis. Even though the amounts of substrate were kept the same between treatments, the temperature changed the decomposer communities as measured by fatty acid composition (unpublished results). In the temperature-quality hypothesis it is assumed that the decomposer community remains the same and that only the substrate availability is modified by temperature. The temperature-quality

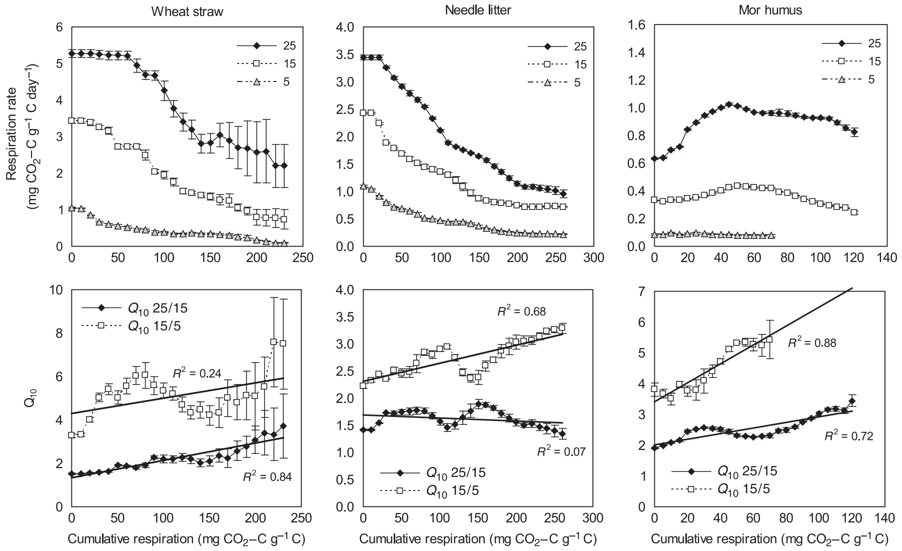

Figure 6. Respiration rates (top) and $Q_{10\text{-const}}$ values for the intervals 5-15°C and 15-25°C (bottom) in wheat straw, needle litter and mor humus in relation to cumulative respiration. The coefficient of determination (R^2) is given for each linear trend line. Error bars indicate 1 SE.

hypothesis may therefore still be valid as such, but masked by a much stronger effect emanating from changes in decomposer community.

Temperature manipulation experiments seem to be a good example of a situation where it is difficult to modify only one variable at a time, while keeping the others constant. Determination of the controlling factor/s in the process puts the definition of quality to the test: do quality and temperature determine the decomposers present, or do the decomposers themselves determine what is high or low quality OM?

The experimental data can be used to evaluate the temperature-quality hypothesis from yet another angle, namely how temperature sensitivity changes with increasing decomposition. When Q_{10} was calculated using the substrates kept at the same temperature during the whole experiment, in five out of six cases Q_{10} increased with decomposition (Fig. 6). This observation is directly in line with the temperature-quality hypothesis, since the quality should decrease during the experiment, leading to increasing Q_{10}.

Q_{10} was also calculated from the change in respiration rates just at a change in temperature. The resulting Q_{10} for needles was higher when the temperature was increased compared with constant or decreased temperature. Q_{10} values at constant and decreased temperature were equal. For humus the pattern was different and less consistent. However, for all significant comparisons, elevated temperature resulted in a higher Q_{10} than calculated from constant treatments. In many cases, elevated temperature resulted in a transient respiration peak (Fig. 7), explaining the Q_{10} results. This peak is most likely a decomposer response, which makes detecting the effect of quality even more complicated.

In conclusion, this experiment provided partial support for the temperature-quality hypothesis and also indicated that temperature effects on decomposers might need more attention.

Because wheat straw behaved very differently between the replicates, it had to be omitted in many of the analyses.

2.5 Paper III

Paper III investigated whether the Q-model could simulate the Norway spruce needle decomposition data from the temperature experiment in *Paper II*. Four different versions of the model were used, using *one* (denoted q_0) or *two* initial quality[1] values of carbon (q_{01} and q_{02}) in combination with decomposer efficiency being either *fixed* (e_0) or *variable* with temperature ($e_{0\text{-}5}$, $e_{0\text{-}15}$, $e_{0\text{-}25}$). The GLUE modelling framework (Beven, 2009) was used to calibrate the model on samples that had been kept at the same temperature during initial and final incubation.

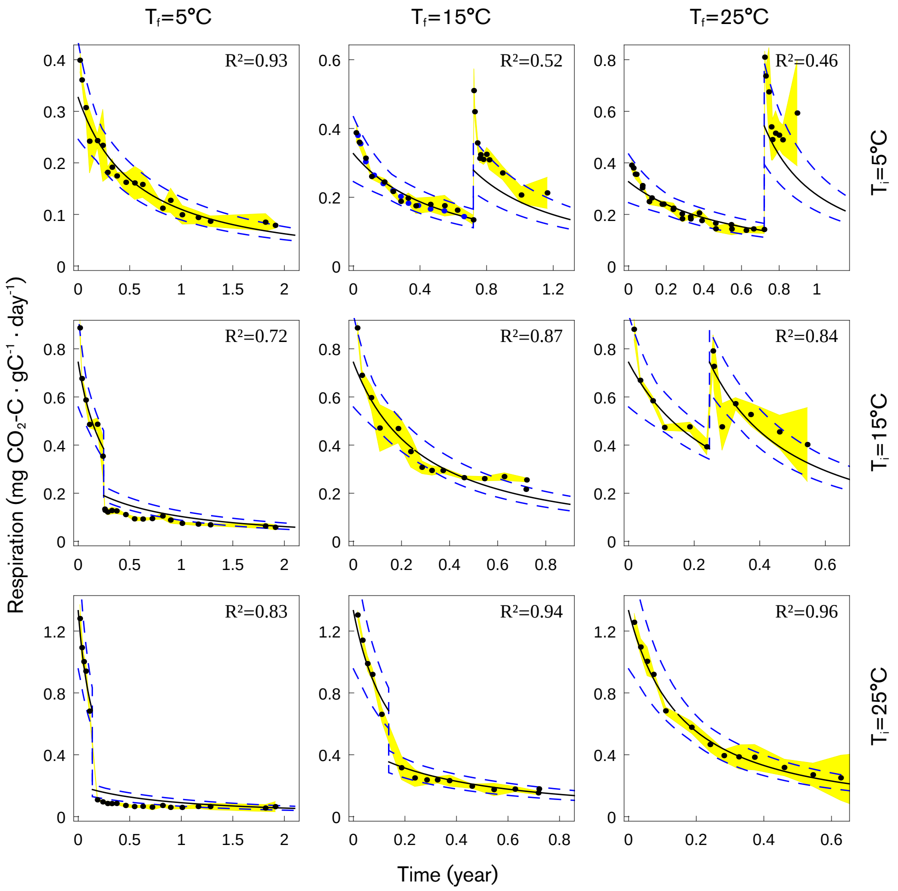

Figure 7. Model predictions of respiration rates for the *one* initial quality, *flexible* decomposer efficiency model and observed respiration rates for all combinations of initial (T_i) and final (T_f) temperatures (5, 15, and 25°C). The other models yielded similar results. Weighted ensemble run predictions are shown (solid black line) with max/min curves (blue dashed lines) for the accepted 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.

The predictive capability of the different model variations was then tested against data in which the needles had been subjected to a temperature change. All four model versions predicted respiration satisfactorily (Fig. 7). The use of two initial quality[I] values made no difference to the respiration in the final incubation, because respiration rates were entirely determined by the higher quality, regardless of temperature. In contrast, when a flexible efficiency was used the respiration rates in the final incubation differed between samples originating from different initial incubation temperatures. On average, the efficiency at 5°C was approximately 10% higher than that at 15 or 25°C. In the long run, decreasing decomposer efficiency with temperature could have a significant effect on soil carbon storage.

The results in *Paper III* indicate that even if the temperature-quality hypothesis is valid, the effects may be small or even undetectable, at least in short-term experiments. Interestingly, the temperature sensitivity of decomposer efficiency had a much stronger effect on quality changes.

2.6 Paper IV

In an experiment by Xiang *et al.* (2008), soils submitted to drying/wetting cycles lost much more carbon than soils incubated at constant optimal moisture level. In *Paper IV* that experiment was repeated and the age of the respired carbon was also measured using ^{14}C dating. Soil samples were collected from the surface and at 1 m depth, weighed into jars and submitted to five drying/wetting cycles. Respired CO_2 was collected at the start and after the last wetting and was analysed for ^{14}C. See Fig. 5a for illustration of the jars used.

The age of the carbon respired from the surface soil samples was initially young, ~280 years, but increased to ~330 years at the end of the experiment. Carbon respired from the soil samples collected at 1 m depth was much older, but decreased in age from 850 to 660 years from the first to the fifth cycle.

Since the mean turnover time (660-850 years) of the deep carbon *respired* was so old, the results challenge the notion that old soil organic matter is old because it is of low quality. The results also raise questions about the conditions in which physically/chemically protected carbon is made available to decomposers.

2.7 Conclusions and future work

The studies reported in *Papers I-IV* answered some questions and raised others, some of which are described in the following section.

In *Paper II* there was a difference in temperature response depending on whether the temperature was increased or decreased. This indicates that the temperature shift might have disturbed the system in a way not explained by theory known to us. Possibly, this could be a decomposer effect, more or less uncoupled from effects of substrate quality. However, other studies have reported an opposite (hysteresis) effect (Chapman & Thurlow, 1998; Hartley *et al.*, 2008).

We wanted to test the hypothesis that the temperature change stressed the decomposers, possibly inducing a metabolic shift to already assimilated carbon, possibly shifting the respiratory quotient. Oxygen probes (Figaro KE-25; see also Turcu *et al.*, 2005) were fitted to the jars in *Paper II* and their output logged. However, it was difficult to detect a change in oxygen concentration with our set-up since we relied on measuring a small change in a large number. The probes used were also highly sensitive to very small temperature and pressure changes and seemed to react to changes of even fractions of a degree in the temperature constant rooms.

Paper IV examined whether the effect of increased availability of SOM could be coupled to increased oxidation during the drying phase and subsequent hydrolysis at wetting. That hypothesis was tested in complementary experiments in which soil was allowed to dry in normal air or in a nitrogen gas atmosphere. After watering, DOC levels in the normal air treatment were 50% higher than in the N_2 treatment (Wetterstedt *et al.*, unpublished data).

The studies described in *Papers I-IV* showed that:

- If the temperature sensitivity of decomposition is modelled as a series of three temperature sensitive processes, unexpected temperature responses occur.
- There were results supporting the temperature-quality hypothesis but there were also results contradicting it.
- Differences in temperature sensitivity when increasing as opposed to decreasing temperature could not be explained using available theory.
- Decomposer efficiency decreases with temperature, which has a higher impact on quality evolution than the temperature-quality effect.
- Old soil organic carbon can be released simply by drying/wetting cycles, indicating it is not present in soil solely by virtue of being of low quality.

3 Afterword

Why is it currently not possible to make general, non site-specific, predictions of decomposition of organic matter and to state with certainty what will happen if the temperature becomes 5°C warmer? Is it because models like that used here or others are in their infancy, or are they established, well developed and close to 'as good as it gets'? What level of precision can we expect to reach in the future, and when developing new models, are there certain areas/certain approaches that might prove more rewarding than others?

One description of the situation is the following (Ågren & Bosatta, 1998) p. 7):

> "Ecology is a subject with many facets. In our endeavours to understand it as completely as possible, we need to make choices of perspectives; all questions are not viewed equally well from the same viewpoint. However, from any particular viewpoint we cannot see the whole system. Thus, by picking a fixed position from which to study the system, we lose information but hopefully what we see becomes more intelligible. The choice of viewpoint is, of course, critical. If we make the wrong choice, the picture we see is blurred and without any clear lines. There are no correct positions, only useful ones. When we happen to find ourselves facing any of these, our picture of the system may become clear and it will be possible to discern patterns and regularities in the system."

By *viewpoint* those authors mean not only place in space and time, but of course also scale or aggregation in space, time, and numbers. On top of that they also mean the theoretical standpoint adopted. The question in the current context is whether the results presented in *Papers I-IV* indicate that we need to change our viewpoint?

I can only answer above questions in a very limited sense, using three examples dealing with them below.

3.1 Selecting system boundaries and scale

Fig. 2 shows a simplified description of the processes involved in decomposition, while Fig. 8 shows some of the simplifications, boundaries and scales involved in experiments dealing with SOM respiration. Kirschbaum (2006) cites some of these factors, and others, as reasons why it is difficult to find consensus about the temperature sensitivity of SOM. Figs. 2 and 8 also illustrate that the experimental design needs to be specific in relation to the theories it is intended to test, since other influencing factors otherwise might render comparison of theory and experiment difficult or useless. Fig. 2 and the Q-model can serve as illustrations of the theoretical standpoint adopted in this work, while Fig. 8 is an illustration of the different scales and boundaries.

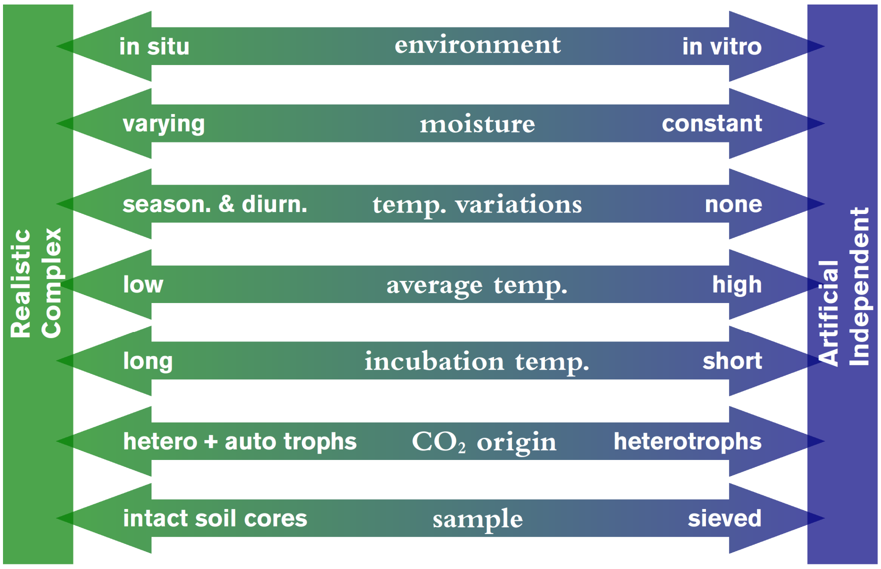

Figure 8. Boundaries in time, space, and complexity. Illustration of the possible choices encountered when measuring soil respiration, displayed on an axis ranging from the more *realistic* and *complex* to the more *artificial* and *independent*. Many of these and other choices differ between experiments, making comparisons difficult.

3.2 Some viewpoints or top-down versus bottom-up

From a more general point of view, theories can be developed to address phenomena at different levels of scale (space, time, number) and can be more or less founded in physical laws. The physical laws can be regarded as setting boundaries *e.g.* on the field in which ecology operates. One interesting and fruitful approach to the study of such boundaries is that placed on organisms by the relative abundance of the elements of which they consist. Because cells and tissues are built up of proteins, fats, *etc.* with fixed proportions of elements, the constraints this places on individual organisms can give rise to a number of predictable patterns at different levels in the ecosystem (Sterner & Elser, 2002). This is quite clearly a bottom-up approach. A quite different approach is that proposed by *e.g.* Lotka (1925) and continued by Odum (1969) and his followers and discussing, among other things, the energy flow through ecosystems. Work on the maximising principles in ecosystems has been summarised in reviews, *e.g.* by Fath *et al.* (2001). This approach focuses on the ecosystem as a system with a 'strategy' to capture *e.g.* as much energy as possible. This is a top-down description.

Considering the above two approaches might be valuable in developing new theories for understanding carbon sequestration. In the following example, stoichiometric theory as well as a pinch of the ecosystems approach are present.

3.3 A final example

One of the conclusions from *Papers I-IV* is that factors other than quality and temperature need to be considered when evaluating the effects of temperature on decomposition. The processes included could be those pictured in Fig. 2. *Papers I-IV* can be placed in a somewhat broader and more complex context with an example by Sterner & Elser (2002, pp. 267), in which the interactions between plants (*e.g.* a tree) and mycorrhizae are discussed in terms of stoichiometry. For the plant, carbon (C) as a structural component and as a source of energy is in relatively high supply because of the ability of plants to photosynthesise. However, once carbon is present in excess, plant growth may be limited by the amount of nutrients (*e.g.* nitrogen and phosphorus) present in the soil. In contrast, mycorrhizae are strictly limited by their access to high quality (energy rich) carbon, but have easier access to N and P. The two organisms can then mutually benefit by making transactions with C in exchange for N or P. The consequences of such exchanges may not be trivial. For example, Heath *et al.* (2005) showed that increased CO_2 concentration can lead to decreased carbon sequestration, most likely as an effect of the plant having an even higher surplus of carbon and benefiting from ‘trading’ more. Trading more with mycorrhizae results in higher decomposition rates, reducing soil carbon and carbon sequestration. The increased CO_2 concentration causing climate change could well have been assumed to compensate for increased respiration of SOM because of plants assimilating more carbon from the air and increasing litter input to the soil. In the case described by Heath *et al.* (2005), however, the effect on SOM was the opposite. This example illustrates that it is not the temperature sensitivity of small scale decomposition alone that defines the effect of climate change and increasing temperature on SOM decomposition, but an intricate relationship between plant, soil and the atmosphere.

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