

Modelling Soil Organic Matter Turnover

K. Sofia Nilsson

*Department of Ecology and Environmental Research
Uppsala*

**Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2004**

Acta Universitatis Agriculturae Sueciae
Silvestria 326

ISSN 1401-6230
ISBN 91-576-6710-1
© 2004 K. sofia Nilsson, Uppsala
Tryck: SLU Service/Repro, Uppsala 2004

Abstract

Nilsson, K. S. 2004. Modelling Soil Organic Matter Turnover.
Doctor's dissertation.
ISSN 1401-6230, ISBN 91-576-6710-1.

This thesis investigates various ways of determining and predicting soil carbon quality. The continuous-quality theory was used to study soil carbon quality changes under perturbations and to explain soil C:N ratios. Also, using the framework of the same theory a comparison of five commonly used soil organic carbon models were done.

The results confirm that NIR spectra in combination with the theory can be used for defining soil organic carbon quality. Decreases in quality in treatments without organic amendments and increases in the treatments with organic amendments are both accurately predicted.

The microbial biomass has been suggested as an indicator of change of soil properties. The continuous-quality theory tends to overestimate the microbial biomass and here the dependence of the mortality rate of microbes on the quality of substrate appears critical for correct predictions of microbial biomass. Nevertheless, the study showed that the amount of microbial biomass carbon tends to increase with increasing inputs of carbon in the soil and that the accumulation of microbial biomass also depends on the quality of these inputs.

The C:N ratio in soils varies between ecosystems and there seems to be no accepted explanation for this variation. The study confirms that the combination of the continuous-quality theory and the growth rate hypothesis lead to predictions about soil C:N ratios that are compatible with both specific experimental evidence and general observations.

The study of different SOC models shows that there is still a long way to go before we will find some generally accepted way of describing turnover of SOC. Not even such a fundamental process as decomposer efficiency can be assigned a value.

Keywords: microbial quotient, organic amendments, C_b , quality, continuous model, CQT.

Author's address: K. Sofia Nilsson, Department of Ecology and Environmental Research, SLU, P.O. Box 7072, SE-750 07 UPPSALA, Sweden.

Contents

Introduction, 7

Background, 7

Calculating quality, 7

Microbial biomass, 8

Carbon:Nitrogen ratio, 8

Modelling, 9

Organic agriculture, 9

Objectives, 11

Materials and methods, 12

Site description, 12

Theory, 13

Results and discussion, 14

Paper I: Using the continuous-quality theory to predict microbial biomass and soil organic carbon following organic amendments, 14

Paper II: Nitrogen:carbon ratios in soil organic matter is determined by the stoichiometric coupling of nitrogen concentration in decomposers to substrate quality, 17

Paper III: Consistency in parameterisations in soil organic carbon models, 17

Paper IV: Near-infrared spectroscopy (NIRS) to measure soil organic matter quality, 19

Conclusions, 20

References, 21

Acknowledgements, 23

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Nilsson, K. S., Hyvönen, R., & Ågren, G. I. Using the continuous-quality theory to predict microbial biomass and soil organic carbon following organic amendments. *European Journal of soil Science*. (In Press)
- II. Ågren, G. I., Nilsson, K. S., Joffre, R. and E. Bosatta. Nitrogen:carbon ratio in soil organic matter is determined by the stoichiometric coupling of nitrogen concentration in decomposers to substrate quality. (Manuscript)
- III. Nilsson, K. S., Ågren G. I. Consistency in parameterisations in soil organic carbon models. (Manuscript)
- IV. Nilsson, K. S., Joffre, R. & Ågren, G. I. Near-infrared spectroscopy (NIRS) to measure soil organic matter quality. (Manuscript)

Paper I is reproduced by permission of the European Journal of soil Science.

Introduction

Background

Soil organic matter, SOM, is a mixture of both new and old material containing everything from simple to complex compounds. Soil organic matter is important in enhancing the quality of the soil both as it increases the stability of the soil and acts as a reservoir of plant nutrients, especially where synthetic fertilizers can not be used as for example in organic farming.

Whether SOM increases or decreases and how fast depends on the balance between inputs and losses of organic matter. A lot of different amendments of organic material can be added to the soil. These contain different proportions of compounds with different degradabilities that will change both the quantity and quality of soil carbon. Due to the large variability of soils and the large background of organic material most soil C changes require periods of decades rather than years to be detectable.

Soils with larger organic matter content are expected to have better physical properties, including an increased abundance of water-stable aggregates, decreased risk of compaction and improved water holding characteristics. Even so it is difficult to find a direct link between increased organic matter and crop yields, since as long as the amount of soil carbon has not become so small as to change the soil properties, the yields are more influenced by the nitrogen content of the amendments than by their carbon content.

It is not only the carbon content that is important, it is also the carbon quality. Since the substrate contains a lot of different compounds, all of the carbon is not equally accessible to the decomposers. The quality is a measure of how accessible the carbon in the substrate is to the microbes, the more accessible the higher the quality and the more easily decomposable is the substrate. When the decomposers feed on the carbon, the fraction that is used for their biomass is called the efficiency i.e. the fraction of carbon going into new microbial biomass per unit of carbon utilized, the rest is respired as carbon dioxide. The carbon compounds produced by the decomposers have a different quality than the carbon they feed on.

However, a carbon quality that suits the microbes is not the same as good soil quality. Soil quality is a much broader term, affected by several factors, among which biological productivity, environmental quality, and plant and animal health all play a role (Karlen *et al.*, 1997).

Calculating quality

A number of different measures of quality of litter exists, this is usually done by measuring various ratios or concentrations, like N concentration, C:N ratio or lignin concentration. But there are some problems with these measures as for example N constitutes such a small percentage of the total litter mass and the N concentration normally is not stable during the whole decomposition process and lignin has a very complex structure and is difficult to measure.

Nuclear magnetic resonance (NMR) has been used extensively (e.g. Baldock et al. 1992, Kinchesh et al. 1995, Mathers et al. 2000) as a way of detecting relative changes in the composition of chemical groups. However, NMR is an expensive technique and not suitable for routine measurements. Moreover, there are so far no direct links between NMR and models.

There is no consensus on how to define and measure the SOM quality, but since quality plays such a central role in the decomposition of organic matter, it would be of importance to be able to do this.

We will show in paper IV that near-infrared spectroscopy combined with the continuous-quality theory provides a means of defining soil organic matter quality in a way that is also consistent with definitions of litter quality, emphasising the continuity between litter and soil organic matter. Near infrared reflectance spectroscopy (NIRS) is an alternative, which has been used to predict both litter decomposability (Gillon et al. 1999) and soil carbon in several studies (Chang et al. 2001). Gillon et al. (1999) also used NIRS to predict both litter mass remaining and decay rate constants. Joffre et al. (2001) also showed how NIRS could be connected to models.

Since in the model each carbon atom in the SOM can be assigned a quality and NIR will give a unique spectral signature in which all the biochemical information is included therefore it is possible to relate NIR spectra to the theoretical carbon quality. By connecting the theoretical quality concept and NIR spectra, predictions of long-term effects on soil organic matter quality and quantity will be possible.

Microbial biomass

The microbial biomass is the living part of the soil organic matter. It has a turnover of 1-2 years (Sparling, 1992), and therefore it responds much faster than the total soil organic matter to changes in management. So when we make changes in farming management, such as the conversion to organic production, we change both the quantity and quality of organic matter in the soil and we can try to monitor the changes in the microbial biomass instead of trying to detect the changes in the total amount of carbon stored which is a much slower process.

The microbial biomass is only a small part of the total soil organic matter, usually less than 5 % and the ratio between microbial biomass carbon (C_b) and soil organic carbon (C_{org}), the microbial quotient (C_b/C_{org}), has been suggested as an indicator of change of soil properties (Sparling, 1992, Ågren & Bosatta, 1998) because the size and activity of the microbial quotient is directly related to the amount and quality of carbon available (Breland & Eltun, 1999). Generally, increases in amounts of organic inputs will lead to increases in the microbial quotient (Breland & Eltun, 1999, Lundquist *et al.*, 1999). Here we have to see if the microbial biomass can be modeled with enough accuracy.

Carbon:Nitrogen ratio

The ratio between carbon and nitrogen in soils varies between grasslands and agricultural soils, with a C:N of typically around 10 (e.g. Burke et al. 1989) and forest ecosystems which have generally higher C:N ratios. The cause of these differences in C:N ratio is a bit unclear and in paper II we have studied whether

the growth rate hypothesis GRH (Sterner & Elser 2002), which says that an organism must increase its concentration of nitrogen and phosphorus when its growth rate increases, because increasing growth rates mean a heavier demand on nitrogen-rich enzymes for growth and on phosphorus-rich ribosomes to produce enzymes, can explain why soils in different ecosystems must have different C:N ratios.

Modelling

Long time field experiments are of course the ideal way of detecting the slow changes in the soil organic carbon but they are time consuming and impossible to perform on all types of soil and management. Therefore models are important in making predictions of soil organic matter quantities and qualities. A model is of course always a simplification of a system. An ecological system is extremely complex, and it is important to single out the most relevant processes. Soil organic matter, SOM, models look at the transformation of carbon in plant-soil systems with the quantity of soil organic components as a state variable.

Several models describing the turnover of carbon in the soil exist. These SOM models are usually either multi-compartment models or continuous models. In the multi-compartment models, the soil organic matter is divided into a number of different compartments or pools, all with different turnover rates. These pools exchange material with each other and also with the surrounding environment, including both inputs and losses; inputs in the form of litter or organic amendments and losses in the form of respiration and leaching. In continuous models the decomposition is a continuous process and division into different pools is not necessary, instead soil organic matter is viewed as litters of many ages added together. In the continuous model we have a more difficult mathematical treatment but we avoid the problems of trying to relate the pools in the model to measured data (Falloon and Smith 2000), to interpret the parameters physically and to make the division between different flows and losses. Instead the set of parameters describing the processes for different compartments in the multi-compartment models are described by functions.

Organic agriculture

I started out this study by looking at differences of organic and conventional agriculture and sustainability then ended up focusing on soil carbon quality.

High-intensity agriculture has with its use of fertilisers, pesticides, new crop varieties and the mechanization been able to considerably increase yields but has also created environmental problems, such as reduced biodiversity, lower soil fertility, increased erosion and eutrophication of lakes. The ability of intensive agriculture to be maintained in the long-term is also questionable. With a growing population there is a need of high yielding agricultural systems, but they also need to be environmentally sound and sustainable in the long- term.

Can organic farming systems meet these demands?

Organic farming is a system based on the concept of sustainability, in which the soil should remain productive over long periods of time without the additions of

synthetic fertilizers, instead it relies on techniques such as the use of crop rotations, animal and green manures and biological pest control.

Perhaps organic farming will be able to increase the yields and prove that it is friendlier to the environment than conventional farming systems have been, but the question that need to be answered is whether organic farming systems can be sustainable in the long term perspective.

In order to assess the sustainability we need to know what happens in the soil after a change from conventional to organic farming practices. Most soil carbon changes require very long times before they can be detected and the short-term changes are not necessarily the same as the long-term changes. Therefore after conversion to organic farming practice long-time periods are required before the impact of the changes on soil carbon and nutrients and their turn-over rates are fully visible.

Objectives

The general objective of this thesis was to investigate various ways of determining and predicting soil carbon quality.

The specific objectives were:

To predict the effects on the microbial biomass of various amendments. (paper I)

To study whether the differences in growth of the decomposers will depend on the substrate quality, such that high quality substrates also require high nitrogen concentrations. (paper II)

To compare 5 commonly used multi-compartment models to see what kind of functions in CQT would be needed to describe the corresponding parameters in the multi-compartment models. (paper III)

To determine whether the theoretical quality concept can be combined with NIR spectra to predict long-term effects on SOM quality. (paper IV)

Materials and methods

Site description

Even though I've only modelled these data, my calibrations of parameters and testing the equations would not have been possible without the data from a field trial so I've decided to include a description of the site here.

The experimental data used in paper (I, III and IV) came from The Ultuna long-term soil organic matter experiment; for more details see Kirchmann et al. (1994). The field experiment is situated at Ultuna, Uppsala, 60° N, 17° E, in central Sweden. The soil is a clay loam (36,5% clay, 41% silt, and 22,5% sand). The experiment was started in 1956 to study the effects of organic amendments and fertilizers on crop yields and soil properties. The experimental plots are 2-by-2 m, and separated by wooden frames, each plot is replicated four times. Measurements on soil C and yield are from Kirchmann et al. (1994) and data on the microbial biomass are from Schnürer et al. (1985), Witter et al. (1993), Witter (1996), and Witter and Kanal (1998). The annual precipitation at the Ultuna site is 570 mm, and the mean annual air temperature is +5.4° C.

The C input to the soil consists of crop residues and organic amendments. The C input from crops consists of belowground plant production, roots, as all aboveground parts are removed at harvest. The organic amendments were applied every second year in amounts of 0.8 kg ash-free organic matter (DW) m⁻². Nine of the original 15 different treatments are studied: black fallow (BF), crop with no N addition (NoN), crop with calcium nitrate addition (N), and six treatments with organic amendments: straw (S), green manure (GM), peat (P), farm-yard manure (FYM), sawdust (SD), and sewage sludge (SS).

Two different techniques for determination of microbial biomass were used: Adenosine triphosphate (ATP) analysis (Jenkinson et al., 1979, Eiland, 1983, Webster et al., 1984) and Fumigation Incubation Technique (FIC) (Jenkinson and Powlson, 1976) with some minor modifications described in Witter et al. (1993). In 1988, 1989 and 1990 the FIC technique (Witter et al., 1993). In 1990 the adenosine triphosphate (ATP) content of the soil was determined as described in Jenkinson and Oades (1979) (Witter et al., 1993). The microbial biomass from the ATP analysis was mainly used to compare with modeled data but the data from the FIC analysis are also included to indicate the variability in the values.

The experimental data used in paper II came from two decomposition experiments involving leaf or needle litters of 36 species were used. Both experiments were conducted using laboratory microcosms at 22 °C with soil moisture maintained at 80% of field capacity. Detailed descriptions are available in Joffre et al (1992) and Gillon et al. (1993, 1994, 1999). For more details see paper II (Table 1).

Theory

In the continuous-quality theory, CQT (Ågren & Bosatta 1998) we have a substrate that is decomposed by a microbial community. The substrate provides the carbon the decomposers need for growth, but it consists of inputs of many ages (cohorts) added together. The cohorts enter the system with an initial quality q_0 , which is a measure of how accessible the carbon is (or the rate at which the decomposers can utilise it). During decomposition it is then converted into a mixture of qualities.

Decomposers extract carbon from this distribution with a rate proportional to the amount of carbon of the respective quality and with a basic, quality-dependent growth rate $u(q)$. A fraction $e(q)$ of the extracted carbon goes into new decomposer biomass while the remainder is lost as respiration; we call e decomposer efficiency. Another consequence of the decomposers assimilation of carbon is a shift in carbon quality towards lower qualities. The average shift in quality of a carbon atom as it is assimilated by decomposers is $\eta_1(q)$.

We will use the following functions

$$e(q) = e_0$$

$$\eta_1(q) = \eta_{11}q$$

$$u(q) = u_0q^\beta$$

I have included some of the most important equations that I use in the thesis.

Equations used in the thesis (see papers 1-4 for notations)

The decrease in quality:

$$\bar{q}(t) = \frac{q_0}{(1 + \beta f_c \eta_{11} u_0 q_0^\beta t)^{\frac{1}{\beta}}}$$

The mean quality of the soil organic matter in all the litter cohorts dating from time 0 to time t :

$$\hat{q}(t) = \frac{1 - e_0 - e_0 \eta_{11} \beta}{1 - e_0 + e_0 \eta_{11} - e_0 \eta_{11} \beta} \frac{1 - \left(\frac{q_t}{q_0}\right)^{\frac{1-e_0}{\eta_{11} e_0} - \beta + 1}}{1 - \left(\frac{q_t}{q_0}\right)^{\frac{1-e_0}{\eta_{11} e_0} - \beta}} q_0$$

The N:C ratio of a cohort :

$$r(q) = \frac{h(q)}{g(q)} = \left[r_0 - \frac{f_{N0}}{f_c} - \frac{f_{N1} q_0}{f_c} \frac{1}{1 - \eta_{11}} \right] \left(\frac{q}{q_0} \right)^{\frac{1}{\eta_{11}}} + \frac{f_{N0}}{f_c} - \frac{f_{N1} q_0}{f_c} \frac{1}{1 - \eta_{11}} \left(\frac{q}{q_0} \right)$$

The accumulation of the soil carbon store:

$$C_s(t) = \frac{I_0 e_0}{f_c u_0 q_0^\beta (1 - e_0 - e_0 \eta_{11} \beta)} \left[1 - \left(\frac{\bar{q}(t)}{q_0} \right)^{\frac{1-e_0}{e_0 \eta_{11}} - \beta} \right] = C_{SS} \left[1 - \left(\frac{\bar{q}(t)}{q_0} \right)^{\frac{1-e_0}{e_0 \eta_{11}} - \beta} \right]$$

The loss of carbon from a system to which the input has been stopped.:

$$C_{BF}(t) = \frac{I_0 e_0}{f_c u_0 q_0^\beta (1 - e_0 - e_0 \eta_{11} \beta)} \left(1 + f_c \eta_{11} \beta u_0 q_0^\beta t \right)^{-\frac{1-e_0}{e_0 \eta_{11} \beta}}$$

The microbial biomass carbon when input is stopped:

$$C_{b,BF}(t) = \frac{f_c}{\mu} \overline{u(q)C}(t) = \frac{I_0}{\mu} \frac{e_0}{1 - e_0} \left(\frac{\bar{q}(t)}{q_0} \right)^{\frac{1-e_0}{\eta_{11} e_0}}$$

The microbial biomass carbon associated with the new material added:

$$C_{b,a(cr)}(t) = \frac{I_{0n}}{\mu} \frac{e_0}{1 - e_0} \left(1 - \left(\frac{\bar{q}(t)}{q_0} \right)^{\frac{1-e_0}{\eta_{11} e_0}} \right)$$

Results and Discussion

Paper I: Using the continuous-quality theory to predict microbial biomass and soil organic carbon following organic amendments

Soil microbial biomass and microbial quotient (the ratio of soil microbial biomass to soil organic carbon) are considered to be useful as rapidly responding indicators of perturbations of soil properties.

Therefore in paper I, I used the CQT to see how well the model is able to predict the effects of the different amendments on the microbial biomass and on the microbial quotient.

The model predicts correctly that the amount of microbial biomass increases for all the treatments with organic amendments compared to the black fallow treatment. Figure 1. The microbial biomass quotient increases also for all the amended treatments, except peat and sewage sludge, and decreases for the other treatments. However, the predicted microbial biomass carbon tend to be larger than the observations, varying by a factor of 4, depending on the type of amendment, which is more than the 2.7-fold variation in soil carbon, figure 2.

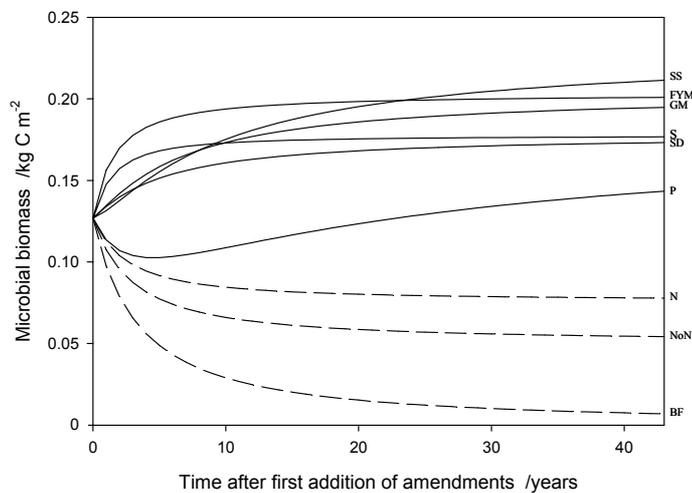


Figure 1. Predicted development of microbial biomass for the different treatments, plotted against time since the start of amendment. Solid lines are treatments with organic amendments; dashed lines are treatments without organic amendments.

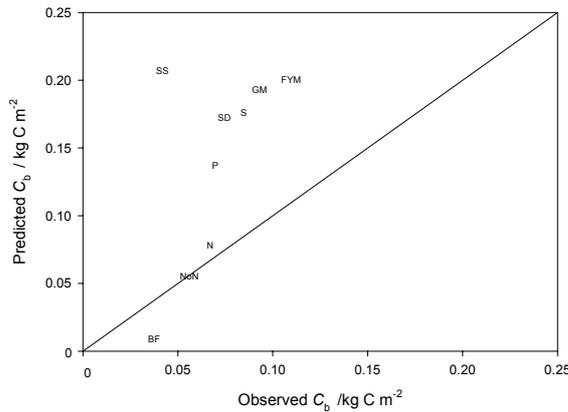


Figure 2. Predicted microbial biomass C plotted against observed microbial biomass C (ATP) in 1990.

The biomass order is the same as initial substrate quality, except that the treatments without additions of extra organic material have less microbial biomasses. Since microbial biomass and microbial quotient are strongly correlated, similar relations are found between predicted and observed microbial quotients as between predicted and observed microbial biomasses.

We attribute these deviations between predictions and observations to our assumption of a constant mortality rate, μ . Instead of being constant, the mortality rate should increase with the quality of the substrate. This could be because different organism groups utilize substrate of differing quality, e.g. bacteria feeding on better quality substrates than fungi. Schnürer *et al.* (1985) showed changes in the composition of the microbial community as a result of the treatments, but they could not interpret their observations in terms of mortality rates.

We cannot adjust the predicted microbial biomasses to the observed ones by manipulating the growth rates without upsetting the soil carbon predictions, which do not depend explicitly on microbial mortality, and the soil carbon predictions have been tested extensively (Ågren & Bosatta 1998).

The microbial biomass and microbial quotient increases with both the amounts of organic matter added (crop residues and amendments) and the quality of the added matter.

Moreover, short term observations can be misleading with respect to both the magnitude and direction of long term changes in biomass and related variables. Special attention must be paid to such amendments as sewage sludge, where contaminants such as heavy metals may determine process rates.

Paper II: Nitrogen:carbon ratios in soil organic matter is determined by the stoichiometric coupling of nitrogen concentration in decomposers to substrate quality

In paper II, the coupling between carbon and nitrogen was studied.

The carbon:nitrogen ratio in soils varies between ecosystems and are in general lower in agricultural soils than in forest soils. The growth rate hypothesis of ecological stoichiometry implies that with increasing growth rate of an organisms must also follow an increasing nitrogen:carbon ratio. In the soil, the differences in growth rates of decomposers will be caused by differences in the quality of the substrate upon which they are feeding.

We do not know the exact shape of the relation between f_N and q but a linear relationship should be a good first approximation

$$f_N(q) = f_{N0} + f_{N1}q$$

Values of the nitrogen concentration in the decomposers f_{N0} and f_{N1} have then been fitted to obtain the best agreement between observed and predicted N:C values. In general, the agreement between observed and predicted nitrogen concentrations corresponds to correlation coefficients exceeding 0.9.

Using the continuous-quality theory for decomposition of soil organic matter we have calculated the consequences of having the decomposer nitrogen concentration increase with litter quality. These theoretical predictions agree with observations from two extensive litter decomposition studies.

For a decomposer efficiency e_0 of 0.25 the steady state C:N in the soil varies between 16 and 25 as the quality of the initial litter decreases from 1.5 to 0.9. This variation is smaller than observed variations. This can be due to a coupling between litter quality and litter nitrogen concentration, we expect that higher litter qualities are also associated with nitrogen-richer systems and that as litter quality increases, we should also see an increase in e_0 . This coupling would lead to steeper relations between steady state C:N and initial litter quality. The other important factor is that we are looking at steady state values of C:N.

Paper III: Consistency in parameterisations in soil organic carbon models

By applying the continuous-quality theory as a framework for transforming five frequently used multicompartiment soil organic carbon, SOC, models: CENTURY (Parton et al. 1987, Parton et al. 1994, Paustian et al. 1992), RothC-26.3 (Coleman and Jenkinson 1996), DAISY (Hansen et al. 1990, Jensen et al. 1997, Mueller et al. 1997) VERBERNE (Verberne et al. 1990, Whitmore et al. 1997) and NCSOIL (Nicolardot & Molina 1994), we were able to give all the models a common form. This made it possible to focus on how the models are structured and parameterised and gives a more in-depth comparison.

In order to describe the dynamics of SOC, three functions are needed, these should describe the rate by which carbon is extracted from each compartment, the

fraction of extracted carbon that is used in respiration by the decomposers and how the remaining fraction of extracted carbon is converted into carbon of other qualities.

There is little consistency between the models in most respect. The qualities (turnover rates) of the compartments vary a lot between models. They have with the exception of ROTHC fairly similar qualities at the lower end of qualities, at the high quality end, there are large differences in which qualities that are included. A major reason for this difference between models might be the differences in timesteps. With a shorter time step it becomes necessary to describe processes with faster rates. Such faster rates might be a consequence of the presence of substrates of higher qualities, but not necessarily so.

We also note a considerable discrepancy in how much rates differ from assumed optimal values; the range is from 8 % of the optimal value in CENTURY to 30 % in ROTHC.

Decomposer efficiency (production-to-assimilation ratio) varies from 0.15 to 0.8 in magnitude between models and also in response to quality. In two models there is no variation with quality, in two other models there is a maximum at intermediate qualities and finally, efficiency increases with quality in NCSOIL but in a stepwise manner from the lowest qualities to the three highest ones, Figure 3.

The recycling of carbon between compartments shows for all models a highly scattered pattern. In part this is a consequence of the fact that not all pools are connected to each other.

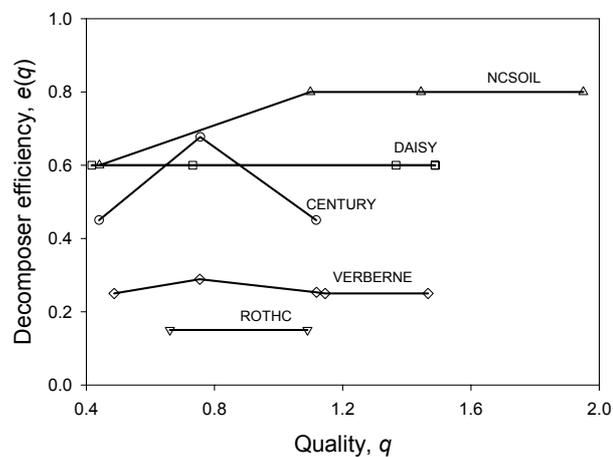


Figure 3. Calculated decomposer efficiency $e(q)$ as a function of quality q for the five models.

Paper IV: Near-infrared spectroscopy (NIRS) to measure soil organic matter quality

Several measures of quality of litter material exist but none has so far been defined for soil organic matter. But as NIR spectra contain all the information on the organic composition of soil samples, it could in combination with the continuous-quality theory be the tool for defining soil organic carbon quality.

For treatments without amendments, the quality is steadily decreasing as a result of inputs being smaller than before the experiment started. In treatments with amendments the quality is increasing although the input of low-quality peat initially leads to a decrease in quality. If the treatments were to be continued until steady state, the black fallow would end up at quality 0 when all was gone whereas the other ones would be ordered according to the initial qualities of the substrates. Both decreases and increases in quality are accurately predicted.

All the calibrations showed that the spectra are closely correlated with soil organic matter quality. However, calibration statistics were always better when the entire spectral information was taken into account than just the infrared region. Figure 4.

The results demonstrate the usefulness of NIRS to reveal and correctly quantify slight modifications of organic matter quality defined according to a theoretical concept of substrate accessibility to decomposers. These promising results show that NIR signature can be linked to synthetic properties of soil organic matter that can be calculated theoretically.

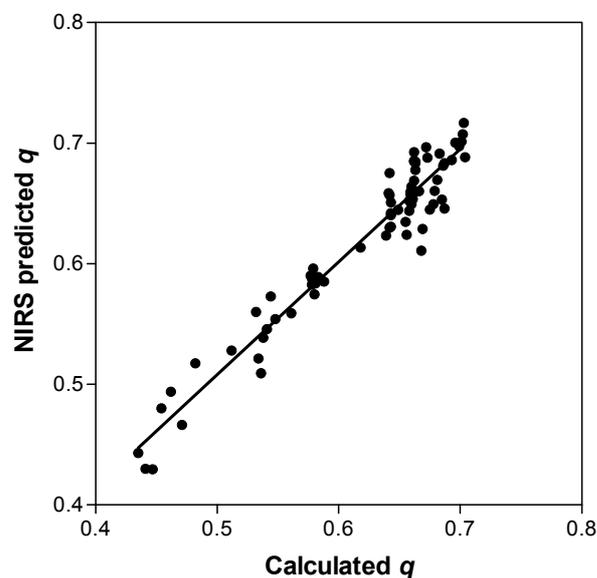


Figure 4. Relationship between soil organic matter quality calculated from Eq. (12) in paper IV and NIRS predicted values (Equation 1 in Table 2 in paper IV). The regression is given by $y = 0.93x - 0.044$.

Conclusions

This study has covered various ways of determining and predicting soil carbon quality.

The study confirmed that NIR spectra in combination with the continuous-quality theory can be used for defining soil organic carbon quality. NIRS can reveal and correctly quantify slight modifications of organic matter quality defined according to a theoretical concept of substrate accessibility to decomposers.

The CQT tends to overestimate the microbial biomass and here the dependence of the mortality rate of microbes on the quality of substrate appears critical for correct predictions of microbial biomass. Nevertheless, the study showed that the amount of microbial biomass carbon tends to increase with increasing inputs of carbon in the soil and that the accumulation of microbial biomass also depends on the quality of these inputs.

The study confirmed that the combination of the continuous-quality theory and the growth rate hypothesis lead to predictions about soil C:N ratios that are compatible with both specific experimental evidence and general observations. Further development requires information from long-term experiments, so that constant parameters can be replaced by functions between variables.

The study of different SOC models showed that there is still a long way to go before we find some generally accepted way of describing turnover of SOC. Not even such a fundamental process as decomposer efficiency can be assigned a value, this indicates that either the term is not used with the same meaning in different models or that we do not know how to assign values; as the analysis with CQT shows (Hyvönen et al. 1998), this parameter is one of the most critical for soil carbon storage.

References

- Ågren, G.I. & Bosatta, E. 1998. *Theoretical Ecosystem Ecology- Understanding Element Cycles*, 233pp. Cambridge University Press, Cambridge.
- Baldock, J.A., Oades, J.M., Waters, A.G., Peng, X., Vassallo, A.M. & Wilson, M.A. 1992. Aspects of the chemical structure of soil organic materials as revealed by solid-state ^{13}C NMR spectroscopy. *Biogeochemistry* 16,1-42.
- Breland, T.A. & Eltun, R. 1999. Soil microbial biomass and mineralization of carbon and nitrogen in ecological, integrated and conventional forage and arable cropping systems. *Biology and Fertility of Soils* 30,193-201.
- Burke, I.C., Yonker, C.M., Parton, W.J., Cole, C.V., Flach, K. & Schimel, D.S. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grasslands soils. *Soil Science Society of America Journal* 53, 800-805.
- Chang, C.W., Laird, D.A., Mausbach, M.J. & Hurburgh, C.R. Jr. 2001. Near-infrared reflectance spectroscopy - principal component regression analyses of soil properties. *Soil Science Society of America Journal* 65, 480-490.
- Coleman, K. and Jenkinson, D.S., 1996. RothC-26.3-A model for the turnover of carbon in soil. In: Powlson, D.S., Smith, P., and Smith, J.U. (Eds.), *Evaluation of soil organic matter models using existing, long-term datasets*. NATO ASI series 1, vol. 38. Springer, Berlin Heidelberg New York, pp. 237-246.
- Eiland, F. 1983. A simple method for quantitative determination of ATP in soil. *Soil Biology & Biochemistry* 15, 665-670.
- Falloon, P. D. and Smith, P., 2000. Modelling refractory soil organic matter. *Biology and Fertility of Soils* 30, 388-398.
- Gillon, D., Joffre, R. and Dardenne, P. 1993. Predicting the stage of decay of decomposing leaves by near infrared reflectance spectroscopy. *Canadian Journal of Forest Research* 23, 2552-2559.
- Gillon, D., Joffre, R. and Ibrahima, A. 1994. Initial litter properties and decay rate: a microcosm experiment on Mediterranean species. *Canadian Journal of Botany* 72, 946-954.
- Gillon, D., Joffre, R. and Ibrahima, A. 1999. Can litter decomposability be predicted by near infrared reflectance spectroscopy? *Ecology* 80, 175-186.
- Hansen, S., Jensen, H.E., Nielsen, N.E. and Svendsen, H., 1990. *Daisy-soil plant atmosphere system model*. Npo- forskning fra Miljøstyrelsen, vol A10, Miljøstyrelsen, Copenhagen, 272 pp.
- Hyvönen, R., Ågren, G.I. and Bosatta, E., 1998. Predicting long-term soil carbon storage from short-term information. *Soil Science Society of America Journal* 62, 1000-1005.
- Jenkinson, D.S. & Powlson, D.S. 1976. The effects of biocidal treatments on metabolism in soil- V. A method for measuring soil microbial biomass. *Soil Biology & Biochemistry* 8, 209-213.
- Jenkinson, D.S. & Oades, J.M. 1979. A method for measuring adenosine triphosphate in soil. *Soil Biology & Biochemistry* 11, 193-199.
- Jenkinson, D.S., Davidson, S.A. & Powlson, D.S. 1979. Adenosine triphosphate and microbial biomass in soil. *Soil Biology & Biochemistry* 11, 521-527.
- Jensen, L.S., Mueller, T., Nielsen, N.E., Hansen, S., Crocker, G.J., Grace, P.R., Klir, J., Körschens, M. and Poulton, P.R., 1997. Simulating trends in soil organic carbon in long-term experiments using the soil-plant-atmosphere model DAISY. *Geoderma* 81: 5-28.
- Joffre, R., Gillon, D., Dardenne, P., Agneessens, R., and Biston, R. 1992. The use of near-infrared reflectance spectroscopy in litter decomposition studies. *Annales des Sciences forestieres* 49, 481-488.
- Joffre, R., Ågren, G.I., Gillon, D. & Bosatta, E. 2001. Organic matter quality in ecological studies: theory meets experiment. *Oikos* 93, 451-458.
- Karlen, D.L., Mausbach, M.J., Doran, J.W., Cline, R.G., Harris, R.F. & Schuman, G.E. 1997. Soil quality: A concept, definition, and framework for evaluation. *Soil Science Society of America Journal* 61, 4-10.

- Kinchesh, P., Powlson, D.S. & Randall, E.W. 1995. ^{13}C NMR studies of organic matter in whole soils: I. Quantitation possibilities. *European Journal of Soil Science* 46,125-138.
- Kirchmann, H., Persson, J. & Carlgren, K. 1994. *The Ultuna Long-term Soil Organic Matter Experiment, 1956-1991*. Department of Soil Sciences, reports and dissertations, Monograph, Uppsala .
- Körschens, M. and Poulton, P.R., 1997. Simulating trends in soil organic carbon in long-term experiments using the soil-plant-atmosphere model DAISY. *Geoderma* 81, 5-28.
- Lundquist, E.I., Scow, K.M., Jackson, L.E., Uesugi, S.I. & Johnson, C.R. 1999. Rapid response of soil microbial communities from conventional, low input, and organic farming systems to a wet/dry cycle. *Soil Biology & Biochemistry* 31, 1661-1675.
- Mathers, N.J., Mao, X.A., Xu, Z.H., Saffigna, P.G., Berngs-Price, S.J. & Perera, M.C.S. 2000. Recent advances in the application of ^{13}C and ^{15}N NMR spectroscopy to soil organic matter studies. *Australian Journal of Soil Research* 38,769-787.
- Mueller, T., Jensen, L.S., Magid, J. and Nielsen, N.E., 1997. Temporal variation of C and N turnover in soil after oilseed rape straw incorporation in the field: simulations with the soil-plant-atmosphere model DAISY. *Ecological Modelling* 99, 247-262.
- Nicolardot, B. and Molina, J.A.E., 1994. C and N fluxes between pools of soil organic matter: model calibration with long-term field experimental data. *Soil Biology & Biochemistry* 26, 245-251.
- Parton, W.J., Schimel, D.S., Cole, C.V. and Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in great plains grasslands. *Soil Science Society of America Journal* 51, 1173-1179.
- Parton, W.J., Ojima, D.S., Cole, C.V. and Schimel, D.S., 1994. A general model for soil organic matter dynamics: sensitivity to litter chemistry, texture and management. *Soil Science Society of America Special publication* 39,147-167.
- Paustian, K., Parton, W.J. and Persson, J., 1992, Modelling soil organic matter in organic-amended and nitrogen- fertilized long-term plots. *Soil Science Society of America Journal* 56, 476-488.
- Schnürer, J., Clarholm, M. & Rosswall, T. 1985. Microbial biomass and activity in an agricultural soil with different organic matter contents. *Soil Biology & Biochemistry* 17, 611-618.
- Sparling, G.P. 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. *Australian Journal of Soil Research* 30, 195-207.
- Sterner, R.W. & Elser, J.J 2002. *Ecological Stoichiometry - The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.
- Verberne, E.L.J., Hassink, J, De Willigen, P., Groot, J.J.R. and Van Veen, J.A., 1990. Modelling organic matter dynamics in different soils. *Netherlands Journal of Agricultural Science* 38, 221-238.
- Webster, J.J., Hampton, G.J. & Leach, F.R. 1984. ATP in soil: a new extractant and extraction procedure. *Soil Biology & Biochemistry* 16, 335-342.
- Whitmore, A.P., Klein-Gunnewiek, H., Crocker, G.J., Klír, J., Körschens, M. and Poulton, P.R., 1997. Simulating trends in soil organic carbon in long-term experiments using the Verberne/MOTOR model. *Geoderma* 81, 137-151.
- Witter, E. 1996. Soil C balance in a long-term field experiment in relation to the size of the microbial biomass. *Biology and Fertility of Soils* 23, 33-37.
- Witter, E. & Kanal, A. 1998. Characteristics of the soil microbial biomass in soils from a long-term field experiment with different levels of C input. *Applied Soil Ecology* 10, 37-49.
- Witter, E., Mårtensson, A. M. & Garcia, F.V. 1993. Size of the soil microbial biomass in a long-term field experiment as affected by different N- fertilizers and organic manures. *Soil Biology & Biochemistry* 25, 659-669.

Acknowledgements

Tack till SJFR som har finansierat denna studie.

Till alla dem som på olika sätt bistått mig under avhandlingsarbetet vill jag rikta ett varmt tack. Detta gäller särskilt professor Göran Ågren vars hjälp varit ovärderlig. Han har alltid haft tid för diskussioner av allt från ekvationer och resultat till stressande av medförfattare.

Tack Riitta för all din hjälp och stöd.

Ett stort tack till Magnus som alltid har tagit sig tid att hjälpa till när datorn strulat.

Tack till alla i systemekologigruppen Göran, Ernesto, Oskar, Magnus, Sveta, Riitta, Martin, Peter, Ann-Sofie och alla andra som suttit med, vi har haft många diskussioner och jag har lärt mig mycket.

Tack också till alla EoM-are både nuvarande och tidigare och till alla i doktorandgruppen, Ni har skapat en väldig trivsamt stämning och det har varit många intressanta och roliga diskussioner vid fika bordet. Inte minst alla roliga hästdiskussioner med Lisette, Riitta och Anne.

Och tack Lisette, Maria och Hanna och alla ni andra som tagit hand om Archie när jag inte har haft tid.