The Interaction between Carbon and Nitrogen during Litter Decomposition

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Cover: Diagram illustrating the interaction between carbon and nitrogen during litter decomposition.
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Abstract

Litter decomposition is essential for the cycling of elements in ecosystems. How carbon (C) and nitrogen (N) interact during litter decomposition is, however, not yet fully understood. This thesis studies litter decomposition with the aim of increasing our understanding of the interactions between C and N. The areas in focus are litter mixtures, mycorrhizal fungi, and various N:C ratios.

The decomposition rate of litter mixtures can differ from that expected on the basis of the decomposition rate of the single components. This thesis shows that changed decomposition rates in litter mixtures can be linked to a transfer of N between the litters.

Besides the typical decomposers, the saprotrophs, also mycorrhizal fungi can decompose organic matter. This thesis explores how mycorrhizal fungi interact with their plant partner under different N availabilities to modify the C and N dynamics of the plant and in the soil. The results indicate that in order to understand how decomposition is influenced by a changing N availability, we need an increased understanding of the decomposer ability of the mycorrhizal fungi and the plant–fungus relation in mycorrhizal associations.

It is problematic to estimate the parameters describing the relation between C and N during decomposition. This thesis shows that the key parameter to estimate is the critical N:C ratio, i.e. the litter N:C ratio at which N immobilisation switches to mineralisation.

Keywords: carbon, nitrogen, litter decomposition, litter mixtures, litter quality, carbon transfer, nitrogen transfer, mycorrhizal fungi, N:C ratio, critical N:C ratio

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Death is not in the nature of things; it is the nature of things.
But what dies is the form. The matter is immortal.
John Fowles

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 Berglund SL, Ågren GI (2012). When will litter mixtures decompose faster or slower than individual litters? A model for two litters. *Oikos* 121(7), 1112-1120.

II Berglund SL, Ågren GI, Ekblad A (in press). Carbon and nitrogen transfer in leaf litter mixtures. *Soil Biology & Biochemistry*, http://dx.doi.org/10.1016/j.soilbio.2012.09.015.

III Berglund SL, Lindahl BD, Clemmensen KE, Ågren GI. Modelling optimal plant growth: Mycorrhizal versus saprotrophic nitrogen mobilisation (manuscript).

IV Ågren GI, Hyvönen R, Berglund SL. The critical N:C ratio as a predictor of litter decomposition and soil organic matter stoichiometry (manuscript).

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The contribution of Linnea Berglund to the papers included in this thesis was as follows:

I Main author. Main part of the data collection. Main part of the analysis.

II Main author. Main responsibility for the experiment. Designed the experiment together with co-authors. Main part of the analysis.

III Main author. Designed the model after discussions with co-authors. Main part of the analysis.

IV Co-author. Discussed the analysis together with co-authors. Contributed to writing the paper.

Abbreviations

C	Carbon
N	Nitrogen
SOM	Soil organic matter

1 Introduction

Litter decomposition is essential for the cycling of carbon (C) and nutrients in terrestrial ecosystems. It is by decomposition that C and nutrients immobilised in the litter are released and once again becomes available to plants. Overall, it is controlled by the interactions between the decomposer organisms, the litter properties, and the abiotic environment (Swift *et al.*, 1979). However, at a more detailed level the interactions are not yet fully understood. One interaction we do not fully understand is the one between C and nitrogen (N).

Besides its scientific interest, understanding how N affects decomposition has become important in a global change perspective. During the last century, the N deposition has increased, mainly as a result of increased production and use of fertilisers and increased combustion of fossil fuels, and it is predicted to continue to increase (Galloway *et al.*, 2008; Galloway *et al.*, 2004). Observations about the effect of N on litter decomposition are, however, conflicting (Hobbie, 2005; Knorr *et al.*, 2005; Fog, 1988). For example, N fertilisation studies show that adding N can increase, decrease, or have no effect on the decomposition rate. A decreased or unchanged decomposition rate, together with an increased plant biomass production, may decrease the concentration of atmospheric CO_2. However, if both the plant biomass production and the decomposition rate increase, the consequence for the atmospheric CO_2 concentration is unclear.

Given the importance of litter decomposition for element cycling in ecosystems, and the uncertainties regarding responses and feedbacks to global change, an increased understanding of the interaction between C and N during decomposition is desirable.

2 Aims

The overall aim of this thesis is to increase our understanding of the interaction between C and N during litter decomposition. The specific areas in focus are:

- Litter mixtures (Papers I and II). The aim is to show that changes in decomposition rates when litters decompose together in mixtures can, at least in part, be explained by an effect of N.
- Mycorrhizal fungi (Paper III). The aim is to explore how stores and flows of C and N between plant and soil are affected by a changing N availability when mycorrhizal fungi can also decompose organic matter.
- N:C ratios (Paper IV). The aim is to examine how to estimate the parameters describing the relation between C and N during decomposition.

3 Methods

In this thesis, Papers I, III, and IV are theoretical studies and Paper II is an experimental study. In Papers I and IV, theoretical statements are compared to empirical data, whereas Paper III is purely theoretical. Before I go into the subject of this thesis and then summarise and discuss the results of the studies, I want to say a few things about theoretical models.

3.1 About models

> *Essentially, all models are wrong, but some are useful.* – George Box

A model is a representation of something, where some properties, important for the use of the model, are included, while other features have been omitted. In this respect, all models are wrong in that they do not include all properties of the thing they represent. The assertion that all models are wrong can also relate to the intended use of the model. Compare this to travel directions. Directions also include only some properties. If someone tells you how to get from A to B, the colours of the houses you are going to pass may not be important and may therefore not be included. The directions may, however, give a correct description of how to get from A to B but still be wrong in the sense that you cannot use them. Suppose the directions are: “From A, cycle north to the intersection X where you turn right, then after the tall red building you will find B on the left side”. Suppose now, on the day you are going from A to B, you have got a flat tire or there is too much snow on the roads, then the cycling directions are of no use. What instead would be more useful are the directions on how to get from A to B by bus. The cycling directions can be considered wrong because they do not help you to get where you want to go.

Let me continue the comparison to travel directions. Directions are often easier to follow the simpler they are. If they are too detailed, you may miss an important turn and get lost on the way. The same applies to models. Adding a parameter to a model may increase how well the model fits to a set of observations. The increased complexity that this entails may, however, cloud the view such that you miss something of interest along your way. In addition, the more complex the model is, the more difficult it may be to parameterise. It is better to start simply and then gradually increase the complexity than to start with too many details and then not even find the way to the first stop. To reach the goal of science, to understand the world, what we need is not the most complex models, but rather, the most useful ones.

4 Litter decomposition

Decomposition is the process by which the remains of living organisms are separated into their constituent elements. Dead organic matter, litter, is broken down into smaller pieces and finally mineralised to inorganic compounds.

4.1 Processes

The action of the decomposers and abiotic factors result in physical and chemical changes of the litter. When the original identity of the litter no longer can be recognised, it is regarded as soil organic matter (SOM). The changes can be attributed to the effects of the processes, leaching, fragmentation, and chemical alteration (Chapin *et al.*, 2002).

- Leaching is the removal of soluble material by the action of water. The soluble material is moved to a different location, usually a lower soil layer, where it can be processed further.
- Fragmentation is the physical breakdown of large pieces into smaller ones, thereby creating new surfaces for the decomposers to colonise.
- Chemical alteration is the chemical change of the litter and is primarily a result of the activity of the decomposers. The changes can occur because decomposers use only a part of a molecule or because they reorganise the molecules, for example in the production of decomposer biomass.

4.2 Carbon and nitrogen dynamics

The decomposers use the organic C in the litter as their primary energy source. As a result of respiration, the amount of C in the litter continuously decreases. An important factor determining the loss of C, besides the production rate of decomposer biomass, is the decomposer growth efficiency, i.e. how much of the assimilated C that is incorporated into new biomass (production-to-assimilation ratio). Like the production rate, the growth efficiency is expected to depend on the quality of the litter and different abiotic environmental factors such as temperature, water availability, and nutrient availability (Manzoni *et al.*, 2012).

The dynamics of N may not follow the same pattern as the dynamics of C. Usually, fresh litter contains too little N relative to the decomposers' need. To balance this, the decomposers immobilise N from the surrounding environment. Consequently, the amount as well as the concentration of N increases. After some time, the litter N concentration becomes larger than the decomposers' requirements, at which point they start to mineralise the excess N in the substrate they assimilate. The N:C ratio at this point, when N immobilisation switches to N mineralisation, is called the critical N:C ratio. Nitrogen, therefore, follows an increasing path, up until the critical N:C ratio is reached, and then a decreasing path. If, however, the N:C ratio of the fresh litter is equal to or higher than the critical N:C ratio, the decomposers will mineralise N from the start and N therefore only follows a decreasing pattern, like C.

4.3 Decomposers

The main part of the decomposer community consists of bacteria and fungi. The other part, the soil animals, influences decomposition by fragmenting the litter, feeding on the bacteria and the fungi, and changing the abiotic environment.

The compounds in the litter are too large for the bacteria and the fungi to ingest directly. Bacteria and fungi therefore excrete enzymes which break down the compounds to smaller ones before they can be absorbed. Some enzymes are very specific in which compounds they can break down whereas others are more general.

The decomposer community has until recently been considered to only include those that get their energy from the litter, that is, the saprotrophs. Now also the mycorrhizal fungi, which get C from their plant partners, are considered to be able to act as decomposers, probably to acquire the nutrients immobilised in SOM (Hobbie *et al.*, 2012; Talbot *et al.*, 2008; Read & Perez-Moreno, 2003).

4.4 Quality

The quality of the litter describes how easily the decomposers can use the litter; the easier it is for decomposers to use, the higher the quality. The quality is mainly determined by the chemical structure of the litter together with the set of enzymes the decomposers produce. Quality can for example be considered the inverse of the number of enzymatic steps required to decompose a compound (Bosatta & Ågren, 1999). If the decomposers lack an enzyme required to decompose a specific compound, they may not be able to use it, and may therefore consider the quality less compared with the decomposers possessing the enzyme.

Because the litter undergoes chemical changes during decomposition, the quality changes, most often towards lower qualities.

5 Litter mixtures

In nature, different litters do not always decompose separately; often they decompose together, in mixtures. The decomposition rate of litter mixtures can differ from the rate expected on the basis of the litter components decomposing separately (Gartner & Cardon, 2004). Most often, the response is positive, i.e. the mixture decomposes faster than the average of the single components. Experimental litter-mixture studies that also have examined N release suggest that this positive non-additive effect in litter mixtures could be coupled to the transfer of N between the litters (Salamanca *et al.*, 1998; McTiernan *et al.*, 1997; Briones & Ineson, 1996; Fyles & Fyles, 1993; Taylor *et al.*, 1989; Chapman *et al.*, 1988).

Whether changes in decomposition rates when two litters decompose together in mixtures could be explained by an effect of N was investigated, in this thesis, both theoretically (Paper I), by formulating and using a model, and experimentally (Paper II).

5.1 Model

In Paper I we formulated a litter mixture model for two litters. It extends the litter decomposition model by Ågren & Bosatta (1998) by describing interactions between two litters during decomposition. The key assumption was that the growth efficiency (production-to-assimilation ratio) of the decomposers responds to the amount of inorganic nitrogen (initial plus mineralised) in the surrounding environment. We then compared the cases where the litters decomposed separately and where the litters decomposed together in a mixture and investigated how this affected the decomposition rates. After conversion of model variables into measured entities we compared model predictions with data from 23 published experimental litter-mixture studies (*Table 1*).

Table 1. *Summary of litter-mixture data used in the prediction-observation comparison of the litter mixture model.*

Source	Species	Litter type[1]	No. of mixtures
Bardgett & Shine (1999)	*Holcus lanatus,* *Lolium perenne*	F	1
Brandtberg & Lundkvist (2004)	*Betula pendula,* *Picea abies*	F	1
Briones & Ineson (1996)	*Betula pendula,* *Eucalyptus globulus,* *Fraxinus excelsior,* *Querqus petraea*	F	3
Conn & Dighton (2000)	*Pinus rigida,* *Quercus* spp.	F	2
Fyles & Fyles (1993)	*Alnus rubra,* *Gaultheria shallon,* *Pseudotsuga menziesii*	F	2
Gartner & Cardon (2006)	*Acer saccharum,* *Quercus rubra*	F	16
Harguindeguy *et al.* (2008)	*Acacia caven,* *Bidens pilosa,* *Hyptis mutabilis,* *Lithraea molleoides,* *Stipa eriostachya*	F	10
Hättenschwiler & Jørgensen (2010)	*Caryocar glabrum,* *Dicorynia guianensis,* *Eperua falcate,* *Platonia insignis*	F	6
Hoorens *et al.* (2002)	*Calamagrostis epigeios,* *Carex rostrata,* *Sphagnum* cf. *recurvum,* *Vicia lathyroides*	F	4
Jonard *et al.* (2008)	*Fagus sylvatica,* *Querqus petraea*	F	1
Liu *et al.* (2007)	*Allium bidentatum,* *Artemisia frigid,* *Stipa krylovii*	F	18
McTiernan *et al.* (1997)	*Alnus glutinosa,* *Betula pendula,* *Fraxinus excelsior,* *Picea abies,* *Picea sitchensis,* *Pinus sylvestris,* *Querqus petraea*	F	21
Montagnini *et al.* (1993)	*Stryphnodendron microstachyum,* *Vochysia ferruginea*	F	1

Quested *et al.* (2002)	*Bartsia alpina,* *Betula nana,* *Empetrum hermaphroditum,* *Vaccinium uliginosum,* *Vaccinium vitis-idaea*	F	8
Quested *et al.* (2005)	*Astragalus frigidus,* *Bartsia alpina,* *Betula nana,* *Empetrum hermaphroditum,* *Pedicularis lapponica,* *Rubus chamaemorus,* *Vaccinium uliginosum,* *Vaccinium vitis-idaea*	F	15
Robinson *et al.* (1999)	*Carex rupestris,* *Dryas octopetala,* *Salix polaris,* *Saxifraga oppositifolia*	R	3
Salamanca *et al.* (1998)	*Pinus densiflora,* *Quercus serrata*	F	3
Sanborn & Brockley (2009)	*Alnus viridis* subsp. *sinuata,* *Pinus contorta*	F	1
Schädler & Brandl (2005)	*Acer platanoides,* *Cerasus avium,* *Corylus avellana,* *Fagus sylvatica,* *Fraxinus excelsior,* *Platanus* x *hispanica,* *Quercus robur,* *Quercus rubra*	F	5
Taylor *et al.* (1989)	*Alnus crispa,* *Populus tremuloides*	F	1
Wang *et al.* (2007)	*Alnus cremastogyne,* *Cunninghamia lanceolata,* *Kalopanax septemlobus*	F	2
Wardle *et al.* (2003)	*Betula pendula,* *Cladina stellaris,* *Empetrum hermaphroditum,* *Hylocomium splendens,* *Picea abies,* *Pinus sylvestris,* *Pleurozium schreberi,* *Salix caprea,* *Vaccinium myrtillus,* *Vaccinium vitis-idaea*	F	45
Xiang & Bauhus (2007)	*Acacia mearnsii,* *Eucalyptus globulus*	F	1

1. F = foliage, R = roots.

A diagram illustrating the litter mixture model is shown in *Figure 1*.

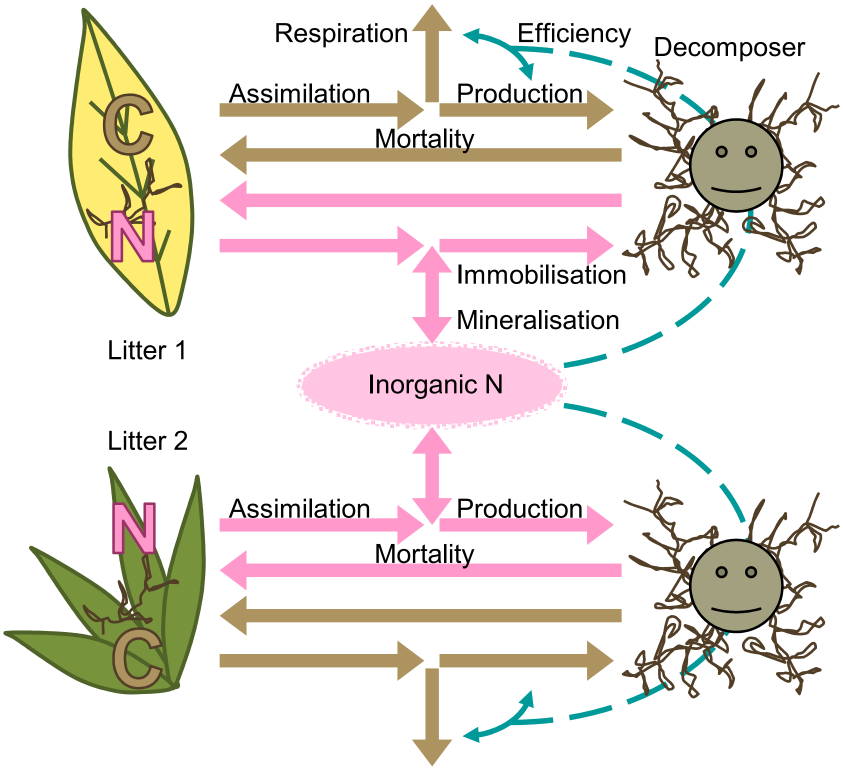

Figure 1. Diagram illustrating the litter mixture model. Brown arrows = C flows, pink arrows = N flows.

Production and mortality of the decomposers were assumed to be in equilibrium with the amount of C in the litter. The C and N dynamics of the two litters ($j = 1, 2$) could then be described by the following equations:

$$\begin{cases} \dfrac{dC_j}{dt} = -\dfrac{uC_j}{e(N_i)} + uC_j = -\left(\dfrac{1}{e(N_i)} - 1\right) u_0 q_j^{\beta} C_j, \quad j = 1,2 \\ \dfrac{dN_j}{dt} = -r_j \dfrac{uC_j}{e(N_i)} + r_d uC_j = \left(-\dfrac{r_j}{e(N_i)} + r_d\right) u_0 q_j^{\beta} C_j, \quad j = 1,2 \\ e(N_i) = e_0 + e_1 N_i \\ N_i + N_1 + N_2 = \text{constant} \end{cases} \qquad [1]$$

Meanings of symbols are summarised in *Table 2*.

Table 2. *Meanings of symbols describing the litter mixture model.*

Symbol	Meaning	Dimension
β	Parameter in decomposer growth rate	-
C_j	Amount of carbon in litter j	mass C
e	Decomposer growth efficiency	-
e_0	Parameter in decomposer growth efficiency	-
e_1	Parameter in decomposer growth efficiency	(mass N)$^{-1}$
N_i	Amount of inorganic nitrogen	mass N
N_j	Amount of nitrogen in litter j	mass N
q_j	Quality of litter j	-
r_d	N:C ratio of the decomposers	mass N (mass C)$^{-1}$
r_j	N:C ratio of litter j	mass N (mass C)$^{-1}$
u	Decomposer growth rate	time^{-1}
u_0	Parameter in decomposer growth rate	time^{-1}

When we compared the cases where the two litters decomposed separately and where the litters decomposed together in a mixture we got the following model predictions:

1. In a mixture, one of the litters will decompose faster and the other one slower than when the litters decompose separately.
2. The relative change in decomposition rate when the litters are mixed will be the same for both litters, but (according to prediction 1) of opposite signs.
3. The decomposition rate of the mixture will lie somewhere between the rates of the two single litters.
4. The decomposition rate of the mixture will be higher than the average of the two single litters (a positive non-additive effect of litter mixing) when the litter of the higher quality also has the largest N mineralisation. If the high quality litter has the smallest N mineralisation, the decomposition rate of the mixture will be lower than the average of the two single litters (a negative non-additive effect).
5. The non-additive effect will be greater the greater the differences in quality and N mineralisation of the single litters.
6. If the non-additive effect of litter mixing is positive, the decomposition rate of the high quality litter in the mixture will have increased and the decomposition rate of the low quality litter will have decreased. If the non-additive effect is negative, the decomposition rate of the high quality litter in the mixture will have decreased and the decomposition rate of the low quality litter will have increased.

The tested model predictions were consistent with a majority of the observations from the litter-mixture studies. An example of the relation between predicted and observed litter mixing effects is shown in *Figure 2*.

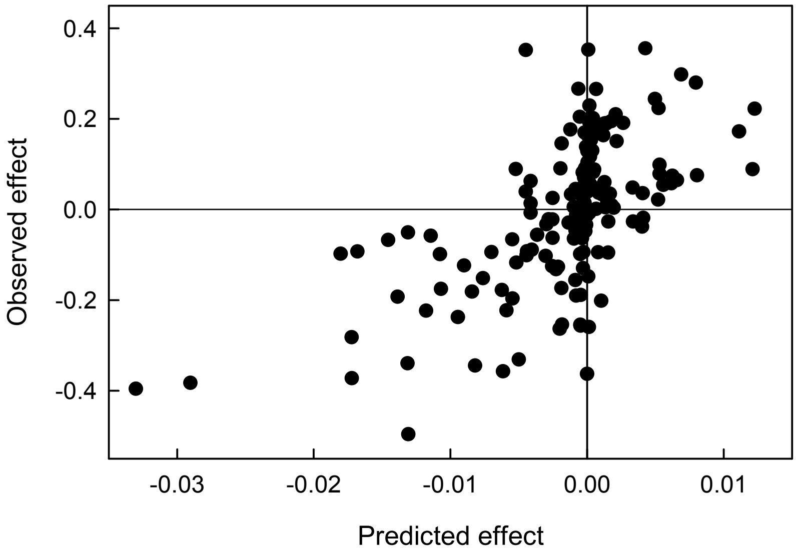

Figure 2. Relation between predicted and observed effects on the decomposition rate of mixing two litters. Each point represents one mixture. Total number of points = 169. Adjusted R^2 = 0.34. Note that the scales for predicted and observed effects are different.

5.2 Experiment

In the microcosm experiment described in Paper II we incubated maize leaves (*Zea mays* L.), pine needles (*Pinus sylvestris* L.), and mixtures of the two (*Figure 3*) and followed transfers and losses of C and N from the litters during decomposition. To follow transfers of C, we used the natural isotopic differences in ^{13}C between the litters (pine, a C_3 plant, is more depleted in ^{13}C than maize, a C_4 plant). To follow transfer of N we labelled half of the material with ^{15}N. We fertilised plants of both species to obtain litters with different initial N concentrations. Two litters and two N levels resulted in four types of single litter microcosms (M+, M−, P+, and P−) and four mixtures of maize and pine (M+P+, M+P−, M−P+, and M−P−). The properties of the litters were analysed after 119 and 190 days of decomposition at constant temperature. Statistical analyses were done using the bootstrap procedure.

Figure 3. Maize leaves (top), pine needles (middle), and a mixture of the two (bottom).

Initial and final C and N concentrations and N:C ratio in the litters in the microcosm experiment is shown in *Table 3*. Fertilised maize litter (M+) had lost 82% of initial C by the end of the experiment, unfertilised maize litter (M−) had lost 72%, fertilised pine litter (P+) had lost 67%, and unfertilised pine litter (P−) had lost 43%. Thus, the C losses for single maize litters were higher than for single pine litters and the C losses for fertilised litters were higher than for unfertilised litters.

Table 3. *Initial (day 0) and final (day 190) C and N concentrations and N:C ratio in the litters. Values for mixtures calculated from values for the constituent litters. Data are mean values, with standard deviation in brackets.*

Litter[1]	C (%)		N (%)		N:C	
	Initial	Final	Initial	Final	Initial	Final
M+	51.4 (1.5)	37.4 (0.4)	3.2 (0.6)	3.8 (0.1)	0.062 (0.010)	0.101 (0.003)
M−	52.3 (0.6)	41.6 (0.2)	1.4 (0.2)	3.1 (0.1)	0.027 (0.003)	0.075 (0.004)
P+	54.2 (2.7)	45.0 (0.7)	2.3 (0.4)	2.5 (0.1)	0.042 (0.006)	0.056 (0.003)
P−	55.2 (1.6)	46.2 (0.5)	1.5 (0.2)	1.7 (0.0)	0.027 (0.003)	0.037 (0.001)
M+P+	52.8 (1.5)	41.4 (1.1)	2.7 (0.3)	2.9 (0.2)	0.052 (0.012)	0.071 (0.007)
M+P−	53.2 (1.1)	42.4 (0.7)	2.3 (0.3)	3.2 (0.1)	0.044 (0.011)	0.077 (0.004)
M−P+	53.2 (1.4)	42.5 (1.0)	1.8 (0.2)	2.9 (0.2)	0.034 (0.007)	0.068 (0.006)
M−P−	53.7 (0.9)	44.3 (1.0)	1.4 (0.1)	2.2 (0.2)	0.027 (0.005)	0.050 (0.003)

1. M+ = fertilised maize, M− = unfertilised maize, P+ = fertilised pine, P− = unfertilised pine.

The measured proportions of initial C remaining in the litter mixtures compared with the expected values, calculated as the average of the proportions C remaining in the single litters, are shown in *Figure 4*. The C losses from the litter mixtures M+P− and M−P+ were significantly ($p<0.001$) higher than expected from C losses in the single litter microcosms, at both day 119 and 190. Mixture M+P− had lost 65% and 70% of initial C at day 119 and 190, respectively, compared with the expected values of 56% and 62 %, and mixture M−P+ had lost 68% and 72%, compared with the expected values of 63% and 69%. In contrast, the M+P+ and M−P− mixtures showed no statistically significant difference between measured and expected C losses.

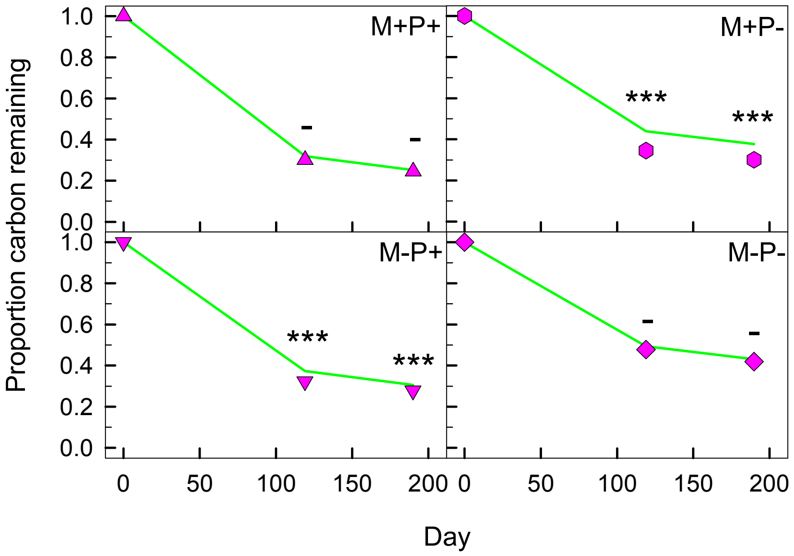

Figure 4. Proportions of initial C remaining in the litter mixtures. Pink symbols = measured values, green lines = expected values based on single litters. Asterisks indicate significant difference between measured and expected proportion remaining in the mixtures; * p<0.05, ** p<0.01, *** p<0.001, - not significant.

The amounts of transferred C, based on the C isotope analysis, are shown in *Figure 5*. There was a bidirectional transfer of C in all mixtures, with a statistically significant net transfer from the pine litters to the maize litters. By adding non-transferred C in a maize litter sample (non-striped part of yellow bars in *Figure 5*) and transferred C in a pine litter sample (striped part of blue bars in *Figure 5*) we got the remaining maize C in the mixture, and vice versa for pine C. The comparison of these values with the values for remaining C of the respective single litter (Figure 2 in Paper II) suggested that the pine litter in mixture M+P− lost more C than when it decomposed separately and that the maize litter in mixture M−P+ lost more C than when it decomposed separately, whereas the C loss of the other litter in these mixtures seemed unchanged.

The amounts of transferred N, based on the N isotope analysis, are shown in *Figure 6*. Nitrogen was also transferred bidirectionally in all mixtures. However, the directions of the net transfer were not the same and not statistically significant for all mixtures. In mixtures M+P+ and M+P− significantly more N was transferred from the maize litter to the pine litter. In mixture M−P+ the net transfer of N was in the opposite direction, with significantly more being transferred from the pine litter to the maize litter. In mixture M−P−, the net transfer of N was not significantly different from zero.

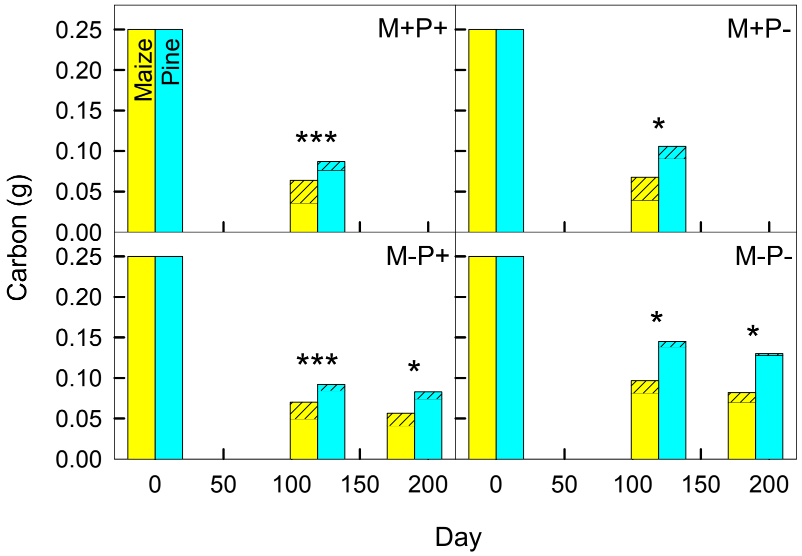

Figure 5. Carbon amounts in the separated litter samples in the mixtures. Yellow = maize samples, blue = pine samples. Striped parts = transferred amounts, i.e. the amount of C that originated from the other litter. Asterisks indicate significant difference between the amounts of C transferred; * p<0.05, ** p<0.01, *** p<0.001, - not significant. Litter samples could not be separated at day 190 for mixtures M+P+ and M+P–.

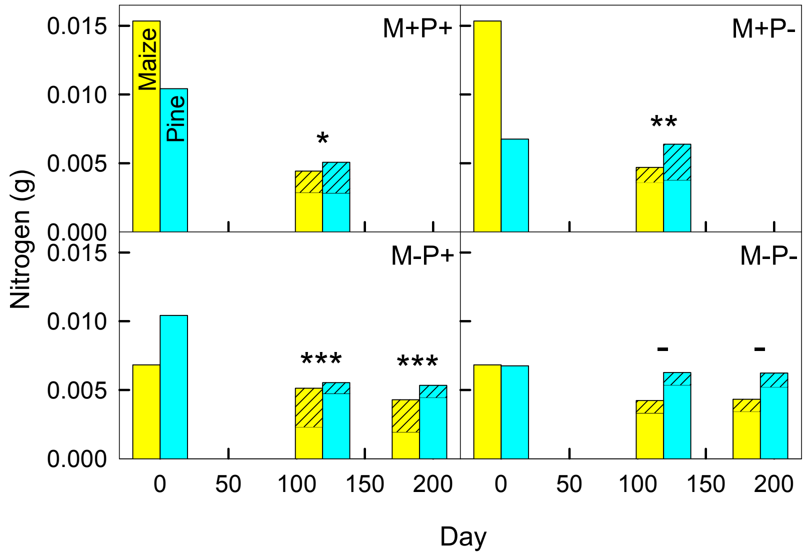

Figure 6. Nitrogen amounts in the separated litter samples in the mixtures. Yellow = maize samples, blue = pine samples. Striped parts = transferred amounts, i.e. the amount of N that originated from the other litter. Asterisks indicate significant difference between the amounts of N transferred; * p<0.05, ** p<0.01, *** p<0.001, - not significant. Litter samples could not be separated at day 190 for mixtures M+P+ and M+P–.

6 Mycorrhizal fungi

To explore how stores and flows of C and N between plant and soil are affected by a changing N availability, when mycorrhizal fungi can also decompose organic matter, we formulated a model (Paper III). The model describes the C and N flows to and from a plant, SOM, saprotrophs, mycorrhizal fungi, and an inorganic N pool. It extends the plant growth and litter decomposition model by Ågren and Bosatta (1998) by incorporating mycorrhiza. The model was formulated such that the mycorrhizal fungi, besides taking up inorganic N, also could decompose SOM to mobilise organic N.

Because the plant provides the mycorrhizal fungi with C, as much as 30% of net fixation has been suggested (Leake *et al.*, 2004), it is generally assumed that less C should be available for growth in mycorrhizal plants, i.e. the C allocation to the fungi is a cost to the plant (Smith & Read, 2008). However, the mycorrhizal fungi should increase the plant's uptake of N and other growth-limiting nutrients, which should compensate for the direct loss of C. The plant's allocation of C to mycorrhizal fungi is, therefore, a balance between direct C costs and potential C gains from increased nutrient access. A further complication is that in a review of the literature, Correa *et al.* (2012) found support for the hypothesis that the C allocation is not a cost to plants in ectomycorrhizal symbioses and that this may be a general characteristic of mycorrhizal symbioses. We therefore studied the system under the two contrasting assumptions: (i) C allocation to mycorrhizal fungi occurs at the expense of plant growth (cost scenario) and (ii) C allocation does not occur at the expense of plant growth (no-cost scenario). We then varied the C allocation level and the efficiency of the mycorrhizal fungi to decompose SOM at various levels of N availability to find the C allocation level that optimised plant biomass. The simulations were run in Mathcad 14.0 and R 2.15.0.

A diagram illustrating the mycorrhiza model is shown in *Figure 7*.

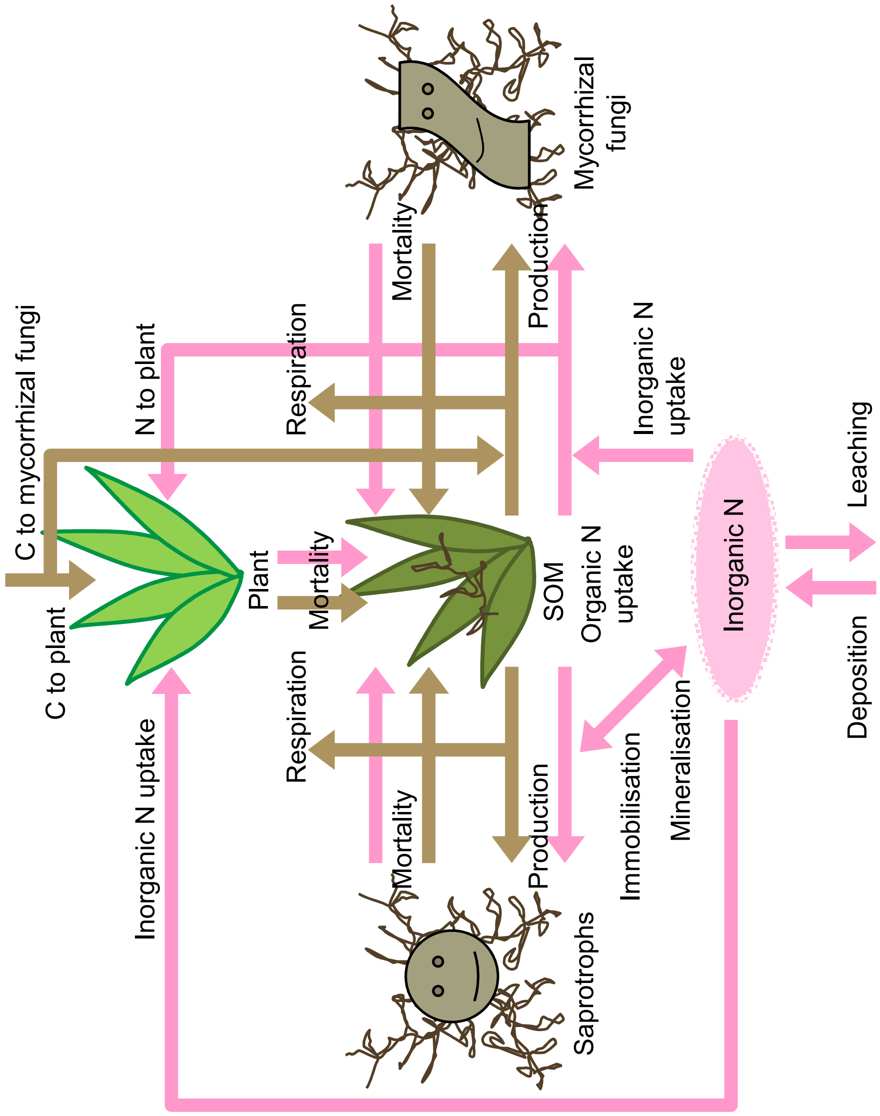

Figure 7. Diagram illustrating the mycorrhiza model. Brown arrows = C flows, pink arrows = N flows.

Production and mortality of the saprotrophs and production and mortality of the mycorrhizal fungi were assumed to be in equilibrium. The C and N dynamics in the plant and the soil could then be described by the following equations:

$$\begin{cases} \dfrac{dC_p}{dt} = \left(1-\delta_2\right) P_N N_p - \mu C_p \\ \dfrac{dC_j}{dt} = \mu C_p - \left(\dfrac{1}{e_s} - 1\right) u C_j - \delta_1 \left(f - e_m \left(1+f\right)\right) P_N N_p \\ \dfrac{dN_p}{dt} = g_p N_i C_p - r_l \mu C_p + \delta_1 \left(r_j f + g_m N_i - r_m e_m \left(1+f\right)\right) P_N N_p \\ \dfrac{dN_j}{dt} = r_l \mu C_p - \left(\dfrac{r_j}{e_s} - r_s\right) u C_j - \delta_1 \left(r_j f - r_m e_m \left(1+f\right)\right) P_N N_p \\ \dfrac{dN_i}{dt} = D + \left(\dfrac{r_j}{e_s} - r_s\right) u C_j - \left(g_p C_p + \delta_1 g_m P_N N_p + \lambda\right) N_i \end{cases} \qquad [2]$$

Meanings of symbols are summarised in *Table 4*.

The C allocation level was expressed as the proportion of net C uptake that the plant allocated to mycorrhizal fungi (δ). In the cost-scenario, when the C allocation to mycorrhizal fungi was considered a cost to the plant, allocating a proportion δ implied that the proportion $1-\delta$ remained for plant growth. In system [2] this was expressed by setting $\delta_2 = \delta_1 = \delta$. In the no-cost scenario, when the C allocation to mycorrhizal fungi was assumed to impose no C cost, $\delta_2 = 0$ and $\delta = \delta_1 / (1 + \delta_1)$ or equivalently $\delta_1 = \delta / (1 - \delta)$.

The N availability was varied by changing the external N addition, the N deposition (D).

The decomposer ability of the mycorrhizal fungi was expressed as a factor *f*, the mycorrhizal SOM assimilation efficiency, times the amount of C from the plant. The higher the *f*, the more efficient the mycorrhizal fungi were to assimilate SOM.

How the plant size varied with the C allocation level (δ) for six N deposition levels (*D*) for the two cost scenarios and for four mycorrhizal SOM assimilation efficiencies (*f*), is shown in *Figure 8*.

Table 4. *Meanings of symbols describing the mycorrhiza model.*

Symbol	Meaning	Value[1]	Units
C_j	Amount of carbon in soil organic matter	-	g C m^{-2}
C_p	Amount of carbon in plant	-	g C m^{-2}
D	Nitrogen deposition rate	0.001-0.011	g N m^{-2} d^{-1}
δ	Proportion of plant net carbon uptake allocated to mycorrhizal fungi	0-0.99	-
δ_1	Carbon allocation parameter	-	-
δ_2	Carbon allocation parameter	-	-
e_m	Growth efficiency of the mycorrhizal fungi	0.25	-
e_s	Growth efficiency of the saprotrophs	0.25	-
f	Mycorrhizal soil organic matter assimilation efficiency	0, 0.25, 0.5, 1	-
g_m	Mycorrhizal inorganic nitrogen uptake parameter	1	m^2 (g C)$^{-1}$
g_p	Plant root inorganic nitrogen uptake parameter	0.01	m^2 (g C)$^{-1}$ d^{-1}
λ	Nitrogen leaching rate	0.01	d^{-1}
μ	Plant mortality rate	0.1	d^{-1}
N_i	Amount of inorganic nitrogen	-	g N m^{-2}
N_j	Amount of nitrogen in soil organic matter	-	g N m^{-2}
N_p	Amount of nitrogen in plant	-	g N m^{-2}
P_N	Plant nitrogen productivity	4	g C (g N)$^{-1}$ d^{-1}
r_j	N:C ratio of the soil organic matter	-	g N (g C)$^{-1}$
r_l	N:C ratio of the plant litter	0.01	g N (g C)$^{-1}$
r_m	N:C ratio of the mycorrhizal fungi	0.1	g N (g C)$^{-1}$
r_s	N:C ratio of the saprotrophs	0.1	g N (g C)$^{-1}$
u	Growth rate of the saprotrophs	0.1	d^{-1}

[1] Parameter values used for results shown in *Figure 8*.

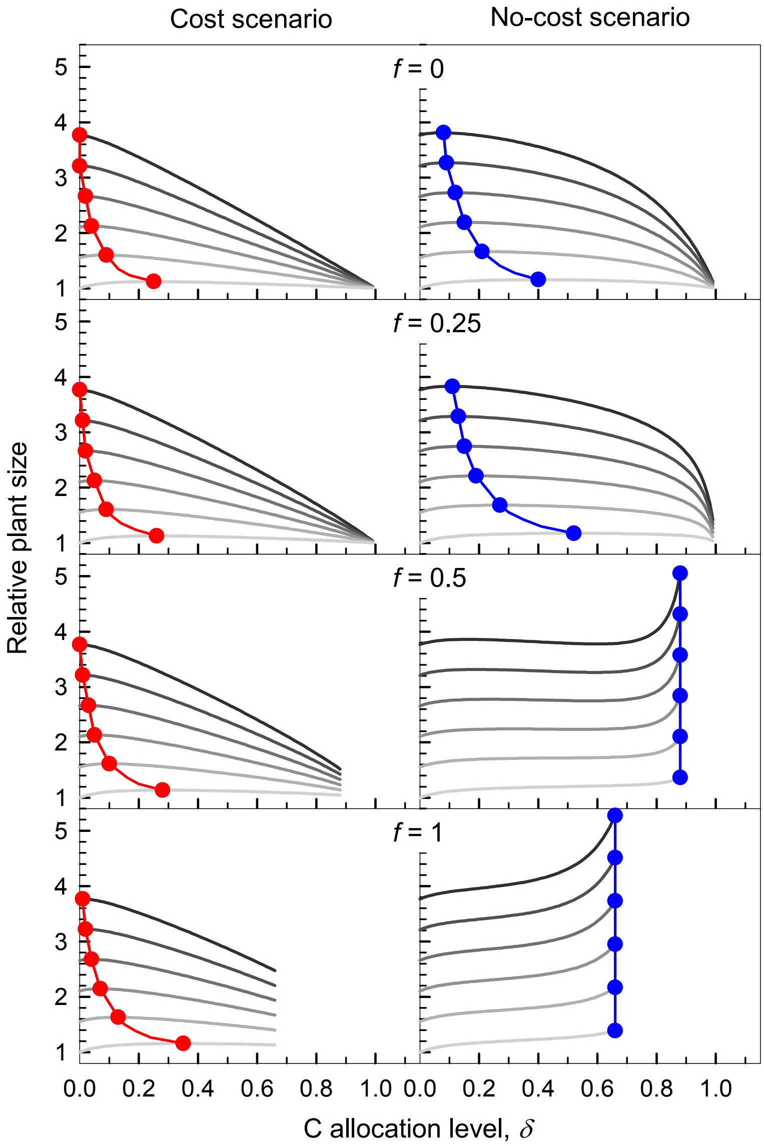

Figure 8. Relative plant size (C_p after 1000 days relative to initial C_p) at different C allocation levels (δ) for six levels of N deposition (D = 0.001, 0.003, 0.005, 0.007, 0.009, and 0.011 g N m^{-2} d^{-1}; increasing D level with increasing gray intensity) for the cost scenario (left side) and the no-cost scenario (right side) for four mycorrhizal SOM assimilation efficiencies (f). Other parameter values are given in *Table 4*. Coloured circles with connecting lines mark the optimum C allocation levels.

To optimise its biomass the plant should, in the cost scenario, allocate less C to the mycorrhizal fungi as the N deposition increases. In the no-cost scenario, the plant should only decrease the C allocation level (δ) with increasing N deposition (D) for low mycorrhizal SOM assimilation efficiencies (f). For high f values, the plant should always allocate C at a certain level to the mycorrhizal fungi, irrespective of the N deposition level. This corresponded to the highest possible C allocation level, i.e. the δ where the mycorrhizal fungi assimilated all material in the SOM pool. Because the decomposer ability depended on the combination of f and δ, and δ always was less than one, it was only when f was sufficiently high that the mycorrhizal fungi were able to assimilate all material in the SOM pool. In this case the saprotrophs would be outcompeted.

When the cases with a constant optimum C allocation level in *Figure 8* are disregarded, the optimum δ increased with increasing f. This pattern was more evident in the no-cost scenario. The more efficient the mycorrhizal fungi were to assimilate SOM (the higher the f), the more C should the plant allocate to the mycorrhizal fungi to optimise its biomass.

7 Nitrogen:carbon ratios

In Paper IV, we examined how to estimate the parameters describing the relation between C and N during decomposition. The relation is simple and depends on only three system properties (Ågren & Bosatta, 1998): (i) initial N:C ratio of the litter (r_0), (ii) N:C ratio of the decomposers (r_d), and (iii) growth efficiency of the decomposers (e_0). An important aspect of this relation is that it is independent of the rate of decomposition; i.e. it does not contain parameters considered to depend on e.g. litter quality and climate.

It is, however, problematic to estimate the parameters r_d and e_0 (r_0 is known) because they are strongly correlated. Manzoni *et al.* (2008) circumvented this problem by assigning a fixed value to r_d and attributed responses to initial litter N:C in decomposition patterns to changes in decomposer growth efficiency. However, decomposer N:C ratios vary at least by a factor of four (Li *et al.*, 2012; Cleveland & Liptzin, 2007), which indicates that the assumption of the same r_d for all systems is an oversimplification.

In Paper IV, we showed that the parameter to estimate is instead the critical N:C ratio (r_c). We derived an expression for r_c and then used data from three different litter-bag decomposition studies (*Table 5*) to validate the usage of this expression. We also showed, based on derivations in Ågren and Andersson (2012) and Ågren and Bosatta (1998), how the critical N:C ratio could be used to predict the steady state N:C ratio in SOM.

Table 5. *Summary of litter data used in the estimation of the critical N:C ratio.*

Source	Species	Litter types[1]	Initial N:C (mg N/g C)
BI (Aber *et al.*, 1984)	*Acer rubrum*	W, B	1.8, 9.0
	Acer saccharum	F, R	16.6, 33.4
	Populus grandidentata	F	16.6
	Quercus alba	F	16.8
	Quercus rubra	F	16.4
	Pinus strobes	F, R, W	8.8, 18.6, 0.8
	Tsuga canadensis	F, B	16.6, 6.0
SWECON[2] (Berg *et al.*, 1991a; b)	*Betula pubescens*	F (g)	34.8
	Picea abies	F (b, g)	8.4 – 36.6, 17.0
	Pinus contorta	F (b, g)	6.8 – 8.4, 21.0
	Pinus sylvestris	F (b, g)	5.8 – 22.8, 30.2
LIDET (Harmon, 2010)	*Acer saccharum*	F	17.0
	Schizachyrium gerardi	F, R	13.4, 16.8
	Drypetes glauca	F, R	42.7, 16.3
	Pinus elliottii	F, R	7.3, 17.5
	Pinus resinosa	F, R	17.5, 26.7
	Quercus prinus	F	21.5
	Thuja plicata	F	13.4
	Triticum aestivum	F	7.8

1. F = foliage, R = roots, W = wood, B = bark. b = brown/senesced material, g = green material; b if not indicated.
2. The same type of litter has been collected in many similar stands, in some cases also in fertiliser trials.

The development of the litter N:C ratio (*r*) during decomposition as a function of the remaining fraction C (*g*) can be shown to be (Ågren & Bosatta, 1998):

$$r = r_d - \left(r_d - r_0\right) g^{e_0/(1-e_0)} \tag{3}$$

Meanings of symbols are summarised in *Table 6*. Expression [3] is valid both when litter quality is assumed constant and when litter quality is allowed to change during decomposition. Because it can be shown that $r_c = e_0 r_d$ (Ågren & Bosatta, 1998), we could rewrite expression [3] to get an expression for the critical N:C ratio:

$$r_c = e_0 r_d = e_0 \frac{r - r_0 g^{e_0/(1-e_0)}}{1 - g^{e_0/(1-e_0)}} \tag{4}$$

Table 6. *Meanings of symbols describing N:C ratios in decomposing litter and SOM.*

Symbol	Meaning	Dimension
β	Parameter in decomposer growth rate	-
C_{ss}	Amount of carbon in soil organic matter at steady state	mass C
e_0	Decomposer growth efficiency	-
g	Fraction remaining carbon	-
η_{11}	Parameter describing rate of quality decline	-
N_{ss}	Amount of nitrogen in soil organic matter at steady state	mass N
r	N:C ratio of the litter	mass N (mass C)$^{-1}$
r_0	Initial N:C ratio of the litter	mass N (mass C)$^{-1}$
r_c	Critical N:C ratio	mass N (mass C)$^{-1}$
r_d	N:C ratio of the decomposers	mass N (mass C)$^{-1}$

To be able to use expression [4], r_c should be constant during decomposition, i.e. the slope of the regression of r_c versus g should be zero. For all data (total = 425), the average slope was −0.4, with a standard deviation of 29.3. Expression [4] could therefore be considered valid to use.

When we plotted the critical N:C ratio (r_c) against the initial litter N:C ratio (r_0), as shown in *Figure 9*, we saw a trend towards increasing r_c with increasing r_0 when all data were used.

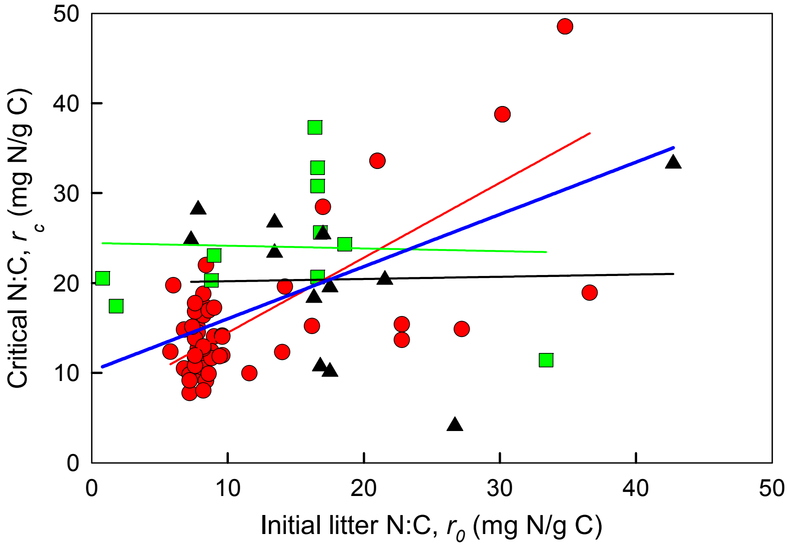

Figure 9. Relations between critical (r_c) and initial (r_0) N:C ratios. Thin lines = regressions for each data base, thick line = regression over all data bases, R^2 = 0.28. Green squares = BI, red circles = SWECON, black triangles = LIDET.

The critical N:C ratio could also be used to predict the steady state N:C ratio in SOM (N_{ss}/C_{ss}). If the litter input rate and r_0 were assumed to be constant and quality changes were disregarded, we got the following expression:

$$\frac{N_{ss}}{C_{ss}} = r_c + (1 - e_0) r_0 \tag{5}$$

Because r_0 generally is smaller than r_c, this expression tends towards r_c. If quality changes were included, we instead got the following expression:

$$\frac{N_{ss}}{C_{ss}} = \frac{r_c}{1 - \beta \eta_{11} e_0} + \left(1 - \frac{e_0}{1 - \beta \eta_{11} e_0}\right) r_0 \tag{6}$$

where β is a parameter determining how rapidly decomposer growth changes with litter quality and η_{11} is a parameter describing the rate of quality decline during decomposition. With standard parameter values ($\beta = 7$, $\eta_{11} = 0.36$, $e_0 = 0.25$), the SOM N:C ratio then tends towards $2.70 r_c$. From the data, where SOM and litter data could be matched, we got the relation between SOM and critical (r_c) N:C ratios as shown in *Figure 10*. A higher r_c correlated with a higher SOM N:C ratio, although the data gave a shallower slope of 1.51 compared with the theoretical value of 2.70.

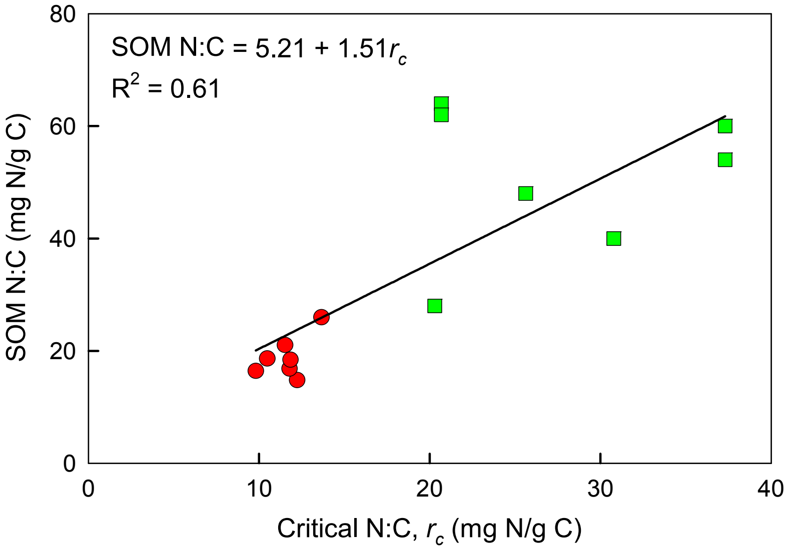

Figure 10. Relation between SOM and critical (r_c) N:C ratios. Green squares = BI, red circles = SWECON.

8 Discussion

The work presented here illustrates that the interactions between C and N are multifaceted and complex, and that their features are still not entirely clear. However, the work presented here also shows that the interactions between C and N are important for the understanding of the litter decomposition process and its controlling mechanisms.

By including an effect of N, here by making the growth efficiency of the decomposers depend on the amount of inorganic nitrogen in the surrounding environment, changes in decomposition rates when two litters decompose together in mixtures could be explained. Not only did this formulation lead to a prediction (prediction 4) of a faster decomposition rate of a mixture compared with the average decomposition rate of the two single litters (a positive non-additive effect of litter mixing), but also of a slower decomposition rate of a mixture (a negative non-additive effect). Positive non-additive effects have previously been suggested to result from an exchange of nutrients between the litters in the mixture (Chapman *et al.*, 1988; Seastedt, 1984). Negative non-additive effects, on the other hand, have been suggested to result from the presence of inhibitory compounds (Chapman *et al.*, 1988). The litter mixture model showed that a transfer of N could explain both faster and slower decomposition rates of litter mixtures compared with the average decomposition rate of the two single litters. Effects from an exchange of N between litters should therefore be accounted for before other factors, such as inhibitory compounds, are introduced as explanatory variables.

According to prediction 4, the decomposition rate of the mixture should be higher than the average of the two single litters when the litter of the higher quality also has the largest N mineralisation and the decomposition rate of the mixture should be lower than the average of the two single litters when the high quality litter instead has the smallest N mineralisation. This prediction together with the positive correlation often seen between high N concentrations and high decomposition rates of litters (e.g. Hobbie, 2005; Enriquez *et al.*, 1993; Melillo *et al.*, 1982) may therefore explain why higher than expected decomposition rates calculated on the basis of the litters decomposing separately are more frequently seen than lower than expected decomposition rates (Gartner & Cardon, 2004). As high quality litters often have higher N concentrations compared with low quality litters, the high quality litter in litter mixtures should also more often have the largest N mineralisation, which according to the model prediction should result in a higher than expected decomposition rate of the mixture. However, when predicting the effect of litter mixing, simply comparing litter N concentrations may be misleading as also litter quality affects N mineralisation.

That a non-additive effect of litter mixing cannot simply be explained by a difference in litter N concentrations is in agreement with the results of the litter mixture experiment. The experimental results suggest that it is the interaction between the litters that determines the effect of mixing, the interaction being a significant net transfer of N. The mixtures of fertilised maize litter and unfertilised pine litter (M+P−) and of unfertilised maize litter and fertilised pine litter (M−P+) both showed higher than expected C losses calculated on the basis of the single litters (*Figure 4*). These mixtures also had a significant transfer of N between the two litters (*Figure 6*). Transfer of N between components in litter mixtures has been shown in other 15N-labelling studies (Lummer *et al.*, 2012; Schimel & Hättenschwiler, 2007). Lummer *et al.* (2012) also investigated losses of mass, but found in their experiment no effect of mixing.

The experimental results also illustrates that the interaction between C and N in litter mixtures is more complex than what is formulated in the litter mixture model. For example, the N concentration and C loss of the fertilised maize litter were much higher compared with the unfertilised pine litter. The expectation for the mixture of fertilised maize litter and unfertilised pine litter (M+P−) on the basis of the model was therefore a positive non-additive effect, which was also observed. The C losses of the fertilised pine litter and the unfertilised maize litter were similar. The expectation for the mixture of those two litters (M−P+) on the basis of the model was therefore a small non-additive effect if any. The observed effect was, however, similar in size to that of mixture M+P−. Another discrepancy between model prediction and experimental results concerns prediction 6. The expectation for mixtures M+P− and M−P+ was that the decomposition rate of the litter in the mixture with highest C loss should have increased and the decomposition rate of the litter in the mixture with lowest C loss should have decreased. The observations rather suggest that the decomposition rate of the low-N litter in the mixtures had increased and that the decomposition rate of the high-N litter was unchanged.

More work is needed to elucidate whether this is a general pattern and what the underlying mechanisms are.

What is more interesting about the experimental results was the substantial transfer of C between the litters in the mixtures (*Figure 5*). This raises questions about the identity of the litters when occurring in mixtures. For example, in mixture M+P+, more than 50% of the C and N in what we physically identified as maize litter was originally in the pine litter and thus this litter could be viewed as being more pine than maize. Unless significant net transfers of C are taken into account, this may give rise to incorrect interpretations of the data. If more C is transferred in one direction than the opposite, the amount of remaining C originally in one litter and the amount of remaining C found in that separated litter sample is not the same. For example, in mixture M+P+, the amount of remaining maize C at day 119 (non-striped part of yellow bar plus striped part of blue bar in *Figure 5*) was not same as the amount of remaining C in the separated maize litter sample (whole yellow bar in *Figure 5*). Previous litter-mixture studies, where the component litters in the mixtures has been separated, have only considered losses in the litter samples. To increase our understanding of the interactions in litter mixtures, future studies also need to take C transfers into account. What further complicates the interpretation is that transferred C and N compounds are also microbially transformed. Therefore the chemical transformations that occur in the litter may be different for different decomposer communities (Wickings *et al.*, 2012).

In the litter mixture studies presented here (Papers I and II) no external N addition and no plants and therefore no mycorrhizal fungi were present. These were, however, included in the mycorrhiza study (Paper III). The results showed that, except for high mycorrhizal SOM assimilation efficiencies (*f*) under the assumption that the C allocation is no cost to the plant (no-cost scenario), the optimum level of C allocation to mycorrhizal fungi decreased with increasing level of N deposition. This is in agreement with field studies reporting a reduction in below-ground C allocation (Högberg *et al.*, 2010), ectomycorrhizal mycelial production (Nilsson & Wallander, 2003), and percentage of roots colonised (Treseder, 2004) as a result of N addition. A decreasing optimum C allocation level with increasing N availability means that, if the plant is assumed to optimise its growth, decomposition of SOM should decrease with increasing N deposition. If, however, the C allocation is no cost and the mycorrhizal fungi have high SOM assimilation efficiencies, decomposition of SOM should remain at the same level when N deposition increases. These results indicate that in order to understand how decomposition is influenced by a changed N deposition, we need an increased understanding of the plant–fungus relation in mycorrhizal associations and the decomposer ability of the mycorrhizal fungi.

An unexpected result was that at lower *f* values the optimum C allocation level was lower than the highest possible level even when C was no cost. For higher C allocation levels than the optimum C allocation level the plant size decreased (*Figure 8*). This was because the incorporation rate of N into the biomass of the mycorrhizal fungi increased faster than the rate by which they acquired N when the C allocation level increased; the mycorrhizal fungi retained proportionally more N with increasing C allocation level. Reduced growth of mycorrhizal plants as a result of high N retention by the mycorrhizal fungi has also been suggested in other studies (Correa *et al.*, 2012; Colpaert *et al.*, 1996).

There are few models describing C and N flows between plant and mycorrhizal fungi that, besides mycorrhizal inorganic N mobilisation, also include mycorrhizal organic N mobilisation. Two other models exist, the MySCaN model by Orwin *et al.* (2011) and the MYCOFON model by Meyer *et al.* (2010). They prescribe, however, how the C allocation decreases with N availability. In the mycorrhiza model presented here, the C allocation level is a parameter, independent of the N availability and the actual allocation is determined by optimising plant growth. We could therefore explore the effect of a changing N availability without a fixed dependence already built into the model.

In addition, neither the MySCaN model nor the MYCOFON model includes mycorrhizal effects on C in SOM; only the uptake of N when SOM is mined for organic N is considered. In the MYCOFON model, for example, organic N is just considered to be a source of N, similar to NH_4 and NO_3. These authors consider the contribution of C in organic N compounds to be a minor source and probably insignificant for the mycorrhizal fungi when the fungi exist in symbiosis. Nevertheless, mining of organic matter for organic N could lead to considerable losses of C. A part of the observed root-induced increase in SOM decomposition (Dijkstra & Cheng, 2007), the so-called rhizosphere priming effect, may be attributed to the decomposition activity of the mycorrhizal fungi. Even if the mycorrhizal fungi do not take up and mineralise soil C, their decomposition activity may still lead to solubilisation and losses of soil C as dissolved organic C. As Talbot *et al.* (2008) emphasise, including the possible soil C loss from mycorrhizal decomposition may be important when predicting soil C dynamics in ecosystems under global change. Because, if also mycorrhizal fungi decompose soil C, the soil C balance depends on ecological factors that affect, not only the saprotrophs, but also the mycorrhizal fungi and their plant partners.

The mycorrhiza model presented in this thesis can be developed further in several ways. One interesting aspect is to explore how other formulations of the mycorrhizal decomposer ability would affect the C and N dynamics in the plant and the soil. The mycorrhizal decomposer ability could, for example, be expressed such that it also depends on the quality and the availability of SOM. Also, as saprotrophs and mycorrhizal fungi may be spatially separated (Lindahl *et al.*, 2007), considering different access to different parts of the SOM pool by the two communities may be desirable.

In both the litter mixture model and the mycorrhiza model presented here, quality changes were disregarded. This may be a valid assumption when short-term processes are studied. When, however, decomposition is studied in a long-term perspective, the effect of quality changes may be large (Hyvönen *et al.*, 1998). Here, this could be seen by the two different expressions for the prediction of the steady state soil N:C ratio ([5] and [6]). By including quality changes the predicted soil N:C ratio was almost three times as large as when quality changes were not considered. From the data the difference seemed to be smaller than this value (*Figure 10*). The number of data points was however small; more data are needed to provide a firm conclusion. An additional difficulty is that relations such as expressions [5] and [6] are assuming SOM N:C to be in steady state with respect to input, a condition that is unlikely to be satisfied in almost any single sample. The match between theoretical variables and measured entities must also be considered when interpreting results.

As the decomposer growth efficiency depends on environmental factors (Manzoni *et al.*, 2012), this raises questions about when the parameters can actually be considered as parameters or should be changed to variables. However, by estimating the critical N:C ratio, which is the product of the decomposer growth efficiency and the decomposer N:C ratio ($r_c = e_0 r_d$), this leaves open the possibility that the decomposer growth efficiency can change in one direction, and the decomposer N:C ratio in the opposite and still give the same r_c. Furthermore, before making the parameters into variables, we must remember that what we need is not the most complex models, but rather, the most useful ones.

To reiterate: the work presented here illustrates that the interactions between C and N are multifaceted and complex, and that their features are still not entirely clear. With this thesis, I wish to have polished some of the facets of the gemstone, the gemstone being the interactions between C and N during litter decomposition.

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