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The effect of nitrogen on the decomposition system

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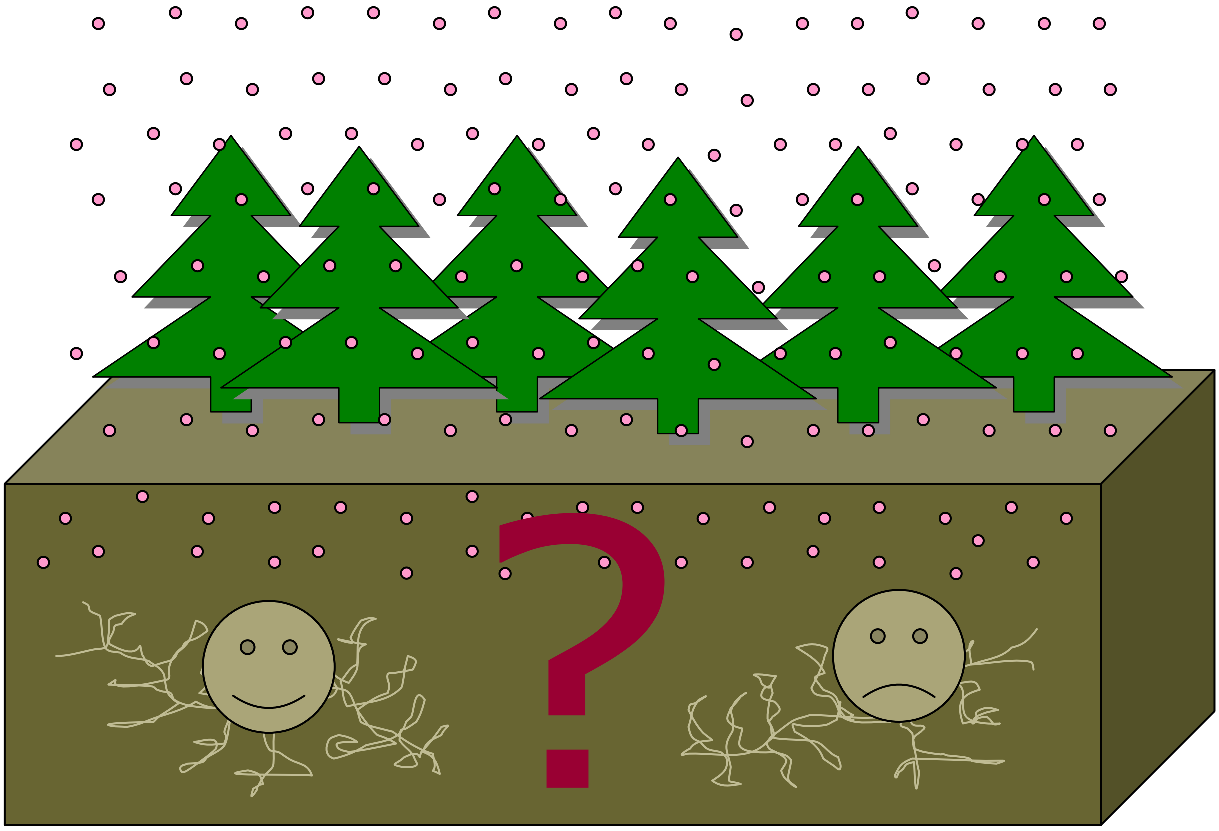

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Abstract

The decomposition system is an important part of terrestrial ecosystems and as such regulated by several factors that are more or less well understood. One of the factors least understood is how decomposition is affected by increased nitrogen deposition. In view of the increased nitrogen deposition of large areas during the last 50 years and an interest in large-scale nitrogen fertilization of forests it has become important to better understand this factor.

In this paper a short description of the decomposition system is given. I also did a literature review of published studies that have examined effects of added nitrogen on decomposition, especially effects on mass loss, microbial respiration, microbial biomass and extracellular enzyme activity. The reported results are conflicting. Overall, the most frequent observation was a zero-effect of nitrogen addition and a smaller, but almost equal, number of reports demonstrated increasing and decreasing rates of decomposition.

I have tried to identify factors that could have interacted with the added nitrogen and caused the variability in effects. Possible interacting factors were: climate, nitrogen source, level of ambient nitrogen deposition, length of measurement period, frequency of nitrogen application, availability of other nutrients, litter quality and change in decomposer properties. The most likely candidate explaining the diverging results seems to be the length of the observation period and if the substrate was litter or soil organic matter. Decomposition over short periods of litter was generally stimulated by nitrogen addition whereas the respiration from soil organic matter rather decreased.

1 Introduction

Although the processes of decomposition may not be readily seen by the human eye they play a significant role in the functioning of ecosystems. Without decomposition there would not be any recycling of nutrients within the ecosystem. Some nutrients would still come from the weathering of parent rocks and deposition but these sources would not be sufficient to sustain the primary production at the prevailing level. The conversion of an element from organic to inorganic form, *mineralisation*, is therefore one of the major functions that is being performed by the decomposition system (Swift et al. 1979).

Even though decomposition is an important part of ecosystem functioning, the factors controlling it are more or less well understood. One of the factors least understood is how decomposition is affected by increased nitrogen deposition. In the last 50 years the global production of reactive nitrogen (i.e. other nitrogen compounds than N_2 e.g. urea, ammonium, nitrogen oxides and nitrate) has increased, which has led to an increased deposition. The main activities responsible for the increase are combustion of fossil fuels and production and use of fertilizers (Matson et al. 2002, Galloway et al. 2003).

In view of the increased nitrogen deposition and also an interest in large-scale nitrogen fertilization of forests it has become important to better understand this factor.

1.1 Aim of the paper

The aim of this paper is to give an introduction and background to the theoretical work and the field of research within which I am going to do my thesis. The focus is being directed at the decomposition system and especially to the effect of added nitrogen on decomposition.

First I give a short description of the decomposition system and then I summarise the results of experiments that particularly have been looking at the effect of nitrogen. The purpose is not to cover all the literature and do a statistical analysis but to give an overview of the results from the experimental work that has been done. Last I go through different factors that might influence how the decomposition system responds to increased nitrogen inputs.

2 The decomposition system

2.1 Components and actors

Any component that enters the decomposition system changes its state; it is the very meaning of the word *decomposition*. This state change is under the influence of many different biotic and abiotic factors, and the result is invariably a decrease in mass of the component. The entering components are called *detritus*, that is: dead plant, animal or microbial material (Swift et al. 1979, Chapin et al. 2002).

The breakdown of the detritus is occurring inside or outside of the *decomposers,* the biological actors in the decomposition system. Bacteria together with fungi are the main part of the decomposer community, the other part being the soil animals (Swift et al. 1979, Chapin et al. 2002).

2.2 Processes

The state change of the detritus can be either physical or chemical in nature, and it can be described as the effect of one of three different processes, namely: leaching, fragmentation or chemical alteration. The term *leaching* refers to the removal of soluble matter by the action of water; the soluble material is washed into a lower layer of the soil where it can be decomposed further (Swift et al. 1979, Chapin et al. 2002).

Leaching is a physical process and so is also the process *fragmentation*. Fragmentation is the reduction in size of the organic matter and it creates new and additional surfaces for the microorganisms to colonise. The fragmentation process is mostly performed by the soil animals although abiotic factors such as freeze-thaw and wetting-drying cycles also fragment the organic matter (Swift et al. 1979, Chapin et al. 2002).

The third and final process, *chemical alteration*, includes the chemical transformation of organic compounds, usually to less complex ones. This reaction is often mediated by the enzymes of bacteria and fungi, but some spontaneous reactions do also occur (Swift et al. 1979, Chapin et al. 2002).

3 Material and methods

I began the literature study by reading the review article “The effect of added nitrogen on the rate of decomposition of organic matter” by Fog (1988). Then I used the database *Web of Science®* and did a “Cited Reference Search” on that article, that is, I searched the database for articles that had cited the article in question. From the list of results, 80 papers (about one fourth of the list) where chosen to be included in my literature study.

All the 80 papers concern the subject decomposition and 51 of those report some sort of experimental investigation of how nitrogen affects the decomposition rate. In almost all of the experiments the effect of nitrogen has been tested by adding nitrogen, that is, by nitrogen fertilization. Comparisons have been made between fertilized and non-fertilized plots and in some experiments more than one level of fertilizer applications have been used.

The results from the experiments: a positive effect, a negative effect or a zero effect of nitrogen, were then counted and summarised. A positive effect of nitrogen is here the same as an increased decomposition rate, a negative effect of nitrogen means the rate was decreased and if no change in the decomposition rate was observed it is here called a zero effect.

The remaining 29 papers have either examined other factors than nitrogen, have investigated the effect of nitrogen on other aspects than the decomposition rate, or have been reviews or more of a theoretical analysis.

4 The effect of nitrogen

There exist several ways to measure decomposition. In the following sections the mostly used approaches in the articles examined and the results obtained are presented.

In one and the same article results from more than one of the ways of measuring decomposition and results from more than one experiment (e.g. results from different field sites) can be reported. Therefore, the total number of observations is larger than the total number of papers.

4.1 Different methods

4.1.1 Mass loss

When studying the effect of nitrogen on the decomposition system some papers have measured the mass loss, also named the weight loss. Several of them have employed the litterbag technique, first taken in use by Bocock and Gilbert (1957). During and at the end of the experiments the weight of the litter in the litterbags has been measured.

The results, regarding the effect of nitrogen on mass loss, from the different experiments are conflicting (Figure 1). Many articles report no effect of nitrogen (e.g. van Vuuren and van der Eerden 1992, Boxman et al. 1998, Hobbie 2005), but some report a positive effect (e.g. Hobbie 2000, Vestgarden 2001), and even a few report a negative effect (e.g. Osono et al. 2006).

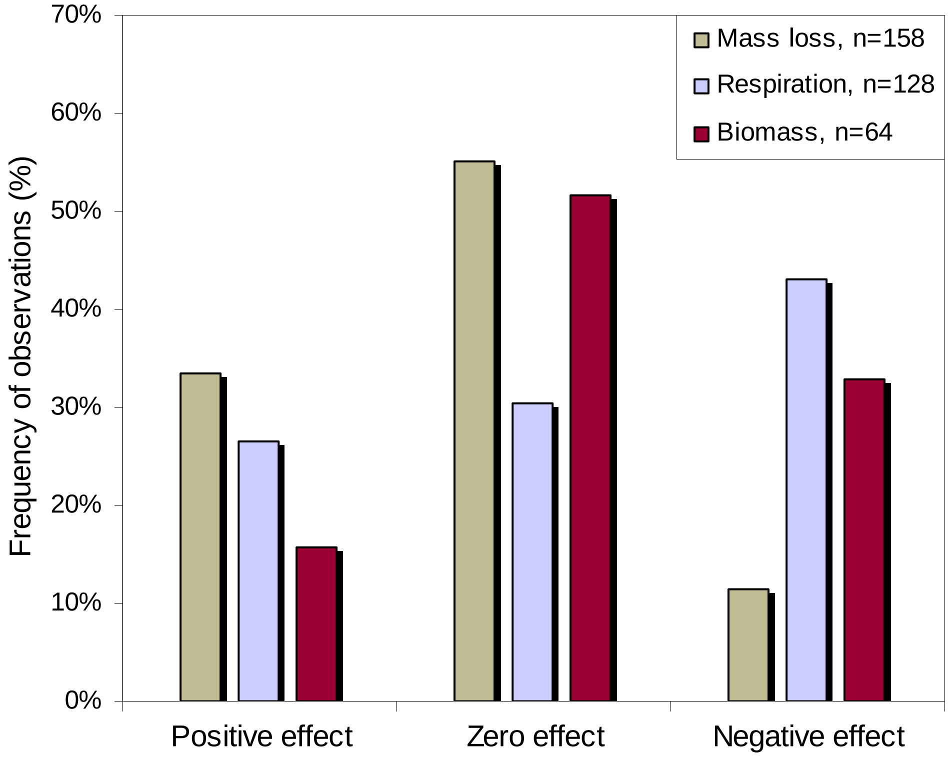

Figure 1: *The frequency (%) of reported results regarding the different effect of nitrogen addition on the rate of decomposition, estimated by different methods (n=total number of observations).*

4.1.2 Respiration

Instead of measuring mass loss, respiration, that is, the production of CO_2, has been used as a measure of mass loss. The amount of CO_2 respired by the decomposers is proportional to the amount of decomposed material. Therefore one can expect that the larger the amount of respired CO_2, the faster the decomposition.

The studied articles report different results of how nitrogen affects the decomposition (Figure 1). It is almost the same number of articles that show a negative effect (e.g. Bowden et al. 2004, Olsson et al. 2005), a positive effect (e.g. Madritch and Hunter 2003, Cleveland and Townsend 2006) and a zero effect of nitrogen (e.g. Micks et al. 2004, Zak et al. 2006).

4.1.3 Biomass

An alternative approach for determining how decomposition is affected by nitrogen is to measure the effect on the decomposers, that is, the microbial biomass. There exist many methods for measuring soil biomass, for example: the fumigation-incubation method (Jenkinson and Powlson 1976), the fumigation-extraction method (Vance et al. 1987), the use of staining (Ingham and Klein 1984, Stamatiadis et al. 1990), phospholipid fatty acid analysis (White et al. 1979) and the substrate-induced-respiration method (Anderson and Domsch 1978).

Not only did the methods vary, but as in previous sections the results also varied (Figure 1). The biomass increased (e.g. Raiesi 2004, Mabuhay et al. 2006), decreased (e.g. Smolander et al. 1994, DeForest et al. 2004b) or was unaffected (e.g. Michel and Matzner 2003, Swanston et al. 2004) by nitrogen additions.

4.1.4 Extracellular enzyme activity

Another way of measure the effect of nitrogen on decomposition is to measure the extracellular enzyme activity (EEA). In decomposition studies the method of measuring the EEA has been in use since the 1990s and it offers a simple way of obtaining functional information on microbial communities (Sinsabaugh et al. 1991).

Of the 51 papers the total number of papers reporting EEA is 15. Comparing the results from the EEA studies is not an easy task. The papers report the activity of many different enzymes and have not always measured the same enzymes. In so far as the same extracellular enzyme activities have been measured, the results differed both between the papers and within the same paper.

4.2 Different kinds of substrate

The results in Figure 1 do not give a clear picture; can we make it clearer? An interesting question is: when measuring decomposition, does it matter if the substrate is litter or if it is soil, or if the litter have been in contact with the soil? What happens if we, instead of the different methods, separate the reported results from Figure 1 into measurements made on litter, measurements made on litter where the litter either have been or still is in contact with soil and measurements made on soil? Can any difference in the reported results be seen depending on the kind of substrate?

According to Figure 2 a difference can be seen. It seems that for litter and litter-soil the decomposition rate is increased after nitrogen additions, whereas it is decreased when the substrate is soil only. It is possible that the effect of added nitrogen somehow depends on the kind of the substrate.

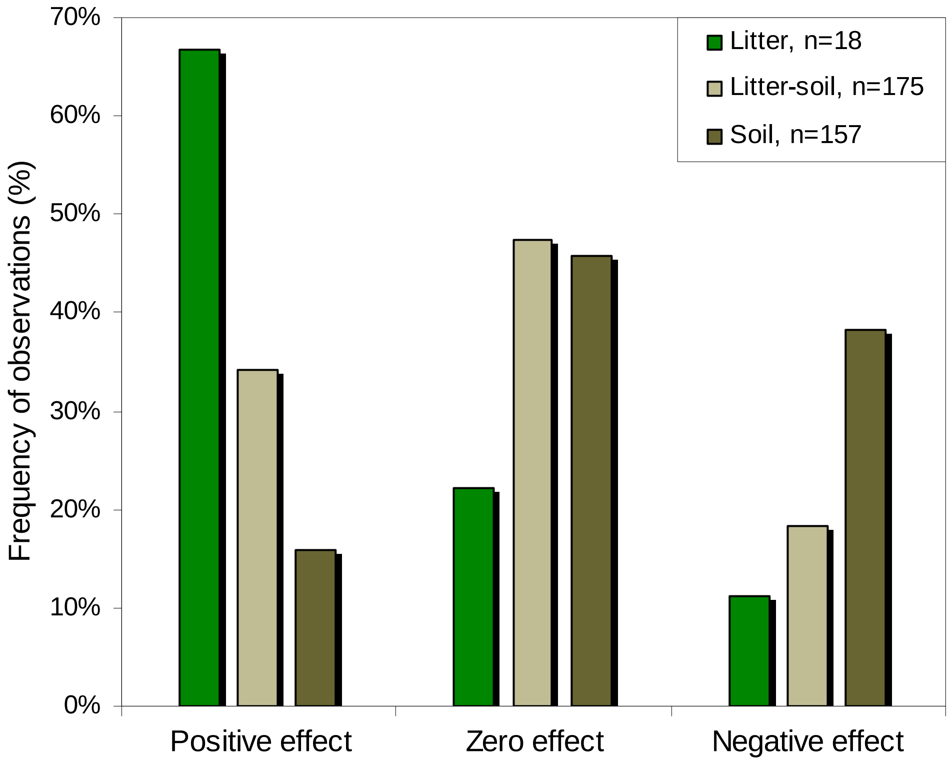

Figure 2: *The frequency (%) of reported results regarding the different effect of nitrogen addition on the rate of decomposition, separated by different kinds of substrate (n=total number of observations).*

5 Interacting factors

The literature study shows that the effect of nitrogen on the decomposition system varies. Overall, the most frequent observation was a zero-effect of nitrogen addition and a smaller, but almost equal, number of reports demonstrated increasing and decreasing rates of decomposition. The obvious question is then: why is it so? Being able to answer that question is not so obvious. But as been noted in the previous section, one part of an answer is that it has to be one or more additional variables or factors that influence how the effect of nitrogen will be. A new question then arises: which other interacting factors than the kind of substrate can there be?

5.1 Abiotic factors

One possible factor is climate; the experiments have been located in different climate zones. Most of the studied experiments have been performed in the temperate zone, but the boreal and the tropical zone are also included. The climatic variables temperature and precipitation are said to be important regulators of the decomposition processes (Swift et al. 1979), it has been shown that they in general exerts a strong influence on litter decomposition rates (Coûteaux et al. 1995).

However, in a review done by Knorr et al. (2005) the mean annual precipitation and temperature did not interact with nitrogen additions to significantly influence the response of the decomposition system. These authors therefore suggest that climate may not be an important factor when it comes to the controlling effect of nitrogen on decomposition.

Another possible factor is the nitrogen source, that is, the type of fertilizer used in the experiments. Nitrogen can be added to the soil in different forms and the possibility exists that the type of the nitrogen source could affect the response on decomposition. Still, in the same review as cited above (Knorr et al. 2005), the evidence for fertilizer type influencing the decay response to nitrogen additions was not strong.

Knorr et al. (2005) points out that little consideration has been given to the background levels of atmospheric nitrogen inputs. They found that, besides the amount of nitrogen applied, also the levels of ambient nitrogen deposition influenced the outcome of the experiments. In areas where the ambient nitrogen deposition was high, the environment might already have been altered prior to the experiment. The additional nitrogen might then not have affected the decomposition to the same degree as if the ambient nitrogen deposition would be low.

The same article also states that the length of the measurement period can influence the direction of the decomposition response. Litter that had decomposed in a shorter period of time were stimulated by nitrogen additions while litter that had decomposed in a longer period of time were inhibited by additional nitrogen. Although time seems to be an interacting factor, the mechanisms behind the time factor also need to be elucidated, that is, why the response change direction after a specific time period.

Besides the length of the experiment, one other possible interacting factor is the frequency by which the nitrogen has been applied. In some experiments the nitrogen has been added only once (e.g. Henriksen and Breland 1999, Wang et al. 2004) and in others it has been applied continuously throughout the experiment (e.g. Hobbie 2000, Compton et al. 2004). Also the intervals between applications differed and in some experiments nitrogen has only been applied during the growing season (e.g. DeForest et al. 2004a, Sinsabaugh et al. 2005). Because the frequency of the nitrogen applications differ between experiments it would be interesting to know whether it is an important interacting factor or not.

Other nutrients like for example phosphorus availability could also be an interacting factor. It might not hold the whole answer because there are reports (e.g. Thirukkumaran and Parkinson 2000) of similar response to nitrogen additions with low and high concentration of phosphorus.

5.2 Biotic factors

Of the possible biotic factors, the first factor that comes in mind is the properties of the litter. The experiments have been done at different locations with different types of vegetation, which produce litter with different chemical properties. Fog (1988) and also Knorr et al. (2005) found that nitrogen additions on average stimulated the decomposition of labile litter (i.e. high content of cellulose), whereas the decomposition of recalcitrant litter (i.e. high content of lignin) was suppressed by the higher nitrogen levels.

This phenomenon could also be distinguished in the papers that I have studied, especially in the articles measuring extracellular enzyme activity. Some articles particularly report ecosystem specific results, the EEA varied between different types of forests. For example in forests with litter high in lignin, nitrogen reduced the phenol oxidase activity (a lignin-degrading enzyme), whereas in forests with low lignin-containing litter nitrogen increased the phenol oxidase activity (Waldrop et al. 2004a, Waldrop et al. 2004b, Waldrop and Zak 2006).

Equal results as the above hold when litters with different lignin content have been collected and then placed to decompose in the same type of forest; the phenol oxidase activity was reduced by nitrogen in the cases where the litter had high lignin content and vice versa (Carreiro et al. 2000, Sinsabaugh et al. 2002). These articles also show an increased activity of cellulose degrading enzymes by nitrogen amendments, especially for low lignin-containing litter.

It seems that litter quality may in part explain the differential response to nitrogen additions, but as with the time factor one would also like to know the underlying mechanisms. What makes the decomposition go faster when nitrogen is added to easily degradable litter, but slower when the litter contains more recalcitrant substances like lignin? I have not found a complete answer to that question.

The last possible factor I will mention is in fact many factors; the decomposers themselves. They are the big actor in the decomposition system and they are different in their ways of degrading the detritus. Changes in the microbial community after nitrogen additions have been observed (Compton et al. 2004, Waldrop et al. 2004a). A shift in the microbial community might also imply that the functioning or properties of the community has changed. This means that the decomposition can operate differently, slower or faster, after than before the nitrogen was added.

Hence, the response of the nitrogen additions may depend on the properties of the original decomposer community and in what way they are changed. Ågren et al. (2001) have distinguished three decomposer properties that each affects the decomposition rate in a specific way. These properties are: decomposer growth rate, decomposer efficiency (production-to-assimilation ratio) and rate of quality decrease (when decomposers transform one substrate into another). Thus, the possible interacting factor is the change in decomposer properties which follows the shift in decomposer community.

6 Conclusion

The effect of nitrogen on the decomposition system varies in direction; positive, negative and no effect have been reported. There appears to be one or more factors that interact with the nitrogen factor which then leads to differing responses of the decomposition system. In this paper different possible interacting factors have been identified. The ones with most support so far seem to be the length of the observation period and the kind and quality of the substrate; although the others should not be forgotten and should be investigated further.

Many experiments have been made, and many more could and should be made. However, in experimental work it is hard to have all the different variables under control. Therefore, more theoretical work could be helpful in the further investigation of the effect of nitrogen on the decomposition system.

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