ELSEVIER

Soil Biology & Biochemistry 40 (2008) 688–698

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Direct and indirect effects of nitrogen deposition on litter decomposition

Peter Manning[a,*], Mark Saunders[a], Richard D. Bardgett[b], Michael Bonkowski[c], Mark A. Bradford[d], Richard J. Ellis[a], Ellen Kandeler[e], Sven Marhan[e], Dagmar Tscherko[e]

[a]*NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*
[b]*Soil and Ecosystem Ecology Laboratory, Institute of Environmental and Natural Sciences, Lancaster University, Lancaster, LA1 4YQ, UK*
[c]*Technische Universität Darmstadt, Fachbereich 10, Biologie D-64287, Germany*
[d]*Institute of Ecology, University of Georgia, Athens, GA 30602, USA*
[e]*Institute of Soil Science, University of Hohenheim, 70599 Stuttgart, Germany*

Received 18 April 2007; received in revised form 6 July 2007; accepted 21 August 2007
Available online 5 November 2007

Abstract

Elevated nitrogen (N) deposition can affect litter decomposition directly, by raising soil N availability and the quantity and quality of litter inputs, and indirectly by altering plant community composition. We investigated the importance of these controls on litter decomposition using litter bags placed in annual herb based microcosm ecosystems that had been subject to two rates of N deposition (which raised soil inorganic N availability and stimulated litter inputs) and two planting regimes, namely the plant species compositions of low and high N deposition environments. In each microcosm, we harvested litter bags of 10 annual plant species, over an 8-week period, to determine mass loss from decomposition. Our data showed that species differed greatly in their decomposability, but that these differences were unlikely to affect decomposition at the ecosystem level because there was no correlation between a species' decomposability and its response to N deposition (measured as population seed production under high N, relative to low N, deposition). Litter mass loss was ~2% greater in high N deposition microcosms. Using a comprehensive set of measurements of the microcosm soil environments, we found that the most statistically likely explanation for this effect was increased soil enzyme activity (cellobiosidase, β-glucosidase and β-xylosidase), which appears to have occurred in response to a combination of raised soil inorganic N availability and stimulated litter inputs. Our data indicate that direct effects of N deposition on litter input and soil N availability significantly affected decomposition but indirect effects did not. We argue that indirect effects of changes to plant species composition could be stronger in natural ecosystems, which often contain a greater diversity of plant functional types than those considered here.

Keywords: Nitrogen deposition; Litter decomposition; Soil enzyme activities; PLFA; C:N ratio; Plant species composition; Decomposer community

1. Introduction

The process of decomposition is vital in regulating ecosystem carbon (C) storage and nutrient cycling (Wardle, 2002), and the rate at which litter decomposes is known to depend upon soil nitrogen (N) availability (Fog, 1988; Knorr et al., 2005). Because human alteration of the N cycle has resulted in an approximate doubling of terrestrial N inputs (Vitousek et al., 1997), this relationship has potentially important implications for the global carbon cycle.

Studies to date have generally shown that the decomposition rate of high quality (i.e. with low lignin content and/or narrow C:N ratio) litter is stimulated by elevated N deposition, but that the decomposition of low quality litter is retarded (Waldrop et al., 2004; Knorr et al., 2005). However, at the ecosystem scale, the relationship between N input rates and decomposition is likely to be far more complex than that observed in simple experiments in which N is added to soil in the absence of living plants (for examples, see Fog, 1988). The reason for this is that N fertilisation affects decomposer organisms both directly and indirectly. Here, we classify direct effects as greater inorganic N availability, stimulation of plant biomass production (Gough et al., 2000; Shaver et al., 2001) and

*Corresponding author. Tel.: +44 207 5922482; fax: +44 1344 873173.
E-mail address: p.manning@imperial.ac.uk (P. Manning).

0038-0717/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2007.08.023

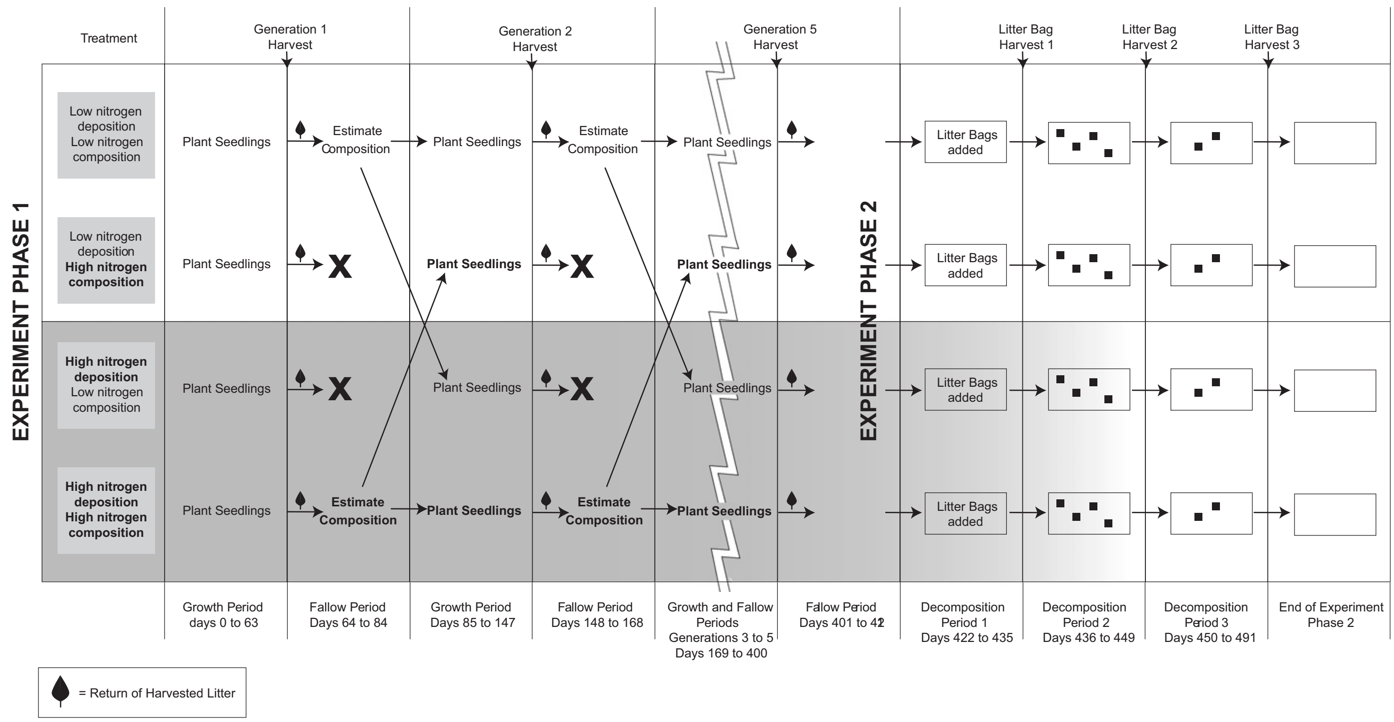

Fig. 1. Design and timeline of the experiment. In the first phase seedlings were planted, grown for 11 weeks and then harvested. The harvested biomass in two of the treatments was used to predict the composition of the next generation. The broken line indicates that the same pattern of planting, harvesting and composition estimation continued over generations 3–5. In the second phase, litter bags were added to the microcosms and harvested at 2, 4 and 8 weeks.

litter inputs, and decreased litter C:N ratio (e.g. Henry et al., 2005). An example of such a direct effect would be the stimulation of decomposer abundance and activity (potentially both microbes and larger soil organisms) by increased C and N inputs resulting in more rapid litter decomposition. We classify indirect effects as those that operate via plant species differences in response to the additional N, resulting in changes to plant species composition. This often shifts plant community composition towards rapidly growing species and these tend to produce high quality litters which decompose rapidly (Suding et al., 2005). Together, these changes mean that high N deposition systems can receive greater and higher quality litter inputs compared to unfertilised ecosystems, and that the species composition, and hence quality, of these inputs will also differ. These processes may be further complicated by the fact that an ecosystem's capacity to decompose plant litter may depend upon previous litter inputs, because they can affect soil physicochemical properties and the activity and composition of decomposer communities (Zak et al., 2003; Porazinska et al., 2003). Earlier litter inputs from a particular species for instance, may cause an increase in the population size of decomposer species (e.g. microarthropods) that are particularly suited to consume that litter species, thus accelerating its decomposition in the future relative to other species.

Here, we describe a two-phase experimental study in which we unravelled direct and indirect effects of N deposition on litter decomposition. We did this in model ecosystems (microcosms) based upon an agricultural field margin community containing eight species of annual herbs. In the first experimental phase, we separated direct and indirect effects by planting the plant species composition of low and high N environments into model ecosystems (indirect effects) that were subject to both low and high rates of N deposition (direct effects) (Manning et al., 2006) (Fig. 1). After five plant generations, soil properties were quantified, and the environments generated by the treatments, which differed in decomposer abundance and activity, pH and N availability, were used as the basis of the second experimental phase. In this phase, we placed litter bags of the eight species (plus two other species with no recent litter input history) into our model ecosystems and measured the effects of the treatments on the decomposition of litter (Fig. 1). We expected direct effects of N deposition on decomposition to operate through stimulation of the decomposer community by increased inorganic N inputs and increased litter C and N inputs. We expected indirect effects of N deposition to operate via the effects of changes in plant composition on the decomposer community, which might feedback to alter rates of decomposition. More specifically, we expected to observe correlations between: (a) plant species response to N in experimental phase one and its litter decomposition rate; and (b) the previous abundance of a plant species in a plot and its litter decomposition rate.