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Effects of long-term nitrogen deposition on fine root decomposition and its extracellular enzyme activities in temperate forests

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ABSTRACT

Resolving the effects of nitrogen (N) on decomposition is ecologically critical for predicting the ecosystem consequences of increased anthropogenic N deposition. Although root litter is the dominant soil carbon (C) and nutrient input in many forest ecosystems, studies have rarely examined how the process of root decomposition is affected by N availability. In a field experiment, we studied the effects of N addition on fine root (<0.5 mm diameter) decomposition using five substrates ranging in initial gravimetric lignin concentrations (from 10.8% to 34.1%) over five years, and made a simultaneous characterization of effects of N on the enzymatic activity of the decomposer community in three temperate forests. Across substrates, asymptotic decomposition models best described the decomposition. The effects of N addition shifted over the course of fine root decomposition, regardless of initial lignin concentrations, with N speeding up the initial rate of decomposition, but ultimately resulting in a larger, slowly decomposing litter fraction (*A*). Such contrasting effects of N addition on initial and later stages of decomposition were closely linked to the dynamics of its extracellular enzyme activity. Our results emphasized the need for studies of N effects on litter decomposition that encompass the later stages of decomposition. This study suggested that atmospheric N addition may have contrasting effects on the dynamics of different carbon pools in forest soils, and such contrasting effects of N should be widely considered in biogeochemical models.

1. Introduction

Decomposition of plant tissues is a fundamental ecosystem process that may influence ecosystem productivity by determining the rate at which nutrients cycle. It also represents an important source of carbon dioxide (CO_2) to the atmosphere, and thus influences the amount of organic carbon (C) stored in the ecosystem. Although more than 5000 papers have been published on the topic of decomposition of plant litter (Institute of Scientific Information Web of Science), key uncertainties remain about how this fundamental ecosystem process is affected by nitrogen (N) availability (Hobbie et al., 2012), especially for externally supplied N. Such uncertainties have impeded their inclusion in biogeochemical and global C models that, with very few exceptions (Moorehead and Sinsabaugh, 2006; Gerber et al., 2010), considered only the effects of substrate N on litter decomposition. Mounting evidence suggests, however, that substrate and externally supplied N may have contrasting effects on different stages of litter decomposition (Berg et al., 1996; Berg and Meentemeyer, 2002; Hobbie, 2005, 2008; Berg et al., 2010; Hobbie et al., 2012). Therefore, resolving such uncertainties about the effects of N on litter decomposition is ecologically crucial in quantifying and predicting the ecosystem consequences of increased anthropogenic N deposition (Galloway et al., 2004).

One key step towards resolving such uncertainties is to understand why the effects of exogenous N addition have substantial, but inconsistent, effects on litter decomposition in published empirical studies (Berg and Wessen, 1982; Berg and Matzner, 1997; Berg, 2000; Carreiro et al., 2000; Knorr et al., 2005; Hobbie, 2005, 2008; Keeler et al., 2009; Hobbie et al., 2012). Specifically, a meta-analysis of N enrichment effects on litter decomposition revealed that N addition generally accelerated the decomposition of substrates with low lignin concentrations but inhibited decomposition of substrates with high lignin concentrations (Knorr et al., 2005). And this interpretation is widely cited in many previous studies of N effects on decomposition (Bragazza et al., 2006; Liu

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et al., 2010; Norris et al., 2013; Yang et al., 2014; Fowler et al., 2015). However, assessing whether the effects of N addition on decomposition generally become independent of initial lignin concentrations in long-term litter studies is still difficult because most of studies reviewed by Knorr et al. (2005) lasted less than two years. Yet two years is not long enough to reveal dynamics in the later stages of this key ecosystem process in most terrestrial environments (Berg and McClaugherty, 2003; Prescott, 2010; Freschet et al., 2013). As a matter of fact, a recent study found that the magnitude and direction of the effects of N addition on aboveground litter decomposition may shift in long-term studies, accelerating the initial decomposition rate but inhibiting decomposition during the later stages of decomposition when lignin degradation dominates (Hobbie et al., 2012). However, most experiments about externally supplied N effects on decomposition do not last long enough to demonstrate whether such inhibitory effects exist during late stages of decomposition, nor are these kinds of N effects considered in biogeochemical models.

Another major uncertainty regarding N effects on litter decomposition is why multiple potential mechanisms of sometimes decreased decomposition rates in N-fertilized experiments may vary among various ecosystems. For example, some studies found that effects of N addition on lignin-degrading enzyme activity can be an important mechanism explaining inhibitory effects of N on decomposition (Carreiro et al., 2000; Sinsabaugh et al., 2002; DeForest et al., 2004; Zak et al., 2008; Hobbie et al., 2012), whereas other studies showing reduction of decomposition by N enrichment observed no evidence for such enzymatic effects (Keeler et al., 2009), or lignin degradation per se was not influenced by N addition (Hobbie, 2008). These contrasting results suggest that further research is needed to elucidate those mechanisms responsible for various effects of N on decomposition and to predict when and where particular mechanisms are important.

Despite the fact that root litter is the dominant soil carbon and nutrient input in many terrestrial ecosystems (Gill and Jackson, 2000; Freschet et al., 2013; Xia et al., 2015), there are just a few studies that have explored the effects of externally supplied N on root decomposition. Our understanding of the effects of external N on decomposition is nearly exclusively based on studies of leaf litter (e.g., Berg, 1986; Berg and Matzner, 1997; Ågren et al., 2001, 2013; Hobbie, 2005, 2008; Aerts et al., 2006). Roots generally decompose within a relatively stable environment within the mineral soil compared with aboveground plant materials which are exposed to fluctuations in temperature and moisture (Silver and Miya, 2001; Prescott, 2010). Consequently, the assumption that the decomposition rates of root and aboveground plant litter would be comparable and equally responsive to the factors influencing decomposition such as climatic conditions, rising atmospheric CO_2 or increased atmospheric N deposition, may result in erroneous predictions of ecosystem C and nutrient cycles (Berg and McClaugherty, 2003; Freschet et al., 2013).

Because N often limits microbial growth on dead plant tissues in terrestrial ecosystems (Vitousek and Howarth, 1991), it is reasonable to expect that elevated atmospheric N deposition would also affect the process of root decomposition from some indirect evidence. First, numerous studies have demonstrated that root litter frequently immobilizes N during its early stage of decomposition (e.g., Lõhmus and Ivask, 1995; Ostertag and Hobbie, 1999; Goebel et al., 2011; Xiong et al., 2012; Sun et al., 2012, 2013), indicating that the N content of fresh litter is insufficient to support the growth and maintenance requirements of decomposer communities. Second, strong positive correlations between initial root litter N concentrations and decomposition rates have been observed in a number of previous studies (Berg, 1984; Silver and Miya, 2001; Fan and Guo, 2010), particularly in the initial stages of decomposition. Third, N-induced changes in the composition or physiology of the microbial community may have significant impacts on decomposition of plant roots. For example, a model study by Ågren et al. (2001) indicated that N induced an increase in decomposition carbon-use efficiency caused by added N can be an important mechanism explaining decreased decay rates of plant litter seen in N-fertilization experiments. Moreover, a meta-analysis of N effects on microbial communities found that N fertilization generally on the average decreased microbial biomass (Treseder, 2008), which has been theoretically considered to have negative effects on decomposition of plant litter (Fog, 1988; Moorehead and Sinsabaugh, 2006; Hobbie et al., 2012).

Mounting evidence suggests that the integrated activities of microbial extracellular enzymes that are involved in cellulose and lignin decomposition have been demonstrated to be correlated with litter decomposition rates, and hence with the turnover rates of organic carbon in a number of different ecosystems (Sinsabaugh and Linkins, 1990; Carreiro et al., 2000; Sinsabaugh et al., 2005, 2008; Zak et al., 2008; Sinsabaugh, 2010). The measurements of enzyme activities would permit the functional responses of the microbial community to elevated atmospheric N deposition to be followed directly rather than indirectly (Carreiro et al., 2000; Sinsabaugh et al., 2002).

In the present study, we focused on fine roots (<0.5 mm in diameter) because these roots have more rapid turnover rates compared with somewhat coarse roots (Eissenstat et al., 2000; Wells and Eissenstat, 2001; McCormack et al., 2012, 2014). Fine roots can dominate total belowground productivity despite their small biomass. At the global scale, approximately one-third of net primary productivity was transferred to the soil through fine root turnover in terrestrial ecosystems (Jackson et al., 1997). In forest ecosystems, this proportion can be as high as 75% (Fogel, 1985; Vogt et al., 1996; Gill and Jackson, 2000). In this study, we conducted a five-year field experiment addressing the significant knowledge gap concerning the effects of externally supplied N on root decomposition and in its simultaneous characterization of N fertilization effects on the carbon-mineralization activities of decomposer community by determining the activities of enzymes that break down cellulose and lignin. The overall objective of this study was to determine how N fertilization influences initial vs. later stages of fine root decomposition separately during long-term decomposition. Specifically, we hypothesized that N addition will speed up fine root (<0.5 mm diameter) decomposition of lignin-poor substrates but will retard that of lignin-rich substrates. We tested this hypothesis by decomposing several substrates varying in their initial lignin and N concentrations over five years in N-fertilized and control treatments.

2. Materials and methods

2.1. Site description and plant material

The study was conducted in the temperate forests at Laoshan Forest Research Station of Northeast Forestry University in Heilongjiang Province, northeastern China (127°30′–127°34′E, 45°20′–45°25′N). The site has a continental temperate monsoon climate, with a strong monsoon windy spring, a warm and humid summer, and a dry and cold winter. Annual precipitation ranges from 600 to 800 mm, most of which falls in July and August. The mean annual air temperature is 2.8 °C, and average January and July air temperature are −19.6 °C and 20.9 °C (unpublished data from Laoshan Forest Research Station). The parent material at the site is granite bedrock and the soil is Hap-Boric Luvisols (dark brown forest soil in Chinese Soil Taxonomic System) with a high organic matter and N content (Gong et al., 1999).