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Influence of nitrogen additions on litter decomposition, nutrient dynamics, and enzymatic activity of two plant species in a peatland in Northeast China

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HIGHLIGHTS

- N additions enhanced decomposition of *V. uliginosum* but not *E. vaginatum* litter.
- *Vaccinium uliginosum* litter decomposed faster than *Eriophorum vaginatum* litter.
- N additions promoted invertase and β-glucosidase activity in both plant litter.
- Altered polyphenol oxidase influenced the response of plant litter to N additions.

GRAPHICAL ABSTRACT

The distribution of the nitrogen addition plots across the experimental field.

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ABSTRACT

Nitrogen (N) availability affects litter decomposition and nutrient dynamics, especially in N-limited ecosystems. We investigated the response of litter decomposition to N additions in *Eriophorum vaginatum* and *Vaccinium uliginosum* peatlands. These two species dominate peatlands in Northeast China. In 2012, mesh bags containing senesced leaf litter of *Eriophorum vaginatum* and *Vaccinium uliginosum* were placed in N addition plots and sprayed monthly for two years with NH_4NO_3 solution at dose rates of 0, 6, 12, and 24 g N m^{-2} $year^{-1}$ (CK, N1, N2 and N3, respectively). Mass loss, N and phosphorus (P) content, and enzymatic activity were measured over time as litter decomposed. In the control plots, *V. uliginosum* litter decomposed faster than *E. vaginatum* litter. N1, N2, and N3 treatments increased the mass losses of *V. uliginosum* litter by 6%, 9%, and 4% respectively, when compared with control. No significant influence of N additions was found on the decomposition of *E. vaginatum* litter. However, N and P content in *E. vaginatum* litter and *V. uliginosum* litter significantly increased with N additions. Moreover, N additions significantly promoted invertase and β-glucosidase activity in *E. vaginatum* and *V. uliginosum* litter. However, only in *V. uliginosum* litter was polyphenol oxidase activity significantly enhanced. Our results showed that initial litter quality and polyphenol oxidase activity influence the response of plant litter to N additions in peatland ecosystems. Increased N availability may change peatland soil N and P cycling by enhancing N and P immobilization during litter decomposition.

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1. Introduction

Peatlands contain vast global carbon (C) pools and act as important sinks (Siegenthaler et al., 2010) due to the slow rates of litter decomposition (Bragazza et al., 2007; Moore et al., 2007). Significant increases in atmospheric nitrogen (N) deposition over ambient levels have been observed for most of the northern peatlands, although the deposition may be relatively small (Galloway and Cowling, 2002). Moreover, global warming is predicted to stimulate soil N mineralization and increase soil available N (Aerts et al., 2006). Increased N availability has important implications for C accumulation in peatland ecosystems where N is a limiting nutrient (Bragazza et al., 2007; Xing et al., 2011). N additions influenced the quality of standing litter in the peatland due to variations in N and phosphorus (P) content and altered enzymatic activity (Song et al., 2017). An improved understanding of litter decomposition and nutrient cycling under N additions in peatlands is needed to better predict the effects of global change on the function of peatlands as C sinks (Bragazza et al., 2012).

Litter decomposition is an important process of C and nutrient cycling in terrestrial and aquatic ecosystems (Knorr et al., 2005; Waring, 2013; Wang et al., 2017). Litter decomposition is influenced by various biotic and abiotic factors, including litter quality, decomposer communities, and external drivers such as climatic factors, anthropogenic N enrichment and global warming (Berg and McClaugherty, 2014; Manninen et al., 2016; Liu et al., 2017). Litter quality is characterized by litter N and P content, lignin and cellulose contents, and lignin:N, C:N, C:P, and N:P ratios. These parameters and their ratios directly influence decomposition because they determine the decomposability of organic material and availability of nutrients to the decomposers (Gong et al., 2015; Zhang et al., 2016; Wang et al., 2017). Litter decomposition is primarily affected by the cellulose and lignin content of the litter (Bragazza et al., 2006; Jiang et al., 2014; Liu et al., 2016). Cellulose, which is the most abundant plant-synthesized biopolymer, usually contains 20%–30% of the C sequestered in plant litter (Berg and Laskowski, 2006). Lignin is the slowest decomposing natural component in plant tissues (Kosheleva and Trofimov, 2008). Therefore, initial litter properties need to be known to meaningfully compare litter decomposition among different plant species.

N plays an important role in determining the rate of plant litter decomposition. N affects decomposition both as an internal chemical component of litter tissue and as an external part of the decomposition environment (Hobbie, 2005; Perakis et al., 2012). The effects of external N additions on litter decomposition have yielded highly variable results. The decomposition rate of high quality litter (i.e., with low lignin content, high N and P contents and low C:N and lignin:N ratios) can usually be stimulated by N additions, whereas the decomposition rate of low quality litter may be slowed by N additions (Knorr et al., 2005; Manning et al., 2008; Gong et al., 2015). Decomposition of easy-to-alter C compounds, which are decomposed mainly during the early stages, can be enhanced by N additions (Berg and McClaugherty, 2008; Brandstätter et al., 2013). By contrast, decomposition of recalcitrant C compounds, which are mainly decomposed during the late stages, is slowed down by N additions (Carreiro et al., 2000; Perakis et al., 2012). N-treated litter enhanced early-stage (0.67 year) and retarded late-stage (2–3 year) decomposition rates (Perakis et al., 2012; Tu et al., 2014). These phenomena imply that litter quality influences the response of litter decomposition to N input.

Enzymes are important drivers of decomposition because they can catalyze the degradation of complex compounds present in litter (Allison and Vitousek, 2004). The activity of different enzymes differs widely among plant species litter (Güsewell and Freeman, 2005). Therefore, litter mass loss rates are significantly influenced by variations in microbial enzyme allocation in diverse plant species litter (Allison and Vitousek, 2004; Waring, 2013). Even the activity of enzymes that do not target N may be affected by N additions (Manning et al., 2008). N additions have suppressed phenol oxidase activity in several studies (Waldrop and Zak, 2006; Jiang et al., 2014), but promoted the activity of the cellulose-degrading enzyme β-glucosidase (Grandy et al., 2013). Investigating litter decomposition by enzymes using N additions will improve the understanding of how C and nutrient cycling respond to N deposition. In peatlands, constraints on phenol oxidase activity because of low oxygen conditions can minimize the activity of hydrolytic enzymes responsible for peat decay (Freeman et al., 2001). Therefore, the effect of N additions on enzyme activity and litter decomposition in peatlands needs further study.

In the Great Xing'an Mountains, located in the Heilongjiang Province, Northeast China, approximately 12% of the land surface is covered by permafrost-affected peatlands (Niu and Ma, 1995). N deposition in this area is reported to be approximately 13.3 kg ha^{-1} $year^{-1}$ (Lu and Tian, 2007). *Eriophorum vaginatum*, a graminoid species, and *Vaccinium uliginosum*, a dwarf shrub species, are two dominant species that constitute the vegetation in this peatland. We previously found that N additions significantly changed the properties of standing litters of these two species (Song et al., 2017). The objective of this study is to clarify the responses of litter decomposition to N additions and identify potential enzymatic mechanisms. We evaluated: (1) how N additions influence *E. vaginatum* and *V. uliginosum* litter decomposition, as well as N and P dynamics; (2) whether N additions affect litter decomposition differently depending on their initial quality, (3) whether litter decomposition is influenced by the response of enzymatic activity to N additions.

2. Materials and methods

2.1. Study site

The study site is located in continuous permafrost peatland in the Great Xing'an Mountains, Northeast China (52.94°N, 122.86°E), and occurs in wide, sloped valleys. It is categorized as poor fen. The average annual air temperature over this area from 1991 to 2010 was −3.9 °C, with the monthly average temperature ranging from −31.9 °C in January to 19.8 °C in July. The average annual rainfall was 450 mm with 45% of the rain falling between July and August. The average air temperatures during the growing season (May through September) in 2012 and 2013 were 12.1 °C and 13.0 °C, respectively, and the corresponding average precipitation was 347.1 and 505.2 mm (based on our observed data). Hydrological conditions of the peatland are mainly controlled by precipitation, no stream source was observed during this study, and the water table is relatively constant. Usually water and soils in the permafrost active layer (about 45–50 cm) remain frozen from October to the next April, and begin to thaw in late April (Wang et al., 2014). The vegetation is dominated by *Eriophorum vaginatum* L., *Vaccinium uliginosum* L., *Chamaedaphne calyculata* L. Moench, *Ledum palustre* L. and *Sphagnum* spp. (Song et al., 2017). The soil of the study site is Glacic Historthels.

2.2. Experimental design

Field measurements of changes in litter mass and quality were conducted using the litterbag method (Aerts et al., 2006). In September 2011, litter of *E. vaginatum* and *V. uliginosum* was collected randomly near the N addition plots. The standing dead *E. vaginatum* leaf litter was clipped, while dead *V. uliginosum* leaf litter was collected from the marsh surface. The samples were thoroughly mixed and air-dried, one subsample was ground and passed through a 0.25 mm mesh to test the initial litter C, N, P, lignin, and cellulose content in triplicate. The initial litter characteristics are listed in Table 1. The remaining litter was used to prepare litter bags made of polyethylene mesh (10 cm × 10 cm) with a 0.5 mm holes, because of the small size of *E. vaginatum* litter. *E. vaginatum* litter was approximately 9 cm in length, similar to the length of the mesh bags. Air-dried litter (8 g) was placed in each litterbag. Four treatments were randomly applied to 12 plots (2 m × 2 m) surrounded by a 1 m-wide buffer strip. These groups were the control