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Nitrogen and phosphorus regulation of soil enzyme activities in acid forest soils

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ABSTRACT

The activities of soil extracellular enzymes are important in governing rates of organic matter decomposition and nutrient cycling in forest ecosystems. Measurements of soil enzyme activities can provide insights on microbial function, in terms of how much energy microbial communities are investing to acquire particular nutrients from OM substrates. In ecosystems enriched with nitrogen (N), phosphorus (P) supply may play an important role in regulating microbial activity, enzyme production, and organic matter decomposition. The response of extracellular enzyme activity to chronic N-enrichment was assessed at a long-term paired watershed N-enrichment experiment, the Bear Brook Watershed in Maine (BBWM) in hardwood and softwood forest types. Specifically, we measured the ambient (extant) activity of C hydrolyzing β-glucosidase (BG) and xylosidase (XYLO), N hydrolyzing N-acetylglucosaminidase (NAG), and P hydrolyzing acid phosphatase (AP) in the watershed subjected to chronic N-enrichment, and in the reference watershed. Secondly, in a series of soil incubations, we characterized the extent to which microbial C and P acquisition were regulated by N and P availability. In these incubations, we measured BG and AP activity response to acute (high-dose fertilizer) nutrient amendments. We hypothesized that soil enzyme activities would respond more to enhanced P availability than N, particularly in the N-enriched watershed. Our results from extant enzyme activity measurements suggest that chronic N-enrichment inhibited rather than stimulated extant soil hydrolytic enzyme activities, which could reflect suppression of microbial biomass and activity. In the acute nutrient amendment incubations, our data indicate that inorganic P was more important than N in regulating soil microbial C and P acquisition in soils from both the N-enriched and reference watersheds. Our results also indicate that the extent to which P availability regulated microbial acquisition of P in O horizon soils was greatest in softwood soils subjected to chronic N-enrichment. Findings from this study suggest that both forest type and soil inorganic P availability could be more important in influencing soil biological response to N pollution than previously recognized.

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1. Introduction

Nitrogen pollution from human activities has dramatically enhanced N availability in terrestrial environments and shifted some ecosystems towards N saturation (Aber et al., 2003; Galloway, 1998; Matson et al., 2002,Vitousek et al., 1997). Global rates of atmospheric N deposition are expected to increase in the coming decades (Dentener et al., 2006; Galloway et al., 2004) despite recent reductions in N deposition in parts of North America and Europe (Driscoll et al., 2003; Fowler et al., 2007). Although N in the environment can act as a pollutant, it is also a commonly limiting nutrient to terrestrial biota and thus, net primary productivity (LeBauer and Treseder, 2008; Vitousek and Howarth, 1991). Organisms require sufficient N supply to maintain a variety of physiological processes, including the synthesis of proteins, energetic nucleotides, pigments (chlorophyll), and nucleic acids. The classic paradigm in northern temperate forests is that N is the primary limiting nutrient to biological productivity. However, increases in the availability of N in these ecosystems could alleviate this

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limitation, and increase the relative importance of other essential nutrients such as phosphorus (P) (Gress et al., 2007; Elser et al., 2009; Phoenix et al., 2004,Vitousek et al., 2010).

Nitrogen-enrichment can alter important soil processes that are mediated by microbial communities, some of which can impact soil P cycling and availability. For instance, a meta-analysis of N-enrichment studies by Knorr et al. (2005) demonstrated that significant inhibition of litter decomposition can occur when N fertilization rates are 2-20× background rates of N deposition. Since litter is an important source of organic P in forest ecosystems, we can expect that lower litter decomposition rates could result in less organic P substrates available for microbes to degrade. Other studies have suggested that N deposition can impede soil organic matter (SOM) decomposition by both suppression of microbial abundance or enzyme activities (DeForest et al., 2004; Ramirez et al., 2010; Stone et al., 2011; Treseder, 2008) or inhibition of specific fungal communities (Frey et al., 2004; Wallenstein et al., 2006). Ecosystem N-enrichment can also enhance the activity of bacterial communities involved in N-mineralization (Aber et al., 1998; Jefts et al., 2004) by reducing C:N ratios in upper soil horizons; this could lead to an increase in N:P ratios in the soil matrix. Collectively, evidence suggests that N-enrichment can promote decomposition of more labile SOM fractions but impede decomposition of more recalcitrant fractions (Zak et al., 2008). These changes in decomposition caused by N-enrichment may stimulate or depress soil C storage, depending on litter quality characteristics (e.g., Waldrop et al., 2004), and the complex interactions among soil microbes, nutrients, or by multiple nutrient limitations.

Recent studies have demonstrated the importance of P in regulating microbial processes (Cleveland et al., 2002), and microbial activity (Liu et al., 2013) in tropical ecosystems, and microbial metabolic rates at the global scale (Hartman and Richardson, 2013). However, the regulation of microbial processes by P in soils subject to high N loading in the Northeastern U.S. has not been well characterized. It is recognized that chronic enrichment with N should enhance the role of P as a limiting nutrient for aboveground productivity in northern temperate terrestrial ecosystems (Gress et al., 2007; Vitousek et al., 2010). However, nitrogen deposition could also enhance the extent to which P is limiting to soil microbial communities by increasing N:P ratios in foliage (Braun et al., 2010; Bytnerowicz and Fenn, 1996), leaf litter and SOM, thereby reducing the amount of P relative to N in substrates for microbial degradation. A recent analysis of foliar chemistry data from 75 sites in the northeastern U.S. by Crowley et al. (2012) demonstrated that foliar N:P ratios increased with increasing N deposition in the Adirondacks, but not for the northeastern U.S. region overall. Furthermore, Naples and Fisk (2010) found that fine root growth responded positively to experimental P additions in mid-age forests in New Hampshire, but not in mature forests. They concluded that changes in nutrient demand with successional growth, and N deposition, can influence the extent of P limitation as stands age. For soil microbes subjected to high N loading, P availability could be more important than previously recognized in regulating microbial biomass and activity, and the rate at which SOM compounds are hydrolyzed.

Microbial production of C, N, and P degrading enzymes is energetically expensive (Allison and Vitousek (2005)), and therefore resource allocation and energetic investment in C and/or P degrading enzymes should theoretically increase with enhanced N availability (Sinsabaugh and Moorhead, 1994). In a meta-analysis of the response of soil phosphatase activity to N and P additions, Marklein and Houlton (2011) demonstrated that across a range of sites on several different continents, phosphatase activity typically increased under high N availability, suggesting accelerated P cycling under N-enrichment. However, the study by Marklein and Houlton only included two studies in temperate forests in the northeastern U.S., and among those two studies, an increase in phosphatase in response to N addition was only demonstrated in mature stands in one of these studies (Naples and Fisk, 2010). More information is needed on how a legacy of enhanced N loading to northeastern forests could influence the extent of P limitation on important ecosystem processes, such as microbial enzyme activity and SOM degradation. In northern hardwoods, studies by Groffman and Fisk (2011), and Weand et al. (2010) suggested no significant influence of N deposition on soil microbial P cycling. However, within northeastern forests, there is reason to expect that P limitation to microbial response to N-enrichment could be different among hardwood and softwood stands because rates of nutrient cycling are generally lower in softwoods compared with hardwoods (e.g. Lovett et al., 2004). If increases in rates of N cycling are not matched by increases in P cycling, then P limitation could be strengthened by N-enrichment; this effect could be more pronounced in softwoods compared with hardwoods because of slower existing rates of P cycling.

We investigated the impacts of long-tern N-enrichment on soil microbial enzyme activity in soils from hardwood and softwood soil types at the Bear Brook Watershed in Maine (BBWM). The BBWM is a long-term paired watershed experiment where forest ecosystem response to chronic N-enrichment and acidification has been studied for over two decades. At the BBWM, Mineau et al. (2013) explored indices of P limitation at watershed-scale using enzyme stoichiometry, and found no difference in stoichiometry to suggest N enrichment had altered soil microbial resource allocation strategies. However, the two forest types at BBWM have different litter quality that could influence microbial response to changes in nutrient availability, but forest type influences on enzyme activity at this site have not been characterized. We developed a set of experiments to determine how forest type and enhanced N and P availability influence soil microbial enzyme activity at the BBWM. To do this, we first measured the ambient (extant) soil enzyme activity from both softwood and northern hardwood soils in reference and treated watersheds. We hypothesized that long-term N-enrichment would accelerate microbial acquisition of C, N, and P compounds, resulting in higher hydrolytic enzyme activity in the N-enriched watershed. Secondly, in short-term soil incubation experiments, we used experimental high dose (acute) addition of inorganic P and N to soils from both the reference and N-enriched watersheds. These incubations were designed to test if P availability was more important than N availability in regulating the activity of C and P hydrolyzing enzymes in soils from both forest types among the N-enriched and reference watersheds. Together, these experiments provide us with novel insights on the nature of nutrient regulation of microbial processes in acid forest soils affected by N pollution.

2. Material and methods

2.1. Site description

The BBWM is a long-term paired watershed experiment located on the southeast slope of Lead Mountain (44° 52′ N., 68° 06′ W.) in eastern Maine. The treated watershed (West Bear; WB) is 11.0 ha and receives bi-monthly additions of $(NH_4)_2\ SO_4$ above the forest canopy, adding 25.2 kg N ha^{-1} yr^{-1} and 28.8 kg S ha^{-1} yr^{-1}, compared with ambient levels of 3.2 kg N ha^{-1} yr^{-1} and 2.4 kg S ha^{-1} yr^{-1} as wet deposition at the nearest National Atmospheric Deposition Program site (Greenville, ME) in 2011. The adjacent untreated watershed (East Bear; EB) is 10.3 ha and serves as an ecological reference.

The BBWM climate is cool and temperate with a mean annual air

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