



Mechanisms driving the soil organic matter decomposition response to nitrogen enrichment in grassland soils



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ABSTRACT

Empirical studies show that nitrogen (N) addition often reduces microbial decomposition of soil organic matter (SOM) and carbon dioxide (CO₂) production via microbial respiration. Although predictions from theoretical models support these findings, the mechanisms that drive this response remain unclear. To address this uncertainty, we sampled soils of three grassland sites in the U.S. Central Great Plains that each have received seven years of continuous experimental nutrient addition in the field. Nitrogen addition significantly decreased the decomposition rate of slowly cycling SOM and the cumulative carbon (C) respired per mass soil C. We evaluated whether this effect of N addition on microbial respiration resulted from: 1) increased microbial carbon use efficiency (CUE), 2) decreased microbial oxidative enzyme activity, or 3) decreased microbial biomass due to plant and/or soil mediated responses to N enrichment. In contrast to our hypotheses – as well as results from N addition studies in forest ecosystems and theoretical predictions – N did not increase microbial CUE or decrease microbial oxidative enzyme activity. Instead, reduced microbial biomass likely caused the decreased respiration in response to N enrichment. Identifying what factors drive this decreased microbial biomass response to N should be a priority for further inquiry.

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1. Introduction

The increased availability of biologically reactive nitrogen (N) has widespread effects on terrestrial ecosystems; N enrichment can lead to biodiversity loss, soil acidification, as well as stimulated plant growth. However, interactions between the carbon (C) cycle and nutrient cycles (such as N) are poorly understood (Ciais et al., 2013) and the extent to which increasing nutrient availability may feed back on the global C cycle remains unknown (Wieder et al., 2015a). This uncertainty is especially important to resolve for the decomposition of soil organic matter (SOM) by soil microorganisms, a process that releases C to the atmosphere as carbon dioxide (CO₂). Soil organic matter contains a significant reservoir of organic C and changes in its decomposition rate in response to N enrichment will impact the net CO₂ exchange between the atmosphere and biosphere.

The effects of N enrichment on microbial decomposition have received considerable research attention to date. Leaf litter and soil

studies conducted across biomes have found that N enrichment often decreases microbial decomposition and respiration (Knorr et al., 2005; Ramirez et al., 2012; Zhou et al., 2014), especially for the leaf litter or SOM pools that cycle slowly (Berg and Matzner, 1997; Hobbie et al., 2012; Riggs et al., 2015). This negative response is particularly paradoxical since N enrichment often increases the input of C belowground via plant litter and root exudates (Liu and Greaver, 2010), which should increase C availability to microbes as well as the decomposition of more slowly cycling SOM (e.g., the priming effect). Although observed decreases in respiration and decomposition of slowly cycling SOM are in accordance with predictions from theoretical models of microbial activity following N addition (Ågren et al., 2001; Moorhead and Sinsabaugh, 2006; Perveen et al., 2014; Schimel and Weintraub, 2003), the biological and chemical mechanisms that underlie the response of SOM decomposition to added N remain uncertain. Are the inhibitory effects of N on SOM decomposition – and slowly cycling SOM decomposition in particular – due to plant biomass, microbial, or soil chemistry-mediated changes that occur in response to N addition? Identifying these mechanisms is key for elucidating how N enrichment will influence soil C sequestration, soil CO₂ emissions, and the global C cycle.

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Microbial decomposition of SOM is influenced by the activity of the microbial decomposer community, as well as the chemistry (or “decomposability”) of the substrates being oxidized. Although microbial community composition shifts in response to N enrichment have been documented in multiple systems (Fierer et al., 2011; Leff et al., 2015; Ramirez et al., 2012), the extent to which they cause significant changes in microbial function – and, importantly, what those changes are – is unknown. A number of microbial mechanisms have been proposed to explain why microbial respiration decreases in response to N addition and are the focus of the study reported here (Fig. 1a). Microbial respiration associated with organic matter decomposition is influenced by decomposer carbon use efficiency (CUE; i.e., C allocation to anabolism (e.g., microbial growth) or catabolism (e.g., decomposition); Fig. 1a, Mechanism 1), the activity of exo-enzymes produced by those decomposers (Fig. 1a, Mechanism 2), as well as the biomass of decomposing microorganisms (Fig. 1a, Mechanisms 3).

First, N might decrease microbial respiration by increasing microbial CUE (Fig. 1a, Mechanism 1) (Ågren et al., 2001; Schimel and Weintraub, 2003). Once microbes acquire C, N addition can alter the allocation of that C to new biomass, enzymes, or maintenance respiration. For example, Schimel and Weintraub (2003) constructed a microbial decomposition model that accounted for microbial growth, enzyme production, and maintenance respiration. They predicted that N addition causes more C to be allocated to microbial growth (assuming N-limited growth) instead of lost via overflow respiration and extracellular enzymes, leading to increased microbial efficiency and reduced respiration following N addition. This could occur either because of shifts in CUE within organisms or, alternately, because of shifts in microbial community composition towards dominance by organisms that acquire C more effectively through increased CUE, leading to a community-wide shift in CUE. A few empirical studies have suggested that microbial CUE increases with N addition (e.g., Thiet et al., 2006), although clear patterns across terrestrial N availability gradients or from N addition studies are lacking. For example, Manzoni et al. (2012) surveyed results from measurements of microbial CUE along natural gradients of soil organic N and found that microbial CUE increased with increasing ambient N concentration; however, experimental N addition had the opposite effect, reducing microbial CUE.

Second, N addition might reduce decomposition because N

directly inhibits oxidative enzymes, which decompose more complex C substrates such as lignin (Fig. 1a, Mechanism 2) (Fog, 1988). Researchers have suggested that lignin degradation may be inhibited by added N if lignin degradation is a mechanism of N acquisition or “N mining” from molecules physically protected by lignin (Craine et al., 2007). Many studies have demonstrated decreased activity of oxidative enzymes under N addition. For example, in a northern temperate forest study system, N decreased phenol oxidase activity (Waldrop et al., 2004), the abundance of functional genes involved in the depolymerization of a variety of complex C molecules (such as lignin) (Eisenlord et al., 2013), as well as the expression of ligninolytic genes (Edwards et al., 2011). However, it is unclear to what extent these enzyme-based mechanisms that lead to decreased respiration hold true in non-forest systems, such as grasslands, where there is less lignin and lignin-degrading microbes (Sinsabaugh, 2010).

Finally, N addition might reduce respiration by decreasing the biomass of the decomposing microbes (Fig. 1a, Mechanism 3). It is well established that N addition tends to decrease microbial biomass (Liu and Greaver, 2010; Treseder, 2008). Nitrogen addition leads to soil acidification (decreasing pH), loss of base cations (e.g., Mg^{2+} and Ca^{2+}), and increased solubility of hydrolyzing cations (e.g., Al^{3+} and Fe^{3+}) (Tian and Niu, 2015). Positive relationships between soil pH and microbial biomass are well established (Wardle, 1992) and microbial biomass may be lower in more acidic soils due to the direct effects of decreased pH on microbial physiology, base cation limitation (Treseder, 2008), or the biologically toxic effects of increased Al^{3+} (Flis et al., 1993). Alternately, low pH soils may inhibit microbial extracellular enzyme activity (Sinsabaugh et al., 2008), leading to decreased microbial access to C, decreased microbial biomass, and reduced respiration. Finally, the increased solubility of hydrolyzing cations at low pH can increase the stabilization of C in organic matter-metal complexes that are inaccessible to microbes, and lead to decreased C availability to microbes and, subsequently, reduced biomass and decomposition (Mueller et al., 2012).

Our objective was to evaluate the microbial mechanisms by which N addition leads to decreased microbial respiration of SOM in grasslands. Specifically, we examined whether N addition decreased microbial respiration and decomposition by 1) increasing microbial CUE, 2) decreasing microbial oxidative enzyme activity, or 3) decreasing microbial biomass. Grassland

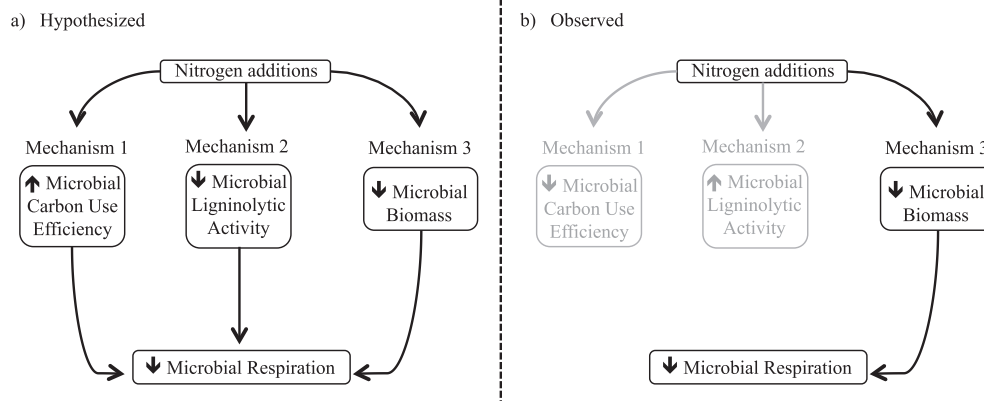


Fig. 1. Hypothesized (a) and observed (b) mechanisms of nitrogen addition effects on microbial respiration. (a) Hypothesized microbial mechanisms by which N might reduce respiration include increased carbon use efficiency (Mechanism 1), decreased ligninolytic enzyme activity (Mechanism 2), and decreased microbial biomass (Mechanism 3). (b) The observed effects of N addition on microbial carbon use efficiency and microbial ligninolytic enzyme activity were opposite to those necessary to explain the decrease in microbial respiration in response to N addition (Panel b, Mechanisms 1 and 2, grayed out). Instead, the negative effects of N addition on microbial biomass, possibly due to decreased substrate decomposability (e.g., higher root tissue N content) and/or effects of reduced soil pH on microbial physiology or Ca availability (but not on Al toxicity or physicochemical protection of SOM), likely explained the observed decrease in microbial respiration (Panel b, Mechanism 3).

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