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Detecting microbial N-limitation in tussock tundra soil: Implications for Arctic soil organic carbon cycling

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ABSTRACT

More than a third of the global soil organic carbon (SOC) pool is estimated to be stored in northern latitudes. While the primary regulators of microbially-mediated decomposition in physically unprotected organic soils are typically attributed to abiotic factors (e.g. temperature and moisture), in extremely nutrient-poor environments such as the Alaskan Arctic tussock tundra, evidence from field studies suggests that low N-availability may also strongly limit microbial growth, and thus the rate of SOC decomposition. However, there have been few direct tests of microbial nutrient-limitation, particularly in Arctic systems. We predicted that during the Arctic summer growing season, when both plants and microbes are competing for mineralized nutrients, N-availability in tussock tundra soil is so low that it will limit microbial biomass production, and thus decomposition potential. We tested this prediction by adding N and C to tussock tundra organic soil and tracking microbial responses to these additions. We used a combination of approaches to identify microbial N-limitation, including changes in microbial biomass, C-mineralization, substrate use efficiency, and extracellular enzyme activity. The Arctic soil's microbial community demonstrated strong signals of N-limitation, with N-addition increasing all aspects of decomposition tested, including extracellular enzyme activity, the rate-limiting step in decomposition. The corresponding C-addition experiment did not similarly influence the microbial activity of the tundra soil. These results suggest that tundra SOC decomposition is at least seasonally constrained by N-availability through microbial N-limitation. Therefore, explicitly including N as a regulator of microbial growth in this N-poor system is critical to accurately modeling the effects of climatic warming on Arctic SOC decomposition rates.

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1. Introduction

Slow decomposition rates in permafrost soils is a major driver in the development of a soil organic carbon (SOC) pool that is estimated to be 1672 Pg—more than twice as much carbon (C) as is in the atmosphere (Schlesinger and Andrews, 2000; Tarnocai et al., 2009). In Arctic tundra organic soils, although the soil organic matter (SOM) is not physically protected (Weintraub and Schimel, 2003), C accumulates and microbial biomass accounts for only 2–4% of the total C (Cheng and Virginia, 1993; Jonasson et al., 1996). The slow decomposition of C-rich material is promoted by the biome's cold climate, which supports the buildup of SOC and concomitant low bio-availability of nitrogen (N), producing a highly N-limited plant community (Shaver and Chapin, 1980, 1986; Chapin

and Shaver, 1989; Giblin et al., 1991). Climate models unequivocally predict that the Arctic will significantly warm during this century (Moritz et al., 2002; Solomon et al., 2007), however, projecting the extent to which warming will alter net Arctic C balance depends upon mechanistically understanding how N-availability regulates tundra SOM decomposition (Mack et al., 2004; Weintraub and Schimel, 2005; Sturm et al., 2008).

Despite the recognition of the intensity of N-limitation to plants in tundra systems (Giblin et al., 1991; Shaver and Chapin, 1986), there have been relatively few direct tests of the potential for microbial nutrient-limitation to limit tundra SOM decomposition (e.g. Jonasson et al., 1996; Mack et al., 2004; Churchland et al., 2010; Lavoie et al., 2011). While N-addition has been demonstrated to drive a wide array of effects on C turnover in a variety of systems, ranging from enhancement to the inhibition of decomposition (e.g. Craine et al., 2007; Cusack et al., 2010), several studies have identified N as a potential regulator of tundra SOC decomposition. This includes both modeling work (Moorhead and Reynolds, 1993) and empirical experiments showing that N-additions to tundra organic soils can

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promote microbial N-immobilization, enhance microbial activity and potential SOC loss (Jonasson et al., 1996; Mack et al., 2004; Churchland et al., 2010; Lavoie et al., 2011). These studies suggest that it is not simply temperature that limits decomposition in this system. To break down plant polymers, microorganisms rely on extracellular enzymes, which are N-rich; when N is limiting, microbial investment in enzymes can control the dynamics of the decomposer system (Schimel and Weintraub, 2003). If N-limitation is extreme enough, it is possible that microbes would lack adequate N to both make the enzymes needed for decomposition and the biomass needed for survival and growth.

Most tundra SOM research has historically focused on temperature (e.g. McKane et al., 1997; Rustad et al., 2001; Walker et al., 2006; Oberbauer et al., 2007; Schuur et al., 2008), SOM chemistry (Giblin et al., 1991; Weintraub and Schimel, 2003), or the interaction between soil chemistry and temperature as a primary regulators of tundra decomposition (Giblin et al., 1991; Nadelhoffer et al., 1991; Hobbie et al., 2000, 2001; Shaver et al., 2006). While these studies have identified site-driven differences in SOM C chemistry (likely driven by differences in chemistry quality of plant litter inputs) as a primary predictor SOM C turnover rates at broad spatial scales, several long-term soil incubation studies have demonstrated that despite substantial and relatively constant rates of C loss for a variety of tundra organic soils, SOM C chemistry remains relatively unchanged, with decomposition of the major chemical fractions being proportional to lignin degradation (Weintraub and Schimel, 2003; Shaver et al., 2006). These findings suggest that tundra SOM consists of a large pool of potentially mineralizable C, with all SOM fractions relatively equally available to microbial attack, despite being in later stages of decomposition (Weintraub and Schimel, 2003; Shaver et al., 2006). However, these studies are not conclusive about the mechanism limiting decomposition of this potentially available material.

Given that nutrient addition experiments suggest microbial productivity in the organic horizon may be at least seasonally N-limited (Moorhead and Reynolds, 1993; Jonasson et al., 1996; Mack et al., 2004; Churchland et al., 2010; Lavoie et al., 2011), and that field studies reveal substantial *in situ* net N-immobilization during the growing season (Giblin et al., 1991), microbial N-limitation appears to be a likely potential regulator of Arctic SOM decomposition. This effect contrasts to N-addition studies in less N-limited soils, where increased N availability is hypothesized to decrease mineralization of recalcitrant N, while not affecting the mineralization rate of more labile N sources (Craine et al., 2007; Janssens et al., 2010).

If N limits tundra organic soil's microbial growth and enzyme synthesis, and hence directly controls decomposition and C-cycling, it would require rethinking biogeochemical models of tundra ecosystems (McKane et al., 1997). Yet, microbial N-limitation is difficult to demonstrate because it is challenging to measure microbial growth in soil and to separate biomass growth from changes in metabolism. It is important to conclusively establish the mechanism by which N controls C-storage in tundra ecosystems (e.g. Sullivan et al., 2007) before reconstructing our paradigms about tundra soil processes.

One challenge in assessing N-limitation to decomposers is that under moderate N-limitation, enzyme production (and thus decomposition) may not be significantly restricted, but cellular growth may be. Under extreme N-limitation, however, microbes may not have adequate N to synthesize the needed enzymes, limiting decomposition itself (Schimel and Weintraub, 2003). Microbial dynamics may therefore be constrained by C, either as quantity (availability) (Waksman and Stevens, 1929; Tate III, 1995) or quality (recalcitrance) (Fontaine et al., 2003); or by N, as a resource for synthesizing either cellular biomass or extracellular enzymes. Limited extracellular enzyme production may drive

secondary C-limitation regardless of the potential C supply (Fontaine et al., 2003; Schimel and Weintraub, 2003).

Separating these different mechanisms requires more sophisticated analyses than simply measuring changes in respiration with C or N-additions. For example, if microbial growth is moderately N-limited, adding C can stimulate microbial respiration without affecting growth, while adding N can reduce respiration but increase growth (Schimel and Weintraub, 2003). If N-limitation is severe however, we hypothesize that adding N would increase extracellular enzyme production and stimulate both respiration and microbial growth. Understanding the nature of microbial responses to additions of limiting resources requires distinguishing the responses of enzyme production, shifts in cellular C-allocation, and overall respiration. Misrepresenting the responses to added resources on microbial processes could misestimate the impact of changing nutrient availability on decomposition dynamics.

To determine whether microbial activity is N limited in an Arctic tundra soil, and to assess the intensity and mechanisms of response to limitation, we performed a laboratory incubation study on soil from an Alaskan tussock tundra site. To ensure that the observed responses to N-addition were due to N as a limiting resource (and not C quality), we contrasted the responses of labile N- and C-addition to soil microbial processes. We used two different concentrations of C and N, and assessed their effects on: respiration, substrate-use efficiency (SUE), cellulase activity, and microbial biomass, which are key indices of the functioning of the soil's microbial community. We hypothesized that summer-collected tussock tundra organic horizon soil is highly N-limited from the microbial perspective, such that adding a labile N source to them will stimulate decomposition by increasing the community's SUE, thereby shifting C allocation towards greater growth and extracellular enzyme synthesis. We postulated that this effect would increase with greater N substrate concentration. In contrast, we hypothesized that additional C would not increase the tundra soil's microbial growth or SUE, although C-mineralization may be stimulated by microbial processing of newly available highly labile C.

2. Materials and methods

2.1. Site description

Experimental soils were collected from moist acidic tundra (MAT) near Toolik Lake, Alaska, USA (68°38'N, 149°34'W). MAT forms on old glacial surfaces (>11,000 years BP). The tussock-forming sedge *Eriophorum vaginatum* L. drives the formation of regular vegetation patterns, with deciduous shrubs, forbs, and herbaceous plants growing between the tussocks. The vegetation in the experimental area is similar to MAT across the Alaskan North Slope, northern Canada, and eastern Siberia (Oechel et al., 1993). There is approximately 0.9×10^6 km² of MAT tussock tundra worldwide (Oechel et al., 1993).

MAT soil is classified as coarse-loamy, mixed, acidic, gelic Typic Aquiturbels (Romanovsky et al., 2011). Mean air temperature during the June–August growing season is 9 °C, with a mean annual temperature of –8.5 °C and total precipitation is on average 350 mm (Deslippe and Simard, 2011). In the growing season, soil temperatures rapidly decline with depth, ranging from 10 to 20 °C at the surface to 0 °C at the bottom of the seasonally thawed active layer, which varies from 30 to 60 cm depth in late July (Shaver et al., 2006).

2.2. Soil collection and initial storage

Eight field replicate soil samples were taken from MAT tundra in July 2002, along random points of arbitrarily laid transects following the methods of Weintraub and Schimel (2003). We

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