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Microbial activity is not always limited by nitrogen in Arctic tundra soils

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ABSTRACT

Both primary productivity and decomposition appear to be limited by low soil nitrogen (N) availability throughout much of the Arctic tundra active growing season, making these ecosystems among the most N-limited in the world. Climate warming may potentially stimulate microbial activities such as N mineralization, which could have cascading long-term effects on Arctic tundra ecosystems. Despite previous evidence of N limitation to microbial decomposition in Arctic tundra, N may not limit microbial activity throughout the entire active season. Labile carbon (C) may be co-limiting for portions of the active season when there is relatively high inorganic N and/or low labile C availability. To assess seasonal variation in the controls on microbial activity, we conducted a series of laboratory incubations with soils collected at the beginning and peak of the active season in two years to examine intra-seasonal and annual variability of soil microbial N limitation in an Arctic moist acidic tundra (MAT) soil. The soil incubations were set-up in a factorial design with treatments of added N or DI water as a control and incubation temperatures of 5 °C and 15 °C. We measured chloroform-labile C and N (as a proxy for microbial biomass), extractable nutrients, C-mineralization and potential enzyme activities. In contrast to previous studies, we found that these metrics of microbial activity were not consistently stimulated by N additions; rather, added N was primarily immobilized by microbes resulting in decreased chloroform-labile C:N ratios. Stimulation of C mineralization by N addition was short-lived and variable between our two sampling dates within a single active season. Additionally, there were differences in temperature sensitivities of C mineralization and contrasting effects of N amendment on enzyme activities between the two study years. These findings suggest that, at times, other factors co-limit microbial activities in MAT soils. The current dogma of universal N-limitation to microbial activity may need to be refined in light of these results, to more accurately predict the fate of the large amounts of C currently sequestered in Arctic tundra soils.

1. Introduction

Arctic tundra ecosystems are believed to be among the most nitrogen (N)-limited in the world. Limited concentrations of available inorganic soil N throughout much of the active growing season (Hobbie and Gough, 2002; Hole, 2004; Weintraub and Schimel, 2005a) occurs due to low rates of N mineralization (Marion and Miller, 1982) and rapid uptake of available N by both plants and microbes (Schimel and Chapin, 1996; Schmidt et al., 1997; Jonasson et al., 1999a; Hole, 2004). Primary productivity (Chapin et al., 1995; Shaver et al., 2001; Gough et al., 2012), microbial decomposition

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(Mack et al., 2004; Sistla et al., 2012), growth of microbial biomass (Sistla et al., 2012), and extracellular enzyme production (Wallenstein et al., 2009; Sistla et al., 2012) have all been shown to be N-limited during the more biologically active Arctic summer season. However, the climate is warming more rapidly in the Arctic than any other region on earth, which could stimulate N mineralization and lead to a cascade of changes in ecosystem structure and function (Schimel et al., 2004; Elberling, 2007).

If N mineralization rates increase in Arctic tundra due to climate warming, the closely coupled carbon (C) cycle may also be affected, with implications for C balance and storage (Weintraub and Schimel, 2003; Mack et al., 2004; Nowinski et al., 2008). Arctic soils and permafrost contain nearly half of the total global soil organic carbon (SOC) pool (Tarnocai et al., 2009). Decomposition of C-rich soil organic matter (SOM) is inhibited for much of the year by high soil moisture and low temperatures, which limits microbial activity and has resulted in the accumulation and persistence of large amounts of mineralizable SOM (Weintraub and Schimel, 2003; Shaver et al., 2006) and low soil nutrient availability (Hobbie and Gough, 2002; Hole, 2004; Weintraub and Schimel, 2005a). However, climate change is ameliorating the environmental constraints on decomposition in Arctic soils. Terrestrial surface air temperatures in the Arctic have increased at nearly twice the global rate (McBean et al., 2005; Anisimov et al., 2007), with the greatest air temperature increases in these areas being experienced during the winter and spring seasons (Serreze et al., 2000). Many important functional changes occur during these seasonal transition periods in Arctic ecosystems, including turnover of microbial communities and shifts in the N cycling processes they mediate (Ernakovich et al., 2014). Increased air temperatures, as well as elevated winter soil temperatures, potentially allow for greater microbial activity over the course of the winter season when the majority of annual N mineralization occurs in the Arctic (Schimel et al., 2004). Greater N mineralization during cool seasons could result in greater soil N availability during the active summer season, which may differentially affect early season and peak season soil microbial processes.

Arctic soils experience extreme seasonal climatic variation and exhibit strong seasonal patterns of biogeochemical cycling (Weintraub and Schimel, 2005a; Buckeridge and Grogan, 2008). Under colder conditions, microbial communities preferentially process labile, N-rich microbial byproducts and net N mineralization occurs (Schimel and Mikan, 2005), while during the warmer active season microbial decomposition of recalcitrant SOM and nutrient-poor plant detritus is prevalent (Baisi et al., 2005; Schimel and Mikan, 2005) resulting in net N immobilization. Additionally, available amino acids and inorganic forms of soil N have been shown to vary throughout the active summer season (Hobbie and Gough, 2002; Weintraub and Schimel, 2005a) with greater N availability early in the growing season followed by a sharp decline mid-season (Weintraub and Schimel, 2005a). This active season decline in available soil N may be attributable to greater plant uptake of soil nutrients during the peak growing season, changes in microbially-driven N mineralization and immobilization (Weintraub and Schimel, 2005b), and/or fluctuating amounts of labile N found in spatially inaccessible pools (Darrouzet-Nardi and Weintraub, 2014).

While N has been demonstrated to be limiting to primary productivity and microbial activity in Arctic ecosystems, the microbial controls on N mineralization and the feedbacks between active-season N variability and microbial activity, as well as temporal variation in these relationships, are still poorly understood. Previous measurements of seasonal variation in active season N availability suggest microbial activity may be most N limited when temperatures are highest at the peak of the active season (Weintraub and Schimel, 2005a,b). However, Song et al. (2010) found temperature sensitivity of SOM decomposition in alpine soils to be positively correlated with labile C availability regardless of soil N availability. This suggests that other factors affecting temperature sensitivity of SOM decomposition may limit the effect of soil temperature on microbial N limitation in Arctic soils. In contrast, the strong seasonality of soil dynamics suggests that patterns of N limitation of microbial processes and biogeochemical cycles should be consistent across years, but no multi-year data sets exist to test this.

To assess seasonal and annual variation in the factors that control microbial C and N cycling, we conducted multiple laboratory-based soil incubations. We addressed the following questions: (1) How does microbial N limitation vary between early and peak season soils within a single active season? (2) Do seasonal patterns in microbial N limitation vary between consecutive growing seasons? and (3) To what extent does soil temperature drive variability in microbial N limitation? Based on previous observations of N variability and temperature effects on microbial activities, we expected to see greater N induced stimulation of microbial activity in soils collected during the peak season than in early season soils, with little variability across years. We also predicted that soils would exhibit greater temperature sensitivity with increased N. In order to answer these questions and test these predictions, we collected soils at two time points during the active season, shortly after thaw and at the peak of the active season, for two consecutive years and conducted laboratory incubations at 5 °C and 15 °C. These experiments shed new light on the extent and drivers of temporal variability of N limitation of microbial activities within Arctic tundra ecosystems.

2. Methods

2.1. Site description

Soil samples were collected from a moist acidic tundra (MAT) site 11 km east of Toolik Field Station at Imnavait Creek (68° 37′ 37″N, 149° 19′ 11″W) on the north slope of the Brooks Range in Alaska. The site consisted of typical MAT tussock vegetation, which is dominated by the tussock forming sedge *Eriophorum vaginatum* L. with primarily mosses (*Sphagnum rubellum* and *Hylocomium splendens*), deciduous shrubs (*Betula nana* and *Salix pulchra*), graminoids (*Carex bigelowii*), and evergreen shrubs (*Vaccinium vitis-idaea*) found between tussocks. The organic soil layer of MAT varies from 0 to 20 cm thick and is composed primarily of the decomposing roots of *E. vaginatum* tussocks (Shaver and Chapin, 1991). Globally, MAT covers approximately 900,000 km^2 (Oechel et al., 1993), with areas of tussock-dominated vegetation similar to our research site found throughout the Northern Slope of Alaska, northern Canada, and eastern Siberia (Bliss and Matveyeva, 1992). The average winter soil temperature and snow depth were determined for both 2010 and 2011 at our study site. Winter soil temperatures were measured at a soil depth of 5 cm from January 1 to April 30 across the sample site. Snow depth was assessed at 60 points near sampling sites in mid-May shortly before the onset of snowmelt.

2.2. Sample collection, preparation, and storage

MAT tussock organic soil samples were collected at the Imnavait site over two consecutive years with sample dates targeting the beginning of the active growing season and the peak time of plant productivity and nutrient demand. Five field samples were collected early in the morning on the dates of June 1,