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Tracking the fate of fresh carbon in the Arctic tundra: Will shrub expansion alter responses of soil organic matter to warming?

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ABSTRACT

Rapid climate warming in the Arctic threatens to destabilize vast stocks of soil carbon (C) that have accumulated over millennia, which could amplify the C-climate feedback. However, climate-induced shrub expansion may counteract these losses if their higher-quality litter (lower C:N) is efficiently incorporated into microbial products and stabilized within the soil. Alternatively, increased C inputs could stimulate microbial decomposition of old soil organic matter (SOM) through priming mechanisms. We investigated whether inputs of low molecular weight carbon (LMW-C) induced SOM priming or retention in soils underlying *Eriophorum vaginatum*, an ubiquitous tussock-forming sedge, and *Betula nana,* a dominant shrub that is expanding its range and coverage across the Arctic. We did not find evidence of priming, defined as an increase in the decomposition of native SOM stocks, from soils underlying either vegetation type. However, microbial respiration of new LMW-C inputs was twice as high in soils underlying *E. vaginatum* than *B. nana,* while belowground retention of new LMW-C inputs was 150% higher in soils underlying *B. nana.* Our results highlight the extraordinary capacity of shrub-colonized soils to retain new C inputs belowground, which may mitigate soil C loss as the Arctic climate warms.

1. Introduction

The vulnerability of vast carbon (C) stocks stored in Arctic soils to rapid climate warming is widely recognized (Crowther et al., 2016; Mack et al., 2004). But, climate warming is also increasing plant productivity, which could either ameliorate or enhance soil C loss (Natali et al., 2012; Sistla et al., 2013). The potential for C inputs to balance losses will depend on how efficiently plant-derived C is incorporated into microbial products, the precursor of soil organic matter (SOM) formation, *versus* converted to CO_2 and released to the atmosphere (Cotrufo et al., 2013). In addition, new plant litter and root exudate inputs might enhance the decomposition of old SOM through a process known as priming (Fontaine et al., 2003; Kuzyakov, 2002). Thus, enhanced plant productivity in the Arctic could either promote the formation of new soil C, or increase losses of native soil C, making vegetation responses to warming a critical regulator of global C cycling.

The net effects of rapid climate change on Arctic soil C stocks are mixed, with evidence of massive greenhouse gas release to the atmosphere (Commane et al., 2017; Crowther et al., 2016; Mack et al., 2004; Schuur et al., 2008), as well as recovery of soil C stocks following perturbation (Jiang et al., 2015; Natali et al., 2012; Sistla et al., 2013). Several responses to warming will likely modulate the balance between C release and storage. Warmer winters (Christensen et al., 2013) are degrading permafrost and deepening active layer thaw depths (Hodgkins et al., 2014; Liljedahl et al., 2016), which could expose newly liberated C to rapid microbial metabolism (Mackelprang et al., 2011; Marín-Spiotta et al., 2014). At the same time, lengthening growing seasons (Ernakovich et al., 2014; Livensperger et al., 2016) have fundamentally altered vegetation composition and productivity (Chapin et al., 1995; Deslippe and Simard, 2011; Sturm et al., 2001), the effects of which are diffusing belowground (Hartley et al., 2012). Specifically, greater plant productivity is expected to increase the release of root exudates belowground (Brüggemann et al., 2011), which are primarily composed of low molecular weight C compounds (LMW-C) (Jones et al., 2009). These LMW-C compounds may stimulate decomposition of native SOM (Hartley et al., 2012; Mack et al., 2004) by inducing a positive priming effect to relieve microbial nutrient limitation (Kuzyakov, 2002). As a result, greater extracellular enzyme

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production could increase nutrient mobilization from native SOM and contribute to net soil C loss (Kuzyakov, 2010). Alternatively, new LMW-C inputs could reduce SOM turnover if microbial substrate use efficiency (SUE) increases and microbial products are stabilized through organo-mineral complexation (Cotrufo et al., 2013; Kallenbach et al., 2016; Schmidt et al., 2011).

The influence of vegetation on belowground nutrient availability may influence the net effect of LMW-C inputs on soil C stocks (Hartley et al., 2012). Widespread increases in primary productivity have been attributed to rapid expansion of *Betula nana* shrubs (Sturm et al., 2001). The success of these shrubs is facilitated by phenotypic traits that allow them to outcompete other species, including *Eriophorum vaginatum,* a dominant tussock-forming sedge (Bret-Harte et al., 2001; Chapin et al., 1995; Deslippe and Simard, 2011; Koyama et al., 2013; Shaver et al., 2001; Sistla et al., 2013). These traits include developmental plasticity (Bret-Harte et al., 2001), formation of N-acquiring and C-sharing ectomycorrhizal networks (Deslippe and Simard, 2011), and snow entrapment, which facilitates over-winter SOM mineralization and release of nutrients for shrub uptake the following spring (Schimel et al., 2004; Sturm et al., 2001). Associations between *B. nana* and N-acquiring ectomycorrhizal networks increase shrub litter and soil N concentrations (Deslippe and Simard, 2011) relative to non-mycorrhizal, N poorer, *E. vaginatum* systems (Sullivan et al., 2007). The difference in N availability belowground could increase the magnitude of priming resulting from new LMW-C inputs in *E. vaginatum* soils, particularly during peak plant productivity when nutrient competition is intensified (Zhu et al., 2016). Thus, cascading effects of *B. nana* expansion may release microbial energetic and nutrient constraints relative to *E. vaginatum* soils, reducing the magnitude of SOM priming.

To test the effect of LMW-C inputs on native soil C stocks, we applied ^{13}C-enriched glucose—a model root exudate (Dijkstra et al., 2011; Strickland et al., 2012)—to Arctic tundra soils underlying *E. vaginatum* and *B. nana*. We used two-pool isotope mixing models to track the proportion of LMW-C converted to CO_2, assimilated in microbial biomass, transformed to dissolved organic matter, and retained in bulk soil. We captured the influence of season on LMW-C fate by amending soils in July (peak biomass), September (senescence), and May (spring thaw). To determine whether LMW-C persisted longer-term, we measured responses 54 and 306 days following amendment. We posit that the fate of LMW-C and the magnitude and direction of priming is driven by SOM stoichiometry (e.g. C:N). With this rationale, we test three predictions: (1) LMW-C input increases SOM turnover, with the largest priming effect—and lowest microbial SUE—in higher C:N soils underlying *E. vaginatum*; (2) the magnitude of these effects vary seasonally and are negatively correlated with soil N concentrations; (3) the proportion of LMW-C retained belowground is positively correlated with microbial SUE.

2. Methods

2.1. Site description

We established study plots in May 2014 in a moist acidic tundra site near Toolik Lake Field Station, Alaska, USA (68° 38′N, 149° 34′W). Mean annual temperature at Toolik Field Station is −8 °C, with average summer temperatures near 10 °C and average winter temperatures near −20 °C (Hobbie and Kling, 2014). Mean annual precipitation is 318 mm, with 43% falling as snow (Schimel et al., 2004). The region is dominated by *Eriophorum vaginatum,* a tussock forming sedge, *Betula nana,* a dwarf birch, and mosses, which together comprise approximately 45% of above and belowground biomass (g m^{-2}) (Hobbie and Chapin, 1998). The soils are classified as Ruptic Histic Aquiturbels (Borden et al., 2010) and have an average pH of 4.9. Average soil C stocks in the top 20 cm were 2150 ± 335 g C m^{-2} in soils underlying *B. nana* and 2282 ± 296 g C m^{-2} in soils underlying *E. vaginatum.* We observed the deepest active layers at our plots in July 2014, averaging 10 cm beneath *B. nana* and > 20 cm beneath *E. vaginatum.* Unfortunately, we did not measure species-specific soil temperatures, however previous research has shown temperatures are similar between graminoid and shrub dominated communities (Bradley-Cook et al., 2016). Thus, although areas colonized by dense, tall shrubs may increase latent heat fluxes (McFadden, 1998) and could reduce temperatures relative to within-tussock soils (Chapin III et al., 1979), these effects are not always propagated belowground (Sturm et al., 2001).

We selected three time periods for our study that represent important seasonal stages in the Arctic: peak productivity (July 24–August 6, 2014), senescence (September 6–September 18, 2014), and thaw (May 19–May 30, 2015). Precipitation and temperature data for each sampling period were acquired from the Toolik Long Term Ecological Research database (Shaver and Laundre, 2010). Cumulative precipitation was 39.6 mm during peak plant productivity, 2.0 mm during senescence, and 55.3 mm during thaw. Mean soil temperatures at 5 cm depth were 9.1 (± 0.6)°C during peak plant productivity, 3.0 (± 0.5)°C during senescence, and 6.65 (± 0.3)°C during thaw. Average annual precipitation and soil temperatures are reported for 2014, 2015, and the ten-year average (2005–2015) in SI Table 1.

2.2. Experimental design

Our experiment consisted of three factors: vegetation type (*B. nana* or *E. vaginatum),* LMW-C addition (amended or control), and month (July, September, or May). We replicated each treatment four times in a fully randomized block design, where each 5 × 5 m^2 block was spaced 10 m apart. Our experimental unit was a PVC collar (10 cm diameter and 15 cm tall), which we installed around a tussock or shrub plant, maintaining a minimum spacing of 1 m between collars.

We installed 12 collars in each block (2 vegetation types * 2 additions * 3 months) in May 2014 and let them equilibrate for 45 days before amending soils within treatment collars with LMW-C. Soils were amended July 28, 2014, September 11, 2014, or May 22, 2015. We amended each collar with ^{13}C-enriched (10 atom%) glucose solution at 640 μg C g^{-1} soil. This corresponded to approximately 36 g glucose m^{-2}, assuming a 10 cm organic horizon and a bulk density of 0.075 g cm^{-3}. The LMW-C addition increased average soil C concentrations in the top 20 cm by 1.7%; we selected this relatively low tracer concentration to avoid inducing a direct C fertilization effect and to minimize impacts on ongoing metabolic processes (Dijkstra et al., 2011). To achieve even distribution throughout the amended soil profile, we added 5 ml of substrate with a 20-gauge needle (Becton Dickinson) at five equidistantly spaced points, continuously injecting substrate from 5 cm depth to the soil surface.

Two additional collars were installed around *B. nana* and *E. vaginatum* plants in each block allowing us to monitor the influence of elevated LMW-C availability on intermediate and long-term Arctic C cycling. These collars were amended July 28, 2014 and harvested either 49 days (September 11, 2014) or 306 days (May 30, 2015) following amendment. Control collars in each block remained undisturbed for the duration of the experiment and were used as background end members in the two-pool isotope-mixing model (see *Data Analysis*).

2.3. CO_2 measurements

LMW-C amended and control (non-amended) soils were measured in the field for CO_2 concentrations (ppm) and $^{13}CO_2$ enrichment (‰) using a Picarro G2101-*i* (Picarro Inc., Sunnyvale, CA, USA) portable cavity ring-down spectroscopy analyzer (CRDSA). The CRDSA was frequently calibrated using high-purity CO_2 calibrant gas with a range of CO_2 concentrations and isotopic values (Cambridge Isotope Laboratories CLM-3783-10; Airgas UHP300). CO_2 concentrations and ^{13}C- CO_2 isotope values were validated with a Li-Cor LI 6252 Infrared gas analyzer (Li-Cor Inc., Lincoln, NE, USA) and a PreCon Delta V IRMS coupled to a GC-isolink unit (Thermo Scientific, Waltham, MA, USA) at