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The seasonal pattern of soil microbial community structure in mesic low arctic tundra

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ABSTRACT

Soil microorganisms are critical to carbon and nutrient fluxes in terrestrial ecosystems. Understanding the annual pattern of soil microbial community structure and how it corresponds to soil nutrient availability and plant production is a fundamental first step towards being able to predict impacts of environmental change on ecosystem functioning. We investigated the composition, structure and nutrient stoichiometry of the soil microbial community in mesic arctic tundra on 9 sample dates in 6 months from winter to fall using phospholipid fatty acid analysis (PLFA), quantitative polymerase chain reaction (qPCR), epifluorescent microscopy and chloroform-fumigation–extraction (CFE). PLFA analysis indicates that the winter microbial community was fungal-dominated, cold-adapted and associated with high C, N and P in the soil solution and microbial biomass. The microscopy data suggest that both bacteria and fungi were active and growing in soils between −5 °C and 0 °C. A significant shift occurred in the PLFA data, qPCR patterns, microscopy and microbial biogeochemistry after the thaw period, resulting in a distinct community that persisted through our spring, summer and fall sample dates, despite large changes in plant productivity. This shift was characterised by increasing relative abundances of certain bacteria (especially Gram +ves) as well as a decline in fungal biomass, and corresponded with decreasing C, N and P in the soil solution. The summer period of low substrate availability (plant–microbe competition) was associated with microbial indicators of nutritional stress. Overall, our results indicate that tundra microbial communities are clearly differentiated according to the changes in soil nutrient status and environmental conditions that occur between winter and post-thaw, and that those changes reflect functionally important adaptations to those conditions.

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1. Introduction

Soil microorganisms are critical to carbon and nutrient fluxes in terrestrial ecosystems. Microbial processing of soil organic matter is determined directly by environmental conditions, and may be indirectly affected by changes in environmental conditions or substrate availability on the composition and relative abundances of the microbes (i.e. the community structure) – for *some* metabolic pathways at least (Schimel et al., 1995; Rinnan et al., 2007). Although the influences of changes in temperature and moisture on microbial activities have been extensively investigated (McKane et al., 1997; Hobbie et al., 2002; Davidson and Janssens, 2006), we know extraordinarily little about the consequences of environmental change for microbial community structure. Therefore, our ability to predict impacts of perturbations such as climate change on microbial structure and function is greatly hindered (Schimel and Gulledge, 1998). Investigating microbial community change is particularly important in Arctic surface soils, where there are strong fluctuations in annual environmental and biogeochemical conditions (Buckeridge and Grogan, 2010), high ecosystem sensitivity to changes in seasonal climate (ACIA, 2005), and a very large and sensitive soil carbon pool that has the potential to impact global atmospheric carbon pools (Schuur et al., 2008; Tarnocai et al., 2009). To date, there have been very few characterisations of Arctic tundra microbial community structure over time (Wallenstein et al., 2007) and only one (from alpine tundra) that linked an observed seasonal switch between fungi in winter and bacteria in summer (Schadt et al., 2003) to a shift in microbial decomposition from recalcitrant to labile substrates respectively (Lipson and Schmidt, 2004). We are still uncertain if larger fungal

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biomass over winter is the result of enhanced winter fungal growth, or residual (frozen) high fall fungal biomass, or if this seasonal shift occurs in non-alpine tundra ecosystems.

Apart from potential shifts in microbial community composition, seasonal variation of the total microbial biomass and the nutrients stored within that biomass in Arctic soils can drive seasonal patterns of nutrient cycling (Wardle, 1998; Jonasson et al., 1999; Schimel et al., 2007; Schmidt et al., 2007). In addition, the synchronicity – or lack of it – between microbial biomass patterns and plant primary production may have consequences for ecosystem-wide nutrient retention. Several authors have proposed that this is a particular concern during the thaw period at the end of snowmelt (Brooks et al., 1998; Jaeger III et al., 1999; Grogan and Jonasson, 2003), when there is a rapid decline in the microbial biomass C, N and P and plant uptake is negligible (Edwards et al., 2006; Buckeridge and Grogan, 2010). In fact, this period may be the most stressful phase in the entire annual cycle for microbes in the surface soil environment because of the physiological impacts of rapid temperature and severe osmotic pressure changes as wet-up occurs (Skogland et al., 1988; Schimel and Clein, 1996; Schimel et al., 2007; Jefferies et al., 2010). In addition, belowground trophic interactions such as increased mesofaunal predation through enhanced soil pore-space connectivity as soil water melts during the thaw period may also contribute to microbial species or functional group turnover (Wardle, 2002). In this study, we investigated the seasonal pattern of the soil microbial biomass, and community structure as well as principal nutrient pools from winter through fall in a mesic low arctic tundra ecosystem. We deliberately sampled from the pre- to post-thaw period at relatively high frequency compared to previous studies to determine if the dynamic environmental fluctuations at that time result in significant changes in the soil microbial communities.

Soil microbial biomass investigations can be accomplished in many ways, with varying agreement between methods (Balkwill et al., 1988; Zelles et al., 1992; Zogg et al., 1997; Bardgett and McAlister, 1999; Fritze et al., 2000; Grayston et al., 2001; Rogers and Tate, 2001). Discrepancies are common and not surprising because many techniques measure different aspects of the soil microbial community. For instance, variation in biomass (total microbial C), may not agree with variation in activity and growth (gene copy numbers). Both of these results may be clouded by changes in community; biomass may increase even as cell abundances decrease if many smaller bacterial cells are being replaced by larger bacterial cells or fungal hyphae. Increased activity may not be evident as increased gene copy numbers if community shifts occur between microbes with many gene copy numbers per cell to microbes with fewer gene copy numbers per cell. However, a combination of methods can provide a more complete description of the microbial community structure than any single method (Strickland and Rousk, 2010). In this study, we measured soil environmental properties and soil carbon, nitrogen and phosphorus pools over nine dates from winter to fall, and used four different methods (chloroform-fumigation, epifluorescent microscopy, phospholipids fatty acid analysis (PLFA) and quantitative polymerase chain reaction (qPCR) of taxon-specific rRNA) to characterize the soil microbial biomass and microbial community structure. With this study we investigated the following hypotheses in low arctic birch hummock tundra:

1. The soil microbial community structure of mesic arctic tundra displays community shifts, functional group crashes and new growth during the thaw period between winter and early spring.
2. Fungal biomass and 18S ITS gene copies in mesic arctic tundra soils are more abundant than bacterial biomass or 16S gene copies in winter and become less dominant in summer.
3. The pre-thaw and post-thaw microbial communities indicate functional group changes that are consistent with the differing environmental conditions of winter as compared to spring, summer and fall.

2. Methods

2.1. Site description and experimental design

This study was conducted in the winter, spring, summer and fall of 2007 at the Tundra Ecological Research Station (TERS) at Daring Lake, Northwest Territories, Canada (64° 50′N, 111° 38′W), 300 km northeast of Yellowknife, in the Coppermine River watershed. The mesic birch hummock ecosystem of our study is located in a valley, midway along a catena. The climate, soils and vegetation-types along this moisture gradient have a circumpolar distribution and this particular site has been previously described (Nobrega and Grogan, 2007, 2008; Buckeridge and Grogan, 2008, 2010; Lafleur and Humphreys, 2008).

2.2. Soil sampling protocol

Daily mean soil temperature was monitored at 5 cm depth over the winter and spring, summer and fall ($n = 4$), using CR 10X dataloggers (Campbell Scientific, Logan, UT). Soil water content was measured gravimetrically (i.e. total water content as ice plus liquid) on each collected soil sample to ~5 cm depth. Snow depth, soil volumetric water content and air temperature were measured as described in Buckeridge and Grogan (2010). All sampling and monitoring occurred in the organic horizon, where the majority of plant rooting and biogeochemical cycling occurs in this ecosystem (Churchland et al., 2010).

Soil samples ($n = 5$) were collected over 9 sample dates over six months, beginning in winter (day 100), when samples were quickly returned to the lab at Queen's University by the next evening and kept just below 0 °C until processing on the following day. Further field samples were collected: in late winter (day 130); in early thaw, at the start (day 139) and end of snowpack thaw (day 147); in late thaw, when soils were just above 0 °C (day 157); in spring (day 169); in late spring, just after the start of bud break of the dominant shrub, *Betula glandulosa* (day 179); in mid-summer (day 192); and in early fall, just after the start of *B. glandulosa* leaf senescence (day 244).

Sampling details have been previously described (Buckeridge and Grogan, 2010). Briefly, sample characteristics such as aboveground vegetation were not pre-selected, but determined by the location of the base of the snowpit. Deep hollows and tall hummocks were avoided and thus interhummock areas were favoured. As thaw approached and vegetation was revealed, this sampling protocol was maintained. Therefore our results incorporate some of the tundra heterogeneity associated with hummocks, interhummocks and hollows. Soil samples were collected from frozen soils by hammering an axe to the depth of the organic layer (average depth 5.3 cm, range 2.9–9 cm), or by cutting out the organic layer with a knife in thawed soils. All samples were stored overnight in plastic bags in a cooler in the field lab then processed the following morning (soils were maintained frozen if collected frozen). Aboveground vegetation and litter was cut off at the moss green-brown transition, soil was chopped (frozen) or crumbled (thawed) into small pieces, large roots were removed, and soils were subsampled for immediate biogeochemical or microbial extraction. We minimized soil handling during soil mixing to limit disturbance of the soil microbial community in the lab at Queen's University and in the field. We were particularly careful to prevent thawing the frozen soils before extraction

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