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Inter-annual and seasonal dynamics of soil microbial biomass and nutrients in wet and dry low-Arctic sedge meadows

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ABSTRACT

Biogeochemical activity occurs year-round in arctic soils, and previous studies from both alpine and arctic tundra sites have revealed that soil microbial biomass (MB) in the active layer reaches an annual peak in winter, and decreases during or shortly after soil thaw. This decline occurs concurrently with, or is followed by, a peak in soil nutrients that provide an important nutritional resource for plant growth. We documented both intra- and inter-annual MB and nutrient patterns in wet and dry sedge meadows near Churchill, Manitoba, Canada between June 2004 and June 2008. Intensive sampling occurred during the winter-spring transition and soils were analyzed for MB, microbial nitrogen, dissolved organic carbon and nitrogen, and inorganic nitrogen. A consistent seasonal pattern was observed wherein large winter MB pools responded negatively to winter warming event, and decreased steeply during soil thaw, suggesting that soil physical factors drive the observed microbial declines. Nutrient pools showed similar seasonal fluctuations, however a post-thaw nitrogen increase was observed in 2006, but not in other years. Inter-annual patterns were similar between wet and dry sedge meadows, including relatively low peak values of all variables by 2008 in both ecotypes, which could be related to observed hydrological changes. As northern climates continue to change, seasonal biogeochemical events that affect the timing and magnitude of nutrient pulses will be altered, with important implications for primary productivity and ecosystem functioning.

1. Introduction

Below-ground microbial activity, and therefore soil organic matter decomposition, occurs in frozen soils during the cold seasons of seasonally frozen environments, and in the active layer of perennially frozen landscapes (Hobbie and Chapin, 1996; Fahnestock et al., 1999; Larsen et al., 2007; Schmidt et al., 2007). Unfortunately, there have been few below-ground biogeochemical studies outside of the growing season in arctic and sub-arctic ecosystems, resulting in a poor understanding of annual patterns and processes despite a desperate need to understand the impacts of changing seasonal weather patterns on these landscapes. Integrating an understanding of these intra-annual (i.e. seasonal) soil microbial and biogeochemical dynamics with inter-annual variation is a key challenge toward understanding current and future impacts of climate change on the ecological functioning of cold regions.

Microbes in frozen arctic ecosystems survive in thin films of unfrozen water when the bulk soil water is frozen. The activity of these 'eutechtophiles' (Deming, 2002) is limited by temperature effects on biochemical processes and indirectly by limited transport of substrates and waste products (Deming, 2002; Agren and Wetterstedt, 2007; Oquist et al., 2009). Microbial processes may be significantly slowed for a period of deep cold in the winter in areas where soil temperatures are below −10 °C (Price and Sowers, 2004), but activity increases again when soils warm above −10 °C, often well before snowmelt (Clein and Schimel, 1995; Brooks et al., 1997; Larsen et al., 2007). Winter microbial respiration results in significant carbon (C) losses from arctic sites during the long cold season, which may result in some sites being a net C source to the atmosphere (Fahnestock et al., 1999; Oechel et al., 2000; Welker et al., 2000; but see Aurela et al., 2004). More specifically, the highest rates of CO_2 production occur during the shoulder seasons rather than during the period of deep cold (Aurela et al., 2004; Brooks et al., 2004; Sullivan et al., 2008) so an understanding of this winter-time C efflux calls for careful examination of both freeze-up and thaw seasons.

When soils thaw, a shift in the microbial community can occur, as observed in alpine tundra sites (Lipson et al., 2002; Schadt et al.,

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2003; Lipson and Schmidt, 2004). The transition from winter to spring to summer is also accompanied by increasing rates of microbial biomass (MB) turnover (Schmidt et al., 2007; Buckeridge and Jefferies, 2007) and changes in substrate use by the microbial community (Lipson et al., 2002; Schimel and Mikan, 2005; Schmidt et al., 2007). Plant root exudates supply labile C in summer, while winter microbes utilize dead plant material (Grogan et al., 2001; Lipson et al., 2002; Schmidt et al., 2007) and microbial cellular products (Schimel and Mikan, 2005). Following plant senescence at the end of the summer, microbes decompose readily available plant litter, while competition for mineral nutrients from plants is waning (Grogan et al., 2001; Nemergut et al., 2005; Schmidt et al., 2007).

Despite ample evidence of microbial activity in winter in cold regions, few studies have measured the changes in microbial and nutrient pool sizes in the active layer of these terrestrial soils outside of the summer growing season. Since they represent the net balance of influx and efflux, tracking these pools can help to highlight periods of changing functional processes, and potential for movement of elements between pools, for example accumulated inorganic nitrogen may be quickly sequestered by plants under the appropriate conditions. Studies conducted in alpine tundra (Lipson et al., 1999), sub-arctic birch forest and heath (Larsen et al., 2007), low-arctic mesic birch hummock tundra (Buckeridge and Grogan, 2010) and low-arctic wet sedge (Edwards et al., 2006) have all observed elevated levels of MB in winter, followed by a decline as soils thaw. The timing of nutrient fluctuations appears to differ across ecosystems, with pulses occurring after the onset of the MB decline in some systems (Brooks et al., 1998; Lipson et al., 1999; Larsen et al., 2007) while elsewhere nutrient availability declines concurrently with MB such that pulses are not detected in early spring (Edwards et al., 2006; Buckeridge and Grogan, 2010). Despite these interesting phenological variations in nutrient availability, winter MB peaks and changes in nutrient availability during the winter-spring transition are common features across these various systems, revealing a biogeochemical pattern that is widespread across seasonally frozen ecosystems.

We documented the seasonal dynamics of soil MB and nutrient pools for four years in wet and dry sedge-dominated tundra ecosystems near Churchill, Manitoba, Canada. Effort was focused on the transition between winter and spring, which is a dynamic time of year that is particularly sensitive to environmental changes (Olsson et al., 2003). As it precedes the summer growing season, this time of year is also important with respect to controls on plant productivity, as plant nutrient uptake can occur very early in spring in these ecosystems (Edwards and Jefferies, 2010). We recognize six different periods in discussing the arctic winter season (Olsson et al., 2003; Buckeridge and Grogan, 2010): early snow (soil temperatures near 0 °C), early cold (freezing of soils), deep cold (declining soil temperatures), late cold (modest increases in soil temperatures), early thaw (soil temperatures step up to approximately −5 °C), and late thaw (soil reaches near-zero temperatures and the soil water transitions to the liquid phase).

The following questions are addressed here: 1) Is the annual pattern of increasing MB and nutrients in winter followed by declines during thaw (Edwards et al., 2006) repeated across multiple years and between two different ecosystem types?; 2) Are inter-annual differences in microbial and nutrient dynamics common between different ecosystem types and therefore attributable to landscape-scale influences?

2. Material and methods

2.1. Site description

Study sites are located near Churchill, Manitoba, Canada, which lies within the ecological transition zone from sub-arctic boreal forest to low-arctic tundra; the sites studied here are representative of the latter landscape. Average monthly air temperatures for Churchill range from −27 °C in January to 12 °C in July, with average monthly precipitation ranging from 16 mm (February) to 68 mm (August) (1971–2000 climate normals; Environment Canada). Vegetation communities are dominated by *Carex aquatilis Wahlenb.*, a rhizomatous sedge that is not known to be mycorrhizal (Muthukumar et al., 2004). Three wet sedge meadow sites were sampled, two of which are adjacent to each other, located approximately 200 m apart (centered at N58° 44.040 W93° 48.365), and the third site being about 5 km away in a low-lying area near to the dry sites described below (N58° 44.783 W93° 53.100). These wet sedge meadows are characterized by the dominance and high productivity of *C. aquatilis*, which is nitrogen (N) and phosphorus (P) co-limited, and reaches an above-ground biomass of 140 g dry tissue m^{-2} (K. Edwards, unpublished data, collected 2004, 2005). The fibrous *C. aquatilis* root system inhabits an organic peat layer approximately 30 cm deep, which is underlain with a mix of sand, silt, and limestone fragments.

Dry sedge meadows included three adjacent sites approximately 500 m apart (centered at N58° 44.767 W93° 53.533), situated less than 1 km from the Hudson Bay coastline. The 5–15 cm of organic soil is underlain with sand. These sites can be saturated in spring, but are relatively dry in summer. *C. aquatilis* is the most abundant vascular plant species, but the flora is diverse relative to the wet sedge and includes *Scirpus caespitosus* L. ssp. austriacus (Pallas) Asch. And Graeb., *Andromeda polifolia* L., *Dryas integrifolia* M. Vahl, *Rhododendron lapponicum* (L.) Wahlenb., and *Salix reticulata* L. Above-ground *C. aquatilis* growth is limited by the availability of both N and P and above-ground biomass of this sedge reaches approximately 35 g dry tissue m^{-2} at the end of the growing season (K. Edwards, unpublished data, collected 2004, 2005).

Soil temperatures were measured in a wet sedge area containing some shrubs (*Salix* spp.) located within 200 m of two of the wet sedge sites used for soil sampling. Temperatures were recorded at 10 cm depth using a Campbell Scientific International CR10X datalogger with type T thermocouples. Readings were taken every 5 min to determine the minimum and maximum daily temperatures. Soil temperatures are not known for the dry sites because no temperature-recording equipment was in place during the time of this study in these or similar sites in the area.

2.2. Soil sampling

Soils were sampled between 11 June 2004 and 3 June 2008, totaling 53 sampling times in the wet meadows and 55 collections from the dry meadows. The majority of sampling dates are represented by six replicates, but fewer than this were collected on 20 Sep 2004, 25 Oct 2004, 1 Apr 2005, and 7 Apr 2005, 23 July 2005, 28 Apr 2006, 1 May 2006, and 15 May 2008, for various logistical reasons. In winter, samples were collected using an axe or CRREL SIPRE permafrost drill. When transport was required for processing (generally September to April), samples were air-freighted in the condition of sampling (either frozen or cold) and extractions were done at the University of Toronto, Canada, within 5 days of sampling.

The upper 1–2 cm of surface material was removed from the samples, including living plant material and litter. For dry site samples, the entire depth of the organic layer was used for extractions (usually less than 12 cm depth) while in the wet site only the upper 15 cm of soil was used. Soils were processed at field moisture levels and chemical extractions were done on soils without thawing. Frozen samples were cut into pieces no larger than 1 cm^3 prior to weighing and extraction using a knife and hammer. Large roots and sticks were removed prior to extraction and although soils were not thoroughly mixed, an attempt was made to portion the soil for all extractions in a representative way.