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Plant functional type affects nitrogen use efficiency in high-Arctic tundra

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ABSTRACT

To unravel the potential effects of climate warming on soil N availability in a high Arctic tundra ecosystem we studied temperature effects on soil mineralization, and N uptake from different soil depths (−3, −10 and −30 cm) by tundra plants. Uptake was assessed using ^{15}N tracer injected directly into mineral soil as $^{15}NH_4Cl$ solution to specifically mimic altered N availability from enhanced mineralization. Net N mineralization rates were very low, suggesting that N is strongly limiting in this system. There was no apparent temperature effect (−2 °C, 5 °C, 10 °C) on mineralization, but net nitrification was strongly limited by temperature – under the −2 °C treatment no nitrification occurred. As a consequence of ongoing mineralization and limited nitrification under freezing conditions, mineral NH_4 may accumulate during the winter season and be available for plant uptake without risk of loss via NO_3^- leaching immediately after snowmelt. Nitrogen uptake niches were clearly stratified by depth. Graminoids (*Carex misandra* and *Luzula arctica*) were most effective at taking up N from deep soil horizons, and recovery in graminoid biomass after one year was independent of ^{15}N injection depth. Recovery of N by the dwarf shrub *Salix polaris* was significantly higher following shallow application (−3 cm) compared to deeper treatments (−10 and −30 cm). Lichens and mosses also showed a decline in N uptake with application depth, and very little N was recovered by lichens and mosses even from −3 cm, in contrast to the strong uptake that has been observed in mosses when N is applied to the vegetation surface. The ability of graminoids to access nutrients from deeper mineral soil may give them an advantage over mosses and dwarf shrubs in warmer high Arctic tundra in acquiring limited available nutrient resources.

1. Introduction

Among the Earth's major biomes, the Arctic is responding most rapidly to global warming (Chapin et al., 2005; Spielhagen et al., 2011). Rising temperatures may cause perturbation in the terrestrial carbon balance due to permafrost thawing (Schuur and Abbott, 2011) and/or increased mineralization of organic matter, releasing plant growth limiting nutrients and thereby increasing the productivity of tundra plants (Sturm et al., 2001; Schimel et al., 2004; Chapin et al., 2005). The Arctic supports globally important biodiversity and has a major influence on the global climate, so it is important to understand how its ecosystems are likely to change in terms of soil carbon, plant cover and vegetation structure. Predicting plant responses to these changes depends on understanding the dynamics of N mineralization, uptake and transport during the short Arctic growing season.

Besides other environmental changes, increased nutrient availability is of key concern for future change in arctic vegetation (Dormann and Woodin, 2002). For example, it has been postulated that snow–shrub interactions have created a positive feedback whereby warming increases nutrient availability, leading to shrub growth and expansion, which in turn leads to deeper snow cover over the shrub canopy, raising winter temperatures and causing further nutrient release (Sturm et al., 2005). Recently, Myers-Smith and Hik (2013) found that abiotic influences of shrub canopy cover alone on nutrient dynamics were weaker than previously asserted. However, increases in temperatures predicted for high latitudes may not necessarily cause greater rates of nitrogen (N) mineralization (Nadelhoffer et al., 1991; Robinson, 2002).

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Despite generally lower net N mineralization in the Arctic compared to temperate ecosystems, N mineralization varies widely across different types of arctic ecosystems (Robinson et al., 1995). Thus understanding climate effects (altered soil temperature, moisture) on N availability is of great importance in strongly N-limited arctic ecosystems.

Based on a recent synthesis of warming experiments in the Arctic, Elmendorf et al. (2012) have shown that shrubs are expanding most in warmer tundra regions, whilst graminoids and forbs are expanding predominantly in colder tundra (areas with a mean July temperature <7 °C). They hypothesise that this might be due to the fact that the tallest growth forms in colder tundra areas tend to be herbs, which can easily prostrate dwarf shrubs, whereas the tallest growth forms in warmer tundra areas are woody (low and tall) shrubs. However, competition for light is only one aspect of interspecific plant competition, and the balance between plant functional types may be affected by availability of other resources. There is evidence for different and complementary strategies to meet N demand by different plant functional groups (Kahmen et al., 2006). Hitherto little attention has been paid to the potential separation of N acquisition niches in high Arctic soils, in contrast to studies in warm tundra (McKane et al., 2002; Grogan and Jonasson, 2003), or tropical and temperate ecosystems (Rowe et al., 2001; Göransson et al., 2008; Houle et al., 2014). The depth at which N uptake occurs is likely to have considerable effects on system-level N use efficiency (Jónsdóttir et al., 1995). Nitrogen availability near the surface will be relatively high during the spring thaw, as a result of N inputs from ice and mineralisation and because water is available (Fig. 1). However, near-surface water and N availability tend to decline rapidly in the dry Arctic spring. Later in the growing season the inorganic N remaining in the system will mainly be deeper in the soil, from where it can only be recycled into the terrestrial ecosystem by deeper-rooting plants.

Ongoing changes in tundra plant composition may have further direct consequences for soil organic matter (SOM) accumulation due to altered litter production and quality, and consequent changes in SOM decomposition. After twenty years of a warming experiment in a moist acidic tussock tundra ecosystem, plant carbon stocks had increased by 50%, without changes in net soil carbon storage (Sistla et al., 2013). On the other hand, another fertilization experiment on the same type of ecosystem similarly stimulated plant productivity, but also stimulated decomposition of soil organic matter, leading to net loss of carbon from the ecosystem after 20 years of fertilization with N and phosphorus (Mack et al., 2004). A common motive of the fertilization experiments is to mimic the higher availability of limiting nutrients expected under changing climate due to higher mineralization rates, or in the case of N to increased deposition. However, whilst surface N fertilisation may provide a reasonable representation of the effects of N deposition, it will not reflect the effects of N mineralization in deeper soil, where the balance of N acquisition structures between plant functional types is different. Surface applications may also lead to a proliferation of roots towards the soil surface, thus disadvantaging deep-rooted species such as graminoids (Mack et al., 2004).

We conducted two sets of experiments specifically designed to: i) study *ex situ* temperature effects on N mineralization in soil profile samples; and ii) track the *in situ* uptake of ^{15}N added into the mineral soil at different depths by tundra plants, both in the short term (10 days after ^{15}N addition) and longer term (one year after addition). We used studies of temperature effects on mineralization and of N uptake from different soil depths to explore how these factors may determine ecosystem responses to warming. Specifically we tested whether soil net N mineralization rates are temperature-dependent over a temperature range from −2 °C to +10 °C. Furthermore, based on previous work (Elmendorf et al., 2012) we predicted that graminoids in the high Arctic may have advantages in a warming climate over other functional groups (lichens, bryophytes and dwarf shrub) in competition for mineral N in the soil.

2. Materials and methods

2.1. Site description

Experiments were done in a high Arctic semi-desert tundra ecosystem surrounding the Kongsfjorden, approximately 2 km west from Ny Ålesund, Svalbard, at the site Leirhaugen (78° 55′ N, 11° 49′ E, 55 m a.s.l.). The area is underlain by continuous permafrost and the mineral soil, developed over limestone, consists of silty clay with interspersed stones. This is overlaid by a thin and discontinuous organic layer. Soil pH increases from 5.71 in the organic horizon to 7.36 in the mineral soil at 20–30 cm depth with mean C/N of 18 in the organic soil and 15 in the mineral soil. Mean annual air temperature over last two decades was −4.5 °C, with July temperatures ranging from 4.6 to 6.9 °C. Annual precipitation is ≈370 mm, which mostly falls as snow between September and May, with the driest month in May (17 mm) and wettest month in September (46 mm). Soil thaw depth is approximately 1 m during the growing season (Roth and Boike, 2001). Tundra vegetation is exposed to reindeer grazing. Reindeer in Ny-Ålesund are descended from animals introduced to the area in 1978, since which time the population has fluctuated with densities up to 0.89 individuals km^{-2} (Aanes et al., 2002; Hayashi et al., 2014).

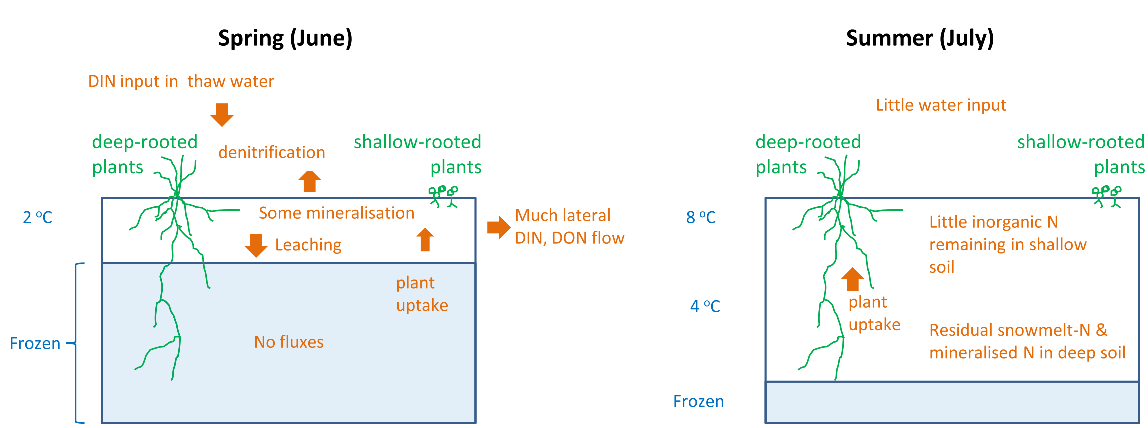

Fig. 1. Conceptual schema of major N flows in Arctic tundra ecosystems, during the spring melt and later in the growing season.