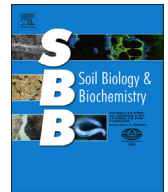




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Shifts in soil microbial community structure, nitrogen cycling and the concomitant declining N availability in ageing primary boreal forest ecosystems

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ABSTRACT

Plant growth in boreal forests is commonly limited by a low supply of nitrogen, a condition that may be aggravated by high tree below-ground allocation of carbon to ectomycorrhizal (ECM) fungi and associated microorganisms. These in turn immobilise N and reduce its availability to plants as boreal ecosystems develop. Here, we studied a boreal forest ecosystem chronosequence created by new land rising out of the sea due to iso-static rebound along the coast of northern Sweden. We used height over the ocean to estimate ecosystem age and examined its relationship to soil microbial community structure and the gross turnover of N. The youngest soils develop with meadows by the coast, followed by a zone of N₂-fixing alder trees, and primary boreal conifer forest on ground up to 560 years old. The young soils in meadows contained little organic matter and microbial biomass per unit area. Nitrogen was turned over at low rates when expressed per area (m⁻²), but specific rates (per gram soil carbon (C)) were the highest found along the transect. In the zone with alder, the amounts of soil C and microbial biomass were much higher (bacterial biomass had doubled and fungal biomass quadrupled). Rates of gross N mineralisation (expressed on an area basis) were highest, but the retention of added labelled NH₄⁺ was lowest in this soil as compared to other ages. The alder zone also had the largest extractable pools of inorganic N in soil and highest N % in plant foliage. In the older conifer forest ecosystems the amounts of soil C and N, as well as biomass of both bacteria and fungi increased. Data on organic matter ¹⁴C suggested that the largest input of recently fixed plant C occurred in the younger coniferous forest ecosystems. With increasing ecosystem age, the ratio of microbial C to total soil C was constant, whereas the ratio of microbial N to total soil N increased and gross N mineralization declined. Simultaneously, plant foliar N % decreased and the natural abundance of ¹⁵N in the soil increased. More specifically, the difference in δ¹⁵N between plant foliage and soil increased, which is related to relatively greater retention of ¹⁵N relative to ¹⁴N by ECM fungi as N is taken up from the soil and some N is transferred to the plant host. In the conifer forest, where these changes were greatest, we found increased fungal biomass in the F- and H-horizons of the mor-layer, in which ECM fungi are known to dominate (the uppermost horizon with litter and moss is dominated by saprotrophic fungi). Hence, we propose that the decreasing availability of N to the plants and the subsequent decline in plant production in ageing boreal forests is linked to high tree belowground C allocation to ECM fungi, a strong microbial sink for available soil N.

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1. Introduction

Despite the abundance of nitrogen (N) in the atmosphere and soil, plant productivity in many forest ecosystems is constrained by the lack of accessible N (Vitousek and Howarth, 1991; LeBauer and Treseder, 2008). This is typically the case for boreal forests (Tamm,

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1991), where higher N availability occurs only locally (Lahti and Väisänen, 1987), especially in groundwater discharge areas (Giesler et al., 1998).

Plant available N is produced as microorganisms decompose organic matter releasing peptides and amino acids, and the further processing of some of this N to ammonium (NH_4^+) and nitrate (NO_3^-). Until a few decades ago, mineralisation of organic N to NH_4^+ and nitrification to NO_3^- were the main foci in this context, but the common observation of lack of net release of inorganic N during the first weeks of soil incubations (eg., Hart et al., 1994a; Priha and Smolander, 1999) called for a shift in thinking. Subsequently, it became more widely known that the plants also take up organic N (Näsholm et al., 1998, 2009) and that various forms of organic N may dominate N uptake in ecosystems with a low soil N supply (Schimel and Bennett, 2004). The occurrence of inorganic N could be viewed as a supply of organic N in excess of the current biological demands of ecosystems (Schimel and Bennett, 2004), which is also dependent on the supply of carbon to the organisms (Hart et al., 1994a). Like peptides and amino acids, inorganic forms of N are rapidly taken up when the supply is low, and may, therefore not be detected when their pool sizes are measured. Thus, low abundances are not in themselves proof that they are not produced or important (e.g., Davidson et al., 1991, 1992; Hart et al., 1994a,b).

Why are pools of available N so low in boreal forests despite inputs of N from N_2 -fixation (DeLuca et al., 2002)? Several mechanisms are possible, for example, losses of N from the soil in recurrent fires typical of boreal forests (Zackrisson, 1977). Another possible mechanism addressed in numerous studies, is that there is a potential for chemical reactions between soil organic matter and inorganic N, e.g. NH_3 (Nömmik and Vahtras, 1982), NO_2^- (Azhar et al., 1986) or organic N forms (Knicker, 2004). Yet another possibility is related to the microorganism's supply of C and N as indicated by the frequent observations of relatively slow release of N from litter or organic matter with a high C/N ratio (Booth et al., 2005, and references therein). This stimulated research on the role of biotic factors like plant-microbial competition for available N (Kaye and Hart, 1997), plant characteristics and plant and microbial community composition, (e.g., Merilä et al., 2002a,b; Leckie et al., 2004; Jerabkova et al., 2006; Boyle-Yarwood et al., 2008).

A study by Lindahl et al. (2007) highlighted the fact that the upper part of the organic layer in a typical boreal forest soil, which consists of a layer of mosses or lichens mixed with above-ground plant litter, is mainly dominated by saprotrophic fungi, but has very few ectomycorrhizal (ECM) fungi, the root symbionts of boreal forest trees. These observations are important, because it means that studies of release of available N forms from litter in litter-bags focus on a stage where saprotrophic fungi dominate and where there are no plant roots. Plants access N through ECM fungi, which dominate in F- and H-horizons deeper down in the organic horizon (Lindahl et al., 2007; Clemmensen et al., 2013) and further down (Rosling et al., 2003). It is in these lower F + H horizons that the availability of N to plants is of greatest interest. Near the litter layer surface the saprotrophs have a higher availability of C and are able to retain more N. Deeper in the profile C supply to saprotrophs is exhausted but ECM fungi are supplied directly with recent photosynthate C from their tree hosts (Yarwood et al., 2009). Therefore, ECM fungi become superior competitors for available N. This is analogous to the combat between saprophytic and ECM fungi for phosphorus demonstrated by Lindahl et al. (2001).

A number of our previous studies support ideas that the links between soil microbial community structure, the supply of C and their combined effects on the microbial N sink capacity and N cycling are of pivotal interest. For example, the microbial cytoplasm rather than abiotic mechanisms was found to be the major immediate sink for ^{15}N (as $^{15}\text{NH}_4^+$ or glycine) injected into the F + H

horizons (Näsholm et al., 1998). Likewise, the immediate retention of $^{15}\text{NH}_4^+$ label was high when cation exchange capacity (CEC) was low and fungal/bacterial ratio was high and the reverse was true when CEC was high and fungal/bacterial ratios were low (Högberg et al., 2003, 2006, 2007a). Because fungi in these (F + H) layers should predominantly be ECM (Högberg and Högberg, 2002; Lindahl et al., 2007; Clemmensen et al., 2013), high fungal/bacterial ratios and N retention, but low N cycling rates (Högberg et al., 2007b) may indicate a role of ECM fungi in N immobilisation.

The idea of ECM mycelium as an efficient N immobiliser was recently supported by Näsholm et al. (2013), based on the fates of labelled C supplied as $^{13}\text{CO}_2$ to the tree canopies and of N injected as $^{15}\text{NO}_3^-$ into the soil. In addition, survey data from N deposition gradients and data from long-term N addition experiments support that the contribution by fungi and bacteria to the soil microbial community may be a useful predictor of the N retention capacity (Demoling et al., 2008; Högberg et al., 2011, 2013, 2014a; Zechmeister-Boltenstern et al., 2011; Blaško et al., 2013). Moreover, the common increase in the natural abundance of the stable isotope ^{15}N , denoted $\delta^{15}\text{N}$, with increasing soil depth in this type of soil is indicative of immobilisation of N in the soil mycelium of ECM (e.g. Högberg et al., 1996; Lindahl et al., 2007; Hobbie and Ouimette, 2009). Thus, the microbial community structure and the microorganisms physiology appear to be pivotal in this context. A key aspect of the F + H horizons of the mor-layer is that the supply of fresh plant photosynthate C to roots, and thus also ECM fungi and associated microorganisms, is low under conditions of high soil N supply, but higher under conditions of low N availability (Hermans et al., 2006; Mäkelä et al., 2008; Högberg et al., 2010).

To test the role of soil microorganisms, especially ECM fungi, as key immobilisers of available N in the soil, we followed changes in C and N cycling with soil age in a replicated chronosequence of boreal forest ecosystems created by iso-static rebound after the last glaciation. The rebound, causes land to rise at a constant rate along the Gulf of Bothnia, creating new land that is colonized by plants and on which developing boreal ecosystems can be studied. More specifically, we address the following questions: (i) How long time does it take for newly developing boreal ecosystems to progress into typical N limitation? (ii) Do shifts in microbial biomass and fungal/bacterial ratios coincide with shifts in N cycling rates and N availability? (iii) Can the decline in N availability be linked to a key role of ECM fungi? Some previous studies have used coastal chronosequences in the same larger region for similar studies. For example, Wallander et al. (2009) found an enrichment in ^{15}N in the soil along with soil depth and increasing age of the ecosystems in a study encompassing systems of up to 7800 years old; they concluded that this enrichment was likely caused by ECM fungi. Merilä et al. (2002a,b, 2010) used younger systems to examine the links between available N and plant-microbial interactions. We focus more than these previous studies on the early and potentially rapid changes of relations among ecosystem age, microbial community composition, and the decline in available N using three replicated transects across ecosystem ages from 25 to 560 years.

2. Methods

2.1. Study sites

The study sites were located within a nature reserve on the island Bjuren (N 63°44', E 20°35') in the Gulf of Bothnia, 15 km SE of Umeå, Sweden. The mean annual (2003–2012) temperature is 5 °C and precipitation is 550 mm. The mean annual N deposition during the same period is 2 kg ha⁻¹. On average, the study area is covered by snow from late October until early May. The rate of the isostatic rebound of the coastline is 8.16 mm per year (Ekman, 1996; Vestøl,

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