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Tamm Review: On the nature of the nitrogen limitation to plant growth in Fennoscandian boreal forests

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ABSTRACT

The supply of nitrogen commonly limits plant production in boreal forests and also affects species composition and ecosystem functions other than plant growth. These interrelations vary across the landscapes, with the highest N availability, plant growth and plant species richness in ground-water discharge areas (GDAs), typically in toe-slope positions, which receive solutes leaching from the much larger groundwater recharge areas (GRAs) uphill. Plant N sources include not only inorganic N, but, as heightened more recently, also organic N species. In general, also the ratio inorganic N over organic N sources increase down hillslopes. Here, we review recent evidence about the nature of the N limitation and its variations in Fennoscandian boreal forests and discuss its implications for forest ecology and management.

The rate of litter decomposition has traditionally been seen as the determinant of the rate of N supply. However, while N-rich litter decomposes faster than N-poor litter initially, N-rich litter then decomposes more slowly, which means that the relation between N % of litter and its decomposability is complex. Moreover, in the lower part of the mor-layer, where the most superficial mycorrhizal roots first appear, and N availability matters for plants, the ratio of microbial N over total soil N is remarkably constant over the wide range in litter and soil C/N ratios of between 15 and 40 for N-rich and N-poor sites, respectively. Nitrogen-rich and -poor sites thus differ in the sizes of the total N pool and the microbial N pool, but not in the ratio between them. A more important difference is that the soil microbial N pool turns over faster in N-rich systems because the microbes are more limited by C, while microbes in N-poor systems are a stronger sink for available N.

Furthermore, litter decomposition in the most superficial soil horizon (as studied by the so-called litter-bag method) is associated with a dominance of saprotrophic fungi, and absence of mycorrhizal fungi. The focal zone in the context of plant N supply in N-limited forests is further down the soil profile, where ectomycorrhizal (ECM) roots become abundant. Molecular evidence and stable isotope data indicate that in the typical N-poor boreal forests, nitrogen is retained in saprotrophic fungi, likely until they run out of energy (available C-compounds). Then, as heightened by recent research, ECM fungi, which are supplied by photosynthate from the trees, become the superior competitors for N.

In N-poor boreal soils strong N retention by microorganisms keeps levels of available N very low. This is exacerbated by an increase in tree C allocation to mycorrhizal fungi (TCAM) relative to net primary production (NPP) with decreasing soil N supply, which causes ECM fungi to retain much of the available soil N for their own growth and transfer little to their tree hosts. The transfer of N through the ECM fungi, and not the rate of litter decomposition, is likely limiting the rate of tree N supply under such conditions. All but a few stress-tolerant less N-demanding plant species, like the ECM trees themselves and ericaceous dwarf shrubs, are excluded.

With increasing N supply, a weakening of ECM symbiosis caused by the relative decline in TCAM contributes to shifts in soil microbial community composition from fungal dominance to bacterial dominance. Thus, bacteria, which are less C-demanding, but more likely to release N than fungi, take over. This, and the relatively high pH in GDA, allow autotrophic nitrifying bacteria to compete successfully for the NH_4^+ released by C-limited organisms and causes the N cycle to open up with leaching of nitrate (NO_3^-) and gaseous N losses through denitrification. These N-rich conditions allow species-rich communities of N-demanding plant species. Meanwhile, ECM fungi have a smaller biomass, are supplied with N in excess of their demand and will export more N to their host trees. Hence, the gradient from low to high

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N supply is characterized by profound variations in plant and soil microbial physiologies, especially their relations to the C-to-N supply ratio. We propose how interactions among functional groups can be understood and modelled (the plant-microbe carbon-nitrogen model).

With regard to forest management these perspectives explain why the creation of larger tree-free gaps favors the regeneration of tree seedlings under N-limited conditions through reduced belowground competition for N, and why such gaps are less important under high N supply (but when light might be limiting). We also discuss perspectives on the relations between N supply, biodiversity, and eutrophication of boreal forests from N deposition or forest fertilization.

Contents

1. Introduction

Boreal forests cover vast areas in the northern circumpolar region (Chapin et al., 2011), which is characterized by long cold winters and short summers. Another important feature is that plant growth is commonly constrained by a low supply of N, i.e. plant growth is enhanced by additions of N (e.g., Tamm, 1991). Tree growth varies with hill-slope position (e.g., Hägglund and Lundmark, 1977), likely because of effects of hill-slope hydrology on the availability of N. Variations in N supply also affects the species composition and other functions of boreal forests.

People dependent on products from the forests and the possibility to clear them for the purpose of agriculture (permanently or temporarily as swidden agriculture) probably recognized already centuries ago the existence of relations between certain plant species and soil fertility. A first more systematic description linking the common forest types (based on descriptions of the field-layer plants) to forest productivity in Finland was given by Cajander (1909, 1926) and Cajander and Ilvessalo (1922). According to these schemes, and followers from Sweden (Arnborg, 1990) and Norway (Kielland-Lund, 1982), ericaceous dwarf shrub communities cover the poorer soils, short herbs are common at intermediate soil fertilities and tall herbs dominate richer soils. The exact causes of these differences in species composition and productivity were not clarified and there is still no commonly accepted explanation of their nature.

This review serves the purpose of describing these patterns and their likely causes in the perspective of recent advances in our understanding of the interactions among soils, soil microorganisms, and plants. We will focus on boreal forests on mineral soils (i.e. make little reference to forests on peat) in Fennoscandia. However, the patterns and processes discussed may be important also in other N-limited forests, e.g., other boreal and temperate forests. For example, forest growth on drained boreal peatlands can likewise be predicted based on the composition of the original field-layer plant community (Hånell, 1988). Moreover, an understanding of these patterns and processes and their underlying causes is essential not only for ecologists interested in the structure and function of these ecosystems, but also pertinent to aspects on forest management (e.g., Hynynen et al., 2005; Mäkinen et al., 2006).

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