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Indications that long-term nitrogen loading limits carbon resources for soil microbes

M.O. Rappe-George ^{a, *}, M. Choma ^b, P. Čapek ^b, G. Börjesson ^a, E. Kaštovská ^b, H. Šantrůčková ^b, A.I. Gärdenäs ^{a, c}

^a Department of Soil and Environment, Swedish University of Agricultural Sciences, P.O. Box 7014, 750 07 Uppsala, Sweden

^b Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czech Republic

^c Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461, 405 30 Gothenburg, Sweden

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Microbial communities in the organic horizon (O-horizon) of forest soils play key roles in terrestrial nitrogen (N) cycling, but effects on them of long-term high N loading, by N deposition or experimental addition, are not fully understood. Thus, we investigated N-loading effects on soil microbial biomass N, carbon (C) and phosphorus stoichiometry, hydrolytic and oxidative enzymes, community composition (via phospholipid fatty acids, PLFA) and soil chemistry of the O-horizon in study plots of three wellstudied experimental Norway spruce (Picea abies) forests in Sweden and the Czech Republic. These forests span substantial gradients in current N deposition, experimental N addition and nitrate (NO_3) leaching. Current N deposition ranges from ~3 kg ha⁻¹ year⁻¹ of N in central Sweden (Stråsan) to ~15 kg ha⁻¹ year⁻¹ of N in SW Sweden (Skogaby) and Czech Republic (Čertovo). Furthermore, accumulated historical N loading during 1950-2000 (which include experimental N addition performed at Stråsan and Skogaby) ranged ~200–~2000 kg ha⁻¹ of N. Across all sites and treatments, current NO_3^- leaching ranged from low (~0.1 kg ha⁻¹ year⁻¹ of N) at Stråsan, to high (~15 kg ha⁻¹ year⁻¹ of N) at Skogaby and Čertovo. We found significantly lower C/N ratios and greater amounts of extractable inorganic N species in the forest soils' O-horizons at the high N loading plots. Microbial biomass and basal respiration decreased under experimental N addition treatments and tended to decrease with increased N deposition. Similarly, activities of hydrolytic enzyme activity associated with N acquisition were lower, although differences in activities at specific sites with the highest and intermediate historical N deposition levels failed statistical significance. Conversely, activities of soil hydrolytic enzymes associated with C acquisition were greater in study plots exposed high N loading. PLFA profiles indicated shifts in microbial community composition induced by long-term N load, towards higher and lower relative abundance of Gram-positive and Gram-negative bacteria, respectively (but no changes in fungal relative abundance). Taken together, our results suggest that long-term N loading of N-limited Norway spruce forests aggravates limitation of other resources, likely of C, for soil microbial communities. Although microbial variables in the soil O-horizon differed between plots exposed to low and high current N loading, microbial variables in plots that leached small amounts and large amounts of NO3 exposed to high N load were similar.

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1. Introduction

* Corresponding author.

Globally, the nitrogen (N) cycle has been altered dramatically by human activities, notably releases of reactive forms of N (Vitousek et al., 1997; Fowler et al., 2013). Fossil fuel burning and animal husbandry are important sources of N released into the atmosphere, some of which is transported long distances and deposited in forest ecosystems (Galloway et al., 2004). Excessive N loading can







E-mail addresses: martin.rappe.george@slu.se (M.O. Rappe-George), chomic@ email.cz (M. Choma), petacapek@gmail.com (P. Čapek), gunnar.borjesson@slu.se (G. Börjesson), ekastovska@prf.jcu.cz (E. Kaštovská), hana.santruckova@prf.jcu.cz (H. Šantrůčková), Annemieke.gardenas@bioenv.gu.se (A.I. Gärdenäs).

saturate forest ecosystems' biotic demands for N, in the short- or long-term, and have undesirable effects such as soil acidification and N loading on other terrestrial ecosystems via N leaching (Aber et al., 1989, 1998). Nitrate (NO_3^-) leaching is pivotal in this context as it is a major pathway of N loss and connected to acidification of soils. Full characterization of the effects of enhanced N input to initially N-limited forest ecosystems requires long-term studies, since such ecosystems frequently have high capacities to retain added N (Aber et al., 1998; Binkley and Högberg, 1997; Johnson, 1992) and some of the responses may only be apparent after prolonged N loading (Aber et al., 1998; Fenn et al., 1998).

The high retention of added N often observed in temperate and boreal ecosystems is likely due to the strength of biotic sinks for N in the soil, notably immobilization by mycorrhizal fungi or freeliving saprotrophs (reviewed by Aber et al., 1998). Accordingly, an important sink for added N is soil organic matter (SOM), in which 50% or more of total added N is frequently retained (Johnson, 1992; Melin et al., 1983). SOM transformations are integral components of terrestrial carbon (C) and nutrient cycles, and are driven by the energy and nutrient requirements of diverse communities of soil organisms, notably fungi and bacteria. Variations in temperature sensitivity of decomposition of SOM fractions and its interactions with soil N availability influence both heterotrophic respiration and net ecosystem productivity and hence play a pivotal role in soilclimate interactions (Gärdenäs et al., 2011). Moreover, climate change might affect responses of microbial communities to enhanced N availability.

As recently discussed (Treseder, 2008; Ramirez et al., 2012; Kopácek et al., 2013). N addition may have both direct and indirect effects on soil microbial communities, with implications for soil C and N cycling. Direct effects include, amongst others, reduction in soil microbial biomass and respiration (Janssens et al., 2010), inhibition of enzymes involved in decomposition of lignin and lignin derivatives (Fog, 1988; Gallo et al., 2004), increased abundance of electron acceptors in the form of NO_3^- (Kopácek et al., 2013), changes in outcomes of competition favoring taxa with high N demands (Fontaine et al., 2003) and/or reductions in rates of decomposition of recalcitrant organic matter due to reductions in needs to mine soil for N (Moorhead and Sinsabaugh, 2006). Reported indirect effects are, for instance, lower dissolved organic C availability as soil acidification may decrease organic C solubility (Kopácek et al., 2013). Another indirect effect is altered resource allocation of trees, whereby reduced tree belowground photosynthate C allocation in response to elevated N availability (Högberg et al., 2010) may cause reduced C availability for microbes and microbial community shift towards loss of ectomycorrhizal fungi (EMF) dominance (Wallenda and Kottke, 1997; Lilleskov et al., 2002; Nilsson and Wallander, 2003) and concomitant reductions in N immobilization (Högberg et al., 2014). Accordingly, reductions in the abundance of fungi, as indicated by a phospholipid fatty acid (PLFA) eukaryotic biomarker linoleic acid ($18:2\omega6,9$), in the organic soil horizon (O-horizon) of boreal forests in response to experimental N addition or ambient N deposition have been linked to reductions in investment of recent photosynthate C from trees to EMF under increased N availability (Högberg et al., 2011, 2014; Bahr et al., 2013). Subsequently, Bahr et al. (2015) reported that soil water inorganic N concentration increased and EMM production decreased following N fertilization in a Norway spruce forest in southern Sweden. However, they found that N + phosphorus (NP)fertilization reduced soil water inorganic N concentration, and further decreased EMM production, suggesting that effects on not only EMF, but also the whole microbial community and N immobilization, warrants further study. van Diepen et al. (2010) reported increased ratios of cyclopropyl/precursor PLFA, interpreted as soil microbial physiological stress, after 12 years of experimental N addition and increased abundance of Gram positive bacterial PLFA biomarkers, considered to be stress tolerant (Balser, 2005), in response to long-term N addition have been reported (Blaško et al., 2013).

In the study presented here we examined effects of long-term N loading (by experimental N addition and N deposition) on soil microbial variables related to soil microbial biomass stoichiometry. enzyme activities and community composition as reflected by phospholipid fatty acid (PLFA) profiles in three Norway Spruce (Picea abies) forests in Sweden and the Czech Republic. The overall aim was to improve understanding of the soil microbial element (C, N and P) stoichiometry, enzyme activities, and community composition under elevated N loading of Norway spruce forests located in the temperate and boreal zones. Furthermore, we assess how these soil microbial variables vary across large ranges of ecosystem N retention and NO_3^- leaching. We hypothesized that long-term N loading to such spruce forest systems will eventually lead to limitation of C resources for the soil microbial biomass, manifested as lower soil C/N ratios, soil microbial biomass and basal respiration, altered enzyme activities reflecting a shift from N to C acquisition and an altered community with greater proportions of stress tolerant functional groups, Gram-positive bacteria, at the expense of fungi and Gram-negative bacteria.

2. Material and methods

2.1. Site description and experimental design

All studied forest sites are long-term monitoring, or experimental, sites located in Sweden and the Czech republic. The soil microbial variables were studied in three Norway spruce (Picea abies L. Karst.) forests (Table 1), located at and called here: Stråsan in central Sweden (60°54'N, 16°01'E), Skogaby in southern Sweden (56°33'N, 13°13'E) and Čertovo in southern Czech Republic (49°10′N, 13°11′ E). These sites have been described by Tamm et al. (1974), Bergholm et al. (1995) and Kopácek et al. (2002), respectively. All sites are dominated by mature Norway spruce forests on acid, haplic podzols. Stråsan had the lowest mean annual temperatures of 3.1 °C, Čertovo intermediate (5.4 °C), while Skogaby is slightly warmer (7.6 °C). The long-term mean annual precipitation is similar at Skogaby and Čertovo (1187 and 1413 mm year⁻¹, respectively), while Stråsan is considerably drier (745 mm year $^{-1}$). The sites cover a strong gradient in historic (1950-2010) N deposition, declining in the order Čertovo (1168 kg N ha^{-1}) > Skogaby $(723 \text{ kg N ha}^{-1})$ > Stråsan (195 kg N ha $^{-1}$, Table 2). Each site is described in more detail below.

2.1.1. Stråsan

Stråsan is the site of a Norway spruce forest optimum nutrition experiment located in central Sweden, approximately 40 km northeast of the city Falun (Table 1). The soil is dominated by medium and fine sand, originating from glacial till (Tamm et al., 1974). In 2010 the average O-horizon depth was 10 cm and the soil Ohorizon C and N contents in the control treatment (N0) were 22.6 Mg C ha⁻¹ and 0.66 Mg N ha⁻¹, respectively (Rappe-George et al., 2013). The current Norway spruce forest was planted in 1958 and in 2010 it had a standing stem volume of 286 m³ ha⁻¹ on bark. Field layer vegetation is sparse, dominated by bilberry (Vaccinium myrtillus L.) and ground vegetation by mosses and lichens. The experiment had a randomized block design with 30 m \times 30 m experimental plots replicated in two blocks and treatments started 1967. Treatments considered in this study are the control (NO), and N addition treatments (N1 and N2, Table 2). The N2 treatment was terminated in 1991 with a total load of 1760 kg ha^{-1} of N, while the N1 treatment is still on-going at a current rate of 30 kg N ha^{-1}

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