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Effects of nitrogen enrichment on belowground communities in grassland: Relative role of soil nitrogen availability vs. soil acidification

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ABSTRACT

Terrestrial ecosystems worldwide are receiving increasing amounts of biologically reactive nitrogen (N) as a consequence of anthropogenic activities. This intended or unintended fertilization can have a wide range of impacts on the above- and belowground communities. An increase in high N availability has been assumed to be a major mechanism enhancing the abundance of above- and belowground communities. In addition to increasing available N, however, N enrichment causes soil acidification, which may negatively affect above- and belowground communities. The relative importance of increased N availability vs. increased soil acidity for above- and belowground communities in natural ecosystems experiencing N enrichment is unclear. In a 12-year N enrichment experiment in a semi-arid grassland, N enrichment substantially increased both above- and belowground plant biomass mainly via the N availability-induced increase in biomass of perennial rhizome grasses. N enrichment also dramatically suppressed bacterial, fungal, and actinobacteria biomass mainly via the soil acidification pathway (acidification increased concentrations of H^+ ions and Al^{3+} and decreased concentrations of mineral cations). In addition, N enrichment also suppressed bacterial-, fungal-feeding, and omnivorous + carnivorous nematodes mainly via the soil acidification pathway (acidification reduced nematode food resources and reduced concentrations of mineral cations). The positive effects resulting from the increase in belowground carbon allocation (via increase in quantity and quality of plant production) on belowground communities were outweighed by the negative effects resulting from soil acidification, indicating that N enrichment weakens the linkages between aboveground and belowground components of grassland ecosystems. Our results suggest that N enrichment-induced soil acidification should be included in models that predict biota communities and linkages to carbon and nitrogen cycling in terrestrial ecosystems under future scenarios of N deposition.

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1. Introduction

Anthropogenic reactive nitrogen inputs to the terrestrial biosphere, originating mainly from fossil-fuel burning and artificial fertilizer application, has increased three- to five-fold over the past century (Galloway et al., 2008). In many areas of the globe and especially in Asia, nitrogen deposition is expected to continue to increase (Zhao et al., 2009). It is well established that increases in nitrogen inputs stimulate plant growth and change plant community structure (LeBauer and Treseder, 2008; Bai et al., 2010; Bobbink et al., 2010). Nitrogen deposition can also result in soil acidification, leading to the suppression of plant growth in grassland (Van Breemen and Van Dijk, 1988; Chen et al., 2013) or forest ecosystems (Berg and Verhoef, 1998; Bobbink et al., 2010). Although nitrogen impacts on plant communities are relatively well understood, we lack a comprehensive understanding of how nitrogen deposition affects belowground organisms and their interaction with plants, even though the belowground community greatly affects ecosystem structure and functioning (Wardle et al., 2004; Bardgett and Wardle, 2010; García-Palacios et al., 2015).

Increased availability of nitrogen for primary production is assumed to greatly increase absolute belowground carbon allocation (Magnani et al., 2007) and therefore to alleviate the carbon limitation for the belowground food web, which relies almost

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entirely on plant-derived nutrients in most terrestrial ecosystems (Pollierer et al., 2007; Zak et al., 2008; Keith et al., 2009). However, while nitrogen deposition increases nitrogen availability, it simultaneously causes soil acidification, which will also affect carbon allocation to soils (and hence the belowground food web) by changing the concentration of H^+ ions and soil base cations (Van Breemen and Van Dijk, 1988; Kuperman and Edwards, 1997). In addition, a number of studies have focused on how the diversity or taxonomic group of belowground communities (mostly soil microbes) changes in response to nitrogen enrichment (Campbell et al., 2010; Ramirez et al., 2010), but the changes lack consistency (Treseder, 2008; García-Palacios et al., 2015). Surprisingly, few studies have simultaneously examined how multiple trophic levels of the belowground food web (e.g., microbes and nematodes) are affected by nitrogen enrichment (Fierer et al., 2009; Eisenhauer et al., 2012). Our incomplete understanding of responses of the belowground food web to nitrogen enrichment limits our ability to predict the impact of future nitrogen deposition on ecosystem productivity and carbon and nitrogen cycling.

Two pathways may primarily determine how nitrogen enrichment affects the belowground food web. In the first pathway, nitrogen enrichment directly increases carbon and nitrogen availability to soil organisms by increasing above- and belowground plant biomass (Ingham et al., 1985; Bardgett and Wardle, 2010). In highly nitrogen-limited environments, this increase in soil nitrogen availability could enhance belowground carbon allocation and thus enhance soil organism activity (LeBauer and Treseder, 2008; Eisenhauer et al., 2012). In the second pathway, nitrogen enrichment alters belowground carbon allocation and soil organisms as a consequence of soil acidification (Van Breemen and Van Dijk, 1988). Soil acidification could suppress plant and belowground communities by increasing concentrations of soil H^+ and Al^{3+} (Berg and Verhoef, 1998; Van Den Berg et al., 2005; Rousk et al., 2010) and by decreasing concentrations of base mineral cations (e.g., Ca^{2+}, Mg^{2+}, and Na^+) (Van Breemen and Van Dijk, 1988; Bowman et al., 2008). Although changes in several specific trophic levels of belowground food webs have been documented in response to nitrogen enrichment in natural ecosystems (Treseder, 2008; Campbell et al., 2010; Ramirez et al., 2010), data are lacking concerning the degree to which increased nitrogen availability vs. acidification explains the effects of nitrogen enrichment on multiple trophic groups in natural ecosystems.

Here, we used data from a 12-year nitrogen enrichment experiment to assess the relative roles of nitrogen availability and soil acidification in determining the effects of long-term nitrogen enrichment on belowground communities in a typical semiarid steppe. First, we determine how nitrogen enrichment affects soil microbes and nematodes, plant variables (aboveground biomass, belowground biomass, and community structure), soil acid cations (H^+ and Al^{3+}), soil base cations (Ca^{2+}, Mg^{2+}, and Na^+), and nitrogen availability (soil NH_4^+–N and soil NO_3^-–N). Second, we determine the relative significance of nitrogen availability and soil acidification in determining nitrogen enrichment-induced changes in components of the belowground food web. Finally, we identify those factors that best explain how nitrogen enrichment affects the belowground food web.

2. Materials and methods

2.1. Study site

This study was conducted at the Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 43°38′N, 116°42′E) of the Chinese Academy of Sciences, which is located in the Xilin River Basin of Inner Mongolia, China, at approximately 1200 m a.s.l. The semi-arid continental climate is characterized by a mean annual precipitation of 334 mm and a mean annual temperature of 0.9 °C (1982–2009). Precipitation mainly occurs in the growing season (June–August), which is coincident with the relatively high temperatures. The site has a dark chestnut soil (Calcic Chernozem according to ISSS Working Group RB, 1998), with a loamy-sand texture (Bai et al., 2010). Before the experiment began, the plant community was dominated by *Leymus chinensis* (Trin.) Tzvel., a C_3 perennial rhizomatous grass that is distributed widely in the Eurasia steppe region (Bai et al., 2004).

2.2. Long-term nitrogen enrichment experiment

The establishment of the nitrogen enrichment experiment was described by Bai et al. (2010) and is described briefly here. In 1999, a 120-m × 70-m area with fairly uniform vegetation was designated within the permanent research plots of IMGERS. The area was divided into 162 5-m × 5-m plots with 1-m buffers. These plots were laid out in a randomized block design with nine replicate blocks. Each replicate block included six levels of nitrogen enrichment (0, 1.75, 5.25, 10.50, 17.5, and 28.0 g of N m^{-2} yr^{-1}) and nitrogen application in the middle of the growing season (July 1–5). Nitrogen was added as commercial, pelletized NH_4NO_3 fertilizer. Because of limitations in available labor, we sampled only five of the nine blocks (total plots is 30, 5 blocks × 6 six levels of nitrogen enrichment).

2.3. Plant sampling

In late August 2010 and 2011, aboveground vegetation was sampled in a 0.5-m × 0.5-m quadrat in each plot. Living vascular plants were sorted into species by clipping and were oven-dried at 65 °C for 48 h and weighed. We classified all plants into five plant functional groups based on life forms as described in Bai et al. (2004): perennial rhizome grasses, perennial bunchgrasses, perennial forbs, shrubs and semi-shrubs, and annuals. Principal component analysis (PCA), based on the biomass of each of the five PFGs, was conducted for each sampling year, and the PC1 scores were used as indicators of plant community structure (Table S1). After the aboveground biomass was sampled, three soil cores (6.5 cm diameter and 0–30 cm depth) were collected in each plot to determine plant belowground biomass. The roots were rinsed from the soil cores under running water, collected on a 1-mm screen, oven-dried at 65 °C, and weighed.

2.4. Soil sampling and analysis

Four soil cores (2 cm diameter, 0–15 cm depth) were randomly collected from each plot and were combined to form one composite soil sample per plot. After the soil was gently mixed and roots were removed, the moist soil was passed through a 2-mm-mesh sieve and separated into two parts. One part was maintained fresh for extraction of microorganisms and nematodes. The second part was air-dried for determination of soil pH and extractable cations (Al^{3+}, Ca^{2+}, Mg^{2+}, and Na^+). A 20-g subsample of moist soil was oven-dried at 105 °C for 24 h to determine soil moisture. Soil pH was measured in a 1:2.5 (soil: water) suspension. NH_4^+–N and NO_3^-–N concentrations were determined by extracting inorganic nitrogen at 100 rpm for 2 h from subsamples (10 g) with 100 ml of 2 mol L^{-1} KCl. Extract was subjected to colorimetric determination on a 2300 Kjeltec Analyzer Unit (FOSS, Höganäs, Sweden). The extractable cations (Al^{3+}, Ca^{2+}, Mg^{2+}, and Na^+) were measured using a modified BCR sequential extraction (Rauret et al., 2000). A 1-g subsample of air-dried soil per sample was placed in a 50-ml polypropylene centrifuge tube. A 20-ml volume of 0.11 mol L^{-1}

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