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Plant functional diversity mediates the effects of vegetation and soil properties on community-level plant nitrogen use in the restoration of semiarid sandy grassland

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ABSTRACT

Species-rich plant communities use nitrogen (N) more efficiently in grassland ecosystems; however, the role of plant functional diversity in affecting community level plant N-use has received little attention. We examined plant N content, stock and N-use efficiency at community-level along a restoration gradient of sandy grassland (mobile dune, semi-fixed dune, fixed dune and grassland) in Horqin Sand Land, northern China. We used the functional trait-based approach to examine how plant functional diversity, reflected by the most abundant species' traits (community-weighted mean, CWM) and the dispersion of functional trait values (FDis), affected N-use efficiency in sandy grassland restoration. We further used the structure equation model (SEM) to evaluate the direct or indirect effects of plant species richness, biomass, functional diversity and soil properties on community-level plant N-use efficiency. We found that plant biomass and its N stock increased following sandy grassland restoration, and there were lower plant N content and higher N-use efficiency in semi-fixed dune, fixed dune and grassland as compared with mobile dune. N-use efficiency was positively associated with plant species richness, biomass, CWM plant height, CWM leaf C:N, FDis and soil gradient, but SEM results showed that species richness, CWM leaf C:N, plant biomass and FDis controlled by soil properties were the main factors exerting direct effects. CWM plant height also had a positive effect on N-use efficiency through its indirect effect on plant biomass. Soil gradient increased N-use efficiency through an indirect effect on vegetation rather than a direct effect. Final SEM models based on different plant functional diversity explained over 74% of variances in N-use efficiency. Effects of plant functional diversity on N-use efficiency supported both the mass ratio hypothesis and the complementarity hypothesis. Our results clearly highlight the important role of plant functional diversity in mediating the effects of vegetation and soil properties on community level plant N-use in sandy grassland ecosystems.

1. Introduction

Nitrogen (N) is a primary limiting resource in determining net productivity in temperate grassland ecosystems (LeBauer and Treseder, 2008). Nitrogen-use efficiency (NUE) can be defined as the amount of biomass produced per unit of N taken up by plants from soil (Fornara and Tilman, 2009; Selmants et al., 2013). NUE has been widely used to analyze the response of plant growth to different N availabilities (Fan et al., 2013; Funk, 2013). Changes in NUE also play an important role in N cycling and retention in terrestrial ecosystems (Knops et al., 2002; Selmants et al., 2013). Plants with high NUE were presumed to be advantageous in the environment of low N availability (Boerner, 1984; Aerts and de Caluwe, 1994), and high community-level NUE may mitigate the effec of N deposition on ecosystem (Selmants et al., 2013). Numerous studies have also reported the complex effects of species identity (Epstein et al., 1998; Vázquez de Aldana and Berendse, 1997), species diversity (Hooper and Vitousek, 1998; Niklaus et al., 2006) and soil properties (Aerts and de Caluwe, 1994; Funk and Vitousek, 2007; Funk, 2013; Selmants et al., 2013) on leaf or community-level N uptake and

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storage in natural ecosystems. The trait-based approach can clearly reveal the effects of plant functional diversity on plant community structure and function (Butterfield and Suding, 2013; Lavorel, 2013; Le Bagousse-Pinguet et al., 2014). However, our knowledge on responses of NUE to those biotic and abiotic factors is still limited. To reveal the driver of NUE is very important for the understanding of N storage, retention and cycling (Selmants et al., 2013; Wilkinson et al., 2015) and how plant adapts to environment with different N availability in natural ecosystems (Vázquez de Aldana and Berendse, 1997).

Plant species differing in their ability to capture, store and release N represent a major driver of N cycling in grassland ecosystems (Knops et al., 2002). Plant communities with higher species richness can use N more completely and efficiently due to species' complementarity in resource use (Tilman, 1997; Hooper and Vitousek, 1998; Mueller et al., 2013; Selmants et al., 2013). Fast-growing plants exhibit high specific leaf area and leaf N content (Kazakou et al., 2007). High plant NUE often resulted from both an increase in biomass and a decrease in leaf N content (An et al., 2005; Aerts and Chapin, 2000; McCulley et al., 2009). High leaf carbon-nitrogen ratio (C:N) is associated with high plant NUE (Aerts and Chapin, 2000; McCulley et al., 2009). Increased soil N availability often leads to a decline in plant NUE because of an enhancement of plant N concentrations (Boerner, 1984; Aerts and de Caluwe, 1994). Nutrient-rich habitats have fast-growing species with high rates of nutrient turnover and nutrient-poor habitats favor slow-growing species with low nutrient-loss rates (Funk and Vitousek, 2007; Fan et al., 2013; Funk, 2013). So, studying effects of plant diversity, plant C:N and soil fertility on community-level plant NUE to improve our understanding of how biotic and abiotic factors influence plant N use, which will in turn be helpful for the management of natural ecosystems.

A number of studies have shown that ecosystem function may be driven by plant functional diversity as reflected by the abundant functional trait values (community-weighted mean, CWM) and the variety of functional trait values (FD) (Butterfield and Suding, 2013; Schumacher and Roscher, 2009). The CWM effects may primarily be attributed to the biomass ratio hypothesis (De Deyn et al., 2008; Lavorel, 2013), while FD effects support the niche complementarity hypothesis (Gamfeldt et al., 2008; Lavorel and Garnier, 2002; Tilman, 1997). According to the mass ratio hypothesis (Grime, 1998), the role of species in the ecosystem is proportional to their biomass; therefore, the most abundant species have the strongest effects on ecosystem processes and properties (Conti and Díaz, 2013; Lavorel, 2013; Butterfield and Suding, 2013). Plant height, leaf dry matter content (LDMC), specific leaf area (SLA) and leaf C:N, as four important traits related to plant size, structural properties and tissue quality, greatly affect the plant growth rate, species richness and biomass (Dechaine et al., 2014; Spasojevic et al., 2014b). Functional dispersion (FDis) represents the mean space of each species, weighted by relative abundances, to the centroid of all species in the community (Spasojevic et al., 2014a), which may be regarded as a surrogate measure of functional richness and functional divergence. In particular, higher FDis may reflect the coexistence of different functional strategies and an increase in niche-complementarity among species (Schleicher et al., 2011; Spasojevic et al., 2014a), thus resulting in higher plant N use in the community. Therefore, examine roles of CWM traits and FDis in affecting ecosystem-level N use can provide profound insights into the mechanism of how plant functional diversity affects ecosystem processes and properties.

Horqin sandy grassland is located in the semi-arid area of southeast Inner Mongolia and is one of the most severely desertified regions of China (Zhao et al., 2005). However, thanks to annual precipitation of 350–500 mm, mobile dunes can be gradually stabilized via vegetative succession after excluding grazing (Liu et al., 2009; Zhang et al., 2005; Zuo et al., 2009). Previous studies have documented that species richness, biomass, soil organic C, total N, electrical conductivity, very fine sand and silt and clay increased along a vegetation succession from sand pioneer plants in mobile dunes to low shrub communities in semi-fixed dunes, then toward annual herbaceous communities in fixed dunes (Liu et al., 2009; Zhang et al., 2005; Zuo et al., 2009, 2012b). Soil properties are the primary driver of plant distribution and community composition following sandy grassland restoration (Zuo et al., 2009). However, little is known about how community-level plant NUE responds to vegetation and soil properties along a restoration gradient of sandy grassland.

In this paper, we used the structural equation model (SEM) to assess the direct and indirect effects of plant diversity, biomass, functional diversity and soil properties on NUE in sandy grassland restoration. We also attempted to identify how CWM traits and FDis affect community-level plant NUE in sandy grassland ecosystems. Specifically, we tested the three hypotheses: (1) community-level plant NUE was positively associated with plant species richness in sandy grassland restoration; (2) high community-level plant NUE was associated with high leaf C:N of the most abundant species, because of a decrease of leaf N content following an increase of biomass in sandy grassland restoration; and (3) increasing functional dispersion (FDis) increased plant NUE due to the effect of niche-complementarity among species.

2. Methods

2.1. Site description

This study area is located in the southwest part of Horqin Sandy Land (42°55′ N, 120°42′ E; 360 m elevation), Inner Mongolia, Northern China. This area has a typical continental semi-arid climate with a warm summer and a very cold winter. The mean annual temperature is around 6.4 °C and mean annual precipitation is 360 mm, with 75% of the total in the growing season of June to September. Soils that consist of coarse and fine sand with loose structure are vulnerable to wind erosion. The pattern of natural vegetation is characterized by a mosaic of sand dunes and grasslands, including mobile dunes, semi-fixed dunes, fixed dunes and grasslands (Liu et al., 2009; Zuo et al., 2012a). Mobile dunes are dominated by sand pioneer plants, *Agriophyllum squarrosum* (an annual forb). Semi-fixed dunes are dominated by the low shrub, *Artemisia halodendron*. An annual forb, *Artemisia scoparia*, is the dominant plant in fixed dunes. Grasslands are dominated by an annual forb, *A. scoparia* and perennial grasses, *Phragmites communis* and *Pennisetum centrasiaticum*.

Within the study area, 24 plots (20 m × 20 m) up to 8 km apart were selected to span a typical restoration gradient of sandy grassland, including mobile dune with less than 10% vegetation cover (MD), semi-fixed dune with 10–60% vegetation cover (SFD), fixed dune with more than 60% vegetation cover (FD) and grassland with more than 60% vegetation cover (G) (Liu et al., 2009; Zuo et al., 2012b). Each habitat type had six replicate plots. Semi-fixed dunes and fixed dunes were naturally restored from mobile dunes by excluding grazing, from approximately 1995 and 1980, respectively. Before grazing exclusion, the landscape of these dune sites was characterized by areas with mobile dunes. Grassland sites also excluded livestock grazing by fencing to restore vegetation from 1996, thus grassland represents a relatively good vegetation type in this region.

2.2. Sampling and measurement

In mid-Aug 2013, five 1 m × 1 m quadrats were set up at the center and the four corners in each plot to carry out vegetation survey