



# Nitrogen deposition and precipitation induced phylogenetic clustering of arbuscular mycorrhizal fungal communities



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## ARTICLE INFO

### Article history:

Received 1 March 2017

Received in revised form

26 July 2017

Accepted 23 August 2017

Available online 4 September 2017

### Keywords:

Glomeromycota

Global climate change

Nitrogen

Precipitation

Phylogenetic clustering

## ABSTRACT

Despite the inarguable importance of arbuscular mycorrhizal fungi (AMF) in terrestrial ecosystems, we know little about how AMF communities shift in response to climate changes. In this study, we investigated the impacts of seven years of precipitation increment and nitrogen (N) addition on the taxonomic and phylogenetic diversity of AMF communities in a temperate steppe of northern China. Phylogenetic patterns were also used to elucidate the ecological processes structuring AMF communities. By 454-pyrosequencing, we detected a total of 71 AMF operational taxonomic units (OTUs), consisting mainly of *Glomeraceae*. In general, N addition reduced but precipitation increment increased AMF abundance including root colonization and fungal biomass. Nitrogen addition also decreased AMF alpha-diversity, including OTU richness, Chao 1 and Faith's phylogenetic diversity. Moreover, permutational multivariate analysis of variance showed that AMF community composition shifted in response to both N addition and precipitation increment. AMF communities were phylogenetically clustered across all experimental treatments, suggesting that environmental filtering was the primary driver of AMF community assembly. Taken together, these findings supported that both N and precipitation shaped the AMF communities, but not altered the ecological processes responsible for the assembly of AMF communities in the temperate steppe.

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## 1. Introduction

Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with the majority of land plants, and provide multiple benefits to their plant hosts, including increased nutrient uptake, improved tolerance to abiotic stress and protection from pathogens (Smith

and Read, 2008). In return, AMF receive photosynthates to meet their demands on carbon resources. The outcome of the symbiosis for the plant host may vary depending on the cost-benefit balance, and can range from mutualism to commensalism or parasitism (Johnson et al., 2015). AMF communities play several important roles in ecosystem functioning through regulating biogeochemical nutrient cycling (Rillig, 2004; Veresoglou et al., 2012), carbon (C) storage (Cheng et al., 2012), soil structure (Rillig and Mummey, 2006), and plant productivity (van der Heijden et al., 1998, 2008). Obviously, our knowledge of the assembly of AMF community could provide valuable clues for understanding ecosystem functioning and dynamics associated with changing environments.

Studies on the community assembly of AMF range considerably in terms of spatial resolution, which could be at local (Dumbrell

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et al., 2010; Caruso et al., 2012; Horn et al., 2014), regional (Hazard et al., 2013) and continental or global (Kivlin et al., 2011; Öpik et al., 2013; Davison et al., 2015, 2016; Bouffaud et al., 2016) scales. Through these studies, it is apparent that the assemblies of AMF communities in natural ecosystems are shaped by multiple processes such as host specificity, environmental filtering, dispersal and stochasticity, while the relative importance of each driver may vary with spatial scales (Vályi et al., 2016). Environmental filters such as soil nutrient availability, soil pH, soil moisture and climate gradient appear to be important predictor for AMF community composition at large spatial scales (Kivlin et al., 2011; Moora et al., 2014; Davison et al., 2015). Besides environmental gradients, plant host is another important variable in driving AMF community assembly. Different grass species or even plant individuals of the same species could harbor different AMF communities (Vandenkoornhuysen et al., 2003; Gosling et al., 2013). Finally, neutral processes such as dispersal limitation also contributed to AMF communities (Kivlin et al., 2011; Davison et al., 2015, 2016). By studying patterns across various environmental gradients, we could have a better understanding about the determinants of AMF community assembly over broad scales. However, up to date little is known about the processes that drive the AMF communities under global climate changes.

Ecological impacts of climate changes on the structure and functioning of an ecosystem can be systematically investigated under experimental manipulations, which could allow a better mechanistic resolution than observational approaches do. Many studies have examined the responses of AMF community composition to environmental manipulations such as nitrogen (N) enrichment (Porrás-Alfaro et al., 2007; Chen et al., 2014; Zheng et al., 2014; Kim et al., 2015) and water additions (Gao et al., 2015; Li et al., 2015). It was found that N and water addition could modulate AMF communities possibly through influences on soil N availability and soil pH (van Aarle et al., 2002; Liu et al., 2012). However, most of these studies relied primarily on taxon-based approaches, while AMF phylogeny may provide additional information about trait-based processes driving the community assembly (Webb et al., 2002), as the functional traits of AMF community are generally conserved (Powell et al., 2009). Environmental filtering might lead to communities in which species are more closely related than expected by chance (phylogenetically clustering), while competitive exclusion might lead to species are less closely related (phylogenetically over-dispersion) (Webb et al., 2002). Some recent studies addressed how experimental drivers mimicking climate change influence the phylogenetic structure of the AMF community (Liu et al., 2015a, b; Mueller and Bohannan, 2015) with inconclusive results. For instance, CO<sub>2</sub> enrichment resulted in phylogenetic clustering of AMF communities while N addition induced no obvious shift in AMF community assembly (Mueller and Bohannan, 2015). By contrast, AMF communities were phylogenetically clustered in unfertilized soil, random under low fertilization treatment and over-dispersed upon high fertilization treatment, suggesting that nutrient availability may change the dominant ecological processes associated with the assembly of AMF communities (Liu et al., 2015a). Obviously, there is still an urgent need for more systematic studies to reveal the potential impacts of climate changes on AMF communities and underlying mechanisms.

The temperate grassland in northern China represents a typical arid and semi-arid region, where N and water are two key factors constraining plant productivity and associated ecosystem functioning (Yang et al., 2011). Moreover, this region is predicted to suffer from a projected higher N deposition and frequency of extreme climatic changes such as increased precipitation

(Ni and Zhang, 2000). In order to examine the potential influences of climate changes on AMF, here we examined the effect of long-term artificial precipitation increment and N addition on AMF diversity, community composition and phylogenetic structure in this temperate grassland. We tested two hypotheses: 1) Nitrogen addition and precipitation increment could alter composition and phylogenetic structure of AMF communities; and 2) Nitrogen addition and precipitation increment can induce shifts in the ecological processes shaping the AMF communities.

## 2. Materials and methods

### 2.1. Study site and sampling

The experimental site is located in a semiarid steppe in Duolun County, Inner Mongolia, China (42° 02' N, 116° 17' E). Mean annual precipitation (MAP) is 385.5 mm and mean annual temperature (MAT) is 2.1 °C. The soil is classified as Haplic Calcisols according to the Food and Agricultural Organization (FAO) of the United Nations classification. The vegetation is typical steppe, and is located in an open high plain with an altitude reaching approximately 1324 m. The experiment was initiated in 2005 with a split-plot experimental design, which involves two levels of precipitation (ambient and increased) applied at the plot scale and four N levels applied to subplots. This experimental design was replicated in seven blocks, and each subplot was 8 m × 8 m with a 1 m wide buffer zone. Thus, there were eight treatments as follows: N0 (control), N5 (5 g N m<sup>-2</sup> yr<sup>-1</sup>), N10 (10 g N m<sup>-2</sup> yr<sup>-1</sup>), N15 (15 g N m<sup>-2</sup> yr<sup>-1</sup>), PN0 (precipitation increment only), PN5 (precipitation increment and 5 g N m<sup>-2</sup> yr<sup>-1</sup>), PN10 (precipitation increment and 10 g N m<sup>-2</sup> yr<sup>-1</sup>), and PN15 (precipitation increment and 15 g N m<sup>-2</sup> yr<sup>-1</sup>). Nitrogen in form of urea was applied twice a year with half in early May and the other half in late June. The precipitation increment plots received 15 mm of simulated precipitation weekly via sprinkling irrigation from June to August. A total of 180 mm (15 mm per week for 12 weeks), equal to 50% of MAP in the study area, was uniformly added to plots during the growth season from 2005 to 2012.

We used a subset of plots (four randomly selected replicates) from each treatment to assess AMF diversity. On August 22, 2012, five soil cores (15 cm deep, 3.5 cm diameter) were randomly collected from each plot and combined into one composite sample, resulting in a total of 32 samples. Composite soil samples were passed through a 2.0 mm sieve to remove roots and debris. Sub-samples were stored at 4 °C for soil chemical analysis, and -80 °C for fatty acid and DNA extraction. At the same time, vegetation coverage was visually estimated for all vascular plant species in each subplot. We calculated Shannon-Wiener index for plant alpha diversity. In each of the sampling plots, plant species richness (SR) was recorded at 6 locations using a 1 m × 1 m quadrat. Above-ground biomass (AGB) were then cut at the ground level, dried at 75 °C for 48 h after being transported to the laboratory and weighed.

### 2.2. Soil chemophysical properties

Soil samples were dried for 48 h at 105 °C to assess soil moisture. Soil pH was determined with a soil to water ratio of 1: 2.5. Soil nitrate and ammonium were extracted with 2 M KCl (soil to water ratio of 1:5), and then measured with a continuous flow analyzer (SAN++, Skalar, Breda, Holland). Soil available phosphorus (AP) was measured using the ammonium molybdate method (Bao, 2005) after extraction with 0.5 M NaHCO<sub>3</sub>. Soil available potassium (AK) was extracted by NH<sub>4</sub>OAc and analyzed by flame atomic

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