



## Phylogenetic structure of arbuscular mycorrhizal community shifts in response to increasing soil fertility



Yongjun Liu <sup>a, b</sup>, Nancy Collins Johnson <sup>c</sup>, Lin Mao <sup>a</sup>, Guoxi Shi <sup>d</sup>, Shengjing Jiang <sup>a</sup>,  
Xiaojun Ma <sup>a</sup>, Guozhen Du <sup>e</sup>, Lizhe An <sup>a, b, \*</sup>, Huyuan Feng <sup>a, \*\*</sup>

<sup>a</sup> MOE Key Laboratory of Cell Activities and Stress Adaptations, School of Life Sciences, Lanzhou University, Lanzhou 730000, China

<sup>b</sup> Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

<sup>c</sup> School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ 86011, USA

<sup>d</sup> University Key Laboratory for Protection and Utilization of Longdong Bio-resources in Gansu Province, Longdong University, Qingyang 745000, China

<sup>e</sup> State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000, China

### ARTICLE INFO

#### Article history:

Received 23 March 2015

Received in revised form

8 July 2015

Accepted 12 July 2015

Available online 26 July 2015

#### Keywords:

Symbiotic fungi

Phylogenetic structure

Ecological process

Competition

Environmental filtering

Resource availability

### ABSTRACT

Understanding the underlying mechanisms driving responses of belowground communities to increasing soil fertility will facilitate predictions of ecosystem responses to anthropogenic eutrophication of terrestrial systems. We studied the impact of fertilization of an alpine meadow on arbuscular mycorrhizal (AM) fungi, a group of root-associated microorganisms that are important in maintaining sustainable ecosystems. Species and phylogenetic composition of AM fungal communities in soils were compared across a soil fertility gradient generated by 8 years of combined nitrogen and phosphorus fertilization. Phylogenetic patterns were used to infer the ecological processes structuring the fungal communities. We identified 37 AM fungal virtual taxa, mostly in the genus *Glomus*. High fertilizer treatments caused a dramatic loss of *Glomus* species, but a significant increase in genus richness and a shift towards dominance of the lineage of *Diversispora*. AM fungal communities were phylogenetically clustered in unfertilized soil, random in the low fertilizer treatment and over-dispersed in the high fertilizer treatments, suggesting that the primary ecological process structuring communities shifted from environmental filtering (selection by host plants and fungal niches) to a stochastic process and finally to competitive exclusion across the fertilization gradient. Our findings elucidate the community shifts associated with increased soil fertility, and suggest that high fertilizer inputs may change the dominant ecological processes responsible for the assembly of AM fungal communities towards increased competition as photosynthate from host plants becomes an increasingly limited resource.

© 2015 Elsevier Ltd. All rights reserved.

### 1. Introduction

Worldwide increases in fertilizer application and nutrient deposition raise the question of how nutrient enriched soil influences biotic communities. Numerous field studies have shown that improved soil fertility increases plant productivity, but also decreases plant species diversity and changes plant community

composition mainly through the enhanced process of competitive exclusion (Rajaniemi, 2002; Hautier et al., 2009; Borer et al., 2014; Liu et al., 2015). Diverse belowground communities of microorganisms interact with plants and serve as key players in biogeochemical cycling (Fitter et al., 2005; Philippot et al., 2013), but in comparison with that of plant community, relative little is known about the patterns and underlying mechanisms of belowground community responses to soil nutrient enrichments. Filling this knowledge gap can help guide management decisions and facilitate predictions of ecosystem sustainability in a changing world.

Arbuscular mycorrhizal (AM) fungi in the phylum Glomeromycota are widespread root-associated microorganisms that are known to be sensitive to fertilization. In general, plants supply associated AM fungi with carbohydrates, and in return, fungi provide soil phosphorus (P) and possibly nitrogen (N) to their host

\* Corresponding author. Room 408, Guiqin Building, Lanzhou University, Tianshui South Road No 222, Lanzhou 730000, China. Tel.: +86 931 8912560; fax: +86 931 8912561.

\*\* Corresponding author. Room 323, Tianyan Building, Lanzhou University, Tianshui South Road No 222, Lanzhou 730000, China. Tel./fax: +86 931 8912537.

E-mail addresses: [yjliu@lzu.edu.cn](mailto:yjliu@lzu.edu.cn) (Y. Liu), [Nancy.Johnson@nau.edu](mailto:Nancy.Johnson@nau.edu) (N.C. Johnson), [lizhean@lzu.edu.cn](mailto:lizhean@lzu.edu.cn) (L. An), [fenghy@lzu.edu.cn](mailto:fenghy@lzu.edu.cn) (H. Feng).

plants (Hodge et al., 2010; Selosse and Rousset, 2011). Mycorrhizal symbioses can also provide plants with other benefits such as protection against root pathogens (Lewandowski et al., 2013) and several types of abiotic stress (Aroca et al., 2007). Furthermore, increasing evidence shows that mycorrhizas influence the structure of plant communities (Klironomos et al., 2011; Yang et al., 2014), the rhizosphere microbiome (Vestergård et al., 2008; Veresoglou et al., 2012), soil structure (van der Heijden et al., 2006; Leifheit et al., 2015), and nutrient cycles (Cheng et al., 2012; Bender et al., 2015). Many experiments have shown that fertilization reduces AM fungal diversity and shifts the community toward dominance of particular species or lineages (e.g. Johnson, 1993; Egerton-Warburton et al., 2007; Alguacil et al., 2010; Liu et al., 2012, 2015; Camenzind et al., 2014). However, neutral or even positive effects of fertilization on AM fungal diversity have also been reported (e.g. Antoninka et al., 2011; van Diepen et al., 2011; Gosling et al., 2013), suggesting that the responses of AM fungal communities to fertilization are influenced by complex interactions of many factors (van Diepen et al., 2011; Vályi et al., 2015).

Although it has long been recognized that fertilization influences the structure of AM fungal communities, the mechanisms responsible for these impacts remain largely unclear. In theory, there are several possible mechanisms by which increasing soil fertility may influence the composition of AM fungal communities including competition among AM fungi and environmental filtering because of fungal preferences or host plant selection. First, fertilization may enhance competition among coexisting AM fungi because plants generally reduce the amount of carbohydrate supplied to mycorrhiza when they are not limited by soil nutrients (Johnson, 2010; Olsson et al., 2010); and, enhanced competition may result in loss of fungal diversity and a shift of the species composition towards dominance of AM fungi that are superior competitors when carbohydrates are limited (Hepper et al., 1988; Johnson, 1993). Second, because species of AM fungi have different niches and are known to prefer to inhabit different soil conditions (Schechter and Bruns, 2008; Alguacil et al., 2010; Dumbrell et al., 2010), fertilization may directly select taxa that grow best in the enriched conditions. Third, there is good evidence that plants actively select AM fungal taxa that best provision nutrients (Parniske, 2008; Kiers et al., 2011; Bever, 2015) and many field studies have shown that certain plants select particular AM fungi (e.g. Vandenkoornhuysen et al., 2003; Veresoglou and Rillig, 2014); thus, the loss of plant species caused by fertilization can lead to significant changes in the AM fungal community (Liu et al., 2012).

Analysis of phylogenetic structure has been used to infer the relative importance of competitive exclusion, environmental filtering, or stochastic process in driving community assembly (Webb et al., 2002). If the phylogenetic niches of organisms are conserved such that more closely related taxa have similar niche-related traits, then competitive exclusion and environmental filtering will generate patterns of phylogenetic over-dispersion and clustering, respectively (Webb et al., 2002). This method was first used in the studies of plant communities (e.g. Webb, 2000; Dinnage, 2009; Parmentier et al., 2014; de Freitas et al., 2014), but is now increasingly used to analyze the community assembly of mycorrhizal fungi (e.g. Lim and Berbee, 2013; Grilli et al., 2014; Horn et al., 2014; Rincón et al., 2014; Shi et al., 2014). A factorial field study of the influence of light and nutrient availability analyzed the phylogenetic structure of AM fungal communities inside roots and determined that environmental filtering structured communities under unfertilized conditions but random process was most important under a low level of fertilization (Liu et al., 2015). The purpose of our current study is to analyze the phylogenetic structure of AM fungal communities across a long-

term fertilization gradient and test the hypothesis that increasing fertilization will cause plants to allocate less photosynthate to their fungal symbionts and increase the relative importance of competitive interactions for structuring AM fungal communities.

We have previously shown that eight years of combined N and P fertilization of an alpine meadow reduces the abundance and diversity of AM fungal communities inside roots (Liu et al., 2012). However, the ecological processes driving these community shifts were not examined. Our current study uses community phylogenetic analysis to study the AM fungal communities in the soil of the same fertilization experimental system as Liu et al. (2012) to better understand the mechanisms by which increasing soil fertility structures AM fungal communities. We chose to identify communities from soil DNA rather than roots because soil contains both active (extraradical hyphae) and dormant (spore) structures of AM fungi and thus may reflect a larger proportion of the total species pool (Alguacil et al., 2014). We predicted that, as in the root-derived results reported in Liu et al. (2012), increasing soil fertility would significantly reduce the diversity of soil-borne AM fungi; and additionally, this reduction should be largely attributed to the enhanced competition process. In particular, the current study aimed to answer the following questions: (1) how do species composition and phylogenetic structure of AM fungal communities respond to a fertilization gradient? (2) Which is the primary ecological process structuring AM fungal communities across a fertilization gradient?

## 2. Materials and methods

### 2.1. Description of study site and fertilization treatment

This study was conducted at the Walaka experimental site (34°00'N, 102°00'E; 3500 m above sea level) of the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University in the eastern Qinghai-Tibetan Plateau of China. This region is a typical alpine meadow ecosystem, where the mean annual temperature is 1.2 °C, the mean annual precipitation is 620 mm, the dominant plants consist mainly of Cyperaceae and Poaceae, the growing season is from May to September, and the diversity of both plants and AM fungi is relatively high (Liu et al., 2012). Since 2001, the experimental site has been fenced and only grazed by yak and sheep every winter from October to April.

The long-term fertilization experiment, with 25 plots (5 rows by 5 columns) consisted of five fertilization levels and five replicates using a randomized block design. Plots were established on a flat area on March 2002. Each plot was 10 × 6-m<sup>2</sup> and separated from the others by a 1-m buffer strip. Five fertilization treatments were generated with 0, 30, 60, 90 and 120 g m<sup>-2</sup> yr<sup>-1</sup> of (NH<sub>4</sub>)<sub>2</sub>HPO<sub>4</sub> fertilizer applied annually from 2002 at the beginning of the growing season, and these treatments are hereafter referred to as F0, F30, F60, F90 and F120, respectively. The corresponding N and P inputs of each treatment are as follows: F0, control; F30, 6.4 g N and 7 g P m<sup>-2</sup> yr<sup>-1</sup>; F60, 12.7 g N and 14.1 g P m<sup>-2</sup> yr<sup>-1</sup>; F90, 19.1 g N and 21.1 g P m<sup>-2</sup> yr<sup>-1</sup>; F120, 25.4 g N and 28.2 g P m<sup>-2</sup> yr<sup>-1</sup>. After eight years of fertilization treatment (in 2010), soil available N and P concentrations gradually increased across the fertilization gradient, while plant species richness decreased dramatically and plant community shifted towards dominance by *Elymus nutans* (Table S1). More details of the changes in soil and plant properties across the fertilization gradient are described in Liu et al. (2012).

### 2.2. Soil sampling and DNA extraction

Soil samples were collected on 20 May, 10 July and 5 September 2010, concurrently with the samples collected for Liu et al. (2012).

Download English Version:

<https://daneshyari.com/en/article/2024466>

Download Persian Version:

<https://daneshyari.com/article/2024466>

[Daneshyari.com](https://daneshyari.com)