Applied Soil Ecology 115 (2017) 60–67

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Shifts in composition and diversity of arbuscular mycorrhizal fungi and glomalin contents during revegetation of desertified semiarid grassland

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ARTICLE INFO

Keywords:
Plant-mycorrhizal association
Community structure
Spore density
Phytoremediation
Caragana microphylla

ABSTRACT

Arbuscular mycorrhizal (AM) fungi may facilitate the revegetation of degraded ecosystems by decreasing abiotic and biotic stresses on pioneer plants. In addition to assessing the AM status of pioneer plants, monitoring the dynamics of an AM fungal community after revegetation can provide key information for the selection of plant-AM fungal combinations that adapt to the disturbed conditions to promote the establishment and growth of mycorrhizal-dependent pioneer plants. Accordingly, species composition, diversity, and spore density of the AM fungal community inhabiting the root zones of 12-year- and 30-year-old planted *Caragana microphylla* were determined in the desertified grassland in northern China. Moreover, the content of glomalin-related soil proteins (GRSP) was measured to assess AM fungal biomass. A total of 23 AM fungal species belonging to *Acaulospora*, *Claroideoglomus*, *Dentiscutata*, *Funneliformis*, *Glomus*, *Rhizophagus*, and *Septoglomus*, were identified. Soil phosphorus availability or organic-carbon content significantly affected AM fungal composition and diversity. However, edaphic properties can explain only approximately 30% of the variations in the AM fungal community. Spore density and GRSP content recorded at the 30-year revegetated dune were significantly higher than those at the 12-year revegetated dune. No significant differences in community composition and diversity of AM fungi were recorded at the dunes with different revegetation duration. This indicates that there might be a certain degree of host-specificity existing in the *C. microphylla*-AM fungal association. Both taxonomic and phylogenetic analyses should be performed in further research to obtain comprehensive information about the composition and dynamics of an AM fungal community during revegetation of the desertified grassland.

1. Introduction

Arbuscular mycorrhizal (AM[1]) fungi, belonging to phylum Glomeromycota (Schussler et al., 2001), can form a mutualistic association with approximately 80% of terrestrial plants (Smith and Read, 2008; van der Heijden, 2004). Such an association can increase the uptake and transport of nutrients and water (Auge, 2001), and enhance the resistance of host plants to pathogen aggression (Newsham et al., 1995). The extraradical mycelia of AM can also bind soil particles and microaggregates (< 250 μm) together to form macroaggregates (> 250 μm) (Chaudhary et al., 2009) and, consequently, increase soil stability and water retention. Due to these key physiological and ecological functions, AM fungal amendment is considered an effective approach to facilitate revegetation in degraded ecosystems, such as desertified shrubland/grassland (Azcon and Barea, 1997; Zhang et al., 2012), mine tailings (Orlowska et al., 2011; Taheri and Bever, 2011), and abandoned agricultural fields (Richter and Stutz, 2002).

Compared to the non-mycorrhizal control, AM fungal inoculation can significantly increase shoot biomass, nutrient concentration, and vegetation recovery in degraded ecosystems (Ouahmane et al., 2007; Urgiles et al., 2014; Zhang et al., 2012). However, neutral or even negative effects of AM fungi on the growth of individual plants or the productivity of vegetation have also been observed and reported (Emery and Rudgers, 2011). Contradictory observations may be attributed to (1) distinct mycorrhizal dependence of different plant species (Azcon and Barea, 1997); (2) lower adaptation of exotic or commercial AM fungi to the harsh environment relative to native AM fungi (Caravaca et al., 2003; Maltz and Treseder, 2015; Taheri and

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[1] Nonstandard abbreviations: AM: arbuscular mycorrhizal; ANOVA: analysis of variation; ASD: active sand dunes; Corg: organic-carbon content; EE-GRSPs: easily extractable glomalin-related soil proteins; GRSP: glomalin-related soil proteins; H′: Shannon-Weaver index; Int: the interspaces between *C. microphylla* shrubs; Pav: phosphorus availability; PVLG: polyvinyl lactoglycerol; RDA: Redundancy analysis; T-GRSPs: total glomalin-related soil proteins; Und: under the canopy of *C. microphylla*.

http://dx.doi.org/10.1016/j.apsoil.2017.03.015
Received 5 October 2016; Received in revised form 17 March 2017; Accepted 17 March 2017
Available online 13 April 2017
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Bever, 2011); (3) some degree of host-specificity existing between AM fungi and their host plants (Sanders, 2002).

Accordingly, in order to successfully utilize AM fungi to enhance the establishment and growth of pioneer plants during the revegetation of degraded grassland, preliminary work needs to be done (1) to assess the AM status of the pioneer plants (Caravaca et al., 2003; Liu et al., 2009); (2) to identify AM fungal composition and monitor its spatiotemporal changes in the root zone of pioneer plants; and (3) to select plant-AM fungal combinations with high adaptation to the harsh environment in the degraded grassland.

During last decade, the AM status of many grass, herb, and shrub species widely distributed in the semiarid area of northern China, have been assessed and reported (Chen et al., 2012; Shi et al., 2007; Tian et al., 2009). For example, Tian et al. (2009) examined 54 plant species (belonging to 18 families) dispersed in the typical steppe grassland in Inner Mongolia, and observed "arbuscules" or "hyphal coils" in the roots of 27 species, and "mycelia" or "vesicles" in 20 other species. Chen et al. (2012) determined the composition and diversity of AM fungi in the root zone of shrubs (i.e., *Caragana korshinskii*, *Artemisia sphaerocephala*, and *Salix psammophila*) dominating in the farming-pastoral zone of Inner Mongolia (China), and revealed distinct impacts of different shrub species on AM fungal diversity. The edaphic properties were supposed to play a key role in shaping the AM fungal community because significantly positive correlations between AM fungal diversity and both soil organic-carbon content and phosphorus availability were recorded (Chen et al., 2012). Likewise, these two soil chemical properties, nitrogen availability and phosphatase activity were found to significantly positively correlate with spore density and content of glomalin-related soil proteins (GRSP) (Bai et al., 2009; Chen et al., 2012; He et al., 2010). These studies reveal the ubiquitous occurrence of AM symbiosis in the semiarid grassland in northern China, and the potential impacts of edaphic properties on AM fungal composition and abundance.

These previous studies were mainly conducted in remnant grassland or shrubland. Few investigations focused on the community structure of AM fungi in the desertified grassland in northern China, where both the aboveground vegetation and belowground environment had experienced severe disturbance. Given the potential impacts of plants and edaphic properties on the composition and abundance of the AM fungal community, we assumed that an increase in vegetation cover and amelioration in soil conditions after revegetation (Su and Zhao, 2003; Yu et al., 2016) can facilitate the recovery of AM fungal symbionts in the desertified semiarid land. Therefore, the present study sheds light on the composition, diversity, and abundance of AM fungi in desertified grassland in northern China, and the shift in these AM fungi-related parameters during revegetation. We hypothesize that (1) since vegetation and soil structure have been severely disturbed at the active sand dunes, both AM fungal species richness and spore density at this habitat are significantly lower than at the revegetated dunes; (2) AM fungal diversity, spore density, and GRSP content recorded at the dune with long revegetated duration are significantly higher than that with short revegetation duration due to an increase in plant cover and improvement of edaphic properties.

2. Materials and methods

2.1. Study site

The study site located in the Wulanaodu village (43°02′N, 119°39′E, 479 m above sea level) in eastern Inner Mongolia (China) is characterized by a temperate and semiarid continental monsoonal climate. The multi-annual (1981–2002) mean temperature and precipitation in this area are 6.3 °C and 310 mm, respectively. Mean monthly temperature, monthly precipitation, and evaporation at the study site throughout the study period are given in Appendix Table A.1. The original landscape was a temperate steppe with sparsely scattered woods (mainly *Ulmus pumila*), and suffered several desertification processes during the last 400 years mainly due to anthropogenic activities such as firewood gathering and overgrazing. After the most recent severe desertification process occurred during the mid-1970s, indigenous perennial shrubs (e.g., *Caragana spp.*, *Salix gordejevii*, and *Artemisia halodendron*) were widely planted in straw checkerboards on the windward slope of active sand dunes from the early 1980s. More details about the background of the study site are available in Yu et al. (2016).

2.2. Soil sampling

Soil samples were collected from three habitats: a 12-year revegetated dune, a 30-year revegetated dune, and adjacent active sand dunes (control). The plant cover of the 12-year revegetated dune was approximately 40%, with randomly distributed *Bassia dasyphylla* and *Corispermum hyssopifolium* beneath the shrubs and at the interspaces during the growth season. The height and crown diameter of *C. microphylla* at this habitat were 90–120 cm and 80–100 cm × 75–90 cm, respectively. The plant cover, height, and crown diameter of *C. microphylla* at the 30-year revegetated dune were above 90%, 70–90 cm, and 65–80 cm × 55–70 cm, respectively. Some annual grasses and herbs, e.g., *Setaria viridis*, *Bassia dasyphylla*, *Chenopodium acuminatum*, and *Salsola collina*, were randomly distributed at this habitat during growth season, with a total cover of less than 10% (Cao et al., 2011). All three habitats were relatively close to each other, with the distances between any two habitats varying from 1 km to 3 km. At each habitat, four 8 × 8 m^2 plots, i.e., replicates, were established at minimum 10-m intervals on the windward slope of a sand dune. For each plot on the revegetated dunes, soil samples (0–10 cm) were collected on August 24th, 2013, and September 4th, 2014, from two sites: (1) under the canopies of five randomly selected *C. microphylla* shrubs with the mean canopy size and mean plant height of the population; and (2) at the interspaces between them. All five soil samples collected under the *C. microphylla* canopies or at the interspaces in the same plot were combined and placed in a plastic bag in the field as one replicate. Five soil samples collected at each plot on the active sand dunes were similarly handled. Insulated containers with ice bags were used to store soil samples during transportation. Prior to analyses, soils were sieved (2 mm) to remove stones, roots, and other organic debris. Air-dried soil samples were used for chemical-property analyses, AM fungal spore extraction, and species identification.

2.3. Soil chemical-property measurements

Soil pH was measured with an Orion Star A211 pH meter (Thermo Scientific, Beverly, MA) using a 1:2.5 soil:water ratio. Soil total organic carbon was determined via combustion of 500 mg air-dried subsamples using an elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). After extraction with 0.5 mol L^{-1} (pH 8.5) sodium bicarbonate, available phosphorus was determined using the molybdenum blue-ascorbic acid method (Olsen, 1954).

2.4. AM fungal spore extraction, species identification, and diversity

AM fungal spores were extracted from each soil sample by wet sieving (40–500 μm mesh size) and sucrose density centrifugation (Ianson and Allen, 1986). The spores were collected on a filter paper and washed with distilled water several times. Spore density was determined under a stereomicroscope at × 45, and a sporocarp was recorded as one unit (He et al., 2010). For species identification, the isolated spores were picked up from the filter paper and mounted in polyvinyl lactoglycerol (PVLG) and PVLG + Melzer's reagent (1:1, v/v). Identification of AM fungi was based on the structural features of each spore, including spore size, color, ornamentations, wall layers, and hyphal attachments. The descriptions of the features of different AM fungi are available online at http://www.invam.wvu.edu/the-fungi/

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