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Changes in arbuscular mycorrhizal fungal attributes along a chronosequence of black locust (*Robinia pseudoacacia*) plantations can be attributed to the plantation-induced variation in soil properties

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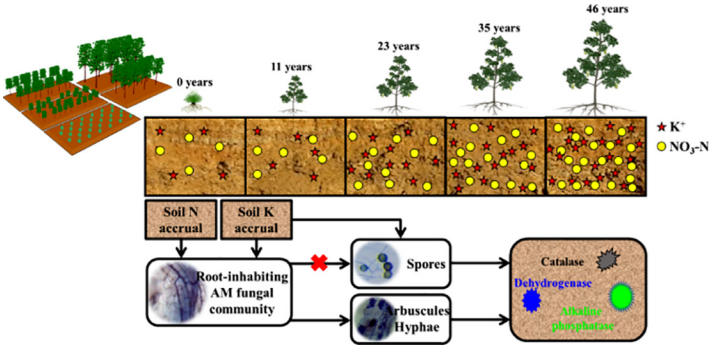
HIGHLIGHTS

- Soil available K and N contents increased as black locust stands aged.
- AM fungal sporulation and colonization varied along the chronosequence.
- Roots and soils hosted different AM fungal communities; the root-inhabiting AM fungal community was affected by stand age.
- The *Claroideoglomus* and *Glomus* genera detected in roots showed significant variation along the chronosequence.
- Soil K and N accrual with increasing stand age is the main reason for the changes in AM fungal attributes.

GRAPHICAL ABSTRACT



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ABSTRACT

Arbuscular mycorrhizal (AM) fungi form symbioses with the majority of terrestrial plant species, and their community influences many important ecosystem processes, including ecological succession. Understanding the successional changes of AM fungal communities in afforested zones over time is of primary interest in forest ecology. Black locust (*Robinia pseudoacacia*) has been widely planted on the Loess Plateau of China to prevent soil erosion. We sampled fine roots and rhizosphere soils in black locust plantations consisting of stands of 0, 11, 23, 35 and 46 years of age to measure soil properties, AM fungal colonization level, and spore density and to describe the composition of AM fungal communities in roots and soils using 454 sequencing. With increasing stand age, AM fungal spore density and soil NO_3-N and available K contents increased, dehydrogenase and alkaline phosphatase activities decreased, and soil catalase activity and the level of root colonization by arbuscules and hyphae first increased and then decreased. Roots and soils hosted different AM fungal diversity and communities. In soils, AM fungal diversity and community composition did not vary with stand age. In roots, the relative abundance of *Claroideoglomus*, together with Chao1 richness and OTU richness, peaked at the intermediate stage (35 years) and then declined, and the relative abundance of *Glomus* decreased linearly with tree age, whereas the relative abundance of the dominant genus *Rhizophagus* did not vary with stand age. Soil available K and NO_3-N largely

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explained the shift in the structure of the root-colonizing AM fungal community along the chronosequence. Soil enzyme activities were also associated with changes in AM fungal spore abundance and root colonization level. All the results presented here suggest that the successional changes in AM fungal communities in black locust plantations occurring over time can largely be attributed to plantation-induced changes in soil nutrient levels.

1. Introduction

Successional taxonomic changes in communities over time are a fundamental property of ecosystems (Soliveres et al., 2016; Gossner et al., 2016). Arbuscular mycorrhizal (AM) fungi are widely distributed in terrestrial ecosystems, forming symbioses with about 80% of all plant species (Smith and Read, 2008). The AM symbiosis is involved mainly in the transport of nutrients to the plant and carbon compounds to the fungus (Smith and Read, 2008). Normally, plants preferentially allocate carbohydrates to the more beneficial symbionts (Bever et al., 2009), and thus the identity and abundance of host plants can shape the AM fungal community (García de León et al., 2016a, 2016b). In addition, AM fungi can improve plant establishment and mitigate the impact of stressful environments (van der Heijden et al., 2008). However, the effects of the AM symbiosis on plant performance depend on the composition of the AM fungal community (Öpik et al., 2009). Thus, it is important to understand AM fungal community dynamics for effective long-term ecosystem management.

Afforestation is an effective way to improve vegetation cover, especially in degraded areas (Nunes et al., 2011). Afforestation can change the composition of plant communities along with soil microclimatic conditions and physicochemical properties (Buscardo et al., 2008; Macdonald et al., 2009; Berthrong et al., 2012). Therefore, there is considerable potential for afforestation to affect a resident AM fungal community. There is evidence that afforestation can affect AM fungal development, distribution, and function (Guo and Han, 2008; Gazol et al., 2016). However, the successional changes in AM fungal attributes in afforested zones over time are largely unknown.

Black locust (*Robinia pseudoacacia*), an N-fixing woody legume originating in the eastern USA, has been extensively naturalized in the temperate regions of North America, Europe, and Asia (Vítková et al., 2017). Black locust grows very rapidly and has high tolerance to drought and soil erosion (Buzhdygan et al., 2016). The occurrence of AM fungi in black locust roots is well documented (Ferrari and Wall, 2008; Callaway et al., 2011), and the AM symbiosis was reported to promote black locust growth considerably (Yang et al., 2014). Furthermore, as planted black locust stands grow and fix atmospheric N_2, they change the vegetation cover and the physicochemical attributes of the soil ecosystem in which mycorrhizas can be active (Yüksek, 2012). Thus, as stands age, the resources available to the mycorrhizal community may change. These changes in soil properties and their potential effects on the structure and function of AM fungal communities are of primary interest in forestry. Liu et al. (2013) reported that a decline in AM fungal spore density in soil planted with black locust as stands age follows an initial increase in spore abundance. Arbuscular mycorrhizal fungal spores are propagules, and thus specific variations in AM spore abundance over time can potentially change the structure of AM fungal communities (Varela-Cervero et al., 2016b). However, the successional changes in AM fungal communities and the reason for these changes are unclear.

The Loess Plateau in western China is a region with distinctive topographical and geological features. This area is characterized by severe land degradation, partly explained by industrial pollution, extreme weather, and the loss of vegetation causing soil erosion (Yuan et al., 2016). In this area, black locust has been planted since the middle of the 20th century to control soil erosion on >70,000 ha (Guo et al., 2005). We selected a chronosequence of black locust plantations of 11, 23, 35, and 46 years of age and the nearby native grassland on the Loess Plateau in China and assessed the influence of afforestation on soil properties and AM fungal attributes over time. We hypothesized that afforestation can induce successional changes in the resident AM fungal community and that these changes are due to the evolving effects of growing trees on soil properties.

2. Materials and methods

2.1. Experimental site

The study was conducted at the Changwu Research Station for Soil and Water Conservation of the Chinese Academy of Sciences in the Wangdonggou watershed region, Shaanxi Province, northwestern China. This region, located in the south of the Loess Plateau, is characterized by a warm temperate subhumid continental climate, with an annual average temperature of 9.4 °C, mean annual precipitation of 575 mm, and a frost-free period of 171 days (China Meteorological Data Service Center). The groundwater level is about 50 to 80 m below the soil surface, which precludes upward capillary flow into the root zone. The soil at the study site has a silty clay loam texture and is covered mostly by native grasses (such as *Bothriochloa ischaemum*, *Arundinella hirta*, and *Artemisia argyi*). Black locust has been planted in the native grassland since 1955, and the planted areas were fenced off to prevent anthropogenic disturbance.

The chronosequence of black locust plantations included plantations of four ages (11, 23, 35, and 46 years old). In addition, the nearby native grassland, with no history of black locust plantation, was sampled as a control. A total of 15 sites (12 black locust plantations and 3 native grassland sites) were sampled. The sampling sites were located within a 700 by 1000-m area at an elevation varying from 1035 to 1145 m above sea level (Fig. S1, Table S1). The average tree heights were 6.91, 10.42, 14.53, and 16.07 m and the average diameters at breast height were 6.58, 10.27, 16.84, and 25.36 cm in the 11-, 23-, 35-, and 46-year-old black locust plantations, respectively. The native grass coverage was 86% to 95% for the grassland sites, 55% to 63% for the 11-year-old black locust plantations, 45% to 57% for the 23-year-old black locust plantations, 35% to 51% for the 35-year-old black locust plantations, and 28% to 43% for the 46-year-old black locust plantations.

In November 2013, roots and rhizosphere soils were sampled. Five soil cores were taken from the top soil layer (0–20 cm) in each native grassland sampling site using a hand-held power sampler, and the cores were pooled to form a single composite sample per site. In each tree-planted site, five trees of similar size were selected, and samples were taken from the four different sides of the trunk. Using a shovel, the sampled roots were traced to the originating tree to ensure identity. The fine feeder roots were sampled directly using hands, scissors, and forceps. Rhizosphere soil samples were collected from these roots by gentle brushing. The root samples were washed in running water, collected on a 0.2-mm mesh sieve, and dried with paper towels. A total of 15 soil samples (12 from the tree-planted sites and 3 from the native grassland sites) were used to determine soil properties and AM fungal spore density and to extract genomic DNA. Only 12 black locust fine root samples were available to measure AM fungal colonization and extract genomic DNA, as there were no black locust roots in the native grassland. All samples were transported to the laboratory on ice and stored in a freezer at −20 °C prior to processing.