



Effects of plant neighborhood on arbuscular mycorrhizal fungal attributes in afforested zones



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ABSTRACT

Arbuscular mycorrhizal (AM) fungi are an important determinant of plant performance, and conversely their community composition greatly depends on host plants and their neighbors. Understanding how the interaction of host plants and their neighbors affects AM fungal communities in afforested zones is of primary interest in forest ecology. We sampled roots and rhizosphere soils in monocultures and mixtures of black locust (*Robinia pseudoacacia*) and oriental arborvitae (*Platycladus orientalis*) to define AM fungal colonization level, spore density and communities using 454 sequencing. Neighboring oriental arborvitae only affected AM fungal community in black locust rhizosphere. For oriental arborvitae, however, growing in a mixture with black locust changed AM fungal colonization, sporulation and communities in the roots and rhizosphere. In particular, neighboring black locust modified the rhizosphere- and root-inhabiting AM fungal pool through improving soil NO₃-N and water contents and reducing soil catalase activity, and the modification in the root AM fungal resource, especially the *Glomus* and *Rhizophagus* genera, further affected AM fungal colonization and sporulation under oriental arborvitae. All the results presented here suggest that both hosts and neighbors can largely affect AM fungal attributes mainly through changing soil nutrient levels and enzyme activity, whereas the reciprocal effects are not always symmetric.

1. Introduction

Arbuscular mycorrhizal (AM) fungi form symbioses with about 80% of terrestrial plant species (Smith and Read, 2008; Brundrett, 2009). The AM symbiosis, a mutually beneficial association between AM fungi and host plant, is principally involved in the transport of nutrients to the plant and carbon compounds to the fungus (Smith and Read, 2008; van der Heijden et al., 2015). Host plants, which supply photosynthates to AM fungi, have been found to preferentially allocate carbohydrates to the more beneficial symbionts (Eom et al., 2000; Vandenkoornhuysen et al., 2002; Wyatt et al., 2014), and this preference induces unequal effect of AM fungal growth rates on different plant species (Bever et al., 1996; Streitwolf-Engel et al., 1997; Klironomos, 2002, 2003). The unequal growth of AM fungi in different host plants may induce changes in AM fungal spatial distribution at the community level (Hausmann and Hawkes, 2009). Some studies have reported that co-occurring

plants in natural ecosystems can host distinct AM fungal communities, a finding that has been attributed to the ecological specificity of the hosts (McGonigle and Fitter, 1990; Helgason et al., 2007; Turrini et al., 2016). Nonetheless, the strength of plant host effects on the AM fungal community remains unclear. It is essential to elucidate interactions among host plants in order to gain a better understanding of the importance of plant host effects on the AM fungal community.

It is known that plant species differ in their patterns of carbon allocation to roots and their production of secondary metabolites and exudation, and that these different patterns may also induce some changes in soil environmental conditions (Eom et al., 2000; Pallardy, 2010). The AM fungi form vast networks which potentially link individual plants within communities, allowing for between-plant two-way trafficking of nutrient resources (Simard and Durall, 2004). Thus, when multiple plant species are present, the neighboring plants may alter the effects of host plant on AM fungi or even change the available

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pool of AM fungi, and therefore have the potential to structure AM fungal communities (Hausmann and Hawkes, 2009; Mummey and Rillig, 2006). Some studies, most of which were conducted in the greenhouse or in invaded systems, have demonstrated that AM fungal community composition is influenced by the identity of the neighboring plants (Mummey et al., 2005; Hausmann and Hawkes, 2009; Morris et al., 2013). However, in artificial forests, the mechanisms by which the neighboring plants affect the AM fungal community are still largely unknown.

Forests play an important role in producing timber, fuel and pulp wood and in supporting ecosystem functions and services such as soil erosion control (Lang et al., 2014). Afforestation, often involving the establishment of monocultures and mixtures, is an effective way to improve degraded areas (Zhang, 2005; Lang et al., 2014). Afforestation changes the vegetation cover, impacting soil microclimatic conditions and physico-chemical properties (Su and Guo, 2007; Antoninka et al., 2011; Yang et al., 2013; Zheng et al., 2014). In general, heterospecific neighborhoods (mixtures) have been more effective than conspecific neighborhoods (monocultures) at maintaining soil properties and supporting plant growth (Guariguata et al., 1995; Carnevale and Montagnini, 2002; Montagnini et al., 2003; Kelty, 2006; Forrester et al., 2005), which means there is considerable potential for afforestation to affect the resident AM fungi and this influence may vary with afforestation type. By determining the relative importance of host plants and neighbors in terms of their effects on AM fungi, we will gain a better understanding of how interactions among plant neighbors play a role in plant-AM fungal feedbacks during the afforestation process.

The Loess Plateau in western China is a region with distinctive topographical and geological features (Peng and Yu, 1995). This area is famous for its deep loess. Due to the special geographic landscape and long history (over 5000 years) of anthropogenic disturbance, the vegetation cover has undergone degradation, exposing the soil to erosion (Zhang, 2000). Restoring the vegetation should therefore improve ecological conditions (Zhang, 2005). Black locust (*Robinia pseudoacacia*), a N-fixing legume tree, has a strong capacity to increase soil N levels (Rice et al., 2004; Tateno et al., 2007). Oriental arborvitae (*Platycladus orientalis*) is a conifer with an expansive root system and a long lifespan (Li and Liu, 2014). Over the last three decades, both black locust and oriental arborvitae have been widely planted as heterospecific and conspecific neighborhoods to control soil erosion. Our previous study, conducted at a 10-year old long-term experimental site established on the Loess Plateau to evaluate the effects of different afforestation types (black locust monoculture, oriental arborvitae monoculture, black locust × oriental arborvitae mixture) on soil erosion, pointed out that (1) oriental arborvitae, as the neighbor of black locust, reduced soil water, NO₃-N and alkaline phosphatase activity, and increased soil Mn level compared with black locust monoculture; and (2) black locust, as the neighbor of oriental arborvitae, increased soil water and NO₃-N levels, but decreased catalase activity compared with oriental arborvitae monoculture (Chen et al., 2017). In this study, we set out to further explicitly test how black locust and oriental arborvitae, evaluated as both a host and a neighbor, drive patterns of AM fungal colonization, sporulation and community composition in roots and rhizosphere soils. We hypothesized that the interactions between host plant and neighbor drive the changes that occur in the resident AM fungal community, in particular through the modification of the properties of the soil environment by the neighbor. The following specific questions are addressed in our study. Do hosts and adjacent plants interact to influence the AM fungal community in roots and rhizosphere? If so, are the changes in root AM fungal community related to the patterns of AM fungal colonization and sporulation? Do the host and neighbors affect AM fungal attributes through changes in soil properties?

2. Materials and methods

2.1. Experimental site and sampling

The study was conducted at Changwu Research Station of Soil and Water Conservation of the Chinese Academy of Sciences in the Wangdonggou watershed, Shaanxi Province, northwest China (longitude 107°42'E, latitude 35°12'N; elevation 1206 m). This study area lies in the southern part of the Loess Plateau and is characterized by a warm temperate sub-humid continental climate with a mean temperature of 9.4 °C. The mean annual precipitation is 575 mm, more than 58% of which falls between July and September (China Meteorological Data Service Center). The groundwater level is about 50–80 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 colonized by native grasses (such as *Bothriochloa ischaemum*, *Arundinella hirta*) and forbs (such as *Artemisia argyi*). Pure stands of black locust and oriental arborvitae and their 50:50 mixtures were established at a 2 × 2 m spacing on the native grassland in 2003, to control soil erosion when the “Grain for Green” project was implemented. To prevent the slope aspect and differences in the initial soil properties from influencing tree growth, all planted areas were selected for uniformity in slope (35°) and soil properties and therefore had the same aspect. The areas were fenced after tree planting to prevent any further anthropogenic disturbance.

In November 2013, i.e. ten years after planting, three stands were selected for each of afforestation types, a total of 9 stands (three for black locust monoculture, three for oriental arborvitae monoculture, and three for black locust × oriental arborvitae mixture) were selected, and in each of these stands, a 20 m × 20 m sampling plot was set up. The distances between plots were ranged from 150 m to 700 m, and this area between plots was used as buffer to prevent root invasion.

In each of these experimental plots, five trees of each species were randomly selected, and soil cores (8 cm in diameter) were collected close to the tree trunk in the 0–20 cm soil layer using a handheld power sampler. All of these samples were transported on ice to the laboratory, where the soil cores from a given tree in each plot were pooled prior to analyses. Roots in the soil cores were shaken to detach loose soil and were then carefully brushed to collect rhizosphere soil. The roots were rinsed in running water, collected on a 0.2 mm mesh sieve, separated from debris by hand, and dried with paper towels. In total, 12 root and 12 rhizosphere soil samples (three from black locust in monoculture, three from oriental arborvitae in monoculture, three from black locust in mixture and three from oriental arborvitae in mixture) were obtained and stored in a freezer at –20 °C prior to processing.

The properties of 12 rhizosphere soil samples have been measured in previous study (Chen et al., 2017) and given as background information here (Table 1). In this study, the same rhizosphere soil samples were used to detect soil-inhabiting AM fungal community composition and measure AM fungal spore density, and the root samples were used to measure AM fungal colonization and detect root-inhabiting AM fungal community composition.

2.2. AM fungal spore density

AM fungal spores were extracted from 15 g of frozen rhizosphere soil by wet sieving and decanting (Gerdemann and Nicolson, 1963), followed by density gradient centrifugation using a 50% sucrose solution (Brundrett et al., 1996). The spores were placed on a white gridded cellulose nitrate filter (1.2-μm pore size) with a pipette, washed with distilled water, then spread evenly and counted under a compound microscope (Olympus Bx51, Japan) at 10 × 10 magnification. Only spores that appeared to be viable (based on color, shape, surface condition, and spore contents) were counted (Yang et al., 2015). The density of AM fungal spores was expressed on a soil dry weight basis.

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