



Arbuscular mycorrhizal fungi inoculation mediated changes in rhizosphere bacterial community structure while promoting revegetation in a semiarid ecosystem



G. Rodríguez-Caballero^{a,*}, F. Caravaca^a, A.J. Fernández-González^b, M.M. Alguacil^a, M. Fernández-López^b, A. Roldán^a

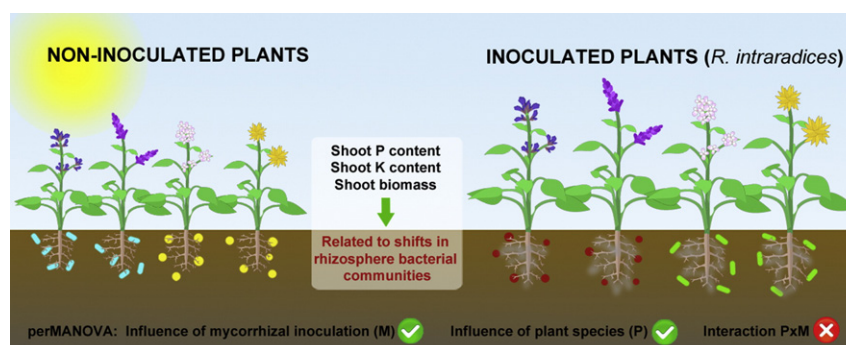
^a CSIC-Centro de Edafología y Biología Aplicada del Segura, Department of Soil and Water Conservation, P.O. Box 164, Campus de Espinardo, 30100 Murcia, Spain

^b CSIC - Estación Experimental del Zaidín, Soil Microbiology and Symbiotic Systems Department, Profesor Alameda, 1, 18008 Granada, Spain

HIGHLIGHTS

- An AMF improved plant performance in the revegetation of a semiarid ecosystem.
- AMF and plant species altered the rhizosphere bacterial community structure.
- AMF-mediated bacterial community shifts were related to plant performance.
- *Anaerolineaceae* family was an indicator of AMF-inoculated rhizospheres.

GRAPHICAL ABSTRACT



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ABSTRACT

The main goal of this study was to assess the effect of the inoculation of four autochthonous shrub species with the arbuscular mycorrhizal (AM) fungus *Rhizophagus intraradices* on the rhizosphere bacterial community and to ascertain whether such an effect is dependent on the host plant species. Additionally, analysis of rhizosphere soil chemical and biochemical properties was performed to find relationships between them and the rhizosphere bacterial communities. Non-metric multidimensional scaling analysis and subsequent permutational multivariate analysis of variance revealed differences in bacterial community composition and structure between non-inoculated and inoculated rhizospheres. Moreover, an influence of the plant species was observed. Different bacterial groups were found to be indicator taxonomic groups of non-inoculated and inoculated rhizospheres, Gemmatimonadetes and *Anaerolineaceae*, respectively, being the most notable indicators. As shown by distance based redundancy analysis, the shifts in bacterial community composition and structure mediated by the inoculation with the AM fungus were mainly related to changes in plant nutrients and growth parameters, such as the shoot phosphorus content. Our findings suggest that the AM fungal inoculum was able to modify the rhizosphere bacterial community assemblage while improving the host plant performance.

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* Corresponding author.

E-mail address: grcaballero@cebas.csic.es (G. Rodríguez-Caballero).

1. Introduction

Mediterranean semiarid ecosystems in Southeast Spain are frequently exposed to erosive processes and vegetation cover losses. This leads to degraded habitats which are especially fragile and endangered by environmental changes such as global warming. The harsh climate conditions and the nutrient scarcity that characterize these areas make the plant establishment more difficult, and thus reduce the effectiveness of restoration programs (Caravaca et al., 2005), which intend to prevent the loss of fertile soil and the desertification progression.

The introduction of autochthonous shrub species, adapted to semiarid environmental conditions and nutrient scarcity, is preferential in the revegetation of Mediterranean semiarid ecosystems (Requena et al., 2001; Caravaca et al., 2005). However, the progressive increase in aridity and land degradation has caused a severe loss of native microbial diversity and functioning (Maestre et al., 2015), which makes plant establishment more difficult in these areas. This is the case for the mycorrhizal potential, which is seriously depleted (Requena et al., 1996; Azcón-Aguilar et al., 2003).

Plant-microbe relationships are decisive for plant growth and survival (Van Der Heijden et al., 2008). In fact, plants are considered as holobionts, with the plant per se and all its associated microbiota comprising a “single dynamic entity” (Vandenkoornhuysse et al., 2015). The main source of these microorganisms is the surrounding rhizosphere soil - which works as a microbial “seed bank” that, together with the local environmental parameters, strongly influences the final composition of the rhizosphere microbial communities (Vandenkoornhuysse et al., 2015). The plant microbiome stimulates germination and plant growth, enhances nutrient acquisition, promotes direct and indirect mechanisms of defense against pathogens and against abiotic stress and influences plant phenology (Berg et al., 2016). Many of these functions might be indirectly influenced by the microbial interactions that occur in the rhizosphere because the resulting plant microbiome could be functionally different (Barea et al., 2005).

The application of microbial inoculants to the plant rhizosphere has been demonstrated to be a suitable strategy for revegetation purposes (Palenzuela et al., 2002; Armada et al., 2015; Mengual et al., 2016). Some native strains of actinobacteria have been successfully used in the revegetation with shrub species of semiarid ecosystems, whose effectiveness was related to increased NPK uptake and plant drought tolerance (Mengual et al., 2016). Meanwhile, arbuscular mycorrhizal fungi (AMF) are one of the best studied plant symbionts (Parniske, 2008) and the beneficial effect of these microbial inoculants on plant establishment - through improvement of plant adaptability and stress tolerance and enhancement of plant nutrient acquisition - has been reported in numerous studies (Jeffries et al., 2003; Van Der Heijden et al., 2008), including studies of revegetation in semiarid degraded areas (Alguacil et al., 2011; Caravaca et al., 2005; Barea et al., 2011). Many studies report that the beneficial effects of AMF may be due to their interactions with rhizobacteria (Artursson et al., 2006). In this regard, AMF mycelial exudates increased the growth and development of soil bacterial community, particularly the relative abundance of Gammaproteobacteria (Toljander et al., 2007). On the other hand, some bacteria can affect spore germination rate and mycelial growth modifying AMF functions on plants (Artursson et al., 2006). Previous findings suggest that microbial interactions involving AMF and nitrogen-fixing, phosphate-solubilizing and plant growth-promoting rhizobacteria, as well as AMF and rhizosphere native bacterial community, can have a beneficial effect on the growth and health of plants and on soil quality (Barea et al., 2005). This synergistic effect on plant growth could be related to enhancement of nutrient uptake to plants, suppression of plant pathogenic fungi and promotion of lateral root growth. Alteration of rhizosphere microbial community has also been proposed as a mechanism responsible of plant growth promotion by AMF (Artursson et al., 2006). However, a better understanding of the complex relationships in the rhizosphere is needed to design effective restoration programs.

It has been reported with a DGGE approach that the AM fungus *G. intraradices*, modified rhizosphere bacterial communities (Vestergård et al., 2008) and that this effect depended on the phenology of the plant (Wamberg et al., 2003). Marschner and Baumann (2003) also employed DGGE to describe changes in rhizosphere bacterial communities which were exposed to *G. intraradices* and *G. mosseae* inoculation, but they suggested that this effect may be partially mediated by the plant as well. In the same way, Marschner and Timonen (2005) concluded that a plant-fungus complex interaction may be affecting the bacterial communities, whereas a study conducted by Söderberg et al. (2002), showed that the AMF effect on the bacterial communities varied depending on the host plant species. More recently, different changes in particular bacterial groups, as a consequence of inoculation with AMF, have been described by the use of PLFA and NFLA (Mechri et al., 2014) and 16S rRNA gene microarrays (Nuccio et al., 2013).

The most commonly used techniques to address this question (DGGE and PLFA) have important resolution limitations and are confined to the most abundant bacterial groups (Zhang and Xu, 2008; Van Elsas and Boersma, 2011), resulting in just a general overview of changes in microbial communities. High-throughput sequencing methods provide more precise tools for the in depth study of soil microbial communities (Zhang and Xu, 2008; Van Elsas and Boersma, 2011). Despite the need to increase our knowledge of symbiosis-associated bacterial communities and the current development of these techniques, there are relatively few studies that deal with the effect of mycorrhizal inoculation on rhizosphere bacterial communities using such molecular tools (Cao et al., 2016; Qin et al., 2016). Besides, none of these studies was performed under natural field conditions or in a semiarid ecosystem.

We hypothesized that the inoculation of four autochthonous shrub species (*Salvia officinalis*, *Lavandula dentata*, *Thymus vulgaris*, and *Santolina chamaecyparissus*) with the AM fungus *Rhizophagus intraradices* would induce direct and/or indirect changes in rhizosphere bacterial community structure, regardless of the host plant species, and that such shifts could be linked to improvements in plant performance. Accordingly, this study aims to determine, through the use of pyrosequencing, whether the application of this mycorrhizal inoculum for revegetation purposes in a semiarid ecosystem mediates changes in the rhizosphere bacterial communities, as well as to analyze the influence of different host plant species on these alterations. Additionally, shifts in soil chemical and biochemical properties driven by the presence of the inoculum are also studied, as well as their relationship to the composition and structure of the resulting bacterial community.

2. Materials and methods

2.1. Study site, plant species and mycorrhizal inoculum

The study was carried out at an experimental site located in the Ecological Park “Vicente Blanes”, El Rellano (province of Murcia, SE Spain; coordinates 38° 12' 50.8" N, 1° 13' 30.9" W). The climate of the area is Mediterranean semiarid, characterized by low and irregular rainfall rates. The annual precipitation recorded during the experimental period (from November 2014 to November 2015) was 315 mm, and the mean temperature was 17.9 °C. The soil in this area is classified as a Typic Torriorthent (SSS 2010) with very little development. It has a silty-clay texture and is poor in organic matter. Therefore, its structural stability is weak.

Four autochthonous shrubs species, representative from semiarid areas in Southeast Spain, were selected for the experiment. *Salvia officinalis* L., *Lavandula dentata* L., and *Thymus vulgaris* L. belong to the *Lamiaceae* family while *Santolina chamaecyparissus* L. belongs to the *Asteraceae*. They are all well adapted to water and nutrient scarcity and are potential candidates for revegetation of this kind of ecosystems (Azcón and Barea, 1997; Padgett et al., 2000; Bochet et al., 2010; Sánchez-Ormeño et al., 2016). Seedlings of each plant species were

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