



Arbuscular mycorrhizal fungal communities in changing environments: The effects of seasonality and anthropogenic disturbance in a seasonal dry forest



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ABSTRACT

The landscape of Mexican seasonal dry forests is affected by various periodic (long and drastic drought) and random (elimination of the forest coverage for agricultural purposes) disturbance events. The community of arbuscular mycorrhizal fungi (AMF) responds to these changes, sporulating and reducing its activity during the dry season, and slowly reestablishing itself following abandonment of cultivated fields. To determine the dynamics of the AMF community in response to natural phenomena and anthropogenic disturbances, we collected soil samples during the wet and dry seasons from plots with different time periods since abandonment of agricultural activity, categorized as early (less than 5 years), middle (11–23 years), and late (over 30 years) age plots. From each plot, AMF spores were isolated and identified in order to estimate abundance, richness and diversity. In addition, the number of infective propagules and value of mycorrhizal inoculum potential were calculated for each plot. Twenty-three species were recorded, for which Glomeraceae and Acaulosporaceae were the most commonly represented families. Significant differences were found in AMF species richness among plots and seasons and the diversity index of AMF was higher than 1.0 in most cases. There were no significant differences in spore abundance. Viable propagules were observed in all soil samples, with fluctuations relating mainly to time since abandonment. Overall, seasonality has a strong influence on AMF diversity but not on AMF infectivity, while time since abandonment had a more important impact.

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Introduction

Seasonal dry forest (SDF) is a plant community that covers 11.26% of the land area of Mexico (Challenger and Soberón 2008). It is distributed in regions that present a highly marked seasonality, for which reason a high percentage of the arboreal elements lose their leaves during the dry season of the year. Primary production in this system is limited by the low levels of available phosphorus present in the soil (Jaramillo and Sanford 1995; García-Oliva and Maass 1998; García-Oliva and Tapia 2001). These plant communities are often cleared for agricultural purposes, increasing the effect of seasonality due to the higher evaporation that occurs when

the soil does not have plant cover or a layer of organic material. In this condition, soil is more exposed to the action of wind and solar radiation, which reduces its capacity for moisture retention (Maass 1995; Whelan 1995) and infiltration, compounding the conditions of drought still further (Maass 1995; Bond and van Wilgen 1996; DeBano et al. 1998) and potentially leading to reduced numbers of below- and above-ground species (Dunphy et al. 2000).

In many cases, however, plant species of SDF are capable of withstanding the effects of seasonality and deforestation because of their association with arbuscular mycorrhizal fungi (AMF) of the phylum Glomeromycota (Violi et al. 2008; Uiboppu et al. 2009). Mycorrhizal interaction takes place in the roots of the host plant, and increases the survival and competitive ability of associated plants due to the presence of a greater root surface area provided by AMF hyphae (Bago et al. 1998). These structures also contribute to an increase in water and nutrient uptake (Fagbola et al. 2001). Moreover, AMF have been shown to increase plant diversity and

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productivity in several ecosystems (van der Heijden et al. 1998; O'Connor et al. 2002), including the tropical forests (Pasqualini et al. 2007).

Conversion of SDF to agricultural land can cause a reduction in the richness and diversity of AMF (Tchabi et al. 2008; Oehl et al. 2010), as well as diminishing the infectivity of propagules (i.e. spores, mycelia and previously colonized roots) capable of colonizing a new host (Aguilar-Fernández et al. 2009; Boerner et al. 1996). Nevertheless, an increase in the abundance of some species has been observed under these conditions, due largely to the fact that certain AMF genera respond differently to the loss of vegetation (Munyanziza et al. 1997): Species of the genus *Glomus* mainly colonize the roots of host plants by means of hyphae, while species of the genera *Gigaspora* and *Acaulospora* mainly colonize through germinating spores (Klironomos and Hart 2002; Gazey et al. 1992; Hart and Reader 2004). Such differences in response among genera may produce changes in AMF community structure during the process of revegetation following cessation of agricultural activity and abandonment of plots. Identification of the AMF species that appear in different successional stages could improve the utilization of these species for the inoculation of seedlings during activities of restoration and reforestation (Oehl et al. 2011). Similarly, the ability to quantify viable propagules in each plot would allow us to more accurately determine the “health” of the ecosystem.

Numbers of soil hyphae and spores may decrease in SDF during the dry season (Moreira-Souza et al. 2003); however, if a plant can maintain its mycorrhizal colonization, it will have competitive advantages with the onset of the rains since the presence of hyphae increases the capacity of the plant to explore the soil for water (Ramos-Zapata et al. 2011) and increases plant production of fine roots, an important process that drives plant growth and reproduction in SDF (Bullock and Solís-Magallanes 1990; Kummerow et al. 1990; Campo et al. 1998).

The SDF of the Nizanda region of Oaxaca, Mexico, undergoes a particularly long drought period that acts to modify the physiognomy, while the natural vegetation is also subject to elimination by slash and burn agricultural practices. This typically takes place over areas of less than one hectare, sometimes with the addition of fertilizers, where maize is grown for auto-consumption. These areas are subsequently abandoned after one or two harvests, depending on the proximity of water (i.e. wells or rivers) (pers. obs.). These agricultural practices have led to heterogeneity in terms of the age of vegetation stands throughout the landscape (Pérez-García et al. 2001). The presence of both events of change (seasonality and anthropogenic disturbance) prompts the question of whether the community of arbuscular mycorrhizal fungi is more influenced by seasonality or by land use changes in the Nizanda area. We predicted that the AMF respond differentially to these events of change, since dormancy is broken with the onset of the wet season, leading to increased diversity. However, a loss of AMF species occurs as a result of the elimination of plant cover by slash and burn practices. AMF community recovers slowly as revegetation takes place. The AMF species present in the secondary vegetation of the Nizanda SDF may then present increased spore production and higher numbers of infective propagules as a consequence of plant re-growth (Shamim et al. 1994; Sanders and Fitter 1992a,b).

The main hypothesis of the present study was that changes in the composition of the AMF community would relate more significantly to time since abandonment of plots than to seasonality, while the propagules capable of initiating colonization would be more affected by seasonality than time since plot abandonment because of the absence and/or latency of hosts. Following abandonment, ruderal plants begin to appear and these maintain AMF infectivity by functioning as temporary hosts. The main goals of this study were to determine whether and how both of these factors, one an environmental condition and the other the

result of agricultural management, could modify the arbuscular mycorrhizal fungal community and its infectivity.

Materials and methods

Study area

The study was conducted near the village of Nizanda, Oaxaca, Mexico (16°39'30" N, 95°00'40" W). The climate of the study area is classified as warm and dry [Aw₀ (w)igw"] with a mean annual temperature of 25 °C and mean annual rainfall of 1000 mm (García 1988). The soil is a sandy clay loam, with pH values between 6 and 6.5, and available P in the soil of between 3.18 and 3.54 ppm (Table 1). There is a marked seasonality in rainfall, with the dry season extending from November to April, and the wet season from May to October (SPP 1984a,b).

The vegetation corresponds to a transition from subtropical very dry forest to subtropical dry forest (Lebrija-Trejos et al. 2008). In this study, we consider the vegetation of this area to be seasonal dry forest (SDF). The SDF landscape comprises tropical low deciduous forest and secondary vegetation of different ages since abandonment of agriculture and is composed of 141 species from 46 families; *Apoplanesia paniculata* C. Presl (Leguminosae), *Amphipterygium adstringens* (Schltdl.) Standl. (Julianiaceae) and *Lysiloma divaricatum* (Jacq.) J.F. Macbr. (Leguminosae) are the dominant species in undisturbed SDF; while areas of late succession secondary vegetation (plots of more than ten years since abandonment) are dominated by *Mimosa tenuiflora* (Willd.) Poir. (Leguminosae) and *Mimosa acantholoba* var. *eurycarpa* (Leguminosae). In areas of early succession secondary vegetation (less than ten years since plot abandonment) the dominant species are *Chamaecrista serpens* (L.) Greene. (Caesalpinaceae) and *Melochia tomentosa* L. (Sterculiaceae) (Lebrija-Trejos et al. 2008). In the study region, mycorrhizal association has been found in the roots of pioneer, early successional and late successional species (pers. obs.) (Table 2).

Study sites

Within an area of 2 km², nine 900 m² plots (30 m × 30 m) were established in selected areas featuring secondary vegetation, derived from slash and burn agricultural practices, at different successional stages. Under this system, small areas of seasonal dry forest are cleared and burned for sowing with maize, then abandoned after one or two harvests (pers. obs.). Plots were classified as: (a) early age (1, 3 and 5 years since abandonment), (b) middle age (11, 16 y 23 years since abandonment), and (c) late age (30, 40 and over 60 years since abandonment). Plots were selected based on the homogeneity of the land and land use history, geological substrate and their topographic position and presence of piedmont landforms (see Lebrija-Trejos et al. 2008). Time since abandonment of the plots was established based on dendrochronological data (Brienen et al. 2009).

Soil sampling

In each of the plots, we randomly collected three 2 kg soil samples. Topsoil (first 15 cm depth of soil) samples were obtained and any recognizable plant material (leaves and stems) within each sample was removed. The AMF spores within each sample were then identified and quantified and the number of infective propagules and mycorrhizal inoculum potential estimated. Samples were taken during the wet season (October 2004) and the dry season (May 2005).

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