



Glomeromycota associated with Mexican native maize landraces in Los Tuxtlas, Mexico



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ABSTRACT

Many native maize landraces are still cultivated by different ethnic groups in Mexico as part of traditional polyculture systems (*milpas*). However, these systems and landraces are being steadily replaced by fertilized monocultures of genetically improved varieties or maize hybrids. Little is known about how such changes may affect the belowground community of maize symbionts. A greenhouse experiment was conducted to assess the composition of the indigenous arbuscular mycorrhizal fungi (AMF) communities colonizing four Popoluca maize landraces and the hybrid Texcoco, and to determine how these communities are influenced by the level of phosphorus fertilization. Fragments of AMF ribosomal DNA (rDNA) were amplified using nested PCR, producing 327 Glomeromycota sequences. Phylogenetic analysis assigned the Glomeromycota sequences into 84 operational taxonomic units (OTUs). This number of OTUs more than doubles the figure previously reported for maize exposed to AMF native inoculum. Exclusive or very heterogeneous maize type-AMF associations were rare. Most AMF species colonized 2–4 maize types. This suggests that the high diversity of AMF in *milpas* is related to the presence of several native maize landraces and that replacement of these landraces with a single hybrid may diminish AMF community richness. All landraces associated with more OTUs under moderate P, compared to low P fertilization, suggesting that low inorganic phosphate (Pi) in *milpas* is limiting symbiotic interactions. However, only 0–20% of OTUs were conserved between different P conditions for each landrace. The Black landrace, which presented the highest AMF colonization and Pi uptake, was associated with the highest number of AMF OTUs, supporting previous suggestions regarding this functional relationship with AMF richness.

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1. Introduction

Maize (*Zea mays* L.) is grown worldwide as a staple food and to manufacture secondary products such as sugar, oil, and protein (FAO, 2006). Mexico is considered the center of origin for maize (Matsuoka et al., 2002) and many native landraces are still cultivated in the country by different ethnic groups as part of traditional polycultures (*milpas*). These systems constitute important genetic resources, not only in terms of different varieties of maize, but also of belowground symbionts, which have co-evolved

with plants in a variety of nutrient deficient and harsh environmental conditions. However, these production systems and landraces are being replaced by fertilized monocultures of genetically improved varieties or maize hybrids (Turrent-Fernández et al., 2012) and little is known about how such management changes may affect the belowground community of mycorrhizal symbionts.

Arbuscular mycorrhizal fungi (AMF) are ubiquitous soil organisms of the phylum Glomeromycota that establish mutualistic symbiotic associations with most land plants (Smith and Read, 2008). AMF are most influential for plants in nutrient deficient soils, in particular where P is limiting (Smith et al., 2011). They facilitate mineral nutrient uptake from the soil in exchange for plant assimilated C (Smith and Read, 2008). In addition to improving plant nutrition, AMF protect their hosts from pathogens

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(Poza and Azcón-Aguilar, 2007) and contribute to the maintenance of variability, stability, diversity and productivity of the plant cover and soil structure (van der Heijden et al., 2006), as well as affecting plant growth traits (Klironomos, 2003).

Despite the considerable role of AMF in terrestrial ecosystems, the relationship between their taxonomic and functional diversity is poorly understood (Krüger et al., 2009). While AMF are not strictly host-specific, it is known that they can exhibit a degree of host-preference (Helgason and Fitter, 2009; Johnson et al., 2003; Scheublin et al., 2004). Plants, on the other hand, may favor specific subgroups of these mycosymbionts (McGonigle and Fitter, 1990; Oliveira et al., 2009). In addition, it is known that the relative abundance of several *Glomus* species decreases significantly in response to chemical fertilization, while other species, including *Entrophospora schenckii*, *Glomus mosseae*, and *Scutellospora fulgida*, remain unaffected (Bhadalung et al., 2005) and maintain their provision of ecosystem services and life history strategies (van der Heijden et al., 1998b).

Around 240 AMF species have been described to date (Oehl et al., 2011), mainly on the basis of spore morphology. However, it is impossible to correlate spore information with specific colonization events in plant roots since spores are typically produced on external hyphae that can easily become detached from the root, and the level of spore production does not reflect the abundance of species in the roots (Clapp et al., 1995). The use of DNA sequencing methods has improved our understanding of AMF diversity and communities associated with roots, particularly because they allow the direct detection of AMF from environmental samples (Öpik et al., 2009, 2013; Wetzel et al., 2014).

AMF fungi associated with maize grown under different management conditions have been studied through morphological identification of spores (Daniell et al., 2001; Jansa et al., 2003) and molecular sequencing (Oliveira et al., 2009; Sasvári et al., 2011). Most of the recent studies based on molecular techniques have found that AMF diversity in maize roots is reduced by agricultural practices such as tillage, fertilization and the introduction of phosphorous-inefficient genotypes (Franke-Snyder et al., 2001; Jansa et al., 2002; Oehl et al., 2003; Oliveira et al., 2009; Sasvári et al., 2011; Toljander et al., 2008), while positive correlations have been found with crop rotation and maize productivity (Maherali and Klironomos, 2007; van der Heijden et al., 1998a; Wagg et al., 2011). Maize varieties differ in terms of the diversity and composition of AMF communities colonizing their roots (Oliveira et al., 2009).

Low P availability limits plant growth in many acid soils of the tropical mountains, such as those where the Popoluca people manage their *milpas* in the Biosphere Reserve of Los Tuxtlas, Mexico (Sangabriel-Conde et al., 2014). Despite this limitation, more than 18 local maize landraces have been developed in this region and are still cultivated in very low input subsistence agricultural systems (Negrete-Yankelevich et al., 2013b). Our research has previously demonstrated that the loss of cultivated plant species in Popoluca *milpas* may have a negative impact on the ability of the mycorrhizal community to colonize maize roots, as well as reducing the availability of P (Negrete-Yankelevich et al., 2013a).

In maize, mycorrhizal symbiosis provides up to 60% of the total P requirement (Nurlaeny et al., 1996). However, AMF species that colonize the roots of maize or soybean exhibit strong host specificity (Gosling et al., 2013). Landraces and hybrids differ in terms of colonization percentage (An et al., 2010) and P absorption capacity (Ortas and Akpinar, 2011; Tchameni et al., 2009), and different AMF species exhibit functional diversity in terms of colonization, maize growth, Pi uptake as well as Pi transporter gene expression (Hao et al., 2008; Klironomos and Hart, 2002; Smith et al., 2000; Tian et al., 2013); nevertheless, increasing the diversity

of AMF in maize roots through co-inoculation leads to higher Pi uptake in shoots (Tian et al., 2013). It has been suggested that if a plant is colonized by several species of AMF that are complementary in their functions (e.g. the uptake of nutrients from different soil pools), they may together prove to be more beneficial to the plant than colonization by any of these species individually (Alkan et al., 2004; Gustafson and Casper, 2006; Koide, 2000). These findings suggest that different maize landraces or hybrids exposed to a diverse native AMF inoculum may associate with specific assemblages of AMF, which could lead to differences in plant Pi uptake.

In a previous study, we evaluated the response of four Popoluca native maize landraces, and the recently introduced hybrid Texcoco, to the presence of native AMF in conditions of low and moderate P input (5 and 65 mg kg⁻¹) (Sangabriel-Conde et al., 2014). The native landrace Black presented colonization percentages (75–80%) that were among the highest reported to date for native maize (Hess et al., 2005; Martinez and Johnson, 2010), as well as the highest shoot P uptake compared with the hybrid Texcoco and the Yellow, White and Red landraces. The hybrid Texcoco, despite showing a high mycorrhizal dependency, exhibited a very low capability to acquire P in low conditions of this nutrient. In contrast, the Black landrace appears to have adaptive mechanisms by which it efficiently obtains P, either directly or through mycorrhizal symbiosis (Sangabriel-Conde et al., 2014). We postulated that these differences in response to AMF colonization among local maize landraces and the hybrid from the Popoluca *milpas* are related to differences in the AMF consortia that colonize each maize type. Since AMF species exhibit functional diversity, maize landraces that are capable of higher Pi uptake may be interacting with a richer fungal community (Tian et al., 2013). In this study, we hypothesize that (1) maize types will differ in terms of the AMF community colonizing their roots, (2) the roots of the Black landrace will be colonized by the highest richness of AMF and the Texcoco hybrid by the lowest, and (3) moderate P fertilization will reduce AMF richness in all the maize types, given the higher possibility for the plant to obtain Pi through the non-mycorrhizal route. To the best of our knowledge, no previous study has tested the effect of indigenous AMF communities on several native maize landraces and under different conditions of P availability.

2. Materials and methods

2.1. Extraction of AMF spores from soil samples

Soil samples were taken from nine Popoluca *milpas* in the communities of Ocotil Chico and Mazumiapan of the Sierra de Santa Marta in Los Tuxtlas, Veracruz, Mexico. AMF spores were extracted from a compound soil sample using the wet sieving and decanting technique (Sieverding, 1991). Briefly, material collected on a 53 µm sieve was dried on plastic trays in the greenhouse for three days at 28–30 °C and subsequently used as an inoculum in a greenhouse experiment (full sampling and extraction details described in Sangabriel-Conde et al. (2014).

2.2. Greenhouse experiments

A complete factorial experimental design was implemented with maize type, inoculation and P fertilization as factors. The most common maize types in Popoluca *milpas* were used: the local maize landraces Yellow (*Púch mok*), White (*Poop mok*), Black (*Luk mok*), and Red (*Tsabats mok*) and the introduced hybrid Texcoco (S-8929, CIMMYT). Two P levels were chosen based on the current levels of P availability in the *milpas* with (moderate P: 65 mg kg⁻¹) or without (low P: 5 mg kg⁻¹) fertilization regimes. Two mycorrhizal treatment levels were applied (inoculated vs.

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