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Soybean cultivation supports a diverse arbuscular mycorrhizal fungal community in central Argentina

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ABSTRACT

Arbuscular mycorrhizal (AM) symbiosis is a key plant-microbe interaction in sustainable ecosystems. Increasing land use intensity poses a threat to AM fungal communities, yet little is known of the impact of agricultural land use on AM fungal communities in many regions and cultivation types. The last few decades have witnessed increased cultivation of soybean worldwide with Argentina becoming one of the major producers. We compared the diversity and taxon composition of AM fungal communities in soybean fields in central Argentina with that in a natural Espinal forest under similar environmental conditions. We sequenced AM fungal DNA from root and soil samples collected from pairs of soybean fields and pristine forest ecosystems. We found that although AM fungal diversity tended to be lower in samples collected from the soybean field, the total number of AM fungal taxa was similar in both agricultural and forest ecosystems. Roots of soybean plants were colonized by diverse communities of AM fungi. AM fungal community composition in roots was primarily driven by host plant identity, but land use type (soybean field versus Espinal forest) was also an important determinant of community composition. The intensity of anthropogenic land use correlated with the proportion of easily-cultured AM fungal taxa, probably due to their efficient colonization strategies and better ability to recover from disturbance. Thus, soybean cultivation has affected AM fungal communities in terms of both diversity and functional attributes, although the diverse AM fungal communities are still present, probably due to the relatively low level of fertilizer application.

1. Introduction

Interest is increasing in the effects of belowground interactions on ecosystem functioning (Bardgett and van der Putten, 2014; van der Putten, 2017). Arbuscular mycorrhizal (AM) fungi (subphylum Glomeromycotina; Spatafora et al., 2016) comprise one of the most ubiquitous groups of soil microbes (Dickie et al., 2014). AM fungi live in symbiosis with the roots of about 80% of terrestrial plant species (Smith and Read, 2008) and provide nutrients (mainly P and N) to their host plants in exchange for plant-assimilated carbon. AM fungi alleviate plant abiotic stress and are able to increase plant resistance to pathogens (Pozo et al., 2015; Smith and Read, 2008). Knowledge is increasing on the geographic distribution and community ecology of these fungi. Recently, Davison et al. (2015) analyzed AM fungal diversity in plant roots based on a systematic global sampling and found that the diversity of natural AM fungal communities varied with respect to environmental variables (precipitation, soil organic C content and pH), and spatial distance.

The seminal paper by Helgason et al. (1998) has led to increased interest in AM fungal communities in agricultural ecosystems. High intensity agricultural land use, associated with mechanical disturbance and abundant application of chemicals, tends to exhibit lower AM fungal diversity than less intensive farming (Ciccolini et al., 2016; Lumini et al., 2011; Moora et al., 2014; Verbruggen et al., 2012), although mechanical disturbance alone may show no effect (Lekberg et al., 2012; de Pontes et al., 2017). Taxon composition of AM fungal communities under high and low intensity agricultural land use is also different (Jansa et al., 2003; Mirás-Avalos et al., 2011; Moora et al., 2014; Xiang et al., 2014). However, more information is needed in order to understand the main trends in AM fungal diversity and community composition under different cropping systems.

Soybean (*Glycine max*) is a widely grown crop that produces significantly more protein per unit area than most other crops (Vollmann, 2016). Soybean cultivation in Argentina has increased significantly

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Table 1
Location and details of sampling; sample source (root or soil), host plant, number of samples (n), number of AM, fungal virtual taxa (VT) and number of glomeromycotina sequences (AMF reads) per site.

Site	Land use	Plant family	Host species	Source	n	AMF VT	AMF reads
1	Espinal forest	*Acanthaceae*	*Justicia tweediana*	Soil	9	40	22790
1	Espinal forest	*Asteraceae*	*Baccharis glutinosa*	Root	8	44	10397
1	Espinal forest	*Asteraceae*	*Conyza bonariensis*	Root	10	59	12269
1	Espinal forest	*Solanaceae*	*Cestrum parqui*	Root	10	22	2080
1	Espinal forest			Soil	6	33	2837
1	Soybean field	*Convolvulaceae*	*Ipomoea nil*	Root	9	47	18484
1	Soybean field	*Fabaceaee*	*Glycine* max	Root	10	49	10948
1	Soybean field	*Poaceae*	*Digitaria sanguinalis*	Root	10	45	7021
1	Soybean field			Soil	9	28	3061
2	Espinal forest	*Acanthaceae*	*Dicliptera squarrosa*	Root	10	44	19703
2	Espinal forest	*Ephedraceae*	*Ephedra triandra*	Root	6	20	3724
2	Espinal forest	*Solanaceae*	*Cestrum parqui*	Root	8	21	552
2	Espinal forest	*Verbenaceae*	*Lantana grisebachii*	Root	10	38	17190
2	Espinal forest			Soil	6	20	745
2	Soybean field	*Commelinaceae*	*Commelina erecta*	Root	7	19	4780
2	Soybean field	*Convolvulaceae*	*Ipomoea nil*	Root	10	24	5245
2	Soybean field	*Fabaceae*	*Glycine* max	Root	10	25	2594
2	Soybean field	*Poaceae*	*Eleusine tristachya*	Root	9	35	6694
2	Soybean field			Soil	6	18	1251

during the last 30 years, from 17.2 million tons in 1996 (Zak et al., 2008) to 61.4 million tons in 2015 (Phélinas and Choumert, 2016). Argentina currently leads the international market for soybean pellets with nearly 57% of world exports, ahead of the United States and Brazil (Phélinas and Choumert, 2016). Soybean is typically grown in neutral or slightly alkaline soils in subtropical climate. Córdoba province in central Argentina is one of the most important soybean cultivation areas with soybean production for the 2014/2015 season being 15.6 million tons. Land use changes have reduced the forest area in the province to only 0.1% of its original area (Phélinas and Choumert, 2016), leaving remnants that are distributed as small and isolated fragments or relics within the agricultural landscape. The typical cropping sequence of soybean plantations includes two years of soybean followed by one year of maize. This cropping system is characterized by rather low fertilization; fertilizers are applied once every three years during maize sowing.

AM fungi stimulate symbiotic nitrogen fixation in legumes under low phosphorus availability (Püschel et al., 2017), hence one may expect a positive effect of AM fungi on soybean performance, especially since fertilizers are not applied to soybean. Indeed, AM fungi increase biomass of soybean plants (Borowicz, 1997; Nurlaeny et al., 1996) and enhance their P uptake (Kelly et al., 2001). In addition, AM fungi may play an important role in mitigating the effects of drought (Grümberg et al., 2015), of heavy metals in the soil (Garg and Bhandari, 2014), and of foliar pathogens (Malik et al., 2017) on soybean. Moreover, the amount of AM fungal spores in the soil of soybean fields (Isobe et al., 2008), as well as the AM fungal colonization rate of soybean roots (Fernández et al., 2011) are negatively related to the amount of P fertilizers applied. The performance of soybean depends not only on the presence, but also on the taxon composition of symbiotic AM fungal community; Cely et al. (2016) were able to increase soybean nutrient content and yield by manipulating the composition of indigenous AM fungal community through addition to the soil of a monospecific AM fungal inoculum.

Although soybean is significantly dependent on AM fungi, and research suggests that AM fungal community in the roots of soybean differs from that in the roots of maize or of a co-occurring weed *Viola arvensis* (Gosling et al., 2013), knowledge of AM fungal diversity and community composition in soybean roots and in the soil of soybean fields is scarce. We addressed the AM fungal communities in central Argentina, by comparing under similar abiotic conditions Espinal forest as a local representative of a natural ecosystem and soybean field as an example of intensively managed agricultural ecosystem. We expect the regular mechanical disturbance and use of pesticides in the soybean field to affect the taxonomic and functional composition of the AM fungal community in both the roots and soil differently compared to that in a natural ecosystem. However, we expect the moderate fertilization rate in our study system to maintain a diverse AM fungal community in the soybean field.

2. Materials and methods

2.1. Study area

Our study site was located in the Espinal ecoregion, a subtropical thorny dry forest in central Argentina. This ecoregion has experienced massive clearing and agricultural expansion since the second half of 19th century, which has intensified during the last few decades. There is a remnant of Espinal forest in La Selva locality, near Las Perdices town (32°36′42″S; 63°57′1″W), ∼100 km southeast of Córdoba city. The landscape comprises a mixture of Espinal forest and arable fields about 330 m above sea level. The climate of the study area is semi-arid with a dry season from April to September (Fehlenberg et al., 2017). Soybean, the region's major crop, is currently limited to an area above ∼500 mm rainfall. Soil type is coarse-loamy, mixed, thermic, typic haplustoll (Parra et al., 2011). Soils are neutral or slightly alkaline across the entire ecoregion and are generally characterized by moderate natural fertility (recently depleted due to intensive agriculture), although some soils (e.g., saline soils, regularly flooded soils) are generally less suited for crop cultivation. Native vegetation in the forest is dominated by *Prosopis alba* Griseb., *Dicliptera squarrosa* Nees, *Justicia tweediana* (Nees) Griseb., *Lantana grisebachii* Stuck. ex Seckt, *Ephedra triandra* Tul., *Cestrum parqui* (Lam.) L'Hér., *Baccharis glutinosa* Pers. and *Conyza bonariensis* (L.) Cronquist. Native vegetation consists of arbuscular mycorrhizal (AM) plants. Soybean fields host weeds: *Commelina erecta* L., *Ipomoea nil* (L.) Roth, *Eleusine tristachya* (Lam.) Lam. and *Digitaria sanguinalis* (L.) Scop. Farmers at the study site sow Roundup Ready™ soybean using a no-tillage method and apply glyphosate as a primary weed killer. Soybean fields receive 100 kg di-ammonium (18% N and 46% P) phosphate /ha during maize sowing (i.e. as crop sequence is 2 years of soybean and 1 year of maize, fertilization occurs once every three years, eight times since 1996).

2.2. Sampling procedure

We targeted AM fungal communities in both plant roots and soil in