



Root colonizing and soil borne communities of arbuscular mycorrhizal fungi differ among soybean fields with contrasting historical land use

Valeria Soledad Faggioli^{a,*}, Marta Noemí Cabello^b, Gabriel Grilli^c, Martti Vasar^d,
Fernanda Covacevich^e, Maarja Öpik^d

^a Instituto Nacional de Tecnología Agropecuaria, EEA Marcos Juárez, Ruta 12 km 36, 2580, Marcos Juárez, Argentina

^b Instituto Spigazzini (Facultad de Ciencias Naturales y Museo, UNLP), Comisión de Investigaciones Científicas de la Prov. de Buenos Aires (CICPBA), Av 53 # 477, 1900, La Plata, Argentina

^c Instituto Multidisciplinario de Biología Vegetal, FCEyN (CONICET-Universidad Nacional de Córdoba), Vélez Sarsfield 1611, CC 495, Córdoba, Argentina

^d Department of Botany, University of Tartu, 40 Lai Street, 51005, Tartu, Estonia

^e Instituto Nacional de Tecnología Agropecuaria, Unidad Integrada EEA Balcarce – CONICET, Instituto de Investigaciones en Biodiversidad y Biotecnología-Fundación para las Investigaciones Biológicas Aplicadas, Ruta 226 km 73.5, 7620, Balcarce, Argentina

ARTICLE INFO

Keywords:

Agriculture
Glycine max
18S rDNA
Mycorrhiza
Land use change
Biodiversity

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) are a key component of soil microbiota in natural and anthropogenic ecosystems. Even though soil type and climate conditioned land uses in the past, soybean cultivation has overrode such limitations and replaced the earlier diverse agro- and natural ecosystems in many countries of South America. We investigated whether actual diversity patterns of local AMF communities were determined by previous land uses and their intrinsic environmental conditions. We sequenced AMF DNA from root and soil samples collected from current soybean fields with three historical land use situations (HLU): agricultural fields, livestock farming and forest sites. We detected overall high AMF richness: 87 virtual taxa (VT) in soil and 69 VT in soybean roots. Mean number of VT per sample ranged from 8.1 to 19.2; it was not affected by HLU nor type of sample, but correlated with soil texture, pH, and plant density. Conversely, AMF community composition did significantly diverge among HLU and type of sample. A distinctive community composition was observed in roots of historical agricultural fields which differed from any other soil and root sample evaluated in this study. We attribute this finding to variations in the abundance pattern of predominant AMF taxa (*Glomeraceae* and *Gigasporaceae*). Our results indicate that soybean cultivation supports relatively high AMF diversity, with apparent legacies from earlier management and natural habitats in the composition of resident AMF communities.

1. Introduction

Arbuscular mycorrhizal fungi (AMF, Glomeromycota; Schüßler et al., 2001) are a key component of the soil microbiota forming obligate symbiosis with roots of ca. 80% of terrestrial plant species (Smith and Read, 2010). It is one of most common and widespread terrestrial plant symbioses and contributes towards plant nutrition, soil structure and other ecosystem services (van der Heijden et al., 2015). AMF diversity and functioning is affected by environmental conditions (Powell and Rillig, 2018) such as altitude and habitat type (Kotlínek et al., 2017), and edaphic and climatic properties (Alguacil et al., 2016). Furthermore, anthropogenic activities have considerable influence on AMF (García de León et al., 2018b). In agroecosystems, soil disturbance (e.g., ploughing), chemical inputs (fertilization, use of pesticides), and limitations on host availability (e.g., continuous monoculture) can

negatively affect diversity of AMF (Druille et al., 2013; Säle et al., 2015; Williams et al., 2017). In addition, grazing and cattle induced changes in soil properties can also have negative impact on AMF diversity in livestock farms (van der Heyde et al., 2017).

Several studies have demonstrated that symbiotic associations between resident AMF species and plant host are related to the identity of both partners (Vályi et al., 2016). Although AMF generally exhibit low host specificity some mutual preferences exist (Davison et al., 2015; Werner and Kiers, 2015; Horn et al., 2014; Martínez-García et al., 2015; Vandenkoornhuyse et al., 2002). Sepp et al. (2018) observed that AMF communities in different habitat types were more similar in the roots of a single host plant species than in soil samples, suggesting a non-random pattern in host-fungal interaction. Further, López-García et al. (2017) found that plants with ruderal traits tended to associate with phylogenetically clustered AMF communities. Therefore, the identity of

* Corresponding author.

E-mail address: faggioli.valeria@inta.gob.ar (V.S. Faggioli).

<https://doi.org/10.1016/j.agee.2018.10.002>

Received 5 June 2018; Received in revised form 26 September 2018; Accepted 4 October 2018

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Table 1

Soil, crop, and climatic variables and root AMF colonization levels in the studied soybean fields with different historical land uses (HLU). Mean values and standard deviation (\pm SD) are shown ($n = 10$). Different letters indicate significant differences among HLU according to Tukey test ($p \leq 0.05$).

HLU	Soil									Soybean		Geographical	
	USDA	P	N	C	pH	EC	Water	Sand	Clay	Root AMF	Plant density	MAP	Altitude
	Classif.	mg kg ⁻¹		%		$\mu\text{S cm}^{-1}$	%			%	pl m ⁻²	mm	m.a.s.l.
Agricultural	Argiudoll	14.6 b (± 6.0)	44.6 (± 22.8)	3.1 a (± 0.4)	6.0 b (± 0.2)	186.5 (± 265.5)	6.9 a (± 0.77)	24.0 a (± 8.2)	76.0 a (± 8.2)	67 a (± 16)	29.3 (± 6.4)	900	119.8 b (± 14.9)
Livestock	Haplustoll	37.9 a (± 23.4)	29.7 (± 23.0)	1.6 b (± 0.6)	6.5 a (± 0.2)	80.0 (± 20.5)	1.5 b (± 0.34)	66.0 c (± 12.4)	34.0 c (± 12.4)	57 ab (± 15)	27.7 (± 7.9)	700	203.3 b (± 53.4)
Forest	Haplustoll	22.0 ab (± 19.7)	55.6 (± 47.1)	3.2 a (± 1.0)	6.4 ab (± 0.6)	155.0 (± 164.8)	6.5 a (± 0.84)	41.2 b (± 14.2)	58.8 b (± 14.2)	48 b (± 18)	37.9 (± 14.4)	800	638.6 a (± 135.8)

MAP: mean annual precipitation.

the crop species may result in the predominance of certain AMF species, leading to the decline or the loss of other species and decrease in overall diversity and mycorrhizal functioning.

During the last decades, many American countries have undergone a drastic expansion of agricultural lands. Soybean (*Glycine max* (L.) Merr.), a legume oilseed crop originating in South Asia and currently one of the most important food crops of the world, is adapted to successful cropping. Indeed, Americas' harvest 84.5% of worldwide soybean production every year (FAO, 2015). In Argentina, the area under soybean cultivation soared from 9.8 mln ha in 1995 to 26 mln in 2016 (SAGPyA, 2017). Concurrently, during the same period, the area used for livestock farms has decreased by 10 mln ha, and forest and shrubland areas' annual decrease has reached 1% (297,000 ha per year; FAO, 2015; SAGPyA, 2017). Subsequently, former livestock farms and natural areas have been gradually converted to soybean fields, and the historical agricultural lands have experienced a strong intensification in management.

The change in land use towards soybean cultivation brings about consequences for above and belowground organisms. Even though no-tillage is the dominant sowing practice in Argentina, and it is less disturbing than conventional ploughing (Albertengo et al., 2013), the use of pesticides and fertilizers coupled with low crop rotation constitute the basis of the intensification of soybean production. In such scenario, local surveys have revealed declining diversity of several groups of soil biota, including ants, prostigmatid mites, earthworms and collembolans (Bedano et al., 2016), bacteria (Ferrari et al., 2015; Figuerola et al., 2015), AMF (Cofré et al., 2017), and saprophytic fungi (Ferrari et al., 2015). In addition, a recent study from Argentinean soybean fields shows somewhat lower AMF diversity and shifted community composition compared to native Espinal vegetation (García de Leon et al., 2018a). Such alteration of biodiversity can alter ecosystem level processes and the ecosystem resilience to further environmental changes (Powell and Rillig, 2018).

In contrast to the developed countries where agriculture was established hundreds of years ago, the change in land use to agriculture in Americas is only a few decades old and its impacts on AMF diversity and functioning are little understood. For example, González-Cortés et al. (2012) observed that the conversion of natural/native forests to avocado plantations and maize fields in Mexico generates a shift in the composition but do not alter the richness of AMF. However, to the best of our knowledge, in Argentina there is a lack of local empirical evidence regarding the consequences of change in land use as well as the intensification of existing agricultural fields on AMF diversity patterns. Surveys based on root-colonizing and soil-borne communities might allow revealing the potential impact of soybean cultivation on AMF communities.

Here we explored AMF diversity in three areas in Argentina that differ in terms of time since land use conversion towards soybean cultivation, and have different historical land uses (HLU), namely,

Agricultural (more than 28 years of intensive soybean cropping), Livestock (28–18 years of soybean cropping in rotation with pastures) and Forest (less than 18 years of intensive soybean cultivation after clearing mountainous native shrub-lands). In order to disentangle the effect of soybean cropping on resident AMF, we addressed AMF both in soil and root samples. While the first allows to gather fungal spores and hyphae contributing towards locally available AMF diversity, intraradical AMF represent the fungi involved in active symbiosis with the plant host (Varela-Cervero et al., 2015; Osborne et al., 2018; Sepp et al., 2018). We expected to find different AMF community composition in soil samples from each HLU because of the combined effect of local conditions and the legacy of earlier land uses. We also expected that AMF communities in soybean roots represent a subset of locally available AMF because of mutual partner preferences.

2. Materials and methods

2.1. Field sites and sampling

The study sites were located in Córdoba province, central Argentina. We targeted current soybean fields in three areas with different edaphic and climatic conditions, which had dictated the predominant historical land uses (HLU): agricultural, livestock farming and forest. Agricultural sites have been under intensive agricultural production for more than 60 years, and 28 under soybean cultivation. The predominant soil type is Argiudoll (USDA, 2014) with high fertility and productivity (INTA, 1978, 1985) (Table S1). Livestock farming sites had been under crop production in rotation with perennial pastures, with a gradual inclusion of soybean cultivation since 1990, and a continuous cultivation since early 2000's. Soil type is mainly Haplustoll with moderate fertility (INTA, 2004). Forest sites had been native shrub forests that were turned into soybean fields during the last 18 years after clearing the native vegetation (*Prosopis* spp., *Acacia* spp., *Zanthoxylum coco* Engl., *Schinopsis marginata* Engl., *Festuca* spp., *Stipa* spp., *Setaria* spp.). They are located in a mountainous area at 500–900 m a.s.l., mainly on Haplustoll soils with high fertility (INTA, 1996, 2004) (Tables 1, S1). Ten sites were sampled in each of the three areas (total of 30 sites). The sites within each HLU were located 10 km (min) to 30 km (max) from each other; HLU regions were located 320 km from each other.

Sampling was conducted when soybean crops were at vegetative or initial reproductive stage (from V3 to R4). We collected roots, rhizosphere soil and bulk soil. Roots were sampled from a set of 20 plants per site and pooled to form one composite sample per site. Briefly, after removing shoots, we collected roots by loosening the soil on the sides of the sowing line with a shovel from 0 to 20 cm of depth. This was possible because soybean root system consists of a coarse primary root with abundant, and superficial secondary roots. Collected root samples were stored on ice until processed within 24 h. In the laboratory, roots were cleaned with tap water, then finest and not lignified secondary roots

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