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The Proceedings of the International Plant Nutrition Colloquium XVI

Title
Arbuscular mycorrhizal colonization and mycorrhizal dependency: a comparison among soybean, sunflower and maize

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Publication Date
2009-04-08

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Introduction

Root colonization with arbuscular mycorrhizal fungi (AMF) has the potential to enhance plant uptake of relatively immobile nutrients, in particular phosphorus (P) and zinc (Bolan, 1991; Cavagnaro, 2008). Contribution of AMF to plant P nutrition is evident in low-P soils (Covacevich et al., 1995, Zhu et al., 2005), but such benefit may not be expected under non-limiting conditions. In this case, the cost of maintaining the symbiosis may exceed the benefit given to the host (Zhu et al., 2005). A useful trait to quantify responsiveness to AMF colonization is the 'mycorrhizal dependency' (MD), calculated as the difference in dry weight between mycorrhizal and non-mycorrhizal plants, and expressed as a percent of dry weight of mycorrhizal plants (Plenchette et al., 1983). Interspecific variation in mycorrhizal colonization has rarely been explicitly explored among crops. Specially, nothing has been reported related to soybean, sunflower and maize that shows the relationship of natural mycorrhization and available soil P. The objective of this work was to compare AMF colonization and MD in soybean, sunflower and maize under contrasting P levels.

Materials and Methods

Field study

In order to assess the indigenous mycorrhizal colonization in soils of the Pampean Region, Argentina, plots with soybean, sunflower and maize with different levels of soil available P were sampled. Roots were sampled at 0-20 cm depth from plants at reproductive stages (R2 – R5). At the same sites, composite soil samples (0-20 cm depth) were taken for measuring available soil P (Bray I). Sample roots were washed and a subsample of fine roots was taken to determine AMF colonization. Roots were stained according to Phillips and Hayman (1970). The percentage of the root colonized was determined by the gridline intersect method across 100 root intersections observed under a binocular microscope (x40) (Giovannetti and Mose, 1980).

Greenhouse experiment

The soil used in the pot experiment was a silty loam Typic Argiudoll with pH 5.5, organic matter 3.6% and available P (Bray 1) 8.4 mg kg^{-1}. Soil was dried and exposed to high temperatures and solar radiation to eliminate indigenous AMF community. Mycorrhizal inoculum was collected from agricultural soils with low P. A composite sample was mixed thoroughly and half of it was steam-pasteurised for 1 h at 100ºC during three consecutive days for the control treatment.

Treatments were arranged in a factorial randomized complete block design with three factors and four replications. Factors were species, P level and inoculum. Species were soybean (*Glycine max* L., Don Mario 4800 RR), sunflower (*Helianthus annuus* L., Paraíso 20) and maize (*Zea mays* L., DK628 RR). The P levels were 0, 12 and 52 mg P kg^{-1} added to the growth media as KH_2PO_4. Plastic 7-L pots were filled with 9 kg growth media prepared with a mix of soil and river sand (1:2 soil:sand v:v). A pre-plant multi-nutrient fertilization was applied. Soybean was inoculated with *Bradyrhizobium* spp. The AMF inoculum was placed in a layer, 6 cm below the surface soil. Each pot received 810 g of fresh weight inoculum. Controls received a similar amount of steamed inoculum. Three seeds were sown per pot and seedlings were thinned to one per pot. Pots were maintained between 60% to 100% field capacity. Plants were grown under natural light at a temperature range of 20 to 30°C.

Plants were harvested 53 days after sowing. Roots were washed and a subsample of fine roots was taken randomly from the root system to determine AMF colonization as described above. Mycorrhizal dependency was calculated by using the Plenchette et al. (1983) formula. Remaining roots and shoot were dried at 60°C to determine dry weight. Phosphorus

concentrations were measured colorimetrically (Murphy and Riley, 1962) after dry ashing.

Data were statistically analyzed by ANOVA and the LSD procedure was used for mean comparisons (P<0.05). An arcsin-square root transformation was conducted on the AMF colonization and MD data to achieve homogeneity of variance around the means. Data for total P uptake were log transformed. The relationship between AMF colonization and available soil P was described through linear-plateau models.

Table 1. Effects of P level and mycorrhizal inoculation on AMF colonization, total biomass, total P uptake and mycorrhizal dependency of soybean, sunflower and maize in the greenhouse experiment.

			AMF colonization	Total biomass	Total P uptake	DM
			(%)	(g plant^{-1})	(mg plant^{-1})	(%)
Soybean	LP	NM		2.01 ab	1.90 c	
		M	46.09 d	7.15 cd	12.08 fg	71.00 d
	MP	NM		4.56 bc	5.45 de	
		M	55.76 e	9.09 d	18.57 gh	46.89 c
	HP	NM		20.57 f	49.85 i	
		M	21.19 bc	20.65 f	52.47 i	3.11 ab
Sunflower	LP	NM		0.51 a	0.38 a	
		M	25.85 c	0.92 ab	0.78 b	42.21 c
	MP	NM		4.51 bc	9.07 ef	
		M	21.85 bc	2.87 ab	4.68 de	-16.05 a
	HP	NM		28.52 g	95.62 j	
		M	11.55 ab	31.81 g	89.96 j	10.59 ab
Maize	LP	NM		2.08 ab	2.09 cd	
		M	14.16 ab	2.30 ab	1.96 c	2.84 ab
	MP	NM		10.42 d	16.51 gh	
		M	6.59 a	14.58 e	19.76 h	20.71 bc
	HP	NM		57.39 h	109.43 j	
		M	5.94 a	64.42 i	102.61 j	10.96 ab
ANOVA						
Species (S)			<0.001	<0.001	<0.001	0.007
P level (P)			<0.001	<0.001	<0.001	0.003
Mycorrhizae (M)				0.001	0.001	
S x P			<0.001	<0.001	<0.001	0.004
S x M				NS	<0.001	
M x P				NS	0.042	
S x M x P				0.014	0.002	

Within a column values followed by the same letter are not significantly different at the 0.05 level using the LSD procedure. NS: non significant differences. NM: non mycorrhizal and M: mycorrhizal.

Results and Discussion

Synchronized soil and root field sampling allowed the characterization of the relationship between the available soil P and indigenous AMF colonization for soybean, sunflower and maize on a wide range of agricultural soils. Our results clearly show that in the field soybean had higher AMF colonization than sunflower and maize (Fig. 1). These results were corroborated under greenhouse conditions (Table 1). AMF colonization in soybean and maize was significantly and negatively correlated with available soil P following linear-plateau function (Fig.1a, 1c).

Covacevich et al. (2007) found a similar relationship for wheat in P fertilization experiments. Our obtained functions indicated that above values of 12.59 mg P kg soil^{-1} the available soil P did not change the AMF colonization in soybean, which remained stable at an average value of 43.2% (Fig. 1a). For maize the threshold value of available soil P was 29.2 mg P kg soil^{-1} and AMF colonization stabilized at 37.5% (Fig. 1c). For sunflower, we could not find any kind of significant relationship between AMF colonization and soil P levels (Fig. 1b). Soybean showed a higher AMF colonization in low P soils (less than 10 mg P kg soil^{-1} (average 64.9%) than maize (54.5%) and sunflower (48.4%). The high colonization levels observed in roots of the three species suggest that this mechanism is highly relevant for P nutrition of crops grown in the Pampean soils, even in P-rich soils, in which the percentage of AMF colonization did not fall below 30%. The importance of AMF symbiosis is not only beneficial in terms of plant nutrition; the external hyphae of AMF have an important role in the aggregation of soils (Degens et al., 1996; Rillig, 2004).

In our greenhouse experiment, soybean and sunflower showed a typical response of AMF colonization to P supply (Table 1). Soybean was the species that most benefited from AMF colonization and its response was determined by P availability. Mycorrhized soybean at low and medium P levels improved P uptake, and this increased total biomass produced. This was reflected in its high values of MD, which was reduced when soil available P was higher. Sunflower showed high MD only at low P treatment although this was not expressed through total plant biomass. Although maize showed low MD values across all P treatments, none of them was negative, so there was no carbon drain in mycorrhized maize plants. Nevertheless, even if AMF colonization is beneficial, it may not necessarily contribute to increased P uptake enough to increase yields (Ryan and Graham, 2002). AMF-host symbiosis is a complex interaction and its impact depends on growth conditions and the host crop. Besides improving P nutrition, other benefits of AMF (nutritional and non-nutritional) should be considered to fully evaluate the cost/benefit balance of AMF colonization.

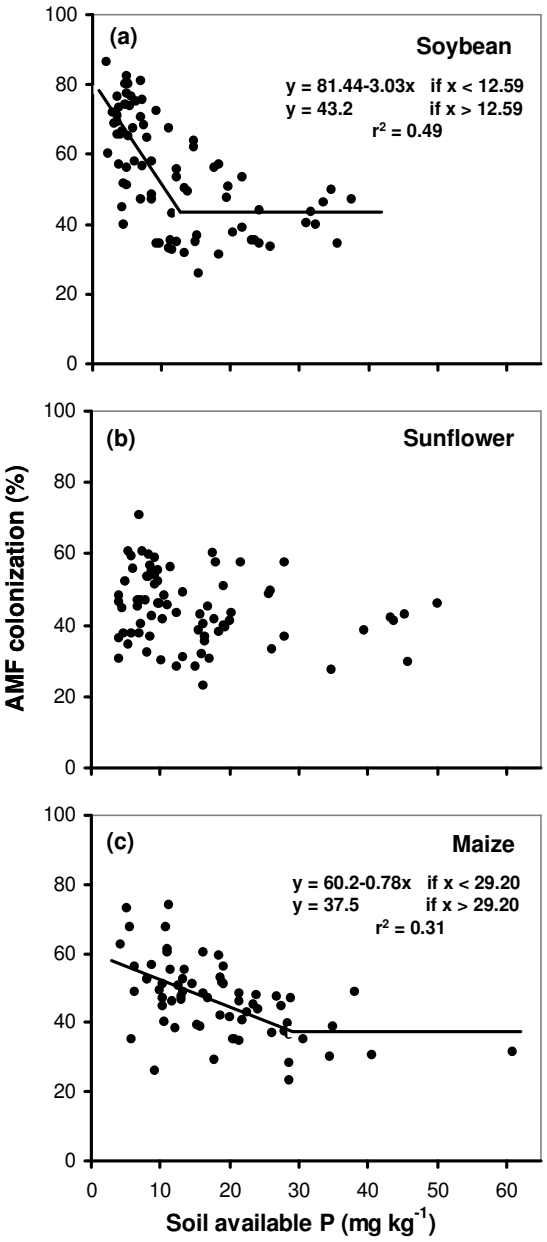

Figure 1. Relationship between arbuscular mycorrhizal fungi (AMF) colonization and soil available P (Bray 1) in the field study for soybean (a), sunflower (b) and maize (c)

Acknowledgements
Financial support was obtained from CONICET (PIP 5432), Universidad de Buenos Aires (UBACYT G622), ANPCYT (PICT 11170 and 931) and IPNI.

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