



High phosphorus availability promotes the diversity of arbuscular mycorrhizal spores' community in different tropical crop systems

Samuel Inocência Alves da Silva¹ · Tancredo Augusto Feitosa de Souza² · Edjane Oliveira de Lucena¹ · Lucas Jónatan Rodrigues da Silva² · Lídia Klestadt Laurindo² · Gislaíne dos Santos Nascimento¹ · Djail Santos¹

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Abstract

We aimed to evaluate the effects of tropical crop systems and phosphorus (P) availability on arbuscular mycorrhizal fungi (AMF) spores' community composition, and soil chemical properties in a Planosol at Tropical ecosystem from Brazilian Northeast. We collected rhizospheric samples containing soil and root fragments in a 5-year field experiment considering two groups of crop systems, i.e., no-till monocropping and agroforestry system, and testing two factors: the cropping system and the soil P availability. We identified the AMF community composition based on AMF spore's morphology. We also characterized the soil chemical properties (e.g., soil pH, soil organic carbon, and available P) at samples level. Crop systems and soil P availability influenced the AMF community composition, and soil chemical properties. We found that: i) the abundance of *Claroideoglossum claroideum*, *C. etunicatum*, *Rhizophagus intraradices*, richness, Shannon's index and Simpson's index were positively correlated with no-till monocropping systems (*Arachis hypogaea*, *Gossypium hirsutum*, and *Vigna unguiculata*) and with all the studied agroforestry systems at low-P availability; and ii) soil pH, and soil organic carbon were positively correlated with no-till monocropping systems (*Arachis hypogaea*, *Glicine hirsutum*, *Glicine max*, and *Sesamum indicum*) at high-P availability, and *Glicine max*, *Sesamum indicum*, *Zea mays*, and agroforestry system at low-P availability. Our results highlight the positive effect of high P on AMF spores' diversity, and the importance to consider both the crop system and soil P availability as key-factors promoting shifts into the AMF community composition and soil chemical properties in Tropical conditions.

Keywords Agroforestry system · AMF spores · Glomeromycota · No-tillage system · Tropical Planosols

Introduction

The interaction between tree species and arbuscular mycorrhizal fungi (AMF) under different P availabilities is important for plant fitness and its resistance to abiotic and biotic stresses

(Tadersoo et al. 2020). The benefits of mycorrhizal symbiosis are closely related with the fine roots by helping the host plant to withstand abiotic and biotic stresses such as drought (Gao et al. 2020), soil anoxic conditions, root-feeding nematodes, and soil borne pathogens (Kariman et al. 2020; van't Padje et al. 2020). This symbiosis also provides the host plants with water and essential plant-nutrients (Boutaj et al. 2020). In tropical environments, AMF can improve various plant physiological mechanisms by increasing growth, nutrient uptake, and yield (Passos et al. 2020). Therefore, understanding the effects of no-till monocropping and agroforestry system in low- and high-P availability on AMF community composition and soil chemical properties in a 5-year field experiment located at the Brazilian tropical seasonal dry forest is of interest in the field of soil ecology and can assist in the design of soil biology and management.

Plant roots support a wide diversity of AMF species by providing the fungi with C-rich exudates (Souza and Freitas 2017) and modifying rhizospheric conditions, i.e., soil pH by

✉ Tancredo Augusto Feitosa de Souza
tancredo.souza@ufsc.br

Samuel Inocência Alves da Silva
samuel-ufpb@hotmail.com

Lídia Klestadt Laurindo
<https://orcid.org/>

¹ Department of Soils, Federal University of Paraíba, João Pessoa, Paraíba, Brazil

² Department of Agriculture, Biodiversity, and Forests, Federal University of Santa Catarina, Campus of Curitibanos, Curitibanos, Santa Catarina, Brazil

H⁺ extrusion (Ramos et al. 2008) and root exudation, i.e., allelopathy (Medeiros et al. 2021). Crop systems (e.g., no-till monocropping and agroforestry systems) can be classified as primary factors driving the succession of the AMF community composition of both annual plant species (e.g., *A. hypogaea*, *G. max*, *G. hirsutum*, *S. indicum*, *V. unguiculata*, and *Z. mays*), and perennial plant species (e.g., *G. sepium*, *Mimosa caesalpiniaefolia*, and *Tabebuia alrea*) as described by Guo et al. (2019), Hontoria et al. (2019), and McKenna et al. (2020). Given that the symbiotic phase among the AMF and plant species are genetically modulated (Souza 2015), plants can initiate the recruitment of specific AMF species by activating genes (e.g., *myc*⁺, *CASTOR*, *DMI*, *SYM**MRK*, etc), and to establish the morpho-physiological contact of the host plant (Souza 2015; Vergara et al. 2019).

In both no-till monocropping and agroforestry systems, plant-AMF interactions within the rhizosphere are generally modulated by soil P availability (Guo et al. 2019; Lei et al. 2020). The continuous use of P fertilization may disturb the AMF activity, i.e., sporulation and root colonization, thus promoting changes in the AMF community structure (Alvarado-Herrejón et al. 2019). The P fertilization practice can also indirectly affect rootability and rhizodeposition by changing soil pH and microbial activity such as the activity of P- and N-metabolism microorganisms (Na et al. 2019). According to Souza and Santos (2018), soil management practices that increase the plant-nutrient availability may weaken the interaction between plant species and AMF because the host does not need to sustain a symbiont inside its roots at high ATP investment. High P input could lead to a negative plant-soil feedback in the rhizosphere of annual plant species by weakening plant resistance induced by AMF against root-feeding nematode and fungal pathogens (Yang et al. 2020). The negative effects of conventional agriculture are well established for annual plant species, but information on the effects of no-till monocropping and agroforestry system into the Brazilian semi-arid is lacking (Sarto et al. 2020; Medeiros et al. 2021).

Various studies have investigated the effects of agriculture (Souza et al. 2015; Chave et al. 2019; Hontoria et al. 2019), and agroforestry system (Guo et al. 2019) on AMF community composition around the world. They have described a negative correlation between the AMF diversity and plant diversity. In such cases the monodominance lead of a plant-AMF simplification. We investigate for the first time in a Planosol at tropical ecosystem how both no-till monocropping and agroforestry systems impact AMF diversity, and soil chemical properties. We anticipated that the agroforestry system would promote positive changes in AMF community composition. To determine the impacts of crop systems (no-till monocropping vs. agroforestry systems), we asked (1) How does AMF community composition vary with crop system? (2) How does P availability influence AMF community

structure in a tropical Planosol from Brazilian Northeast? In this context, we hypothesized that (i) the diversity of AMF species decreases with monocropping system at high-P availability; and ii) the variation in the AMF community composition is correlated with changes in soil chemical properties. Thus, we tested whether the AMF community, and soil properties might change at crop systems under low and high soil P availability.

Material and methods

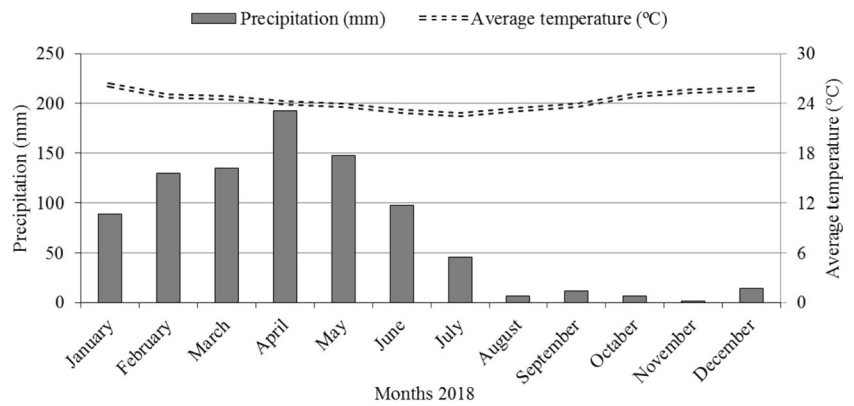
Study sites

The experimental area was located at the experimental perimeter from EMEPA (Statal Research Company from Paraiba), Alagoinha, Paraiba, Brazil (6°57'00" S, 35°32'42" W, altitude of 317 m a.s.l.). The climate is tropical wet and dry climate (As' type according to the Köppen climate classification), with 995 mm of total annual precipitation and mean annual air temperature of +26.4 °C. Total monthly precipitation (mm), and mean air temperature (°C) from Alagoinha, Paraiba, Brazil from January to December 2018 (Fig. 1) were obtained online: <https://portal.inmet.gov.br/>, and <http://www.aesa.pb.gov.br/aesa-website/meteorologia-chuvas/>. The soil of the experimental area was classified as Planosol, with stagnant water profile and abrupt textural difference (e.g., presence of B_t horizon) between A horizon and B horizon (WRB 2006).

Experimental design

The field experiment has been conducted since 2013 using a randomized block design. In our study we considered a split-plot scheme with four blocks. In each block, we have nine treatments (e.g., divided into the two groups of crop systems) as plots (38 × 20 m), soil available P levels (e.g., low-P and high-P availability) as subplots (19 × 20 m), and 10 repetitions (e.g., sampling points located near the rows following 2 m of distance between each other) per subplot. Our treatments were divided into two main groups which simulated the follow systems: AF Group = Agroforestry systems (AF); and NTFS Group = No-till monocropping farming systems. Within AF group, we considered the following plant species combination into the plots: AF1 = [*G. sepium* (Jacq.) Steud. + *Z. mays* L. + *B. decumbens* Stapf.]; AF2 [*M. caesalpiniaefolia* Benth. + *Z. mays* L. + *B. decumbens* Stapf.]; and AF3 [*T. alrea* (Manso) Benth. & Hook. f. ex S. Moore + *Z. mays* L. + *B. decumbens* Stapf.]. Whereas for the NTFS group, we considered the following annual monocropping systems as plots: *A. hypogaea* L., *Gossypium hirsutum* L., *Glycine max* (L.) Merrill, *S. indicum* L., *Vigna unguiculata* (L.) Walp. and *Z. mays* L. Each plot had 38 × 20 m, and soil and crop's management following recommendations according Cavalcanti (2008)

Fig. 1 Total monthly precipitation (mm) and mean air temperature (°C) from January to December 2018 at the experimental area, Alagoinha, Paraíba, Brazil. Data obtained online: <https://portal.inmet.gov.br/>, and <http://www.aesa.pb.gov.br/aesa-website/meteorologia-chuvas/>



and specific recommendations according “iLPF net” (<https://www.redeilpf.org.br/>). All the plant combinations from AF groups are widely recommended into the Brazilian Northeast by the “iLPF net” as the best crop systems for semiarid environments because their resistance to abiotic stresses such as drought. For the no-till monocropping farming systems all annual plant species but *G. max* (L.) Merrill are widely used by the Brazilian smallholder farmers located into the tropical seasonal Brazilian dry forest (e.g., Caatinga ecoregion).

To better characterize the plant environment of our studied treatments, we described plant variables (e.g., shoot and fine root dry biomass, and plant yield), and some soil variables (e.g., litter deposition and Olsen’s available P) from the first year of the experiment. For plant variables, we selected 10 plants per subplot during flowering stage, that were harvested at the ground level. For the AF group, we estimated tree dry biomass using the allometric equations proposed by Laurindo et al. (2020). To estimate fine root (diameter: < 2 mm) dry biomass, we collected roots from the soil samples of each collected plant during flowering stages within soil monoliths (20 × 20 × 20 cm). Fine roots were washed using a 0.5-mm nylon mesh bag. We sorted fine roots into living and dead roots based on morphology and condition. Only living roots were considered to estimate dry biomass. Into the AF groups, fine roots included both tree and herbaceous species because it was difficult to distinguish between these precisely. Fine root dry biomass (g) was determined after drying the samples for 48 h at 70 °C. The plant yield of annual species was estimated by collecting 10 plants of each studied annual plant species during seed maturity stage (Fig. 2).

Soil samples to characterize AMF community composition and soil chemical properties were collected in 2018 inside the field experiment considering two groups of crop systems, i.e., no-till monocropping and agroforestry systems. The soil environment was characterized by measuring litter deposition and estimating Olsen’s P at both low- and high-P availability. Before collecting the soil monoliths, an area of 20 × 20 cm on the soil surface was delimited for separately sampling the litter

layer. Litter deposition (LP) was calculated by the following equation: $LP (g\ cm^{-2}) = DDPF (g) / 400\ cm^{-2}$. Where, DDPF is the dry dead plant fragments deposited on the monolith surface; and $400\ cm^{-2}$ is the basal area of each soil monolith. Samples of each subplot from monoliths were air-dried and passed through a 2-mm sieve. Available P was determined using the Olsen’s P protocol (Olsen et al. 1954)(Table 1).

AF1 = *G. sepium* + *Z. mays* + *B. decumbens*; AF2 = *M. caesalpiniaefolia* + *Z. mays* + *B. decumbens*; AF3 = *T. alrea* + *Z. mays* + *B. decumbens*. ^a Independent sample t test comparing Low- × High-P groups. ns: not significant; * $p < 0.05$; and ** $p < 0.01$.

AMF community characterization

During each month (i.e., from January to December 2018), we collected three soil samples containing soil plus root fragments by each subplot (i.e., considering low- and high-P availability) within each experimental plot. All samples were collected at a soil depth of 0 to 20 cm. Each sample was divided in two portions. The first one to chemically analyse soil properties, and the second one to characterize AMF community composition by AMF species identification. We extracted AMF spores from each soil sample using the wet sieving protocol as described by Gerdemann and Nicolson (1963), followed by centrifugation using sucrose gradient (Jenkins 1964). First, the AMF spores were sorted under a dissecting microscope by their morphology (e.g., Acaulosporoid, Gigasporoid, Glomoid, and Radial-Glomoid) (Souza 2015). Next, the spores were identified in microscope using polyvinyl alcohol lacto-glycerol (PVLG), and Melzer’s reagent (Souza 2015). During taxonomical identification, we considered the morphological characteristics of the spore walls and presence of special structures (e.g., layer’s ornamentation, germination shield or orb, *peridium*, small bulbs on subtending hypha, and inner walls). The identification of AMF species was realized by consulting the International Culture collection of arbuscular mycorrhizal fungi database available on the

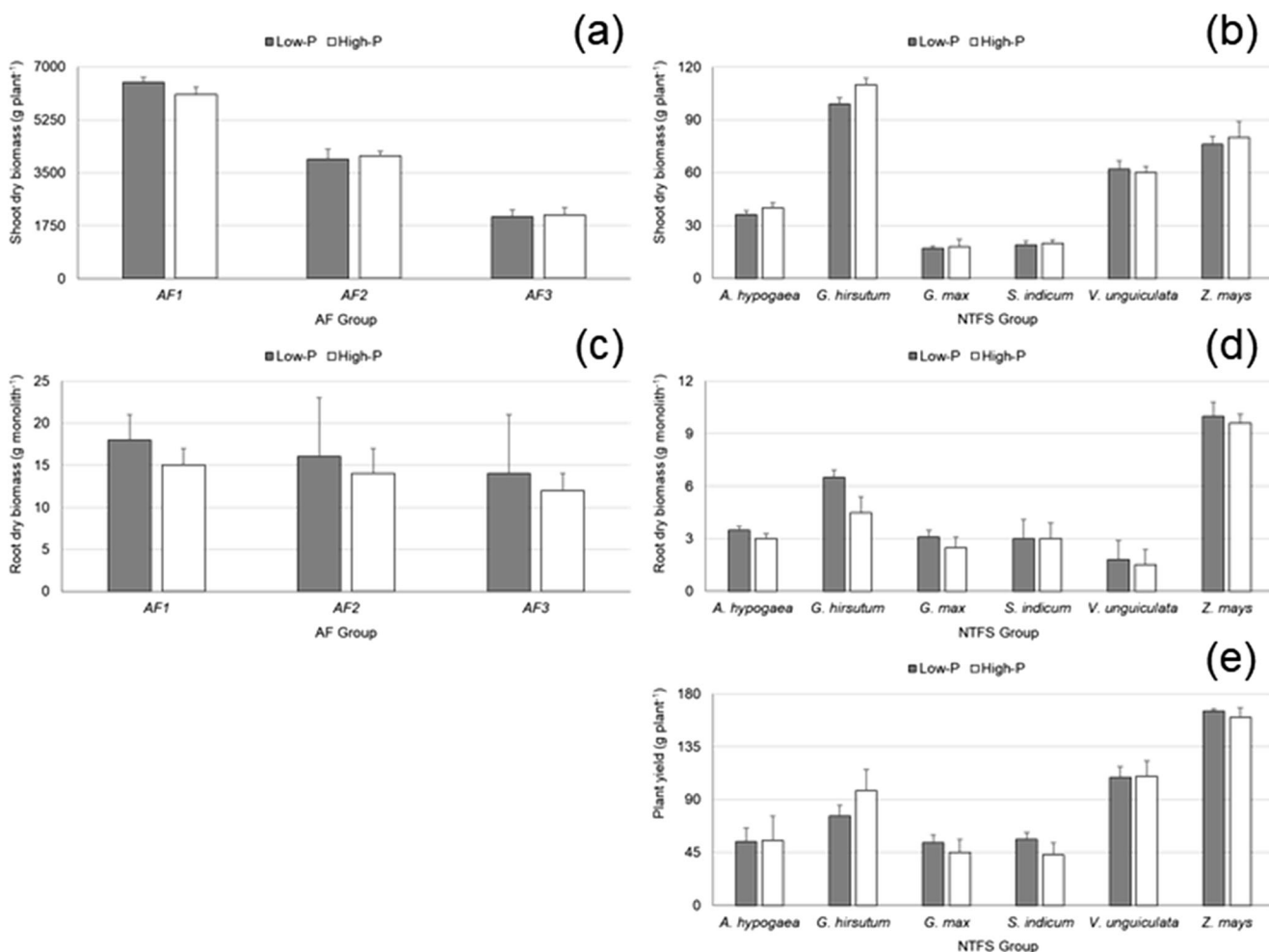


Fig. 2 Shoot dry biomass (g plant^{-1} , a, b), root dry biomass (g monolith^{-1} , c, d) and plant yield (e) from AF and NTFS groups as affected by soil P availability. The values are means (\pm SD, $N=40$). Shoot dry biomass (SDB) from AF group was estimated by using the following

equation: $\text{SDB} (\text{g plant}^{-1}) = [0.36 \times \text{DBH}^{1.86}] / 1000$. DBH = Diameter at breast height (cm). Root dry biomass was estimated from soil monoliths with $20 \times 20 \times 20$ cm

INVAM (<http://invam.caf.wvu.edu>). We used the AMF classification adjusting new recently updated taxa (Oehl

et al. 2011; Sieverding et al. 2011; Goto et al. 2012). As we did not aim to evaluate the seasonal variation of AMF

Table 1 Subplots characterization (litter deposition and Olsen’s P content) into each studied crop system (Mean \pm SD, $N=40$) before to start the field experiment

Crop systems	Litter deposition (g cm^{-2})		Low- vs. High P ^a	Olsen’s P (mg dm^{-3})		Low- vs. High P
	Low-P	High-P		Low-P	High-P	
<i>No-till monocropping system group</i>						
<i>A. hypogaea</i>	0.13 \pm 0.02	0.14 \pm 0.01	0.98 ^{ns}	8.5 \pm 0.5	13.9 \pm 1.3	9.31*
<i>G. hirsutum</i>	0.45 \pm 0.03	0.43 \pm 0.02	0.83 ^{ns}	7.3 \pm 1.2	11.9 \pm 1.9	9.86*
<i>G. max</i>	0.16 \pm 0.05	0.15 \pm 0.01	0.90 ^{ns}	8.9 \pm 0.6	14.5 \pm 1.8	10.54**
<i>S. indicum</i>	0.26 \pm 0.04	0.25 \pm 0.01	0.86 ^{ns}	8.1 \pm 0.8	14.9 \pm 2.3	11.93**
<i>V. unguiculata</i>	0.20 \pm 0.02	0.21 \pm 0.01	0.85 ^{ns}	7.4 \pm 1.2	13.7 \pm 1.9	10.89**
<i>Z. mays</i>	0.10 \pm 0.01	0.14 \pm 0.01	0.91 ^{ns}	9.1 \pm 0.4	15.3 \pm 2.4	12.34**
<i>Agroforestry system group</i>						
AF1	0.19 \pm 0.03	0.23 \pm 0.03	0.98 ^{ns}	4.3 \pm 0.3	9.3 \pm 1.2	10.78**
AF2	0.18 \pm 0.02	0.26 \pm 0.02	0.99 ^{ns}	5.4 \pm 0.5	8.7 \pm 1.9	9.97*
AF3	0.13 \pm 0.01	0.26 \pm 0.05	1.03 ^{ns}	4.9 \pm 0.9	6.9 \pm 0.9	7.89*

community composition, in our results we showed the mean AMF's abundance, and ecological indices (e.g., Chao, Shannon, Simpson and Pielou's indices).

Soil sampling

We determined the following soil chemical properties: soil pH, total organic carbon, and available phosphorus. First, the soil pH was determined in a suspension of soil and distilled water (1 : 2.5, v: v, soil: water suspension). Next, the total organic carbon was determined through rapid dichromate oxidation method as described by Okalebo et al. (1993). Finally, the available P was determined as described by Olsen et al. (1954).

Data analysis

All analyses in our study were carried out using R software (R Core Team 2018). For all variables we tested normality by Shapiro-Wilk test. Also, we assessed homogeneity of variances using Bartlett's test. The normality test was performed using the “*shapiro.test*” function, and the homogeneity test was performed using the “*dplyr*” package. To compare AMF community composition and soil chemical properties, we used two-way ANOVA followed by the Bonferroni test at 5% of probability. We performed non-metric multidimensional scaling (NMDS) using the “*metaMDS*” function of the “*vegan*” package to analyse differences between crop system and soil P availability in terms of AMF composition using Euclidean dissimilarities (Schmitz et al. 2020). Here, we performed a PERMANOVA, 9999 permutations) to determine differences in AMF composition using “*adonis*” function of the “*vegan*” package. To investigate a possible relationship between soil chemical properties and biotic (AMF species) variables, a CCA was used examining the similarity or dissimilarity in the AMF community composition of plots along the crop systems and soil P availability. The CCA was performed using the “*ggord*” and “*ordiplot*” of the “*vegan*” package.

Results

AMF community composition as influenced by crop system and soil P availability

The ecological indices varied between the crop system ($p < 0.001$), soil P availability ($p < 0.05$), and their interaction ($p < 0.001$). The highest values of Chao's index were found on plots with *A. hypogaea*, *V. unguiculata*, and all the agroforestry systems (AF1, AF2, and AF3) at high soil P availability. For the AMF diversity and AMF dominance (Shannon and Simpson's indices), we found the highest values on plots with *A. hypogaea*, *G. hirsutum*, *V. unguiculata*, and AF3 at high-P

availability. Finally, for the evenness index (Pielou's index), we found the highest values on plots with *A. hypogaea*, and AF1 plots at high-P availability. For *G. hirsutum* plots, we did not find significant differences on Chao's index, Shannon's index (diversity), Simpson's index (dominance), and Pielou's index (evenness) between high- and low-P availability (Table 2).

Soil chemical properties as influenced by crop system and soil P availability

We observed significant differences on soil pH ($p < 0.05$), soil organic carbon ($p < 0.001$) and available P ($p < 0.001$) between the studied crop system and soil P availability. For soil pH, we found the highest values on plots at high-P availability with *G. max* and *S. indicum*, while at low-P availability the highest values were found on plots with all agroforestry systems (AF1, AF2, and AF3). For soil organic carbon, we found the highest values at high-P availability with all no-till monocropping systems but *V. unguiculata* and AF3, while on low-P availability the highest values were found with *A. hypogaea*, and *G. hirsutum* plots. For the available P, the highest values at high-P availability were found with *G. hirsutum* plots, while on low-P availability, we found the highest values with *A. hypogaea* plots (Table 3).

The principal components analysis of the AMF community composition and soil chemical properties revealed that in different plots, these variables changed as a function of crop systems and soil available P conditions. According to the factor loadings of the principal components analysis, the abundance of *C. claroideum*, *C. etunicatum*, *R. intraradices*, richness, diversity (H') and dominance (C) were positively correlated with no-till monocropping systems (*A. hypogaea*, *G. hirsutum*, and *V. unguiculata*) and agroforestry system (AF1, AF2, and AF3) at low-P subplots (Fig. 3a), while the soil pH, and soil organic carbon were positively correlated with no-till monocropping systems (*A. hypogaea*, *G. hirsutum*, *G. max*, and *S. indicum*) at high-P subplots, and *G. max*, *S. indicum*, *Z. mays*, and agroforestry system at low-P subplots (Fig. 3b).

Discussion

We demonstrated the influences of crop system and soil P availability on AMF community composition at AMF species level (Table 2), and on soil chemical properties (Table 3). Our results improved the understanding of the AMF responses to both no-till monocropping (e.g., *A. hypogaea*, *G. hirsutum*, *G. max*, *S. indicum*, *V. unguiculata*, and *Z. mays*) and agroforestry systems (Freschet et al. 2015; de Stefano and Jacobson 2018; Basirat et al. 2019; Melo et al. 2020). Our results detected dissimilar patterns of plant species (e.g.,

Table 2 Effects of crop system and soil P availability on AMF ecological indices (Richness, diversity, dominance, and evenness). The values are means (\pm SE, $n = 548$)

Crop system	Richness		H'		C		J	
	High-P	Low-P	High-P	Low-P	High-P	Low-P	High-P	Low-P
<i>A. hypogaea</i>	10.1 \pm 0.1 aA	8.2 \pm 0.2 bA	2.2 \pm 0.2 aA	2.0 \pm 0.1 bB	0.9 \pm 0.1 aA	0.8 \pm 0.3 bB	1.6 \pm 0.2 aA	1.4 \pm 0.1 bB
<i>G. hirsutum</i>	10.2 \pm 0.2 aA	11.4 \pm 0.5 aA	2.2 \pm 0.1 aA	2.2 \pm 0.3 aA	0.9 \pm 0.1 aA	0.9 \pm 0.1 aA	1.6 \pm 0.1 aA	1.6 \pm 0.3 aA
<i>G. max</i>	8.1 \pm 0.2 bA	5.0 \pm 0.6 dB	0.8 \pm 0.1 dA	0.8 \pm 0.2 dA	0.8 \pm 0.1 bA	0.8 \pm 0.2 bA	1.4 \pm 0.1 bA	1.1 \pm 0.1 cB
<i>S. indicum</i>	7.3 \pm 0.3 bA	6.2 \pm 0.1 cA	1.7 \pm 0.3 cA	1.6 \pm 0.2 cA	0.8 \pm 0.3 bA	0.8 \pm 0.2 bA	1.2 \pm 0.3 cA	1.2 \pm 0.1 cA
<i>V. unguiculata</i>	10.1 \pm 0.5 aA	9.1 \pm 0.1 bA	2.2 \pm 0.2 aA	2.0 \pm 0.2 bB	0.9 \pm 0.2 aA	0.8 \pm 0.2 bB	1.6 \pm 0.8 aA	1.4 \pm 0.2 bB
<i>Z. mays</i>	8.2 \pm 0.1 bA	7.2 \pm 0.9 cA	0.8 \pm 0.2 dA	0.8 \pm 0.2 dA	0.8 \pm 0.3 bA	0.8 \pm 0.1 bA	1.4 \pm 0.1 bA	1.3 \pm 0.2 bA
AF1	10.2 \pm 0.6 aA	8.2 \pm 0.6 bA	1.9 \pm 0.2 bA	1.9 \pm 0.4 bA	0.8 \pm 0.1 bA	0.8 \pm 0.1 bA	1.7 \pm 0.1 aA	1.4 \pm 0.1 bB
AF2	11.3 \pm 0.5 aA	8.3 \pm 0.5 bB	2.0 \pm 0.1 bA	1.9 \pm 0.4 bA	0.8 \pm 0.2 bA	0.8 \pm 0.1 bA	1.5 \pm 0.2 bA	1.4 \pm 0.1 bB
AF3	10.3 \pm 0.4 aA	8.0 \pm 0.4 bA	2.2 \pm 0.1 aA	1.9 \pm 0.4 bB	0.9 \pm 0.4 aA	0.8 \pm 0.1 bB	1.4 \pm 0.3 bA	1.4 \pm 0.1 bA

AF1 = *G. sepium* + *Z. mays* + *B. decumbens*; AF2 = *M. caesalpiniaefolia* + *Z. mays* + *B. decumbens*; AF3 = *T. alrea* + *Z. mays* + *B. decumbens*.¹ Different small and capital letters show differences between crop system, and P availability, respectively by the Bonferroni's test ($p < 0.05$).

perennial plant species showing higher biomass than the annual plant species), root morphology (e.g., taproot vs. fibrous root), and crop systems (e.g., monocropping vs. agroforestry system) under field conditions (Fig. 2).

AMF community was characterized based on AMF spores' morphology, which allowed us to understand the AMF investment for future symbiosis as an effect of the current plant-AMF symbioses that occurred in our field experiment. First, AMF species colonized the fine roots (Table S1) to establish the symbiotic process. Next, they improved plant performance (Fig. 2), and finally, they sporulate as influenced by the host plant (Table S2). According to many studies, the AMF

sporulation is a highly carbon demanding process that starts during the plant senescence, i.e., when the AMF mycelium starts to be nutrient-limited (Souza and Freitas 2017; Liu et al. 2019; Medeiros et al. 2021). In our study, it is an important point because in the agroforestry system treatments, we have trees with a 5-years life cycle, whereas we have annual crops dominating the monocropping systems. It was expected to find in the agroforestry system less AMF spores than in the monocropping system (Deveautour et al. 2021). This hypothesis was supported for all studied agroforestry systems showing an average of 34.5% less AMF spores than the monocropping systems.

Table 3 Effects of crop system and soil P availability on soil pH, soil organic carbon (SOC, g kg^{-1}), and available P (mg dm^{-3}). The values are means (\pm SE, $n = 2160$)

Crop system	Soil pH		SOC (g kg^{-1})		Available P (mg dm^{-3})	
	High-P	Low-P	High-P	Low-P	High-P	Low-P
<i>A. hypogaea</i>	5.63 \pm 0.04 cB	6.10 \pm 0.04 bA	7.52 \pm 0.30 aB	8.50 \pm 0.04 aA	13.83 \pm 1.53 bB	23.02 \pm 0.21 aA
<i>G. hirsutum</i>	5.72 \pm 0.21 cA	5.82 \pm 0.06 cA	7.10 \pm 0.13 aB	8.62 \pm 0.02 aA	40.20 \pm 2.67 aA	16.81 \pm 1.54 bB
<i>G. max</i>	6.54 \pm 0.07 aA	6.33 \pm 0.02 bB	7.52 \pm 0.27 aB	8.23 \pm 0.02 bA	12.63 \pm 0.95 bA	12.34 \pm 0.02 bA
<i>S. indicum</i>	6.61 \pm 0.14 aA	6.53 \pm 0.14 bA	7.63 \pm 0.50 aA	7.60 \pm 0.01 cA	7.42 \pm 0.57 cA	6.82 \pm 0.13 cB
<i>V. unguiculata</i>	6.02 \pm 0.13 bA	5.91 \pm 0.01 cA	7.04 \pm 0.07 bB	8.01 \pm 0.01 bA	3.60 \pm 0.04 dB	5.04 \pm 0.11 dA
<i>Z. mays</i>	6.32 \pm 0.09 bA	5.62 \pm 0.01 cB	7.71 \pm 0.21 aA	7.23 \pm 0.06 dB	4.72 \pm 0.33 dB	8.13 \pm 0.11 cA
AF1	6.10 \pm 0.37 bB	6.80 \pm 0.03 aA	7.82 \pm 0.44 aA	7.41 \pm 0.04 cB	13.71 \pm 4.92 bA	6.82 \pm 0.18 cB
AF2	5.31 \pm 0.02 dB	6.82 \pm 0.03 aA	7.50 \pm 0.27 aA	7.40 \pm 0.04 cA	3.02 \pm 0.01 dB	6.83 \pm 0.18 cA
AF3	6.02 \pm 0.26 bB	6.83 \pm 0.03 aA	6.82 \pm 0.12 bB	7.40 \pm 0.04 cA	2.25 \pm 0.49 eB	6.82 \pm 0.18 cA

AF1 = *G. sepium* + *Z. mays* + *B. decumbens*; AF2 = *M. caesalpiniaefolia* + *Z. mays* + *B. decumbens*; AF3 = *T. alrea* + *Z. mays* + *B. decumbens*.¹ Different small and capital letters show differences between crop system, and P availability, respectively by the Bonferroni's test ($p < 0.05$).

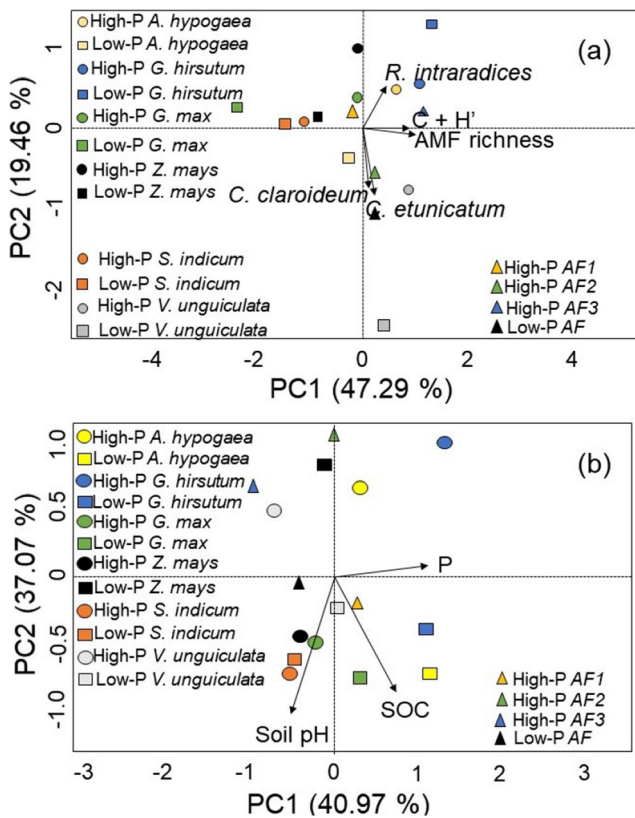


Fig. 3 Profile of arbuscular mycorrhizal fungi community composition (a), and soil chemical properties (b) plotted as Principal Component Analysis (PCA) of samples collected from different crop system and soil available P conditions. The two axes represent 66.75%, and 78.04% of data variance, respectively. Only high significant values are shown ($p < 0.001$). Agroforestry system are represented as follows: AF1 = *G. sepium* + *Z. mays* + *B. decumbens*; AF2 = *M. caesalpiniaefolia* + *Z. mays* + *B. decumbens*; AF3 = *T. alrea* + *Z. mays* + *B. decumbens*

Our field study determined the significant effects of crop systems and soil P availability on the AMF spore abundance (Table S2), richness (Chao’s index), diversity (Shannon’s index), dominance (Simpson’s index) and evenness (Pielou’s index) (Table 2)(Liu et al. 2019; Soonvald et al. 2020). In tropical soils, the soil P availability is considered as the most important factor that drives AMF richness and diversity in agroforestry and monocropping systems (Belay et al. 2020). However, in both agroforestry and monocropping systems, the effect soil P availability on AMF community composition was positive in all studied treatments. Thus, our statement about the agroforestry system as the best treatment promoting positive changes on AMF community composition when compared to the no-till monocropping system was not supported. In general, we found the highest values of richness, diversity, dominance, and evenness (Table 2) on subplots with high-P availability. These phenomena may be related with the higher root dry biomass production (Fig. 2 and Table S2) at the high- P availability when compared to the low root dry biomass at the low- P availability sites (Impastato and

Carrington 2020). The observed changes in the AMF community were primarily driven by the varying soil chemical properties (e.g., soil pH, soil organic carbon, and available P). Soil pH, soil organic carbon, and available P mainly explained the succession of the AMF community assemblage (Table 3, and Fig. 3).

Acid soils may reduce the abundance of AMF species with large spores (e.g., *Gigaspora* species), and select AMF species with less dense mycelial networks (e.g., *Glomeraceae* species) (Wang et al. 2021). On the other hand, soil organic carbon may improve AMF community composition by creating favourable condition to glomalin-related soil protein production and root activity (Wei et al. 2019). Finally, high P availability usually decreases the abundance of *Gigaspora* and *Scutellospora* species (Zhang et al. 2020). In our study, we found that crop systems which promoted (i) soil acidification (e.g., *A. hypogaea*, *G. hirsutum*, and AF2 at high P sites, while *G. hirsutum*, *V. unguiculata*, and *Z. mays* at low P sites); ii) soil rhizodeposition (e.g., *A. hypogaea*, *G. hirsutum*, *G. max*, and *V. unguiculata* at high P sites); and iii) soil fertility (e.g., *G. hirsutum* at high P sites) have promoted the AMF-plant interaction by inducing *Claroideoglomeraceae* and *Glomeraceae* spore germination (e.g., *Claroideoglomus*, and *Rhizophagus*) and hyphal growth rate into these soil conditions during our field study. Like the results found in our study for agroforestry and monocropping systems (Wang et al. 2017; Liu et al. 2020), the reducing of *Gigaspora* and *Scutellospora* species might make the agroforestry system much more prone to the negative plant-soil feedback than the monocropping systems.

The shifts in the AMF community composition in high-P availability affected the richness, diversity, dominance, and evenness (Table 2) of the AMF species for specific crop systems (e.g., *A. hypogaea*, *G. max*, *G. hirsutum*, *V. unguiculata*, and *Z. mays*). Previous studies on the variation in the AMF community detected substantial changes into the AMF community structure as affected by host traits (Šmilauer et al. 2019; Higo et al. 2020; Pires et al. 2020). Consistently, we found that crop systems determined the AMF community structure and the abundance of *R. intraradices*, *C. clarioideum*, and *C. etunicatum*. In the present study, the ecological indices of AMF community were positively correlated with high-P availability. This finding suggests a P-soil-driven succession pattern of the AMF assemblages in accordance with host species (Higo et al. 2020). In addition to AMF-plant feedback, plants can establish and alter their relationship with AMF species initiatively trough rootability (e.g., root exudation), which vary in diversity, intensity, and quantity over plant developmental stages (e.g., growth stage vs. reproductive stage) and plant nutritional status modulated by soil fertility (Tsiknia et al. 2020; Deveautour et al. 2021). This condition indicated that both the plant species and soil nutrient availability can drive the succession of AMF community in

semi-arid conditions in the rhizosphere of annual and perennial plants via the modification of rootability and rhizodeposition patterns. By contrast, the soil P availability cannot directly explain the shift in the AMF community by its own. Considering that the nutritional requirements of both monocropping and agroforestry systems were satisfied with fertilization during seedling (unpublished data), our results indicate that (i) into the monocropping systems (e.g., *A. hypogaea*, *G. hirsutum*, *G. max*, and *V. unguiculata*) and the agroforestry system (e.g., AF1 and AF2) the host plants increased their ability to recruit and structure their rhizosphere to AMF from *Glomeraceae* and *Claroideoglomeraceae*; (ii) the plots with high soil carbon content showed the highest values of biomass production, rootability which was promoted by the studied crop systems (e.g., *A. hypogaea*, *G. max*, *G. hirsutum*, *V. unguiculata*, and *Z. mays*). In the first one, soil properties were influenced by rootability and rhizodeposition processes (Fig. 3) at high P availability, while in the second one is related to the effects of crop systems that promoted changes on soil chemical properties, such as improving plant nutrient availability (Gebremikael et al. 2016). In semi-arid ecosystems the high-quality organic residues deposition (e.g., litter) promote both rhizodeposition and biological activity next to the root zone (Deveautour et al. 2021). These results agreed with our previous hypothesis that soil ecosystem with high contents of H^+ (e.g., acid soils) and organic compounds (e.g., root exudates) can promote soil chemical properties, soil organic carbon pools, and root system as described by Delgado-Baquerizo et al. (2018). Also, based on the importance of the relationship between host plants and AMF species in semi-arid conditions for plant growth and health (Souza and Freitas 2017; Souza and Santos 2018), we hypothesized that the shifts patters of AMF community structure, which is mainly driven by crop systems, will endanger the plant-soil feedback over the year. Further experimentations with plants inoculated with *R. intraradices*, *C. claroideum*, and *C. etunicatum*, which are based on AMF isolated and aggregated effect with annual and perennial plants under different P-fertilization rates (Fig. 3) can be useful in testing our main hypothesis.

Conclusion

The AMF community, and soil chemical properties responded differently to the changes in soil conditions promoted by the studied crop systems (e.g., no-till vs. agroforestry system) and soil P availability. The AMF community was directly affected by soil properties at both low- and high- P availability, which may suggest a P-soil-driven succession pattern of the AMF assemblages in accordance with host species. The significant abundance of *C. claroideum*, *C. etunicatum*, and *R. intraradices* in our study may suggest shifts into both

rootability and rhizodeposition patterns. Hence, the monocropping with *A. hypogaea*, *G. max*, *G. hirsutum*, *V. unguiculata*, and *Z. mays* in a no-till farming promoted soil carbon content, thus creating favourable conditions to AMF sporulation; and the agroforestry system increased the host plants ability to recruit and structure their rhizosphere to AMF from *Glomeraceae* and *Claroideoglomeraceae*.

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Declarations

Ethics approval We confirm that this manuscript that not been published elsewhere and is not under consideration by another journal. All Authors have approved the manuscript and agree with submission to *Biologia*. We have read and have abided by the statement of ethical standards for manuscripts submitted to *Biologia*.

Competing interests The authors declare that they have no conflict of interest.

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