



## SOIL SCIENCE

# Arbuscular mycorrhizal fungi community in coffee agroforestry, consortium and monoculture systems

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**Abstract:** Understanding the effects of different production systems on arbuscular mycorrhizal fungi (AMF) can help to interpret interactions between their components and to define management strategies. As a result, our study was conducted on soils under three coffee production systems (one homogeneous and two heterogeneous) and in a native forest located in the Bahia state, Brazil. This study aimed to answer the following questions: 1) Does the organization and management of the coffee production system affect the occurrence and diversity of AMF?; and 2) Is the seasonality effect similar between systems? To do so, soil samples (0-10 cm depth) were collected at two times of the year (rainy and dry). Number of spores (NS) and average richness did not show differences between the systems, only between seasons. There was a reduction in NS in the dry season (1.4 and 2.7 spores g<sup>-1</sup> soil) in relation to the rainy season (3.8 to 12.5 spores g<sup>-1</sup> soil). The influence of coffee production systems was observed in the presence and absence of some AMF species. The AMF community was shown to be related to the plant species composition of the system, which was reflected in the dissimilarity of heterogeneous systems in relation to the coffee monoculture system.

**Key words:** *Grevillea robusta*, *Coffea arabica*, *Musa* spp., Mycorrhizae, seasonality.

## INTRODUCTION

Coffee (*Coffea arabica* L. and *C. canephora* Pierre) is widely cultivated in Brazil and constitutes one of the most important products for the national and world economy, giving the country the title of largest producer and exporter of coffee in the world. The state of Bahia is the fourth largest coffee producer among the Brazilian states, with relevant participation in regional development with an annual production of about 3.8 million 60-kilo sacks of coffee (CONAB 2020).

The coffee production system most adopted is monoculture in full sun. However, adopting systems which optimize land use and enable biological and socioeconomic benefits has been

gaining importance nationally and worldwide. Agroforestry systems (AFS) are considered the land use models which most ecologically resemble native forests (Nair 1993, Gama-Rodrigues 2004, Miccolis et al. 2016). In these systems there is the association of agricultural crops with tree components which enables an increase in the entry of organic matter into the soil, and as a consequence favors improving its chemical, physical and biological characteristics. In addition, AFS can contribute to greater diversity in the microbial community and soil fauna, which act as biological control agents and soil conditioners (Young 1994).

Understanding the effects of different production systems on soil quality can assist in interpreting interactions between its components and in defining management strategies (Marshall 2000). Arbuscular mycorrhizal fungi (AMF) are among the biological attributes of the soil which are considered sensitive to changes in the environment. These organisms form symbiotic associations in the roots of host plants (Pereira et al. 2018). Thus, plants are able to meet the demands of the AMF for carbon compounds through this relationship (Moreira & Siqueira 2006, Ghazanfar et al. 2016), while fungi favor absorption of nutrients from the soil (Mergulhão et al. 2014). In addition, AMF provide several other benefits such as favoring moisture retention, aggregate formation, soil stability (Nobre et al. 2015) and stimulating the primary defense system of plants to attack pathogens (Mechri et al. 2014), which increases their tolerance to biotic stress caused by diseases (Calvo-Polanco et al. 2016, Meddad-Hamza et al. 2017).

The occurrence of AMF is regulated by several biotic and abiotic factors which influence the abundance and survival of infectious propagules (Mello et al. 2012) and the richness of communities (Sousa et al. 2014, Ferreira et al. 2018), altering the root colonization process in plants (Rocha et al. 2020, Moreira et al. 2019). Among these factors there are climatic conditions, the cultivation system organization (homogeneous or heterogeneous) and the adopted management (Martínez-García et al. 2012, Carrenho et al. 2010).

The climate directly controls forming an association and establishing AMF communities due to temperature variations and water availability, and indirectly according to the plants' demand for water and nutrients which is higher at certain times of the year (Santos et al. 2014). Similarly, the cultivation system also

influences the AMF community according to its characteristics (Posada et al. 2016). For example, a homogeneous (monoculture) system tends to provide a less favorable environment to root colonization and diversity of AMF species when compared to heterogeneous systems such as AFS or a native forest (Siqueira et al. 2010, Prates Júnior et al. 2019). This is because the species composition of the system interferes with plant-fungus interactions because AMF occurrence and distribution are conditioned by the existence of suitable hosts (Verbruggen et al. 2012) and by the release of root exudates (Ajeesh et al. 2015). In addition, implementing management techniques such as soil movement also affects the AMF as it causes hyphae disruption, and as a consequence propagule and spore exposure, thus decreasing their infectious capacity (Jasper et al. 1991, Kabir et al. 1997, Caproni et al. 2003, Hu et al. 2015).

Several studies on the AMF community have been carried out in Brazil on monoculture crop systems, agroforestry systems and native forests (Loss et al. 2009, Ferreira et al. 2012, Costa et al. 2013, Santos et al. 2014, Lima et al. 2015, Souza et al. 2016, Durazzini et al. 2016, Pereira et al. 2018, Martins et al. 2019). However, studies comparing different coffee production systems are still scarce (Bonfim et al. 2010, Durazzini et al. 2016), especially those which evaluate native forest as a reference system.

Given the above, our study aimed to answer the following questions: 1) Does the organization and management of the coffee production system affect the occurrence and diversity of AMF community?; and 2) Is the seasonality effect similar between systems? To do so, the AMF community in three coffee production systems (one homogeneous and two heterogeneous) and in a native forest (which was used as a reference) were evaluated. It was assumed that the production system causes different

magnitudes of change in the structure and composition of the AMF community according to its organization and management.

## MATERIALS AND METHODS

### Area descriptions

The study was conducted in the district of Lucaia, municipality of Planalto, Southwest region of the state of Bahia, Brazil. Three coffee production systems and a natural vegetation area were evaluated: (1) AFS - *Coffea arabica* L. with *Grevillea robusta* agroforestry system, 17 years old and spacing 3.5 x 15.0 m (between trees) and 1.5 x 2.5 m (among coffee trees) (14° 44' 58" S and 40° 32' 21" W); (2) BC - *Coffea arabica* L. with banana (*Musa* spp.) consortium, aged 17 years old, including drastic coffee pruning (Stumping) at the age of eight, and established in 1.5 x 4 spacing, 0 m (among coffee trees) and 1.0 x 16.0 m (among banana trees) (14° 45' 01" S and 40° 31' 24" W); and (3) MC - *Coffea arabica* L. monoculture, 15 years old, with two stumpings and 1.5 x 2.5 m spacing (14° 45' 08" S and 40° 32' 27" W); and (4) NF - native forest, which was used as a reference system and is located in an area adjacent to the coffee systems (14° 44' 52" S and 40° 31' 21" W).

The native forest fragment has vegetation classified as Semi-deciduous Seasonal Forest and a total area of about 30 hectares. It is a forest with relatively low arboreal stratum (between 10 and 15 m high), with a predominance of the *Parapiptadenia* and *Anadenanthera* genera (IBGE 2012) and intermediate regeneration stage according to criteria described in CONAMA Resolution #01/1994 (Brasil 1994), since it has not been submitted to any intervention for over 20 years.

The AFS was established from opening furrows with planting fertilization (20 Mg ha<sup>-1</sup> of simple superphosphate) and annual organic

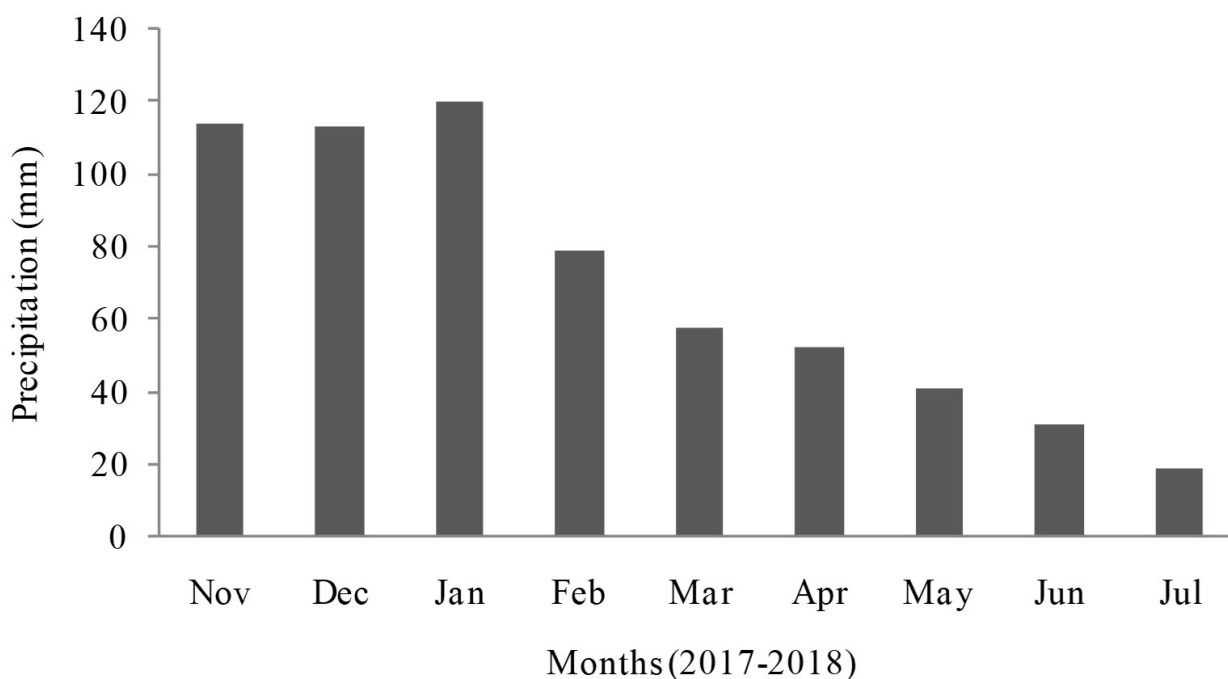
cover-maintenance fertilization (32 Mg ha<sup>-1</sup> of bovine manure). Soil tillage with plowing, harrowing and furrowing, planting fertilization (20 Mg ha<sup>-1</sup> of simple superphosphate) and annual maintenance (17 Mg ha<sup>-1</sup> of urea and 33 Mg ha<sup>-1</sup> of NPK 20-00-20) were adopted in the BC and MC systems. Maintenance was performed twice a year in all systems with clearing to control spontaneous herbs.

The region has a tropical altitude climate (Cwb) according to the Köppen classification, with an average altitude of 923 meters above sea level (SEI 2013), average annual temperature of 19.2°C and an average annual rainfall of 750 mm. The monthly rainfall data from September 2017 to July 2018 are shown in Figure 1. The soil in the studied areas is classified as Oxisol according to the USDA-Natural Resources Conservation Service classification (Soil Survey Staff, 2014), and dystrophic Yellow Latossol according to the Brazilian Classification System (Santos et al. 2018a).

### Soil and litter sampling

First, four plots of 20 m x 20 m (400 m<sup>2</sup>) were demarcated randomly in each system, ensuring a minimum distance of 10 m between plots. The soil and litter collections were carried out in the months of December 2017 (beginning of the rainy season) and April 2018 (beginning of the dry season).

Random soil sampling was performed after removing (cleaning) the litter, collecting 10 individual samples (depth 0-10 cm) which were gathered to form a composite sample from each plot. The accumulated surface litter was collected with a square wooden template of 0.25 m<sup>2</sup> (0.5 m x 0.5 m) which was randomly thrown over the area of each plot. The litter samples were dried in an oven at 65°C, then weighed on a precision scale (0.01g) and the dry mass results were converted to Mg ha<sup>-1</sup>.



**Figure 1.** Monthly rainfall recorded at the station closest to the study site (municipality of Vitória da Conquista, Bahia, Brazil), from September 2017 to July 2018 (Source: INMET 2020).

The soils were chemically characterized according to Table I following the procedures described by EMBRAPA (2017): pH in water; extractable P and K by Mehlich<sup>-1</sup>; Ca<sup>2+</sup>, Mg<sup>2+</sup> and Al<sup>3+</sup> exchangeable with 1 mol L<sup>-1</sup> of KCl; and organic matter by oxidation with 0.4 mol L<sup>-1</sup> of K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>.

#### Spore extraction, counting and identification

First, 50 g of each soil sample were used to extract the arbuscular mycorrhizal fungi (AMF) spores, adopting an adapted procedure described for nematodes according to the wet-sieving methodology (Gerdemann & Nicolson 1963) and centrifugation in density gradient with water and 45% sucrose (Jenkins 1964). Next, spore counting and species identification were performed using a stereoscopic microscope, referring to the Schenck & Pérez manual (1988) and the international collection website of AMF - INVAM (2020, <https://invam.wvu.edu/>).

#### Data analysis

The number of AMF spores counted in 50 cm<sup>3</sup> of soil was transformed into the abundance of spores g<sup>-1</sup> of soil. Furthermore, total spore richness, mean richness and occurrence frequency have been calculated in each of the four plots (repetitions) per site.

The obtained data were analyzed for normality (Shapiro-Wilk) and homogeneity (Cochran and Bartlett test) of the error variances, and converted when necessary. Parametric data were subjected to analysis of variance (ANOVA) when found, according to a completely randomized design (CRD). Multiple comparisons of the means were performed between times and between treatments by the Tukey test at 5% significance when ANOVA showed a significant result in the F-test ( $p < 5\%$ ). The analyzes were performed using the Assisat<sup>®</sup> v.7.7 statistical software program.

**Table I. Chemical attributes and humidity of Dystrophic Yellow Latossol (depth 0-10 cm) under three coffee production systems and in native forest.**

System	pH	P	SOM	K	Ca	Mg	H+Al	SB	E	Soil moisture	
										Moist	Dry
	H <sub>2</sub> O	mg dm <sup>-3</sup>	g dm <sup>-3</sup>	----- cmolc dm <sup>-3</sup> -----							
AFS	6.2	41.5	21.0	0.5	3.8	2.6	2.7	6.9	7.0	12.9	13.0
BC	6.2	26.5	17.0	0.6	5.0	2.2	3.3	7.7	7.8	12.6	14.2
MC	7.2	27.0	15.5	0.7	4.0	2.8	1.4	7.4	7.4	12.7	13.0
NF	5.5	3.5	30.0	0.2	4.0	3.0	7.1	7.1	7.3	18.1	19.7

In which: AFS = agroforestry system coffee with *Grevillea robusta*, BC = banana coffee, MC = monoculture coffee, NF = native forest, SOM = soil organic matter, H+Al = potential acidity, SB = sum of soil bases, E = effective soil CEC, soil moisture = moisture at the time of collection.

The presence-absence of the AMF species (occurrence or non-occurrence of species, respectively), accumulated litter and soil moisture data were complementarily submitted to a principal component analysis (PCA) using the Addinsoft XLSTAT® Version 2020.1.3 (1995-2020) program. This analysis was performed to synthesize the multidimensional variation of the treatments in a diagram and order them into the components according to their similarities around the measured soil variables. The interrelationships between attributes of soil, litter, spore numbers and AMF richness were analyzed using Pearson's 5% correlation using the SAEG® v.9.1 program.

## RESULTS

The variation pattern in litter accumulation between the systems was the same at both times of the year (Table II). The highest value was observed in the native forest (12.26 Mg ha<sup>-1</sup>), followed by AFS (6.07 Mg ha<sup>-1</sup>), which was not distinguished from the consortium (3.66 Mg ha<sup>-1</sup>), which in turn was similar to monoculture (0.78 Mg ha<sup>-1</sup>).

A total of 16 AMF species were identified and presented different occurrence frequencies according to the systems and time of year (Table

III). Of this total, 15 species occurred in the rainy season and ten species in the dry season. This was reflected in greater total species richness in the rainy season for all studied systems (Table II), although the average richness only showed differences between seasons in the NF. Following this same pattern, a reduction in the number of spores (NS) was observed in the dry season for most systems. The total density in the rainy season varied from 3.8 to 12.5 spores g<sup>-1</sup> soil, while the density in the dry season was between 1.4 and 2.7 spores g<sup>-1</sup> soil (Table II).

Although no significant variations were observed between the systems regarding the number of spores and AMF richness (Table II), significant correlations were observed between mean species richness and soil pH ( $r = -0.66$ ;  $p < 0.05$ ), litter ( $r = 0.67$ ;  $p < 0.05$ ), soil moisture ( $r = 0.87$ ;  $p < 0.05$ ) and SOM ( $r = 0.70$ ;  $p < 0.05$ ). In addition, differences were observed regarding the presence and absence of AMF species (Table III). The *Acaulospora denticulata*, *Acaulospora mellea*, *Acaulospora scrobiculata* and *Claroideoglossum etunicatum* species only occurred in coffee production systems. *Glomus macrocarpum* and *Sclerocystis clavispora* occurred in all systems studied at both times of the year. *Acaulospora tuberculata*, *Gigaspora* sp. and *Racocetra persica* exclusively occurred in

**Table II. Accumulated litter (Mg ha<sup>-1</sup>), average number of spores (in 50 g of soil) and richness of arbuscular mycorrhizal fungi species in three coffee production systems and in native forest at two times of the year.**

Systems	Litter		NS		TR		AR	
	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry
AFS	6.16 Ab	5.98 Ab	202.5 Aa	70.25 Ba	9	5	4.5 Aa	2.75 Aa
BC	3.93 Abc	3.38 Abc	626.75 Aa	126.75 Ba	10	6	5.25 Aa	3.25 Aa
MC	0.84 Ac	0.72 Ac	193.00 Aa	136.75 Aa	10	10	5.50 Aa	4.25 Aa
NF	14.17 Aa	10.34 Ba	474.25 Aa	81.75 Ba	11	6	5.50 Aa	3.25 Ba

In which: Litter = accumulated dry phytomass on the soil, NS = number of spores, TR = total richness, AR = average richness.

Different capital letters within rows compare season for each measurement, and different lower case letters in columns indicate differences using the Tukey test at 5% significance.

the native forest during the rainy season. On the other hand, *Claroideoglossum etunicatum* only occurred in monoculture in the dry season, and *Sieverdingia tortuosa* occurred in all systems in the rainy season and in almost all of them in the dry season.

The most abundant genera in the two seasons considering all the studied systems were *Acaulospora* and *Glomus* (Table III), representing approximately 56% of the total number of AMF identified.

When analyzed together using PCA, the accumulated litter, soil moisture and presence and absence of AMF species explained more than 86% of the variation between treatments using the first two principal components in the two studied seasons (87.0% in the rainy season) and 92.6% in the dry season) (Figure 2). The graphic dispersion of the treatments in relation to the axes showed a similar pattern between the two periods (Figure 2b and 2d), with isolation of the NF (next to the principal component 1, PC1) and the MC (next to the principal component 2, PC2), which were in different quadrants. It also showed clustering of AFS and BC, which were located in the same quadrant between PC1 and PC2.

Eigenvalues of 63.5% for PC1 and 23.5% for PC2 were verified in the rainy season. The variables most associated with PC1 (and

therefore the most prevalent for differentiating the native forest, AFS and BC) were: litter, moisture and *A. scrobiculata*, *A. tuberculata*, *Am. Leptoticha*, *Gigaspora* sp., *R. persica* (Figure 2a, Table IV). In turn, the variables most strongly associated with PC2 and consequently with MC were *A. denticulata*, *A. foveata*, *A. mellea*, *Glomus* sp.1 and *Glomus* sp. (Figure 2a, Table IV).

The PCA for the dry season presented eigenvalues of 52.3% (PC1) and 40.4% (PC2). In addition to the *A. mellea* and *A. scrobiculata* species, litter and moisture were among the variables most associated with PC1 in the dry season following a similar pattern to the rainy season. The most important variables for PC2 were the *Am. Leptoticha*, *C. pellucida*, *Cl. etunicatum* and *G. glomerulatum* species (Figure 2c, Table IV).

## DISCUSSION

The greater litter accumulation in the NF can be attributed to the species composition and diversity in the native ecosystem which enables greater plant residue additions. This highlights the significant contribution of the tree component to the litter supply and also explains the fact that the AFS has the second most significant accumulation, although without distinction from the BC. Likewise, the smaller

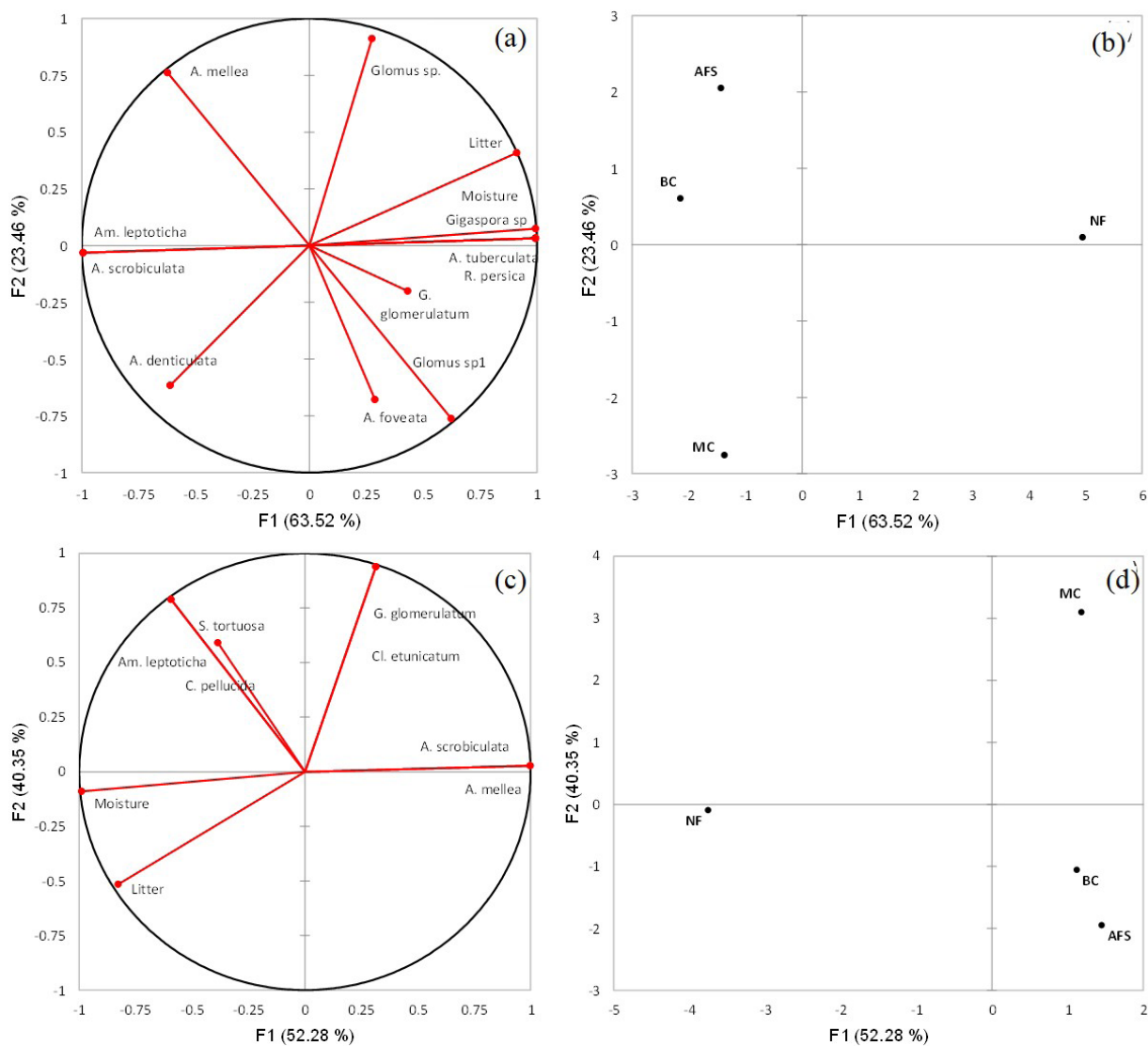
**Table III. Frequency of occurrence (%) of arbuscular mycorrhizal fungi species at two times of the year in three coffee production systems and in native forest.**

Species	AFS	BC	MC	NF
	Rainy season			
<i>Acaulospora denticulata</i> Sieverding & Toro.	0	25	25	0
<i>Acaulospora foveata</i> Trappe & Janos.	0	25	25	25
<i>Acaulospora mellea</i> Spain & Schenck.	25	75	0	0
<i>Acaulospora scrobiculata</i> Trappe.	25	25	50	0
<i>Acaulospora tuberculata</i> Janos & Trappe.	0	0	0	25
<i>Ambispora leptoticha</i> (Schenck & Smith) Morton & Redecker.	50	100	75	0
<i>Cetranspora pellucida</i> (T.H. Nicolson & N.C. Schenck) Oehl, F.A. Souza & Sieverd.	25	25	50	25
<i>Gigaspora</i> sp.	0	0	0	50
<i>Glomus glomerulatum</i> Sieverding.	50	0	75	50
<i>Glomus macrocarpum</i> Tulasne & Tulasne.	100	100	100	100
<i>Glomus</i> sp.1	0	0	50	25
<i>Glomus</i> sp.	25	25	0	100
<i>Racocetra persica</i> Oehl, Souza & Sieverd.	0	0	0	25
<i>Sclerocystis clavisporea</i> (Trappe) Almeida & Schenck.	100	100	75	75
<i>Sieverdingia tortuosa</i> Schenck & Smith.	50	25	25	50
	Dry season			
<i>Acaulospora mellea</i> Spain & Schenck	50	75	25	0
<i>Acaulospora scrobiculata</i> Trappe	25	25	25	0
<i>Ambispora leptoticha</i> (Schenck & Smith) Morton & Redecker	0	0	50	25
<i>Cetranspora pellucida</i> (T.H. Nicolson & N.C. Schenck) Oehl, F.A. Souza & Sieverd	0	0	25	25
<i>Claroideoglomus etunicatum</i> (W.N. Becker & Gerdemann) C. Walker & A. Schübler	0	0	25	0
<i>Glomus glomerulatum</i> Sieverding	0	0	50	0
<i>Glomus macrocarpum</i> Tulasne & Tulasne	100	100	100	100
<i>Glomus</i> sp.1	25	25	25	50
<i>Sclerocystis clavisporea</i> (Trappe) Almeida & Schenck	50	100	50	75
<i>Sieverdingia tortuosa</i> Schenck & Smith	25	0	50	50

amount of litter stocked in the monoculture compared to NF and AFS is explained by the system's homogeneous characteristic which provides less diversity and less litter. In evaluating different coffee production systems, Meylan et al. (2017) observed a greater amount of litter in the shaded systems with *Erythrina*

and or with banana in relation to the system in full sun.

Litter accumulation was maintained in most of the studied systems when comparing the seasons, with the exception of the native forest which showed a significant increase in the rainy season (Table II). The fact that it only varied in the NF is related to the typical seasonal pattern



**Figure 2.** Diagram of the ordering of variables and treatments in the rainy season (a and b) and in the dry season (c and d) produced by the principal components analysis of the presence-absence of arbuscular mycorrhizal fungi, litter and soil moisture in three coffee production systems and in native forest in Planalto, Bahia, Brazil.

of semi-deciduous seasonal forests, with litter deposition peaks coinciding with the end of the dry season as a vegetation response to climatic variation (Dias & Oliveira-Filho 1997, Santos Neto et al. 2015, Barreto-Garcia et al. 2019), which in turn is reflected in greater litter accumulations at the beginning of the rainy season. These larger accumulations are usually associated with the influence of rain which creates more favorable conditions for leaf renewal and due to leaves

and branches falling by mechanical action (Dias & Oliveira-Filho 1997, Vendrami et al. 2012).

The reduction in the number of species, NS and richness in the dry season indicates that only the species which are more resistant to water deficit conditions would present reproduction and dispersion structures in the dry season. This denotes that the AMF community becomes less complex in low water availability conditions, thus preserving the most tolerant species (Santos et al. 2014). Despite this,



**Table IV.** Factor loadings and variability explained by the axes in the principal component analysis (PCA) of the presence-absence of arbuscular mycorrhizal fungi, litter and soil moisture in three coffee production systems and in native forest in the rainy and dry seasons in Planalto, Bahia, Brazil.

Variables/ Treatments	Rainy season			Variables/ Treatments	Dry season		
	PC1	PC2	PC3		PC1	PC2	PC3
	<b>Factor loadings</b>				<b>Factor loadings</b>		
Litter	<b>0.912</b>	0.409	-0.042	Litter	<b>-0.828</b>	-0.516	-0.221
Moisture	<b>0.994</b>	0.074	-0.083	Moisture	<b>-0.989</b>	-0.090	0.117
A. denticulata	-0.612	<b>-0.616</b>	-0.497	A. mellea	<b>0.998</b>	0.028	0.050
A. foveata	0.288	<b>-0.679</b>	-0.675	A. scrobiculata	<b>0.998</b>	0.028	0.050
A. mellea	-0.623	<b>0.762</b>	-0.177	Am. leptoticha	-0.592	<b>0.789</b>	-0.165
A. scrobiculata	<b>-0.994</b>	-0.032	0.102	C. pellucida	-0.592	<b>0.789</b>	-0.165
A. tuberculata	<b>0.994</b>	0.032	-0.102	Cl. etunicatum	0.314	<b>0.939</b>	-0.141
Am. leptoticha	<b>-0.994</b>	-0.032	0.102	G. glomerulatum	0.314	<b>0.939</b>	-0.141
G. glomerulatum	0.431	-0.201	<b>0.880</b>	S. tortuosa	0.386	0.591	<b>0.709</b>
Gigaspora sp	<b>0.994</b>	0.032	-0.102				
Glomus sp1	0.623	<b>-0.762</b>	0.177				
Glomus sp.	0.275	<b>0.912</b>	-0.306				
R. persica	<b>0.994</b>	0.032	-0.102				
Variability %	63.519	23.461	13.020	Variability %	52.278	40.345	7.377
Cumulative %	63.519	86.980	100.000	Cumulative %	52.278	92.623	100.000

no significant differences in soil moisture were observed between the seasons of the year in all studied sites (Table I), which must be related to the fact that the soil was sampled on only one date, and therefore did not reflect average humidity conditions. According to Mangan et al. (2004), seasonality affects the occurrence of AMF as the species produce their spores at different times of the year, and these become physiologically active in seasons which are more conducive to their development. Reductions in the number of spores in the dry season were also observed by Khaekhum et al. (2017) and Ramos-Zapata et al. (2011) in eucalyptus stands and coastal dunes, respectively.

The absence of variation in NS and average richness between systems suggests that the coffee production systems did not cause changes in these attributes for the AMF community under

the studied conditions. However, variations in NS were observed by Bonfim et al. (2010) and Durazzini et al. (2016) when comparing agroforestry coffee systems with monoculture coffee systems.

The occurrence of the *Acaulospora denticulata*, *Acaulospora mellea*, *Acaulospora scrobiculata* and *Claroideoglomus etunicatum* species only in the coffee production systems is in line with the results found by Fernandes & Siqueira (1989), who observed the occurrence of these same species (except *Acaulospora denticulate*) in coffee plantations in the south of Minas Gerais. This reveals a high adaptation of these species to the edaphoclimatic conditions prevalent in coffee ecosystems (Theodoro et al. 2003). For example, *Acaulospora mellea* was one of the species most commonly found in coffee

plantations in Colombia and Mexico (Posada et al. 2016).

The presence of *Glomus macrocarpum* and *Sclerocystis clavispora* in all systems studied and at both times of the year suggests that these fungi have adapted well to the conditions of all studied systems. *Glomus macrocarpum* is usually reported as a species with a high capacity to adapt to stress and climatic variations, and therefore it is commonly found in different environmental conditions (Carvalho et al. 2012, Ferreira et al. 2012, Carneiro et al. 2015, Silva et al. 2016). On the other hand, the occurrence of *Sclerocystis clavispora* is more common in the dry season (Al-Yahya'ei et al. 2011, Silva et al. 2016, 2019).

The exclusivity of *Acaulospora tuberculata*, *Gigaspora* sp. and *Racocetra persica* in the native forest is possibly related to the characteristics of this environment which is more biologically complex than coffee systems, has higher levels of organic matter in the soil and is less subject to temperature and moisture variations. This would favor the survival of more demanding species in climate and soil conditions. Several records of the occurrence of these species are found in the literature (Santos et al. 2014, 2018b, Pereira et al. 2018, Silva et al. 2019).

The presence of *Claroideoglomus etunicatum* only in the dry season is also in agreement with several studies which found the occurrence of this species being associated with water restriction periods, including in studies by Pedone-Bonfim et al. (2018) and Teixeira-Rios et al. (2013) in dry tropical forests, and Sousa et al. (2013) in cultivated areas in the semi-arid region of Brazil. On the other hand, the fact that this species only occurred in the MC suggests that the system provided some factor favorable to its occurrence or sporulation, such as the pH which was relatively higher in this system (Table I). Corroborating this hypothesis, a significant

negative correlation was observed between mean species richness and soil pH. According to Zhu et al. (2007), soil pH is a factor which directly or indirectly influences AMF diversity since it can compromise the nutrient availability for the fungus or for the plant.

The occurrence of *Acaulospora denticulata*, *Acaulospora foveata*, *Acaulospora mellea*, *Acaulospora tuberculata*, *Gigaspora* sp., *Glomus* sp. and *Racocetra persica* species only in the rainy season (Table III) shows that water availability was a limiting factor to sporulation. In turn, the occurrence of *Sieverdingia tortuosa* in all systems in the rainy season and in almost all the systems in the dry season is explained by the fact that this species is considered generalist, and can therefore occur in preserved or disturbed natural environments and in times with high or low water availability (Santos et al. 2014, Silva et al. 2016).

The greater abundance of the *Acaulospora* and *Glomus* genera can be attributed to the fact that they produce smaller spores and in greater quantity, being less influenced by seasonal changes when compared to other genera such as *Gigaspora*, which have larger spores (Sousa et al. 2014). These genera are generally found with great frequency in a wide range of forest ecosystems (Davison et al. 2015, Soteris et al. 2015, Silva et al. 2016, Bonfim et al. 2016, Araújo et al. 2019, Pagano et al. 2019, Becerra et al. 2019) and also in agricultural ecosystems (Oehl et al. 2017, Cristo et al. 2018, Vieira et al. 2020).

A similar dispersion pattern of treatments between the rainy season (Figure 2a and 2b) and dry season (Figure 2c and 2d) in the PCA with AFS and BC clustering and MC and NF isolation demonstrates that AMF dynamics in the studied systems remain between the seasons. The dissimilarity of NF and MC (Figures 2b and 2d) can be attributed to differences in the litter and soil moisture accumulation in these treatments

(Tables I and II). The native forest provides greater litter (Table II) and organic matter accumulation in the soil (Table I) due to not suffering anthropic influence and presenting a great diversity of plant species, whereas monoculture causes smaller organic residue entry and a less diverse litter due to its homogeneity characteristic, in addition to presenting only one host species. This would be influencing the occurrence of some AMF species. An example of these are the *Gigaspora* sp., *A. tuberculata*, and *Racocetra Perssica* species which were found exclusively in the native forest, the *Glomus* sp. species which was only absent in the MC, and *Am. Leptoticha* and *A. scrobiculata* which did not occur in the NF. In line with this explanation, significant positive correlations were found between mean species richness and litter, soil moisture and SOM. According to Verbruggen et al. (2012), the occurrence and distribution of AMF species are related to contemporary ecological processes such as the existence of one or more hosts, and environmental factors such as organic matter content, soil temperature and moisture which act on the fungal community, conditioning its abundance and diversity.

In turn, the ASF and BC grouping (Figures 2b and 2d) can be explained by the fact that these systems are made up of more than one plant species. Thus, the vegetation structure and composition (with the presence of the arboreal component in the AFS and the banana tree in the BC) would provide a specific environment for the AMF, with more diversified litter and a more balanced microclimate when compared to the MC. In other words, the heterogeneous systems would be exercising a similar influence in the AMF community, while the MC (as previously discussed) is distinguished by being composed of a single plant species presenting restriction in the entrance and diversity of organic residues and being more prone to disturbance.

## CONCLUSIONS

Although not presenting an effect on spore density and average species richness, coffee production systems cause changes in the presence or absence of arbuscular mycorrhizal fungi (AMF) species. The AMF community was shown to be related to the species composition of the productive system, which was reflected in a similar influence by the heterogeneous systems (agroforestry coffee-grevillea system and banana-coffee consortium), and distinct from the coffee monoculture and native forest in terms of effect on the fungal community. The species distribution and number of spores was shown to be influenced by climatic conditions with a reduction in the dry season, but without differentiation between the studied systems.

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WTB: conceptualization, data curation, formal analysis, investigation, methodology and writing – original draft; PABBG: conceptualization, formal analysis, methodology, supervision and writing – review & editing; OJS: methodology and resources; RNS: data curation, formal analysis and supervision; MSS: investigation and methodology. All authors critically reviewed the manuscript and approved the final version.

