



Agronomía Colombiana

ISSN: 0120-9965

Universidad Nacional de Colombia, Facultad de Agronomía

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Agronomía Colombiana, vol. 37, no. 3, 2019, September-December, pp. 239-254
Universidad Nacional de Colombia, Facultad de Agronomía

DOI: <https://doi.org/10.15446/agron.colomb.v37n3.74008>

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Diversity of arbuscular mycorrhizal fungi communities associated with cape gooseberry (*Physalis peruviana* L.) crops

Diversidad de comunidades de hongos formadores de micorrizas arbusculares asociados a los cultivos de uchuva (*Physalis peruviana* L.)

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ABSTRACT

The diversity of arbuscular mycorrhizal fungi (AMF) communities in agricultural systems depends on biotic and abiotic factors as well as on cultural practices. This research aimed to evaluate the diversity of AMF present in an altitudinal transect cultivated with cape gooseberry (*Physalis peruviana* L.). A set of 13 soil samples from cape gooseberry plantations located in the Colombian Andean mountains in the provinces of Cundinamarca and Boyaca were collected during dry (0-20 mm/month) and rainy (150-330 mm/month) seasons between 1500 and 3000 m a.s.l., in order to establish the relationship between the altitudinal characteristics and AMF diversity. The evaluation of the abundance of spores and species and diversity indexes showed the presence of 46 AMF species in the dry season and 31 in the rainy season. This shows the high diversity of AMF in the tropical Andes with spore abundance between 20 and 120 spores 10 g⁻¹ of soil in the rainy season and between 127 and 1531 spores 10 g⁻¹ of soil in the dry season.

Key words: diversity, richness, Colombian Andes, Glomeromycota.

RESUMEN

La diversidad de las comunidades hongos formadores de micorrizas (HFMA) en sistemas agrícolas depende de factores bióticos y abióticos, así como de prácticas culturales. La investigación tuvo como propósito evaluar la diversidad de los HFMA presentes en un transecto altitudinal (1500 a 3000 msnm) cultivado con uchuva (*Physalis peruviana* L.). Se recolectaron 13 muestras compuestas de suelo de plantaciones de uchuva localizadas en Los Andes colombianos de los Departamentos de Cundinamarca y Boyacá, durante las temporadas seca (0-20 mm/mes) y lluviosa (150-330 mm/mes), para establecer la relación entre las características altitudinales y la diversidad de HFMA. La evaluación de la abundancia de esporas y especies e índices de diversidad evidenció la presencia de 46 especies de HFMA en época seca y 31 en época de lluvias. Esto muestra la alta diversidad de HFMA en los Andes tropicales, con una abundancia entre 20 y 120 esporas 10 g⁻¹ de suelo en temporada de lluvias y entre 127 y 1531 esporas 10 g⁻¹ de suelo en época seca.

Palabras clave: diversidad, riqueza, Andes Colombianos, Glomeromycota.

Introduction

One of the symbiotic associations with the greatest geographic and botanical distributions is the interaction between arbuscular mycorrhizal fungi (AMF), which covers more than 80% of plant species and is found in a great diversity of ecosystems (Brachmann and Parniske, 2006; Bonfante and Genre, 2008). A bi-directional exchange of nutrients is the basis of this association (Breuninger and Requena, 2004; Genre *et al.*, 2005, 2008), which favors plant nutrition and plant tolerance to biotic or abiotic stress (Van der Heijden and Sanders, 2002; Smith and Read, 2008; Smith and Smith, 2011). To understand this complex

symbiotic association, it is necessary to know the environment in which it is developed and the factors that affect the establishment and functioning of AMF communities. Many factors affect the dynamics of this symbiosis, such as geophysical factors (i.e. altitude) or the different stages of plant development that influence the composition of AMF communities (Husband *et al.*, 2002a, b; Oehl *et al.*, 2006; Senés *et al.*, 2014). Senés *et al.* (2014) evaluated the composition of AMF communities in the Peruvian Andes in potato crops at four different altitudes from 2,658 to 4,075 m a.s.l., and they found a direct relationship between altitude and the community composition of AMF species. Some factors that affect the structure, diversity and distribution of AMF

Received for publication: 3 August, 2018. Accepted for publication: 3 December, 2019

Doi: 10.15446/agron.colomb.v37n3.74008

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communities are soil microorganism populations (Garbaye, 1994; Gehring and Whitham, 2002), agricultural practices, such as logging, burning, use of fertilizer and tillage (Jansa *et al.*, 2003), and indirectly microclimate and topography (Johnson, *et al.*, 1992; Kernaghan, 2005).

Cape gooseberry (*Physalis peruviana* L.) belongs to the Solanaceae family and is distributed in the wild highlands of the South American Andes (Pérez, 1996; Trillos *et al.*, 2008), its place of origin (Morton, 1987; Bartholomäus *et al.*, 1990; Medina, 1991; Criollo and Ibarra, 1992; Chia *et al.*, 1997). In Colombia, the optimal conditions for its cultivation include altitudes between 2300 and 2800 m a.s.l., temperatures between 13 and 17°C, relative humidity between 70 and 80%, and precipitation between 600 and 1100 mm/year (Fischer, 2000; Espinal *et al.*, 2005). The interest in working with this plant species is based on the fact that the plant is native to the Andes and has a wide range of edapho-climatic adaptations (Fischer, 2000) that may be related to its ability to associate with AMF.

The objective of this study was to evaluate AMF diversity in Andean soils cultivated with cape gooseberry to determine if the composition of AMF communities is modulated by altitude. The possible effect of altitude on the establishment of AMF communities is fundamental for understanding symbioses and finding behavioral patterns in AMF communities that would allow a better management of agroecosystems.

Materials and methods

Soil sampling

Sampling was performed on an altitudinal transect between 1500 and 3000 m a.s.l. Composite samples of cape gooseberry rhizospheric soils were collected at 13 sites. At each site 4 kg (15 subsamples) of soils were collected at a depth of 0-20 cm, in duplicate, for physicochemical and AMF analysis (Tab. 1). From each sample, 200 g were taken for analysis of the abundance and diversity of AMF spores, in duplicate. The remaining soil was stored to be used as inoculum or as a source of spores for a plant tramp assay. Two samplings were carried out: one in the rainy season (150-330 mm/month) and the other in the dry season (0-20 mm/month).

Isolation and identification of AMF spores

For each sample, the number of spores 10 g⁻¹ of soil was determined according to the methodology described by Gerdermann and Nicholson (1963), with modifications. The percentage of AMF colonization was estimated using the Trypan Blue differential staining methodology by Phillips and Hayman (1970) and Giovannetti and Mosse (1980) with modifications. The taxonomic classification of the AMF was performed at the species level based on the morphology of the spores. The spores were isolated and arranged in sheets with polyvinyl lactic acid-glycerin (PVLG) (Koske and Tessier, 1983) and, in some cases, with a mixture (1:1 v/v) of PVLG with Melzer (Brundrett *et al.*,

TABLE 1. Sampling sites, altitude, soil taxonomy, soil pH, organic matter (OM) and phosphorus (P) content in Cundinamarca and Boyaca.

Location	Nomenclature	Taxonomic classification	Altitude (m a.s.l.)	pH		OM (%)		P (mg kg ⁻¹)	
			R	D	R	D	R	D	
Cundinamarca	Zipacon	Z1	2675	5.9	5.1	16.0	11.15	24.3	49.0
		Z2	2627	6.0	5.1	17.8	13.15	13.8	39.0
	Granada	G1	2380	5.9	5.18	16.6	13.63	32.6	63.1
		G2	2302	5.5	5.18	22.5	14.34	54.0	50.4
		G3	2250	5.5	5.15	14.7	12.68	12.0	30.3
		G4	2000	5.4	5.00	8.3	9.34	5.0	30.4
	Mosquera	M1	2560	5.6	5.10	6.1	14.22	35.0	53.0
Boyaca	Alban	A	1639	6.0	5.14	12.8	12.92	3.6	70.1
	Combita	C1	2869	4.9	5.3	7.1	14.40	32.7	53.1
		C2	2930	5.0	5.21	8.6	14.60	62.4	62.2
		C3	2750	5.2	5.2	10.7	14.46	15.8	36.8
	Arcabuco	A1	2575	5.6	5.07	8.3	12.58	9.4	81.8
		A2	2636	5.0	5.11	9.4	11.97	19.6	68.3

R: Rainy, D: Dry.

1994). The isolated and identified spores corresponded to the two sampling periods, dry season (<20 mm/month) and rainy season (150-350 mm/month). The classification codes of Schenck and Pérez (1990) and INVAM (International Culture Collection of Vesicular Arbuscular Mycorrhizal Fungi (<http://invam.caf.wvu.edu/cultures/cultsearch.htm>)) were used, along with scientific publications as support for the genus or species classification (Morton and Benny, 1990; Blazkowski, 1991; Morton and Redecker, 2001; Schüßler *et al.*, 2001; Oehl and Sieverding, 2004; Walker and Schüßler, 2004; Blaskowski *et al.*, 2006, 2008; Sieverding and Oehl, 2006; Palenzuela *et al.*, 2008; Alves Da Silva *et al.*, 2009; Oehl *et al.*, 2008, 2010, 2011 a, b, c, d; Goto, *et al.*, 2011; Redecker *et al.*, 2013).

Diversity index

Density (DE), richness (R), relative abundance (RA), isolation frequency (IF), Shannon-Wiener diversity index (H'), uniformity index (E), Simpson dominance index (D) and Simpson-Gini diversity index (Y) were used to determine AMF diversity in each sample and between all 13 samples collected. Indices were applied at the species level (Franken-Snyder *et al.*, 2001; Zhang *et al.*, 2004; Rodríguez *et al.*, 2005; Zhao and Zhao, 2007; Kwasna *et al.*, 2008; Chiffot *et al.*, 2009).

Statistical analysis

Correlations were performed between spore diversity, abundance and richness of species. Multiple regressions were used for the diversity indexes and abundance and richness variables, as well as correlations between diversity variables, using the SAS program, version 10.

Results and discussion

AMF Communities

The presence of plant-AMF symbiotic associations was measured as percentages of colonization of cape gooseberry roots and the total number of spores present in the rhizosphere of the plant to verify the interaction of these AMF communities with the plant.

The results showed that the highest percentages of colonization occurred during the rainy season for most municipalities (Fig. 1), except for G1, A2 and A, with values between 7.4 and 68.5%. Municipalities G4, A1, C3 and G2 were noted for having a higher percentage of colonization, and lower values were seen in G1, A2 and Z2. In the dry season, the colonization range was between 2 and 22%. The higher values were recorded in G1, G4, A and A2, and the lowest were seen in G3, C1 and Z2 (Fig.1). In all samples evaluated, the

presence of AMF associated with roots of cape gooseberry plants was registered, independent of colonization rates, demonstrating that it is a mycotrophic species.

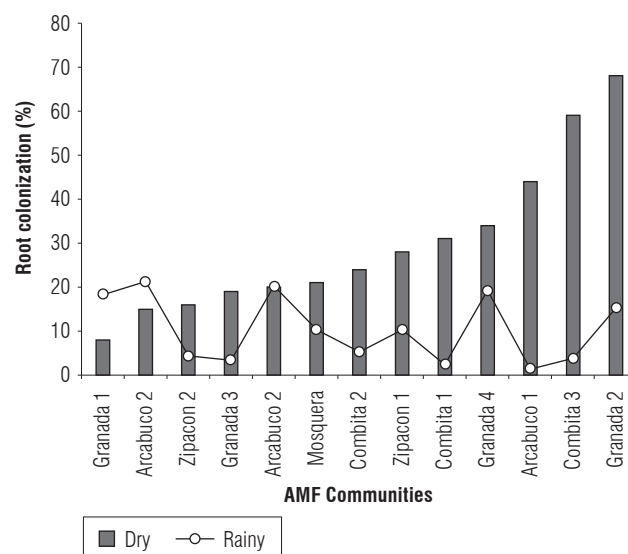


FIGURE 1. Natural colonization levels (%) of cape gooseberry roots by AMF at two sampling seasons, dry and rainy.

The number of spores varied between 20 and 120 spores 10 g^{-1} of soil during the rainy season. The higher spore number values were seen in municipalities A and C1, and the smallest amount was recorded in Z1. However, the dry season presented the highest spore values, between 170 and 1531 spores 10 g^{-1} of soil, in G3 and G4, respectively (Fig. 2).

During the rainy season, a negative correlation was observed in the number of spores, since the highest number of spores was recorded at the lowest altitudes. During the dry season, the correlation was positive, since a greater number of spores was observed at higher altitudes. These results agree with publications that show how, under water stress conditions, AMF sporulate by increasing the production of spores 10 g^{-1} of soil (Caproni *et al.*, 2003; Roveda *et al.*, 2012; Pagano *et al.*, 2013).

Taxonomic identification of AMF

A total of 46 species, grouped in 16 genera, 11 families and 5 orders, were taxonomically identified, illustrating the great diversity of AMF found in the Colombian Andean soils. The distribution of species and genera of AMF identified in each of the evaluated locations during dry and rainy seasons can be seen in Table 2. The results show 23 species for Alban, 12 for Mosquera, 25 for Zipacon and 35 for Granada, the latter presenting the greatest diversity of AMF species. Three types of spores that had not previously been described were found: two of them corresponded to the genus *Glomus* and the other was found from the genus

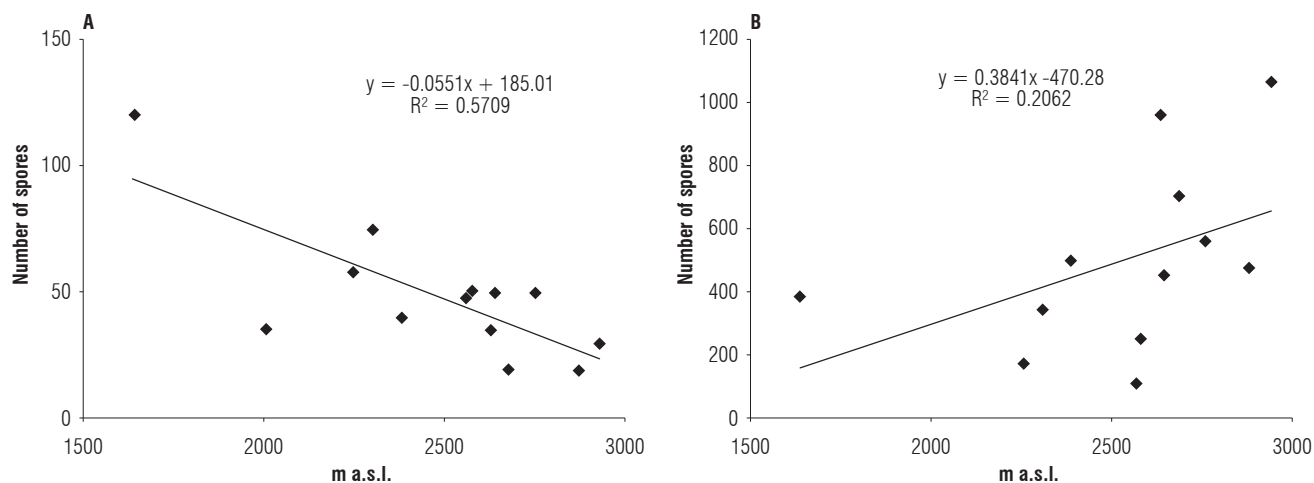


FIGURE 2. Relationship between altitude and number of AMF spores grown with cape gooseberry in the provinces of Cundinamarca and Boyaca. a) Rainy season and b) dry season.

Acaulospora (Personal communication from F. Oehl and E. Sieverding), which were isolated from the soils of Granada, Zipacon and Combita. In the altitudinal transect (1636–2675 m a.s.l.) of the province of Cundinamarca, between 4 and 18 species were found in the soils during the rainy season and between 18 and 33 were found in the dry season in consolidated zones of cape gooseberry production (more than 20 years). For the altitudinal transect of the province of Boyaca (2572 to 2869 m a.s.l.), between 6 and 13 species were identified in the rainy season and between 11 and 17 in the dry season, in a zone that is considered as new for cape gooseberry cultivation (between 5 and 7 years).

It is important to point out that five AMF species were not identified in soils of the consolidated zones of cape gooseberry production in Cundinamarca: *Acaulospora* sp2, *A. scrobiculata*, *A. rehmi*, *A. colombiana* and *Paraglomus laccatum*. In a recent crop production in the province of Boyaca, 13 AMF species were not identified: *Glomus* sp1, *Rhizoglomus fasciculatum*, *R. proliferum*, *Funnelformis geosporum*, *F. coronatus*, *F. monosporum*, *Septoglomus constrictum*, *Claroideoglomus walkeri*, *Acaulospora longula*, *A. morrowiae*, *Acaulospora* sp1, *Intraspora* sp. and *P. occultum*. Mahdai *et al.* (2017) reported a higher density of AMF spores associated with a coffee crop (256 spores 100 g⁻¹ soil) at higher altitudes (1400 m a.s.l.) as compared to lower altitudes (700 m a.s.l.) in the mountains of Saudi Arabia.

AMF species

The total number of species in the rainy season was 31, while in the dry season it was 46. Regardless of the sampling time, the highest number of species was observed in sample G4, followed by A, while the lowest values were observed in G1 and G3.

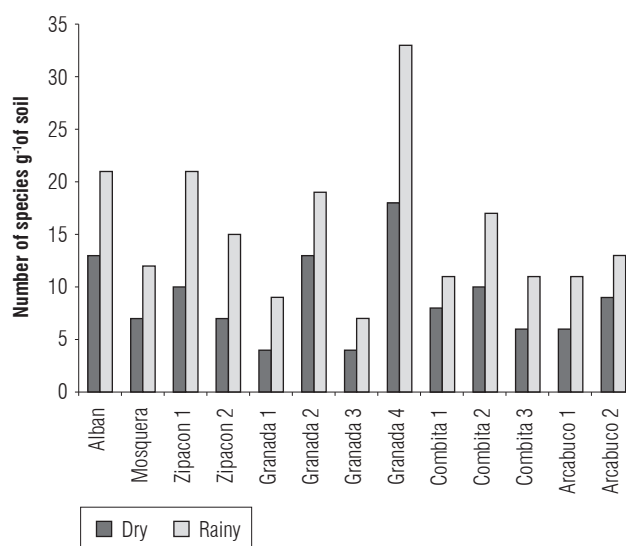


FIGURE 3. Number of AMF species (10 g⁻¹ of soil) identified in the cape gooseberry crop in Cundinamarca and Boyaca at two sampling seasons, dry and rainy.

At the seasonal level, a high diversity in AMF communities was also observed, which was expressed as a higher number of spores, richness and relative abundance of species in the dry season compared to the wet season in which higher levels of root colonization were detected. Similar results have been obtained by several authors in the dry season (Pagano *et al.*, 2013; Guadarrama *et al.*, 2014; Rabelo *et al.*, 2014) as well as in the wet season (Guadarrama and Álvarez-Sánchez, 1999). The seasonal variation of the communities was evident by the differences found in the number of species between the dry (46) and rainy (31) seasons, of which 32.6% of the species were not isolated in the rainy season. These results are in agreement with previous reports on seasonal variations of AMF communities

TABLE 2. Distribution of AMF genus and species in soil samples cultivated with cape gooseberry in an altitudinal transect between 1636 and 2869 m a.s.l. (R: Rainy, D: Dry).

Location	Cundinamarca																Boyaca										
	ALBAN		MOSQUERA		ZIPACON				GRANADA				COMBITA				ARCABUCO										
	A		M		Z1		Z2		G1		G2		G3		G4		C1		C2		C3		A1		A2		
Sample season	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	
Species																											
Glomus macrocarpum	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Glomus brohuttii		*			*	*			*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Rhizoglomus intraradices	*	*	*	*	*	*	*	*			*	*			*	*			*				*	*	*	*	
Rhizoglomus aggregatum															*						*			*			
Rhizoglomus irregulare		*				*																		*			
Glomus sinuosum		*																*									
Glomus microcarpus		*		*		*	*	*	*	*			*	*	*	*	*	*	*	*	*	*	*			*	
Glomus sp1					*	*	*	*			*	*			*	*											
Glomus sp 2						*					*				*				*								
Rhizoglomus fasciculatum						*					*				*												
Rhizoglomus proliferus	*	*									*	*			*												
Funnelliformis mosseae	*	*	*	*				*			*	*			*	*	*	*	*	*				*	*	*	
Funnelliformis geosporus	*			*	*	*									*												
Funnelliformis coronatus						*									*												
Funnelliformis monosporus		*				*									*												
Simioglomus hoi		*																			*		*				
Septoglomus constrictum															*												
Clareidoglomus clarioideum	*	*	*	*		*	*	*		*	*	*		*	*	*	*	*	*	*	*	*	*		*	*	*
Clareidoglomus etunicatum		*				*		*		*	*	*		*	*	*	*	*	*	*		*		*	*	*	
Clareidoglomus drummondii				*												*	*										
Claroideoglomus luteum				*			*	*			*	*		*	*	*			*								
Claroideoglomus walkeri											*																
Diversispora celata	*														*									*	*	*	
Diversispora versiformis															*										*	*	
Entrophospora infrequens					*	*		*		*	*	*		*	*			*	*	*	*	*	*	*	*	*	*
Entrophospora nevadensis					*		*				*			*	*			*	*	*	*	*	*	*	*	*	
Acaulospora longula											*			*	*												
Acaulospora morrowiae					*	*	*	*							*												
Acaulospora sp 1		*									*				*												
Acaulospora sp 2																								*	*	*	
Acaulospora sp 3							*				*			*	*	*	*	*	*	*							
Acaulospora scrobiculata	*	*		*												*	*										
Acaulospora rehmi	*	*																							*	*	
Acaulospora spinosa															*				*	*	*	*	*	*	*	*	
Acaulospora denticulata							*	*		*	*		*	*	*							*	*	*	*	*	
Kuklospora colombiana																		*	*	*	*	*	*	*	*	*	
Pacispora sp	*	*	*	*		*		*						*	*	*	*	*	*	*	*	*	*	*	*	*	
Scutellospora nodosa	*	*					*		*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	

CONTINUATION TABLE 2. Distribution of AMF genus and species in soil samples cultivated with cape gooseberry in an altitudinal transect between 1636 and 2869 m a.s.l. (R: Rainy, D: Dry).

Location	Cundinamarca																Boyaca										
	ALBAN		MOSQUERA		ZIPACON				GRANADA				COMBITA				ARCABUCO										
	A		M		Z1		Z2		G1		G2		G3		G4		C1		C2		C3		A1		A2		
Sample season	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	R	D	
Species																											
Racocetra tropicana		*		*	*							*	*			*	*					*					
Cetospora pellucida	*	*								*		*				*	*			*							
Intraspora sp		*	*		*	*										*	*					*					
Archeospora trappei						*	*												*								
Ambispora sp	*	*															*								*		
Ambispora appendicula						*	*												*								
Paraglomus occultum						*			*							*											
Paraglomus laccatum																			*								
Species	13	21	7	12	10	21	7	15	4	9	13	19	4	7	18	33	8	11	10	17	6	12	6	11	9	13	

(Courty *et al.*, 2008; Davey *et al.*, 2012; Bonfim *et al.*, 2013; Guadarrama *et al.*, 2014). Some authors have reported similar effects of the rainy season on root colonization to those obtained in the present study (Rabatin, 1979; Allen, 1983; Lodge, 1989; Miller, 2000; Miller and Sharitz, 2000), while other authors observed no effect (Bryla and Duniway, 1997; Ming and Hui, 1999). The presence of spores and the different levels of root colonization showed the existence of an active interaction between AMF and cape gooseberry plants in the Andean soils. The dry season increased the number of spores.

In the present study, a high number of spores was found in 10 g of soil, both in the rainy season (20-120 spores g⁻¹) and dry season (170-1531 spores g⁻¹). These values were higher than those reported by Jayachandran and Shetty (2003) for the wetlands of the Everglades (18-124 spores g⁻¹) and by Lopes *et al.* (2013) in humid forests and pastures in Brazil (2.5 and 77.9 spores g⁻¹), where the number of species varied between 31 and 46 for the rainy and dry seasons, respectively. These values are similar to those reported in the Chilean Andes (39 species) (Castillo, 2005; Castillo *et al.*, 2005), in the Amazonian-pasture forest in Brazil (36 species) (Lopes *et al.*, 2013), and in the forests of Mexico (37 species) (Violi *et al.*, 2008). A lower diversity of species has been reported in the dunes in Brazil (25 species) (Stümer *et al.*, 2013), forests (13-29 species) and pasture lands (18 species) of Mexico (Gavito *et al.*, 2008; Fernandes *et al.*, 2009; Guadarrama *et al.*, 2014), tropical humid forests of Colombia (18 species) (Peña-Venegas *et al.*, 2007), forests in Brazil (Aidar *et al.*, 2004; Zandavalli *et al.*, 2008; Moreira *et al.*, 2009; Bonfim *et al.*, 2013; Rabelo *et al.*, 2014) and in

general in various studies that have demonstrated a range of 12-26 species 10 g⁻¹ of AMF (Wilson *et al.*, 1992; Wang *et al.*, 2008).

The high number of spores identified in the present study, associated with high species diversity from the ecological point of view, is a reflection of the history of the establishment of communities in a specific environment. It can be considered a reserve bank that may contains AMF adapted to various environmental conditions with the potential to associate with different hosts at a particular moment in time, with different growth strategies and adaptive mechanisms to the dynamic changes of the environment (Hijri *et al.*, 2006; Oehl *et al.*, 2006; Moebius-Clune *et al.*, 2013). From the agronomic point of view, the high diversity represents the high potential presented by the Andean ecosystems for the establishment of symbiotic associations. Although this was an analysis of agroecosystems with semi-intensive use, AMF diversity was high, contrary to that reported by different authors on the reduction of AMF diversity in agricultural systems (Mason *et al.*, 1992; Munyanziza *et al.*, 1997; Cowden and Peterson, 2009). This study verified the presence of “generalist” species (according to Oehl *et al.*, 2003). These are AMF species that can be isolated under different soil and climatic conditions, in contrast to “specialist” species that only occur under specific soil or climatic conditions. Generalist species can be isolated under different edaphic conditions and at different altitudes, showing their high tolerance for diverse soil and climatic conditions, including: *G. macrocarpum*; *G. brouhettii*; *G. microcarpum*, *C. claroideum*, *C. luteum*, *E. infrequens* and *E. nevadensis*. The existence of “generalist”

species has been reported by different authors (Oehl *et al.*, 2003, 2010; Castillo, 2005; Öpik *et al.*, 2006; Guadarrama *et al.*, 2007; Stümer and Siqueira, 2008). *Glomus macrocarpum* has been reported as a “generalist” species in several ecosystems and agroecosystems (Oehl *et al.*, 2004; Castillo *et al.*, 2005; Oliveira Freitas *et al.*, 2014; Rabelo *et al.*, 2014). Guadarrama *et al.* (2014) identified 10 species considered as generalist, while Rabelo *et al.* (2014) identified 4 generalist species among 40 identified species.

In the case of fungi of the genus *Glomus*, their predominance in diverse edaphoclimatic conditions was reported in several plant species (Gavito *et al.*, 2008; Wang *et al.*, 2008; Schnoor *et al.*, 2011; Boonlue *et al.*, 2012; Mahdhi *et al.*, 2017). The high presence of species of the genus *Glomus* was probably associated with their high sporulation capacity favoring the colonization of roots in different environments, especially in environments with agronomic operations (Caprioni *et al.*, 2003; Rabelo *et al.*, 2014). This quality results in the species of this genus being more abundant in manmade systems, especially in agroecosystems like the one in the present study, where fungi of the order Glomerales and specifically species of the genus *Glomus* showed wide dispersion and high abundance in soils of the Colombian Andes.

Other species of fungal genera, such as *Acaulospora* and *Glomus*, predominate in the Chilean Andes (Castillo, 2005; Castillo, *et al.*, 2005), showing similarity to those found in this study in Colombia, possibly because of the affinity of some of the edaphic characteristics, such as the presence of volcanic ash (allophane), soil acidity, low P contents in the soil and high organic matter (OM), although they differ in altitude and latitude. In contrast, in studies in the Peruvian Andes Sénes *et al.* (2014) found that *Funneliformis mossseae* was the most predominant species in both the soil and root of potato plants. This species is an early stage colonizer and seems to be adapted to frequent soil disturbances, such as contamination by hydrocarbons, fungicides, heavy metals, salinity, drought and cold climates (Abdel-Azeem *et al.*, 2007; Huang *et al.*, 2007; Zarei *et al.*, 2010; Hassan *et al.*, 2011; Krishnamoorthy *et al.*, 2014).

The increment of the available phosphorus in the soil produced a reduction of AMF root colonization, which was previously reported by Jansa *et al.* (2009) and Selvam and Mahadevan (2002). Low levels of phosphorus in the soil favor and promote the establishment and development of symbiosis, and therefore, AMF multiplication. Phosphorus deficiency in the soil is one of the main activators of recognition signals between plants and HFMA (Ramírez

and Rodriguez, 2010). It was found that 32% of AMF species, especially Glomerales, were favored by increasing the contents of this element in the dry season, while 17.4% were negatively affected in the wet season. This type of interaction has been previously reported (Jeffries *et al.*, 1988; Sieverding, 1991; Oehl *et al.*, 2003; Landis *et al.*, 2004; Uhlmann, *et al.*, 2004; Bashan *et al.*, 2007), showing correlations between phosphorus contents and richness and abundance of AFM species. There are reports of the presence of HFMA in soils with high phosphorus contents (Davidson and Christensen, 1977; Allen and MacMahon, 1985), showing the great versatility of adaptation that AMFs have. The soils of the Andean region have high phosphorus fixation, so at relatively high phosphorus levels, but with low availability, the abundance of certain HFMA species can be favored.

The tolerance of some species to edaphoclimatic conditions is a desirable characteristic of species considered “generalist” since it allows species to be easily adapted to changes in the environment. This is a common situation in agroecosystems, where the edaphic environment is modified by cultural practices associated with crops. In addition, the identification and use of “generalist” species can facilitate the establishment of symbiosis under different conditions in cape gooseberry because of the high mobility of the crop as an escape mechanism for diseases. The high frequency of isolates along the altitudinal transect of some species showed the high adaptability of these species to conditions of biotic stress and strong changes in agroecosystems from practices such as fertilizer applications (Sturmer and Siqueira, 2008; Zangaro and Moreira, 2010). In this study, species such as *G. macrocarpum* were seen under rainfall conditions below 20 mm/month as well as with rainfall between 150 and 300 mm/month, while other species only occurred in the dry season.

In the case of AMF species considered as “specialists”, because their presence is associated with specific conditions (climate, soil or both), it was found that *R. aggregatum*, *R. irregulare*, *G. sinuosum*, two species of *Glomus* sp., *F. coronatus*, *F. monosporum*, *S. hoi*, *S. constrictum*, *C. walkeri*, *E. nevadensis*, *Acaulospora* sp, *P. occultum* and *P. laccatum* were exclusively associated with climate, while *S. constrictum*, *C. walkierii*, *Acaulospora* sp2 and *P. laccatum* were associated with the soil type, specifically soils cultivated with *Physalis peruviana*. These AMF characteristics, which present a “specialist” behavior for soil types, climate and moisture regimen, have been reported in AMF community analysis studies in tropical ecosystems, such as humid forests and semi-arid zones of Brazil and Africa, in tropical

savannas and the Swiss Alps (Landis *et al.*, 2004; Uhlmann *et al.*, 2004; Lekberg *et al.*, 2007; Oehl, *et al.*, 2010). Although they are not ecologically similar to the Colombian Andes, they showed a trend of AMF behavior. Rabelo *et al.* (2014) identified 26 intermediate and 19 exclusive species or specialists in communities composed of 40 species. The identification of “specialist” species allows species to adapt to specific stresses, which can occur both in space and time because of anthropic intervention or global or local phenomena, such as climate change and variation.

Relative abundance and species richness of AMF

The relative abundance exhibited higher values in the dry season than in the rainy season, related to the greater number of species collected and identified at that time. A relative abundance of more than 71% was obtained for the sample from G4, whereas for that same sample in the rainy season, only 60% was reached. The samples from G1 and G3 had the lowest relative abundances. It is evident that in C1, A2 and G2, the relative abundance of the species was higher in the rainy season, while in the other samples it was always higher in the dry season (Fig. 4).

Species richness varied between 1.57 and 8.30 in the dry season and between 0.87 and 4.95 in the rainy season, reflecting the differences between the two sampling periods. The highest species richness values were observed in the samples from A and G4, and the lowest values in G1 and G3.

Frequency of species isolates in soil samples

In the rainy season, the frequency of isolation ranged between 7.6% from isolated species in a sample to 100%

of isolated species in all samples. According to Oehl *et al.* (2003), this analysis allows the determination of “generalist” species (15%), such as *G. macrocarpum*, *G. brohutii*, *C. claroide*, *C. etunicatum*, *G. microcarpum*, *G. intraradices* and *E. infrequens*, which were isolated from a high number of samples in rainy and dry seasons with a clear predominance of *Glomus* species in terms of isolation frequencies. The species that can be considered as “specialists” corresponded to 8.7% of the species: *Septoglomus constrictum*, *Claroideoglomus walkierii*, *Acaulospora* sp2 and *Paraglomus laccatum*, as they were isolated in a single sample and in one single season.

Of the total species 45.6% showed the highest frequency of isolation in the dry season (21), and only 4 showed higher frequency in the rainy season (*Rhizoglomus proliferum*, *A. longula*, *A. rehmii* and *Archeospora tropeii*). We observed that only 4 species (*G. macrocarpum*, *Glomus* sp2, *Diversispora celata* and *Kuklospora colombiana*) had the same frequency of isolation in the dry and rainy seasons, compared to the total species isolated in each season.

Only 32.6% of the species (15) were isolated in the dry season: *Rhizoglomus agregatum*, *R. irregulare*, *G. sinuosum*, two species of *Glomus* sp, *F. coronatus*, *F. monosporum*, *Simioglomus hoi*, *S. constrictum*, *C. walkeri*, *E. nevadensis*, *Acaulospora* sp, *P. occultum* and *P. laccatum*. These were “specialists” for the wet regime rather than for soil type or altitude. According to the scale proposed by Zhang *et al.* (2004), the dominant species in the rainy season were *G. macrocarpum*, *G. brohutii*, *G. intraradices* and *C. claroideum*, and in the dry season *G. macrocarpum*, *G. brohutii*,

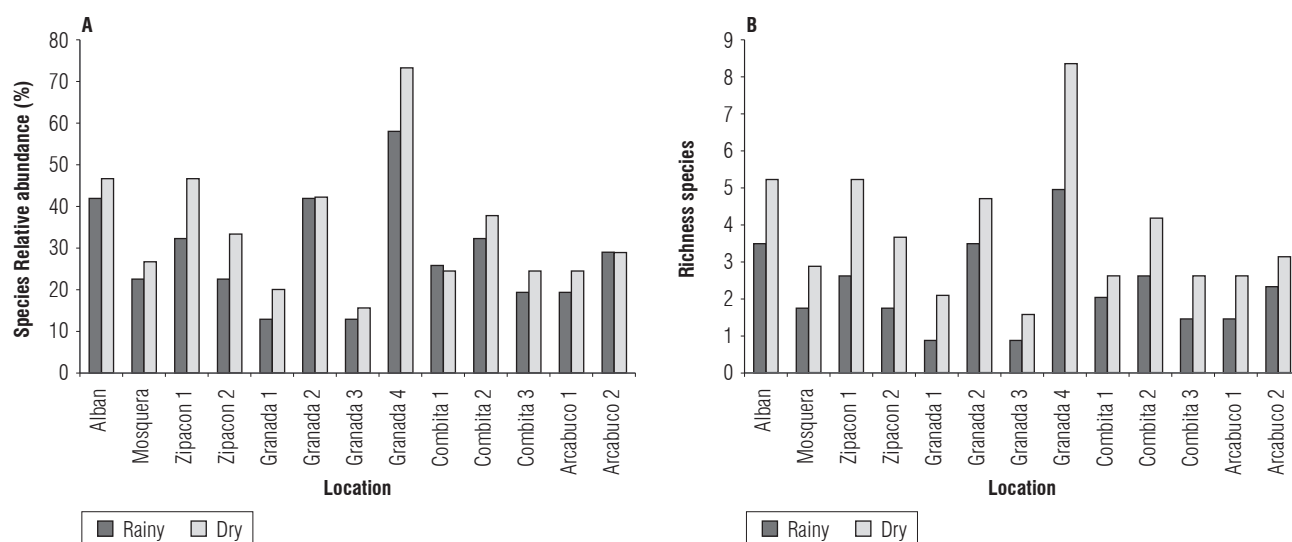


FIGURE 4. Relative abundance (a) and richness (b) of AMF species (g^{-1} of soil) in soils cultivated with cape gooseberry in Cundinamarca and Boyaca in rainy and dry seasons.

G. intraradices, *G. microcarpus*, *F. mosseae*, *C. claraideum*, *C. etunicatum*, *E. infrequens*, *E. nevadensis*, *Pacispora* sp. and *Scutellospora* sp. The rare species in the rainy season were *C. drummondii* and *Ambispora* sp., and for the dry season, they were *S. constrictum*, *C. walkeri*, *A. longula*, *Acaulospora* sp2, *A. rehmi*, *Archeospora troppei*, *Ambispora appendicula* and *P. laccatum*. Regardless of the season, *G. macrocarpum*, *G. brohuttii*, *G. intraradices* and *C. claraideum* were dominant, and most of the rare species in the

dry season were not isolated in the rainy season, except for *A. longula*, *A. rehmi*, *Archeospora troppei* and *Ambispora appendicula*.

Figure 5 shows the abundance of spores for each of the identified species in each community. We determined that although a species may be present in all evaluated communities, its abundance can vary widely.

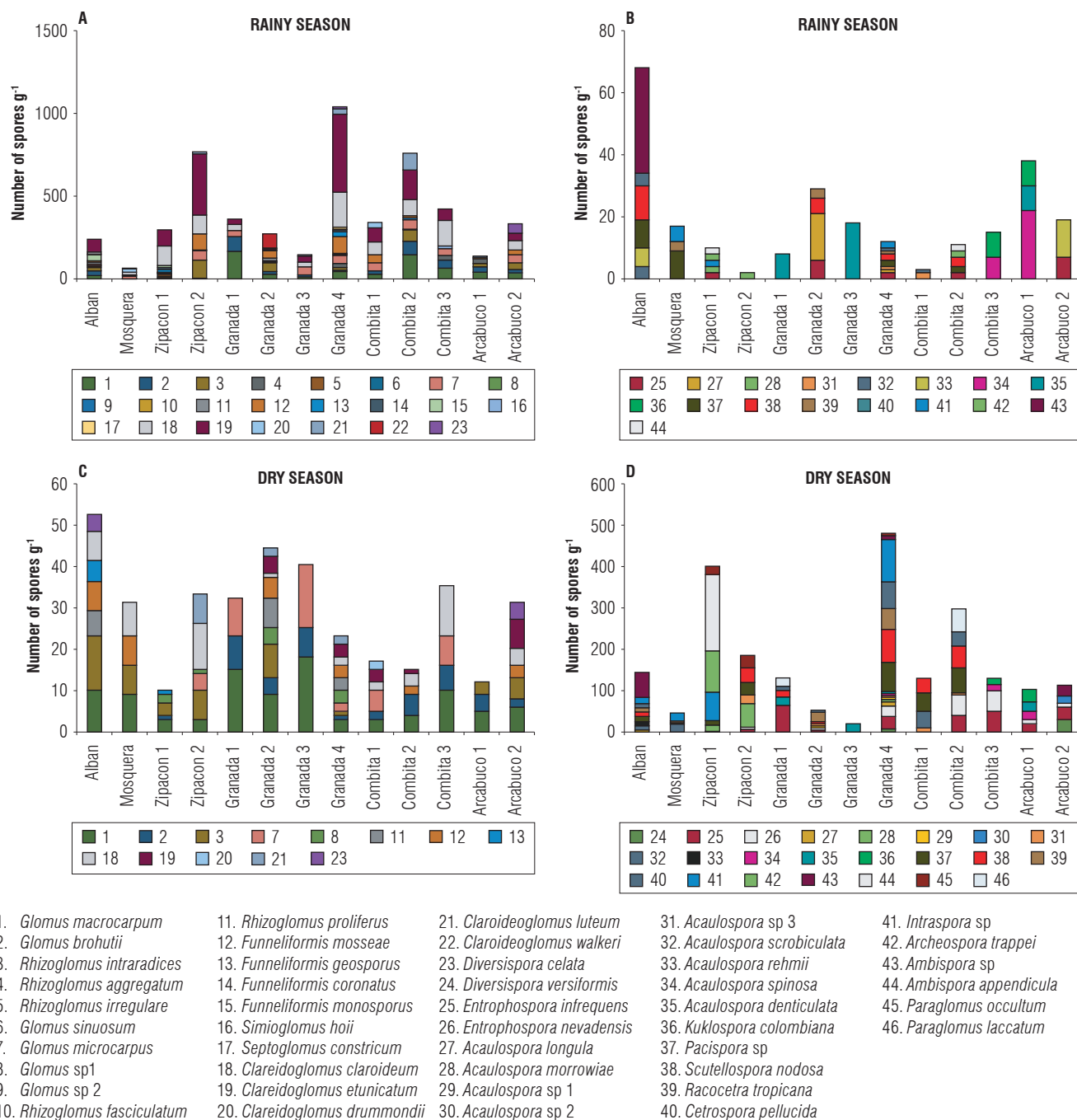


FIGURE 5. Abundance of spores for each of the species identified in the rainy (a and b) and dry (c and d) seasons.

Shannon-Wiener Index (H')

In the rainy season, Shannon-Wiener diversity indexes were found between 1.33 and 2.8, considered as mean values according to Gove *et al.* (1999). The locations G4, A, Z1, C2 and A2 had mean levels of diversity related to the number of species found in the samples (Fig. 6A). In the dry season, the values were similar, with variations between 1.12 and 2.5 with the highest levels of diversity in A2, A1, C2, C1, M, G2 and Z1. It is interesting to observe how in the same location but in a different sampling area the levels of diversity may vary widely either by soil type or agronomic management of the lots.

Uniformity index

This index had a range between 0 and 1, with 1 as the maximum value when all species are present in equal abundance

and it decreases when the dominance extent of a species or morphotype occurs (Hurlbert, 1971).

Two measures of uniformity were considered: between samples and inside each sample. Results are presented in Figure 6 (B and C). In the first case, for the rainy season differences in uniformity between the samples were observed when the identified species had variations between 0.06 in Z1 and 0.82 in G4, representing values of low uniformity for Z1 and high uniformity for G4 in relation to the other sampling sites according to Hurlbert (1971). This indicates that Z1 had few species with high disparity with the other samples. In the dry season, there was greater homogeneity between the samples with values between 0.29 (G4) and 0.65 (A2), showing a more homogeneous distribution of the species. When measuring the uniformity per sample

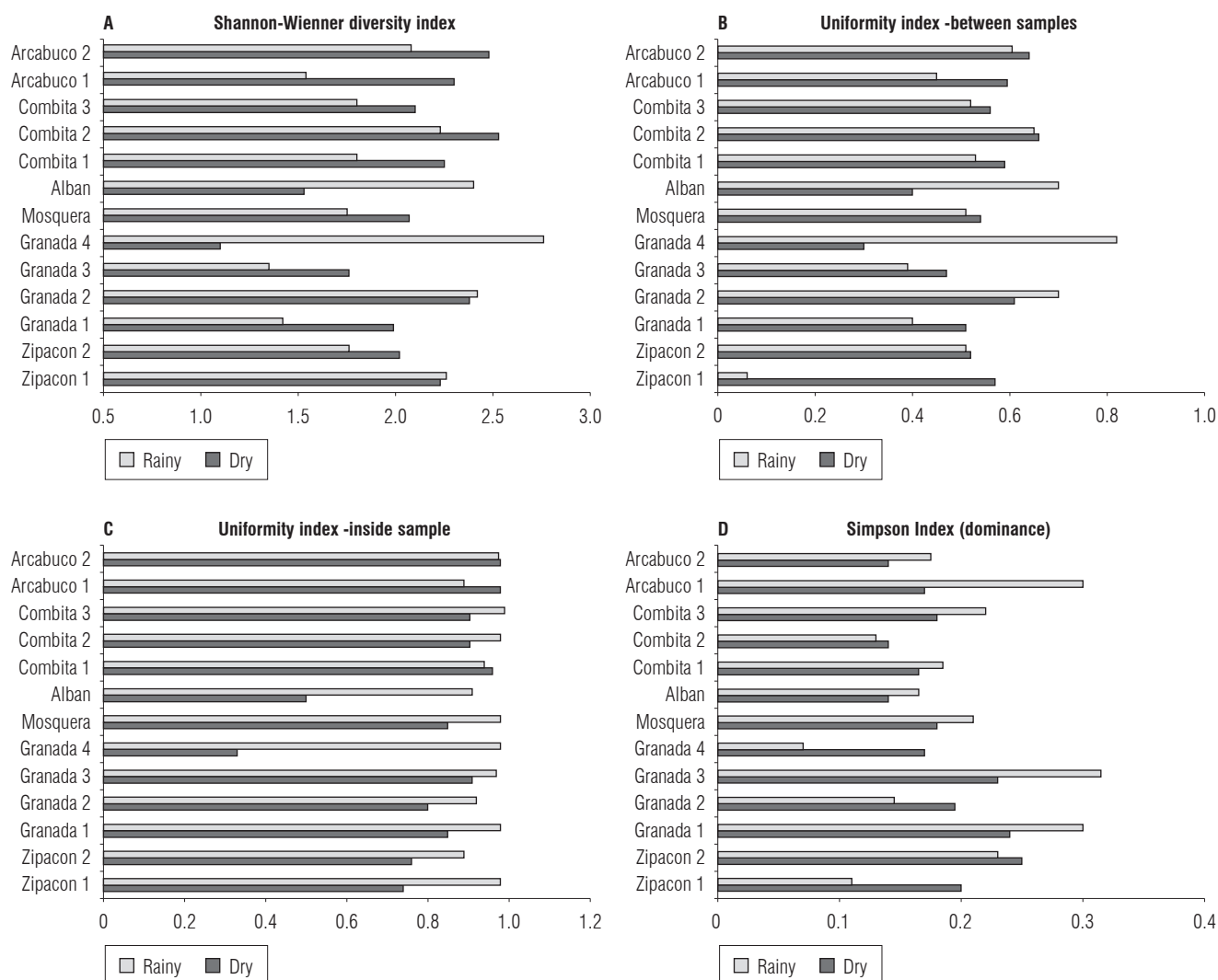


FIGURE 6. Indexes of diversity of AMF species isolated in cape gooseberry in the provinces of Cundinamarca and Boyaca during the rainy and dry seasons. a) Shannon-Wiener Diversity Index; b) Uniformity Index between samples; c) Uniformity Index inside samples and d) Simpson Index (dominance).

(ratio of number of spores to total spores in the sample), in the rainy season, there was a low number of spores the values were very close to 1 in all of the samples reflecting similar values of spores per species in each of the samples. In the dry season, the values were high but with greater variations, with a range between 0.32 in G4 and 0.91 in G3, showing wide variations in the number of spores of each species present in the sample.

Simpson's Dominance Index:

Simpson's Dominance Index shows the highest values for samples G1, G3 and A1 during the rainy season and for Z2, G1 and G3 in the dry season, signifying that these samples had dominant species (Bouza and Covarrubias, 2005). This is consistent with the results of the Uniformity Index since these were the same samples that showed lower uniformity values (Fig. 6D).

The estimated diversity indexes corroborated the hypothesis of high diversity of AMF in these systems, with low-average levels of uniformity between and within the analyzed samples and with species dominance in some of the analyzed communities, especially in those that had a low number of species. The Shannon-Wiener diversity index values recorded for cape gooseberry (1.1 to 2.8) showed that, while the host affects AMF diversity (Vandenkoornhuyse *et al.*, 2002), edaphic conditions and altitude also play an important role. This is evident in the ranges of diversity found in the evaluated altitudinal transect where the variations were mainly environmental and not from the host. However, the host component can be evaluated by comparing the values of the present study with those obtained by Helgason *et al.* (1998) and Tanja *et al.* (2004), who reported ranges from 0.4 in agricultural soils to 2.3 in forests, with higher values in cape gooseberry. It is important to consider the characteristics of the cape gooseberry crop since it is a species that is cultivated in agricultural fields but is also in the process of domestication. Cape gooseberry originated from Andean ecosystems, where the diversity centers of the species are found and has been adapted to these ecosystems with restrictive soil-climatic conditions, possibly through co-evolution processes with AMF. Additionally, these results indicate that the tropical Andes of Colombia are a niche with broad AMF diversity.

The previous results confirm the existence of high AMF diversity in the ecosystems of the tropical Andes. Although only cape gooseberry soils were sampled, the number of AMF species was higher to that identified with a greater variety of hosts as mentioned previously. The identification of "generalist" or "specialist" species is very important for

the establishment of the AMF-cape gooseberry association since this is a "nomadic" crop that changes with location, soil, climate and altitude. Due to this, AMF species with high adaptability to different climatic and altitude conditions may have a greater possibility of establishing symbiosis than those affected by edaphic changes. Knowing the factors that can affect the abundance of species allows the creation of practices that favor the presence of species of interest for an ecosystem or an agroecosystem.

Conclusions

This research contributed to our knowledge of AMF diversity in the cape gooseberry (*Physalis peruviana* L.) production system in the evaluated altitudinal transect (1500-3000 m a.s.l.). It also determined the relationship between diversity, abundance and composition of communities with the characteristics of the soils in which these communities of fungi associated with cape gooseberry plants are established. This is the first time this kind of research has been carried out in the Andes.

The presence of spores and different levels of root colonization showed the existence of an active interaction between AMF and cape gooseberry plants in Andean soils. This high diversity can be considered as a reserve bank of AMF species adapted to the conditions in the Colombian Andes, which will allow the establishment of symbiotic associations for sustainable and competitive agricultural systems.

Acknowledgments

The authors would like to thank Dr. F. Oehl and Dr. E. Sieverding for their assistance in the identification of the AMF, Dr. Ian Sanders for his recommendation for the PhD internship at the Agroscope Research Center in Zurich and the managers of Agroscope, Zurich for their acceptance of the doctoral internship under the direction of Dr. Fritz Oehl.

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