

Mycotrophy of endemic plants of the white sand savannas of Pinar del Río, Cuba

Micotrofía de plantas endémicas de las sabanas de arenas blancas de Pinar del Río, Cuba

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ABSTRACT

The knowledge of mycorrhizal status of plants is very important both from ecological and conservation point of view, even more for endangered species and fragile ecosystems. Thus, this study aimed to evaluate and characterize the arbuscular mycorrhizal status of 20 Cuban endemic species present in the white sand savannas of Sabanalamar, Pinar del Río. Plants were sampled in October 2009 (end of the rainy season) and April 2010 (end of the following dry season). All species were arbuscular mycotrophic, and most of them showed high values of mycorrhizal colonization and visual density. No relationship was detected between seasonality and mycorrhizal association at the ecosystem level. Three plant groups were identified based on mycorrhizal association levels which suggests different strategies of mycorrhizal functioning. The *Paris*-type morphology was identified in all species. The *Arum* and Intermediate types were also present in 35 % and 15 % of the plant species, respectively, and always accompanied by the *Paris*-type. Root colonization by dark septate endophytes, fine endophyte and ectomycorrhiza were also observed in 19, seven and one species, respectively. This work contributes to the knowledge and characterization of the arbuscular mycorrhizal status of Cuban endemic species, as well as the reporting of other fungal root associations. Colonization by fine endophyte in Cuban plants is recorded for the first time.

Keywords: arbuscular mycorrhiza, *Arum-Paris continuum*, fungal root endophytes, mycorrhizal functioning, sandy soils

RESUMEN

El conocimiento del estatus micorrízico de las plantas es muy importante tanto del punto de vista ecológico como conservacionista, aún más para especies amenazadas y ecosistemas frágiles. Por tanto, este estudio tuvo como objetivo evaluar y caracterizar el estatus micorrízico arbuscular de 20 especies endémicas cubanas presentes en las sabanas de arenas blancas de Sabanalamar, Pinar del Río. Las plantas fueron muestreadas en octubre del 2009 (final de la estación lluviosa) y en abril del 2010 (final de la estación seca siguiente). Todas las especies resultaron micrótrofas arbusculares, y en su mayoría con altos valores de colonización micorrízica y densidad visual. No se detectó relación entre la estacionalidad y la asociación micorrízica a nivel de ecosistema. De acuerdo al grado de asociación micorrízica se identificaron tres grupos de plantas, lo cual sugiere diferentes estrategias de funcionamiento micorrízico. La morfología tipo-*Paris* se identificó en todas las especies. Las morfologías tipo-*Arum* e Intermedia se identificaron en el 35 % y 15 % de las especies vegetales, respectivamente y siempre acompañadas del tipo-*Paris*. Se observó además, la colonización por endófitos oscuros septados, endófito fino y ectomicorriza en 19, siete y una especie, respectivamente. Este trabajo contribuye con el conocimiento del estatus micorrízico arbuscular de especies endémicas cubanas, así como al registro de otras asociaciones fúngicas. Se registra por primera vez la colonización por endófitos finos en plantas cubanas.

Palabras clave: micorrizas arbusculares, *continuum Arum-Paris*, endófitos fúngicos de raíz, funcionamiento micorrízico, suelos arenosos

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INTRODUCTION

Over a century, an important proportion of mycorrhizal research has focused on identifying mycorrhizal association of plant species (Brundrett 2009). It is estimated that more than 80 % of plant species are mycorrhizal and about 70 % are arbuscular mycotrophic (Brundrett & Tedersoo 2018, Soudzilovskaia & al. 2020).

Arbuscular mycorrhiza (AM), the most common type of mycorrhiza, is a symbiotic association between roots of a wide variety of plants and obligate symbiotic fungi of the phylum *Glomeromycota* (Schüßler & al. 2001, Tedersoo & al. 2018). This symbiosis is biotrophic, normally mutualistic and largely

based on the bidirectional nutrient transfer between both symbionts, sometimes complemented by additional benefits for plants, such as drought and disease tolerance (Smith & Read 2008).

Based on the internal morphology of the plant-fungus association, arbuscular mycorrhiza has been classified into *Arum*-type and *Paris*-type, which represent the extremes of the structural continuum of AM symbiosis. Arbuscules and hyphal/arbusculate coils are the structures that characterize *Arum*-type and *Paris*-type, respectively (Dickson 2004, Dickson & al. 2007). They are the main sites for phosphorus release to the host plant (van Aarle & al. 2005). Dickson & al. (2007) proposed

that a single morphological type prevails within a plant family, however other researchers have asserted that colonization morphology is also influenced by the fungal species and it is not necessarily constant within plant or fungal genera (Cavagnaro & al. 2001, Federmann & al. 2010).

Although AM fungi are the most common fungi associated with plant roots (Brundrett & Tedersoo 2018, Soudzilovskaya & al. 2020), root endophyte communities include diverse fungi that represent a wide range of taxa and ecological roles (Jumpponen & al. 2017). Their record, even not being the main purpose of study, is important and provides the basis for more exhaustive future studies.

Despite efforts to record the root fungal associations, only about 15 000 species had been assessed (Soudzilovskaya & al. 2020), remaining the mycorrhizal status of numerous plant species of many habitats still unknown. On the other hand, there are still no standardized criteria for the diagnosis of mycorrhizal status of plants species, though the recording of fungal structures present and quantification of fungal colonization are keys to support it (Brundrett 2009). Cuba is not out of this reality, and although it has a high floristic richness and endemism (González Torres & al. 2016), only a few studies about the mycotrophy of Cuban plants has been published (Herrera & Ferrer 1980, Ferrer & Herrera 1985, 1988, Rodríguez-Rodríguez 2013, Rodríguez-Rodríguez & al. 2013, 2014, Furazola & al. 2020). Moreover, only the more recent included the quantification and description of mycorrhizal colonization (Rodríguez-Rodríguez & al. 2013, 2014, Furazola & al. 2020).

With the intention to continue the study of mycorrhizal status of Cuban plants, and especially endemic plants of fragile ecosystems, we aimed to determine and characterize the AM status of 20 endemic plants species of the white sand savannas of Sabanalamar, Pinar del Río, Cuba, and evaluate the seasonal variation of AM root colonization at community level.

MATERIALS AND METHODS

Characterization of study site

This study was conducted at the Managed Floristic Reserve San Ubaldo-Sabanalamar ($22^{\circ}9'2''$ lat. N, $84^{\circ}3'15''$ long. W and $22^{\circ}3'54''$ lat. N, $84^{\circ}57'23''$ long. W), in Southwestern of Pinar del Río (Municipality Guane), Cuba. It is included in the phyto-geographical district *Sabaloense* according to Borhidi (1996) or White Sand Savannas (Sabana de Arenas Blancas) according to Samek (1973). The vegetation of this region corresponds to a seminatural savanna (Capote & Berazaín 1984) on quartzite sandy soil and their flora is highly specialized, and characterized by a high endemism, mostly threatened (Cejas & Herrera 1995, Urquiola & al. 2010). The soil present is classified as Arenosol according to IUSS Working Group WRB (2014) and the bioclimate as thermoxerochimetic, mainly dry with three to four months of drought per year (Vilamajó 1989).

The sampling area was within the Sabanalamar conservation site. Field samples were performed in October 2009 (end of

the rainy season) and April 2010 (end of following dry season). The average temperature and the rainfall accumulated in the rainy season (May-October 2009) were 26.8°C and 706.4 mm, respectively, and in the dry season (November 2009-April 2010) they were 21.3°C and 190.1 mm (data obtained from the Meteorological Station Isabel Rubio, Pinar del Río).

Soil sampling and characterization

Composted samples from the superficial layer of soil (10 sampling points, 0-20 cm depth) were collected in both season for the chemical and physical characterization of the study area. The determination of soil moisture, soil acidity (pH_{KCl}), phosphorus (P_2O_5) and potassium (K_2O) available, exchangeable cations (Ca^{2+} , Mg^{2+} , Na^+), cationic exchange capacity (CEC), and organic matter content (OM) was performed according to Gardner (1986), NRAG 878-879 (1976), NC 51 (1999), NC 52 (1999) and NC 65 (2000). The results interpretation of the soil analysis was performed according to Paneque & Calaña (2001).

Species tested

Twenty plant species (15 herbs, four shrubs and a tree) belonging to 18 genera and 12 families (Table I) were evaluated. These were selected based on the quantitative biological distribution of plant species found in the province, which is characterized by a predominance of herbs, followed by shrubs and then trees (Urquiola & al. 2010). All studied species are endemic and typical of the white sand savannas, being 85 % of them exclusives of Western Cuba (Cejas & Herrera 1995, Urquiola & al. 2010).

Root sampling and mycorrhizal assessment

The sampling was carried out randomly, when the small plant populations or isolated individuals were found. Five individuals per species were sampled, being selected no more than two individuals from the same population. Considering that the herbaceous plants were predominant and most of the species are threatened with diminished populations, a larger number of individuals per species were not sampled. Root sampling of herbs often included the loss of the individual.

For each species, root samples were collected, air dried, and stored until processing. Fine roots (diameter ≤ 2 mm) were separated, washed with tap water and cut into 1 cm segments. Then, they were mixed to form a single sample per species, rinsed, cleared and stained with Trypan Blue (0.05 %) according to Phillips & Hayman (1970), with Herrera-Peraza & al. (2004) modifications.

Mycorrhizal colonization variables of stained roots were assessed under stereo microscope CARL ZEISS Axioskop 2 Plus at 40 to 80 \times magnifications. The AM colonization and AM visual density rates were determined according to Giovannetti & Mosse (1980) and Herrera-Peraza & al. (2004) methodologies, respectively.

The record of typical intra-radical (arbuscules, hyphal/arbusculate coils, vesicles, spores) and extra-radical (auxiliary cells)

structures of AM fungi, and the determination of morphological types (*Arum*, *Paris*, or Intermediate) of AM association were carried out by more detail microscopic analyses of stained roots. For that, root segments were mounted in polyvinyl alcohol lactoglycerol (PVLG) on microscope slides and examined at 200 to 1 000 \times magnifications using a light microscope CARL ZEISS Axioskop 2 Plus. Additionally, if a non-arbuscular mycorrhizal fungal structure was observed, it was also recorded. The AM status of plant species was established by recording of AM fungal structures and quantification of AM colonization.

Statistical analysis

One Way Analysis of Similarity (ANOSIM) was used to test the effect of seasonality for quantitative variables measured. Each ANOSIM test was performed based on a Euclidean distance matrix using 9 999 permutations. For this, the value of each species was used as replicates per season, thus, the analysis showed the mycorrhizal behavior at community level. The species were clustered according to their response to mycorrhizal colonization and visual density variables by hierarchical cluster analysis using the unweighted pair-group average (UPGMA) algorithm and Euclidean distance. Permutational multivariate analysis of variance (PERMANOVA), also using a Euclidean distance matrix and 9 999 iterations, was performed to detect statistically significant differences between the plant groups formed by the cluster analysis. All statistical analyzes were performed using the program *PAST v.3.25* (Hammer & al. 2001).

RESULTS

Chemical and physical characterization of soil

The main soil properties of sampling area in the rainy season were: soil moisture = 5.50 %, pH_{KCl} = 3.95, P₂O₅ = 15 mg dm⁻³, K₂O = 50 mg dm⁻³, Ca²⁺ = 1.53 cmol_c dm⁻³, Mg²⁺ = 0.96 cmol_c dm⁻³, Na⁺ = 0.86 cmol_c dm⁻³, CEC = 6.36 cmol_c dm⁻³ and OM = 15.7 g kg⁻¹, whereas in the dry season were: soil moisture = 0.59 %, pH_{KCl} = 4.18, P₂O₅ = 46.5 mg dm⁻³, K₂O = 78.5 mg dm⁻³, Ca²⁺ = 1.92 cmol_c dm⁻³, Mg²⁺ = 0.7 cmolc dm⁻³, Na⁺ = 0.88 cmol_c dm⁻³, CEC = 6.61 cmol_c dm⁻³ and OM = 20.8 g kg⁻¹. In general, the soil properties were similar in both season, showing the high acidity and the very low fertility of the study area. Only soil moisture and P₂O₅ varied seasonality, although their values were very low in both seasons.

Quantified mycorrhizal variables

All plant species examined showed evidence of arbuscular mycorrhizal colonization (Table I). The mycorrhizal colonization ranged between 4 % and 100 % in the rainy season and between 8 % and 100 % in the dry season. Overall, the average was 67.18 ± 5.89 % and 65.25 ± 6.95 % in the rainy and dry season, respectively, without seasonal variation (ANOSIM, R = -0.016, p = 0.601).

The visual density ranged between 0.06 % and 21.73 % in the rainy season, and between 0.13 % and 31.56 % in the dry season. The average of visual density for rainy and dry season was 6.09 ± 1.29 % and 9.25 ± 2.03 %, respectively. It was not influenced by season either (ANOSIM, R = 0.003, p = 0.358).

Plants species were clustered in three groups based on both mycorrhizal variables (Figure 1). The Group I was formed by species with the highest values of mycorrhizal attributes in both seasons. A Group II included the species with intermediate values and the Group III contained only two species with very low values of mycorrhizal attributes. The mean values of the mycorrhizal variables (Table II) were much higher in Group I than in Group II and Group III. They differed statistically from each other (PERMANOVA, F = 33.79, p = 0.0001) (Table III).

Fungal structures and AM internal morphology

A wide range of AM fungal structures was observed in plant roots (Table IV, Figure 2). Terminal and intercalary vesicles were observed in all species, showing a wide variety of forms spanning from ovoid, box-shaped to irregularly lobed (Table IV, Figure 2 A-B). Additionally, spinous, and knobby auxiliary cells were observed (Table IV, Figure 2 C-D). Hyphal coils were found in all species (Table IV, Figure 2 E-F), whereas arbusculate coils were only seen in eight species (Table IV). Arbuscules were observed in seven species (Table IV, Figure 2 H-I) and intraradical spores in 11 species (Table IV). Only three species showed hyphal coils attached to longitudinal hyphae (Table IV, Figure 2G). In addition, structures of other fungal endophytes were also identified. Fine endophytes (Table IV, Figure 2J) were observed in seven species, dark septate endophytes (Table IV, Figure 2 K-L) in all the species, excepting *Plinia orthoclada* and ectomycorrhiza-like structures only in *Lechea cubensis* (Figure 2M).

The *Paris*-type was the main AM morphology observed, which was present in all species. The *Arum* and Intermediate morphologies was also identified in 35 % and 15 % of the species, respectively, always accompanied by the *Paris*-type (Table IV). Consequently, all plant families exhibited the *Paris*-type morphology, and four families (Asteraceae, Cistaceae, Melastomataceae and Phyllanthaceae) exhibited both extremes of the AM morphological continuum (*Paris* and *Arum* types). The Intermediate morphology was only found in the Arecaceae and Asteraceae families. The latter was the only family with the three morphological types of the AM morphological continuum.

DISCUSSION

Arbuscular mycorrhizal association is very important in highly competitive environments (Read & al. 1976, van der Heijden & Horton 2009) and their wide occurrence in all species examined of the white sand savannas of Sabanalamar supports this statement. The high levels of mycorrhizal colonization (> 50 % according to Read & al. 1976, Soudzilovskaia & al. 2020) of most species may be due to the low fertility and moisture of the quartzite sandy soil, where, the development of AM symbiosis could play a key role as a palliative for these deficiencies (Smith & Read 2008, Smith & al. 2010). Likewise, the AM visual density observed was high comparing with other results in Cuban natural and managed ecosystems (Herrera-Peraza & al. 2004) as well as with AM inoculation experiments (Terry-Alfonso & al. 2013, Ley-Rivas & al. 2017). Studies by Furrazola & al. (2015) at several sites under different

TABLE I**Plant species studied from the white sand savannas of Sabanalamar, Pinar del Río, Cuba**

*: Strict endemism of white sands of Western Cuba according to Cejas & Herrera (1995) and Urquiola & al. (2010). BT: Biological type. Conservation Status according to González-Torres & al. (2016): CR: Critically Endangered, EN: Endangered, V: Vulnerable, A: Threatened, NT: Near Threatened. Mycorrhizal variables evaluated: MC: Mycorrhizal colonization rate, VD: Visual density rate, D: Dry season, R: Rainy season.

TABLA I**Especies de plantas estudiadas de las sabanas de arenas blancas de Sabanalamar, Pinar del Río, Cuba**

*: Endémico estricto de las arenas blancas de Cuba occidental según Cejas & Herrera (1995) y Urquiola & al. (2010). BT: Tipo biológico. Estado de Conservación según González-Torres & al. (2016): CR: Peligro Crítico, EN: En Peligro, V: Vulnerable, A: Amenazado, NT: Casi Amenazado. Variables micorrízicas evaluadas: MC: Tasa de colonización micorrízica, VD: Tasa de densidad visual, D: Período seco, R: Período lluvioso.

Taxa	BT	Conservation Status	MC _R (%)	MC _D (%)	VD _R (%)	VD _D (%)
Arecaceae						
<i>Colpothrinax wrightii</i> Griseb. & H. Wendl. ex Voss	Tree	EN	96.0	90.0	21.73	21.12
Asteraceae						
<i>Neja marginata</i> (Griseb.) G. L. Nesom	Herb	EN	66.0	84.0	2.91	6.77
* <i>Erigeron bellidiastroides</i> Griseb.	Herb	EN	90.5	95.0	7.11	14.52
* <i>Pectis juniperina</i> Rydb.	Herb	CR	100	100	6.78	13.79
Cistaceae						
* <i>Lechea cubensis</i> Legg.	Herb	EN	4.0	8.0	0.06	0.13
Ericaceae						
* <i>Kalmia ericoides</i> C. Wright ex Griseb.	Shrub	CR	56.0	41.0	2.37	1.91
Eriocaulaceae						
* <i>Paepalanthus retusus</i> C. Wright	Herb	CR	50.0	12.5	3.77	0.71
* <i>Syngonanthus lagopodioides</i> (Griseb.) Ruhland	Herb	EN	10.5	12.0	0.60	0.36
Euphorbiaceae						
* <i>Croton cerinus</i> Müll. Arg.	Herb	A	61.5	85.5	2.06	21.80
* <i>Croton crasspedotrichus</i> Griseb.	Herb	VU	64.0	95.5	3.90	31.56
Malvaceae						
<i>Sida brittonii</i> León	Herb	NT	85.0	39.5	5.68	0.99
* <i>Waltheria arenicola</i> A. Rodr.	Herb	CR	57.5	45	3.06	2.85
Melastomataceae						
* <i>Miconia wrightii</i> (Griseb.) Triana	Shrub	CR	85.0	64.0	15.91	5.47
* <i>Arthrostemma cubense</i> A. Rich.	Shrub	NT	95.0	86.0	13.23	6.84
Myrtaceae						
* <i>Plinia orthoclada</i> Urb.	Shrub	CR	47.0	44.5	3.17	2.53
Phyllanthaceae						
* <i>Phyllanthus echinospermus</i> C. Wright	Herb	EN	95.0	100	14.70	22.19
Poaceae						
* <i>Aristida sandinensis</i> Catasús	Herb	EN	81.0	91	2.74	11.98
* <i>Aristida fragilis</i> Hitchc. & Ekman	Herb	CR	73.0	69	5.09	2.44
* <i>Cenchrus distichophyllus</i> Griseb.	Herb	CR	54.0	56	2.67	4.95
Polygalaceae						
<i>Polygala squamifolia</i> C. Wright ex Griseb.	Herb	LC	73.0	86.5	4.19	12.18

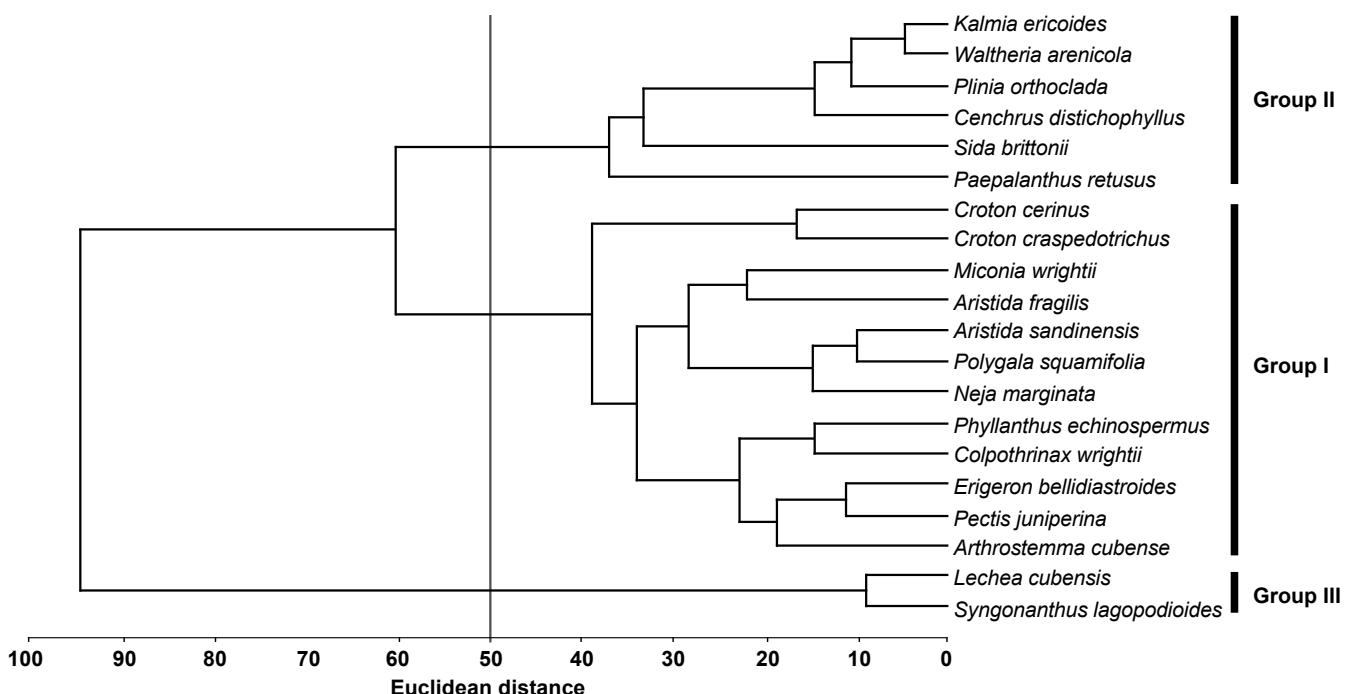


Fig. 1. Plant species clustering according to mycorrhizal colonization and visual density variables in dry and rainy seasons in the white sand savannas of Sabana- lamar, Pinar del Río, Cuba.

Fig. 1. Agrupamiento de las especies de plantas en función de las variables colonización micorrízica y densidad visual en período seco y lluvioso en las sabanas de arenas blancas de Sabanalamar, Pinar del Río, Cuba.

TABLE II

Mean values ± standard error of mycorrhizal variables of the plant groups formed by Hierarchical Cluster Analysis in the white sand savannas of Sabanalamar, Pinar del Río, Cuba

MC: Mycorrhizal colonization rate. VD: Visual density rate. D: Dry season. R: Rainy season. n: Number of species per group.

TABLA II

Valores medio ± error estándar de las variables micorrízicas de los grupos de plantas formados por el Análisis de Agrupamiento Jerárquico en las sabanas de arenas blancas de Sabanalamar, Pinar del Río, Cuba
 MC: Tasa de colonización micorrízica. VD: Tasa de densidad visual. D: Período seco. R: Período lluvioso. n: Número de especies por grupo.

Group	n	MC _R (%)	MC _D (%)	VD _R (%)	VD _D (%)
I	12	87.21 ± 3.21	81.63 ± 3.99	14.22 ± 2.47	8.36 ± 1.85
II	6	39.75 ± 5.94	58.25 ± 5.58	2.32 ± 0.63	3.45 ± 0.49
III	2	10 ± 2	7.25 ± 3.25	0.25 ± 0.11	0.33 ± 0.27

TABLE III

Pairwise PERMANOVA comparison between the plant groups formed by a Hierarchical Cluster Analysis based on variables: mycorrhizal colonization and visual density

TABLA III

Comparación por pares mediante PERMANOVA entre los grupos de plantas formados por el Análisis de Agrupamiento Jerárquico basado en las variables: colonización micorrízica y densidad visual

Treatment	F	p
Group I vs. Group II	28.19	0.0001
Group I vs. Group III	50.92	0.013
Group II vs. Group III	15.44	0.0336

TABLE IV

Fungal root structures and internal morphology of arbuscular mycorrhiza in plant species studied from the white sand savannas of Sabanalamar, Pinar del Río, Cuba

AM: Arbuscular mycorrhiza. DSE: Dark septate endophytes. FE: Fine endophyte. A: Arbuscule. HC: Hyphal coil. AC: Arbusculate coil. V: Vesicle. AuC: Auxiliary cells. LH+HC: Longitudinal hypha attached to hyphal coil. SH: Septate hypha. MS: Microsclerotium. FH: Fine branching hypha. ALS: Arbuscule-like structure. +/-: Presence/Absence.

TABLA IV

Estructuras fúngicas radicales y morfología interna de las micorrizas arbusculares en las especies de plantas estudiadas de las sabanas de arenas blancas de Sabanalamar, Pinar del Río, Cuba

AM: Micorrizas arbusculares. DSE: Endófitos oscuros septados. FE: Endófito fino. A: Arbúsculo. HC: Enrollado hifal. AC: Enrollado arbusculado. V: Vesícula. AuC: Células auxiliares. LH+HC: Hifa longitudinal unida a enrollado hifal. SH: Hifa septada. MS: Microesclerosio. FH: Hifa fina ramificada. ALS: Estructura semejante a arbúsculo. +/-: Presencia/Ausencia.

Taxa	AM structures							AM internal morphology			DSE structures		FE structures		
	A	HC	AC	V	AuC	S	LH+HC	Arum type	Paris type	Intermediate type	SH	MS	FH	V	ALS
Arecaceae															
<i>Colpothrinax wrightii</i>	-	+	+	+	+	-	+	-	+	+	+	+	-	-	
Asteraceae															
<i>Erigeron bellidiastroides</i>	+	+	+	+	-	+	+	+	+	+	+	+	-	-	
<i>Neja marginata</i>	+	+	-	+	-	-	+	+	+	+	+	+	-	-	
<i>Pectis juniperina</i>	+	+	-	+	-	-	-	+	+	-	+	+	-	+	
Cistaceae															
<i>Lechea cubensis</i>	+	+	-	+	-	-	-	+	+	-	+	+	-	-	
Ericaceae															
<i>Kalmia ericoides</i>	-	+	-	+	-	-	-	-	+	-	+	+	+	-	
Eriocaulaceae															
<i>Paepalanthus retusus</i>	-	+	-	+	-	-	-	-	+	-	+	+	+	-	
<i>Syngonanthus lagopodioides</i>	-	+	+	+	-	+	-	-	+	-	+	+	-	-	
Euphorbiaceae															
<i>Croton cerinus</i>	-	+	+	+	-	+	-	-	+	-	+	+	+	-	
<i>Croton crassipedotrichus</i>	-	+	+	+	-	-	-	-	+	-	+	+	-	-	
Malvaceae															
<i>Sida brittonii</i>	-	+	-	+	-	+	-	-	+	-	+	+	-	-	
<i>Waltheria arenicola</i>	-	+	-	+	-	+	-	-	+	-	+	-	-	-	
Melastomataceae															
<i>Miconia wrightii</i>	+	+	-	+	+	-	-	+	+	-	-	+	-	-	
<i>Arthrostemma cubense</i>	+	+	-	+	-	+	-	+	+	-	+	+	-	-	
Myrtaceae															
<i>Plinia orthoclada</i>	-	+	+	+	-	+	-	-	+	-	-	-	-	-	
Phyllanthaceae															
<i>Phyllanthus echinospermus</i>	+	+	-	+	-	+	-	+	+	-	+	-	+	+	
Poaceae															
<i>Aristida sandinensis</i>	-	+	+	+	+	+	-	-	+	-	+	+	+	-	
<i>Aristida fragilis</i>	-	+	+	+	-	+	-	-	+	-	+	+	+	-	
<i>Cenchrus distichophyllus</i>	-	+	-	+	-	-	-	-	+	-	+	+	-	-	
Polygalaceae															
<i>Polygala squamifolia</i>	-	+	-	+	-	-	-	-	+	-	+	+	-	-	

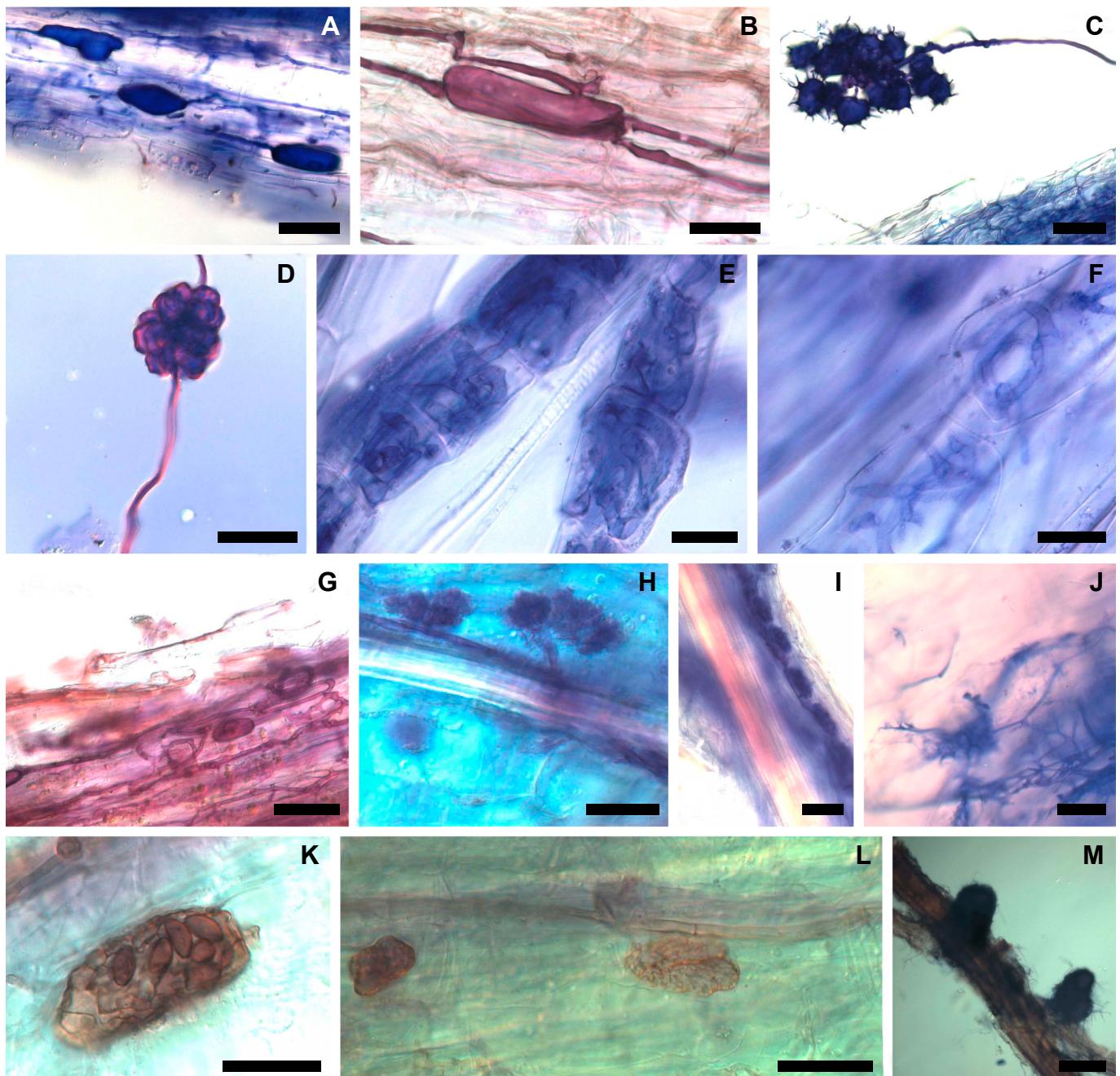


Fig. 2. Fungal root structures of the plant species studied from the white sand savannas of Sabanalamar, Pinar del Río, Cuba. Arbuscular mycorrhizal: vesicles in *Erigeron bellidiastroides* (A) and *Kalmia ericoides* (B), auxillary cells in *Arthrostemma cubense* (C) and *Aristida sandinensis* (D), hyphal coils in *Plinia orthoclada* (E) and *Syngonanthus lagopodiooides* (F), hyphal coil attached to longitudinal hypha in *Colpothrinax wrightii* (G), arbuscules in *Arthrostemma cubense* (H) and *Miconia wrightii* (I). Fine root endophyte: fine branching hypha in *Phyllanthus echinospermus* (J). Dark septate endophytes: microsclerotium in *Polygala squamifolia* (K) and microsclerotium and septate hyphae in *Sida brittonii* (L). Ectomycorrhiza in *Lechea cubensis* (M). Scale bars: 50 µm (A, C-D, G and I), 20 µm (B, E-F, H and J-L), 200 µm (M). Photos: R.M. Rodríguez-Rodríguez.

Fig. 2. Estructuras fúngicas en las raíces de las especies de plantas estudiadas de las sabanas de arenas blancas de Sabanalamar, Pinar del Río, Cuba. Micorrizas arbusculares: vesículas en *Erigeron bellidiastroides* (A) y *Kalmia ericoides* (B), células auxiliares en *Arthrostemma cubense* (C) y *Aristida sandinensis* (D), enrollados hifales en *Plinia orthoclada* (E) y *Syngonanthus lagopodiooides* (F), enrollado hifal unido a hifa longitudinal en *Colpothrinax wrightii* (G), arbúsculos en *Arthrostemma cubense* (H) y *Miconia wrightii* (I). Endófito fino: hifa fina ramificada en *Phyllanthus echinospermus* (J). Endófitos oscuros septados: microesclerosio en *Polygala squamifolia* (K) y microesclerosio e hifa septada en *Sida brittonii* (L). Ectomicorriza en *Lechea cubensis* (M). Barras de escala: 50 µm (A, C-D, G e I), 20 µm (B, E-F, H y J-L), 200 µm (M). Fotos: R.M. Rodríguez-Rodríguez.

land use within the Managed Floristic Reserve San Ubaldo-Sabanalamar (2008-2010) obtained values of mycorrhizal attributes comparable to ours. The high AM fungal spore density ($> 5\,000$ spores 100 g^{-1} soil) reported by these authors for the region suggests a high mycorrhizal inoculum potential, that alongside the soil low fertility could explain the level of AM association developed in most plants.

Most studies show the effect of seasonality on AM colonization (Becerra & al. 2009, Bencherif & al. 2016, Cavagnaro & al. 2019); however, some others show no effect (Clark & al. 2009, Zangaro & al. 2013). In our study no relationship was detected between seasonality and mycorrhizal colonization variables at the ecosystem level. This suggests that specific plant-fungus interaction determine the behavior of the symbioses. On the other hand, the coexistence of plant groups with different degree of association shows different strategies of mycorrhizal functioning and nutrient exchange in the white sand savannas of Sabanalamar and with it, the dynamic equilibrium of the ecosystem.

Identification of AM fungal structures during the diagnosis supported the AM status of all plant species. Special importance had the identification of arbuscules and hyphal/arbuscular coils, main responsible for exchange plant-AM fungus (Cavagnaro & al. 2003, van Aarle & al. 2005). *Lechea cubensis* and *Syngonanthus lagopodioides* showed very low rates of mycorrhizal colonization and visual density, so they could have been classified as endophytic Glomeromycotan Fungus Colonization (GFC) according to Brundrett (2009). However, the presence of arbuscules and hyphal coils in *L. cubensis* and hyphal coils and vesicles in *S. lagopodioides* supports the classification of both species as arbuscular mycotrophic. On the other hand, the simultaneous presence of vesicles and auxiliary cells in some host plants indicate the concurrent colonization by different taxonomic orders of AM fungi.

The *Paris*-type morphology predominated at the study site. This agrees with the conclusion of several authors (e.g., Brundrett & Kendrick 1990, Yamato & Iwasaki 2002, Becerra & al. 2007), where the *Paris*-type morphology is dominant in natural ecosystems and herbaceous plants. Additionally, the coexistence of both AM morphologies within plants of white sand savannas of Sabanalamar also suggests different strategies for nutrient exchange, not only within the ecosystem, but also within the same plant species.

Fine endophyte and dark septate endophytes were the main non-AM endophytes found coexisting with AM fungi in the roots of the plants studied. The first, once named *Glomus tenuis* (Greenall) I. R. Hall, was considered until recently as arbuscular mycorrhiza. It has been confirmed within *Mucoromycota* phylum and renamed as an *Planticonsortium tenuis* (Greenall) C. Walker & D. Redecker (Walker & al. 2018). This endophyte was not previously recorded in Cuban plants. Like us, other authors (Postma & al. 2007, Bueno & al. 2018a) have recorded their co-occurrence with AM fungi in root samples. Ecological role of fine endophyte is little understood, although a recent study

by Hoysted & al. (2019) provides evidence that they form nutritional mutualism with vascular plants related to carbon-nitrogen exchange. Dark septate endophytes, the other endophyte, is a miscellaneous group of ascomycetous anamorphic fungi that colonize root tissues intracellularly and intercellularly. They cause different effects in plants, varying from negative, neutral, to positive (Mandyam & Jumpponen 2015). They were identified cohabiting with AM fungi in most species, coinciding with several previous reports (Mandyam & Jumpponen 2008, Bueno & al. 2018b, Lugo & al. 2018, Rayment & al. 2020). Some of these studies (e.g., Mandyam & Jumpponen 2008, Bueno & al. 2018b) suggest that dark septate endophytes may compete with AM fungi for root colonization. However, others (Monica & al. 2015, Lugo & al. 2018) show synergy between both fungal groups. In our study, the high arbuscular mycorrhizal colonization in most species coexisting with dark septate endophytes does not seem to indicate competitive interference with AM root colonization. Anyway, further studies about the co-occurrence of AM fungi, fine endophyte and dark septate endophytes in Cuban plants and ecosystems are needed to understand their possible interactions and relationships.

In short, all the species assessed are arbuscular mycotrophic, which is consistent with the AM status recognized for their botanical families (Wang & Qiu 2006). *Cistaceae*, *Myrtaceae* and *Ericaceae* families also host ectomycorrhizal and ectendomycorrhizal species (Wang & Qiu 2006, Brundrett 2009) but, only *Lechea cubensis* (*Cistaceae*) showed evidence of ectomycorrhizal colonization. Ericoid mycorrhiza, exclusive to the *Ericaceae* family (Wang & Qiu 2006) was no identified in *Kalmia ericoides*.

CONCLUSIONS

Our study allowed to characterize qualitative and quantitatively the AM status in 20 endemic plant species of white sand savannas of Sabanalamar, Pinar del Río, Cuba. Identification of AM structures together with quantification of mycorrhizal colonization allowed confirm the AM mycorrhizal status, as well as, the characterization of the internal morphology of the association in all the species assessed. No relationship was observed between the AM colonization levels and seasonality at the ecosystem level, and the *Paris*-type internal morphology was dominant in the plants and ecosystem. Other fungal endophytes were also recorded in all species. Our work is a continuation of the studies about mycotrophy of Cuban plants. It also constitutes a starting point for future researches related to relationships and interactions of root fungal communities.

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AUTHORS' CONTRIBUTIONS

R.M. Rodríguez-Rodríguez conceived and designed the research, performed the field sampling and laboratorial works, processed the data and wrote the manuscript. J.A. Sánchez performed the statistical analysis, contributed to the discussion of results and critical revision of manuscript. P.P. Herrera identified the vegetal material, provided their ecological information and contributed to the revision of manuscript.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The authors declare that they have no conflict of interest.

Ethics approval: All authors have carried out fieldwork and data generation ethically, including obtaining appropriate permitting.

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