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RESEARCH ARTICLE

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Fungal diversity and colonization in roots seed trees of *Swietenia macrophylla* King (Magnoliophyta: Meliaceae) in the tropical rainforest of Laguna Om, Quintana Roo, Mexico

Guadalupe SÁNCHEZ-REYES[1], Luis A. LARA-PÉREZ[1], Luis A. SÁENZ-CARBONELL[2], Víctor H. RODRÍGUEZ-MORELOS[3], Fernando CASANOVA-LUGO[1], Angélica NAVARRO-MARTÍNEZ[4], Carlos A. PUCH-HAU[5] and Iván OROS-ORTEGA[1*]

[1] Tecnológico Nacional de México, Campus Instituto Tecnológico de la Zona Maya. Ctra. Chetumal-Escárcega km 21.5, Ejido Juan Sarabia, Quintana Roo, 77960 Mexico. [2] Centro de Investigación Científica de Yucatán. Calle 43 No. 130, Col. Chuburná de Hidalgo, Mérida, Yucatán, 97200 Mexico. [3] Université Catholique de Louvain, Earth and Life Institute, Mycology, Croix du Sud 2, Box L7.05.06, 1348 Louvain-la-Neuve, Belgium. [4] El Colegio de la Frontera Sur. Av. Centenario km 5.5. Chetumal, Quintana Roo, 77014 Mexico. [5] Tecnológico Nacional de México, Campus Instituto Tecnológico Superior de Valladolid, Ctra. Valladolid-Tizimín, km 3.5, 97780 Valladolid, Yucatán, Mexico.

*Correspondence should be addressed to Iván Oros-Ortega: ivanoros1109@hotmail.com

Abstract

Aim of study: (i) To investigate the diversity of arbuscular mycorrhizal fungi (AMF) associated with the roots of seed trees stands in a conserved and natural population of mahogany (*Swietenia macrophylla*), based on rDNA sequences; and (ii) to evaluate the dual colonization by AMF and dark septate fungi (DSF), showing the types of fungal colonization patterns in the dry season..

Area of study: Tropical rainforest of Ejido Laguna Om, Quintana Roo, Mexico.

Materials and methods: We evaluated the AMF and DSF colonization in secondary root segments of ten adult trees of mahogany. We analysed the diversity of AMF in one composite sample of mahogany roots (three trees) using 18S rDNA gene with Illumina MiSeq platform.

Main results: Through metabarcoding 14 virtual taxa belonging mainly to the genus *Glomus* and *Diversispora* were obtained, VTX00186 being the most abundant. The percentages of colonization for the different fungal structures were hyphae 80%, vesicles 18%, coils 2%, and arbuscules 0.5%; for DSF, 60% hyphae and 12% microsclerotia. The *Paris*-type colonization predominated with 61% in the roots.

Research highlights: The knowledge of the AMF diversity present in natural mahogany forests will allow the selection of species for inoculation management seeking to enhance seedling survival and growth of this species.

Additional key words: arbuscular mycorrhiza fungi; dark septate endophytes; symbiosis; mahogany; tropical tree; virtual taxon.

Abbreviations used: AMF (arbuscular mycorrhizal fungi); DSF (dark septate fungi); VT (virtual taxa).

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Introduction

The big-leaf mahogany (*Swietenia macrophylla* King) is a tree mainly found in natural wet and dry tropical forests worldwide, in a wide variety of climatic and edaphic conditions (Mayhew & Newyon, 1998; Navarro-Martínez et al., 2018). Big-leaf mahogany is a highly appreciated fine timber that is an economically important and emblematic species from the Neotropics (Langbour et al., 2011; Navarro-Martínez et al., 2020). Its natural distribution includes fragmented populations from southeastern Mexico along the Atlantic coast of Central America and northern South America, occupying a large geographical arc south of the Amazon, between Brazil, Colombia, Peru and Bolivia (Lamb, 1966; Snook, 1996). This tropical tree has been intensively exploited and subjected to international trade for over 300 years, showing, therefore, a decline in its population size and increased fragmentation in several areas of its natural distribution (Navarro & Hernández, 2004; Grogan et al., 2010). Mexico reports a loss of 76% of the tropical evergreen forest areas containing mahogany trees by the end of the 20th century (Calvo et al., 2000). The original distribution of mahogany in Peru and Bolivia decreased by 4% and 8%, respectively, while a region between Venezuela and Bolivia, underwent 58 million hectares of deforestation until 2001 (representing 20% of the original distribution) (Kometter et al., 2004). In contrast, the Yucatan Peninsula, specifically in protected areas and forest *ejidos* in Quintana Roo and Campeche, harbors semievergreen and semideciduous forests with abundant and conserved populations of mahogany (Navarro-Martínez et al., 2018, 2020). Currently, mahogany is a preferred species for reforestation and the establishment of commercial plantations throughout tropical America (Negreros-Castillo et al., 2018).

Vascular plants host a great variety of soil fungi, being susceptible to soil-borne pathogens, but plant roots are also colonized by non-pathogenic fungi like arbuscular mycorrhizal fungi (AMF) and dark septate fungi (DSF) (Mandyam & Jumpponen, 2005). Remarkably, AMF (belonging to Glomeromycota phylum) are an important ecological and economics group of soil fungi forming symbiotic associations with the vast majority of plants (Wang & Qiu, 2006; Brundrett & Tedersoo, 2018; Chen et al., 2018), including most forest tropical species (Stürmer et al., 2018). In this association, these fungi receive their carbon sources from the plants in exchange for water and minerals (e.g., P, N). As such, they play critical roles in the biogeochemical cycle of C, N and P (van der Heijden et al., 2015). Most tropical forest species have different grades of dependence on AMF, depending on successional stages or soil fertility (Danieli-Silva et al., 2010; Schüßler et al., 2016).

The AMF symbiosis deserves more attention in tropical ecosystems, especially in degraded tropical regions where the availability of nutrients such as phosphorus is a limiting factor in plant growth. Different studies have addressed the identification of AMF spores within the rhizosphere and root colonization (i.e., vesicles and arbuscules) of seedling and mahogany trees in Neotropical natural areas (Herrera & Ferrer, 1980; Rodriguez-Morelos et al., 2014), young plantations in the Amazon region (Noldt & Bauch, 2001; Pereira et al., 2014) and agroforestry systems and tropical forests of Southeast Asia where mahogany was introduced for cultivation (Dhar & Mridha, 2006, 2012; Shi et al., 2006, 2007; Mridha & Dhar, 2007; Nandi et al., 2014). However, the taxonomic identity of the specific AMF species colonizing the roots of *S. macrophylla* remains unknown. An increasing number of case studies report Glomeromycota molecular diversity from ecosystems worldwide (Husband et al., 2002; Lara-Pérez et al., 2020. A unique molecular operational taxonomic unit (MOTU) nomenclature – virtual taxa (VT) –, was performed to classify AMF rRNA sequences, as implemented in a public database MaarjAM (http://www.maarjam.botany.ut.ee; Öpik et al., 2010, 2014). Then a consistently named system of small-subunit (SSU) rRNA gene sequence phylogroups can be used as a proxy for species and/or higher-level organism identification in ecological research (Öpik et al., 2014).

According to Rodriguez et al. (2009), the DSF (Class 4 endophytes) are distinguished as a functional group based on the presence of darkly melanized septa, and their restriction to plant roots, primarily ascomycetous fungi that are conidial or sterile and that form melanized structures such as inter- and intracellular hyphae and microsclerotia in the roots. DSF are found worldwide and coexist often with different mycorrhizal fungi. They have been reported from 600 plant species including plants that have been considered non-mycorrhizal (Jumpponen & Trappe, 1998). However, studies of endophytic fungi carried out in tropical forests are limited to fungal species that colonize the aboveground part of the plant (Arnold et al., 2000; Cannon & Simmons, 2002; Silva et al., 2018). Lately, 55 endophytic fungi (Class 2 endophytes) were isolated from the roots of mahogany monoculture and identified by their rDNA ITS1 region (Rodriguez et al., 2009; Maulana et al., 2018). A close relationship between DSF and AMF with P availability and uptake in plants was suggested. Whereas DSF increases the pool of P in the rhizosphere, AMF are responsible for P transfer to the host, with co-colonization of plants by dual fungal colonization suggesting a synergistic outcome (García et al., 2012; Della Monica et al., 2015).

In the present study, the specific objectives were to (i) describe the diversity of AMF in the roots of *S. macrophylla*, based on rDNA sequences and (ii) evaluate the dual colonization by AMF and DSF, showing the types of fungal colonization patterns.

Material and methods

Study area and sampling design

This study was conducted in permanent plots of *S. macrophylla* seed trees, within a natural tropical rainforest from Ejido Laguna Om (18°25'60"N & 89°7'60"W), municipality of Othón P. Blanco, Quintana Roo, Mexico. The dominant accompanying plant species include *Manilkara zapota* (L.) P. Royen, *Vitex gaumeri* Greenm, *Lysiloma latisiliquum* (L.) Benth, *Brosimum alicastrum* Sw. and *Acacia collinsii* Saff. The climate is warm subhumid with rains in summer and winter. The average temperature is 26°C and the annual precipitation is 1290 mm (INEGI, 2016).

Ten adult seed trees of mahogany were selected, at a distance of at least 100 m between individuals, for sampling mycorrhizal roots. Select trees had ages of 32.6 ± 4.6 years, basal diameter (± SD) of 1.4 ± 0.43 m and height (± SD) of 12.3 ± 3.21 m. Samples were obtained during the dry season of 2016, from February to April, removing the organic matter and digging up to 20 cm depth; secondary roots anchored to the supporting mahogany roots were collected. After removing adhering soil, samples were deposited in hermetic bags and microtubes of 1.5 mL;10 cm of additional roots were placed in cetyltrimethyl ammonium bromide (CTAB) buffer solution as described by Harrison et al. (1994), for their temporary preservation and subsequent laboratory analysis.

Mycorrhizal and DSF colonization

To determine the degree of mycorrhizal and DSF colonization, we used the method of Phillips & Hayman (1970) as modified by Kormanik et al. (1980). Secondary root segments of 1-2 cm were used, KOH (10% w/v) was added to permeate and clarify the cells, then root segments were autoclaved for 10 min at 121 °C (68977.59 Pa), then H_2O_2 (10% v/v) was added for 10 min to remove pigments, then roots were acidified with HCl (10% v/v) for 3 min, and stained with trypan blue in an autoclave for 10 min at 121 °C.

To evaluate fungal colonization, three replicates of 15 root segments of 1 cm each (45 cm total per tree), were placed in parallel on a slide and fixed with glycerin for observation under a microscope a 10x and 40x. We analyzed a total of 450 cm of root for this study, and only stained cenocitic hyphae, coils, vesicles, and arbuscules were counted to determine AMF colonization. The mean percentages of these fungal structures in all root segments were used in our analysis. To quantify dark septate fungal colonization, we counted the presence of hyphae that were both septate and melanized with thick walls, and microsclerotia. The fungal structures observed were recorded with a Nikon D850 camera. The presence of intracellular and intercellular hyphae, as well as *Arum*-type arbuscules and *Paris*-type arbuscules, and the percentage of total colonization was quantified. The *Arum*-type colonization is characterized by intercellular hyphae and well-defined arbuscules; *Paris*-type consists of intracellular hyphae, the presence of coils or coils with rudimentary arbuscules; and the *intermediate* is the combination of the two patterns of colonization (Dickson, 2004). The data were analyzed with the non-parametric U-Mann Whitney test ($p < 0.05$), in the PAleontological STatistics (PAST) program.

DNA extraction and bioinformatics

Genomics DNA was extracted from 300 mg of a composite sample of mahogany roots (three trees) using the DNeasy Plant Mini Kit (QIAGEN, Hilden, Germany) following the manufacturer´s instructions with 50 mL of elution buffer. DNA was sent to the Research and Testing Laboratory (Lubbock, TX, USA) for Illumina MiSeq sequencing, targeting a partial sequence of the small-subunit (SSU) 18S rRNA gene. To perform sequencing reactions, the methodology reported by Lara-Pérez et al. (2020) was followed.

Denoising, homopolymers, and chimeric sequences were removed using UCHIME (Edgar et al., 2011). Virtual taxa (VT) were assigned with Blast search against the MaarjAM AMF database with sequence similarity ≥ 97%, and choosing the sequences with the highest values for the phylogenetic tree. We used the VT concept that allows standardization, as well as binomial taxonomic nomenclature, and comparison between studies where phylogenetically defined sequence variations correspond roughly to species-level taxa. We employed MaarjAM database described by Öpik et al. (2014) for the identification of environmental sequences. Application of

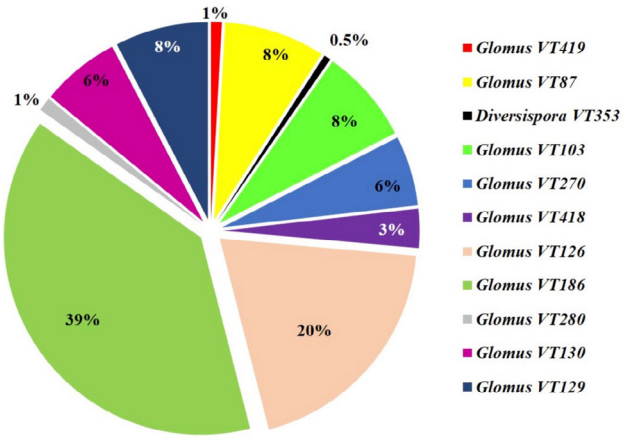

Figure 1. Relative abundance (%) of virtual taxa of arbuscular mycorrhizal fungi associated with secondary roots of mature trees of *Swietenia macrophylla.*

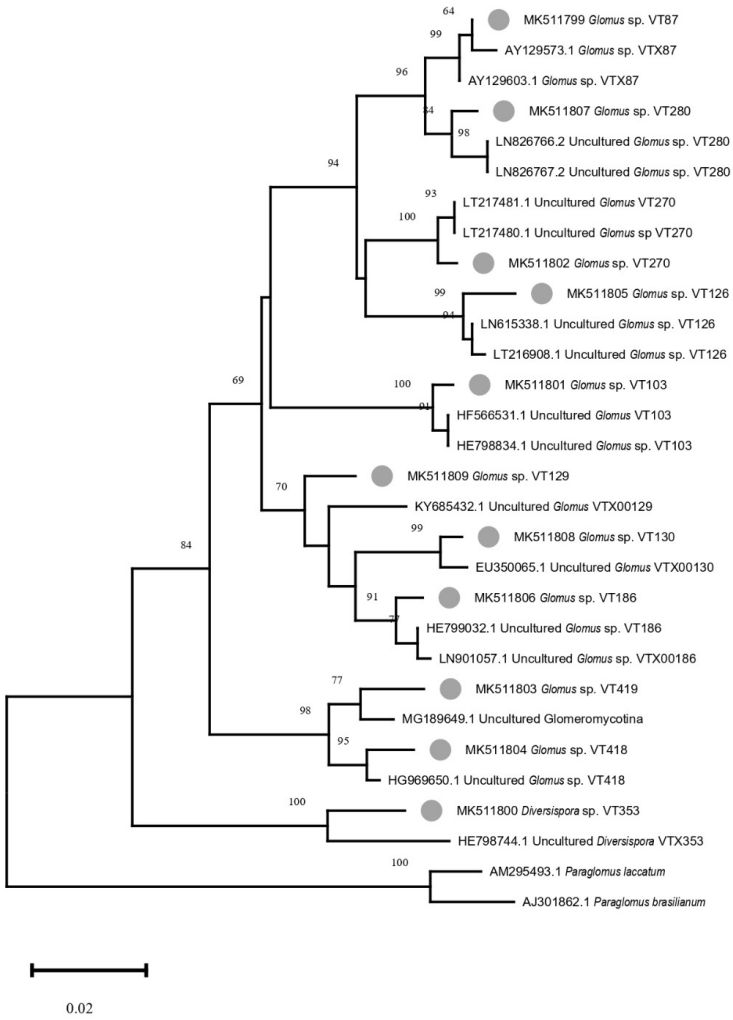

Figure 2. Phylogenetic tree of representative sequences of arbuscular mycorrhizal fungi virtual taxa associated with secondary roots of *Swietenia macrophylla*. Reference sequences from the MaarjAM database (Öpik et al., 2010). Bootstrap support values > 50 (999 iterations) are shown. Sequences from the present study are indicated with gray circles. New sequences have been submitted to the NCBI database (accession numbers from MK511799 to MK511809).

VT is becoming widespread, and the MaarjAM database is increasingly used as a reference for environmental sequence identification.

Representative sequences for each VT were chosen for phylogenetic analysis. The phylogenetic tree was performed using the Neighbor-joining methodology with the MEGA 7 program (Tamura et al., 2007) with the Kimura-2 model (Kimura, 1980), and the bootstrap method (Felsenstein, 1985) with 1000 replicates as support for the branches. Sequences of *Paraglomus laccatum* (AM295493) and *Paraglomus brasilianum* (AJ301862) were obtained from the NCBI database (www.ncbi.nlm.nih.gov) and used as outgroup. Representative sequences of each VT were submitted to the NCBI database under accession numbers from MK511799 to MK511809.

Results

Metabarcoding

In total, we obtained 2840 reads and designated VT based on sequence similarity with a minimum identity ≥ 97%. Eleven VTs were obtained, that correspond to *Glomus* sp. (10) and *Diversispora* sp. (1). The four most abundant VT were VT186, VT126, VT129, and VT87 in order of priority (Figs. 1 and 2).

Colonization by fungal groups

In the present study, the co-occurrence of interactions of fungi like AMF and DSF were observed in mahogany

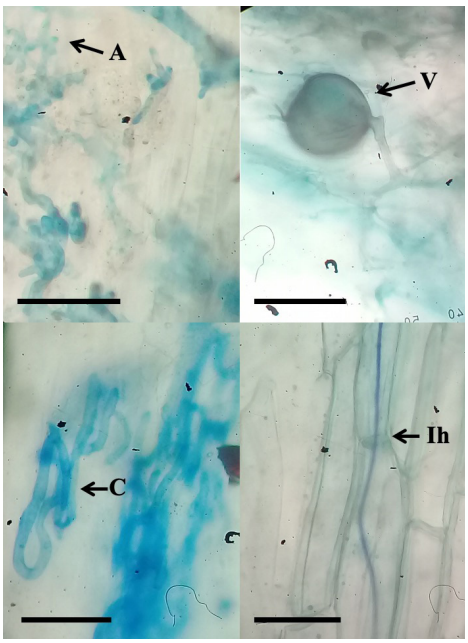

Figure 3. Arbuscular mycorrhizal fungi structures in secondary roots of mature trees of *Swietenia macrophylla*. A, arbuscules; V, vesicles; C, coils; Ih, intracellular hyphae. Bar: 50 µm.

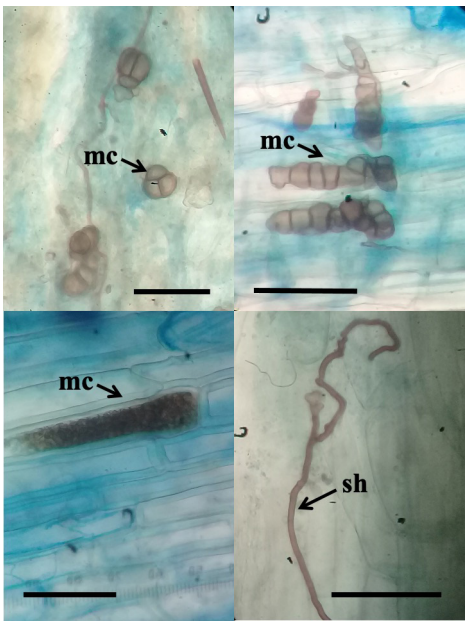

Figure 4. Dark septate fungi structures on secondary roots of mature trees of *Swietenia macrophylla*: mc, microsclerotia; sh, septate hyphae. Bar: 50 µm.

roots. Different AMF structures such as hyphae, coils, vesicles, and arbuscules were identified (Fig. 3). Septate hyphae and microsclerotia corresponding to DSF were also observed (Fig. 4). We found significantly ($p < 0.05$) higher colonization of AMF than DSF. The roots of adult mahogany trees presented 80% of AMF colonization, while DSF fungal structures were present in 66% of root-length colonization (Fig. 5a). Hyphae were the most frequent structures in mahogany roots with 80% colonization, followed by vesicles with 18%, coils 2%, and arbuscules with 0.5%. Septate hyphae were observed in 60% and microsclerotia in 12 % of root length colonization (Fig. 5b).

Mycorrhizal colonization

Mycorrhizal colonization on mahogany roots was mainly *Paris*-type, characterized by intracellular hyphae and arbuscules, with 62% of root length colonization. The intermedia type colonization was 7% and the *Arum*-type was detected in only 4% of the root length (Fig. 5c).

Discussion

The great majority of the VT detected in this study belonged to the Glomeraceae, which is the most widespread and largest family within the phylum Glomeromycota that includes 16 genera (Wijayawardene et al., 2022). Nowadays, comparisons between AMF diversity studies are difficult due to the scarcity of studies in natural tropical ecosystems, and the different methods used (e.g., spore identification, PCR-cloning, Terminal Restriction Fragment Length Polymorphism, pyrosequencing) (Rodríguez-Echeverría et al., 2017). A high diversity of AMF colonizing the roots of woody species from tropical forests has been reported (Husband et al., 2002). However, morphological and molecular studies on colonized roots by AMF in neotropical rain forests are still limited.

In general, a high predominance of Glomeraceae has been observed by spore identification within the rhizosphere of mahogany mature trees, like in agroforestry systems established in Bangladesh (Dhar & Mridha, 2006, 2012; Mridha & Dhar, 2007), tropical evergreen forest (plantation) in China (Shi et al., 2006, 2007), or young plantations in the Atlantic Forest in Brazil (Pereira et al., 2014). However, Rodríguez-Morelos et al. (2014) observed a weaker predominance of Glomeraceae in mature trees of tropical rain forests in Mexico; they reported 21 AMF spore morphotypes, primarily of Glomeraceae (52.3%) and Acaulosporaceae (38%). Indeed, in general co-dominance by Glomeraceae and Acaulosporaceae in the tropical forest has been suggested (Leal et al., 2013). Our study showed a single VT belonged to the Diversisporaceae family. Likewise, an AMF spore morphotype (e.g. *Diversispora aurantium*) was identified whatever the phenological stage of mahogany (Rodríguez-Morelos et al., 2014). We recorded a VT (*Glomus macrocarpum*), previously reported as the dominant AMF in the mahogany plantations

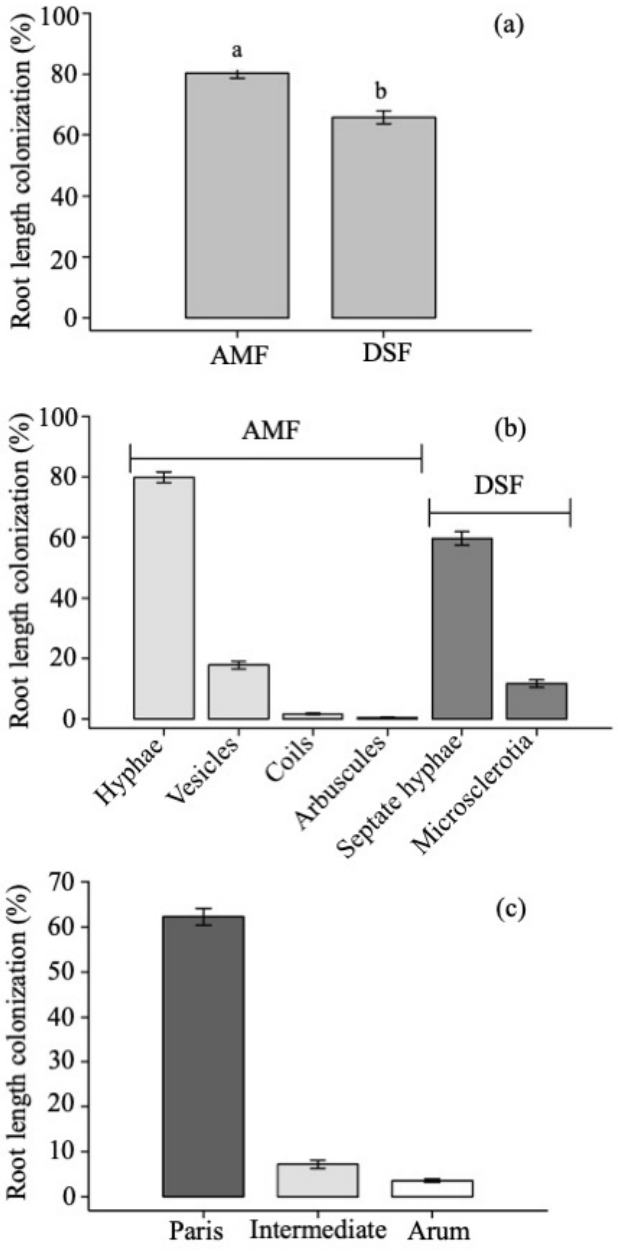

Figure 5. Percentages of root length colonization on secondary roots of *Swietenia macrophylla* mature trees by: (a) arbuscular mycorrhizal fungi (AMF) and dark septate fungi (DSF); (b) AMF (hyphae, vesicles, coils and arbuscules) and DSF (septate hyphae and microsclerotia); (c) AMF colonization types; intermediate colonization is the combination of *Arum*-type and *Paris*-type colonization. Values are presented as means ± SE ($n = 10$). Different letters above the histogram bars indicate significant differences between groups ($p<0.05$, U-Mann Whitney test).

(Pereira et al., 2014). Members of Acaulosporaceae, Ambisporaceae, Gigasporaceae and Paraglomeraceae previously reported in mahogany rhizosphere were not found colonizing roots (Rodríguez-Morelos et al., 2014). These groups are characterized by a limited ability to colonize the roots (Hart & Reader, 2002; de Souza et al., 2005). Conversely, the Glomeraceae family allocates energy to high intraradical colonization (e.g., arbuscules, vesicles, coils, and unspecialized hyphae) (de Souza et al., 2005). Root colonization levels for individual fungi strongly depend on the host tree species and the colonization strength does not correlate with plant growth promotion (Schüßler et al., 2016).

Results from studies based on the isolation of glomerospores from the rhizosphere of mahogany and the molecular approach in this study indicate that the predominant AMF species belong to the genus *Glomus*. Certain species in this family have been shown to be easily propagated in trap cultures, which can be used to obtain inoculum for commercial forest plants (Schüßler et al., 2016). The interaction between these species and mahogany seedlings has been demonstrated to improve their relative growth rate and water potential, both of which are key factors in increasing seedling survival in commercial plantations and restoration programs (Rajan et al., 2020). The first step in this process is to isolate the AMF from seed tree stands in conserved and natural populations of mahogany, and then to test the different effects of single AMF species or consortia in controlled environments (Holste & Kobe, 2017). An alternative method is to collect roots from mahogany to generate trap cultures and obtain the species associated with the target species, although this approach is less successful than using soil to increase inoculum. The percentage of root length colonization by DSF is high, which could be significant for nutrient acquisition by established adult plants and seedlings. It is noteworthy that some species of the DSF can be isolated and cultured successfully using basic techniques (Maulana et al., 2018).

In this study, a high AMF colonization (80%) in mahogany roots was observed. Meanwhile, colonization between 30% and 69.3% was reported from plantations of introduced populations of mahogany in Southeast Asia (Shi et al., 2006; Mridha & Dhar, 2007; Dhar & Mridha, 2012; Nandi et al., 2014) and 53.2% was noticed on mahogany plants after two years in Costa Rica (Holste & Kobe, 2017). A pot experiment found a percentage of root colonization between 27.4% and 44.9% according to AMF inoculation after 180 days (Rajan et al., 2020). Our findings show different percentages of root colonization in mahogany compared to previous works, where they have studied various environments such as natural and introduced populations (Shi et al., 2006; Mridha & Dhar, 2007; Rajan et al., 2020). However, all works showed that mahogany is consistently colonized by AMF.

Our results showed mainly *Paris*-type colonization in roots. Similarly, a predominant presence of *Paris*-type colonization was observed in Meliaceae trees of natural forest (Smith & Smith, 1997; Shi et al., 2006). Noldt & Bauch (2001) recorded in roots of mahogany seedlings, under plantation, structures of the *Arum*-type,

with appressoria penetration and coiled hyphae with a high frequency of vesicle and arbuscules. *Arum*-type colonization is more commonly found in crop plants while *Paris*-type is more common in plants from natural ecosystems (Matekwor Ahulu et al., 2005), although several studies (Dickson, 2004; Yamato, 2004) have found that AMF morphological structures appear to be dependent on individual plant species, the fungal species involved, and environmental conditions (e.g. salinity, drought). Additionally, these fungal symbionts have been reported to be functionally distinct (Jumpponen, 2001). In our study, the simultaneous occurrence of DSF and AMF were observed which is consistent with the findings of Muthukumar et al. (2006) and Zhao et al. (2016), in tropical ecosystems. Also, Rodríguez-Morelos et al. (2014) recorded a percentage of mahogany root length colonization by DSF between 6.09% (trees) and 5.5% (seedlings). However, despite the mix colonization, we do not know the functions in Meliaceae. Further investigations need to be done towards the identity of the fungi and to carry out an experimental assay to test their functions, and to consider implementation in mahogany seedling production. More recently, 55 endophytic fungi (Class 2 endophytes according to Rodriguez et al., 2009) were isolated from a *S. macrophylla* plantation and identified by the rDNA ITS1 region (Maulana et al., 2018) elucidating a high DSF diversity associated with mahogany roots.

Remarkably, inoculation of tropical tree seedlings with AMF can improve tree growth and viability, but efficiency may depend on plant and AMF genotype (Schüßler et al., 2016). Particularly, a differential effect of AMF inoculation on mahogany was noticed lately (Holste & Kobe, 2017; Rajan et al., 2020). Furthermore, dual colonization by AMF and DSF may aid plants in surviving in highly stressed environments (Della Monica et al., 2015; Zhao et al., 2016).

Conclusions

The roots of *S. macrophylla* display a mixed colonization pattern, with both AMF and DSF. Percentage of root length colonization was significant higher in AMF than DSF. Among the AMF, there was a predominance of the *Paris*-type colonization in the roots, while the presence of septate hyphae characterized the DSF; AMF and DSF were colonized. Through metabarcoding, 14 virtual taxa (VT) belonging mainly to the genus *Glomus* and *Diversispora* were obtained, VTX00186 being the most abundant. However, information on the diversity and the effect of the dual colonization by AMF and DSF on tropical trees remains unknown. Studies of dual colonization by AMF and DSF would deserve more attention due to the little knowledge about the diversity and potential of these fungi in association with tropical plants. Studies related to the production of fungal inoculum for the production of tropical plant species are necessary. Despite its paramount importance, currently, there is only limited use of these fungi in reforestation programs on a large scale.

Authors' contributions

Conceptualization: I. Oros-Ortega, L. A. Lara-Pérez.
Data curation: L. A. Lara-Pérez, C. A. Puch-Hau, F. Casanova-Lugo.
Formal analysis: C. A. Puch-Hau, A. Navarro-Martínez, F. Casanova-Lugo.
Funding acquisition: I. Oros-Ortega, L. A. Sáenz-Carbonell.
Investigation: G. Sánchez-Reyez, L. A. Lara-Pérez**,** I. Oros-Ortega.
Methodology: G. Sánchez-Reyez, L. A. Lara-Pérez, L. A. Sáenz-Carbonell.
Project administration: I. Oros-Ortega.
Resources: I. Oros-Ortega, L. A. Sáenz-Carbonell.
Software: C. A. Puch-Hau, L. A. Lara-Pérez.
Supervision: I. Oros-Ortega, L. A. Lara-Pérez.
Validation: A. Navarro-Martínez, V. H. Rodríguez-Morelos.
Visualization: F. Casanova-Lugo.
Writing – original draft: G. Sánchez-Reyes, I. Oros-Ortega, V. H. Rodríguez-Morelos, L. A. Lara-Pérez.
Writing – review & editing: G. Sánchez-Reyes, L. A. Lara-Pérez, L. A. Sáenz-Carbonell, V. H. Rodríguez-Morelos, C. A. Puch-Hau, F. Casanova-Lugo, A. Navarro-Martínez, I. Oros-Ortega**.**

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