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Symbiotic relationships between arbuscular mycorrhizal fungi and wild accessions of *Selenicereus undatus* in the Peruvian Amazon

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Summary

The Pitahaya, also known as dragon fruit, is a crop whose demand in the Peruvian market has grown significantly due to its nutraceutical properties. However, species within the genus Selenicereus are highly susceptible to various pathogens. In this context, arbuscular mycorrhizal fungi (AMF) not only exhibit remarkable adaptability to adverse conditions but also contribute to protecting plants against pathogens, enhancing their health and resilience.

The present study aimed to report the symbiotic relationship between AMF and wild accessions of *Selenicereu undatus*, assessing the presence of fungal structures (hyphae, arbuscules, vesicles) in the roots, the diversity of AMF in rhizospheric soil, and the confirmation of AMF-DNA in the roots. For this purpose, soil and root samples were collected from two wild pitahaya accessions in the Peruvian Amazon. The results revealed the presence of 16 AMF species across eight genera, with the genus Acaulospora being the most abundant. Furthermore, the Cabo Aberto Leveau accession exhibited a higher colonization rate (38%) compared to the Bellavista accession (22%). Molecular analysis successfully amplified a DNA band of approximately 1500 base pairs, confirming the presence of AMF-DNA in the roots of both accessions evaluated. These findings lay the groundwork for advancing studies focused on the potential of AMF associations with pitahaya cultivation and developing technologies for sustainable agricultural systems.

Key words: *Selenicereus undatus*; Arbuscular Mycorrhizal Fungi; Symbiosis; Diversity.

Introduction

Selenicereus spp. (formerly Hylocereus), commonly known as dragon fruits, are perennial, shrubby, and epiphytic cactus species from the Cactaceae family, characterized by their succulent, green, and photosynthetic cladodes (Korotkova et al., 2017). The mesocarp of the fruit exhibits a wide range of colors, from yellow to red-violet, with white or reddish-purple pulp de-pending on the species. There are three main forms: one with white pulp and red skin (*Selenicereus undatus*), another with red pulp and red skin (*S. costaricensis*), and a third with white pulp and yellow skin (*S. megalathus*). Among these, *S. undatus* being the most widely distributed species globally. These genera occur in Peru, Colombia, Bolivia, Ecuador, and Venezuela (González-Trujillo et al., 2020; Verona-Ruiz et al., 2020). In Peru, *S. undatus*, *S. monacanthus*, *S. megalanthus*, and *S. costaricensis* are commercially cultivated in the provinces of San Martín, Amazonas, Piura, and Lambayeque (Ostolaza, 2014).

These genus holds significant economic importance due to its nutraceutical properties, including anti-inflammatory, antioxidant, anticancer, and hepatoprotective effects. Additionally, it promotes bone system development due to its high vitamin C content (Corzo-Rios et al., 2017; Verona-Ruiz et al., 2020). In Peru, the demand for dragon fruits has surged in recent years, leading to an exponential rise in production, rising from 156.9 tons in 2019 to 4,178.9 tons in 2023 (Midagri, 2021).

Studies conducted in India revealed that *S. undatus* is highly susceptible to anthracnose caused by *Colletotrichum siamense*, reducing plant yield by 30% (Abirami et al., 2019). Additionally, the nematode *Meloidogyne incognita* has been reported to affect the root system of *S. monacanthus*, posing a significant threat to the crop due to root rot, which hinders optimal plant development (Souza et al., 2022).

Beneficial microbial communities are also present in the soil, notably arbuscular mycorrhizal fungi (AMF). These fungi form symbiotic associations with 70%-90% of existing plant taxa by developing hyphae, vesicles, and arbuscules – hallmarks of AMF colonization. In this symbiotic relationship, plants and AMF exchange vital nutrients: the fungi provide essential elements such as phosphorus and nitrogen, while receiving carbohydrates from the host plants in return (Piliarová et al., 2019). These associations not only enhance plant growth but also strengthen host defense mechanisms, mitigating damage caused by nematodes, pathogenic fungi, and other harmful microorganisms (Corazon-Guivin et al., 2024).

In Peru, 93 AMF species, spanning 24 genera and 9 families, have recently been reported (Vega-Herrera et al., 2022). Among these, the families Acaulosporaceae and Glomeraceae, and the genera Acaulospora and Glomus, are the most representative, particularly in the Amazon region (Corazon-Guivin et al., 2023; Pineda-Lázaro et al., 2024). In recent years, AMF have been studied through morphological analyses and molecular markers, leading to the discovery of new species (Błaszkowski et al., 2024; Corazon-Guivin et al., 2021). These studies, based on the SSU-ITS-LSU rDNA region, have revealed the large diversity of these microorganisms (Aguila et al., 2022; Corazon-Guivin et al., 2020; De la Sota

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RICALDI et al., 2023). Numerous studies on the functional benefits and diversity of AMF have shown that over a dozen species possess significant potential to enhance plant growth, improve nutrient assimilation, and even suppress root pathogens and pests in various agricultural crops (CORAZON-GUIVIN et al., 2023, 2024; SÄLE et al., 2021).

In San Martín, studies on AMF diversity in coffee plantations have identified 35 spe-cies, with Acaulospora and Glomus being predominant (CORAZON-GUIVIN et al., 2021). Similarly, in *Theobroma cacao*, molecular analyses identified eight AMF species (VALLEJOS-TORRES et al., 2022). A recent study reported 18 AMF species associated with *Myrciaria dubia*, a native Amazonian species, with Acaulospora being the most prevalent genus (PINEDA-LÁZARO et al., 2024).

To date, only one study has been conducted on *Selenicereus polyrhizus*, in which AMF were inoculated in plants during the acclimatization process (DEWIR et al., 2023). There are no studies on the interaction of these microorganisms with wild populations of *S. undatus*. This research gap presents a valuable opportunity to explore the natural symbiotic interactions between AMF and Selenicereus, which could have significant implications for both agriculture and biodiversity conservation in the Peruvian Amazon.

In this context, the present study aimed to investigate the establishment of symbiosis between AMF and *S. undatus*, focusing specifically on: i) Identifying the presence of intra-radical fungal structures characteristic of AMF symbiosis, such as vesicles, hyphae, and arbuscules; ii) Confirming the presence of AMF-DNA in the roots of *S. undatus* through molecular techniques; and iii) Evaluating the diversity of AMF species in soils associated with *S. undatus* in the Province of San Martín, Peru, through morphological spore analysis.

Materials and methods

Site description and sample collection

Rhizospheric soil samples were collected from two wild accessions of *Selenicereus undatus* (Fig. 1), located in the district of Cabo Alberto Leveau, San Martín Province (6°43'13.20"S, 76°16'1.16"W, 331 masl), and the district of Bellavista, Bellavista Province (7°4'25.54"S, 76°34'16.47"W, 278 masl), both within the San Martín region (Fig. 2A, B).

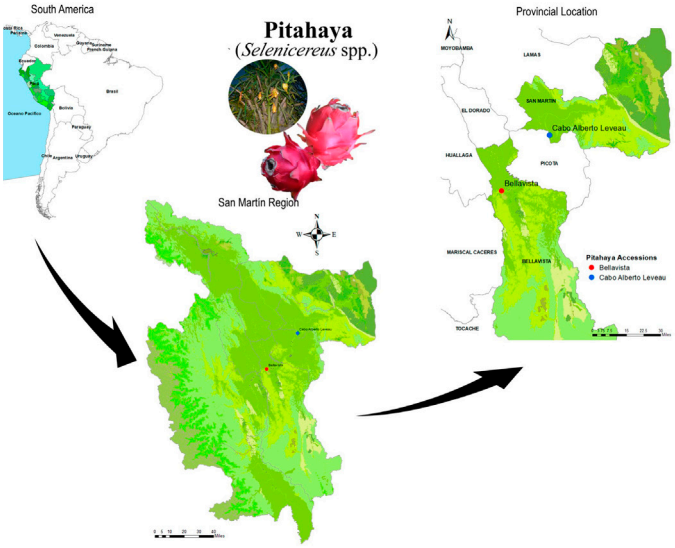

Fig. 1: Geographical location of the accessions of *Selenicereus undatus*, collected in the districts of Bellavista and Cabo Alberto Leveau.

The cladodes from these wild accessions were cultivated in our germplasm bank (Fig. 2C). Based on the characteristics of the resulting fruits, we confirmed their identity as *Selenicereus undatus* (red skin with white pulp) as shown in Fig. 2D and 2E. For each accession, samples were collected from two plants, as wild pitahaya populations typically consist of a few individuals. The collection of biological samples was conducted under a scientific research permit for wild flora (RDG No. D000330-2021-MIDAGRI-SERFOR-DGGSPFFS with authorization code No. AUT-IFL-2021-035), issued by the National Forest and Wildlife Service (SERFOR). Sampling involved extracting 10 g of root systems and 1.5 kg of soil, composed of three equidistant subsamples taken 0.5 m from the main stem of each plant, at a depth corresponding to the arable layer (15-20 cm). Soil samples were stored in polyethylene bags, while root material was placed in moist paper towels and kept in a thermal container at 4 °C for transport to the Biology and Molecular Genetics Laboratory at the National University of San Martín for further analysis. In the laboratory, roots were washed with tap water and cut into segments of 1-2 cm. A portion of the roots (100 mg) was preserved at -80 °C for molecular analysis, while the remaining root material was stored in test tubes with 70% ethanol to determine AMF colonization. Soil samples were air dried at room temperature for 48 hours, sieved through a 5 mm mesh to remove roots and stones, and then stored in sealed bags at 4 °C until analysis.

Fig. 2: Representative images of *Selenicereus undatus* in its wild habitat and under cultivation. (A) Wild plant in the district of Cabo Alberto Leveau (Province of San Martín); (B) Wild plant in the district of Bellavista (Province of Bellavista); (C) Cultivation of wild accessions of *S. undatus* in a germplasm bank; (D) Mature fruit of *S. undatus* with red skin; (E) Cross-section of the *S. undatus* fruit showing white pulp with numerous black seeds. Bar = 5 cm.

Extraction, quantification, and morphological characterization of spores

Spores were extracted using the wet sieving technique (Gerdemann and Nicolson, 1963). Specifically, 50 g of rhizospheric soil were diluted in 1 L of water, followed by filtration through sieves of 250 µm and 38 µm mesh size. This process was repeated five times. The resulting material from sieving underwent two centrifugation steps: the first at 2054 × g for 3 minutes, and the second in 60% (w/v) sucrose solution for 1 minute at 1048 × g. The suspended material was washed with distilled water and placed in 120 mm Petri dishes. Spores were grouped according to their morphological similarity and subsequently mounted in polyvinyl lactoglycerol (PVLG) and a mixture of PVLG with Melzer's re-agent in a 1:1 ratio. Species identification of arbuscular mycorrhizal fungi (AMF) was conducted using a taxonomic approach, evaluating spore morphological traits (color, size, shape). Taxonomic key characters as proposed by Oehl et al., 2011, the classification of orders, families, and genera as suggested by Baltruschat et al., 2019, and resources from the International AMF Conservation Center website (https://invam.ku.edu/species-descriptions; accessed November 2022) were used.

Intraradical colonization of AMF

The analysis of AMF colonization in *S. undatus* root systems followed the protocol of Vierheilig et al., 1998. Five grams of roots were softened in a 10% KOH solution for 15 minutes, followed by bleaching with hydrogen peroxide (H_2O_2) for 1 minute. The bleached roots were stained with Parker ink (5.7%) and stored in lactoglycerol for 24 hours. Twenty root segments (1 cm) were mounted on microscope slides and examined at 20× magnification, as proposed by McGonigle et al., 1990. During the analysis, a total of 60 points were assessed, evenly distributed along three parallel lines across 20 root segments mounted on slides, with three slides per plant. The percentage of mycorrhizal colonization was determined by calculating the proportion of points exhibiting characteristic colonization structures (hyphae, arbuscules, and vesicles) relative to the total number of points evaluated.

Molecular analysis

Genomic DNA (gDNA) was extracted from 50 mg of roots per accession using the cetyltrimethylammonium bromide (CTAB) protocol. Two consecutive PCR amplifications were performed to target a ~1500 bp fragment of AMF ribosomal DNA, encompassing partial SSU, ITS1, 5.8S, ITS2, and partial LSU regions. Primers SSUmAf/LSUmAr and SSUmCf/LSUmBr were used (Krüger et al., 2009), following the protocol established by Corazon-Guivin et al., 2019. PCR products were separated on a 1.2% agarose gel, visualized, and rec-orded using an omniDOC Gel Documentation System (Cleaver Scientific). To obtain the sequences of the host plant (*S. undatus*), extracted DNA was amplified with three molecular markers (matK, psbA-trnH, trnL-trnF) following the conditions out-lined by Tineo et al., 2020. Amplified fragments were sequenced by Macrogen Inc. (Seoul, South Korea), and the resulting sequences were deposited in GenBank (Accessions: PQ661626, PQ661627, PQ661628, PQ661943, PQ661944 and PQ661945). These generated sequences contribute to the molecular characterization of *Selenicereus undatus*, offering valuable data for future phylogenetic studies and aiding in the precise identification of this species within its genus. Additionally, these sequences provide a foundation for investigating the genetic diversity and evolutionary relationships of *S. undatus* within the Cactaceae family.

Physicochemical soil analysis

A comprehensive soil analysis was conducted for each sample, quantifying physical properties (sand, silt, clay) and chemical attributes: pH, cation exchange capacity (CEC), organic matter (OM), nitrogen (N), phosphorus (P), potassium (K), and base saturation (Bas. Sat.). Additionally, exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) and aluminum concentrations (Al^{3+}) were assessed. Climatic conditions, including average temperature, precipitation, and humidity, were obtained from the National Meteorology and Hydrology Service of Peru (SENAMHI) via data from the nearest weather station (https://www.senamhi.gob.pe/?p=estaciones).

Results

Symbiotic association between AMF and *Selenicereus undatus*

Morphological and molecular analyses approaches were used to characterize the relationship between Arbuscular Mycorrhizal Fungi (AMF) and radicular system of wild accessions of *S. undatus*. Our analysis shows the presence of various fungal structures such as arbuscules, vesicles, and hyphae (Fig. 3A, B), and also the quantification of colonization was recorded to 26% and 16% for the two wild accessions (Cabo Alberto Leveau and Bellavista).

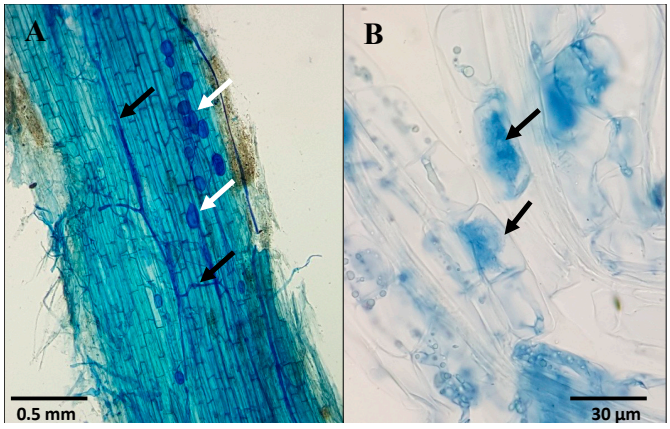

Fig. 3: Arbuscular mycorrhizal colonization in *Selenicereus undatus*. (A) hyphae (black arrows) and vesicles (white arrows); (B) arbuscules (black arrows).

To confirm the specificity of AMF to the root system of *S. undatus*, was amplified a ~1500 bp fragment of AMF ribosomal DNA using SSUmAf/LSUmAr and SSUmCf/LSUmBr primers and the presence of AMF-DNA in the roots of both wild *S. undatus* accessions was detected (Fig. 4A, B).

AMF diversity associated with *Selenicereus undatus*

Base on morphological characterization approaches we explored the diversity of AMF associated to *S. undatus* with the quantification of abundance, species richness and colonization of AMF in the rhizospheric soil present in the ecosystem of two wild accessions. The analysis by spore morphology evidenced five families, eight genera, and 19 species of AMF (Tab. 1), representing 20% of the AMF species reported across Peru's classical natural regions: Coast, Andes, and Amazon.

Edaphoclimatic characteristics of *Selenicereus undatus* accessions

Results from soils and climatic analyses in the provinces of Bellavista and Cabo Alberto Leveau reveal key differences, particularly in sand and clay content, as well as exchangeable cations (Ca^{2+}, Mg^{2+}), and precipitation levels (Tab. 2). These variations partly explain differences in the colonization, abundance and AMF richness observed between the two wild *Selenicereus undatus* accessions. In

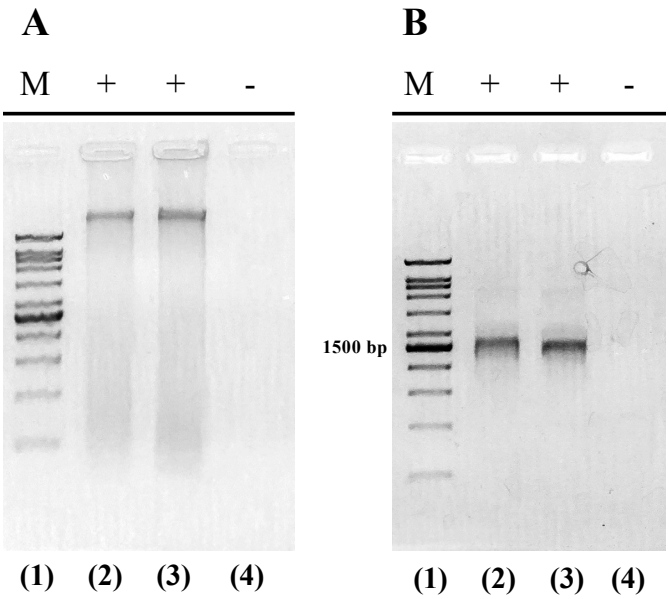

Fig. 4: Gel electrophoresis: (A) Lane 1: (M) 10 Kb molecular marker (Invitrogen, USA), Lane 2-3 (+) Genomic DNA (Cabo Alberto Leveau and Bellavista), Lane 4: (-) negative control, no DNA was added; (B) PCR reaction, Lane 1: (M) 10 Kb molecular marker (Invitrogen, USA), Lane 2-3: (+) 1500 bp fragments of mycorrhizal DNA (Cabo Alberto Leveau and Bellavista), Lane 4: (-) negative control reaction, no DNA was added.

Tab. 1: Abundance, species richness and colonization of arbuscular mycorrhizal fungi in the rhizospheric soil of two wild accessions.

Species AMF	Wild accessions	
	Bellavista	Cabo Alberto Leveau
Diversisporales		
Acaulosporaceae		
Acaulospora mellea	8	340
Acaulospora morrowiae	-	4
Acaulospora foveata	-	12
Acaulospora scrobiculata	-	4
Acaulospora sp. 1	4	-
Acaulospora sp. 2	-	16
Entrophosporales		
Entrophosporaceae		
Entrophospora claroidea	16	16
Entrophospora etunicata	8	-
Entrophospora infrequens	-	16
Glomerales		
Glomeraceae		
Funneliformis geosporus	24	160
Funneliformis mosseae	4	-
Glomus microcarpum	8	24
Glomus macrocarpum	-	64
Septoglomus constrictum	4	-
Rhizoglomus fasciculatum	-	72
Gigasporales		
Gigasporaceae		
Gigaspora decipiens	8	-
Gigaspora gigantea	-	48
Scutellosporaceae		
Scutellospora sp. 1	-	8
Scutellospora sp. 2	-	32
Spores/50 g of soil	84	816
Species richness	9	14
AMF colonization (%)	22	36

contrast, the higher sand content in Cabo Alberto Leveau (56.36% versus 41.25% in Bellavista) improves soil conditions by enhancing aeration and water infiltration, creating an environment more beneficial to AMF development and colonization. The difference in soil texture results in a higher colonization rate (36% versus 22%), increasing spore abundance (816 spores/50 g soil versus 84 spores/50 g soil), and greater species richness (14 species versus 9) in Cabo Alberto Leveau (Tab. 1). This emphasizes the relationship between soil texture and the dynamics of AMF diversity and abundance, where the soil conditions in Cabo Alberto Leveau facilitate both higher spore production and a greater number of AMF species.

Discussion

The lower colonization rate in the natural conditions of wild pitahayas may be attributed to the higher availability of host plants and the specificity AMF is exhibit when the symbiosis is establishing with their hosts (Geml, 2017), because in ecosystems with high plant density and diversity, AMF have multiple options for symbiosis establishment. The abundance of potential hosts results in a broader distribution of AMF among the various available plants, thereby reducing the intensity of colonization in each individual host (Van der Heijden et al., 2008). Furthermore, in environments with a wide diversity of plant species, AMF may preferentially associate with plants that provide more favorable conditions for their development, such as more extensive root systems, root exudates or soil conditions that promotes colonization (Johnson et al., 1997). Our findings show the possible influence of ecological communities' in the establishment of AMF symbiosis with *S. undatus* that is still unexplored in the Amazonian ecosystems. However, fifteen species identified in our study had been previously documented in the Peruvian Amazon, in crops such as *Coffea arabica*, *Theobroma cacao*, *Plukenetia volubilis*, and *Myrciaria dubia* (Corazon-Guivin, et al., 2023; Vega-Herrera et al., 2022; Pineda-Lázaro et al., 2024; Vallejos-Torres et al., 2022). These findings not only confirm the presence of these species in agricultural systems but also in undisturbed natural areas of the Peruvian Amazon, where rhizospheric soil samples were collected for this study. Additionally, the detection of four unidentified species as *Acaulospora* sp. 1, *Acaulospora* sp. 2, *Scutellospora* sp. 1 and *Scutellospora* sp. 2 suggests significant potential to expand the recorded diversity of these microorganisms in Peru. This is particularly relevant because 11 new AMF species have been reported in the Peruvian Amazon in recent years (Błaszkowski et al., 2024; Corazon-Guivin et al., 2022; Corazon-Guivin et al., 2019, 2020; Corazon-Guivin et al., 2023). On the other hand, the impact of soil physical, chemical, and climatic conditions on the development and colonization of AMF has been well documented (Corazon-Guivin et al., 2022; Zhang et al., 2021). For our study, the higher clay content in Bellavista's soil may limit AMF sporulation, also fine clay particles reduce soil aeration and drainage, creating less favorable conditions for spore diversity and abundance (Vieira et al., 2020). Different from Cabo Alberto Leveau, where the clay content is less with more sand proportion and also the precipitation in more in Cabo Alberto Leveau than Bellavista (1,623.90 mm versus 722.60 mm) maintaining favorable soil moisture levels for growth and development of AMF. Higher precipitation levels ensure adequate soil water content, which is critical for spore germination and the extension of AMF hyphae, promoting higher colonization rates and overall AMF activity

Tab. 2: Physical chemical and climatic characteristics of the sampling sites.

Soil properties	Wild accessions	
	Bellavista	Cabo Alberto Leveau
pH	7.1	6.2
EC (µS/cm)	193.7	212.6
OM (%)	2.1	2.85
P (ppm)	16.2	16.4
K (ppm)	185.2	192.1
N(%)	0.1	0.10
Texture		
Sand (%)	41.3	56.4
Silt (%)	27.2	25.1
Clay (%)	31.5	18.5
CEC	20.0	16.0
Bas. Sat. (%)	100.0	100.0
Changeable cations		
Ca^{+2}	17.45	14.12
Mg^{+2}	1.32	0.96
K^{+2}	0.50	0.50
Na^{+}	0.60	0.60
Al^{+3}	0.00	0.00
Temperature (°C)	27.7	24.1
Relative Humidity (%)	88.5	86.2
Precipitation (mm)	723	1624
Altitude (masl)	278	331

(Carrillo Aguilar et al., 2021). Regarding exchangeable cations, Bellavista showed higher concentrations of Ca^{2+} (17.45 meq/100 g versus 14.12 meq/100 g) and Mg^{2+} (1.32 meq/100 g versus 0.96 meq/100 g). While nutrients are essential for plant-AMF interactions, their excess can disrupt the soil's ionic balance, indirectly affecting AMF colonization and abundance (Chen et al., 2023). In contrast, the lower cation levels in Cabo Alberto Leveau may improve the environment for AMF colonization, supporting robust symbiotic development. Excessive calcium and magnesium concentrations can saturate the exchangeable sites on soil particles, thereby reducing the bioavailability of phosphorus and other essential nutrients that are crucial for AMF activity. This explains the lower colonization rates observed in Bellavista. In contrast, the lower cation concentrations in Cabo Alberto Leveau create more favorable conditions for AMF, promoting higher spore abundance and greater species diversity. The *S. undatus* accession from Cabo Alberto Leveau exhibited greater spore abundance, with *Acaulospora mellea*, and *Funneliformis geosporus* being the most representative species. *Acaulospora mellea* shows variable abundance depending on soil texture and seasonality, proliferating more easily in soils with high sand concentration or high drainage levels (Aker et al., 2022). On the other hand, *Funneliformis geosporus* is highly tolerant to arid soils, enabling host plants to have greater access to water and nutrients, leading to higher spore production (Lara-Pérez et al., 2017).

Conclusions

This study reveals the first report about the symbiotic relationship between AMF and wild accessions of *Selenicereus undatus*, demonstrating the presence of hyphae, arbuscules, and vesicles in the root systems, and also the DNA detection of AMF in *S. undatus* roots. At the same way, morphological analysis of spores discloses substantial AMF diversity associated with the rhizospheric soil of wild *S. undatus*, where Acaulospora genus being the more dominant. Finally, the edaphoclimatic characteristics provide insights into AMF behavior, highlighting their influence on diversity and abundance. These findings suggest the importance of further studies to explore the symbiosis of AMF in *Selenicereus undatus* and its relationship with natural ecosystems.

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Conflict of interest

No potential conflict of interest was reported by the authors

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