 Chilean J. Agric. Anim. Sci., ex Agro-Ciencia (2025) 41(2):264-278.
https://doi.org/10.29393/CHJAAS41-24ARAM60024

ISSN 0719-3890 online

# DIVERSITY OF ARBUSCULAR MYCORRHIZAL FUNGI ACROSS TWO PRODUCTION SYSTEMS OF SOURSOP (*Annona muricata* L., 1753) IN MEXICO

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## ABSTRACT

**Soursop (*Annona muricata* L., 1753) is a valuable tree native to Mexico and other regions of Central and South America, known for its edible fruit and medicinal properties. Few studies have examined the interactions between *Annona muricata* and arbuscular mycorrhizal fungi (AMF). However, understanding the biology, ecology, diversity, and limiting factors of AMF is essential for their agricultural application. This study aimed to compare the diversity parameters of AMF associated with *Annona muricata* under conventional and agroecological production systems in Nayarit, Mexico. The high-input (HT) field received periodic fertilization and irrigation, whereas the low-input (HNT) field did not receive either. AMF spores were extracted for morphological identification and the abundance and diversity index were estimated. Soil characterization included measurements of pH, potassium, phosphorus, magnesium, calcium, and nitrogen. The diversity index and percentage of root colonization by AMF were higher in the HNT field compared to the HT field. These findings suggest that AMF communities associated with *Annona muricata* under organic or agroecological management (low-input) exhibit greater diversity of species than those in conventional cultivation systems (high-input).**

**Keywords:** agroecosystem, AMF diversity, AMF species, mycorrhization, soursop cultivation.

## INTRODUCTION

*Annona muricata* L. (1753) is a perennial tree native to Mesoamerica. Its fruit is mainly consumed fresh in juices, nectars, and ice creams. In recent years, this species has gained considerable attention for its medicinal properties, including cytotoxic, antioxidant, antimicrobial, larvicidal, insecticidal, and antidiabetic activities (Al Kazman et al., 2022). Research has focused on the phytochemical composition of *Annona muricata* and its potential use in modern medicine, but little is known about its interspecific interactions, especially with rhizosphere microorganisms.

The rhizosphere microbiome plays a crucial role in nutrient cycle and ecosystem productivity

Recieved: March 3, 2025 Accepted: August 14, 2025

(Sun et al., 2021; Trivedi et al., 2020). Among its key members are arbuscular mycorrhizal fungi (AMF), which form mutualistic associations with most terrestrial plants. The fungal mycelium penetrates the cortical cell wall, forming arbuscules within the root. Simultaneously, the external hyphal network facilitates the translocation of essential nutrients such as ammonium ($NH_4$), phosphorus (P), zinc (Zn), and copper (Cu) from the soil to the host plant (Parihar et al., 2020).

AMF extraradical hyphae extract P from the soil through P importers and convert it into polyphosphate (Thangavel et al., 2022). Nitrate is absorbed via nitrate transporters (NRT) and ammonium transporters (AMT), and converted into arginine. Arginine binds to polyphosphate, and both compounds are transported into the intraradical hyphae, where they are delivered to the host plant (Thangavel et al., 2022). AMF take up assimilated carbon (C) from the host through the photosynthetic process, thus forming a mutualistic symbiosis; the C and nutrient transfer occurs through chemical transmission (Parihar et al., 2020).

AMF spores germinate and establish physical contact with host plant roots through a hyphopodium. The fungus then penetrates root cortical cells, forming arbuscules surrounded by a periarbuscular membrane (Thangavel et al., 2022; Parihar et al., 2020). Plants hydrolyze sucrose into glucose (Thangavel et al., 2022), and transport it to cortical cells via phloem and sucrose transporters (SUT); which then deliver it to AMF (Parihar et al., 2020). Other sugar transporters, such as monosaccharide transporters (MST) and Sugars Will Eventually be Exported Transporters (SWEET), are also involved in this process (Parihar et al., 2020; Thangavel et al., 2022). The intraradical mycelium transports C to the extraradical hyphae (Parihar et al., 2020). Additionally, AMF rely entirely on host-supplied fatty acids (FAs) since they lack the biosynthetic machinery to synthesize them (Bell et al., 2024).

Conventional management practices rely on pesticides, herbicides, and chemical fertilizers. These inputs negatively impact the ecosystem, affecting soil quality and stability, as well as biological processes (Li et al., 2024). Hence, agroecological practices have attracted attention in recent years; farmers base these low-input practices on maintaining sustainable agricultural systems that prevent soil erosion, conserve biodiversity, and enhance the function of beneficial soil microorganisms (Prates et al., 2019), such as AMF. These microorganisms represent a great potential to increase crop yield while avoiding agrochemicals (Madawala, 2021). Nonetheless, in order to effectively harness this technology, it is imperative to understand both the diversity and abundance of AMF species associated to key crops, as well as the conventional practices that reduce AMF diversity within agroecosystems.

Certain agricultural activities, such as long-term crop monocultures, reduce AMF diversity by favoring plant species that release selective root exudates (Agnihotri et al., 2017). In addition, tillage disrupts AMF hyphal networks and reduces spore density, while high fertilizer inputs further decrease AMF abundance and diversity in agroecosystems (Li et al., 2024). Moukarzel et al. (2024) reported that organic vineyard systems in New Zealand supported higher AMF diversity and distinct community composition compared to conventional systems. Similarly, Liu et al. (2022) demonstrated that the combination of no-tillage and biologically based organic fertilization significantly increased species richness, evenness, and overall diversity of AMF communities in winter wheat fields compared to conventional practices. Additionally, Heuck et al. (2024) found that organic management systems harbored unique and functionally beneficial AMF taxa largely absent under conventional agriculture, suggesting that organic practices can partially mitigate the negative effects of intensive farming on AMF communities.

Currently, the diversity of AMF species associated with *Annona muricata* remains poorly characterized. Sarwade et al. (2011) reported associations of the genera *Glomus* and *Acaulospora* with *A. squamosa* and the genera *Glomus*, *Acaulospora* and *Gigaspora* with *Annona reticulata*. A related study by González et al. (2024) investigated the abundance of AMF species associated with *Annona muricata* trees in the same Compostela region and soil propagation, identifying 13 AMF species across seven genera. The present study builds upon that research, focusing specifically on the diversity of AMF species.

The diversity of AMF associated with *Annona muricata* remains poorly documented, particularly under different management systems. This knowledge gap limits our understanding of how agricultural practices influence beneficial soil fungi in this species. Therefore, this study aimed to evaluate AMF diversity in the rhizosphere of *Annona muricata* under conventional and agroecological production systems in Nayarit, Mexico. We hypothesize that intensive management (high-input production system) would negatively impact AMF communities, resulting in lower diversity under intensive management. This research contributes to a better understanding of the ecological impact

of management intensity on AMF and supports sustainable cultivation strategies for soursop.

## MATERIALS AND METHODS

**Study sites.** The study was conducted in two field sites located cultivated with *Annona muricata* in the municipality of Compostela, Nayarit, Mexico. Both sites have a warm sub-humid climate (Aw) with an average annual temperature of 22.9 °C, ranging from a minimum of 15.7 °C, and a maximum of 30.2 °C. During the dry season (May), the average monthly temperature is 24.1 °C. The mean annual rainfall is 971.4 mm. The study sites were managed under two different productions systems: i) high-input (HT), characterized by annual fertilization via fertigation, a micro-spray irrigation system and adequate weed control; ii) low-input (HNT), characterized by the absence fertilization or irrigation, the presence of livestock activity and grass-type weeds (Table 1).

**Soil sampling.** Rhizospheric soil samples were collected during the dry season (May 2018) from both study sites. The HT field covered an area of 10 ha with a 12-15% slope, while the HNT field covered 5 ha with a 35-40% slope. At each site, three-year-old *Annona muricata* trees were randomly selected – four trees from the HT site and five from the HNT site. From each selected tree, four rhizospheric soil subsamples were taken at a depth of 0-15 cm, following the method described by Zhu et al. (2020). All sampled trees showed no visible signs of disease or pest infestation and had comparable canopy size and vigor. To minimize edge effects and ensure representing sampling, only trees located at least 10 m from field borders were included. The subsamples were mixed, air-dried, stored at room temperature (22 °C), and kept out of direct sunlight for further analysis (Edwards et al., 2024).

**Soil analysis.** Total rhizospheric soil contents of N, P, K, Ca, and Mg were measured using extracts obtained through wet digestion. Briefly, 500 mg of soil were digested with 4 mL of $H_2SO_4$ and $HClO_4$ (2: 1, v/v) and left to stand for 24 h. Subsequently, 30% $H_2O_2$ was added, the mixture was allowed to digest at up to 200 °C. The resulting extracts were then washed. Total N was carried out following the Kjeldahl method. Total P was determined using the ammonium molybdate colorimetric method (Chapman and Pratt, 1979), while available P was quantified following the Bray and Kurtz (1945) method. Exchangeable K, Ca, and Mg were determined by flame photometry.

**Colonization rates and spore density of arbuscular mycorrhizal fungi (AMF).** Spores were extracted from 100 g of dry soil through sieving and decantation (Gerdemann and Nicolson, 1963), and the samples were centrifuged in a 50% sucrose gradient. Subsequently, spores were observed and counted under a stereoscopic microscope (Leica EZ4 HD®, Leica Microsystems, Germany).

Roots were placed in plastic cassettes and embedded in 10% KOH overnight. The KOH solution (10%) was the refreshed, and the roots were autoclaved at 121 °C and 1.0546 kg $cm^{-2}$ for 5 min. After autoclaving, roots were rinsed with distilled water and placed in 10% $H_2O_2$ at 100 °C for 5 min. Roots were newly rinsed with water and treated with 1 N HCl at room temperature for 10 min. The samples were then stained with 0.02% trypan blue at 95 °C for 10 min. Root

**Table 1. Main agronomic traits of soursop (*Annona muricata*) plantations under different production systems in Compostela, Nayarit, Mexico.**

| Production systems | Localization | Plantation type | Crop system | Fertilization (N-P-K) | Density (trees $ha^{-1}$) | Elevation (m.a.s.l.) |
|---|---|---|---|---|---|---|
| HT | 21° 07′ 35.2′′ N 105° 12′ 12.5′′ W | Monoculture, slope of 12-15% | Intensive, with micro-spray irrigation | 130-130-130 Annual through irrigation system | 830 | 148 |
| HNT | 21° 12′ 48′′ N 105° 03′ 10′′ W | Monoculture, slope of 35-40% | Semi-natural, without irrigation | 00-00-00 | 400 | 188 |

HT: High-input field, HNT: Low-input field, N-P-K: nitrogen–phosphorus–potassium ratio, m.a.s.l.: meters above the sea level.

sections were mounted on microscope slides, and the percentage of mycorrhizal colonization was assessed according to the method described by McGonigle et al. (1990), based on the presence of characteristic structures such as arbuscules (A), coils (C), and vesicles (V); hyphal colonization was expressed as total colonization.

**Taxonomic identification and determination of AMF diversity.** AMF spores extracted from soil samples were taxonomically identified. Dry soil (50 g) from each sample was processes using a wet sieving and decanting method (Gerdemann and Nicolson 1963), followed by centrifugation in a 50% sucrose gradient to isolate the spores. Selected spores were extracted and placed on microscope slides. A drop of polyvinyl alcohol in lactoglycerol (PVLG) mixed with Melzer's reagent in a 1:1 ratio was added to each slide. Spores were observed under a microscope (Leica DM750 model) to examine cell wall structures. The microscope was equipped with a Leica ICC50E integrated digital camera. Image capture and analysis were performed using the Leica Application Suite V 3.3.0. (2016; Leica Microsystems Ltd. Switzerland).

AMF spores were identified considering the species descriptions of specialized sources, including the Arbuscular Mycorrhizal Fungi Phylogeny (University of Tübingen, 2024), the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM, 2024), and the Glomeromycota database curated by Janusz Błaszkowski (West Pomeranian University of Technology, 2024). The classification of AMF spores was conducted following the system proposed by Redecker et al. (2013).

Alpha diversity of a community is assessed through species richness and community structure parameters, including: species richness (S), defined as the total number of species registered in the community; species abundance (N), which corresponds to the number of individuals per species; Margalef index (d), which relates the number of species to the total number of individuals, and probability accumulation functions (Clench and Linear Dependency equations), which estimates the probability of detecting a new species. Community structure parameters include abundance indices that determine the distribution of the species in the community. The Simpson index (D) gives more weight to dominant species, and it is measured in an interval from 0 to 1. Species equity or diversity was measured using the Shannon-Weaver index (H′), which ranges from 0 to 3.5, with higher values indicating greater diversity.

Simpson, Shannon-Weaver, and Margalef diversity indices were calculated, and the ecological diversity of both study sites was compared by a T-Hutchenson test ($P \leq 0.05$). Additionally, expected species accumulation curves (Clench and Linear Dependency) were calculated.

**Statistical analysis.** Prior to conducting parametric tests, the assumptions of normality and homogeneity of variances were evaluated using the Shapiro–Wilk and Bartlett's tests, respectively, both implemented in Statgraphics Centurion XV. When assumptions were not met, equivalent non-parametric tests were applied.

Soil variables, including electrical conductivity (EC), and the rhizospheric contents of N, P, K, Ca, and Mg, were compared using the Kolmogorov-Smirnov and T-student statistical test ($P \leq 0.05$). In addition, the colonization percentage and the number of spores from both study sites were compared using a T-Student test ($P \leq 0.05$). Moreover, Pearson's correlation analysis ($P \leq 0.05$) was performed between the colonization percentage and number of spores and soil analysis variables of the sampled sites. All statistical analyzes were performed using Statgraphics Centurion XV software.

Simpson, Shannon-Weaver, and Margalef diversity indices were calculated using Primer 6 version 6.1.16 & Permanova software, version 1.0.6 2013. Ecological diversity between the two study sites was compared by a T-Hutchenson test ($P \leq 0.05$). Species accumulation curves (Clench and Linear Dependency) were generated using EstimateS and Statistica statistical softwares. The total expected richness (asymptote a / b) was determined based on these models. The Clench model was defined by the equation , while the linear dependency model followed the equation, where $x$ represents the sampling effort (number of samples); $y$ represents the observed species; $a$ indicates the rate of increase of new species, and $b$ is a parameter related to the shape of the curve.

Redundancy analysis (RDA) was initially conducted using OriginPro version 9.9.0.225. The following AMF species were excluded from the analysis due to their low frequency (less than 30%). Due to software limitations, a Hellinger transformation could not be applied to the species abundance matrix, and analyses were then performed using untransformed raw data. Moreover, OriginPro does not support permutation-based significance testing or variance inflation factor (VIF) diagnostics.

A subset of the most ecologically relevant environmental variables was selected based on their strength and significance in Pearson correlation analyses with AMF colonization

and spore density. The final model included the following variables: total nitrogen (Nt), available phosphorus (Pd), total phosphorus (Pt), exchangeable potassium (Ki), total potassium (Kt), exchangeable calcium (Cai), and total calcium (Cat).

The RDA formula used was:

RDA: Y = Nt + Pd + Pt + Ki + Kt + Cai + Cat

where Y represents the Hellinger-transformed species composition matrix.

Due to the lack of residual degrees of freedom in the full RDA model, statistical validation through permutation tests was not possible.

## RESULTS AND DISCUSSION

Differences were observed in mycorrhizal colonization, chemical soil characteristics, as well as in the diversity, richness, and abundance of AMF species.

In the two soursop field sites under study, 13 AMF species were identified based on spore morphology (Fig. 1). These species belong to seven genera: *Acaulospora*, *Claroideoglomus*, *Funneliformis*, *Rhizophagus*, *Sclerocystis*, *Scutellospora* and *Septoglomus* (Fig. 2). The most abundant species were *Funneliformis geosporum*, *Acaulospora kentinensis* and *Rhizophagus intraradices*, with a relative abundance of 45.85, 18.97 and 15.81%, respectively (Table 2). Likewise, *F. geosporum*, *A. kentinensis*, and *Scutellospora dipurpurescens* were found at the two sampling fields, while the species *Acaulospora excavata*, *A. mellea*, *A. morrowiae*, *Claroideoglomus claroideum*, *C. etunicatum*, *Rhizophagus fasciculatus* were only identified in the HNT field (Table 2). Five species of the genus *Acaulospora*, representing 38% of the total genera, were observed in both sites. The abundance of *Acaulospora* species in *Annona muricata* rhizosphere may be attributed to the acidic conditions of the soil. Some studies have confirmed that *Acaulospora* species are well-adapted to acidic soils. For instance, Gaonkar and Rodrigues (2020) showed that *Acaulospora* species were dominant in mangrove soils with low pH levels (5.8).

Lauriano-Barajas and Vega-Frutis (2018) previously reported the presence of AMF morphospecies in Nayarit state. In their study, nine morphospecies were identified in the cloud forest, including *C. etunicatum*, *S. constrictum*, *Claroideoglomus* sp., *Acaulospora* sp., and five unidentified species. These species were also observed in the present study (Table 1).

There are few studies on AMF species associated with *Annona muricata* or the genus *Annona*. However, Sarwade et al. (2011) reported the symbioses between *Glomus* sp. and *Acaulospora* sp. with *A. squamosa*, and among the

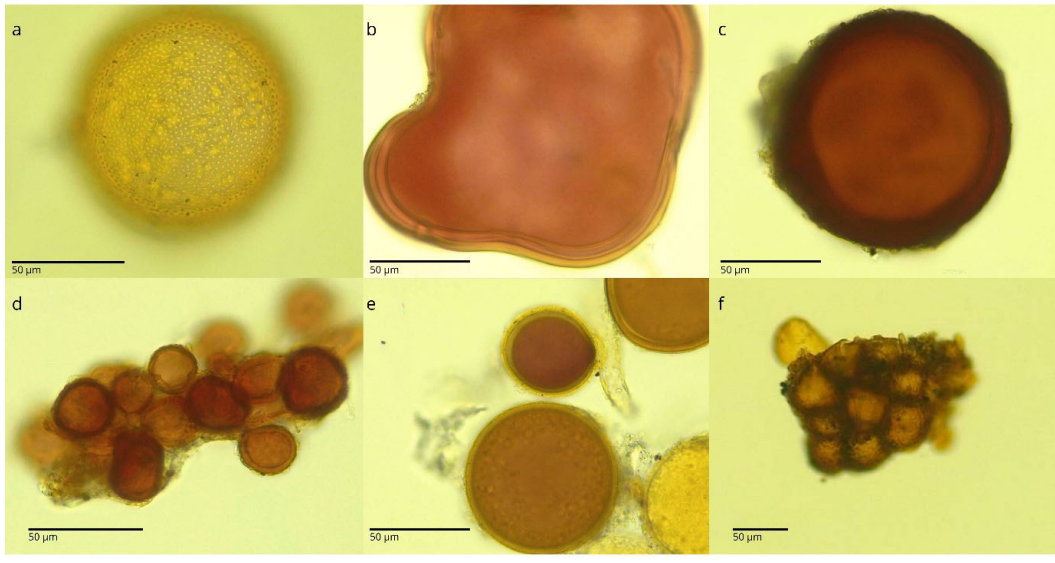


**Fig. 1. Microphotographs of AMF species found in *Annona muricata* rhizosphere of two sites under different production systems in Compostela, Nayarit, Mexico. a. *Acaulospora kentinensis*; b. *Scutellospora dipurpurescens*; c. *Septoglomus constrictum*; d. *Rhizophagus fasciculatus*; e. *Acaulospora spinosa*; f. *Sclerocystis sinuosa*. Bars 50 µm.**

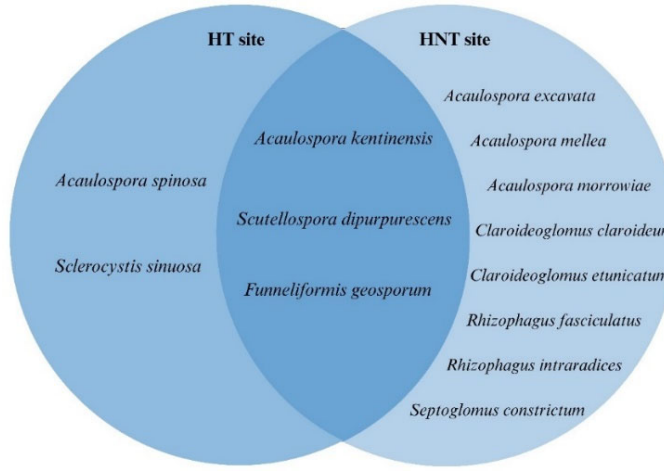


**Fig. 2. Distribution of AMF morphospecies associated with *Annona muricata* at two sites under different productions systems in Compostela, Nayarit, Mexico. Species names according to Schübler and Walker (2010). HT: High-input field, HNT: Low-input field.**

genera *Glomus* sp., *Acaulospora* sp., and *Gigaspora* sp. with *Annona reticulata*.

In the present study, the genera *Funneliformis*, *Acaulospora*, and *Scutellospora* were found at both evaluated fields, with the genus *Funneliformis* being the most abundant. In addition, the genus *Claroideoglomus* was recorded exclusively in the HNT field. These findings agree with Masebo et al. (2023), who compared AMF species richness profiles between organic and conventional cultivation sites and they observed a higher presence of *Claroideoglomus* in organic systems. Similarly, Jansa et al. (2014) reported a decrease in the abundance of *C. claroideum* associated to the use of mineral fertilizers. This decline is explained by the varying sensitivity of AMF species across different genera to soil disturbance (Guadarrama et al., 2014). Zeng et al. (2021) described that the diversity and abundance of AMF generally decreases in conventional management systems. This decline may be due to the utilization of mineral fertilizers and synthetic pesticides, giving rise to detrimental impacts on AMF communities; however, a more comprehensive understanding of these adverse effects requires further in-depth research.

It has been described that, under field conditions, the influence of fertilizers like P on the structure of the AMF community may be variable (Liu et al., 2016). In the present study, however, the high P content in the HT site may have influenced the community structure. Research has demonstrated that the diversity and abundance of AMF decline when there are high levels of available P in the soil (Ma et al., 2023). Nevertheless, P fertilization does not always reduce AMF diversity; its impact depends on form of the fertilizer, sampling times, and the host plant species under study (Liu et al., 2016). Additionally, Liu et al. (2016) reported variations in the AMF community associated with the soil N/P ratio in response not only to fertilizer application but also to factors such as soil properties, environmental conditions, cultivation stage, and soil depth (Liu et al., 2016).

In addition to the type of soil fertilization management, factors such fungicide application, management intensity, tillage practices, site history, monoculture systems, cultivation of non-mycotrophic species, and soil aggregation can also influence the structure of the AMF community (Agnihotri et al., 2022; Zinati et al., 2025). In the present study, the HNT exhibited a greater abundance and species richness (González-López et al., 2024; Table 3). Similarly, the Shannon-Weaver index indicated a higher diversity at the HNT site compared to the HT site (González-López et al., 2024), and the Margalef diversity index further confirmed that the HNT field exhibited higher diversity than the HT field (Table 3). Regarding the Simpson index (dominance index), the HT field showed a greater dominance than the HNT field (González-López et al., 2024). The composition of the AMF communities was different in both sites.

The a / b ratio obtained from the Clench model were 7.5 and 14.3 expected species for the HT and HNT sites, respectively (Table 3). Therefore, evaluation of the species inventory using the species accumulation curve of the Clench model showed a proportion of registered species of 66.6%

**Table 2. Relative abundance (RA) of AMF associated with *Annona muricata* at two sites under different production systems in Compostela, Nayarit, Mexico.**

| AMF Species | Production systems | | | AMF Species | Sampling field | | |
|---|---|---|---|---|---|---|---|
| | HT | HNT | RA | | HT | HNT | RA |
| *Acaulospora excavata* Ingleby & C. Walker | | X | 0.40 | *Funneliformis geosporum* (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler | X | X | 45.85 |
| *Acaulospora kentinensis* (C.G. Wu & Y.S. Liu) Kaonongbua, J.B. Morton & Bever | X | X | 18.97 | *Rhizophagus fasciculatus* (Thaxt.) C. Walker & A. Schüßler | | X | 1.19 |
| *Acaulospora mellea* Spain & N.C. Schenck | | X | 0.40 | *Rhizophagus intraradices* (N.C. Schenck & G.S. Sm.) C. Walker & A. Schüßler | | X | 15.81 |
| *Acaulospora morrowiae* Schenck, Spain, Sieverd. & How | | X | 1.58 | *Sclerocystis sinuosa* (Gerd. & B.K. Bakshi) | X | | 0.40 |
| *Acaulospora spinosa* C. Walker & Trappe | X | | 1.98 | *Scutellospora dipurpurescens* J.B. Morton & Koske | X | X | 5.93 |
| *Claroideoglomus claroideum* (N. C. Schenck & G. S. Sm.) C. Walker & A. Schüßler | | X | 1.98 | *Septoglomus constrictum* (Trappe) Sieverd., G.A. Silva & Oehl | | X | 3.56 |
| *Claroideoglomus etunicatum* (W.N. Becker & Gerd.) C. Walker & A. Schüßler | | X | 1.98 | | | | |

HT: High-input field, HNT: Low-input field. X: Presence of the species. Species names according to Redecker et al. (2013).

and 76% for the HT and HNT fields, respectively (Table 3). Regarding the LD model, the expected number of species was 5.4 and 11.2 for the HT and HNT sites, respectively. Additionally, the proportion of recorded species was 92% for the HT site and 98% for the HNT site. However, the coefficient of determination from the Clench model was 0.99 for both sites (Table 3), indicating the likelihood of finding additional AMF species in these study sites. Moreover, the present study may underestimate the richness and diversity of AMF species, as spore varies between seasons; some species sporulate in late spring, whereas others sporulate in late summer (Prates et al., 2019).

Soil properties differed between the two study sites. The HT field exhibited significantly higher levels of available P and lower levels of exchangeable K and Ca compared to the HNT field ($P \leq 0.05$; Table 4).

**Table 3. Species richness, abundance, diversity indices, and expected species richness of AMF spores at two *Annona muricata* sites under different production systems in Compostela, Nayarit, Mexico.**

| Diversity parameters and sampling effort | Study sites | | Significance (*p-value*) |
|---|---|---|---|
| | HT | HNT | |
| Species abundance (N) | 35 | 218 | 0.0000 |
| Margalef index (d) | 1.1251 | 1.8572 | - |
| Asymptote[a] (a,b) Clench Model[b] | 7.5 | 14.3 | - |
| Asymptote[a] (a,b) LD Model[c] | 5.4 | 11.2 | - |
| r Clench Model | 0.9917 | 0.9991 | - |
| $R^2$ Clench Model | 98.35% | 99.83% | - |
| r LD Model | 0.9847 | 0.9967 | - |
| $R^2$ LD Model | 96.97% | 99.35% | - |

HT: High-input field, HNT: Low-input field. [a]Expected number of species calculated as a/b. [b]Clench model function:. $y = (ax) / 1 + bx$. [c]Linear Dependence model function (LD): $y = a / b * (1 - e^{-bx})$ . r: correlation coefficient between sampling units and observed species. $R^2$: coefficient of determination between variables sampling units and observed species.

**Table 4. Chemical soil characteristics of the rhizosphere soil from *Annona muricata* at two sites under different production systems in Compostela, Nayarit, Mexico.**

| | | $P_a$ | $N_e$ | $K_e$ | $M_{gt}$ | $Mg_e$ | $Ca_t$ | $Ca_e$ | Mycorrhizal variables | |
|---|---|---|---|---|---|---|---|---|---|---|
| Site | EC | (mg kg$^{-1}$) | | | | | | | MC (%) | SD |
| HT | 0.4± 0.2a | 103± 2a | 270± 65a | 338± 90a | 478± 12a | 278± 3a | 12,130±1538a | 1,455± 111a | 32± 2a | 277± 24a |
| HNT | 0.1± 0.04a | 52± 9b | 193± 20a | 1491± 45b | 561± 53a | 231± 22a | 18,562±1650b | 1,834± 227a | 58± 6b | 618± 36b |

HT: High-input field, HNT: Low-input field, EC: electrical conductivity (dS m$^{-1}$), P: phosphorus, N: nitrogen, K: potassium, Mg: magnesium, Ca: calcium. t: total, a: available, e: exchangeable. MC: mycorrhizal colonization (% of root length colonized); SD: spore density (spores per 100 g of dry soil). Values for MC and SD were previously published in González-López et al. (2024). Different letters within each column indicate significant differences according to the Kolmogorov-Smirnov test ($P \leq 0.05$), ± standard error (EC, $N_e$, $K_e$, $Mg_t$, $Mg_e$, $Ca_t$, $Ca_e$) and to the T-student test ($P \leq 0.05$), ± standard error ($P_a$, MC and SD).

Elevated P availability in the HT field may have important ecological implications for arbuscular mycorrhizal fungi (AMF), as it is known to suppress root colonization by reducing the mutualistic nutrient exchange between plants and fungi (Peña-Venegas et al., 2021; Miao et al., 2023). Under such conditions, the mutualistic exchange of resources between plants and AMF is reduced, and plants tend to acquire P directly from the soil, leading to a decline in AMF diversity and niche breadth (Miao et al., 2023).

This reduction in AMF diversity may also be associated with decreased decomposition activity and a shift in nutrient acquisition strategies by the host plant, which further limits AMF functionality under high-P conditions. Additionally, high P inputs promote deterministic assembly processes within AMF communities, favoring species tolerant to elevated P and excluding those adapted to low P environments (Miao et al., 2023). This shift results in less diverse but more competitive fungal assemblages, which may persist under high P conditions but offer reduced functional contributions to nutrient cycling. Such dynamics may explain the lower AMF colonization and spore density observed in the HT field.

The reduced K availability in the HT field may also have ecological consequences for AMF, as potassium plays a central role in plant physiological processes, such as osmoregulation, carbohydrate translocation, and root growth stimulation (Kumar et al., 2024). These enhance root exudation, creating a favorable rhizospheric environment that supports AMF colonization (Albornoz et al., 2024). Moreover, soil K contributes to osmotic regulation in plants, and fluctuations in its availability can indirectly affect AMF community composition and functionality (Albornoz et al., 2024).

In the HT field, a lower AMF spore density was observed (González-López et al., 2024). Mycorrhizal colonization also differed notably

between the two sites. In the HT field, a total colonization was observed with distinct contributions from "coils", vesicles and arbuscules. In contrast, the HNT field exhibited a higher level of colonization, within a larger proportion of "coils" and arbuscule formations compared to the HT field (González-López et al., 2024).

González-López et al. (2024) showed a higher AMF spore density in non- technified sites. This result agreed with Toprak (2017), who also observed a greater spore density in low-input farming systems. Given that the present study is a continuation of González-López et al. (2024), it is reasonable to infer that the HNT site maintains a high spore density. Furthermore, studies have shown that high-input agricultural practices can negatively affect AMF spore density, likely due to factors such as excessive fertilization, tillage, and pesticide use (Elbon and Whalen, 2015). Other research has reported no significant effects of agricultural practices on spore density, suggesting that AMF responses may vary depending on soil type, crop species, and local environmental conditions (Liu et al., 2016). Regarding the degree of mycorrhizal colonization, Knerr et al. (2019) reported higher colonization levels under organic farming systems or unconventional management. These results align with the present study, which reported 58% in the HNT site and 32% in the HT site (González-López et al., 2024). The higher spore density and colonization rates observed in the HNT site may attributed to agronomic management practices. Conventional agricultural practices that affect AMF include crop rotation, tillage, application of fertilizers, pesticides and fungicides, soil aggregation, and the cultivation of genetically modified plants (Agnihotri et al., 2017).

Pearson's correlation analysis showed that total P and K, exchangeable K, and total Ca content significantly influenced spore density and mycorrhizal colonization percentage (Table 5). Available P showed a negative correlation with mycorrhizal colonization percentage. Available P content was 98% higher in the HT field, and total P was 94% higher in the HT field (Table 2 and González-López et al., 2024). In addition, the correlation between spore density and mycorrhizal colonization percentage with total P content was negative, and available P content and mycorrhizal colonization percentage were negatively correlated (Table 3). The inhibition of AMF by high P levels can be considered a negative feedback mechanism that allows the plant to save energy under optimal nutritional conditions without the fungal symbiote (Peña-Venegas et al., 2021). Several authors have shown that phosphorus fertilization may affect AMF colonization differently depending on the form and availability of P in soil. While some report reductions in colonization under high P conditions (Prates et al., 2019), others highlight the role of AMF in enhancing P uptake under low availability scenarios (Qi et al., 2022).

Edaphic characteristics differ between the study sites due to conventional agricultural practices, which may explain the decrease in spore density and colonization indices observed in the HT field (Table 5). A study conducted by Nafady and Elgharably (2018) showed that the AMF response to the available P is variable; fertilization with P can positively or negatively influence spore production. However, our findings suggest that applying fertilizers in the soursop crop may cause a decrease in spore density and mycorrhizal colonization percentage of native AMF species.

The correlation between total and exchangeable K and spore density and mycorrhizal colonization percentage was positive (Table 5). This agrees with Egboka et al. (2022), who reported a positive correlation between the K present in the soil and the spore density and diversity index. This increased spore density may be associated to the role that K plays in plant metabolism (Kumar et al., 2024).

Ca total content was 52% higher in the HNT field and showed a positive correlation with spore density and mycorrhizal colonization percentage (Table 5). Although the relationship between AMF development in roots and Ca

**Table 5. Pearson's correlation coefficients between response variables, spore density (SD) and mycorrhizal colonization (MC), and soil chemical properties of the soil of both commercial soursop sites from Compostela, Nayarit, Mexico.**

| | PMC | pH | EC | $P_t$ | $P_a$ | $N_t$ | $N_a$ | $K_t$ | $K_e$ | $Mg_t$ | $Mg_e$ | $Ca_t$ | $Ca_e$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SD | 0.80* | 0.77* | -0.26 | -0.75* | -0.64 | 0.34 | -0.22 | 0.81* | 0.89* | 0.32 | -0.38 | 0.70* | 0.30 |
| MC | -- | 0.70 | -0.27 | -0.75* | -0.75* | 0.34 | -0.33 | 0.77* | 0.81* | 0.17 | -0.13 | 0.95* | 0.63 |

*Significant correlation (*P≤0.05*). EC: electrical conductivity (dS $m^{-1}$), P: phosphorus, N: nitrogen, K: potassium, Mg: magnesium, Ca: calcium. t: total, a: available, e: exchangeable.

supplementation is poorly understood, some studies have indicated that Ca is essential for AMF colonization. For instance, Cui et al. (2019a) demonstrated the synergy between AMF and exogenous $Ca^{2+}$ in peanut plants, revealing that the application of Ca $(NO_3)_2 \cdot 4H_2O$ at a concentration of 6 mM significantly enhanced root colonization by the AMF species *F. mosseae*. Additionally, Cui et al. (2019b) found that exogenous $Ca^{2+}$ application up-regulated the expression levels of specific genes involved in AMF symbiosis (*AhRAM1* and *AhRAM2*). These findings are consistent with the present study, which found a positive correlation between Ca and spore production, and colonization percentage (Table 3). However, further research is needed to better understand the interaction between Ca and HMA development in plants. Our understanding of the relationships between soil characteristics, spore density, and mycorrhizal colonization percentage still needs to be improved. However, the present study reports a positive correlation between soil pH and spore density (Table 5). Highly acidic or alkaline soils can suppress the germination of spores and presymbiotic hyphal growth; however, Muthukumar et al. (2014) reported that the optimum pH for spore germination is linked to the pH of the soil from which the AM fungus originated. The variation in soil pH can alter the concentration of many nutrients and toxic ions in the soil, thereby affecting the development and function of AMF (Birhane et al., 2020).

Table 5 shows the positive correlation observed between mycorrhizal colonization percentage and spore density. These two variables are closely related, as the factors that promote or hinder AMF sporulation similarly influence root colonization. In annual plants, spore density and colonization rate can increase simultaneously during growing stages. Nevertheless, this relationship is influenced by other factors, such as soil characteristics and cultivation stage, and may vary in each specific case (Ma et al., 2023).

According to the RDA analysis, which was used to determine the effect of chemical soil variables (pH, $P_t$, $P_d$, $K_t$, $K_e$, $N_t$, $Ca_t$, and $Ca_e$) on the AMF community in *Annona muricata* rhizosphere, the selected soil variables collectively explained 94.9% of the total constrained variation in AMF composition (Fig. 3).

Although statistical validation of the full RDA model was not feasible due to the lack of residual degrees of freedom, the ordination diagram indicated that *F. geosporum*, *A. kentinensis*, *R.*

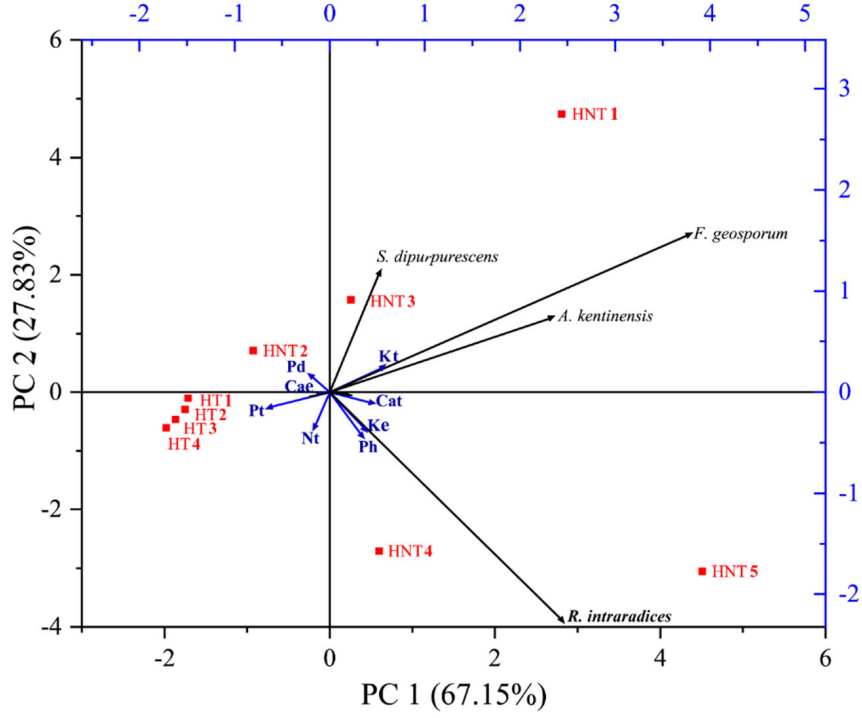


**Fig 3. Redundancy analysis of soil variables (blue vectors) and AMF abundance (black vectors). Sampled sites are shown in red. The first two components explained 94.98% of the total variance. Pa, available phosphorous. Pt, total phosphorous. Nt, total nitrogen. Kt, total potassium. Ke, exchangeable potassium. Cat, total calcium. Cae, exchangeable calcium.**

*intraradices*, and *S. dipurpurescens* were more abundant in the HNT site, which also exhibited higher concentrations of total potassium (Kt) (Fig. 3). These patterns may reflect a potential influence of Kt on the relative abundance of certain AMF species in agroecological systems.

The HNT management system exhibited heterogeneity in AMF species richness and soil properties; some sites had more AMF species than other sites, while HT sites were homogeneous, with low diversity and lower Kt, Ke, and Ca levels than HNT sites (Fig. 3).

Some authors observed the relation between some AMF genera and soil chemical properties. For instance, Liu et al. (2022) observed that *Glomus* abundance in winter wheat fields of northwest China was driven positively by available P and pH.

Our results agreed with those of Melo et al. (2019), who found that Mg and K contents in the soil influence the abundance of Glomeraceae members. Moreover, K content positively affected other AMF families, such as Gigasporaceae and Diversisporaceae. Some authors suggest that this effect could result from compensation for the ionic imbalance induced by high Na levels in soils, as K addition can help maintain cellular water balance (Zhang et al., 2021). Nonetheless, further research is required to clarify the relationship between soil nutrients and AMF diversity.

Agroecological practices mitigate the impacts of conventional agriculture by decreasing competition among native AMF species and the toxicity of agrochemicals; the high levels of diversity found in agroecological systems may be related to the availability of niches due to the heterogeneity of the site (Prates et al., 2019).

Although our findings are consistent with previous reports, they should be interpreted with caution due to the exploratory nature of the RDA and the lack of formal statistical validation. Further research involving larger sample sizes, multi-seasonal sampling, and complementary molecular techniques is recommended to confirm the observed patterns.

This study was constrained by its single-season sampling design and a relatively small number of biological replicates per site, largely due to logistical challenges associated with mature orchards. Additionally, the exclusive use of morphological identification may have resulted in an underestimation of AMF diversity. Despite these limitations, the findings provide valuable preliminary insights into the potential influence of agricultural management practices and soil chemical properties on AMF community structure in *Annona muricata* orchards.

## CONCLUSIONS

Data confirmed that AMF communities associated with *Annona muricata* under organic or agroecological management (low-input field, HNT) exhibited greater species richness, abundance, and diversity compared to those in a conventional production system (high-input field, HT). A total of 13 species belonging to seven genera were identified, with *Funneliformis geosporum*, *Acaulospora kentinensis*, and *Rhizophagus intraradices* being the most abundant. Genera such as *Claroideoglomus, Rhizophagus*, and *Acaulospora* were more prevalent under HNT conditions, while fewer and less diverse taxa were found under HT management. Notably, statistical analyses revealed that available phosphorus (P) was negatively correlated with both AMF colonization and spore density, while total potassium (K) and calcium (Ca) showed positive correlations with these variables. Additionally, the redundancy analysis (RDA) indicated that the higher abundance of dominant AMF species in the HNT site could be associated with increased K and Ca levels. These findings underscore the influence of agronomic practices on soil nutrient dynamics and their cascading effects on AMF diversity and structure. Therefore, reduced chemical input and minimal soil disturbance promote richer AMF communities, supporting the use of sustainable practices in soursop cultivation.

Future research should focus on evaluating seasonal dynamics of AMF communities, assessing the influence of other agronomic factors such as tillage and agrochemical use, and determining how changes in AMF diversity impact nutrient uptake and fruit productivity in *Annona muricata*. Elucidating these relationships will help optimize sustainable management strategies for this crop.

## ACKNOWLEDGEMENTS

This study was partially financed by projects of the Plant Pathology Laboratory at Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco A.C. (CIATEJ), Mexico, and the FOMIX-Michoacán CONACyT (MICH-2010-03-148208). A. M. González-López thanks SECIHTI (CONAHCYT) for providing the scholarship for her master's studies.

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