frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 10 December 2025
DOI 10.3389/fevo.2025.1702917

OPEN ACCESS

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RECEIVED 10 September 2025
REVISED 18 November 2025
ACCEPTED 24 November 2025
PUBLISHED 10 December 2025

CITATION
Cáceres-Mago K, Cáceres A, Ávila-Lovera E and Tezara W (2025) Effect of arbuscular mycorrhizal fungi on the physiological traits and growth of three woody species from a tropical dry forest. *Front. Ecol. Evol.* 13:1702917. doi: 10.3389/fevo.2025.1702917

Effect of arbuscular mycorrhizal fungi on the physiological traits and growth of three woody species from a tropical dry forest

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The tropical dry forests (TDFs) of the Macanao Peninsula (Margarita Island, Venezuela) have been severely degraded by open-cast sand mining for over four decades, reducing vegetation cover and disrupting soil biological processes, including those mediated by arbuscular mycorrhizal fungi (AMF). To assess whether enriching native AMF communities can improve plant performance, we evaluated the physiological traits and growth of three woody species (*Bulnesia arborea, Caesalpinia mollis* and *Piptadenia flava*) grown for eight months under greenhouse conditions in noninoculated (NI) and inoculated (I) treatments, both using the same non-sterile forest soil to ensure that inoculation represented enrichment of the native AMF community, which reflects realistic restoration scenarios. Species differed markedly in their responses: in *B. arborea*, AMF enrichment increased net photosynthetic rate and stomatal conductance by 50% and 31%, respectively, and significantly enhanced the maximum rate of RuBisCO carboxylation and biomass accumulation; in *C. mollis*, inoculation increased CO_2-saturated photosynthetic rate but did not affect growth; and in *P. flava*, inoculated plants showed greater shoot biomass and root length despite no detectable changes in photosynthetic parameters. These species-specific responses suggest that *B. arborea* may hold potential for future restoration testing in the Macanao Peninsula, and further ecological evaluation is needed before selecting species for restoration.

KEYWORDS

gas exchange, chlorophyll fluorescence, fungal inoculation, photosynthesis, restoration

1 Introduction

Tropical dry forests (TDFs) constitute over 40% of the world's tropical forests (Murphy and Lugo, 1995) and comprise tree communities adapted to warm climates and seasonal droughts (Santos et al., 2022; Oyedeji, 2023). These ecosystems are among the most threatened due to anthropogenic activities, which degrade soil properties, vegetation structure, and environmental conditions (Fajardo et al., 2013; Ávila-Lovera et al., 2023; Mesa-Sierra et al., 2025). Recognized for their high endemism and timber species richness, TDFs are rapidly disappearing, emphasizing the need for research and restoration efforts in this biome (Banda et al., 2016; Shahzad et al., 2024). Restoring degraded areas is crucial for conserving biodiversity and improving ecosystem services, particularly when native species are used (Bertolazi et al., 2025).

Soil disturbance during deforestation, such as that caused by opencast mining, disrupts essential biological processes, including those mediated by arbuscular mycorrhizal fungi (AMF), key mutualistic symbionts in terrestrial ecosystems (Xu et al., 2023a). AMF form associations with most tropical and dryland plant species, enhancing the uptake of water and nutrients (particularly P and N) while providing protection against root pathogens (Wahab et al., 2023). Through their extensive extraradical mycelium and the production of glomalin, AMF improve soil aggregation and water retention, thereby enhancing plant stomatal conductance, transpiration, and photosynthetic performance (Shukla et al., 2025; Zaman et al., 2025). These functions are particularly critical in arid and semi-arid ecosystems such as TDFs, where limited water and nutrient availability constrain plant establishment and survival, and AMF enhance plant drought tolerance by improving root absorptive capacity, hydraulic continuity, and water-use efficiency during dry periods (Shukla et al., 2025). Beyond individual plant benefits, AMF promote long-term soil recovery and ecosystem resilience through improved soil structure and organic matter stabilization (Li et al., 2024). This ecological facilitation underlies their growing use in restoration programs of degraded TDFs, where AMF enhance seedling establishment, water relations, and overall soil functionality, offering a sustainable bio-alternative to chemical fertilization.

In the Macanao Peninsula, Margarita Island, Venezuela, four decades of open-cast sand mining have caused severe deforestation and habitat destruction (González, 2007). Mining is considered one of the main causes of deforestation in the region, involving excavation and a transport system, with negative impacts that lead to soil erosion, damage to wildlife habitat, and changes in soil hydrology (Chambi-Legoas et al., 2021; Moulatlet et al., 2023). Studies in TDFs impacted by mining suggest that native species from mature forests can thrive in disturbed sites, supporting their use in ecological restoration plans (Ávila-Lovera et al., 2023; Bertolazi et al., 2025).

Research in Macanao has demonstrated that AMF inoculation enhances growth, physiological performance, and survival of native plants under both drought and well-watered conditions (Cáceres et al., 2014; Tezara et al., 2014). For instance, *Piscidia carthagenensis* (Fabaceae) inoculated with native AMF exhibited improved gas exchange and water-use efficiency compared to control plants planted in a disturbed area (Kalinhoff, 2012). Eight years postrevegetation, soil quality improvement, including enhanced chemical and microbiological properties, was observed in restored sites (Sierraalta et al., 2021).

Despite evidence that AMF enhance physiological parameters such as photosynthetic rate, stomatal conductance, and water potential under drought stress (Frosi et al., 2016; Chen et al., 2020; Rani et al., 2023), their role remains underexplored in restoration plans for Macanao's semi-arid ecosystems. To address this knowledge gap and support restoration planning, three native woody species with contrasting functional traits were selected to test their responses to AMF enrichment using an inoculum obtained from soils of the Macanao TDF (Table 1). *Bulnesia arborea*, *Caesalpinia mollis*, and *Piptadenia flava* were chosen based on the following criteria: (a) they are all native species, (b) they present rapid growth, and (c) they belong to families of high ecological importance in these TDFs and associated xerophytic scrubs. *B. arborea* is a dominant species in the riparian deciduous forest of the Macanao Peninsula. Both *C. mollis* and *P. flava* belong to the Fabaceae family, the most species-rich in Venezuelan TDFs and the largest group present in the study area (Fajardo, 2007). Furthermore, *C. mollis* is classified as vulnerable (VU) according to the Red Book of Venezuelan Flora (Huérfano et al., 2020), warranting special conservation attention. These species are also ecologically important for the yellow-shouldered parrot (*Amazona barbadensis*), an endangered species endemic to the region. *B. arborea* and *C. mollis* are the primary trees used for nesting during the reproductive period, while the flowers and fruits of *B. arborea* and the seeds of *P. flava* are a significant part of the parrot's diet (González, 2007; Rojas-Suárez, 2014).

This study evaluated how AMF enrichment, through the inoculation of native communities, influences the physiological performance and growth of these three woody species, focusing on gas exchange, photochemical activity, and biomass production. We hypothesized that AMF enrichment would promote species-specific responses reflecting their contrasting adaptations to

TABLE 1 Tree plant species studied in a tropical dry forest of the Macanao Peninsula, including family, leaf habit, and means ± SE of height and diameter at breast height (DBH) (modified from Ávila-Lovera et al., 2019).

Species	Family	Leaf habit	Height (m)	DBH (cm)
Bulnesia arborea (Jacq.) Engl.	Zygophyllaceae	Drought deciduous	13.3 ± 2.9	95.0 ± 22.7
Caesalpinia mollis (Kunth) Spreng.	Fabaceae	Drought deciduous	8.7 ± 0.7	54.9 ± 8.7
Piptadenia flava (Spreng. ex DC.) Benth.	Fabaceae	Evergreen	3.8 ± 0.9	11.7 ± 2.7.

drought, water-use efficiency, and nutrient acquisition strategies. The outcomes of this study aim to inform restoration strategies for degraded areas in Macanao, contributing to global efforts to recover TDFs—an ecosystem of high conservation priority, yet often overlooked compared to tropical wet forests.

2 Materials and methods

2.1 Study area

The field component of this study was conducted in the Macanao Peninsula, a mountainous region in the western part of Margarita Island (10°56′–11°06′N; 64°10′–64°25′W), approximately 38 km off the coast of mainland Venezuela. The climate of Macanao is semi-arid, with a mean annual temperature of 27° ± 0.3°C and an average annual precipitation of 524 mm ± 87 mm, based on climate data recorded from 1986 to 2006 at the San Francisco de Macanao meteorological station (11°01′30″N, 64°17′26″W; Ávila-Lovera et al., 2019). Precipitation peaks occur in August, with a secondary, smaller peak in December, while the dry season extends from January to June (Fajardo et al., 2013).

Sand extraction in the region has been ongoing for over 46 years, and following the abandonment of mining sites, vegetation recovery is notably slow due to the removal of the soil seed bank and the region's characteristic aridity (González, 2007).

The TDF of the Macanao Peninsula represents a mature plant community dominated by *Spondias mombin* (Anacardiaceae), *Lonchocarpus punctatus* (Fabaceae), *Handroanthus chrysanthus* (Bignoniaceae), *Handroanthus serratifolius* (Bignoniaceae), *Bulnesia arborea* (Zygophyllaceae), and *P. carthagenensis* (Fabaceae) (González, 2007). This forest serves as the reference ecosystem prior to disturbance, with its lowland areas among the plant communities most threatened by sand mining. Excavated areas are typically abandoned after mining activities, allowing for natural regeneration of vegetation in and around the mine sites, although this process is extremely slow and is often interrupted by the resumption of mining activities after 20–25 years of abandonment.

2.2 Field measurements

To compare the physiological performance of greenhouse-grown plants with that of adult trees in the study area, gas exchange and photochemical activity traits were assessed in adult trees from the TDF located in the Macanao Peninsula during the rainy season of the year (see details below).

2.3 Greenhouse experiment

The greenhouse experiment was carried out at the Institute of Experimental Biology, Central University of Venezuela, located in Caracas (10°24′N, 67°36′W; 1200 masl). The greenhouse was covered with transparent polyethylene and maintained under natural light conditions. During the experiment, air temperature ranged from 20°C to 26°C, relative humidity varied from 83% to 65%, maximum photosynthetic photon flux density reached 550 μmol m^{-2} s^{-1}, and vapor pressure deficit ranged between 0.4 and 1.6 kPa. Measurements were taken at 08:00 and 13:00 hours, indicating relatively stable microclimatic conditions with moderate daily fluctuations (see Supplementary Table S1 for microclimatic values in both the greenhouse and the field).

Seeds were collected from relatively undisturbed xerophytic scrubs and deciduous forests in the surroundings of mining activity areas. They were stored in plastic bags in a cool environment until transferred to the greenhouse. In the greenhouse, seeds were planted in germination trays, and after the emergence of the first true leaves, 60 seedlings of each species were transplanted into 3 kg polyethylene bags and assigned to two experimental treatments: (1) nonsterile control, with 30 seedlings of each species planted in unsterilized forest soil without AMF inoculum (not inoculated (NI)), and (2) inoculated treatment, with 30 seedlings of each species planted in unsterilized forest soil supplemented with 50 g of AMF inoculum (inoculated (I)). Plants were watered regularly throughout the experiment, and after 8 months of growth (240 days), gas exchange, photochemical activity, response curves of photosynthesis (A) to intercellular CO_2 concentration (C_i) (A/C_i curves), and growth variables were measured.

It is important to note that both treatments were established using the same unsterilized forest soil to preserve the native microbial and AMF community naturally present in the substrate. This approach provided ecologically realistic conditions that simulate field restoration scenarios, where soils are never sterile. Therefore, the I treatment represents an enrichment of the native AMF community compared with the NI treatment.

2.4 Soils and AMF inoculum

The soil used in the greenhouse experiment was collected from the TDF of the study area and was characterized as moderately alkaline, with a pH of 7.87 ± 0.08, low P concentration (7.37 ppm ± 1.02 ppm), high N concentration (0.74% ± 0.04%), and elevated soil organic matter content (13% ± 6.3%), according to the classification criteria of the Ministerio de Obras Públicas (MOP) (1972).

To characterize the native AMF community present in these soils, AMF spores were extracted from rhizospheric soil samples collected from adult individuals of the studied plant species. Spores were isolated from 5 g of soil (in triplicate) using the wet-sieving, decanting, and sucrose centrifugation method described by Sieverding et al. (1991). Only intact spores with visible lipid reserves were counted under a stereomicroscope (× 40), and results were expressed as the number of spores per 100 g of dry soil. Morphological identification of AMF morphospecies was based on spore characteristics such as size, wall type and number, color in water and in polyvinyl alcohol mounting medium, reaction to Melzer's reagent, and other diagnostic features such as

ornamentation, subtending hyphae, or scars when present. Morphospecies were identified using the descriptions and identification keys of Schenck and Pérez (1990) and the International Culture Collection of Arbuscular Mycorrhizal Fungi (INVAM, https://invam.ku.edu/species-descriptions). The AMF community identified in these soils (Table 2) represents the natural assemblage used as the basis for preparing the mixed inoculum.

The AMF inoculum was then prepared using the trap pot method, which consists of preparing a suitable substrate for fungal development and using a highly mycotrophic plant species to promote rapid root colonization and sporulation, generating infective AMF propagules in the soil (Sieverding et al., 1991). For this purpose, plants of *Vigna luteola*, a highly mycotrophic herbaceous legume (Hernández et al., 2000), were grown in pots containing fresh soil from the TDF to obtain a mixed AMF inoculum (Bever, 1994). After 8 months of cultivation, the aerial parts of the plants were harvested, and the roots were preserved as part of the inoculum. This method allowed an increase in the AMF propagule density in the substrate, reaching 860.67 spores per 100 g of soil ± 120.81 spores per 100 g of soil, between 12 and 30 times higher than the spore density found in the rhizospheric soil of the studied species (Table 2).

Additionally, root samples from the experimental greenhouse plants were collected at harvest and examined microscopically to verify the presence of mycorrhizal structures, confirming that the seedlings had established AMF colonization during the experiment. Fine root fragments were cleared in 10% KOH, acidified with 1% HCl, stained with trypan blue (Phillips and Hayman, 1970), and examined under a light microscope (Nikon Eclipse E200, Tokyo, Japan) for the presence of hyphae, vesicles, and arbuscules.

2.5 Instantaneous gas exchange

Net photosynthetic rate (A), transpiration rate (E), and stomatal conductance (g_s) were measured in leaves of five trees per species in the field and 10 individuals per species per treatment in the greenhouse between 08:00 and 11:00 hours using an open-system portable infrared gas analyzer (CIRAS-II, PP Systems Inc., Amesbury, MA, USA) connected to a leaf chamber PLC(B) at a CO_2 concentration of 400 μmol mol^{-1} ± 10 μmol mol^{-1}, a leaf chamber temperature of 29.0°C ± 0.3°C, leaf-to-air vapor pressure deficit (Δ_W) of 1.6 kPa ± 0.01 kPa, and photosynthetic photon flux density (PPFD) of 1,500 μmol m^{-2} s^{-1} ± 50 μmol m^{-2} s^{-1} (light was provided by a LED-based light unit from the same manufacturer).

TABLE 2 Morpho-species of arbuscular mycorrhizal fungi (AMF) isolated from tropical dry forest soils in the Macanao Peninsula.

Morpho-species	Family	*B. arborea*	*C. mollis*	*P. flava*
Diversispora spurca	Diversisporaceae	X		
Diversispora cf. tortuosum	Diversisporaceae	X		
Entrophospora infrequens	Entrophosporaceae			
Funneliformis geosporum	Glomeraceae	X	X	
Gigaspora 1	Gigasporaceae			
Gigaspora 2	Gigasporaceae			
Glomus sp. 1	Glomeraceae			
Glomus sp. 2	Glomeraceae	X		X
Glomus sp. 3	Glomeraceae		X	
Glomus sp. 4	Glomeraceae		X	X
Glomus sp. 5	Glomeraceae	X		
Glomus sp. 6	Glomeraceae			
Rhizophagus aggregatus	Glomeraceae		X	X
Rhizophagus intraradices	Glomeraceae			
Sclerocystis sinuosa	Glomeraceae			X
Sclerocystis sp. 1	Glomeraceae	X		
Sclerocystis sp. 2	Glomeraceae	X	X	X
Septoglomus deserticola	Glomeraceae	X	X	
Total number of morphotypes of AMF		8	6	5
Spore density (spores 100 g^{-1} soil)		27.3 ± 6.1	71.0 ± 4.6	61.7 ± 40.2

Those that were present in the rhizospheric soil of the studied species, and their total spore density under natural conditions in the TDF in the Macanao Peninsula, are indicated by an X. Spore density is the average count ± standard error (n=3) of the total number of spores per 100 g soil (courtesy of Dr. Kalinhoff).

Instantaneous measurements were made on fully expanded healthy leaves. Intercellular CO_2 concentration (C_i) was calculated by the program in the CIRAS, after Farquhar et al. (1980). Instantaneous water-use efficiency was estimated as WUE=A/E.

2.6 A/C_i curves

For each species, A/C_i curves (n=5) were determined in well-irrigated plants in both treatments (NI and I) by decreasing atmospheric CO_2 concentration (C_a) from 400 µmol mol^{-1} to zero, and then progressively increasing C_a from zero to 1,800 µmol mol^{-1}. The CO_2 was provided by a cylinder filled with pure gas connected to the IRGA. Conditions during A/C_i measurements were the same as in the instantaneous measurements. The A/C_i curves were fitted to an empirical equation where $A=b + d\ e^{kCi}$ (Tezara et al., 2003). Carboxylation efficiency (CE) was calculated from the initial slope of the curve, and the CO_2 compensation point was calculated as Γ=Ln $(-\ b/d)/k$. Relative stomatal limitation (L_s) was calculated as $L_s=100 \times (A_o - A)/A_o$, where A_o is A at $C_i=C_a$ and A is the net photosynthesis rate measured at C_i=280 µmol mol^{-1} (Farquhar and Sharkey, 1982). Relative mesophyll limitation (L_m) was calculated as $L_m=100 \times (A_I - A_{NI})/A_I$, where A_I is A of leaves in inoculated plants at C_i=800 µmol mol^{-1}, and A_{NI} is A of leaves in noninoculated plants at the same C_i (Jacob and Lawlor, 1991). Thus, L_m is a measure of the capacity of the mesophyll to fix CO_2 at saturating C_i, and its value in inoculated plants was assumed to be minimum. Maximum rate of RuBisCO carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}), and triose phosphate utilization rate (TPU) were calculated from the A/C_i curves using the model proposed by Sharkey (2015).

2.7 Chlorophyll *a* fluorescence of PSII

Maximum quantum yield of PSII (F_v/F_m) was measured on attached dark-adapted leaves at predawn in well-irrigated plants using a fluorometer (PAM 2100, WALZ, Effeltrich, Germany) following the protocol described by Genty et al. (1989). Variable fluorescence (F_v) is $F_m - F_0$, where F_0 and F_m are dark-adapted minimum and maximum fluorescence, respectively. Relative quantum yield of PSII at steady-state photosynthesis was calculated as $\Phi_{PSII}=(F'_m - F_s)/F'_m$, where F_s and F'_m are fluorescence at steady-state photosynthesis and maximum fluorescence in light, respectively. Electron transport rate through PSII (J) was estimated as $J=\Phi_{PSII} \times PPFD \times \alpha \times 0.5$, where α is the fraction of incident PPFD absorbed by the leaf, assumed to be 0.84 (Krall and Edwards, 1992). The photochemical ($q_P=(F'_m - F_s)/(F'_m - F'_0)$) and nonphotochemical ($q_N=1 - (F'_m - F'_0)/(F'_m - F'_0)$) quenching coefficients were also calculated. Fluorescence parameters were measured simultaneously on the same leaves where gas exchange was measured in five trees per species in the field and 10 plants per species per treatment in the greenhouse.

2.8 Growth variables

After physiological measurements in the greenhouse, 10 plants per species per treatment were harvested to carry out a growth analysis. The number of leaves of each plant was counted, and the shoots and roots were separated. Roots were washed, and soil particles were removed. Total root length was measured using the WinRHIZO Pro program (version 2003b, Regent Instrument, Quebec, Canada). Shoots and roots were dried in an oven at 60°C for 48 h and weighed to determine shoot, root, and total biomass. The shoot–root ratio (S:R) was determined by dividing the shoot dry mass by the root dry mass. Based on the total plant biomass, the mycorrhizal response index (MRI) was calculated as MRI=[(DW(I) – DW(NI))/DW(I)] × 100, where DW(I) is the dry weight of the inoculated plant and DW(NI) is the dry weight of the noninoculated plant. The MRI is considered an indirect indicator of the plant's response to AMF inoculation and of the functional effectiveness of the mycorrhizal symbiosis, as it does not directly quantify root colonization by fungi but rather the functional outcome of that colonization on plant performance, expressed here in terms of growth (biomass).

2.9 Statistical analysis

Data analysis was performed using Statistica v10 (StatSoft Inc., Tulsa, OK, USA). A one-way analysis of variance (ANOVA) was conducted to determine the significant differences in the variables evaluated among species in the field. In the greenhouse experiment, a two-way ANOVA was applied to all response variables, using species and inoculation treatment as fixed factors. Prior to the analysis, the assumptions of normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test) were verified, and data were transformed when necessary to meet these criteria. When significant effects were detected, Tukey's *post-hoc* test was used for mean comparisons at a significance level of p=0.05. All results are presented as means ± standard error (SE). Graphical representations were produced in SigmaPlot 14.0 (Systat Software, San Jose, CA, USA).

3 Results

3.1 Field measurements

The three tree species studied differed significantly in height, with *B. arborea* and *C. mollis* being deciduous and *P. flava* evergreen (Table 1). Significant differences were found in almost all the physiological traits related to gas exchange (E, g_s, and WUE) and in q_N among the species in the field (Table 3). Values of A ranged from 4.9 to 6.4 µmol m^{-2} s^{-1}, showing no significant differences among species. In contrast, E (1.9–3.2 mmol m^{-2} s^{-1}), g_s (162.3–423.1 mmol m^{-2} s^{-1}), and WUE (1.8–2.9 mmol mol^{-1}) differed significantly

TABLE 3 Physiological traits measured in the field during the wet season for adult trees from TDF.

Physiological traits	*B. arborea*	*C. mollis*	*P. flava*	*p*
Gas exchange (n=5)				
A (μmol m^{-2} s^{-1})	5.2 ± 0.7 a	4.9 ± 0.6 a	6.4 ± 2.0 a	0.3257
E (mmol m^{-2} s^{-1})	3.2 ± 0.9 b	2.8 ± 0.6 b	1.9 ± 0.2 a	0.0000*
g_s (mmol m^{-2} s^{-1})	162.3 ± 23 a	291.9 ± 56 a	423.1 ± 74 b	0.0000*
WUE (mmol mol^{-1})	2.9 ± 0.2 b	1.9 ± 0.1 a	1.8 ± 0.3 a	0.0002*
Photochemical activity (n=5)				
F_v/F_m	0.81 ± 0.007 a	0.83 ± 0.004 a	0.83 ± 0.007 a	0.2733
J (μmol e^- m^{-2} s^{-1})	75.1 ± 6 a	74.7 ± 5 a	75. 8 ± 7 a	0.2900
ϕ_{PSII}	0.13 ± 0.01 a	0.14 ± 0.01 a	0.11 ± 0.01 a	0.2532
q_P	0.22 ± 0.02 a	0.22 ± 0.02 a	0.19 ± 0.02 a	0.5081
q_N	0.94 ± 0.007ab	0.93 ± 0.008 a	0.96 ± 0.003 b	0.0318*

Gas exchange traits include net photosynthetic rate (A), transpiration rate (E), stomatal conductance (g_s), and water use efficiency (WUE). Photochemical activity traits include maximum quantum yield (F_v/F_m), electron transport rate (J), relative quantum yield of PSII (Φ_{PSII}), photochemical quenching (q_P), and nonphotochemical quenching coefficient (q_N). Data are shown as mean ± standard error. *p-values indicate statistical significance ($p \leq 0.05$) based on Tukey's test for comparisons among species.

($p < 0.001$) among species. *P. flava* differed significantly from the other two species, with notably higher g_s values, whereas *B. arborea* showed the highest WUE. Photochemical activity parameters showed no signs of photoinhibition, as F_v/F_m values remained between 0.81 and 0.83 during the study period. Values of J (74.7–75.8 μmol e^- m^{-2} s^{-1}), Φ_{PSII} (0.11–0.14), and q_P (0.19–0.22) did not differ among species (Table 3).

3.2 Greenhouse experiment

A total of 18 AMF morphospecies were identified in the soils of the TDF of the Macanao Peninsula, which were used to produce the native inoculum applied in the greenhouse experiment. The AMF community was dominated by species of the genus *Glomus* (nine species), followed by *Sclerocystis* (three species), and *Diversispora*, *Gigaspora*, and *Rhizophagus* (two species each). The remaining AMF genera were represented by a single species. This composition reflects the naturally occurring AMF community in the study area and was used to inoculate the seedlings of *B. arborea*, *C. mollis*, and *P. flava*.

3.2.1 Effects of AMF inoculation on physiological traits

The effects of AMF inoculation on physiological traits were species-dependent (Supplementary Table S2). The AMF inoculation in *B. arborea* plants caused a significant increase in A (p=0.0001) and g_s (p=0.0409) of 50% and 31%, respectively, compared to the NI plants, with no significant differences in E, C_i, and WUE (Figure 1). A significant species × inoculation interaction was observed for A (p =0.0177), but not for g_s, E, C_i, or WUE. *B. arborea* showed higher A, g_s, and E than *C. mollis* and *P. flava*. Significant species effects were observed in leaf photochemical activity parameters such as F_v/F_m (p=0.0002), J (p=0.0038), Φ_{PSII} (p=0.0018), and q_N among species, while q_P was not affected. However, no significant effects of inoculation or species × inoculation interactions were detected for the photochemical variables.

Analyzing the A/C_i curves, significant increases in A_{sat} were found in *B. arborea* and *C. mollis* plants inoculated with AMF, whereas in *P. flava*, inoculation had a negative effect on the photosynthetic capacity, decreasing A_{sat} (Figure 2). Inoculation significantly increased V_{cmax} in *B. arborea* (p =0.0560, Figure 3), and a significant species × inoculation interaction was observed for J_{max} (p=0.0107) and TPU (p=0.0094). For all species, no changes in Γ, L_s (58 μmol mol^{-1} and 18.33%, respectively), or L_m were observed between treatments, species, or due to the species × inoculation interaction (Figure 3).

Overall, AMF enrichment enhanced photosynthetic performance only in *B. arborea*, while *C. mollis* and *P. flava* showed no consistent improvements, underscoring the species-specific nature of the physiological responses to the symbiosis.

3.2.2 Effects of AMF inoculation on plant growth

AMF inoculation and species significantly influenced most growth variables, while species × inoculation interactions were generally not significant (Supplementary Table S3). Inoculation did not significantly affect the number of leaves, although this trait differed among species ($p < 0.0001$).

Inoculation with AMF resulted in larger plants and a greater root system overall (Figure 4). AMF inoculation significantly increased root and total biomass in *B. arborea* (p=0.0217 and p=0.0126, respectively) and shoot biomass and root length in *P. flava* (p=0.0254 and p=0.0061, respectively). Inoculation did not significantly affect S:R, although species differences were significant ($p < 0.0001$). The values obtained for the S:R ratio indicate that, in all treatments, the plants showed a greater allocation of biomass to

10.3389/fevo.2025.1702917

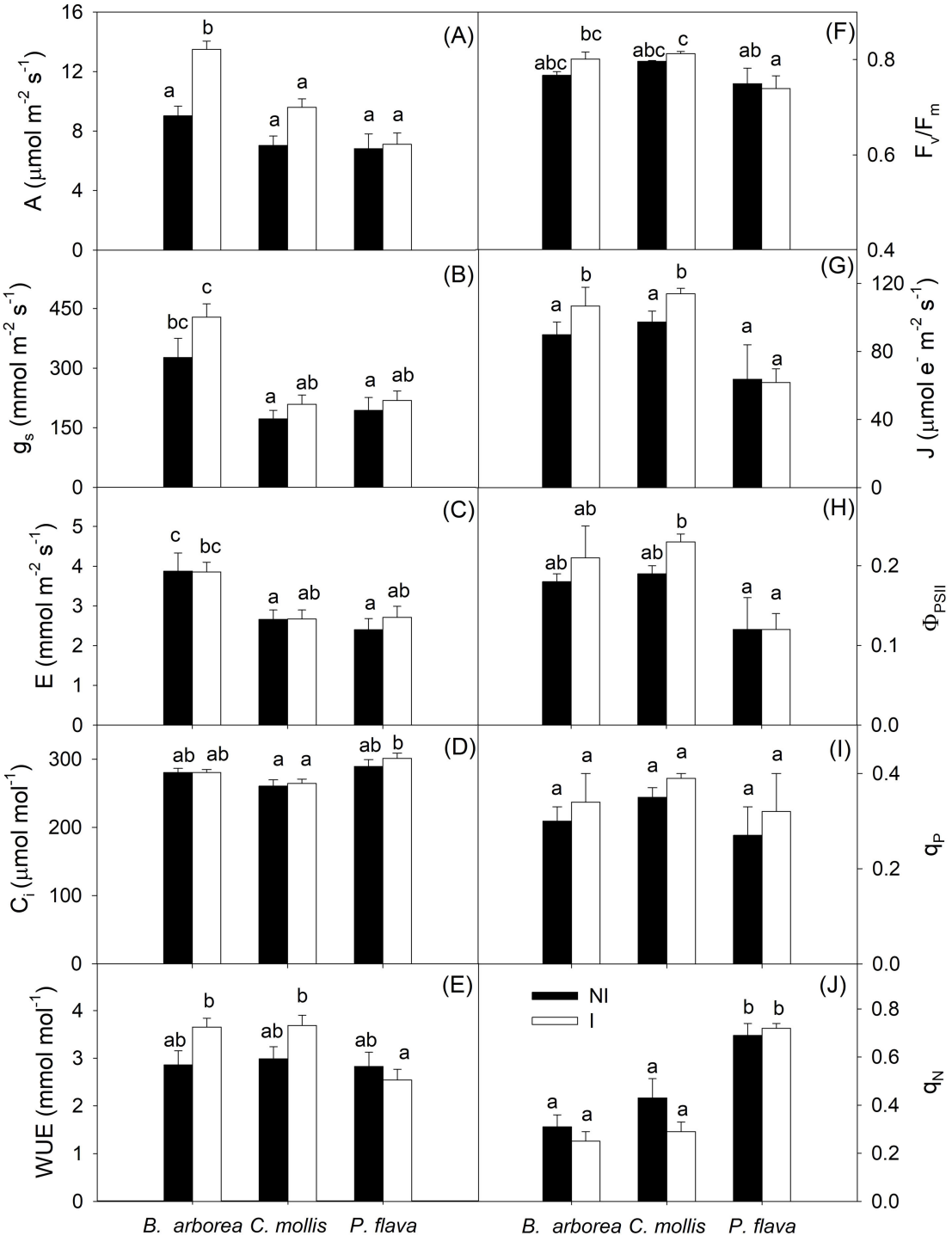

FIGURE 1
Instantaneous gas exchange parameters in the greenhouse: **(A)** net photosynthetic rate [A], **(B)** stomatal conductance [g_s], **(C)** transpiration rate [*E*], **(D)** intercellular CO_2 concentration [C_i], **(E)** water use efficiency (WUE), and photochemical parameters: **(F)** maximum quantum yield [F_v/F_m], **(G)** electron transport rate [*J*], **(H)** relative quantum yield of PSII [Φ_{PSII}], **(I)** photochemical quenching coefficient [q_P], and **(J)** nonphotochemical quenching coefficient [q_N] measured in leaves of *B. arborea*, *C. mollis*, and *P. flava*, in noninoculated (black bars) and AMF-inoculated (white bars) plants. Values are means ± standard error (n=10). Different letters indicate statistical differences at $p \leq 0.05$.

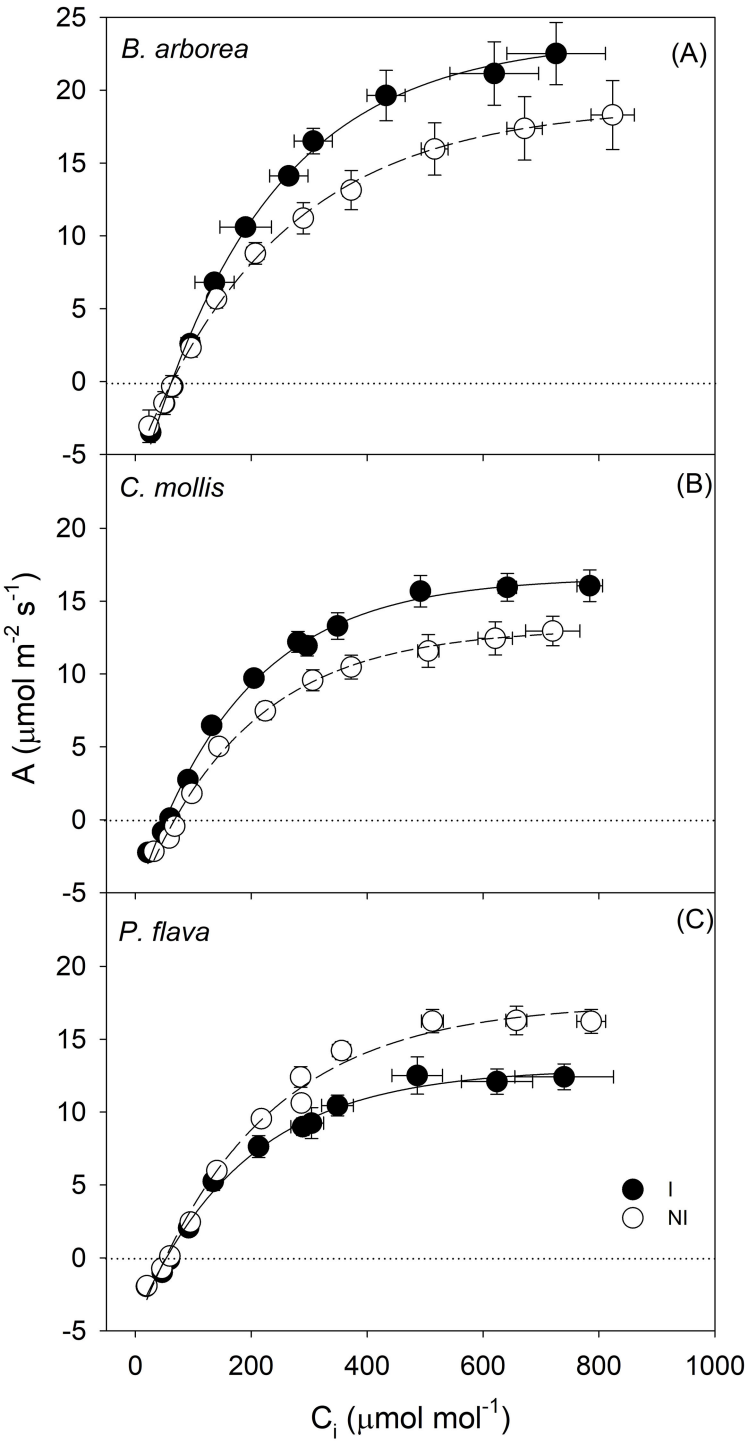

FIGURE 2
Responses of leaf photosynthetic rate (*A*) to intercellular CO_2 concentration (C_i) in leaves of **(A)** *B. arborea*, **(B)** *C. mollis*, and **(C)** *P. flava*, in noninoculated (black circles) and AMF-inoculated (white circles) plants. Values are means ± standard error (n=5), and standard errors are shown when larger than the symbol size.

the aboveground part (Figures 4, 5). Species effects were significant for all biomass and root traits, and no significant species × inoculation interactions were detected. *B. arborea*, *C. mollis*, and *P. flava* responded to AMF inoculation, albeit to different degrees, with MRI of 31%, 3%, and 23%, respectively.

Growth responses to AMF enrichment were also species-dependent, with marked biomass increases in *B. arborea*, partial enhancement in *P. flava*, and no significant effects in *C. mollis*, confirming that the magnitude of AMF-induced growth stimulation varied among host species.

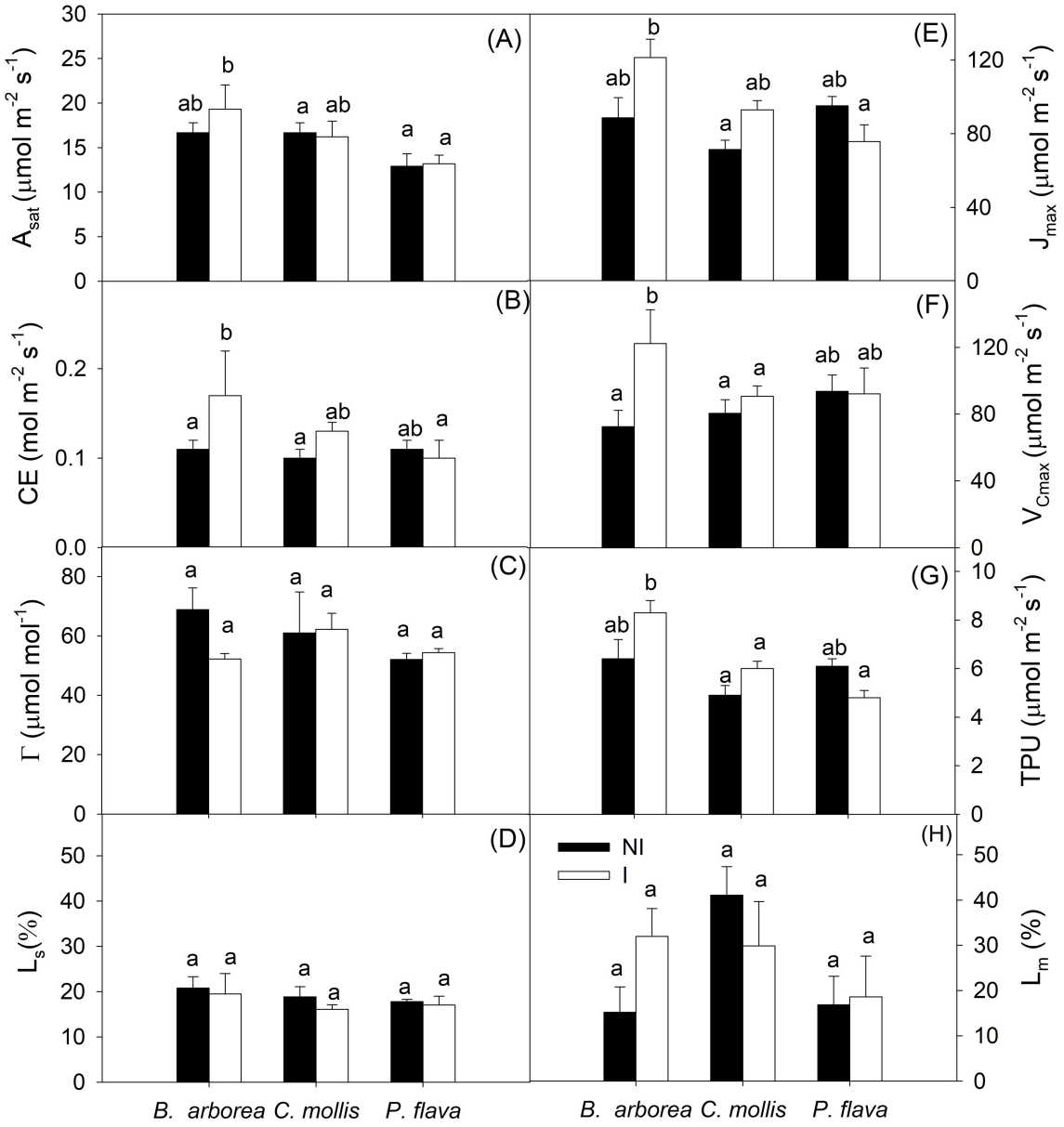

FIGURE 3
Effect of inoculation with AMF on **(A)** C_i-saturated photosynthetic rate [A_{sat}], **(B)** carboxylation efficiency (CE), **(C)** CO_2 compensation point [Γ], **(D)** relative stomatal limitation [L_s], **(E)** maximum carboxylation rate [V_{Cmax}], **(F)** maximum rate of electron transport [J_{max}], **(G)** rate of triose phosphate utilization (TPU), and **(H)** relative mesophyll limitation [L_m] in the three tree species studied: *B. arborea*, *C. mollis*, and *P. flava*. Noninoculated (black bars) and AMF-inoculated (white bars) plants. Values are means (n=4) ± standard error. Different letters indicate statistical differences at $p \leq 0.05$.

4 Discussion

Our results showed that enrichment of the native AMF community via inoculation enhanced certain physiological traits and promoted growth in native plant species, with the most pronounced effects observed in *B. arborea*. In *P. flava*, plant growth also increased following AMF inoculation, although no significant differences were detected in its physiological traits, suggesting species-specific functional responses to AMF. These findings highlight the importance of evaluating the compatibility between native AMF consortia and target plant species when designing restoration strategies for disturbed areas. In this context, specific AMF strains may be more effective with certain hosts, depending on their functional traits and ecological adaptations (Wu et al., 2024). Therefore, large-scale restoration programs should consider the use of compatible or locally adapted AMF inoculum, rather than generalist strains, to optimize plant establishment, growth, and ecosystem recovery.

Adult trees evaluated in the field showed significant differences in gas exchange parameters (E, g_s, WUE), with the physiological performance of *B. arborea*, *C. mollis*, and *P. flava* being consistent with values previously reported in the same forest during the wet

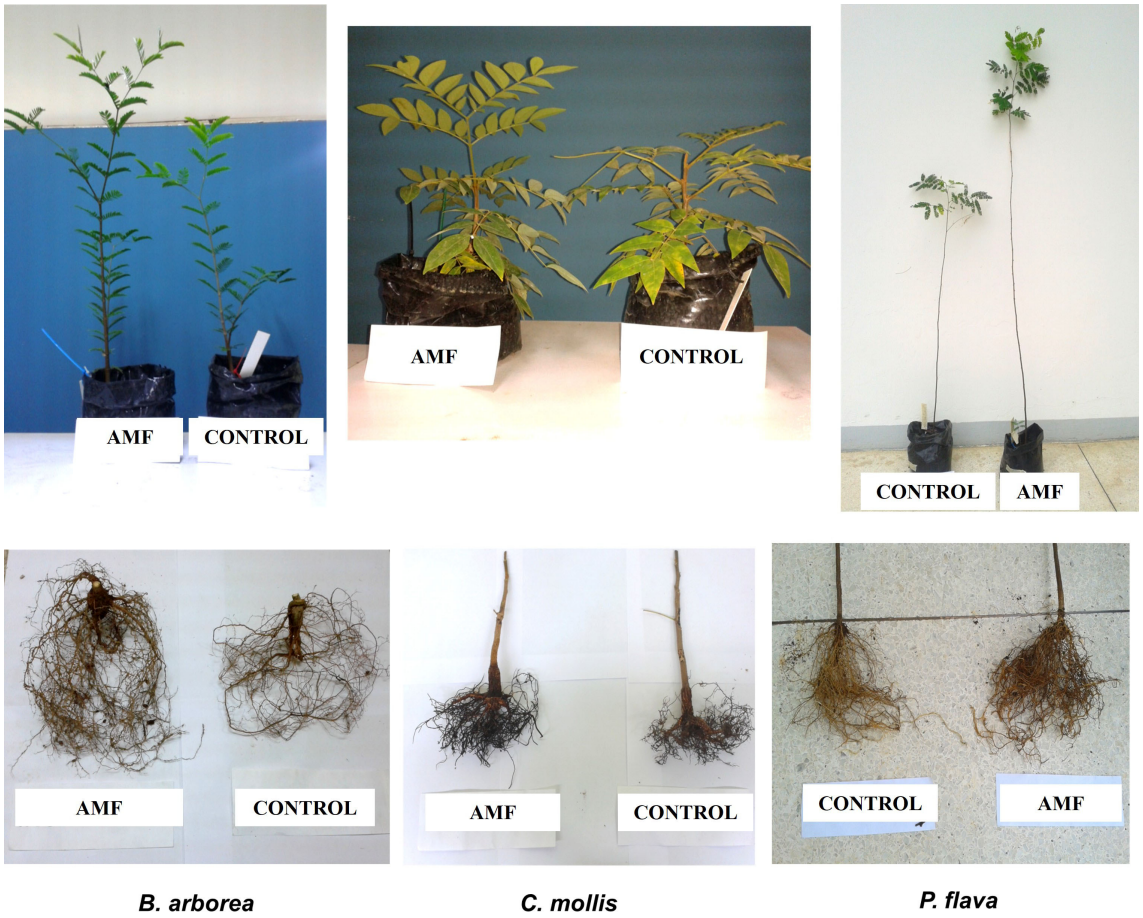

FIGURE 4
Growth of *Bulnesia arborea*, *Caesalpinia mollis*, and *Piptadenia flava* plants after 240 days in the greenhouse with AMF inoculation and without inoculation (control).

season (Ávila-Lovera et al., 2019). Compared with greenhouse plants, trees in the field likely experienced greater environmental stress, as indicated by the lower *A* values in *B. arborea* and *C. mollis*. The higher light intensity, temperature, and vapor pressure deficit in the field likely imposed stronger evaporative demands, leading to reduced photosynthetic performance compared with the more stable and moderate greenhouse conditions.

The AMF community identified in soils of the Macanao Peninsula TDF shared similarities with those reported for the Caatinga dry forests in Brazil, where *Glomus* and *Gigaspora* were likewise common; however, *Acaulospora* was the predominant genus in those ecosystems (Teixeira-Rios et al., 2018; da Nóbrega Veras et al., 2024). AMF are widely distributed symbiotic fungi, yet many taxa possess physiological and ecological adaptations to specific environments, including semi-arid ecosystems, where factors such as rainfall and soil properties influence AMF community structure (Sousa et al., 2018; da Nóbrega Veras et al., 2024). Interestingly, *B. arborea* exhibited the highest response to mycorrhization (MRI of 31%), despite belonging to the Zygophyllaceae family, which has previously been described as mycorrhizal-free (Varma, 1999). The high MRI value suggests a functional response to the inoculum, consistent with effective AMF symbiosis. Our findings are consistent with reports of AMF colonization in other Zygophyllaceae species (Ramos-Zapata et al., 2013; Alrajhei et al., 2022; Xu et al., 2023b).

Fabaceae species are known to associate simultaneously with AMF and rhizobia, and previous studies have documented reciprocal influences between these symbionts: AMF infection can increase nodule number and biomass, whereas rhizobia inoculation may reduce AMF hyphal colonization of roots (Larimer et al., 2014). In addition, the mixed inoculum used in this study was likely enriched not only in AMF propagules but also in rhizobia, as *V. luteola* formed root nodules during trap culture. These combined factors may help explain the comparatively lower mycorrhizal response observed in *C. mollis* and *P. flava*, not necessarily reflecting limited AMF colonization capacity, but rather the concurrent contribution of nitrogen-fixing symbiosis or nutrient enrichment from the inoculum to plant growth—aspects that should be considered in future studies aimed at selecting species for restoration.

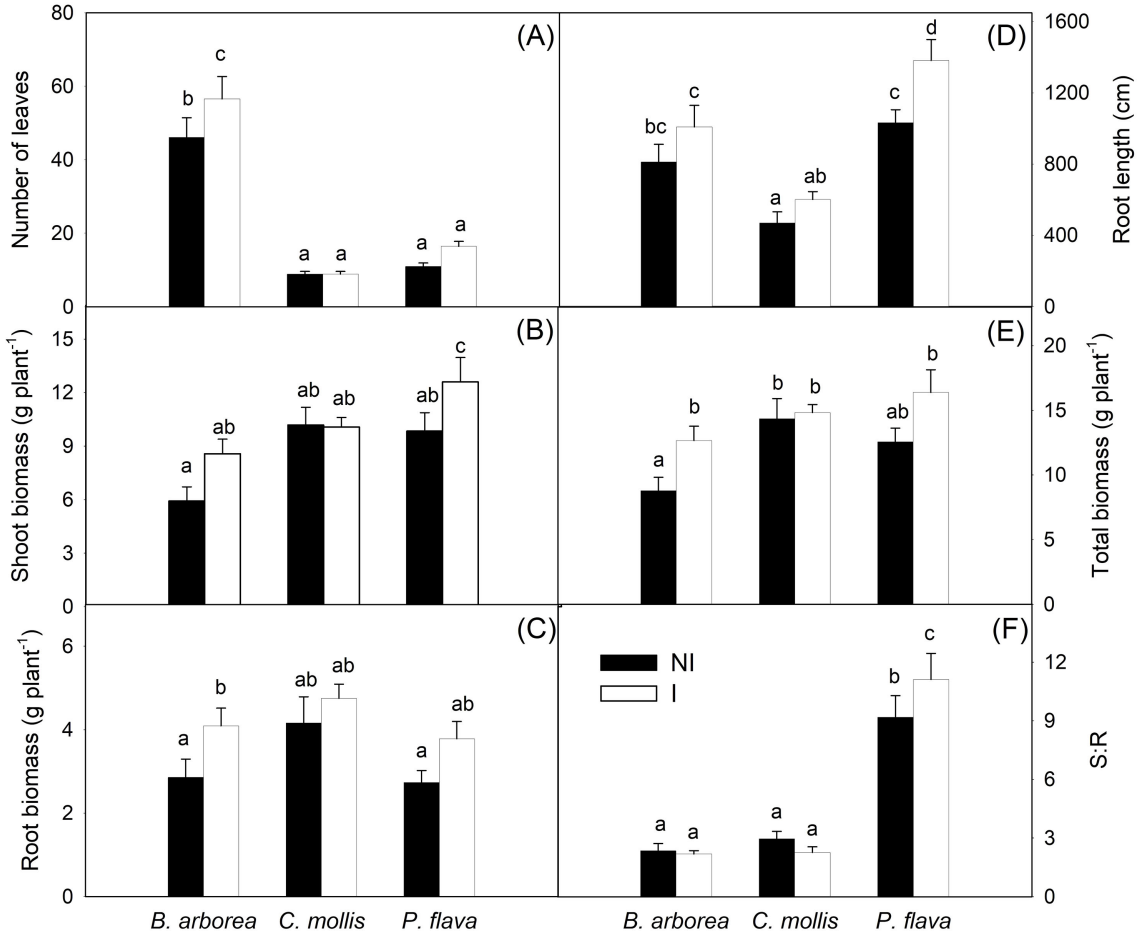

FIGURE 5
Growth variables measured in *B. arborea*, *C. mollis*, and *P. flava*, in noninoculated (black bars) and AMF-inoculated (white bars) plants, including **(A)** number of leaves, **(B)** shoot biomass, **(C)** root biomass, **(D)** root length, **(E)** total biomass, and **(F)** shoot–root ratio (S:R) (n=10). Values are means ± standard error. Different letters indicate statistical differences at $p \leq 0.05$.

4.1 Effects of AMF inoculation on physiological traits

Enrichment of the native AMF community through inoculation improved the physiological performance of *B. arborea*, increasing *A* and *g*s, with minor effects on photosynthetic capacity except for V_{cmax}. Similar responses have been reported in other woody species from semi-arid ecosystems, which exhibited enhanced *A*, g_s, *E*, and/or WUE following AMF inoculation (Barros et al., 2018; Chen et al., 2020). These improvements likely reflect enhanced water uptake, carboxylation efficiency, and RuBP regeneration, supported by the observed increases in g_s, V_{cmax}, and J_{max}. Since all plants were grown under optimal irrigation in the greenhouse, the benefits of AMF enrichment could be even more pronounced under water-limited conditions (Püschel et al., 2021).

The effects of the AMF inoculum were not evident in fluorescence parameters for any of the plant species studied, suggesting that photochemical activity, light use rate, or energy dissipation as heat were unaffected by AMF enrichment. *B. arborea* and *C. mollis* maintained F_v/F_m values near the optimal range for healthy plants (~ 0.83; *sensu* Maxwell and Johnson, 2000), while *P. flava* showed lower values, suggesting partial PSII impairment. These results are consistent with reports for other semi-arid shrub species associated with AMF (Martínez-García et al., 2011; Yang et al., 2022; Bertolazi et al., 2025).

Photosynthetic limitations often arise from constraints in RubisCO carboxylation (V_{cmax}) and electron transport (J_{max}; Farquhar et al., 1980; Amthor, 1995). In this study, *B. arborea* plants subjected to AMF enrichment through inoculation showed increased *A* and A_{sat}, as well as V_{cmax}, indicating that AMF promoted photosynthesis by enhancing RuBisCO carboxylation capacity. Similar effects have been reported in other species, where AMF inoculation improved RubisCO activity and photosynthetic efficiency (Tezara et al., 2014; Chen et al., 2017). Increases in A_{sat} have also been reported in plants inoculated with AMF, where the symbiosis alleviated photosynthetic limitations caused by biochar-induced reductions in N and P availability through enhanced V_{cmax} and J_{max} (Yang et al., 2022).

4.2 Effects of AMF inoculation on plant growth

The significant increase in *B. arborea* growth after AMF enrichment through inoculation could be associated with improved nutrient uptake and assimilation through enhanced root biomass and photosynthetic activity (Khan et al., 2022). This increase in root biomass, combined with the extensive extra-root mycelium of AMF, allows the inoculated plants to extract more water and nutrients (mainly P) from the soil for subsequent translocation to the aboveground parts (White, 2019). In *P. flava*, some growth variables also increased following AMF enrichment, but these changes cannot be explained by the physiological traits measured here, as no changes in photosynthetic performance were detected. The enhancement in shoot biomass and root length, without changes in leaf number, root biomass, or total biomass, suggests that the symbiosis influenced specific growth components rather than overall carbon gain. This apparent decoupling between photosynthesis and growth could reflect early resource allocation to structural development or the carbon costs of sustaining the fungal partner, which can offset potential benefits to photosynthetic activity. Overall, these species-specific responses highlight the complexity of AMF–plant interactions and their dependence on the functional traits of both partners.

Beyond improving plant physiological performance and growth, enrichment of the native AMF community can exert long-term effects on soil recovery and microbial community dynamics. Through glomalin production and hyphal network formation, AMF contribute to soil aggregation, carbon sequestration, and nutrient cycling, enhancing soil stability in degraded dry ecosystems (Wu and Zou, 2017; Li et al., 2024). These processes favor the establishment of other beneficial soil microorganisms, promoting a more complex and resilient rhizosphere community (Boyno et al., 2025). Although this study was limited to 8 months under greenhouse conditions, the sustained physiological and growth responses observed suggest that AMF enrichment could have lasting benefits if maintained under field conditions. The use of native AMF inoculum, as applied here, may thus accelerate the reestablishment of soil biological functions disrupted by mining activities, ultimately improving soil health and supporting ecosystem resilience. Future research should include long-term monitoring of soil structure and fertility parameters, such as glomalin content, aggregate stability, and nutrient availability, together with microbial and biochemical analyses, to evaluate the persistence of AMF effects and their contribution to ecosystem restoration in the dry forests of Macanao and other tropical dry ecosystems worldwide.

5 Conclusion

Bulnesia arborea, *C. mollis*, and *P. flava* showed different responses to inoculation both in growth variables and in physiological traits, and it is well documented that these responses vary depending on the species, the inoculum, and the environmental conditions. AMF enrichment improved both growth and physiological performance in *B. arborea* during the first months of growth, corresponding to the most critical stage of plant establishment and survival, especially in arid and semi-arid ecosystems. Therefore, *B. arborea* may hold potential for future restoration efforts in the TDFs of the Macanao Peninsula, and further ecological evaluation is required before its selection for restoration programs. In contrast, the AMF enrichment could represent a carbon cost for *P. flava*, potentially affecting its photosynthetic capacity; however, it would be advisable to conduct experiments under water stress conditions to assess whether inoculation with AMF elicits a positive response when water is limiting. Overall, our results advance the understanding of plant responses to AMF and support the development of restoration strategies through the enrichment of native AMF communities. Our findings, together with evidence from other studies, suggest that the improvement in photosynthetic capacity and growth is not general across species, and species-specific responses and interactions with AMF inoculum are necessary to study to determine with certainty whether this symbiotic relationship is beneficial for plants.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

KC-M: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing, Resources. AC: Conceptualization, Investigation, Methodology, Resources, Supervision, Writing – review & editing. EÁ-L: Investigation, Writing – review & editing, Resources. WT: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Funding

The author(s) declare that no financial suppor was received for the research, and/or publication of this article.

Acknowledgments

We would like to thank Jenny De Almeida for the help provided in the greenhouse measurements and Carolina Kalinhoff for providing data on the AMF morpho-species present in the rhizosphere of the studied species.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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