Unveiling native mycorrhizal fungi diversity: insights into growth performance, nutrient uptake, and root system robustness in caper-bush (*Capparis spinosa* L.) seedlings

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A B S T R A C T

This study investigates the role of native arbuscular mycorrhizal fungi (AMF) in enhancing the growth performance, nutrient uptake, and root system robustness of caper bushes (*Capparis spinosa* L.), a key species for rehabilitating marginal lands in the Mediterranean region. The primary aim is to identify AMF communities in the rhizosphere soils of caper bushes and evaluate their effects on seedling growth and nutrition. Greenhouse experiments were conducted over two years in Morocco's Safi region, using two seedling groups: one inoculated with a newly identified native AMF complex, and another uninoculated (control) group. Numerous AMF morphotypes were discovered in the rhizospheric soils under mature caper-bush plants, predominantly from the *Glomus* genus. Soil analysis revealed a sandy loam texture and high alkalinity. Results showed that AMF inoculation significantly enhanced plant biomass (~135 %), root length (~58 %), and the number of secondary roots (~141 %) compared to controls. Mycorrhizal dependency was approximately 58 %. Furthermore, inoculated plants showed substantial improvements in mineral nutrient levels: potassium (K^+), calcium (Ca^{2+}), phosphorus (P), magnesium (Mg^{2+}), iron (Fe^{2+}), and zinc (Zn^{2+}), with increases ranging from ~1.5 to ~3 times that of non-inoculated plants. The fresh and dry weights of mycorrhizal plants also increased by ~87 % and ~135 %, respectively. Additionally, the specific absorption rates for these nutrients were enhanced, with increases ranging from ~7 % to ~170 %. These results highlight pre-transplant AMF inoculation as a promising strategy to enhance caper-bush growth and nutrition in challenging environments. Future research should focus on optimizing AMF inoculation for caper-bush cultivation and exploring its potential for land restoration.

1. Introduction

Agricultural output and agroindustry are substantial economic and livelihood sectors across the Mediterranean region, particularly in rural areas. However, climate change progressively threatens their stability, impacting gross domestic product, trade balances, and food security. Reliance on rainfed crops, crucial for rural economies and livestock, exacerbates vulnerabilities to climatic variability [1]. To address these challenges, Mediterranean countries, including Morocco, have implemented subsidies to promote agricultural investments, particularly in export-oriented and climate-resilient crops [2]. The cultivation of *Capparis spinosa* (caper bush) has gained prominence as part of these initiatives, especially in Morocco's Safi region, due to its ability to thrive in semi-arid conditions and poor soils, making it a sustainable choice for

rainfed agriculture [3]. This drought-resistant shrub has emerged as a strategic crop for diversification, offering economic benefits by creating jobs, particularly for women, and providing stable incomes for smallholder farmers. Additionally, Morocco's leadership in caper production and export generates significant economic benefits, contributing to trade balance improvements [4,5]. The integration of caper bush reflects a strategic approach to addressing environmental and economic challenges while aligning with Mediterranean efforts to enhance food security, adapt to climate variability, and sustain rural economies. With approximately 350 species, the *Capparis* genus offers diverse economic, nutritional, and industrial benefits, extending its utility to the cosmetics industry and for honey production and ornamental purposes [6]. Historically, the caper bush has been integral to traditional Moroccan pharmacopeia, renowned for its medicinal properties, including diuretic, antidiarrheal, antirheumatic, antispasmodic, and appetite-stimulant effects. Recent phytochemical and biological research has further validated these therapeutic attributes, identifying bioactive compounds in various parts of the plant, such as flavonoids, alkaloids, and antioxidants, which contribute to its pharmacological potential [7,8].

Despite its natural resilience, caper bush faces several biotic and abiotic challenges, particularly in arid and semi-arid regions, significantly affecting global crop productivity [9]. Biotic pressures, such as fungal and viral infections, also severely impact natural caper bush populations, leading to infestations that damage both root and shoot systems. The shift from semi-wild cultivation to more industrialized farming practices has further intensified these challenges, exacerbating the vulnerability of caper-bush harvests to pest outbreaks and disease [10]. The combined or individual stresses of salinity and drought significantly impair the growth, quality, and yield of caper plants, posing a major challenge to their cultivation and yield [11,12]. These abiotic stressors disrupt physiological and biochemical processes such as water uptake, photosynthesis, and ionic homeostasis, leading to reduced plant vigor and lower crop yields. The resilience of caper plants to harsh environmental conditions highlights their adaptability. However, prolonged or extreme exposure to salinity and drought can still overwhelm their natural defenses, underscoring the need for improved agronomic practices and stress-mitigation strategies to sustain productivity [4,13].

Certain microbes inhabit plant surfaces in nature, while others form stronger interactions, colonizing plant tissues inter- or intracellularly. Some act as disease-causing pathogens, while others promote plant growth as mutualistic symbionts in the rhizosphere [14,15]. Approximately 70–90 % of terrestrial plants form symbiotic relationships with mycorrhizal fungi, classified into seven or more types based on distinct morphological traits, structure, and function [16,17]. Among these, arbuscular mycorrhizal fungi (AMF) are the most abundant and widely distributed, playing a key role in plant nutrition and stress tolerance [18]. Building a mutualistic relationship with AMF is a beneficial way for plants to deal with harsh environments because it helps them grow, absorb water, obtain minerals, and resist biotic and abiotic stress [19, 20]. AMF are particularly significant in Mediterranean ecosystems, which endure prolonged degradation due to anthropogenic activities and challenging climatic conditions characterized by lengthy, arid summers and rare, torrential precipitation [2,21]. This degradation destroys plant communities and soil, particularly in dry and semi-arid areas [22,23]. Loss of underground microbial diversity is often linked to soil degradation, which changes the relationships between plants and microbes and lowers the density, diversity, and effectiveness of AMF [24]. In Morocco, rainfed agricultural areas, commonly used for caper cultivation, are exposed to continuous wind and water erosion, resulting in soil fertility loss and degradation, further exacerbating the need for sustainable agricultural practices [25]. Developing and protecting these areas is crucial to ensure sustainable agriculture that meets immediate needs while mitigating environmental impacts. The targeted management of soil biodiversity aligns with ecological engineering concepts, promoting ecological intensification for better and more sustainable agriculture [26].

The AMF community plays a pivotal role in soil biota, contributing positively to agroecological plant management and enhancing crop production in response to challenges like industrialization and climate change [26,27]. Using native AMF inoculum emerges as a relevant biotechnological method for revegetation, reforestation, and improving the fertility and quality of degraded habitats [19,28]. Despite the well-documented benefits of AMF in enhancing plant resilience and growth, there is a significant gap in understanding the native AMF communities associated with *Capparis spinosa*, particularly in Moroccan soils. While Mediterranean ecosystems, including those in Morocco, host a variety of AMF species [19,29–31], little is known about the specific mycorrhizal relationships in Moroccan *Capparis spinosa* populations. This study hypothesizes that the native AMF communities in Morocco's Safi region play a crucial role in enhancing the growth and nutrient uptake of caper seedlings, particularly under abiotic stress conditions such as drought and salinity [4,13]. By exploring the diversity and functional role of these AMF communities, the study seeks to fill the knowledge gap regarding how these unique microbial associations influence caper bush productivity and sustainability.

The primary purpose of this study was to establish a preliminary inventory of the AMF communities associated with caper bushes in Morocco's Safi region, using morphological approaches to identify the species present. Additionally, this study sought to assess the mycorrhizal dependency of caper seedlings by examining the effects of a newly characterized consortium of native AMF on their growth performance and nutrient absorption efficiency.

2. Materials and methods

2.1. Soil sampling

In March 2020, soil samples were gathered from the rhizosphere beneath mature caper plants in four plantation areas within Morocco's Safi region. Safi Province experiences a semi-arid climate, encompassing three climatic zones: oceanic (coast), semi-arid (Abda), and arid (Ahmer). Classified as BSh (steppe climate) by Köppen and Geiger, the region has an average annual rainfall of 350 mm and an average temperature of 19.0 °C [32]. Approximately 25 kg of rhizospheric soil per station was randomly collected at a depth of ~35–~45 cm, with ~5 kg taken explicitly from around the secondary roots of each plant. These samples were blended to create a uniform substrate and included as part of the fungal inoculum used in this study.

2.2. Mycorrhizal inoculum production

The inoculum consisted of a mixture of indigenous AMF (Mixed-AMF species) in rhizosphere soil samples (which contained ~1394 spores per 100 g). The spore material was obtained through maize (*Zea mays*) due to its high germination colonization rate, early sensitivity to mycorrhizal formation, and abundant root growth. Also, trap culture has been employed to enrich the naturally associated native mycorrhizal complex with the caper-bush plants. The trap culture technique was used following the method outlined by Ouahmane et al. [19]. Initially, maize seeds were sterilized with a 1 % sodium hypochlorite (NaOCl) solution on the surface for 15 min, washed with distilled water multiple times and germinated at a temperature of 25 °C (for 48 h) before sowing. Five pregerminated maize seeds (rootlets ~1–2 cm long) were transplanted into each 1 kg pot containing a mix ($1\nu/1\nu$) of sterilized rhizospheric soils/sandy soil (121 °C for 1 h on three consecutive days) for four months under the greenhouse condition.

2.3. General soil characteristics

A portion of the soil samples collected beneath the caper was air-dried, crushed, sieved (2 mm), and analyzed for soil physical and

Table 1

Physicochemical properties of rhizospheric soils associated with *Capparis spinosa* L. in Morocco's Safi region.

Physical and chemical soil parameters	Values
pH (H_2O)	8.3 ± 0.1
Electrical conductivity (EC) (dS m^{-1})	0.39 ± 0.6
Calcium carbonate ($CaCO_3$) (%)	17.93 ± 9.05
Total organic carbon (TOC) (%)	2.13 ± 0.78
Soil organic matter (SOM) (%)	3.7 ± 2.2
Total phosphorus (P) (mg/g)	1.6 ± 0.2
Potassium (K) (mg/g)	5.8 ± 0.7
Calcium (Ca) (mg/g)	47.3 ± 3.2
Magnesium (Mg) (mg/g)	7.3 ± 0.1
Sodium (Na) (mg/g)	0.8 ± 0.1
Iron (Fe) (mg/g)	14.3 ± 0.5
Zinc (Zn) (mg/g)	0.07 ± 0.0
Sand (%)	67.3 ± 0.6
Clay (%)	9.8 ± 0.03
Loam (%)	22.9 ± 0.4
Soil texture	Sandy loam

Data are means ± SEM of three replicates.

chemical parameters (Table 1). The soil was mixed with deionized water (1:5, *v/v*) for an hour. Then, a pH meter (Model Mi150 pH Bench Meter) and an EC meter (Model Mi170 Bench Meter) were used to measure, calculate, and set the electrical conductivity (EC) and pH of the water [33]. The soil texture was determined using the pipetting method, which involves breaking down organic matter with hydrogen peroxide and spreading chemicals with hexametaphosphate. Sand particles (50 and 2000 μm) were directly determined after sieving under jet water. The silt (<50 μm) and clay fractions dissolved in the water filtrate were calculated [34]. The soil texture classification was described using the USDA soil textural triangle method. The Bernard calcimeter method was used to find out how much total carbonate ($CaCO_3$) was in soil samples. This method measures how much CO_2 is released when HCl is added to the samples [35]. Total organic carbon (TOC) content was measured using the Walkley-Black method, as described by Wang et al. [36]. Excess potassium dichromate in a sulfuric medium at a controlled temperature oxidizes organic carbon. A solution of Mohr's salt was used to measure the extra potassium dichromate in the presence of diphenylamine coloring. The percentage of organic matter (% OM) was calculated from TOC levels in the soil using the van Bemmelen factor (1.724). Genin et al. [37] mentioned equations for calculating the rates of TOC and OM. The analysis of specific mineral elements in soil samples was conducted using the detailed procedure outlined below.

2.4. Seed treatment

Seeds of the caper-bush were collected in August 2019 at the same soil sampling stations in the Safi region, where caper-bush plants grow abundantly in both spontaneous and cultivated states. After immersing the seeds in a 3 % NaOCl solution for 10 min, they underwent three rinses with double-distilled water to sterilize them. Following a 30-min scarification pretreatment with concentrated sulfuric acid, the seeds underwent a 200 mg L^{-1} Gibberellic acid soak and a thorough distilled water wash. This pretreatment provides the most significant proportion of seed germination [4]. The seeds were soaked in water for 12 h to remove traces of the chemical agents. Afterwards, the seeds were placed on sterilized and moist filter paper in 9-cm-diameter disposable Petri dishes (20 seeds/dish). They were incubated in the dark in an incubator

at 24 ± 1 °C for germination until the radicles appeared.

2.5. Experimental procedures

After breaking dormancy, we selected uniformly pre-germinated seeds and sowed them in bulk trays with sterilized black peat. Following the rooting period, we gently transplanted robust seedlings into experimental pots measuring ~47.5 cm in top diameter, ~13.5 cm in height, and ~40 cm in bottom diameter. The pots were disinfected with a 5 % NaOCl solution to prevent contamination. The experimental design included a single factor with non-inoculated (control) and inoculated plants using a mixture of indigenous AMF. Inoculated plants grew in test containers filled with a substrate consisting of 1 kg of rhizosphere soil, 700 g of washed and sterilized river sand, 250 g of sterilized black peat, and 50 g of fungal inoculum (infected root fragments and rhizospheric soils from maize trap culture). The mycorrhizal inoculum was placed close to the seedling roots to encourage fungal infection. Non-inoculated plants received the same sterilized substrate, with a filtrate aliquot (<20 mm) from autoclaved inoculum added to supply a general microbial population without AMF propagules. The plants were randomly arranged in a complete block design with 35 replicates for each treatment. Daily watering with potable water was provided as needed. The cultivation spanned two years, from April 15, 2019, to April 15, 2021, in a sunlit greenhouse under natural daylight conditions. Temperatures during the experiment ranged from a maximum of ~29.1 °C in July to a minimum of ~10 °C in November, with a relative humidity of 60–80 %. The average daylight duration was approximately 10 h.

2.6. Caper plant measurements and analysis

2.6.1. Morphological features and biomass production

After 24 months of planting, various morphological attributes and biomass production were estimated. The length of the main shoot and root was evaluated using a self-retracting metal tape measure, and the diameter of the basal stem was calculated using digital Vernier calipers. The numbers of leaves, branches, internodes, and secondary roots were also recorded. These growth parameters were measured during and after the seedlings' culture period. To assess the impact of mycorrhization on the growth and mineral nutrition of caper plants, ten randomly chosen plants from each treatment were uprooted from the containers, and their root parts were gently rinsed. The fresh weight (FW) of each sample was immediately calculated after harvesting using an electronic precision balance (0.001g). Subsequently, the plant shoots and roots were oven-dried at 110 °C for 24 h to obtain their dry weights (DW). The mycorrhizal dependency (MD), representing the contribution of AMF to the growth of caper plants, was calculated as follows [38]:

$$MD \% = \frac{[(DW \text{ of mycorrhizal plants} - DW \text{ of non} - \text{mycorrhizal plants})]}{DW \text{ of mycorrhizal plants}} \times 100$$

The specific absorption rate (SAR) of a nutrient, indicating the quantity absorbed per unit of root dry mass, can be estimated using the formula proposed by Azcón-Aguilar et al. [39]:

$$SAR = \frac{\text{Plant nutrient uptake (mg)}}{\text{Root mass (g)}}$$

The SAR is an important parameter that quantifies plant roots' efficiency in absorbing nutrients per unit of root mass. In this study, SAR is used to evaluate the impact of AMF inoculation on the nutrient uptake

efficiency of *C. spinosa* L. seedlings.

2.6.2. Plant and soil mineral analysis

Approximately 0.5 g of the previously dried and powdered material was meticulously weighed and then disintegrated in porcelain crucibles. The breakdown was followed by calcination in muffle furnaces at ~550 °C for 5 h, with the ash temperature gradually increasing, to determine the total mineral content of shoots and roots. Subsequently, the ash samples underwent chemical digestion using a freshly prepared acid mixture (9 mL) of HNO_3 (65 %) and HCl (37 %), with a ratio of 1:3 (*v/v*). The samples were gently heated over a water bath (90 °C) to ensure complete digestion, and the test tube walls were rinsed with deionized water to prevent sample loss. After digestion, the acid-digestible solution was filtered through Whatman filter paper 42 (2.5-µm particle retention). The extracts were then diluted to 50.0 mL with deionized water and stored in volumetric flasks [4]. This protocol was also applied to dry and finely powdered rhizosphere soil samples. Major elements (P, Ca, K, Mg, and Na) and minor elements (Fe, Zn) were measured using multitype inductively coupled plasma atomic emission spectrometry (ICPE-9000, Shimadzu Inc.). Operational conditions included Radio Frequency Power (kW): 1.20, Plasma Gas (L.min^{-1}): 14.0, Auxiliary Gas (L.min^{-1}): 1.20, Carrier Gas (L.min^{-1}): 0.70, Exposure Time (sec): 10 Sensitivity: Wide Range, View Direction: Axial, and Wavelengths: Ca 183.801, Fe 235.489, Mg 383.826, K 766.490, Na 589.592, P 177.499, and Zn 213.856. The results were expressed as mg g-1 of dry matter for both major (P, Ca, K, Mg, and Na) and minor elements (Fe and Zn).

2.7. Mycorrhizal colonization rate in caper roots

Representative samples of fresh fibrous roots taken from 10 mycorrhizal individual plants were cleared and stained according to Phillips and Hayman's method [40], slightly modified to highlight fungal structures. Selected root sections were cleared with 10 % (*w/v*) potassium hydroxide (KOH) at 90 °C for 3 h to remove their cytoplasmic and nuclear contents, then immersed in hydrochloric acid HCl (5 %) for 5 min to neutralize the alkalinity due to KOH. Next, they were stained with 0.05 % (w/v) trypan blue in lactoglycerol (1*v*/1*v*/1*v* of distilled water, glycerol, lactic acid) for ½ h at 90 °C. After each step, each sample was thoroughly rinsed with distilled water to eliminate any traces of KOH, HCl, and excess trypan blue. The stained root bits were cut into approximately one-cm-long fragments, arranged parallel to each other on a microscopic slide in five replicates of ten root fragments each, and then carefully crushed with the coverslip. A random sample of non-inoculated plant roots was tested to check for fungal infections. The preparations were evaluated under a microscope at 40× magnification, and the mycorrhizal colonization in plant roots was estimated according to the method described by Trouvelot et al. [41]. This assessment includes the degree of root colonization, i.e., mycorrhizal frequency (F%), as well as mycorrhizal intensity (M%) and abundance of arbuscular formations (A%) in ~1-cm-long root sections. Root colonization was calculated automatically with the software "Mycocalc" (INRA of Dijon).

2.8. AM fungi identification and diversity

The investigation focused on the presence, abundance, and diversity of AMF associated with caper (*Capparis spinosa*) plants. Wet sieving and decanting, followed by sucrose gradient centrifugation, were both used to extract AMF spores from rhizospheric soil [42]. Initially, rhizospheric soil samples were sieved with a 2 mm sieve, and a soil-water mixture (100 g/1000 mL) was passed through stacked sieves ranging from 500 µm to 45 µm with forced water spray. The contents of the 45-µm sieve were entirely covered with a water-sucrose solution (50 % *w/v*) and centrifuged at 1500 rpm for 10 min. The spores were identified at the morphotype scale based on criteria like size, color, shape, wall structure, and hyphal ornament using specific keys (INVAM) (Fig. 1). Spore counts and numbers for each morphotype were stereomicroscopically recorded. The spore density (spores per 100 g of air-dried soil), species richness (total morphotypes), and relative abundance (spores of one morphotype divided by the total spores in all samples) were computed. We used the Shannon-Weaver index (H′) and the Pielou equitability index (J′) to show the variety of AMF morphotypes taken from rhizospheric soils in four areas in the Safi region.

2.9. Data analysis

The results are presented as means with standard deviations. Statistical significance between the averages of each measured parameter in AMF-inoculated and uninoculated caper plants was evaluated using a student t-test, with n = 35 replicates for each treatment. The Bonferroni correction was applied to adjust the significance threshold for multiple comparisons. Effect sizes (Cohen's d) were calculated to assess the magnitude of AMF inoculation effects. Assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene test) were verified for all data. AMF morphotype diversity was explored using the paleontological statistics program PAST (Version 3.24). All data were
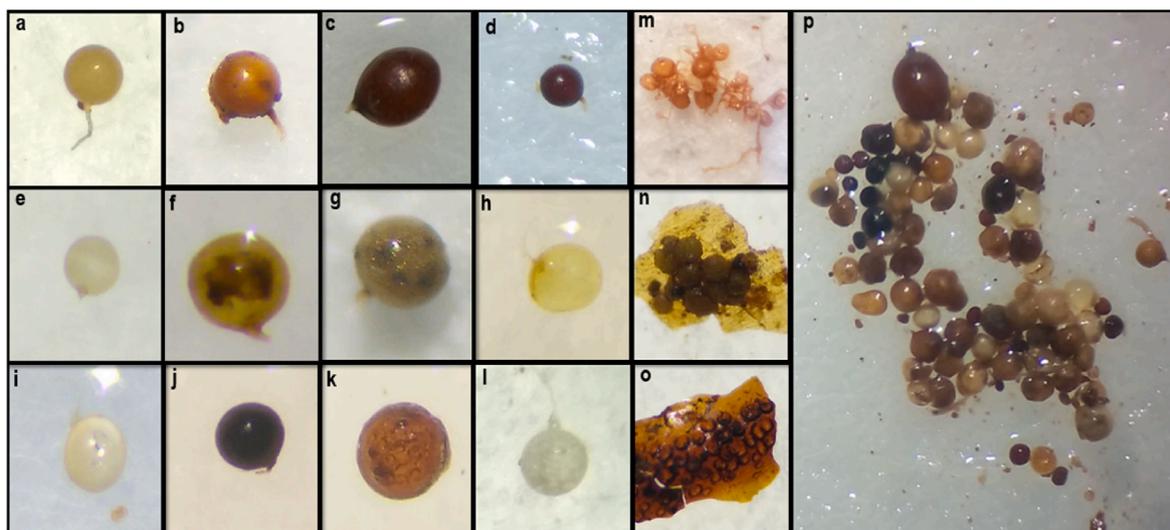

Fig. 1. Diversity of AMF morphotypes isolated from rhizosphere soil of *C. spinosa* in Morocco's Safi region. [Spores morphotypes (a to l), sporocarp (m), spores clusters (n and o) and mixture of AMF complex (p)].

statistically analyzed using the SPSS package (version 28.0).

3. Results and discussion

3.1. Physicochemical characteristics of caper-bush rhizosphere soil in the Safi region

This study provides the first comprehensive evaluation of the associated microbiota and physicochemical properties of *Capparis spinosa* L. rhizospheric soils in Morocco's Safi region. Soil analyses (Table 1) revealed sandy-loam textures with an alkaline pH ranging from ~8.16 to ~8.52. Electrical conductivity (EC) values were consistent across sites, between 0.33 and 0.39 dS m^{-1}. Total calcium carbonate ($CaCO_3$) content varied from ~14.24 % to ~23.65 %. The low EC, attributed to minimal rainfall and low $CaCO_3$ solubility, indicates non-saline soils, in line with Holford and Mattingly's [43] assertion that calcareous soils typically exhibit low salinity. These characteristics suggest *C. spinosa*'s potential use in the reclamation of saline and calcareous soils. Organic matter contents showed moderate variation, with total organic carbon (TOC) ranging from ~1.5 % to ~5.9 % and soil organic matter (SOM) from ~1.35 % to ~2.91 %. These values are consistent with the findings of El Arnabi et al. [44], who reported SOM contents of 1.4–4 % for Safi soils, confirming the regional patterns. Enhancement of TOC, nutrients, and moisture through organic mulch application, as demonstrated by **Rabani et al.** [45], is beneficial for *C. spinosa* cultivation, while the plant's natural canopy improves soil microclimate by providing shade [7]. *C. spinosa* is a rupicolous and xerophytic species exhibiting exceptional ecological versatility. It thrives in a range of soils—alfisols, regosols, and lithosols—and substrates including rocky outcrops, coastal zones, sand dunes, and even building joints. The species adapts to silty clay, sandy, rocky, and gravelly soils with low SOM, favoring well-drained sandy to sandy-loam soils with a pH of 7.5–8.0, but tolerating calcareous and moderately clayey soils. Regional studies corroborate these findings. In Morocco, El Arnabi et al. [44] reported clayey textures and pH values from slightly acidic (6.91) to slightly alkaline (7.46). In Tunisia, *C. spinosa* grows in soils with pH 7.2–8.6 and textures ranging from silty to rocky [46]. Algerian soils supporting *C. spinosa* also exhibit alkaline pH, sandy-loam to loamy textures, and high limestone with variable SOM [47]. In Lebanon, optimal conditions include a pH of 7.8 ± 1 and clay to sandy-loam textures [48]. In Iran, *C. spinosa* flourishes in silty loam to sandy clay loam soils with neutral to slightly alkaline pH, consistent with Mediterranean vegetation adapted to dry coastal environments [12,49]. Turkish populations of *C. spinosa* L. and *C. ovata* Desf. similarly thrive in slightly to moderately alkaline sandy-loam soils rich in organic matter and $CaCO_3$ [50]. Controlled experiments further emphasize soil texture's critical role in caper cultivation. Taghvaei et al. [51] demonstrated that *C. spinosa* plantlets achieved the highest root biomass in sand- or sand/perlite-based media. Similarly, Damizadeh [52] found that sandy or sandy-loam soils promoted optimal survival of *Capparis decidua* seedlings. These findings suggest that incorporating sand into growth substrates enhances drainage and root aeration, thus supporting vigorous plant development. Therefore, the sandy-loam soils of the Safi region provide a highly suitable substrate for *C. spinosa*, with favorable pH, organic matter

levels, and salinity conditions. These properties underline the plant's ecological resilience and its potential role in sustainable agriculture, particularly in the rehabilitation of degraded semi-arid lands.

3.2. Mycorrhizal community in caper-bush rhizosphere

In this study, we present the first characterization of the mycorrhizal community associated with *Capparis spinosa* L. (caper-bush) in the Safi region of Morocco. Our analysis focused on the rhizosphere soil beneath mature caper-bush plants at four distinct locations. A morphological assessment of arbuscular mycorrhizal fungi (AMF) spores identified 11 to 12 distinct morphotypes, distinguished by spore shape, size, structure, and color. Notably, sporocarps and spore clusters were also detected (Fig. 1). The quantification of AMF spores per 100 g of rhizospheric soil ranged from approximately 1074 to 1548, depending on the sampling location (Table 2), with a peak of ~1074 spores observed in one of the sites. This significant abundance of native AMF spores suggests that the rhizosphere of *C. spinosa* supports a potentially beneficial mycorrhizal community, which may enhance the plant's ecological resilience and agricultural productivity.

Further characterization of the mycorrhizal complex was carried out using rhizospheric soils from sampling sites A, B, C, and D (Table 2), along with a trap culture. The identified AMF assemblages revealed the dominance of several genera, with *Glomus* accounting for ~80–84 % of the population, followed by *Rhizophagus* (~12–16 %), *Gigaspora* (~1–3 %), *Acaulospora* (~0.5–2.5 %), *Paraglomus* (~0.5–2 %), and *Sclerocystis* (~0.5–1 %). These genera contribute uniquely to mycorrhizal symbiosis, influencing the ecological dynamics of *C. spinosa* and potentially bolstering its tolerance to environmental stresses. *Glomus*, in particular, is recognized for its remarkable adaptability and widespread distribution across diverse ecosystems, from arid to tropical regions. This genus not only enhances soil fertility but also supports plant growth, promotes biodiversity, and improves tolerance to both abiotic and biotic stress factors ([4,13]; Öpik et al., 2010). Recent global discoveries further highlight the pivotal role of *Glomus* species in sustaining agricultural ecosystems [53,54].

The occurrence of the genera *Rhizophagus*, Gigaspora, *Acaulospora*, *Paraglomus*, and *Sclerocystis* at certain sampling locations aligns with earlier studies that have documented their presence in Moroccan rhizospheres [19,29,31,55,56]. These findings suggest that at least *Glomus, Rhizophagus,* and *Gigaspora* may be generalist AM fungi, capable of forming symbiotic relationships with a wide range of plant species. However, further research is required to explore the ecological niches and specific roles of these genera in the context of *C. spinosa* growth and resilience. Several environmental factors, such as soil texture, nutrient availability, moisture content, and plant-fungus compatibility, are known to influence the composition and structure of AMF communities [57,58]. Additionally, the reduction in AMF species richness is often linked to increased land use and anthropogenic disturbance [59], highlighting the importance of preserving natural habitats to maintain fungal biodiversity.

To assess the diversity of the AMF morphotypes across the sampling sites, we applied several diversity indices, including Shannon's diversity index (H'), Pielou's evenness index (E), and Simpson's dominance index

Table 2
The abundance of AMF spores in the rhizospheric soils of *Capparis spinosa* L. across four sampling stations in Morocco's Safi region.

Locations	AMF spore/100 g of rhizospheric soil[a]											
	a	b	c	d	e	f	g	h	i	j	k	l
Station A	105	326	112	335	45	37	21	208	97	112	14	78
Station B	113	317	134	329	68	34	31	197	85	127	21	92
Station C	79	289	121	348	72	43	37	218	88	81	37	54
Station D	68	214	128	217	35	0	11	137	57	92	8	107

[a] The number of AMF spores per 100 g of dry-weight rhizospheric soil for each morphotype; a to l = AMF morphotypes; Station A, B, C and D = Sampling sites of rhizospheric soils.

Table 3

Diversity index of AMF spores associated with *Capparis spinosa* L. at four sampling stations in Morocco's Safi region.

Diversity indices	Sampling stations			
	A	B	C	D
Morphotype richness (S)	12	12	12	11
Total number of spores/100g soil	1490	1548	1467	1074
Simpson's dominance (D)	0.14	0.13	0.14	0.14
Simpson's index (1-D)	0.86	0.87	0.86	0.86
Shannon's diversity index (H')	2.153	2.209	2.195	2.127
Pielou's Evenness index (E)	0.72	0.76	0.75	0.76
Equitability (J)	0.87	0.89	0.88	0.87

Station A, B, C and D = Sampling sites of rhizospheric soils.

(D). The values of Shannon's diversity index ranged from ~2.127 to ~2.209, indicating moderate to high diversity across the rhizospheres of *C. spinosa* at all sampling locations (Table 3). Pielou's evenness index (E) varied between ~0.72 and ~0.76, reflecting a relatively even distribution of AMF morphotypes at these sites. Simpson's dominance index (D) was low and remained stable across all locations, ranging from ~0.13 to ~0.14, which suggests that no single AMF genus overwhelmingly dominates the community. These diversity indices are comparable to those reported by **Ouallal et al.** [60] in studies of AMF diversity in the rhizosphere of *Argania spinosa* in Morocco, supporting the conclusion that the *C. spinosa* rhizosphere is home to a diverse and stable AMF community. The diversity indices observed in this study are indicative of healthy and balanced interactions between *C. spinosa* and its mycorrhizal partners. The consistent Shannon and Pielou indices across different sampling locations suggest that the rhizosphere of *C. spinosa* provides a conducive environment for the coexistence of a wide range of AMF morphotypes. Moreover, the equitability values (J) further affirm the observed variability in AMF diversity across the different sampling sites. These findings highlight that *C. spinosa* may serve as an ideal host for a diverse mycorrhizal community, which plays a key role in the plant's ecological success.

The variability in mycorrhizal community composition and diversity across the different sampling sites is likely influenced by several factors, including soil properties (e.g., pH, nutrient availability, moisture), as well as climatic conditions [18,61,62]. The rhizosphere of *C. spinosa* likely represents a dynamic and resilient habitat for mycorrhizal fungi, where environmental factors such as soil moisture and nutrient availability interact with plant root exudates to shape the structure and function of the AMF community. These interactions are fundamental to the ecological and biogeochemical processes that sustain soil health and plant productivity, particularly in arid and semi-arid environments.

3.3. Mycorrhizal colonization and root interaction

The results of this study confirm the successful colonization of *Capparis spinosa* L. roots by the native arbuscular mycorrhizal fungi (AMF) complex isolated from the Safi region. All inoculated plants demonstrated visible mycorrhizal colonization across the lateral roots, with an average colonization frequency of approximately 53.75 % and an intensity of about 21.36 % (Table 6). These levels of colonization are consistent with findings on medicinal plants and xerophytic species that are naturally adapted to Mediterranean-type climates, as well as many semi-arid and arid environments [17,19,29,56,63–65]. Microscopic analysis revealed well-developed intraradical mycorrhizal structures: 37.53 % were intracellular hyphae, 31.89 % were vesicles, and 15 % were arbuscules. The predominance of hyphae and vesicles over arbuscules suggests a functional symbiosis focused on nutrient storage and transport, vital for survival under semi-arid conditions [66]. Vesicles serve as reservoirs for lipids and other nutrients, helping AMF endure environmental stresses [16]. The lower proportion of arbuscules may reflect environmental constraints such as soil moisture variability, which is known to reduce arbuscule formation without impairing overall

mycorrhizal functionality [66]. The absence of colonization in uninoculated control plants, as confirmed by microscopic observations, underscores the critical role of AMF inoculation in establishing effective symbiotic relationships with *C. spinosa*. This observation is consistent with earlier findings where non-inoculated caper seedlings showed no mycorrhizal colonization under either water-deficit or saline conditions. Our findings are also consistent with previous studies evaluating *C. spinosa* mycorrhizal colonization under abiotic stress. Under varying water-deficit stress (WDS) levels, colonization rates increased from 41.7 % under well-watered conditions to 55.3 % at moderate WDS, then slightly declined to 51.7 % at severe stress [4]. Similarly, under NaCl-induced salinity stress (NSS), colonization peaked at low salinity (~52.2 %) but dropped significantly to ~15.7 % under severe NSS [13]. These patterns suggest that moderate environmental stresses can stimulate mycorrhizal association, whereas extreme conditions impair colonization efficiency. The stable and moderately high colonization achieved in the current study under standard soil conditions (~53.75 %) confirms the adaptability and infectivity of the native AMF complex, particularly under low-stress or moderately challenging environments. The morphology of the colonization observed points toward an Arum-type mycorrhizal pattern, characterized by intercellular hyphae and abundant vesicle formation. This morphology is often associated with efficient water and nutrient transport, advantageous under the variable soil moisture conditions typical of semi-arid ecosystems [65]. The dominance of *Glomus* species in the AMF complex likely contributed to the strong colonization observed. *Glomus* spp. are widely recognized for their ecological plasticity, high infectivity, and ability to form robust symbioses across a range of environmental conditions (Öpik et al., 2010). Their abundance in the inoculum may explain the relatively high proportion of vesicle structures recorded, which is characteristic of *Glomus*-dominated communities (Błaszkowski, 2012).

3.4. Growth promotion and biomass enhancement via AMF

Plants inoculated with the native AMF complex exhibited significantly improved growth parameters, including the number of leaves, branches, nodes, and collar stem diameter. Statistical significance was observed with p-values <0.001 for plant height (Table 4). Over the course of two years in nursery conditions, AMF-inoculated plants demonstrated significantly greater biomass in both shoots and roots (p < 0.001), with total dry and fresh weights surpassing non-inoculated plants by ~135.27 % and ~86.85 %, respectively. Additionally, AMF inoculation resulted in a marked increase in root length and the number of secondary roots, with increases of ~57.98 % and ~141.42 %, respectively. The root-to-shoot ratio remained statistically consistent at ~1.34 for both treatments (Fig. 2). The observed increase in plant growth and biomass with AMF inoculation highlights the critical role that AMF play in improving plant growth, particularly in nutrient-poor

Table 4

Growth parameters of *Capparis spinosa* L. seedlings cultivated with or without a mixture of native arbuscular mycorrhizal fungi after 2 years under greenhouse conditions.

Growth parameters	Treatments		t-test
	Control	Mixture of AM fungi	
Plant height (cm)	42.7 ± 3.6	53.8 ± 1.9	*
Number of leaves (plant^{-1})	50.7 ± 7.12	90 ± 12.54	***
Number of branches (plant^{-1})	7.9 ± 1.02	16.4 ± 2.6	***
Number of nodes (plant^{-1})	104.6 ± 6.9	164.5 ± 10.8	***
Collar stem diameter (mm)	6.43 ± 0.44	9.1 ± 0.43	***
Main root length (cm)	28.7 ± 1.44	45.3 ± 2.34	***
Number of secondary roots (plant^{-1})	16.9 ± 3.5	40.8 ± 6.7	***

The data are presented as means ± standard errors for n = 10 replicates. Statistical significance between control and AMF treatment groups was determined using Student's t-test (*, $p < 0.05$, ***, $p < 0.001$).
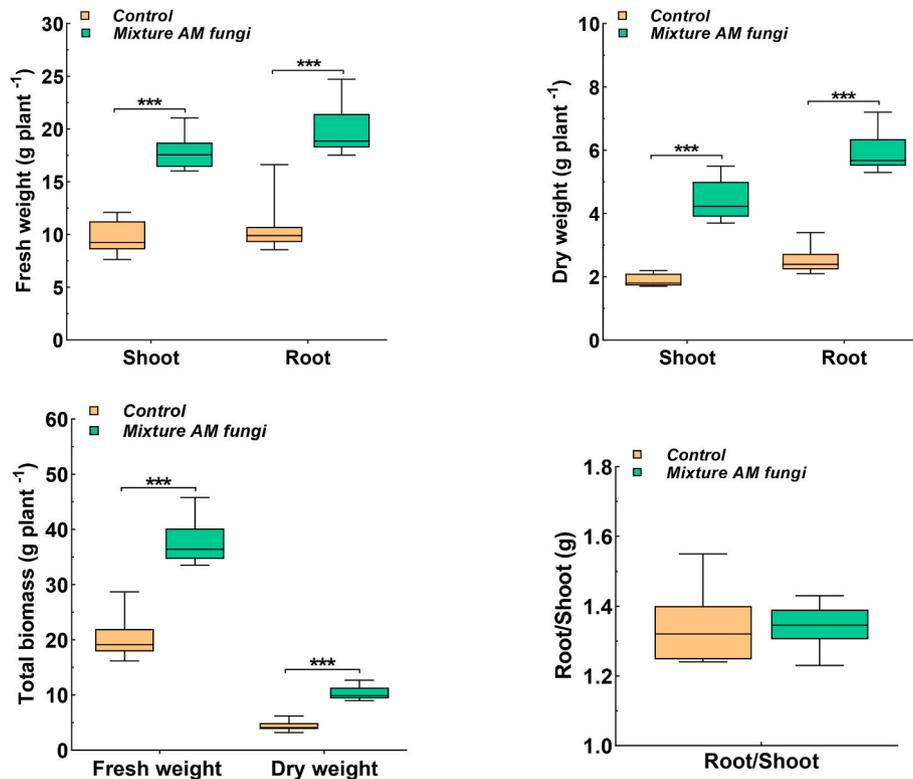
Fig. 2. Influence of native mixtures of AM fungi on fresh and dry weights and total biomass in the shoot and root of *C. spinosa* seedlings under nursery conditions. The bar charts represent means and standard errors of means based on n = 10 replicates for each part (shoot or root). Significant differences between control and mixture AMF treatments were determined using the Student's *t*-test, denoted by three asterisks (***, $p < 0.001$).

and stressed environments. Mycorrhizal fungi enhance plant growth by extending the root system, allowing plants to access more water and nutrients from the soil. This phenomenon is well-documented by Smith and Read [66], who found that AMF symbiosis improves plant growth by increasing the volume of soil explored by the plant roots. In line with Azcón-Aguilar et al. [39], who demonstrated significant biomass increases in plants under nutrient-limited conditions, our findings also suggest that AMF promote plant growth primarily through enhanced phosphorus (P) uptake, a crucial nutrient often limited in arid soils. Sieverding [67] emphasized that AMF increase root length and density,

improving nutrient acquisition efficiency, particularly in nutrient-poor environments like the semi-arid conditions in which this study was conducted. Similarly, Bouskout et al. [4] showed that AMF promote root expansion, facilitating better access to water and nutrients under drought stress. The increase in root length (~57.98 %) and the number of secondary roots (~141.42 %) in this study aligns with the work of Ouahmane et al. [30], who found that mycorrhizal fungi, particularly native strains, significantly enhance root system architecture, leading to improved nutrient uptake. Pugnaire and Esteban [68] further support this, concluding that AMF inoculation led to more extensive root systems
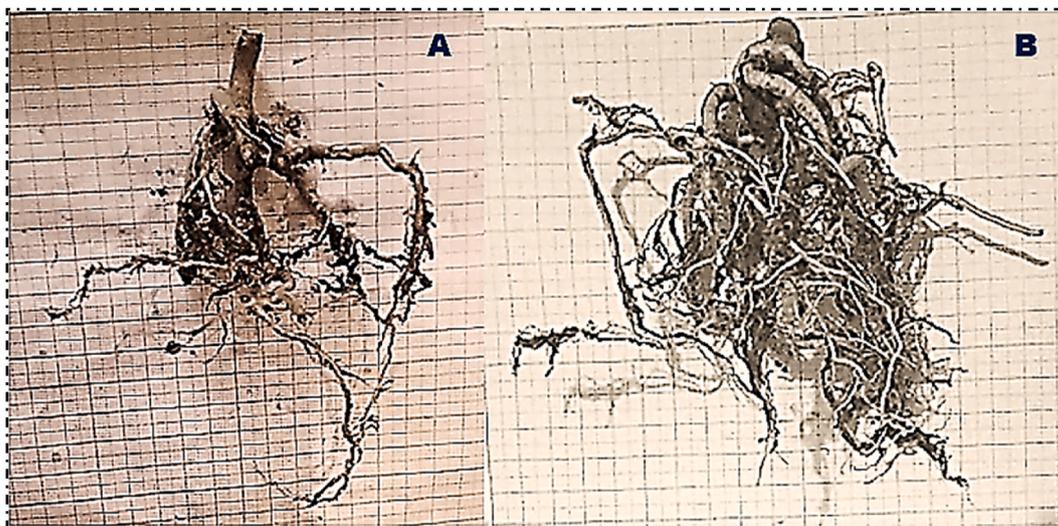

Fig. 3. Root system architecture for non-mycorrhizal (control) (A) and mycorrhizal (B) plants of *C. spinosa* L. after two years of cultivation in a greenhouse conditions.

in plants growing under low nutrient conditions. Moreover, the maintenance of a stable root-to-shoot ratio (~1.34) indicates balanced plant growth, with AMF facilitating efficient resource allocation between roots and shoots. This finding is consistent with Hashmi et al. [69] who observed that AMF contribute to optimal resource allocation in plants, leading to increased overall growth and productivity, especially under water-limited conditions.

Increased root length and secondary root formation are indicative of a more extensive root system, which improves nutrient uptake capacity. This could be particularly beneficial in semi-arid conditions where soil fertility is limited, and the plant must maximize its nutrient acquisition ability. The increase in lateral root formation, which is often correlated with improved nutrient and water absorption, supports findings by Outamamat et al. [31], who reported similar root system modifications under AMF inoculation.

Moreover, the consistent root-to-shoot ratio of ~1.34 in both treatments suggests that while AMF enhanced root development, they did so without compromising shoot growth. This indicates an efficient allocation of resources, with AMF helping plants maximize both root and shoot growth to ensure optimal productivity (Fig. 3).

3.5. Nutrient uptake enhancement in AMF-inoculated plants

AMF-inoculated plants showed significantly higher concentrations of phosphorus (P), iron (Fe^{2+}), and zinc (Zn^{2+}) in the shoot parts, with p-values <0.05 for P and Fe^{2+}, and <0.001 for Zn2+. In the root system, significant differences were observed for phosphorus and zinc at $p < 0.01$, and for magnesium (Mg^{2+}) at $p < 0.05$. Additionally, the concentration of macronutrients such as potassium (K^+) and calcium (Ca^{2+}) increased by 1.5 times, sodium (Na^+) by nearly twice, phosphorus and magnesium by approximately 2.5 times, and iron and zinc by more than three times (Table 5). The enhancement in nutrient uptake observed in AMF-inoculated plants reflects the role of AMF in increasing the bioavailability of essential nutrients. Smith and Read [66] and Reid and Hayes [70] highlight that AMF symbiosis facilitates nutrient uptake, particularly for immobile nutrients like phosphorus, by extending the root system and enhancing nutrient exploration beyond the root zone. This ability of AMF to improve nutrient uptake is critical in semi-arid soils where nutrients like phosphorus are often bound to soil particles and unavailable to plants. The significant increase in micronutrient concentrations, such as Fe^{2+} and Zn^{2+}, is particularly notable, as these nutrients are often less available in calcareous and alkaline soils.

Table 5
Mineral contents in shoots and roots of *Capparis spinosa* plants without (Control) or with a mixture of native AM fungi after 24 months of culture in nursery conditions.

Mineral nutrient	Shoot		t-test	Root		t-test
	Control	Mixture AMF		Control	Mixture AMF	
P (mg g^{-1} DW)	1.52 ± 0.07	2.27 ± 0.21	*	1.65 ± 0.09	2.41 ± 0.13	**
K$^+$ (mg g^{-1} DW)	17.93 ± 1.58	20.21 ± 0.1	ns	11.86 ± 0.35	11.87 ± 0.95	ns
Ca^{2+} (mg g^{-1} DW)	12.43 ± 0.33	15.54 ± 1.46	ns	8.96 ± 0.23	9.52 ± 1.53	ns
Na$^+$ (mg g^{-1} DW)	34.48 ± 3.80	46.79 ± 10.9	ns	8.12 ± 0.43	9.57 ± 1.21	ns
Mg^{2+} (mg g^{-1} DW)	4.60 ± 0.29	5.56 ± 0.86	ns	1.98 ± 0.72	3.48 ± 0.39	*
Fe^{2+} (mg g^{-1} DW)	0.62 ± 1.19	4.40 ± 2.21	*	2.53 ± 0.08	4.28 ± 1.10	*
Zn^{2+} (mg g^{-1} DW)	0.032 ± 0.003	0.059 ± 0.001	***	0.024 ± 0.001	0.035 ± 0.001	**

The data are presented as means ± standard errors for n = 10 replicates. Statistical significance between control and AMF treatment groups was determined using Student's t-test (*, *p* < 0.05, **, *p* < 0.01, ***, *p* < 0.001).

Sieverding [67] emphasized that AMF can solubilize micronutrients, thereby increasing their bioavailability. Similarly, Wang et al. [71] reported that AMF significantly enhance the uptake of iron and zinc, which are critical for various enzymatic processes and metabolic functions within the plant. Bouskout et al. (20022, 2024) also found that AMF inoculation improved the micronutrient status of plants under drought and salt stresses, highlighting the importance of AMF in alleviating micronutrient deficiencies under adverse environmental conditions. The observed increases in macronutrients such as potassium, calcium, and magnesium further underscore the role of AMF in improving overall plant nutrition. Pugnaire and Esteban [68] and Zhang et al. [59] similarly noted that AMF improve the availability of these essential macronutrients, which are critical for plant physiological processes like photosynthesis, osmoregulation, and cell wall formation. The positive influence of AMF on nutrient uptake in this study reinforces the findings of Outamamat et al. [31], who observed similar nutrient increases in other plant species following AMF inoculation. These findings confirm the broad-spectrum nutrient-enhancing effect of AMF, which is particularly beneficial in nutrient-limited environments like the semi-arid soils studied here.

3.6. Ecological implications and soil quality enhancement

AMF-inoculated plants showed substantial improvements in the specific absorption rate (SAR) of key nutrients, including Fe^{2+}, Zn^{2+}, P, Mg^{2+}, Na^+, Ca^{2+}, and K^+. The SAR for Fe^{2+}, Zn^{2+}, and P increased by approximately 170 %, 101 %, and 48 %, respectively, compared to non-inoculated controls. Statistical analysis confirmed that the improvements in SAR for Fe^{2+}, Zn^{2+}, and P were highly significant ($p < 0.01$), while increases for Mg^{2+}, Na^+, and K^+ were significant at $p < 0.05$ (Fig. 4). The increased SAR values for key nutrients such as phosphorus, iron, and zinc further underscore the critical role of AMF in enhancing nutrient uptake efficiency. As Wang et al. [71] and Zhang et al. [59] have reported, AMF increase the surface area for nutrient absorption by extending their hyphal networks, thus improving access to nutrients that are poorly mobilized in the soil, especially in semi-arid environments where soil fertility is often limited. AMF also contribute to soil quality improvement, particularly through the enhancement of soil aggregation. As highlighted by Sieverding [67], AMF hyphal networks promote soil aggregation, which improves soil structure and water retention. This is crucial in semi-arid regions where soil erosion and water scarcity are pressing issues. The positive impact of AMF on soil structure has also been documented by Rhoades et al. [72], who emphasized the role of AMF in reducing soil erosion and enhancing water infiltration in arid regions. The ability of AMF to improve soil quality aligns with the findings of Ouahmane et al. [29] and Caravaca et al. (2005), who demonstrated that AMF inoculation improves the physical and chemical properties of degraded soils. Additionally, AMF enhance microbial activity in the rhizosphere, promoting nutrient cycling and organic matter decomposition. This is consistent with the work of Etesami [73] and Andrade et al. [74], who showed that AMF symbiosis alters the microbial community in the rhizosphere, improving soil nutrient cycling and microbial diversity.

In this study, the mycorrhizal dependency (MD) of *Capparis spinosa* was estimated at 58 %, reflecting a substantial reliance on arbuscular mycorrhizal fungi (AMF) for biomass production under nutrient-deficient, semi-arid conditions. This finding aligns with previous research demonstrating that AMF symbiosis significantly enhances nutrient acquisition, particularly of phosphorus and nitrogen, under edaphic stress [69,75]. Notably, comparable or higher MD values for *C. spinosa* have been reported by Bouskout et al. [4,13], who quantified MD under drought and salinity stress and found dependency levels exceeding 60 %, highlighting the critical role of AMF in conferring tolerance to abiotic stress. In comparison, *Cupressus atlantica* showed moderate and comparable MD (~40–50 %) in degraded soils [19], whereas *Ceratonia siliqua* expressed low-moderate MD (~32–34 %)

Table 6

Mycorrhizal colonization parameters of AMF-inoculated caper-bush (*Capparis spinosa* L.) plants after two-years of cultivation in a greenhouse conditions.

Treatment	Colonization frequency (F%)	Colonization intensity (M%)	Arbuscules abundance (A%)	Hyphae (%)	Vesicles (%)
	%		(No/cm root)		
AMF	53.75 ± 5.13	21.36 ± 2.7	7.15 ± 1.1	37.53 ± 4.8	31.89 ± 3.2
Control	0 (nd)	0 (nd)	0 (nd)	0 (nd)	0 (nd)

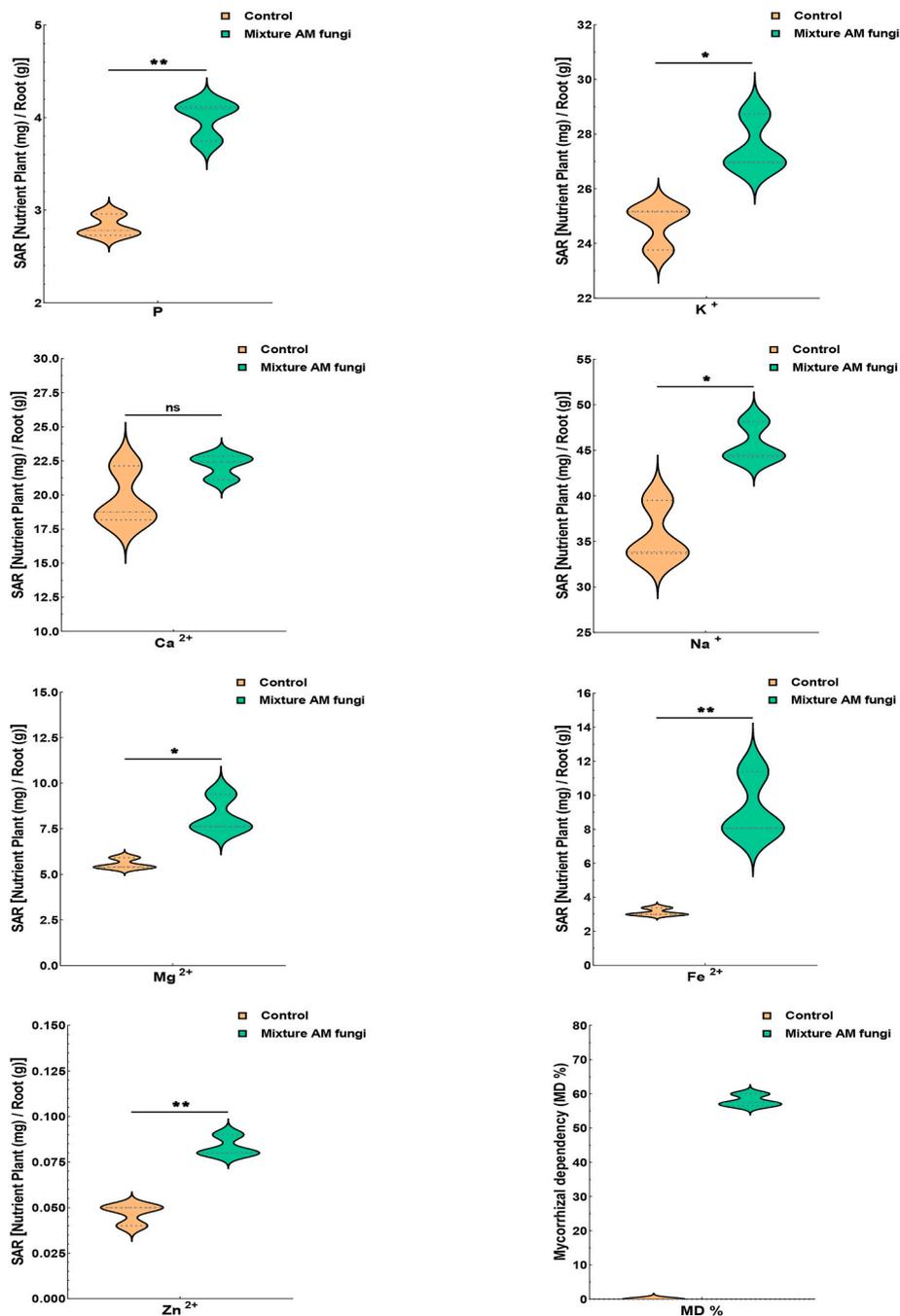Values are Means of n = 3 repetitions; nd = not found.

Fig. 4. Mycorrhizal dependency and specific absorption rate (SAR, mg per g root mass) for both macro and micronutrients was compared between mycorrhizal (+ Mixture AMF) and non-mycorrhizal (Control) caper plants. The bar chart illustrates means and standard errors based on n = 10 replicates. Significant differences between control and mycorrhizal treatments were determined using the Student's *t*-test, denoted by asterisks (* for $p < 0.05$, ** for $p < 0.01$, and "ns" for no significance at $p < 0.05$).

under similar conditions [56], emphasizing species-specific variation in mycorrhizal responsiveness. These differences are shaped not only by intrinsic plant traits but also by environmental context and fungal identity; indeed, native AMF strains have consistently shown greater effectiveness in arid zones than exotic ones [19,70]. Overall, the MD observed in this study reinforces the ecological and functional significance of AMF in supporting *C. spinosa* growth and underscores the need for selecting locally adapted fungal strains in sustainable land management and restoration strategies. Selecting appropriate AMF strains is therefore essential for optimizing plant growth and productivity in nurseries. Monosporal cultures offer a promising tool for selecting high-infectivity strains that are well-adapted to the edaphic conditions of crops species [31].

Overall, this study demonstrates the significant potential of AMF as biofertilizers to enhance plant growth, nutrient uptake, and soil quality, particularly in semi-arid and degraded soils. However, further research is required to optimize AMF inoculation protocols, including the selection of native AMF strains and the development of efficient inoculum production methods. Several studies suggest that using native AMF strains can lead to better plant growth and nutrient uptake in semi-arid conditions, where AMF are naturally adapted [4,13,29,68]. Moreover, understanding the role of AMF in the mycorrhizosphere, as highlighted by Zhang et al. [59], will provide insights into how AMF interact with other soil microorganisms to improve soil health and nutrient cycling. Future studies should also explore the long-term benefits of AMF inoculation, particularly in field trials, to assess the persistence of AMF symbiosis and its impact on ecosystem restoration and agricultural productivity.

4. Conclusion

This study is the first to explore rhizospheric microbes associated with *Capparis spinosa* L. (caper-bush) and analyze the physicochemical properties of the soil. A key finding is the composition and abundance of arbuscular mycorrhizal fungi (AMF) spores in symbiosis with wild caper plants in the rhizosphere. We evaluated the effects of a newly identified AMF complex on caper seedlings in greenhouses over two years. AMF-colonized plants showed significant improvements in leaf and branch production, biomass, stem elongation, collar diameter, root development, nutrient uptake, and flower bud yield. These results highlight the vital role of AMF in supporting *C. spinosa* in environments characterized by water scarcity and drought. While AMF inoculation shows promising benefits under controlled conditions, scaling this technique for commercial cultivation requires addressing challenges such as inoculum production, costs, and field implementation. Future research should focus on optimizing these aspects, alongside molecular analysis using ITS sequencing to identify AMF species and their functional traits. Long-term field trials are essential to validate greenhouse findings and assess the feasibility of AMF inoculation in real farming conditions.

CRediT authorship contribution statement

Mohammed Bouskout: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Writing – review & editing, Conceptualization. **Said ElJebri:** Writing – review & editing, Software. **Yaseen Khan:** Writing – review & editing, Visualization, Validation. **Ibrahim A. Saleh:** Writing – review & editing, Funding acquisition. **Mohammad K. Okla:** Writing – review & editing, Visualization, Funding acquisition. **Saud S. Al-Amri:** Writing – review & editing, Funding acquisition. **Sujat Ahmed:** Writing – review & editing. **Hanane Dounas:** Writing – review & editing. **Lahcen Ouahmane:** Supervision, Conceptualization, Validation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All relevant data generated or analyzed during this study are included in this published article.

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