



Spatio-temporal dynamics and edaphic drivers of arbuscular mycorrhizal fungi associated with *Pancratium maritimum* L. in coastal dunes of Oran (North-Western Algeria)

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(Manuscript received 18 September 2025; Accepted 6 May 2026; Online published 30 May 2026)

ABSTRACT: This study investigated spore density, community structure, and diversity of arbuscular mycorrhizal fungi (AMF), and root colonisation in *Pancratium maritimum* L. in coastal dunes of Cap Falcon (Oran coast, North-Western Algeria). Spatial and seasonal variation were assessed across three sites over four seasons (2018–2019). Physicochemical properties of rhizosphere soils were analysed, and AMF spores were extracted by wet sieving and centrifugation, followed by morpho-taxonomic identification and ecological index calculation. Root colonisation was assessed after histochemical staining. Two-way ANOVA evaluated spatial and seasonal variation, while Canonical Correlation Analysis (CCA) explored relationships between soil physicochemical properties and AMF spore density, community structure, diversity and colonisation. Significant spatio-temporal variation ($p < 0.05$) was observed for most soil and AMF variables, reflecting dynamic AMF symbiosis in limestone-rich, nutrient-poor coastal dune soils. 15 AMF species belonging to 7 genera and 4 families of the phylum Glomeromycota were identified, with a clear predominance of the family Glomeraceae, particularly the genus *Glomus*. Mean AMF spore density reached 49.24 spores per 100 g of dry soil, and mycorrhizal frequency remained consistently high, indicating strong mycotrophy of *P. maritimum*. Spatial differences reflected the influence of local soil conditions, while seasonal patterns showed higher colonisation intensity in spring and increased spore density and diversity in autumn. CCA revealed that AMF diversity and spore density were positively associated with soil calcium carbonate, electrical conductivity and sand content, whereas root colonisation was mainly associated with available phosphorus and soil organic matter.

KEY WORDS: AMF diversity, community structure, mycorrhizal colonisation, soil physicochemical properties.

INTRODUCTION

Pancratium maritimum L. (1753) is one of the many psammophilous coastal plant species with specific adaptations that enable them to thrive in a restrictive habitat. Belonging to the *Amaryllidaceae* family, this species is well adapted to sandy substrates, well-drained in foredunes, coastal hind-dunes and embryonic dunes and is often found among shrubby vegetation in consolidated dunes (De Castro *et al.*, 2016). This species is highly resistant to drought and salinity (Khedr *et al.*, 2003; Grassi *et al.*, 2005; Perrone *et al.*, 2015). It is perennial, 30 to 60 cm high, glabrous, with a large, oval bulb (Julve, 2018), which generally generates one inflorescence per season, sometimes two, with a flowering period from June to September. It is a geophyte capable of vegetative reproduction through the formation of bulbils (Zahreddine *et al.*, 2004). Its geographical distribution is extensive, encompassing the Mediterranean region, southern Europe, extending eastwards to the Transcaucasus, North Africa (comprising Morocco, Algeria, Tunisia, Libya, and Egypt), western Asia (including Cyprus, Lebanon, Syria, Palestine, and Turkey), and the southeastern United States (specifically, the Carolina region). Its distribution

extends to parts of the Atlantic coast, the Black Sea, and the Caspian Sea (El Hadidy *et al.*, 2011; De Castro *et al.*, 2020). It is a medicinal and ornamental species, known for its physiological, phytochemical and pharmacological properties (Berkov *et al.*, 2004; Giovino *et al.*, 2015; Rokbeni *et al.*, 2016; Carfagna *et al.*, 2021). In its natural habitat, *P. maritimum* faces severe environmental constraints such as nutrient-poor soils, prolonged drought periods, high temperatures, strong winds, and salinity (Novo *et al.*, 2004; Fenu *et al.*, 2013). However, these harsh conditions favor the presence and activity of symbiotic soil microorganisms such as arbuscular mycorrhizal fungi (AMF), which form symbiotic relationships with plant roots and contribute to improving plant adaptation to the environment (van der Heijden *et al.*, 2015). The formation of a vast hyphal network by these fungal organisms enables the root system to access water and nutrients over a greater volume of soil (Kakouridis *et al.*, 2022). They play a considerable role in the reproductive phenology of plants, while concomitantly enhancing their resistance to abiotic and biotic stresses (Vázquez-Santos *et al.*, 2019; Wahab *et al.*, 2023). Symbiosis with arbuscular mycorrhizal fungi (AMF) has been demonstrated to enhance plant resilience to drought by optimising water and nutrient efficiency,

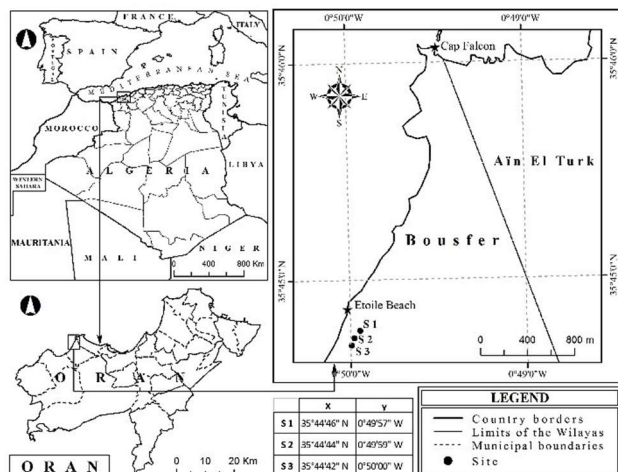


Fig. 1. Geographical location of the study area (Etoile Beach in the Commune of Bousfer, Wilaya of Oran, North-Western Algeria). Scale bar: 200 m.

modulating hormonal homeostasis and mitigating oxidative stress (Rapparini and Peñuelas, 2014; Liu *et al.*, 2016; Wang *et al.*, 2024). Arbuscular mycorrhizal fungi (AMF) have been shown to facilitate plant adaptation to high soil salinity by increasing the uptake of essential nutrients and regulating the exclusion or compartmentalisation of toxic ions such as sodium (Hajiboland, 2013; Tivane *et al.*, 2020). Furthermore, AMF play a crucial role in the bioremediation of contaminated dune soils by improving plant tolerance to heavy metals and facilitating their accumulation, thereby helping to reduce their environmental impact (Gaur and Adholeya, 2004). Despite the ecological importance of mycorrhizal symbiosis for dune plants, research on AMF in coastal dune ecosystems remains constrained by technical challenges and divergent research priorities. Consequently, studies on the mycorrhizal colonisation of numerous species, including *P. maritimum*, remain extremely limited (Giovannetti and Nicolson, 1983; Çakan and Karataş, 2006; Camprubí *et al.*, 2010; De Castro *et al.*, 2018; Tsiknia *et al.*, 2021). In Algeria, research on mycorrhizal associations in dune species remains scarce (Tabti and Bendimered-Mouri, 2022a, 2022b), with most of the research concentrated on *Acacia saligna* (Labill.) H.L.Wendl., of the *Fabaceae* family, in the Terga sandpit of the wilaya of Ain Témouchent, in the far west of Algeria (Nehila *et al.*, 2015; Bouazza *et al.*, 2015). To our knowledge, no studies have been conducted on arbuscular mycorrhizal associations of *P. maritimum* in Algeria, and the subject remains poorly documented worldwide. Against this backdrop, the present study aims to assess AMF spore density, community structure, and diversity, together with root colonisation, associated with *P. maritimum* across spatial and seasonal gradients in the coastal dunes of Oran (North-Western Algeria). In this context, the following research questions were addressed: (i) Do AMF spore

density, community structure and diversity, together with root colonisation of *P. maritimum*, vary among the studied coastal dune sites? (ii) Do seasonal variations influence AMF spore density, community structure, diversity and root colonisation in the rhizosphere of *P. maritimum*? (iii) To what extent do soil physicochemical properties drive the spatial and temporal variability of AMF communities? Based on these questions, the following hypotheses were formulated. First, AMF spore density, community structure and diversity, and root colonisation are expected to differ significantly among sites in response to local variations in soil physicochemical properties. Second, seasonal variation is expected to influence these AMF parameters, whereas species richness is expected to show limited seasonal variation. Third, soil physicochemical properties are expected to be major drivers of AMF spore density, community structure, diversity and root colonisation.

MATERIALS AND METHODS

Study area

The present study was conducted in the dune region of Cap Falcon and Bousfer coast, located in the western part of the Oran province, at the extreme west of Algeria (Fig. 1). This area is characterised by a semi-arid Mediterranean climate, marked by prolonged periods of drought throughout much of the year (Aimé and Penven, 1982). The vegetation is heterogeneous, with specific adaptation to the sandy substrate, which is naturally poor in water and mineral elements and highly permeable.

Site selection and sampling of plant and rhizosphere material

Based on the natural availability and spatial distribution of *P. maritimum* within the study area, three representative coastal dune sites (S1, S2 and S3) were selected (Figs. 1–2). At each site, five individuals were randomly selected per season during 2018–2019 as independent replicates in semi-mobile dunes characterised by sparse vegetation typical of Mediterranean coastal ecosystems. Root systems were excavated to a depth of approximately 20 cm to assess root colonisation, and rhizosphere soil was collected for physicochemical analyses, AMF spore density determination, and subsequent identification. The sampling sites, located in the Etoile-Plage area, corresponded to the following coordinates: S1 (35°44'46" N, 0°49'57" W), S2 (35°44'44" N, 0°49'59" W), and S3 (35°44'42" N, 0°50'00" W) (Fig. 1). These sites were selected to ensure comparable ecological conditions while allowing the assessment of spatial and seasonal variation in AMF-related parameters.

Physico-chemical analysis of rhizosphere soils: Rhizosphere soil samples were analysed to determine their physicochemical properties, given their key role in

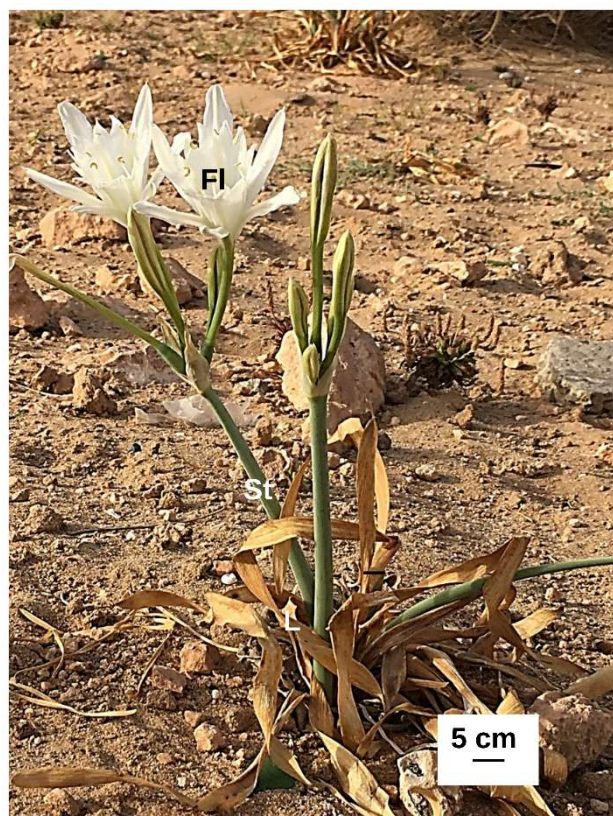


Fig. 2. *Panocratium maritimum* in its natural setting (L: Leaf, St: Stem, Fl: Flower). Scale bar: 5 cm.

shaping plant–fungus interactions. The analyses included particle size determination using the Robinson pipette method (Gee and Or, 2002), moisture content by the gravimetric method (Mathieu *et al.*, 2003), pH measured by potentiometry, and electrical conductivity by conductivity (Mathieu *et al.*, 2003), organic carbon content determined using the modified Walkley-Black method (Nelson and Sommers, 1996), and organic matter content calculated using the formula (1):

$$OM\% = OC\% \times 1.724 \quad (1)$$

where: OM is the organic matter content; OC is the organic carbon content and 1.724 is a constant.

Total nitrogen is determined by the Kjeldahl method (1883), and assimilable phosphorus by the Olsen method (1954). Total limestone using the Bernard calcimeter (Mathieu *et al.*, 2003) and active limestone using the Drouineau method (1942).

Extraction, enumeration and morphological identification of AMF spores: AMF spores were extracted from rhizosphere soils using the wet sieving and decanting method described by Gerdemann and Nicolson (1963). Trap cultures using sorghum as a host plant were established to facilitate the morphological identification of AMF species. Spores retained on sieves with mesh sizes ranging from 500 μm to 32 μm were recovered by centrifugation in a sucrose solution following the method of Jenkins (1964). The recovered spores were rinsed with

water and counted to determine spore density. Morphological identification was performed separately by microscopic examination using polyvinyl–lactoglycerol (PVLG) (Omar *et al.*, 1979) and Melzer (1:1, v/v). Morphological identification was based on spore colour, size, wall structure, and hyphal attachment (Schenck, 1990; Błaszowski, 2012; Souza, 2015; Stürmer *et al.*, 2020).

Root staining and quantification of mycorrhizal colonisation: Histochemical staining of the roots with Trypan Blue was performed according to the method described by Phillips and Hayman (1970). After clarification in a 10% potassium hydroxide solution at 90 °C for 20 minutes, rinsing, and acidification with 2% lactic acid, the roots were stained with 0.05% (W/V) Trypan blue. Microscopic observations were performed using an Axio Scope A1 microscope (Carl Zeiss, Germany) after fixation and mounting in glycerol. The presence of endomycorrhizal structures, including hyphae, arbuscules, and vesicles, was recorded. Root colonisation was assessed using the method of Trouvelot *et al.* (1986), based on the calculation of seven colonisation parameters: F% (2), M% (3), m% (4), v% (5), V% (7), a% (8) and A% (10), whose formulas are as follows:

-- **F (%)**: mycorrhizal frequency

$$F\% = (n/N) \times 100 \quad (2)$$

where: N is the total number of fragments observed and n is the number of mycorrhizal root fragments.

-- **M (%)**: mycorrhizal intensity in the root system

$$M\% = (95n_5 + 70n_4 + 30n_3 + 5n_2 + n_1)/N \quad (3)$$

where: n_5 , n_4 , n_3 , n_2 and n_1 represent the number of mycorrhized fragments recorded as 5, 4, 3, 2 and 1, respectively. Class 5: more than 90%, class 4: between 50% and 90%, class 3: between 10% and 50%, class 2: less than 10%, class 1: trace, and class 0: no mycorrhization.

-- **m (%)**: mycorrhizal intensity in colonised root fragments

$$m\% = M \times (N/n) = M \times 100/F \quad (4)$$

-- **v (%)**: vesicle abundance in colonised root fragments

$$v\% = (100mV_3 + 50mV_2 + 10mV_1)/100 \quad (5)$$

in which mV_3 , mV_2 and mV_1 are the percentages of **m**, V_3 , V_2 and V_1 respectively, calculated according to the following formula:

$$mV_3 = ((95n_5V_3 + 70n_4V_3 + 30n_3V_3 + 5n_2V_3 + n_1V_3)/n) \times 100/m \quad (6)$$

also for mV_2 and mV_1 .

where: n_5V_3 is the number of fragments marked 5 with V_3 , n_4V_3 the number of fragments marked 4 with V_3 ;

V_0 : no vesicles; V_1 : a few vesicles (10%); V_2 : moderately abundant vesicles (50%); V_3 : abundant vesicles (100%).

-- **V (%)**: vesicle abundance in the root system

$$V\% = v \times (M/100) \quad (7)$$

-- **a (%)**: arbuscule abundance in colonised root fragments

$$a\% = (100mA_3 + 50mA_2 + 10mA_1)/100 \quad (8)$$

where: mA_3 , mA_2 and mA_1 are the percentages of **m**, denoted A_3 , A_2 and A_1 , respectively, with:

$$mA_3 = ((95n_5A_3 + 70n_4A_3 + 30n_3A_3 + 5n_2A_3 + n_1A_3) \times 100/m) \quad (9)$$

same for A_2 and A_1 .

A_0 : no arbuscules; A : a few arbuscules (10%); A_2 : moderately abundant arbuscules (50%); A_3 : very abundant arbuscules (100%).

-- **A (%)**: arbuscule abundance in the root system

$$A\% = a \times (M/100) \quad (10)$$



Statistical analysis of results

All statistical analyses were performed on five replicates per site and per season. Data normality was assessed using the Shapiro–Wilk test for all edaphic and arbuscular mycorrhizal parameters (Shapiro and Wilk, 1965). Homogeneity of variances was verified using Levene’s test prior to the application of parametric analyses. A two-way analysis of variance (ANOVA) was performed to evaluate the effects of site, season and their interaction (site \times season) on all the parameters studied. When significant differences were detected, mean comparisons among treatments were carried out using Tukey’s honestly significant difference (HSD) test at the 5% significance level (Tukey, 1949). In addition, Fisher’s least significant difference (LSD) test was applied to confirm specific pairwise differences among sites and seasons (Fisher, 1935). Based on the identification and enumeration of spores, species richness, diversity, and evenness of arbuscular mycorrhizal fungal communities were evaluated using the S, H (11), E (12), and Cs (13) indices, calculated according to the formulas proposed by Shannon and Weaver (1949), Pielou (1966), and Sørensen (1948):

S: Species richness by counting the number of taxa present; H: Shannon-Wiener Diversity index:

$$H = - \sum \frac{N_i}{N} \log_2 \left(\frac{N_i}{N} \right) \quad (11)$$

where: N_i is the number of individuals of a species at a given site, and N is the total number of individuals of all species at that site.

– E: Equitability index of Pielou:

$$E = H / \log_2 S \quad (12)$$

where S is the total number of species.

– Cs: Sørensen’s Similarity Index to measure the similarity between two samples:

$$Cs = 2 \times J / a + b \quad (13)$$

where: a and b are the number of species present in the two compared sites, respectively, and J is the number of species common to both sites.

Canonical Correspondence Analysis (CCA) was performed to examine the relationships between soil physicochemical parameters (independent variables) and AMF spore density, community structure, diversity and colonisation parameters (dependent variables). Two sets of analyses were performed: (i) to explore the relationships between soil physicochemical parameters and AMF spore density (SD), together with community structure and diversity, represented by species richness (S), Shannon diversity index (H) and Pielou’s evenness (E); and (ii) between soil physicochemical parameters and AMF root colonisation parameters, including mycorrhizal frequency (F); mycorrhizal intensity in the root system (M); mycorrhizal intensity in colonised root fragments (m); vesicle abundance in colonised root fragments (v); vesicle abundance in the root system (V); arbuscule abundance in colonised root fragments (a); arbuscule abundance in the root system (A). All statistical analyses and graphical representations were performed

using IBM SPSS Statistics software (version 27; IBM Corp., Armonk, NY, USA).

RESULTS AND DISCUSSION

Physicochemical properties of rhizosphere soils

The analysis of rhizosphere soil parameters associated with *P. maritimum* revealed characteristics typical of sandy substrates (Table 1). Significant spatial differences ($p < 0.05$) were observed between the three sites studied, within the same season, for all edaphic parameters, except in winter for electrical conductivity (EC), total nitrogen (TN) and assimilable phosphorus (AP), and in spring for total nitrogen, sand, silt and clay. Significant seasonal variations ($p < 0.05$) were observed for all the parameters analysed, with the exception of electrical conductivity (EC) for site S2 and sand and silt for sites S1 and S2. Granulometric analyses revealed a sandy texture at all three sites, characterised by a very high sand content (often $> 95\%$), a low silt content, and an extremely low clay content (usually $< 0.05\%$), which explains the low moisture content ($< 4\%$). Although sandy soils typically have good aeration, they have limited water and nutrient retention, as well as limited anionic and cationic exchange capacity (Hatimi and Tahrouche, 2007). Salinity was null at all three sites. The maximum electrical conductivity value was recorded in autumn at site S1 ($F = 16.94$, $p = 0.0003$), while the minimum value was recorded in summer at site S3 ($F = 14.45$, $p = 0.0006$). The pH values varied between 8.09 ± 0.014 (site S3 in summer) and 8.67 ± 0.01 (site S2 in autumn), indicating that coastal dune soils are basic due to their high carbonate content, which comes from a variety of sources, including aeolian sediments, carbonate rock formations, mollusc shell deposits and shell fragments (Philippon and Salomon, 1995). Total and active limestone levels exceeded 25% and 5%, respectively, confirming the highly calcareous nature of the soils. High total limestone values were recorded for the rhizosphere soil at site S1 in autumn ($F = 433$, $p < 0.05$) and spring ($F = 112$, $p < 0.05$), while the lowest values were recorded in winter for the soil at site S3 ($F = 243$, $p < 0.05$). The analyses indicate that the levels of carbon, organic matter, assimilable phosphorus and total nitrogen were all below the standard norms. The sparse vegetation limits the supply of organic matter, resulting in soil poor in essential nutrients. Furthermore, it has been demonstrated that an increase in calcium ions (Ca^{2+}) in the soil precipitates phosphorus (P), rendering it immobile (Wahid *et al.*, 2020). As demonstrated by Le Tacon (1978), the rate of mineralisation is significantly slower in calcareous soils, which consequently limits the availability of nitrogen. The rhizosphere soil at site S1 exhibited the highest levels of (ACaCO₃, OC and OM), while that at site S2 demonstrated the lowest levels. The rhizosphere soil at site S3 exhibited maximum values for (SM and clay) and minimum values for (pH, EC and TCaCO₃).

**Table 1.** Results of physico-chemical analyses of *Pancreatium maritimum* rhizosphere soil for the three sites during the four seasons.

Rhizosphere Soil Parameters	Site	Seasons			
		Spring	Summer	Autumn	Winter
SM (%)	S1	1.33 ± 0.013 ^{Ac}	0.78 ± 0.03 ^{Bc}	2.35 ± 0.01 ^{Cc}	3.98 ± 0.007 ^{Dc}
	S2	0.96 ± 0.015 ^{Ab}	0.44 ± 0.02 ^{Bb}	2.4 ± 0.01 ^{Cb}	3.82 ± 0.006 ^{Db}
	S3	1.57 ± 0.013 ^{Aa}	1.26 ± 0.02 ^{Ba}	2.15 ± 0.015 ^{Ca}	3.8 ± 0.008 ^{Da}
pH	S1	8.58 ± 0.02 ^{Aa}	8.31 ± 0.01 ^{Ba}	8.24 ± 0.03 ^{Ba}	8.47 ± 0.02 ^{Ca}
	S2	8.44 ± 0.055 ^{Ab}	8.52 ± 0.014 ^{Bb}	8.67 ± 0.01 ^{Cb}	8.28 ± 0.03 ^{Db}
	S3	8.33 ± 0.03 ^{Ab}	8.09 ± 0.014 ^{Bc}	8.41 ± 0.035 ^{Cc}	8.2 ± 0.016 ^{Db}
EC (mS/cm)	S1	0.165 ± 0.009 ^{Aa}	0.282 ± 0.023 ^{Ba}	0.315 ± 0.008 ^{Ba}	0.195 ± 0.013 ^{Ca}
	S2	0.154 ± 0.015 ^{Aa}	0.198 ± 0.025 ^{Ab}	0.230 ± 0.016 ^{Ab}	0.175 ± 0.014 ^{Aa}
	S3	0.250 ± 0.011 ^{Ab}	0.129 ± 0.006 ^{Bc}	0.220 ± 0.011 ^{Ab}	0.189 ± 0.010 ^{Ca}
OC (%)	S1	0.984 ± 0.002 ^{Ac}	0.156 ± 0.003 ^{Bc}	0.172 ± 0.004 ^{3Cc}	0.212 ± 0.001 ^{Dc}
	S2	0.262 ± 0.01 ^{Ab}	0.198 ± 0.012 ^{Bb}	0.13 ± 0.004 ^{Cb}	0.049 ± 0.007 ^{3Db}
	S3	0.912 ± 0.01 ^{Aa}	0.165 ± 0.003 ^{Bc}	0.203 ± 0.002 ^{Ca}	0.072 ± 0.001 ^{3Da}
OM (%)	S1	1.7 ± 0.0037 ^{Ac}	0.27 ± 0.005 ^{Bc}	0.3 ± 0.0072 ^{Cc}	0.37 ± 0.0016 ^{Dc}
	S2	0.453 ± 0.018 ^{Ab}	0.343 ± 0.02 ^{Bb}	0.23 ± 0.0068 ^{Cb}	0.085 ± 0.013 ^{Db}
	S3	1.58 ± 0.02 ^{Aa}	0.29 ± 0.0042 ^{Bc}	0.35 ± 0.0033 ^{Ca}	0.13 ± 0.0014 ^{Da}
TN (%)	S1	0.057 ± 0.002 ^{Aa}	0.037 ± 0.003 ^{Ba}	0.019 ± 0.0027 ^{Ca}	0.01 ± 0.0028 ^{Ca}
	S2	0.052 ± 0.008 ^{Aa}	0.026 ± 0.003 ^{Bb}	0.015 ± 0.003 ^{Ba}	0.023 ± 0.007 ^{Ba}
	S3	0.047 ± 0.0043 ^{Aa}	0.013 ± 0.001 ^{Bc}	0.068 ± 0.0032 ^{Cb}	0.027 ± 0.0028 ^{Da}
AP (ppm)	S1	7.2 ± 0.27 ^{Aa}	5.5 ± 0.74 ^{Ba}	2.57 ± 0.34 ^{Ca}	3.97 ± 0.08 ^{Ca}
	S2	6.74 ± 0.7 ^{Aa}	7.8 ± 0.17 ^{Ab}	3.39 ± 0.22 ^{Bb}	5.77 ± 0.26 ^{Ab}
	S3	8.25 ± 0.2 ^{Aa}	4.28 ± 0.15 ^{Ba}	5.61 ± 0.16 ^{Cc}	5.19 ± 0.2 ^{Cb}
TCaCO ₃ (%)	S1	35.5 ± 0.19 ^{Ab}	33.1 ± 0.15 ^{Bb}	37.4 ± 0.2 ^{Cb}	30 ± 0.18 ^{Db}
	S2	34 ± 0.12 ^{Aa}	28.74 ± 0.26 ^{Ba}	31.61 ± 0.09 ^{Ca}	32 ± 0.17 ^{Ca}
	S3	32 ± 0.19 ^{Ac}	30.1 ± 0.13 ^{Bc}	34.4 ± 0.082 ^{Cc}	27.35 ± 0.09 ^{Dc}
ACaCO ₃ (%)	S1	7 ± 0.068 ^{Ab}	6.24 ± 0.13 ^{Bb}	8.5 ± 0.03 ^{Cb}	5.14 ± 0.01 ^{Db}
	S2	6.1 ± 0.027 ^{Aa}	4.02 ± 0.02 ^{Ba}	5.45 ± 0.02 ^{Ca}	4.31 ± 0.01 ^{Dc}
	S3	5.19 ± 0.02 ^{Ac}	6.05 ± 0.02 ^{Ba}	7 ± 0.009 ^{Cc}	4.52 ± 0.01 ^{Da}
Granulometry (%)					
Sand	S1	97.43 ± 0.28 ^{Aa}	96.8 ± 0.38 ^{Aa}	98.15 ± 0.32 ^{Aa}	97.26 ± 0.47 ^{Aa}
	S2	95 ± 0.55 ^{Aa}	93.64 ± 1.55 ^{Ab}	96.2 ± 0.64 ^{Ab}	92 ± 1.65 ^{Ab}
	S3	96.48 ± 0.97 ^{Aa}	97.6 ± 0.37 ^{Aa}	98 ± 0.14 ^{Aa}	93.26 ± 0.6 ^{Bb}
Silt	S1	2.55 ± 0.28 ^{Aa}	3.17 ± 0.4 ^{Aa}	1.84 ± 0.32 ^{Aa}	2.7 ± 0.47 ^{Aa}
	S2	4.97 ± 0.54 ^{Aa}	6.2 ± 1.5 ^{Ab}	3.76 ± 0.63 ^{Ab}	7.9 ± 1.64 ^{Ab}
	S3	3.5 ± 0.97 ^{Aa}	2.38 ± 0.37 ^{Aa}	2 ± 0.14 ^{Aa}	5.57 ± 0.55 ^{Ba}
Clay	S1	0.017 ± 0.006 ^{Aa}	0.025 ± 0.007 ^{Aa}	0.01 ± 0.006 ^{ABa}	0.04 ± 0.003 ^{Aa}
	S2	0.023 ± 0.004 ^{Aa}	0.16 ± 0.04 ^{Bb}	0.034 ± 0.007 ^{Cb}	0.1 ± 0.01 ^{Bb}
	S3	0.019 ± 0.008 ^{Aa}	0.016 ± 0.007 ^{Ba}	0 ± 0.00 ^{Ca}	1.17 ± 0.07 ^{Dc}
Texture	S1	Sandy			
	S2	Sandy			
	S3	Sandy			

Data are presented as mean ± standard deviation of five replicates. Values with the same letter are not significantly different between seasons (uppercase) and between sites (lowercase) according to Fisher's LSD test at the 5% threshold. SM: soil moisture; EC: electrical conductivity; OC: organic carbon; OM: organic matter; TN: total nitrogen; AP: assimilable phosphorus; TCaCO₃: total limestone; ACaCO₃: active limestone.

AMF Spore density estimation

The AMF spore density in the rhizosphere of *P. maritimum* showed a significant difference in winter at site S1 ($F = 5.53, p = 0.008$) and in autumn at sites 2 and 3 ($F = 4.66, p = 0.01$ and $F = 3.45, p = 0.04$, respectively), while during the other seasons, it recorded statistically similar values (Fig. 3). Significant variations were also observed between sites in spring ($F = 5.08, p = 0.02$) and summer ($F = 7.52, p = 0.007$). The peak density was recorded in autumn, with an average of 70.4 ± 2.84 spores/100 g of dry

soil at site S1, compared to 31.6 ± 4.23 spores/100 g of dry soil at site S2 in summer. Considering the annual averages per station, the values ranged from 40.85 ± 5.9 spores/100 g (site S2) to 57.75 ± 6.65 spores/100 g of dry soil (site S1), reflecting spatial heterogeneity and conditions favourable to sporulation, probably due to the relatively high OC and OM contents at site S1, but below standard norms. Furthermore, seasonal analysis across all stations shows a maximum average density in autumn (61.87 ± 5.4 spores/100 g of dry soil) and a minimum value in winter

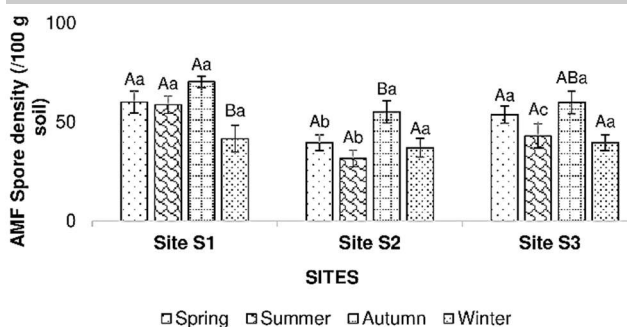


Fig. 3. Results of the estimation of the AMF spore density of *Pancratium maritimum* in the soil rhizosphere at the three sites (S1, S2 and S3) during the four seasons. Values accompanied by the same letter are not significantly different between seasons (uppercase) and between sites (lowercase) according to Fisher's LSD test at $p \leq 0.05$.

(39.4 ± 4.96 spores/100 g of dry soil), indicating the marked influence of seasonal conditions on spore sporulation in the soil. The seasonal trends observed in spore density can be attributed to increased sporulation at the end of the growing season, which corresponds to the autumn months (Greipsson and El-Mayas, 2000; Rodríguez-Echeverría *et al.*, 2008; Su *et al.*, 2011). The average spore density of AMF was 49.24 / 100 g of dry soil. Błaszczkowski and Czerniawska (2011) found that spore density in the coastal dunes of Bornholm (Denmark) was low, ranging from 0 to 153 spores/100 g of dry soil. A comparison between the different dune species reveals that it is five times higher than that estimated for *Artemisia halodendron* (10.03 spores/100 g of dry soil), higher than that estimated for *Chenopodium glaucum* (24.28 spores), but lower than that counted for *Polygonum lapathifolium* (94.40 spores) in Chinese dunes (Wang *et al.*, 2021). This value is also higher than that estimated for *Lotus creticus* (41 spores) in the northwestern Algerian dunes (Nehila *et al.*, 2015). Still, it remains relatively close to that observed in our study. The difference in densities can be attributed to factors such as plant communities, edaphic parameters such as soil pH, nutrient availability and soil texture, as well as climatic characteristics, including temperature, precipitation and seasonal variations (Escudero and Mendoza, 2005; Xu *et al.*, 2017; Vieira *et al.*, 2019).

Diversity and structure of AMF

Fifteen AMF species belonging to seven genera and four families of the phylum Glomeromycota were identified (Schüßler, Schwarzott & C. Walker). The Glomeraceae family (Piroz. & Dalpé emend C. Walker & Schüßler), including the *Glomus* genus (Tul. & C. Tul. emend C. Walker & A. Schüßler), comprises multiple species (*Glomus* spp.), the *Rhizophagus* genus (C. Walker & A. Schüßler) includes *Rhizophagus* sp, the *Funneliformis* genus (C. Walker & Schüßler) is represented by *Funneliformis* sp, and the *Septoglomus*

genus (Sieverd., G.A. Sliva & Oehl) by *Septoglomus* sp. The *Acaulosporaceae* family (Gerd. & Trappe) includes the genus *Acaulospora* (Gerd. & Trappe emend. Berch) with *Acaulospora* spp., and the *Gigasporaceae* family (Morton & Benny) includes the genus *Gigaspora* (Gerd. & Trappe) with *Gigaspora* spp. Finally, the *Diversisporaceae* family (C. Walker & Schüßler) includes the genus *Diversispora* (C. Walker & Schüßler), to which *Diversispora* sp. belongs (Fig. 4). The coexistence of several taxa reflects marked functional diversity. The Glomeraceae family and the *Glomus* genus were the most dominant, reflecting their ecological plasticity and dominance in sandy soils. It has been demonstrated that AMF species diversity plays an essential role in plant resilience and performance, particularly in stressful environments such as coastal dunes (Da Silva *et al.*, 2015). It improves the ability of plants to adapt to nutrient-poor soils, which is essential for their survival in such extreme conditions (Hart and Klironomos, 2003; van der Heijden and Scheublin, 2007). The present results are consistent with those of De Castro *et al.* (2018), who reported a predominance of Glomeraceae taxa, including *Rhizophagus* and *Glomus*, along with members of the *Diversisporales*, in *P. maritimum* from Mediterranean coastal dunes using molecular approaches. This convergence suggests that AMF communities associated with *P. maritimum* are structured by environmentally tolerant taxa adapted to coastal sandy habitats. It also supports the widely accepted view that arbuscular mycorrhizal symbioses exhibit low host specificity, allowing plants to associate with a broad range of AMF taxa shaped by local environmental conditions (Smith and Read, 2008; Öpik *et al.*, 2010). Despite these similarities, some differences in the composition of AMF communities between the two studies may be attributed to methodological and ecological factors. The present study relied on morphotaxonomic identification of spores isolated from the rhizosphere, whereas De Castro *et al.* (2018) employed molecular sequencing approaches targeting fungal DNA within root tissues. These methodological differences are known to influence the detection of AMF taxa. In this context, molecular approaches provide complementary insights into AMF diversity within plant roots, notably by detecting non-sporulating or cryptic taxa, whereas morphological analyses remain essential for assessing sporulation patterns and soil AMF community structure (Stockinger *et al.*, 2010; Öpik *et al.*, 2013). In addition, molecular methods may be affected by primer bias, differential DNA amplification, and incomplete reference databases, potentially leading to the underestimation of certain fungal lineages (Stockinger *et al.*, 2010; Öpik *et al.*, 2013). Several authors have emphasised that morphological identification remains a fundamental tool for the ecological and quantitative assessment of AMF communities (Brundrett, 1991; Oehl *et al.*, 2011). These

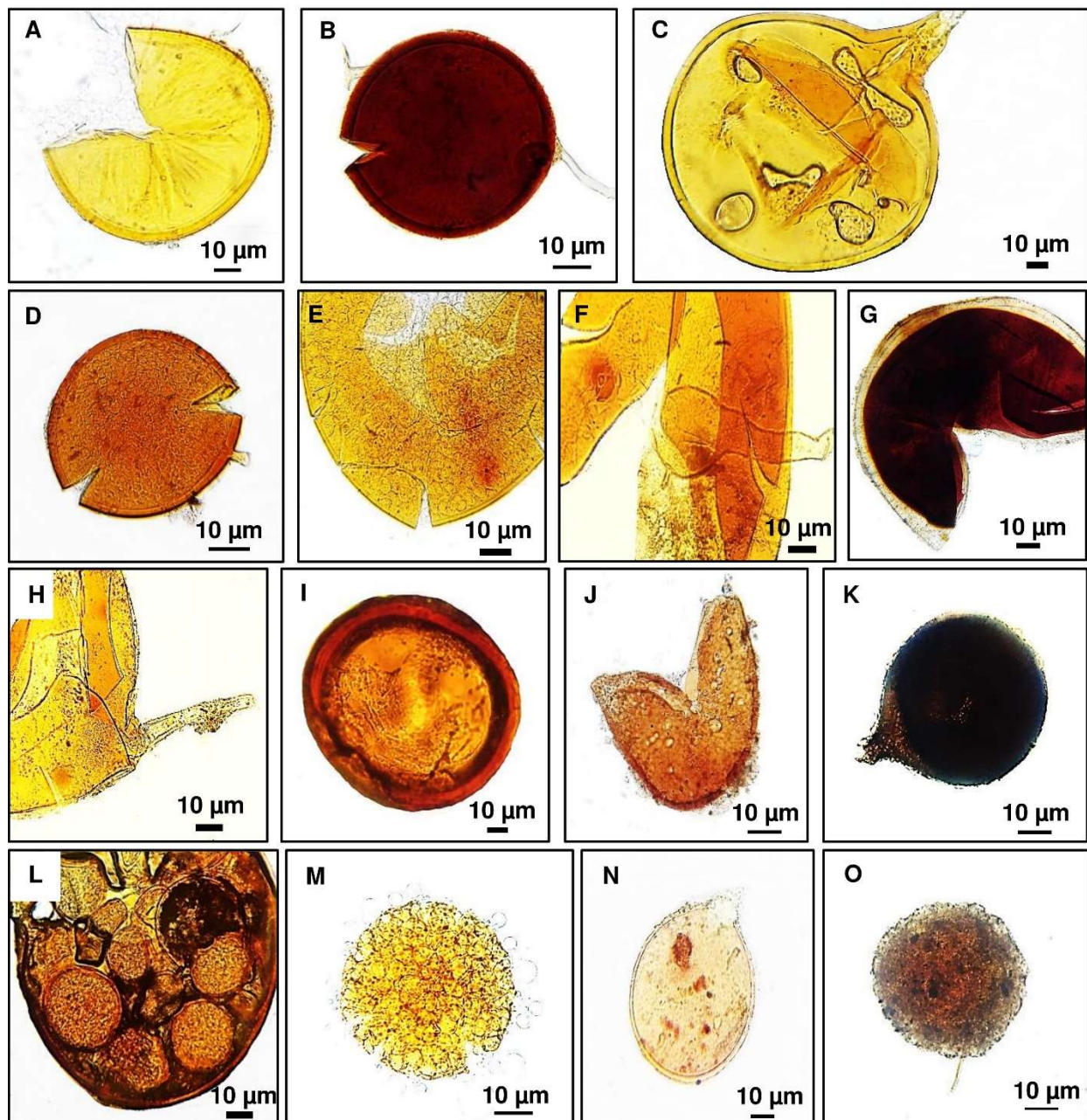


Fig. 4. Morphotypes of AMF spores isolated from trap cultures and rhizospheric soil of *Pancratium maritimum* observed by light microscopy in PVLG + Melzer reagent (400 ×). **A:** *Glomus* sp 1 (globose spore, 97.2 µm in diameter, with a multilayered wall continuous); **B:** *Rhizophagus* sp (glomoid spore, 81 µm in diameter, with a smooth external wall, showing a red dextrinoid reaction); **C:** *Funneliformis* sp (spore measuring 212.5 µm in diameter with a funnel-shaped base); **D:** *Glomus* sp 2 (glomoid spore, 75.7 µm in diameter, with a multilayered wall, and a continuous subtending hypha); **E:** *Glomus* sp 3 (large globose spore measuring 423 µm in diameter); **F:** *Gigaspora* sp 1 (large-spored morphotype, 486 µm in diameter, with a thick wall and a sporogenous bulb); **G:** *Acaulospora* sp 1 (acaulosporoid spore, globose, 100 µm in diameter, with multiple wall layers and an internal dextrinoid wall, appearing dark red-violet); **H:** *Gigaspora* sp 2 (large spore, 468 µm in diameter, with sporogenous bulb); **I:** *Acaulospora* sp 2 (acaulosporoid, globose, 127 µm in diameter, with several distinct wall layers); **J:** *Glomus* sp 4 (subglobose globose spore measuring µm in diameter); **K:** *Septoglomus* sp (glomoid spore, 77.6 µm in diameter, dark brown); **L:** sporocarp of *Diversispora* sp (235 µm in diameter, globose spores with diverse wall structures, often aggregated into sporocarps); **M:** *Acaulospora* sp 3 (ornamented acaulosporoid spore measuring 81.6 µm in diameter); **N:** *Glomus* sp 5 (subglobose globose spore, 46 µm in diameter, with multilayered wall); **O:** *Glomus* sp 6 (spore has a thick, 66 µm in diameter, multilayered wall with a subtending hypha present). Scale bars: 10 µm.

**Table 2.** Species richness (S), Shannon–Weaver diversity index (H) and Pielou’s evenness (E) of AMF in rhizospheric soils of *Pancratium maritimum* at the three studied sites across the four seasons.

Indices/ Seasons	S1			S2			S3		
	S	H	E	S	H	E	S	H	E
Spring	13.0 ± 0.70	2.05 ± 0.035	0.8 ± 0.011	14.0 ± 1.73	1.88 ± 0.045	0.69 ± 0.011	12.0 ± 0.70	2.19 ± 0.049	0.81 ± 0.011
Summer	13.0 ± 0.70	2.33 ± 0.039	0.91 ± 0.011	14.0 ± 0.70	1.64 ± 0.045	0.6 ± 0.014	14.6 ± 0.54	1.98 ± 0.051	0.72 ± 0.014
Autumn	12.4 ± 0.54	2.48 ± 0.045	0.98 ± 0.011	15.0 ± 1.30	2.34 ± 0.030	0.87 ± 0.011	14.8 ± 0.44	2.56 ± 0.041	0.93 ± 0.011
Winter	12.0 ± 0.70	1.86 ± 0.048	0.74 ± 0.014	14.0 ± 1.73	1.89 ± 0.040	0.7 ± 0.011	15.0 ± 2.16	1.96 ± 0.041	0.71 ± 0.011

S: Species richness; H: Shannon-Weaver index; E: Pielou equitability index. Values are expressed as mean ± SD (n = 5).

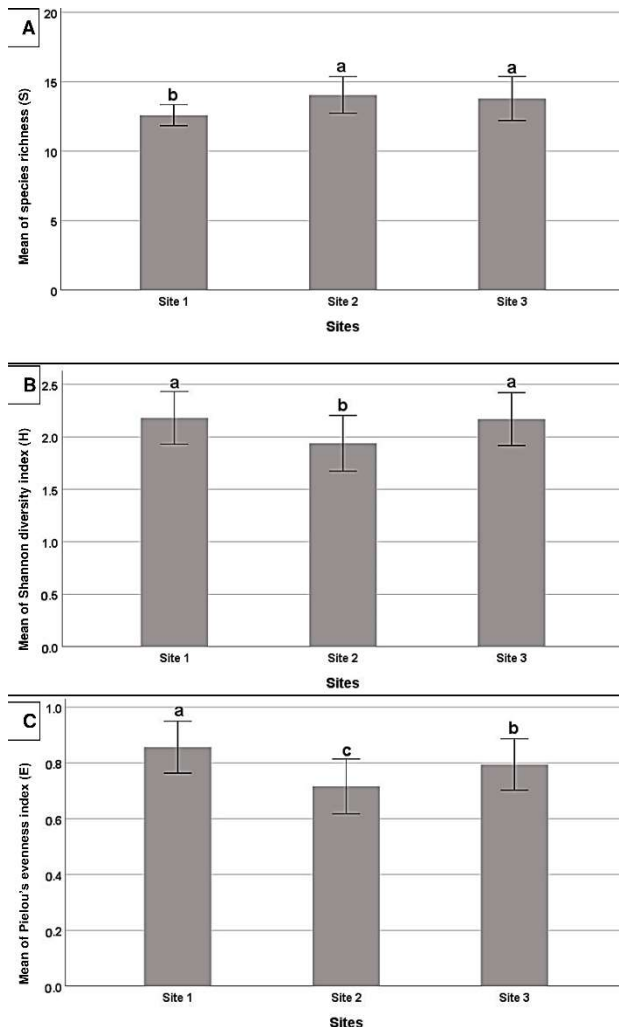


Fig. 5. Site effect on diversity indices in the rhizosphere of *Panocratium maritimum* (mean ± SD): **A.** species richness (S), **B.** Shannon diversity index (H), and **C.** Pielou’s evenness index (E). Bars with different letters indicate significant differences among sites (Tukey’s test, $p \leq 0.05$).

approaches are increasingly complemented by molecular techniques, allowing a more comprehensive and integrative evaluation of AMF community composition. Comparable AMF taxa have also been reported in other Mediterranean coastal dune ecosystems. For instance, the genera *Glomus*, *Acaulospora* and *Gigaspora* have been recorded in association with *Lotus creticus* in the

Algerian coastal dunes of Terga-plage, located approximately 70 km from the present study area (Bouazza *et al.*, 2015). At a broader spatial scale, Stürmer *et al.* (2013) reported that AMF communities in coastal dunes may exhibit relatively similar compositions even across distances of up to 150 km. However, variations in community composition may also occur at smaller spatial scales, suggesting that local environmental conditions and site-specific factors play an important role in structuring AMF assemblages (Wolfe *et al.*, 2007). Species richness (S) was significantly higher at sites S2 and S3 compared with site S1 (Fig. 5A; Table 2), indicating marked spatial variability in AMF communities in the studied coastal dunes. This spatial heterogeneity is generally associated with variations in edaphic characteristics, including soil texture, salinity, organic matter content and nutrient availability, even at low concentrations, which are recognised as major drivers of AMF diversity and community composition (Smith and Read, 2008; Öpik *et al.*, 2010). The spatial patterns observed in AMF diversity indices suggest that the structure of fungal communities differed among the studied sites. While species richness was lower at site S1, the relatively high values of the Shannon diversity index and Pielou’s evenness indicate a more balanced distribution of taxa within the community. In contrast, site S2 exhibited lower diversity and evenness values despite a relatively high species richness, suggesting a stronger dominance of a limited number of taxa (Fig. 5B,C; Table 2). Such patterns indicate that community structure may vary independently of species richness, reflecting differences in the relative abundance and distribution of taxa within each site. Similar patterns have been reported across diverse ecosystems, where AMF communities frequently exhibit contrasting relationships between species richness and evenness depending on local environmental conditions and ecological filtering processes that shape fungal community assembly (Öpik *et al.*, 2010; Davison *et al.*, 2015). These observations also suggest that AMF communities associated with *P. maritimum* are able to maintain functional stability across heterogeneous dune habitats, despite differences in local soil conditions. Species occurring in these environments often show a high degree of ecological tolerance and adaptive capacity to stressful conditions typical of coastal dune systems, including nutrient limitation, substrate



Table 3. Two-way ANOVA results showing the effects of site, season and their interaction (site × season) on AMF Species richness (S), Shannon–Weaver diversity index (H) and Pielou's evenness (E).

Source of variation	Species richness S			Shannon-Weaver index H			Pielou equitability index E		
	df	F	p-value	df	F	p-value	df	F	p-value
Site	2	9.185	0.000***	2	199.585	0.000***	2	649.847	0.000***
Season	3	2.017	0.124 ^{ns}	3	499.497	0.000***	3	854.295	0.000***
Site × Season	6	2.577	0.030 [*]	6	75.447	0.000***	6	122.634	0.000***

ns: not significant. *: $p < 0.05$; ***: $p < 0.001$; df: degree of freedom

Table 4. Sørensen similarity index of AMF communities between the three sites across the four seasons.

	S1–S2	S1–S3	S2–S3
Spring	0.92	0.92	1.00
Summer	0.92	0.92	1.00
Autumn	0.89	0.89	1.00
Winter	0.89	0.89	1.00

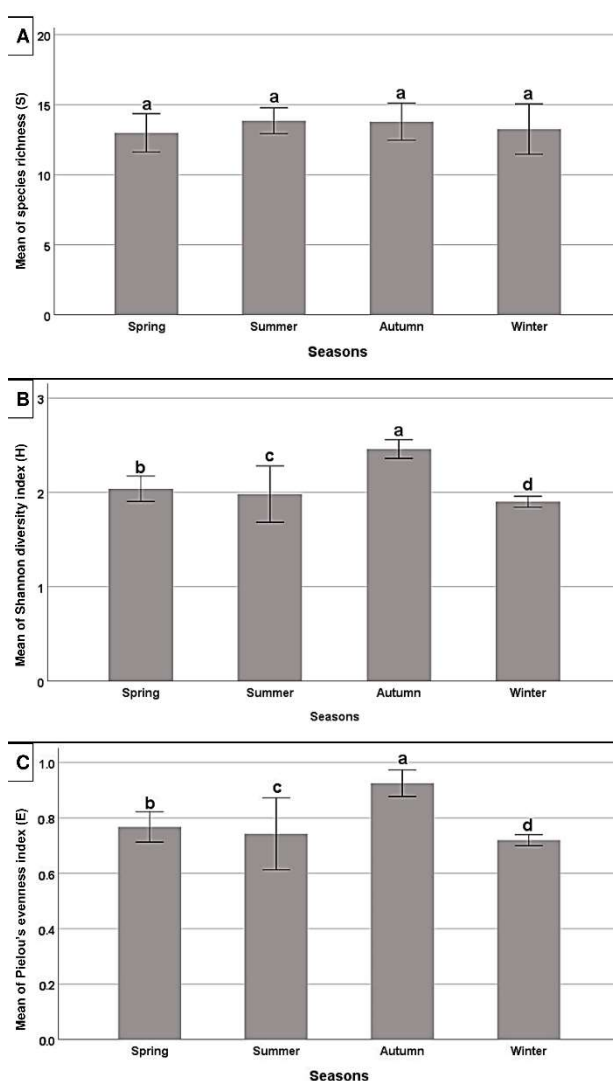


Fig. 6. Seasonal variation in diversity indices in the rhizosphere of *Panocratium maritimum* (mean ± SD): **A.** species richness (S), **B.** Shannon diversity index (H), and **C.** Pielou's evenness index (E). Bars with different letters indicate significant differences among seasons (Tukey's test, $p \leq 0.05$).

instability and drought stress (Augé, 2001; Maun, 2009). Species richness remained relatively stable across seasons, with no significant differences observed (Fig. 6A), suggesting the presence of a relatively persistent propagule reservoir in dune soils. Such stability has been reported in semi-arid ecosystems, where AMF communities often exhibit limited short-term seasonal variation, driven by the persistence of fungal propagules and the dominance of ecologically tolerant taxa (Santos-González *et al.*, 2007; Davison *et al.*, 2015; Janoušková *et al.*, 2023). In contrast, the Shannon and Pielou indices exhibited significant seasonal variation, with maximum values observed in autumn and minimum values in winter, while intermediate values were recorded in summer and spring (Fig. 6B, C). This pattern indicates that seasonal factors primarily influence the relative distribution and abundance of taxa rather than their presence. These fluctuations may be related to variations in soil moisture and temperature, as well as host plant phenology, which regulate fungal activity, root colonisation, and sporulation in dune environments (Augé, 2001; Smith and Read, 2008). Autumn thus appears to provide more favourable and stable ecological conditions. Two-way analysis of variance showed that both site and the site × season interaction significantly affected AMF richness, diversity, and evenness (Table 3). The interaction between site and season significantly influenced all diversity indices (Fig. 7A–C), indicating that AMF community responses strongly depend on local environmental conditions. The highest values of richness and diversity were recorded at site S3 in autumn, whereas the lowest values were observed in summer or spring, depending on the site. These patterns reflect the combined effects of spatial heterogeneity and temporal dynamics and are consistent with ecological models emphasising the role of environmental filtering in shaping fungal community assembly (Öpik *et al.*, 2010; Nemergut *et al.*, 2013; Kraft *et al.*, 2015). The Sørensen similarity index indicated high to very high similarity among sites across seasons (Table 4). The particularly strong similarity between sites S2 and S3 suggests the existence of a common core of taxa adapted to the ecological constraints of coastal dunes. The slightly lower similarity observed for site S1 may be related to edaphic differences, especially carbonate content, or to moderate seasonal influences. This inter-site stability probably reflects the functional resilience of AMF communities in ecosystems

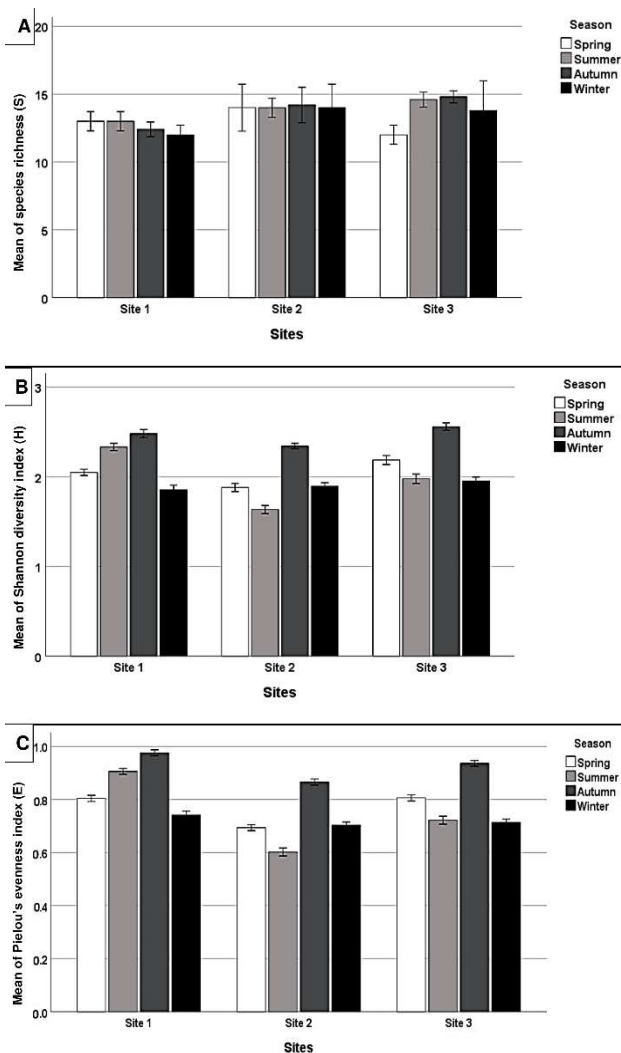


Fig. 7. Interaction effect of site and season on diversity indices in the rhizosphere of *Pancratium maritimum* (mean \pm SD): **A.** species richness (S), **B.** Shannon diversity index (H), and **C.** Pielou's evenness index (E).

exposed to harsh environmental conditions. The three indices (S, H and E) reached their highest values in autumn and their lowest values in spring and summer, reflecting seasonal fluctuations in environmental conditions and host plant activity. These findings indicate that spatial factors represent the primary drivers of AMF diversity, whereas seasonal variations mainly regulate community structure and evenness.

AMF root colonisation

Microscopic observation showed AMF structures in *P. maritimum* roots (Fig. 8). These structures are classified as Arum-type, a classification that has already been observed in several other dune plants, including *Retama sphaerocarpa*, *Phleum arenarium*, *Gypsophila paniculata*, *Centaurium littorale*, *Linaria loeselii*, *Aster tripolium* and *Plantago maritima* (Druva-Lusite and

Ievins, 2010). The average mycorrhizal frequency (F) was highest (100%), regardless of site and season, indicating no significant variation (Fig. 9). This reflects a high degree of dependence of this plant on AMF for its growth and survival. The high mycorrhizal frequency values are comparable to those reported for other dune plants: 100% for *Picris hieracioides*, *Melilotus officinalis* and *Daucus carota*, 92% for *Croton rhamnifolius* and *Acacia tortuosa* in the coastal dunes of Venezuela (Alarcón and Cuenca, 2005) and for *Lotus creticus* in the north-western coastal dunes of Algeria (Nehila *et al.*, 2015). A comparative analysis of the results of various studies on the mycorrhizal status of *Pancratium maritimum* reveals heterogeneity in mycorrhizal colonisation rates. Çakan and Karataş (2006) demonstrated that this species was not mycorrhizal in Turkish coastal dunes, while Giovannetti and Nicolson (1983) identified a percentage ranging from 38% to 72% in Italian dunes. Tsiknia *et al.* (2021) and Camprubí *et al.* (2010) reported rates of 65% and 74%, respectively, in Greek and Spanish dunes. The other parameters of mycorrhizal colonisation (M, m, v, V, a and A) showed significantly different mean values between seasons at each site ($p < 0.05$) but did not vary significantly between sites during the same season, except for the vesicle abundance in colonised root fragments (v) in spring ($F = 6.61$, $p = 0.01$) and winter ($F = 4.22$, $p = 0.04$), the vesicle abundance in the root system (V) ($F = 5.38$, $p = 0.02$) and the arbuscule abundance in colonised root fragments (a) ($F = 13.91$, $p = 0.0001$) in winter. For all sites considered, site S1 had the maximum value of $57.16 \pm 4.82\%$ in spring and the minimum value of mycorrhizal intensities (M and m) of $32.2 \pm 2.52\%$ in autumn, illustrating their sensitivity to seasonal fluctuations. As the mycorrhizal frequency was at its maximum, the mycorrhizal intensities (M) and (m) were equal by definition (Equation (4)). The vesicles appeared throughout the year and remained more dominant than the arbuscules, which appeared only in winter and summer. The highest vesicle abundance values (v and V) were recorded at site S1 in spring (63.25% and 33.16%, respectively), while the lowest were observed at site S3 in autumn (27.14% and 9.7%, respectively). The highest arbuscule abundances (a and A) were recorded at site S2 in winter (56.9% and 27.16%, respectively), while the lowest were recorded at site S3 in summer (22.82% and 12.1%, respectively). These observed fluctuations may be related to edaphic and climatic factors or to the phenology of the host plant, which directly influences mycorrhizal structures and their abundance (Enebe and Erasmus, 2023). Vesicles are more abundant and more frequent than arbuscules because they serve as storage and survival structures, which are particularly useful in arid soils, whereas arbuscules, which ensure nutritional exchanges, are less frequent because metabolic activity is reduced under stressful conditions (Madouh *et al.*, 2025).

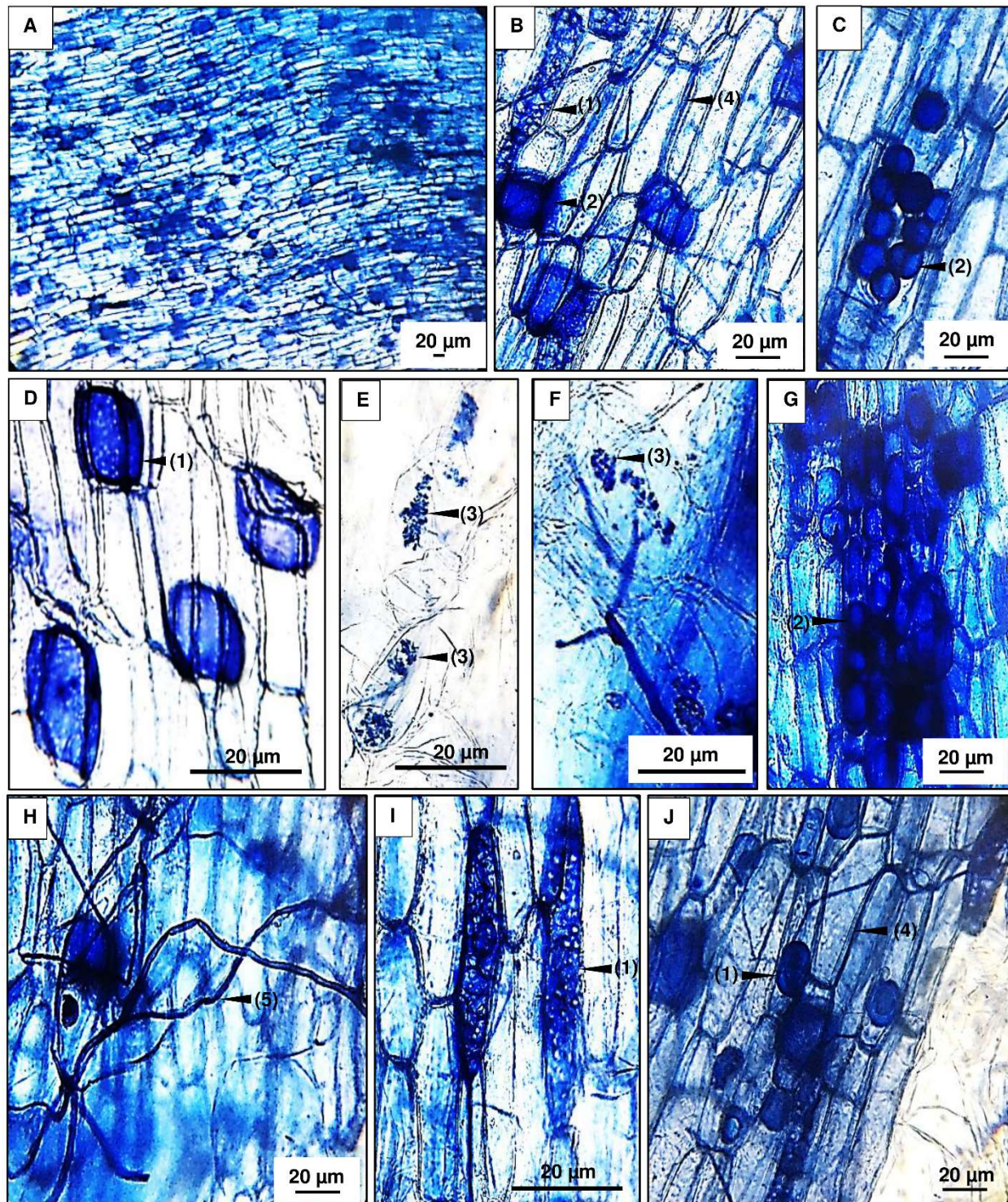


Fig. 8. AMF structures with Trypan blue-stained *Pancretium maritimum* roots. Numbers refer to: (1) vesicles; (2) intraradical spores; (3) arbuscules; (4) intraradical hyphae; (5) extraradical hyphae. **A.** Overview of a heavily colonised root segment showing multiple AMF intraradical structures within cortical cells; **B.** large intraradical vesicles (1) occupying entire cortical cells, associated with intraradical hyphae (4) and an intraradical spore (2); **C.** intraradical spores (2) arranged in a sporocarp-like cluster, globose to subglobose, with thick well-defined wall layers; **D.** large elongated vesicles (1); **E.** arbuscules (3) appearing as densely stained dot-like clusters within cortical cells; **F.** arbuscules (3) showing characteristic dichotomous branching with fine hyphal ramifications; **G.** intraradical spores (2) of variable morphology forming dense clusters within the root cortex; **H.** entangled extraradical hyphae (5) forming an external hyphal network; **I.** large intraradical vesicles (1) densely packed within cortical cells; **J.** Subglobose terminal vesicles (1) of variable size within cortical cells, associated with intraradical hyphae (4). Magnifications: A (100 ×), B, D, F, G, H and I (400 ×); C, E and J (1000 ×). Scale bars: 20 µm.

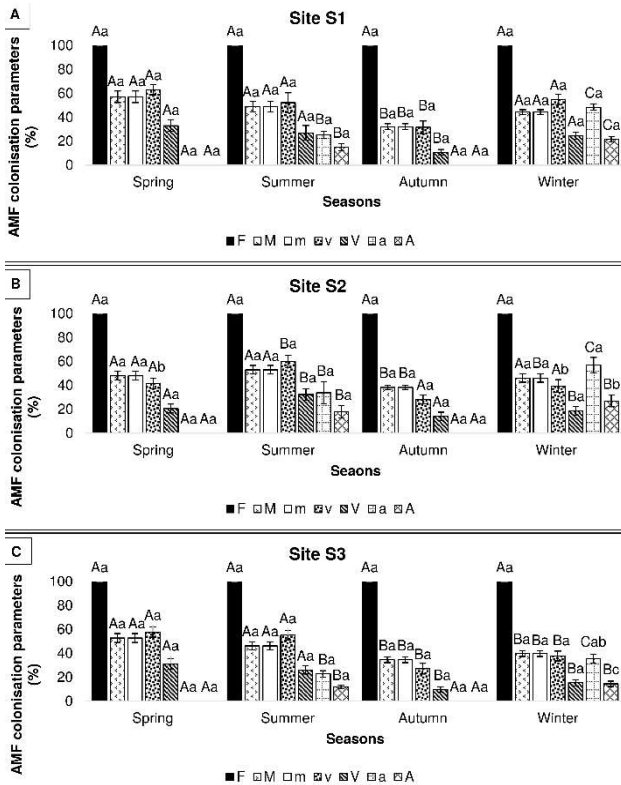


Fig. 9. Variation in arbuscular mycorrhizal colonisation parameters of *Pancratium maritimum* across three sites (S1 (A), S2 (B) and S3 (C)) and four seasons. Data are presented as averages of five replicates. Values accompanied by the same letter are not significantly different between seasons for the same site (upper case) and between sites for the same season (lower case) according to Fisher's LSD test at the 5% threshold, **F**: mycorrhizal frequency; **M**: mycorrhizal intensity in the root system; **m**: mycorrhizal intensity in colonised root fragments; **v**: vesicle abundance in colonised root fragments; **V**: vesicle abundance in the root system; **a**: arbuscule abundance in colonised root fragments; **A**: arbuscule abundance in the root system.

Table 5. Canonical Correlation Analysis of relationships between soil physicochemical parameters and AMF spore density, community structure and diversity.

Correlation	Correlation coefficient	Eigen value	P values
1	0.987	37.453	0.000***
2	0.904	4.485	0.000***
3	0.870	3.106	0.000***
4	0.601	0.565	0.007**

** : $P < 0.01$. *** : $P < 0.001$.

Relationships between soil physicochemical properties and AMF spore density, community structure, diversity and root colonisation

Canonical Correlation Analysis (CCA) was used to examine the relationships between soil physicochemical parameters and AMF spore density, community structure, diversity and colonisation parameters. Some colonisation parameters (F, m, a and A) were not included in the CCA. The variable F showed no variance (F = 100% for all samples), while the variable m was perfectly collinear

with M, indicating redundant information. In addition, the parameters a and A contained zero values and were therefore excluded from the analysis. Consequently, these variables were excluded from the canonical model to avoid statistical bias. CCA revealed four possible and statistically significant canonical correlations between soil physicochemical parameters and AMF spore density, community structure and diversity (Table 5). The first three canonical correlations showed very strong relationships, with correlation coefficients ranging from 0.87 to 0.98, and were highly significant ($P < 0.001$). The fourth canonical correlation showed a moderate relationship ($r = 0.60$) but remained statistically significant ($P < 0.01$) (Table 5). The first canonical function explained the largest proportion of the shared variance between the two sets of variables. Soil physicochemical parameters contributed 25.5% to this canonical relationship, while the AMF community variables (species richness (S), Shannon diversity index (H), Pielou's evenness (E) and spore density (SD)), contributed 70.6% to the same canonical axis. The first canonical function indicated positive associations between active calcium carbonate, electrical conductivity, total calcium carbonate and sand content, and AMF diversity indices, including Shannon diversity, Pielou's evenness and spore density, whereas species richness showed a weak negative association (Fig. 10A). These results suggest that the physicochemical characteristics of sandy coastal soils play an important role in structuring AMF communities. Coastal dune soils are typically characterised by high sand content, low nutrient availability and high carbonate concentrations, which create selective environmental conditions favouring AMF taxa adapted to these constraints (Maun, 2009; Öpik *et al.*, 2010; Estrada *et al.*, 2013; van der Heijden *et al.*, 2015). High sand content may improve soil aeration and drainage, which can enhance fungal sporulation and the persistence of AMF propagules in soil (Jasper *et al.*, 1989; Smith and Read, 2008). Similarly, electrical conductivity and carbonate-rich substrates may influence fungal diversity by selecting tolerant taxa capable of maintaining symbiotic interactions under alkaline conditions (Öpik *et al.*, 2010; Tabti and Bendimered-Mouri, 2022 b). The positive relationship observed between carbonate content and AMF diversity indices may reflect the ecological specialization of certain AMF taxa capable of colonising calcareous soils.

Relationships between soil properties and AMF root colonisation

CCA also revealed significant relationships between soil physicochemical parameters and AMF root colonisation parameters (Table 6). Three canonical correlations were identified, all showing strong relationships with correlation coefficients ranging from 0.84 to 0.97, and all were highly significant ($P < 0.001$)



Table 6. Canonical Correlation Analysis of relationships between soil physicochemical parameters and AMF root colonisation parameters.

Correlation	Correlation coefficient	Eigen value	P values
1	0.973	17.884	0.000***
2	0.960	11.868	0.000***
3	0.848	2.558	0.000***

***: $P < 0.001$

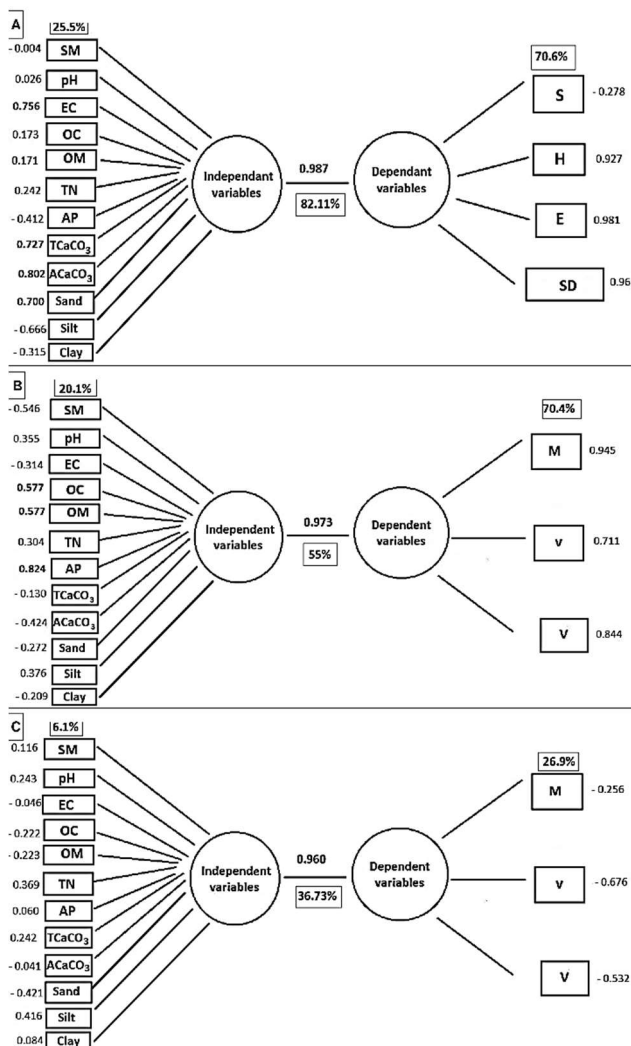


Fig. 10. Canonical functions relating soil physicochemical parameters to AMF community attributes and root colonisation parameters: **A.** first canonical function for AMF community structure, diversity and spore density; **B.** first canonical function for root colonisation parameters; **C.** second canonical function for root colonisation parameters. S: species richness; H: Shannon diversity index; E: Pielou's evenness; SD: spore density.

(Table 6). The first canonical function accounted for the largest proportion of shared variance between soil properties and colonisation parameters. Soil physicochemical variables contributed 20.1% to this canonical relationship, whereas the dependent variables representing mycorrhizal intensity and vesicle abundance contributed 70.4%. The first canonical function revealed

positive relationships between available phosphorus (AP) and soil organic matter (derived from organic carbon) and AMF root colonisation parameters, particularly mycorrhizal intensity (M) and vesicle abundance (V and v) (Fig. 10B).

The positive associations observed between soil organic matter and AMF colonisation intensity suggest that carbon-rich substrates may stimulate intraradical fungal development, a relationship consistent with the role of organic matter in sustaining microbial activity and improving conditions for symbiotic establishment (Vanlalmalsawmi *et al.*, 2025). In addition, phosphorus availability can regulate mycorrhizal symbiosis by influencing plant carbon allocation to fungal partners and controlling the development of intraradical structures such as vesicles and arbuscules (Smith and Read, 2008; Bonfante and Genre, 2010; Kiers *et al.*, 2011; Smith *et al.*, 2011). The second canonical function explained an additional 6.1% of the shared variance between the two sets of variables, while the root colonisation parameters contributed 26.9% to this canonical relationship (Fig. 10C). This means that although soil physicochemical properties are very important in determining how intensely mycorrhizal colonisation occurs, other ecological factors such as plant phenology, climatic variability, and microbial interactions may also affect AMF colonisation dynamics (Kiers *et al.*, 2011; van der Heijden *et al.*, 2015; Rillig *et al.*, 2019).

CONCLUSION

The study highlights spatial and seasonal patterns in AMF spore density, community structure, diversity, and root colonisation associated with *P. maritimum* in the coastal dunes of Oran. The findings demonstrate that AMF function as key biotic drivers of plant persistence under the restrictive edaphic conditions of Mediterranean coastal dunes, characterised by low nutrient availability, high calcium carbonate content, and substrate instability. AMF communities were dominated by Glomeraceae members, underscoring the crucial ecological role that adaptable and stress-resistant taxa play in sustaining symbiotic relationships in heterogeneous environments. Despite marked spatial and temporal variability in spore density, community structure and diversity, and colonisation parameters, species richness remained relatively stable, suggesting the persistence of AMF propagules and the resilience of dune-adapted fungal assemblages. Soil physicochemical properties were identified as key factors shaping AMF spore density, community structure, diversity and root colonisation. AMF spore density and diversity were positively associated with calcium carbonate, electrical conductivity and sand content, whereas root colonisation was more closely related to available phosphorus and soil organic matter. *P. maritimum* exhibited a high degree of mycotrophy, with



consistently elevated colonisation levels across sites and seasons, confirming the important role of AMF in enhancing plant tolerance and ecological resilience in coastal dune ecosystems. These findings support the idea that AMF are key mediators of plant-soil relationships in conditions where nutrients are scarce and physical stability is low. Future research should prioritise long-term monitoring to assess the temporal stability of AMF communities under increasing climatic variability. The integration of molecular approaches, including high-throughput sequencing, will be important to refine diversity assessments and detect cryptic taxa. In addition, investigating the functional traits of dominant AMF taxa will enhance our understanding of their contribution to plant adaptation to various stress factors. From an applied perspective, the use of native AMF consortia represents a promising, ecologically grounded strategy for the restoration and sustainable management of Mediterranean coastal dunes, ecosystems that are increasingly threatened by climate change and anthropogenic pressures.

ACKNOWLEDGMENTS

We would like to express our sincere gratitude to the directors and teams at the Plant Biodiversity: Conservation and Valorisation Laboratory (UDL Sidi Bel Abbès, Algeria) for providing the necessary equipment and products. We would also like to thank the General Directorate of Forests (DGF) in Oran, particularly the teams from the Boutlelis forest districts (Wilaya of Oran), for their valuable assistance and support in the field.

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