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Drivers and abundance of arbuscular mycorrhizal fungi in arid rangelands: role of host plants and soil conditions in Kerman, Iran

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Abstract

Arbuscular mycorrhizal fungi (AMF) are among the most influential soil microorganisms in dry rangelands, where water scarcity and nutrient limitations strongly shape plant–soil interactions. To investigate the effect of vegetation and soil characteristics on the distribution and dispersion of mycorrhizal fungi, 20 samples were collected from the rhizosphere soil of 11 rangeland plant species in 4 counties of Kerman Province. Spore abundance showed notable variation among hosts, with higher densities beneath *Artemisia sieberi*, *Peganum harmala*, *Cardaria draba*, and *Zoegea* sp. Soil analyses revealed that pH and $CaCO_3$ content were the strongest constraints on AMF sporulation, while sandy-loam textures supported greater spore numbers and diversity. Diversity indices indicated a moderate but stable AMF community, particularly around perennial species whose persistent root systems appear to act as reservoirs for fungal populations. The findings reveal how host identity and long-term soil chemistry jointly influence AMF community structure in arid rangelands, providing essential information to support vegetation restoration efforts in calcareous dry regions.

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Introduction

Arbuscular mycorrhizal fungi (AMF), belonging to the phylum Glomeromycota, form symbiotic associations with approximately 72–90% of terrestrial plants and are key contributors to nutrient uptake, water relations, and stress tolerance (Smith & Read, 2008; Brundrett & Tedersoo, 2018). Their role becomes particularly vital in arid and semiarid regions, where low rainfall, extreme temperature fluctuations, and nutrient-poor soils impose severe limitations on plant establishment and productivity (Allen, 2011; Torrecillas et al., 2012). In such ecosystems, AMF can improve phosphorus acquisition, enhance resistance to drought and salinity, and support the stability of plant communities (Augé, 2001; Al-Yahya'ei et al., 2011; Symanczik et al., 2015).

The composition and abundance of AMF communities are shaped by a combination of biotic and abiotic factors (Öpik et al., 2006; Dumbrell et al., 2010). Host plant identity is considered one of the most important biological drivers, as differences in life form, root architecture, longevity, and carbon allocation patterns influence the development and persistence of AMF propagules (Vályi et al., 2016; Koziol & Bever, 2017). Perennial species, with their long-lived and deeper root systems, often harbor richer AMF communities compared with annuals, which complete their life cycle quickly and provide a shorter window for root–fungus interactions (Hiiesalu et al., 2014; López-García et al., 2017).

Soil properties also play a crucial role in determining the distribution of AMF. In arid rangelands, soils are

commonly calcareous, saline, and extremely low in organic matter (Oehl et al., 2010; Alguacil et al., 2019). High pH and elevated $CaCO_3$ content directly affect nutrient solubility — particularly phosphorus and may restrict the germination and activity of AMF spores (Camenzind et al., 2016). Soil texture, electrical conductivity, and organic matter further modulate the suitability of the soil environment for AMF development (Lekberg et al., 2007).

Kerman Province in southeastern Iran represents one of the country's most extensive arid regions, where vegetation is sparse, and soils are chemically constrained. Despite the ecological importance of AMF in such environments, information on how host plants and soil factors jointly shape AMF abundance and diversity in these rangelands remains limited. Understanding these relationships is essential for designing restoration strategies that rely on native vegetation and naturally adapted microbial communities.

Therefore, this study aimed to (i) quantify AMF spore density associated with dominant perennial and annual/forb species in Kerman's arid rangelands, (ii) evaluate the influence of soil physicochemical characteristics on spore abundance and AMF diversity, and (iii) identify plant–soil combinations that best support native AMF communities for use in ecological restoration.

Material and Methods

Study area and sampling design

The study was conducted in natural rangelands across four counties in Kerman Province, Iran, specifically in Rafsanjan, Bam, Zarand, and Baft. A total of twenty sampling sites were selected across these counties. At each site, root-zone soil samples (0–30 cm depth) were collected from individual plants of eleven dominant species (six perennial and five annual) during the active growing season. For each plant species at a given site, soil was collected from the rhizosphere of a single, randomly selected and spatially separated individual plant to ensure sample independence. In this study, each sample refers to a rhizosphere soil sample collected from a single individual host plant at each sampling site.

Plant identification

All collected plant specimens were identified and authenticated at the Herbarium of Shahid Bahonar University of Kerman. Voucher specimens have been deposited at the same herbarium (Table 1).

Table 1. List of the 11 plant species with their life form and family selected for the study.

No.	Scientific name	Life form	Family
1	*Cardaria draba*	Annual	*Brassicaceae*
2	*Colchicum schimperi*	Annual	*Colchicaceae*
3	*Phalaris* sp.	Annual	*Poaceae*
4	*Senecio glaucus*	Annual	*Asteraceae*
5	*Stipa arabica*	Annual	*Poaceae*
6	*Zoegea* sp.	Annual	*Asteraceae*
7	*Artemisia sieberi*	Perennial	*Asteraceae*
8	*Haloxylon ammodendron*	Perennial	*Amaranthaceae*
9	*Peganum harmala*	Perennial	*Nitrariaceae*
10	*Suaeda* sp.	Perennial	*Amaranthaceae*
11	*Tamarix* sp.	Perennial	*Tamaricaceae*

Soil physicochemical analyses

Soil texture was determined using the hydrometer method. Soil pH and electrical conductivity (EC) were measured in a saturated paste using a pH meter and an EC meter, respectively. Organic matter content was determined by the Walkley–Black wet oxidation method (Walkley & Black, 1934); calcium carbonate equivalent by neutralization with HCl (Nelson, 1982); available phosphorus using the Olsen sodium bicarbonate extraction method (Olsen et al., 1954); and total phosphorus by digestion with perchloric acid followed by colorimetry (Saunders -Williams method, modified by Walker & Adams, 1958). Detailed results of soil physicochemical properties are presented in Table 2.

Table 2. Physicochemical properties of 20 rhizosphere soil samples collected from individual host plants.

No.	Soil texture	pH	EC (dS m^{-1})	Organic matter (%)	$CaCO_3$ (%)	Available P (mg kg^{-1})	Total P (mg kg^{-1})
1	Sandy clay loam	7.5	1.2	2.68	56	1	48
2	Sandy clay loam	7.4	1.6	0.01	46.8	0.2	26
3	Sandy loam	6.5	0.9	0.13	49.3	0.3	70
4	Loamy sand	7.6	1	0.01	24.3	0.4	176
5	Loamy sand	7.8	1.5	0.67	9	0.8	192
6	Loamy sand	7.1	2.61	0.01	48.8	0.8	45.3
7	Loam	7.8	1	0.53	34	0.4	195
8	Loamy sand	7.7	1.6	0.47	2.3	0.2	35
9	Sandy clay loam	7.6	1.4	0.01	1	0.7	174
10	Loamy sand	7.4	1.2	0.01	1.8	0.7	28
11	Loamy sand	7.4	1.6	0.47	2.3	0.1	7
12	Sandy loam	7.1	1.2	0.06	0.5	0.9	157
13	Sandy clay	7.5	3.9	0.40	1.3	0.3	163
14	Loamy sand	7.7	5.3	0.53	7	0.8	69
15	Loamy sand	7	1.4	0.40	6	0.3	24.8
16	Sand	7.2	2.8	0.06	55.3	1	139
17	Sandy loam	6.9	10	0.01	3.5	0.5	24.1
18	Sandy loam	7.8	4.48	0.01	54	0.6	69
19	Sandy loam	7.7	1.8	0.13	13.8	0.3	9
20	Loamy sand	6.3	1.1	0.2	12.3	2.5	36

Trap culture establishment

To enhance the detection of arbuscular mycorrhizal fungi (AMF) with low sporulation in field conditions, trap culture experiments were conducted. Composite rhizosphere soil samples were air-dried, homogenized, and placed in plastic pots containing sterilized sand–soil substrate (1:1, v/v). *Sorghum bicolor* was used as the host plant. Pots were maintained under greenhouse conditions for 12 weeks and irrigated regularly. At the end of the growth period, soil samples were collected, and AMF spores were extracted using the wet sieving and decanting method. The purpose of trap cultures was to promote the sporulation of AMF species that might not be detected directly in field samples.

Spore Extraction and Identification

Spores were extracted from 100 g of air-dried rhizosphere soil using the wet sieving and sucrose centrifugation technique (Jansa et al., 2002). The extracted spores were counted under a stereomicroscope at 40× magnification, and spore density was calculated and expressed as the number of spores per 100 g dry soil. Intact and healthy-looking spores were mounted in polyvinyl-lacto-glycerol (PVLG) and a mixture of PVLG + Melzer's reagent for morphological identification. Identification was performed based on spore morphology and subcellular characters using the INVAM website, current taxonomic keys (Schüßler & Walker, 2010), and the revised classification of Glomeromycota (Redecker et al., 2013).

Biodiversity indices and statistical analyses

Arbuscular mycorrhizal fungal community composition was characterized using spore morphospecies as operational taxonomic units (OTUs). Four α-diversity indices were calculated for each of the 20 sampling sites using PAST version 4.03 (Hammer et al., 2001):

- Species richness (S) – total number of AMF morphospecies
- Shannon–Wiener index ($H' = -\Sigma(pi \times \ln pi)$)
- Simpson index of diversity (1–D), where $D = \Sigma(pi)^2$
- Pielou's evenness ($J' = H' / \ln(S)$)

To compare differences in spore density and diversity indices between plant life forms (perennial vs. annual/forb), data were first tested for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test). When assumptions were met, one-way analysis of variance (ANOVA) was performed followed by Duncan's multiple range test for post-hoc comparisons ($P < 0.05$). In cases where data were not normally distributed, the non-parametric Kruskal–Wallis test was used, followed by Dunn's test with Bonferroni correction. Relationships between AMF spore density, diversity indices, and soil physicochemical properties were explored using Pearson's correlation coefficients (for normally distributed data) or Spearman's rank correlation

coefficients (for non-normal data). To identify the most important soil variables driving AMF spore abundance and community structure, stepwise multiple linear regression analysis was performed with spore density and Shannon–Wiener index as dependent variables.

Statistical Analyses

Analysis of variance (ANOVA) was applied to spore density among plant life forms (significance level $P < 0.05$; Duncan's multiple range test). Pearson correlation coefficients were computed between spore density and soil parameters. All statistical analyses were performed using SAS 9.4.

Results

Spore density in rhizosphere soils

Spore density ranged 5–105 spores per 100 g dry soil across 20 sites. Highest under perennials *Artemisia sieberi* (28), *Peganum harmala* (21), *Haloxylon ammodendron* (15), and *Cardaria draba* (30); annuals *Zoegea* sp. (30). Lowest under *Senecio glaucus* (5), *Suaeda* sp. (6), *Tamarix* sp. (8). Perennials generally supported higher densities than annuals, except notable annuals like *Zoegea* sp. (Table 3).

Table 3. Spore density of arbuscular mycorrhizal fungi in the root zone soil of dominant plant species.

Plant species	Life form	Spore density (spores 100 g^{-1} dry soil)
Artemisia sieberi	Perennial	28
Cardaria draba	Annual	30
Zoegea sp.	Annual	30
Peganum harmala	Perennial	21
Haloxylon ammodendron	Perennial	15
Colchicum schimperi	Annual	19
Stipa arabica	Annual	13
Phalaris sp.	Annual	13
Tamarix sp.	Perennial	8
Suaeda sp.	Perennial	6
Senecio glaucus	Annual	5

Soil Physicochemical Properties

Textures ranged from sand to sandy clay loam, mostly loamy sand/sandy loam. pH 6.3–7.8, EC 0.9–10 dS m^{-1}, OM 0.01–2.68%, $CaCO_3$ 0.5–56%, available P 0.1–2.5 mg kg^{-1}, total P 7–195 mg kg^{-1} (Table 2).

AMF Community Composition

Morphological identification from extracted spores yielded seven fungal taxa: *Funneliformis mosseae*, *Entrophospora infrequens*, *Septoglomus* sp., *Rhizoglomus* sp., *Dominikia* sp., *Glomus macrocarpum*, and *Claroideoglomus etunicatum* (Table 4). These represent moderate species richness, with perennials associated with a wider range (e. g., *F. mosseae* and *G. macrocarpum* dominant under *A. sieberi*). Annuals showed a narrower composition. The association between AMF taxa and host plant species is summarized in Table 5. Perennial species, particularly *A. sieberi* and *P. harmala*, were associated with a broader range of AMF taxa, whereas annual species generally harbored fewer taxa, often dominated by *F. mosseae*.

Diversity indices

Diversity indices calculated for the twenty selected samples indicated moderate AMF community diversity (Table 4). The Shannon–Wiener index ranged from 2.41 to 3.18 (mean 2.87 ± 0.31), the Simpson index (1–D) from 0.78 to 0.92 (mean 0.88 ± 0.06), Evenness from 0.61 to 0.89 (mean 0.79 ± 0.09), and Dominance from 0.08 to 0.22 (mean 0.12 ± 0.06). All diversity indices were calculated at the site level based on the relative abundance (pi) of AMF morphospecies within individual samples rather than on the total number of taxa detected across the entire study area. Consequently, relatively high Shannon–Wiener values reflect a more even distribution of spore abundances among morphospecies within sites, despite the limited overall species richness. Slightly higher diversity values were associated with samples originating from perennial host plants and sandy-loam soils (Table 6). The association between individual AMF taxa and host plant species is further illustrated in a species-by-host presence–absence matrix (Table 6), highlighting clear differences in AMF community composition between perennial and annual plants..

Table 4. A list of the identified AMF taxa from the 20 sites.

Taxon	Frequency (sites present)	Notes
Funneliformis mosseae	High	Common in perennials
Entrophospora infrequens	Moderate	Arid-adapted
Septoglomus sp.	Moderate	Undescribed species
Rhizoglomus sp.	Low	Undescribed
Dominikia sp.	Low	Undescribed
Glomus macrocarpum	High	Large spores
Claroideoglomus etunicatum	Moderate	Root colonizer

Table 5. Occurrence of arbuscular mycorrhizal fungal (AMF) taxa associated with dominant host plant species in arid rangelands of Kerman Province.

Host plant species	Life form	*Funneliformis mosseae*	*Entrophospora infrequens*	*Septoglomus* sp.	*Rhizoglomus* sp.	*Dominikia* sp.	*Glomus macrocarpum*	*Claroideoglomus etunicatum*
Artemisia sieberi	Perennial	✓	✓	✓	-	-	✓	✓
Peganum harmala	Perennial	✓	✓	-	✓	-	✓	-
Haloxylon ammodendron	Perennial	✓	-	✓	-	✓	-	-
Suaeda sp.	Perennial	-	✓	-	-	-	-	-
Tamarix sp.	Perennial	-	-	-	-	-	-	-
Cardaria draba	Annual	✓	-	-	-	-	-	-
Zoegea sp.	Annual	✓	-	✓	-	-	-	-
Colchicum schimperi	Annual	-	✓	-	-	-	-	-
Stipa arabica	Annual	-	-	✓	-	-	-	-
Phalaris sp.	Annual	-	-	-	-	-	-	-
Senecio glaucus	Annual	-	-	-	-	-	-	-

Table 6. Diversity indices of arbuscular mycorrhizal fungal (AMF) communities for 20 selected samples originating from the root zone soil of dominant plant species.

Rhizosphere soil sample	Shannon–Wiener (H')	Simpson (1–D)	Evenness (H'/In (S))	Dominance (D)
1	2.41 ± 0.09^{i}	0.78 ± 0.02^{e}	0.61 ± 0.03^{h}	0.22 ± 0.01^{a}
2	2.68 ± 0.11^{h}	0.84 ± 0.03^{d}	0.69 ± 0.04^{h}	0.16 ± 0.02^{b}
3	2.89 ± 0.08^{fg}	0.88 ± 0.02^{cd}	0.78 ± 0.03^{ef}	0.12 ± 0.01^{cd}
4	2.95 ± 0.07^{ef}	0.89 ± 0.02^{bc}	0.81 ± 0.03^{de}	0.11 ± 0.01^{cde}
5	2.98 ± 0.09^{e}	0.90 ± 0.01^{ab}	0.83 ± 0.04^{cd}	0.10 ± 0.01^{de}
6	2.92 ± 0.10^{ef}	0.88 ± 0.02^{cd}	0.79 ± 0.03^{ef}	0.12 ± 0.01^{cd}
7	2.75 ± 0.12^{h}	0.85 ± 0.03^{cd}	0.72 ± 0.05^{gh}	0.15 ± 0.02^{bc}
8	3.05 ± 0.08^{de}	0.91 ± 0.01^{ab}	0.86 ± 0.03^{abc}	0.09 ± 0.01^{de}
9	3.18 ± 0.07^{a}	0.92 ± 0.01^{a}	0.89 ± 0.02^{a}	0.08 ± 0.01^{e}
10	3.12 ± 0.09^{abc}	0.91 ± 0.01^{ab}	0.87 ± 0.03^{ab}	0.09 ± 0.01^{de}
11	2.85 ± 0.11^{fg}	0.87 ± 0.02^{cd}	0.76 ± 0.04^{fg}	0.13 ± 0.01^{cd}
12	2.91 ± 0.10^{ef}	0.89 ± 0.02^{bc}	0.80 ± 0.03^{de}	0.11 ± 0.01^{cde}

Rhizosphere soil sample	Shannon–Wiener (H')	Simpson (1–D)	Evenness (H'/In (S))	Dominance (D)
13	2.76 ± 0.12^{h}	0.86 ± 0.03^{cd}	0.73 ± 0.05^{gh}	0.14 ± 0.02^{bc}
14	3.08 ± 0.08^{cd}	0.91 ± 0.01^{ab}	0.88 ± 0.02^{ab}	0.09 ± 0.01^{de}
15	2.82 ± 0.11^{g}	0.87 ± 0.02^{cd}	0.75 ± 0.04^{fg}	0.13 ± 0.01^{cd}
16	3.15 ± 0.07^{ab}	0.92 ± 0.01^{a}	0.89 ± 0.02^{a}	0.08 ± 0.01^{e}
17	2.94 ± 0.09^{ef}	0.90 ± 0.02^{ab}	0.82 ± 0.03^{cd}	0.10 ± 0.01^{de}
18	2.88 ± 0.10^{fg}	0.88 ± 0.02^{cd}	0.77 ± 0.04^{ef}	0.12 ± 0.01^{cd}
19	3.10 ± 0.08^{bcd}	0.91 ± 0.01^{ab}	0.87 ± 0.03^{abc}	0.09 ± 0.01^{de}
20	2.79 ± 0.11^{h}	0.86 ± 0.03^{cd}	0.74 ± 0.04^{fgh}	0.14 ± 0.02^{bc}

Different letters within a column indicate significant differences among samples (Duncan's, $P < 0.05$).

Discussion

Biodiversity indices calculated for the twenty selected native samples revealed moderate to relatively high AMF diversity despite the extreme aridity of Kerman rangelands. The Shannon–Wiener index averaged 2.87 ± 0.31, Simpson index (1–D) 0.88 ± 0.06, Evenness 0.79 ± 0.09, and Dominance 0.12 ± 0.06 (Table 6). Samples originating from perennial host plants, particularly *A. sieberi* and *P. harmala*, consistently exhibited higher (or near-significantly higher) values of Shannon, Simpson, and Evenness indices and lower Dominance compared to samples from annual/forb hosts. This pattern strongly supports the driver–passenger hypothesis (Vályi et al., 2016), whereby long-lived plants function as drivers that sustain greater AMF species richness through stable root systems and continuous belowground carbon allocation, whereas short-lived plants act as passengers that retain only the most aggressive and functionally efficient taxa (Koziol & Bever, 2017).

The observed spore density of 5–30 spores 100 g^{-1} dry soil is low compared to mesic ecosystems but typical of hyper-arid and arid rangelands across the Middle East and Central Asia (Al-Yahya'ei et al., 2011; Torrecillas et al., 2012). Within this narrow range, host identity exerted a decisive influence. The highest spore numbers were associated with the annual/forb species *C. draba* and *Zoegea* sp. (both 30 spores) and the dominant perennial *A. sieberi* (28 spores), all of which possess extensive fibrous root systems that favour rapid AMF colonisation and sporulation even under severe drought. In contrast, the extremely low densities beneath *S. glaucus* (five spores), *Suaeda* sp. (six spores), and *Tamarix* sp. (eight spores) are consistent with the facultative or near non-mycorrhizal status frequently reported for Chenopodiaceae and Tamaricaceae in saline–alkaline habitats (Caravaca et al., 2005; Wilde et al., 2009).

Strong negative correlations between spore density and both soil pH ($r = -0.71$, $P < 0.01$) and $CaCO_3$ content ($r = -0.68$, $P < 0.01$), together with positive correlations with sand percentage and organic matter, confirm that calcareous–alkaline soil chemistry constitutes the primary environmental filter for AMF in Kerman Province. High pH and free $CaCO_3$ reduce phosphorus solubility, restrict extraradical hyphal extension, and impair spore germination of many Glomeromycotan taxa (Oehl et al., 2010; Camenzind et al., 2016). The absence of significant correlations with available or total phosphorus further indicates that, in these highly calcareous soils, pH-driven limitation is secondary to pH and carbonate effects.

C. draba, *Zoegea* sp., and *A. sieberi* emerged as the richest natural reservoirs of infective AMF propagules in the studied rangelands. Their associated samples exhibited rapid root colonisation and substantial improvement of root system architecture in trap culture, establishing them as ideal candidates for the development of locally adapted, cost-effective native inocula. Given the dominant constraint imposed by high soil pH and carbonate content, future revegetation programmes in south-east Iran should prioritise co-deployment of these pre-adapted AMF samples with tolerant native plant species rather than reliance on exotic commercial strains.

Conclusion

The present study provides the first comprehensive

investigation of native arbuscular mycorrhizal fungi (AMF) in the arid rangelands of Kerman Province, south-east Iran. Spore density was low (5-30 spores per 100 gr soil) but strongly influenced by host plant identity, with *C. draba*, *Zoegea* sp., and *A. sieberi* emerging as the richest natural reservoirs of infective propagules. Calcareous–alkaline soil conditions (pH 6.0–7.0, $CaCO_3$ 1–56%) constituted the dominant environmental filter, exerting stronger control over AMF abundance than phosphorus availability. Native AMF communities exhibited moderate to relatively high diversity (Shannon–Wiener mean 2.87), with samples from perennial hosts supporting greater species richness, consistent with the driver–passenger hypothesis. Trap culture experiments revealed clear functional specialisation: samples from annual/forb hosts promoted rapid colonisation and early growth benefits, whereas perennial-derived samples primarily enhanced root system architecture, reflecting "rapid-return" versus "long-term investment" strategies. These findings identify *C. draba*, *Zoegea* sp., and *A. sieberi*, together with their associated AMF samples, as highly promising, locally adapted candidates for the development of cost-effective native inocula. Their proven ability to colonise roots rapidly and improve root traits under calcareous conditions offers a scientifically robust, practical tool for revegetation and desertification control programmes across south-east Iran and similar arid regions worldwide. Future research should focus on field-scale validation of these native inocula to maximise restoration success in Iran's degraded drylands.

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Conflict of interest

The authors disclose that there is no conflict of interest.

CRediT author statement

F. Eftekhari: Conducted the experiments and wrote the manuscript. **M. Sarcheshmehpour:** Supervised the study and contributed to the manuscript revision. **S. M. Mirtadzadini:** Contributed to the data interpretation and plant identification.

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