Environmental and Experimental Botany 201 (2022) 104982

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Native arbuscular mycorrhizal fungi improve growth, biomass yield, and phosphorus nutrition of sorghum in saline and sodic soils of the semi–arid region

Priyanka Chandra, Awtar Singh [*], Kailash Prajapat, Arvind Kumar Rai [*,1], Rajender Kumar Yadav

ICAR-Central Soil Salinity Research Institute, Karnal 132 001, Haryana, India

A R T I C L E I N F O

Keywords:
AMF
Plant–microbe interaction
Phosphorus nutrition
Glomalin
Funneliformis mosseae
Funneliformis geosporum
Responsiveness

A B S T R A C T

Exploiting symbiotic plant-microbe interactions with arbuscular mycorrhizal fungi (AMF) adapted to hostile soil can be a promising approach for enhancing crop productivity and tolerance to salinity and sodicity-related stresses in salt-affected agroecosystems. This study was conducted to characterize the native mycorrhizal ecotype and its responsiveness to sorghum in saline and sodic soils under controlled conditions. The AMF spore density in sodic soil under the rice-wheat cropping system was greater than in the sorghum-based systems. The spore density was greater under sodic compared to saline soils. The sequence of the amplified fungal ribosomal DNA of the 18 S region of the isolated culture from the rice-wheat system under sodic soil conditions showed the *Funneliformis mosseae* and *Funneliformis geosporum* as the dominant AMF species. The colonization and arbuscular abundance of *Funneliformis sps.* inoculated sorghum was greater for sodic and normal soil, respectively. Plant height and fresh and dry biomass of AMF inoculated plants were greater in normal soil followed by sodic and saline soils. Sodic soil showed a greater increase in root-to-shoot ratio compared to saline soils. The P content, P uptake, and K^+/Na^+ were greater in AMF inoculated soils. The increase in Olsen's-P in AMF inoculated soils was in the order of normal > sodic > saline soils. Sodic soils showed a maximum 15–35 fold increase in the EE-GRSP and DE GRSP because of AMF inoculation ($P \leq 0.05$). Dehydrogenase and alkaline phosphatase enzymes were greater in AMF inoculated ($P < 0.05$). The soil electrical conductivity, glomalin, and arbuscular abundance alone explained about 76 % variability in the plant response to AMF inoculation in these soils. This study concludes that the use of native AMF with the important cropping system can be an agronomically sound option to cope with abiotic stress in salt-affected soils.

1. Introduction

Salt-affected soils (SAS) are the chemically degraded soils constrained by high osmotic and matric stress for crop plants because of excessive soluble salts and exchangeable sodium (Basak et al., 2020). About 20 % of global croplands have become less productive or, in extreme cases, uncultivable wastelands because of land degradation associated with soil salinization (Anon, 2020). High osmotic and matric stress in these soils narrow down the range of plant utilizable water (Akhter et al., 2004; Sheldon et al., 2017). Besides, low water availability, the cationic and anionic composition of the soil solution of salt-affected soils also interferes with the availability and uptake of nutrients even at relatively higher soil fertility status (Singh and Abrol, 1985; Sundha et al., 2017). The excess accumulation of salts in the rhizosphere adversely affects crop growth. An abundance of electrolytes in the solution of saline soils also reduces the activity of microorganisms with slows down the utilization of substrate because of imbalance and/or deficiency/ toxicity of essential nutrients (Rai et al., 2021a; Soni et al., 2021). On the other hand, higher soil pH and the presence of carbonates and bicarbonate eventually affect root development and nutrient uptake (Ghollarata and Raiesi, 2007; Rengasamy, 2016). Specifically, changes in P solubility, complexation, precipitation–

* Corresponding authors.
E-mail addresses: priyanka.chandra@icar.gov.in (P. Chandra), awtar.singh1@icar.gov.in (A. Singh), kailash.prajapat@icar.gov.in (K. Prajapat), ak.rai@icar.gov.in (A.K. Rai), rk.yadav@icar.gov.in (R.K. Yadav).
[1] orcid.org/0000-0002-8045-9828

https://doi.org/10.1016/j.envexpbot.2022.104982
Received 12 April 2022; Received in revised form 30 June 2022; Accepted 1 July 2022
Available online 6 July 2022

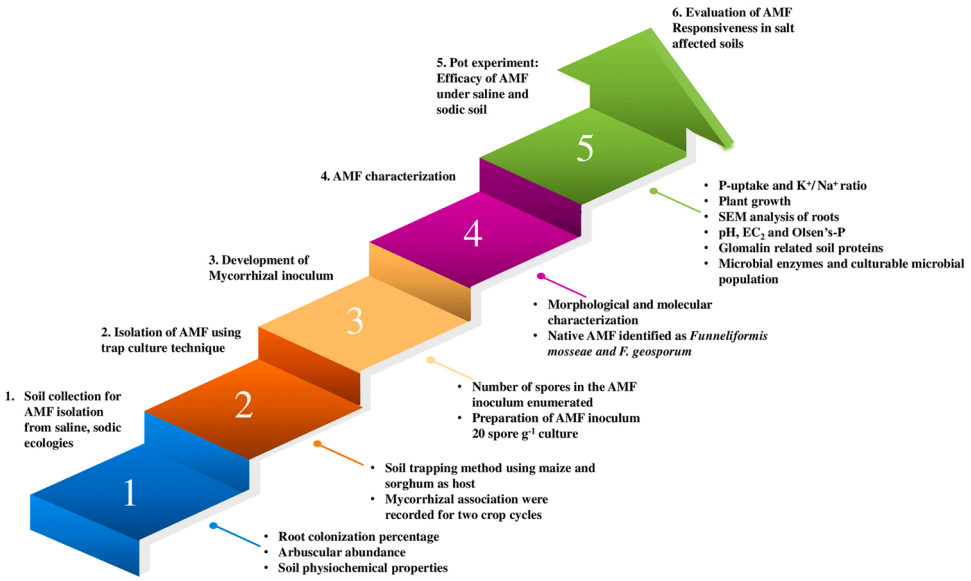


Fig. 1. Technical roadmap of the steps involved in the study of native AMF in salt–affected soils.

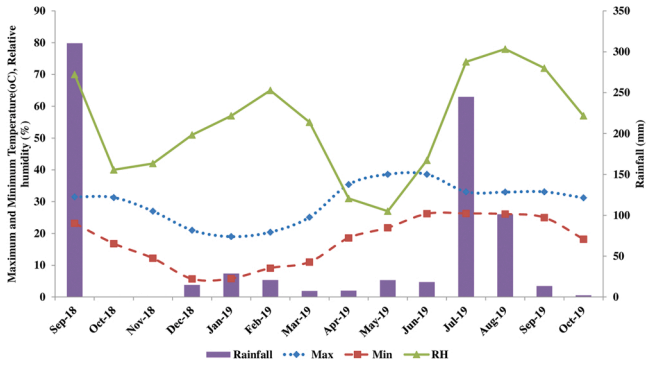


Fig. 2. Monthly Meteorological data of experimental site during the cropping season.

dissolution, and speciation affect the soil P dynamics because of changes in soil solution activity of Na^+, Ca^{2+}, Mg^{2+}, and SO_4^{2-}(Shariatmadari et al., 2006; Sharpley, 1983). The replenishment of P to the depletion zone around the roots is restricted because of the slow desorption-diffusion in highly tortuous sodic (Jalali and Kolahchi, 2009; Sundha et al., 2022) and saline soils of poor soil–plant water relation (Sheldon et al., 2017).

One key to successful cropping in these soils may be enhancing the mutualistic association of crops with beneficial arbuscular mycorrhizal fungi (AMF). The AMF is the obligate biotrophs deriving mutual benefits of the partnership by the improved acquisition of water and mineral nutrients, in exchange for photosynthetically fixed carbon, ultimately helping in plant growth and development and mediating the terrestrial nutrient cycling (Giovannini et al., 2020; Teste et al., 2020; Wu et al., 2022). This association had special significance in water and nutrient uptake, especially phosphorous (P) and micronutrients of poor dissolution and transport in these soils (Bindraban et al., 2020). Mycorrhizal fungal hypha associated with plant roots forms a structural relationship to extend the plant root absorptive surface area to increase the reach of the root system and improve the translocation of growth–limiting resources (Bindraban et al., 2020; Ruiz-Lozano et al., 2012; Smith et al., 2011). The symbiosis with AM fungi can also ameliorate abiotic stresses including salt stress in plants. AM symbiosis also confers the tolerance against abiotic stress by reducing Na^+ uptake and translocation (Selvakumar et al., 2018). Besides improving plant nutrition the substantial hyphal biomass produced by AMF also plays critical roles in improving soil structure, porosity, pore size distribution, water use efficiency, and activity of the beneficial microorganisms (Ellouze et al., 2014; Gosling et al., 2006; Wilson et al., 2009). However, the effectiveness of the symbiosis depends upon soil types, plant genotypes, and environmental stresses in many agroecosystems (Cobb et al., 2016; Rai et al., 2021b).

Exploiting symbiotic plant-microbe interactions tailored for specific soil environments is now gaining increased attention as an alternative to intensive farming (Briat et al., 2020; Cobb et al., 2016; Rai et al., 2021b). It is necessary to understand the potential benefit of a mutualistic partnership with AMF for enhancing crop productivity and tolerance to salinity and sodicity-related stresses in these agroecosystems. Previous studies had established the advantage of indigenous AMF communities adapted to stressed soil environment in strengthening the mutualistic association in cultivated crop plants (Lambert et al., 1980; Querejeta et al., 2006). Therefore, it seems reasonable to take advantage of the indigenous AMF community for higher mycorrhizal responsiveness in crops under saline and sodic soil. These AMF ecotypes adapted to extreme soil conditions (Sylvia and Williams, 1992) can beneficially develop partnerships with crop plants in stressed ecosystems (Dodd and Thomson, 1994). Therefore, this study examined the mycorrhizal responsiveness of sorghum in a mutualistic association with a native mycorrhizal isolate from degraded soil with low P fertility and higher pH and electrical conductivity.

Sorghum [*Sorghum bicolor* (L.) Moench] is cultivated for grain, and biomass under rainfed semi-arid and arid regions worldwide (Kumar et al., 2012; Rai et al., 2022). It is a tolerant crop plant for salt-affected soils and rainfed/drought conditions. Sorghum is also regarded as an ideal crop for diversification as sorghum production uses minimal agricultural inputs and responds well to AMF inoculation (Abdelhalim et al., 2020). We hypothesized that in saline and sodic soil conditions establishing the partnership between adapted native AMF with sorghum will result in increased productivity and stress tolerance. Keeping these points in view, the primary objectives of our study were to (i) characterize the native mycorrhizal spores from degraded lands trapped using different hosts; (ii) assess their responsiveness to sorghum in saline and sodic soils; and (iii) characterize the host-AMF interactions in contrasting soils.

2. Material and methods

Herein, the abundance of the native AMF was studied in salt–affected

Table 1
The initial physiochemical properties of three soil types used in the study.

	Unit	I	II	III
Sand	%	62.6	56.4	31
Silt		15.2	25	46
Clay		22.2	18.6	23
Soil texture		Sandy clay loam	Sandy loam	Loam
Soil pH_2 (1:2 soil: water)		8.30	8.28	9.0
Electrical conductivity (EC_2; 1:2 soil: water)	dS m^{-1}	0.27	2.3	1.2
EC_e	dS m^{-1}	0.94	8.05	4.2
Organic carbon	g kg^{-1}	5.80	3.20	3.40
$KMnO_4$-N	kg	127.64	128.64	132.4
Olsens-P	ha^{-1}	13.33	14.6	15.2
NH_4OAc-K		246.0	230.67	264.0
Soil Saturation extract parameters				
Na^+	me	2.08	78.09	35.34
K^+	L^{-1}	0.26	0.24	0.14
Ca^{2+}		8.1	16	2
Mg^{2+}		2.7	2.5	2.4
CO_3^{2-}		Nil	Nil	Nil
HCO_3^-		1.8	3.5	2.5
Cl^-		1	15.75	11.25
USDA classification		*Typic Natrustalf*	*Hasplustepts*	*Typic Ustochrepts*
Collection site		ICAR–Central Soil Salinity Research Institute (CSSRI)	Nain experimental farm, ICAR-CSSRI, Panipat	Farmer's field at Jodhpur village Patiala district, Punjab.
Longitudes (∘)		28.717° N,	29°19′7.09″ N,	30°05'20.6"N,
Latitude (∘)		73.967° E	76°47′30.0″ E	76°33'03.4"E
Elevation (m. a.s.l)		244	231	256
Soil type		Normal soil	Saline soil	Sodic soil

soils under different cropping systems. The isolated spores were characterized using morphological and molecular techniques and the responsiveness of the native inoculation in comparison to uninoculated control soils was studied under saline and sodic soil using the standard methodology (Sections 2.1–2.6). Different steps involved in the study are depicted in the technical road map (Fig. 1).

2.1. Soil sample collection for AMF isolation

The native mycorrhizal fungi were isolated from the rhizospheres of the rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* (L.) Moench), pearl millet [*P. glaucum* (L.) R. Br.], mustard (*Brassica juncea* L.) and wheat (*Triticum aestivum* L) plants growing in highly saline and sodic soil from different locations (Supplementary Table 1). Rice, sorghum, and pearl millet are raised in the rainy season, while, mustard and wheat are raised in the winter season. Rice is a tolerant crop that can grow in saline as well as sodic soils with sufficient water availability. While, sorghum, pearl millet, mustard, and wheat are the semi-tolerant crops adapted well to salinity, sodicity, as well as rainfed/drought conditions (Abrol et al., 1988; Rai et al., 2022; Singh et al., 2022). Soil samples, were collected aseptically in the autumn season (March 2018) from the sites under these crops with varying salinity and sodicity. The abundance of the AMF spores was studied by wet sieving (Gerdemann and Nicolson, 1963). Briefly, ten-gram soil was agitated vigorously with 100 mL of water, and the supernatant was decanted and centrifuged for ten min. The centrifuged samples were observed under a stereomicroscope at 40 × magnifications for quantification. The efficiency of the native AMF in developing a partnership with maize plants was evaluated by sowing the surfaces sterilized seeds in soil: sand mixture (3:1 v/v). Seeds of both the crops were surface sterilized by dipping for five min in 1 % NaOCl solution followed by five times washings with sterilized distilled water. The mycorrhizal colonization and arbuscular abundance were studied in roots 30 days after sowing following the method described in Section 2.1.1. The sodic soil under long-term rice-wheat crop rotation was collected from the Patiala (30°05'20.6"N; 76°33'03.4"E; Altitude: 256 m above Sea level), Punjab, India showing greater spore density, and mycorrhizal colonization was identified for isolation of AMF using trap culture technique.

2.1.1. Root colonization and arbuscular abundance

The roots fragments (≈2.0 cm) were boiled in 10 % (w/v) KOH solution till they turned transparent and further stained using trypan blue in lacto-glycerol (0.05 % v/v) (Phillips and Hayman, 1970). The one cm fragments of stained roots were mounted onto microscope slides and observed at 100–400x magnification under an optical microscope. The root colonization percentage was calculated using the Eq. (1):

$$\text{Root } colonization\ (\%) = \frac{\text{RN} \times 100}{\text{TN}} \quad (1)$$

where, RN and TN are the number of root fragments colonized and total root fragments examined, respectively.

The arbuscular abundance was also observed by counting the number of arbuscules present in the root segment. The arbuscular abundance (%) was calculated using the Eq. (2):

$$\text{Arbuscular } abundance(\%) = \frac{\text{No. of arbuscules in the root segments} \times 100}{\text{Total no. of root segments } examined} \quad (2)$$

2.2. Isolation of native mycorrhizal culture

The soil trapping method was used to isolate native AMF species using maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) (Yao et al., 2010). The soils were mixed with sand (3:1, v/v) and then transferred into fifty pots of 24 cms diameter having a capacity of carrying 12 kg soil. Rooting behaviour of maize and sorghum differ significantly, even in the early growth period at 6 leaf stage (25–30 days after sowing) maize produces three times greater root biomass compared to sorghum (Singh et al., 2010). Therefore, the experiment was conducted in pots carrying 10 kg of soil to avoid the limitation of soil volume on root proliferation of both crops. The surface–sterilized seeds of both sorghum and maize were sown in 25 (5 sets × 5 replications) pots each under natural conditions. After 7 days of sowing, plants were thinned and five plants were maintained in each pot. Plants were irrigated on alternate days to maintain the moisture content at 60 % of field capacity. The

Table 2
Physiochemical properties and AMF spore densities of rhizospheric soils along with their AMF association status in different cropping systems; numbers followed by different letters (A–B) are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; SEm± : standard deviation; n = 3.

Factors	Soil properties						AMF abundance		
	pH_2	EC_2 (dS m^{-1})	Organic Carbon (g kg^{-1})	$KMnO_4$–N (kg ha^{-1})	Olsens–P (kg ha^{-1})	NH_4OAc–K (kg ha^{-1})	Spore density (no. of spores/100 g soil	Mycorrhizal colonization (%)	Arbuscular abundance (%)
Cropping system									
Pearl millet–mustard	$8.3±0.3^{AB}$	$4.9±3.0^{A}$	$4.3±0.5^{A}$	$129.4±16.6^{AB}$	$15.8±3.7^{AB}$	$250.9±37.4^{AB}$	$70.2±23.3^{AB}$	$27.8±2.1^{A}$	$7.7±2.5^{AB}$
Rice–wheat	$8.6±0.4^{A}$	$2.6±2.3^{A}$	$3.9±0.5^{A}$	$134.7±33.3^{A}$	$17.6±3.8^{A}$	$269.1±35.1^{A}$	$78.7±25.3^{A}$	$27.3±5.5^{A}$	$11.6±5.4^{A}$
Sorghum–mustard	$8.1±0.1^{AB}$	$3.9±1.9^{A}$	$3.7±0.6^{A}$	$122.0±2.9^{B}$	$12.7±0.1^{B}$	$225.0±3.8^{B}$	$56.3±3.4^{B}$	$25.8±0.3^{A}$	$5.8±0.7^{B}$
Sorghum–wheat	$8.0±0.1^{B}$	$6.0±0.9^{A}$	$4.4±0.1^{A}$	$128.0±2.5^{AB}$	$12.7±0.6^{B}$	$225.8±5.2^{B}$	$52.8±2.1^{B}$	$26.2±0.7^{A}$	$8.3±2.5^{AB}$
Soil salinity status									
Sodic soil	$8.8±0.2^{A}$	$1.0±0.3^{B}$	$4.2±0.3^{A}$	$141.8±35.8^{A}$	$19.9±2.5^{A}$	$292.6±17.7^{A}$	$90.3±22.3^{A}$	$28.1±6.1^{A}$	$11.6±5.9^{A}$
Saline soils	$8.0±0.1^{B}$	$5.6±1.5^{A}$	$3.9±0.6^{A}$	$123.4±6.1^{B}$	$13.0±0.6^{B}$	$225.8±4.6^{B}$	$56.2±9.2^{B}$	$26.3±0.8^{A}$	$7.8±2.6^{A}$

meteorological data of the experimental site during the experimental period is presented in Fig. 2. Pots were fertilized with the recommended doses of fertilizers (17.9 mg P kg^{-1} and 44.6 mg N kg^{-1} soil). Each set of 5 pots for sorghum and maize was harvested at 15, 30, 45, and 60 days after sowing. At each harvesting, the aboveground part was cut from the crown and their fresh weight was measured. The dry matter was determined after drying the plant samples at 60 °C in a hot air oven. The roots were carefully removed from the pots and washed on a sieve with a water jet followed by rinsing with distilled water. At each harvesting, the fresh weight was measured and roots were cut into two cm fragments and mixed evenly. The chopped root mass was stored at 4 °C for the analysis of mycorrhizal association and colonization. A portion of the root mass was oven–dried (60 °C) for recording dry matter content and further chemical analysis. Approximately 50 g fresh roots from the 60 days of harvesting was mixed in the same pots and surface-sterilized seeds of sorghum and maize were resown and the second cycle of the crop was raised following the condition as described for the first crop cycle. The mycorrhizal association and other parameters were recorded for both crop cycles.

2.3. Preparation of mycorrhizal inoculum

The mycorrhizal inoculum was developed using the method described by Gopal et al. (2018). Briefly, maize roots harvested at 60 days after sowing were recovered separately from each pot of the second crop cycle and washed on a sieve with a water jet followed by five times washing with sterilized distilled water and examined for the AMF colonization. About 5.0 g of roots showing higher AMF association were chopped into 2 cm pieces and mixed in 1.0 kg sterilized soil: sand mixture (3:1 v/v). The soil and sand mixture was sterilized for three days consecutively at 121 °C for one hour. After mixing the root bits in soil and sand mixture refilled in plastic pots of 1.0 kg capacity, 5–6 surface-sterilized maize seeds were sown in each pot. Pots were watered with sterilized distilled water following the cultural practices described earlier. Pots were weekly supplied with 0.5 × Hoagland solution used for AMF mass production (Gopal et al., 2016). After 50 days of growth, watering was stopped to impose drought stress and promote sporulation. After 60 days of growth mixture of root bits and soils containing spores and other AMF propagules were examined for final spore counts and used as inoculum for further evaluation of AMF partnership under saline and sodic soil. The number of spores in the AMF inoculum was enumerated using the wet sieving method (Gerdemann and Nicolson, 1963). The spore population was approximately 20 g^{-1} in AMF inoculum.

2.4. Characterization of AMF

2.4.1. AMF spore isolation and morphological characterization

After the establishment of the trap cultures, AMF spores were extracted from the trap culture by the wet sieving (Gerdemann and Nicolson, 1963). The spores and their subcellular structures were examined using an optical microscope (1000 ×) (Omar et al., 1978). Slides for microscopic examination were prepared by mounting the material on a slide containing a drop of polyvinyl–lacto–glycerol and Melzer's reagent mixture (4: 1, v/v). The AMF was classified based on the data provided by the International Culture Collection of Arbuscular and Vesicular Mycorrhizal Fungi (INVAM) (http://invam.wvu.edu/-the-fungi/species-descriptions) and other available reports (Błaszkowski and Czerniawska, 2006; Rajeshkumar et al., 2015; Redecker et al., 2013).

2.4.2. Molecular identification

Molecular characterization for identification of AMF was outsourced from The Energy and Resources Institute (TERI), New Delhi, India. The standard protocol of TERI for spore DNA extraction was followed and further amplification was carried out as described by Lee et al. (2008).

Table 3
Correlation matrix for soil properties and AMF parameters; ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	pH_2	EC_2 (dS m^{-1})	Organic carbon (g kg^{-1})	$KMnO_4$–N (kg ha^{-1})	Olsen's–P (kg ha^{-1})	NH_4OAc–K (kg ha^{-1})
Spore density (no. of spores/100 g soil	0.83***	–0.61*	0.12^{ns}	0.72**	0.59*	0.60*
Mycorrhizal colonization (%)	0.31^{ns}	–0.21^{ns}	0.020^{ns}	0.64*	0.19^{ns}	0.19^{ns}
Arbuscular abundance (%)	0.14^{ns}	–0.11^{ns}	–0.16^{ns}	0.0^{ns}	–0.03^{ns}	–0.09^{ns}

Briefly, The healthy spores obtained were immersed for 30 min in a solution of sodium chloro (4–methylbenzene–1–sulfonyl) azanide (2 %), and streptomycin (100 μg mL^{-1}) (Gopal et al., 2018). After washing with sterilized deionized water spores were aseptically crushed in PCR tube containing 10 μl of 1: 1 ratio of 10 × PCR buffer and sterilized deionized water. Then, the extracted DNA was amplified with universal primer and LSU–SSU based primers. Gel electrophoresis of the PCR product was carried out on 1 % agarose gel in TAE buffer. The amplified sequence was deduced by BLAST against the NCBI database to find the closest relative. The identified nucleotide sequences of 18 S rDNA were deposited in NCBI.

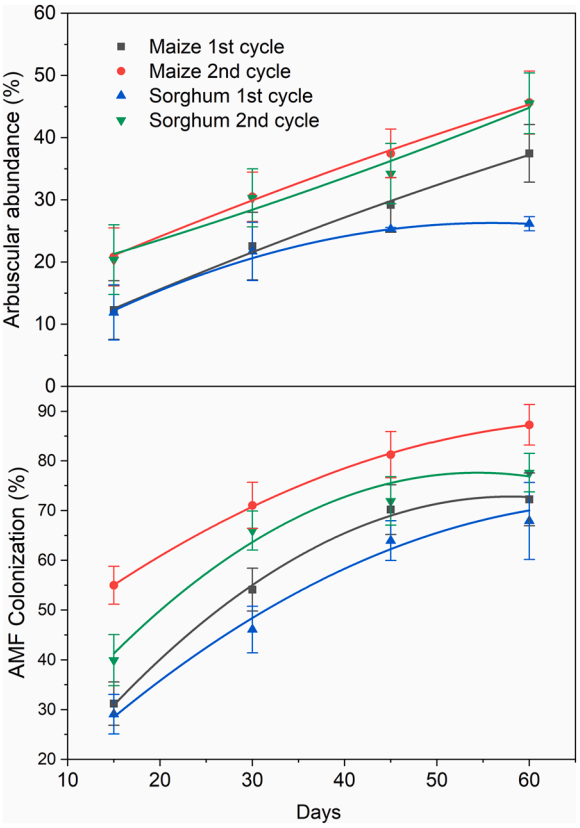


Fig. 3. Temporal change in (a) Mycorrhizal colonization and (b) arbuscular abundance in roots of maize and sorghum in the first and second cycle of trap culture in sodic soils under rice–wheat cropping system with higher spore density from Patiala district, Punjab, India; capped lines on data points are standard deviations; $n = 5$.

2.5. Pot experiment

A pot experiment was carried out at ICAR-Central Soil Salinity Research Institute (CSSRI), Karnal, India, located in a semi-arid, warm, and temperate climate (28.717° N, 73.967° E, 244 m above mean sea level). The physicochemical properties of the soils used for the pot

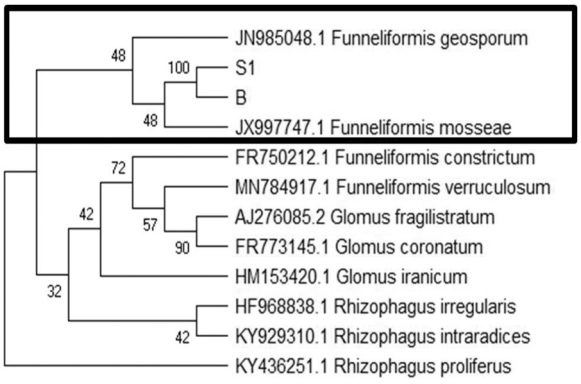


Fig. 4. Phylogenetic relationships based on 18 S rDNA sequencing and related nearest neighbour sequences of two groups of AMF spores isolated after the second cycle of trap culture from sodic soils under rice-wheat cropping system with higher spore density from Patiala district, Punjab, India; the tree was constructed using closely related sequences based on Euclidean distance and Bootstrap values higher than 50 % are shown; number in parenthesis is the nucleotide accession number in Genbank; the constructed phylogenetic tree confirmed that the two investigated species are in the same branch with *F. mosseae* (B) and *F. geosporum* (S1).

Table 4
Variation in the shoot-root system traits of sorghum and maize as influenced by AMF colonization; numbers followed by different letters in the column are significantly different at $P \leq 0.05$ using Duncan's Multiple Range Test; ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Crop	Time (days)	First cycle							Second cycle						
		Fresh biomass (g)		Dry biomass (g)		Dry matter (%)		Shoot root ratio	Fresh biomass (g)		Dry biomass (g)		Dry matter (%)		Root shoot ratio
		Root	Shoot	Root	Shoot	Root	Shoot		Root	Shoot	Root	Shoot	Root	Shoot	
Maize	15	1.3 ^{D}	32.6 ^{D}	0.89^{D}	6.91 ^{D}	37.1	21.23 ^{A}	0.08 ^{C}	1.77 ^{D}	41.6 ^{D}	0.68^{D}	6.64 ^{D}	38.6 ^{AB}	16.1 ^{B}	0.10
	30	3.0 ^{C}	57.2 ^{C}	1.17 ^{C}	11.39 ^{C}	38.2	19.92 ^{A}	0.10 ^{B}	3.24 ^{C}	65.0 ^{C}	1.36 ^{C}	13.2 ^{C}	42.1 ^{A}	20.3 ^{A}	0.10
	45	5.4 ^{B}	76.2 ^{B}	2.23^{B}	15.67 ^{B}	40.7	20.56 ^{A}	0.14 ^{A}	5.54 ^{B}	83.2 ^{B}	1.92^{B}	16.1 ^{B}	34.8 ^{B}	19.3 ^{A}	0.12
	60	6.8 ^{A}	111.6 ^{A}	2.75 ^{A}	19.84 ^{A}	40.2	17.79 ^{B}	0.14 ^{A}	7.38 ^{A}	115.6 ^{A}	2.82 ^{A}	22.7 ^{A}	38.2 ^{AB}	19.6 ^{A}	0.12
Sorghum	15	1.8 ^{D}	40.0 ^{D}	0.60 ^{D}	7.98 ^{D}	31.3 ^{B}	20.0	0.07 ^{C}	1.33 ^{D}	40.6 ^{D}	0.58 ^{D}	8.1 ^{D}	44.0	20.0	0.07 ^{C}
	30	3.2 ^{C}	55.0 ^{C}	1.28 ^{C}	10.33 ^{C}	39.8 ^{A}	18.9	0.12 ^{B}	3.86 ^{C}	60.4 ^{C}	1.69 ^{C}	12.4 ^{C}	43.7	20.6	0.13 ^{B}
	45	5.6 ^{B}	81.2 ^{B}	2.33 ^{B}	15.37 ^{B}	40.9 ^{A}	18.9	0.15 ^{A}	6.22 ^{B}	88.0 ^{B}	2.60^{B}	18.0 ^{B}	41.7	20.4	0.14 ^{AB}
	60	7.6 ^{A}	124.0 ^{A}	2.94 ^{A}	24.30 ^{A}	38.63 ^{A}	19.5	0.12 ^{B}	7.89 ^{A}	120.4 ^{A}	3.76 ^{A}	24.6 ^{A}	47.8	20.5	0.15 ^{A}
Crop		***	**	ns	*	ns	ns	ns	ns	ns	**	*	*	*	*
Time		***	***	***	***	*	ns	***	***	***	***	***	ns	ns	**
Crop * Time		ns	*	ns	***	ns	ns	ns	ns	*	*	ns	ns	ns	**

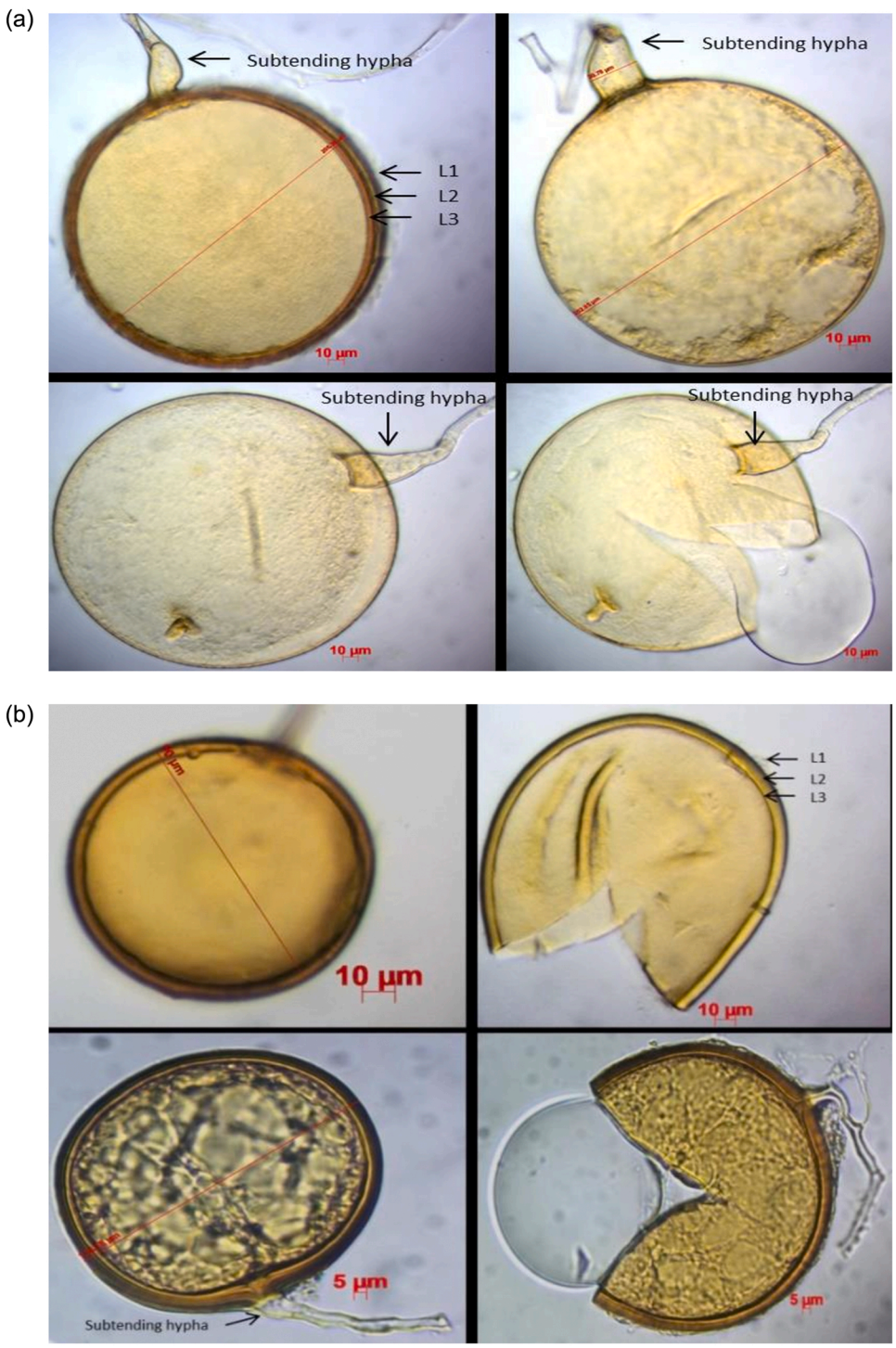


Fig. 5. Morphology of two groups of AMF spores isolated after the second cycle of trap culture from sodic soils under rice–wheat cropping system with higher spore density from Patiala district, Punjab, India: (a) yellowish-brown colored spores of *Funneliformis mosseae*; spore size: 150–210 µm; intact spores are having subtending hyphae attached, spore wall structure has three layers, Layer 1 (L1), Layer 2 (L2), and Layer 3 (L3); (b) yellowish–brown colored spores of *Funneliformis geosporum*: spore size: 80–170 µm; spore wall has three layers, Layer 1 (L1), Layer 2 (L2), and Layer 3 (L3), spores are attached with subtending hyphae.

experiment collected from three sites are presented in Table 1. The 10.0 kg air-dried and sieved soil was filled in pots. The details of the treatments imposed include NSI0: normal soil (EC_e 0.9 dS m^{-1}; pH_2 8.30) without AMF inoculation; NSIM: normal soil (EC_e 0.9 dS m^{-1}; pH_2 8.30) with AMF inoculation; SSI0: saline soil (EC_e 8.05 dS m^{-1}; pH_2 8.28) without AMF inoculation; SSIM: saline soil (EC_e 8.05 dS m^{-1}; pH_2 8.28) with AMF inoculation; SOI0: sodic soil (EC_e 4.2 dS m^{-1}; pH_2 9.00) without AMF inoculation; SOIM: sodic soil (EC_e 4.2 dS m^{-1}; pH_2 9.00) with AMF inoculation. Treatments were arranged in a randomized block design with five replications. The performance of native AMF was evaluated using sorghum (*cv.* Hybrid *Mayur*) grown in the rainy season (June-July) for fodder purposes. In each pot, 5–6 surface-sterilized sorghum seeds inoculated with AMF inoculum were sown. For inoculation, 250 g of seeds were mixed with 50 g AMF inoculum and 80 mL of carboxymethyl cellulose (1 % w/v) solution (Rai et al., 2021b). Untreated seeds were sown in uninoculated pots. After germination excess plants were thinned to maintain three plants in each pot. The crop was fertilized with urea and DAP used as the sources of N and P. The uniform dose of P (17.9 mg kg^{-1}) and N (44.6 mg kg^{-1}) were applied in each pot. Half of N and the full amount of P were mixed soil before sowing the seed. Remaining N was applied equally in two splits at 30 DAS and 45 DAS. Pots were watered at regular intervals using deionized water to

Table 5
Effect of AMF inoculation on sorghum growth and biomass production under different soil types; NSI0: normal soil uninoculated; NSIM: normal soil inoculated with AMF; SAI0: saline soil uninoculated; SAIM: saline soil inoculated with AMF; SOI0: sodic soil uninoculated; SOIM: sodic soil inoculated with AMF; I0: uninoculated; IM: inoculated with AMF; means with different capital letters within column are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; ns $P > 0.05$; *** $P < 0.001$.

Treatment	Plant height (cm)	Fresh biomass (g pot^{-1})		Dry biomass (g pot^{-1})		Dry matter (%)		Root: shoot ratio
		Shoot	Root	Shoot	Root	Shoot	Root	
NSI0	112.6^{A}	139.4^{BC}	11.4^{BC}	28.1^{BC}	2.06^{CD}	20.2^{A}	18.1^{CD}	7.5^{CD}
NSIM	117.4^{A}	196.6^{A}	23.0^{A}	34.4^{A}	5.90^{A}	17.5^{A}	26.2^{A}	17.1^{A}
SAI0	80.0^{D}	119.8^{C}	9.9^{BC}	20.9^{D}	1.51^{DE}	17.4^{A}	15.3^{D}	7.3^{CD}
SAIM	105.4^{B}	167.6^{AB}	13.4^{B}	31.1^{AB}	3.10^{B}	19.2^{A}	23.1^{B}	10.3^{B}
SOI0	92.0^{C}	125.8^{C}	8.02^{C}	24.2^{CD}	1.25^{E}	19.3^{A}	15.9^{D}	5.2^{D}
SOIM	113.0^{A}	178.4^{A}	13.3^{B}	31.5^{AB}	2.70^{BC}	17.7^{A}	20.4^{BC}	8.8^{BC}
I0 *vs* IM	***	***	***	***	***	ns	***	***

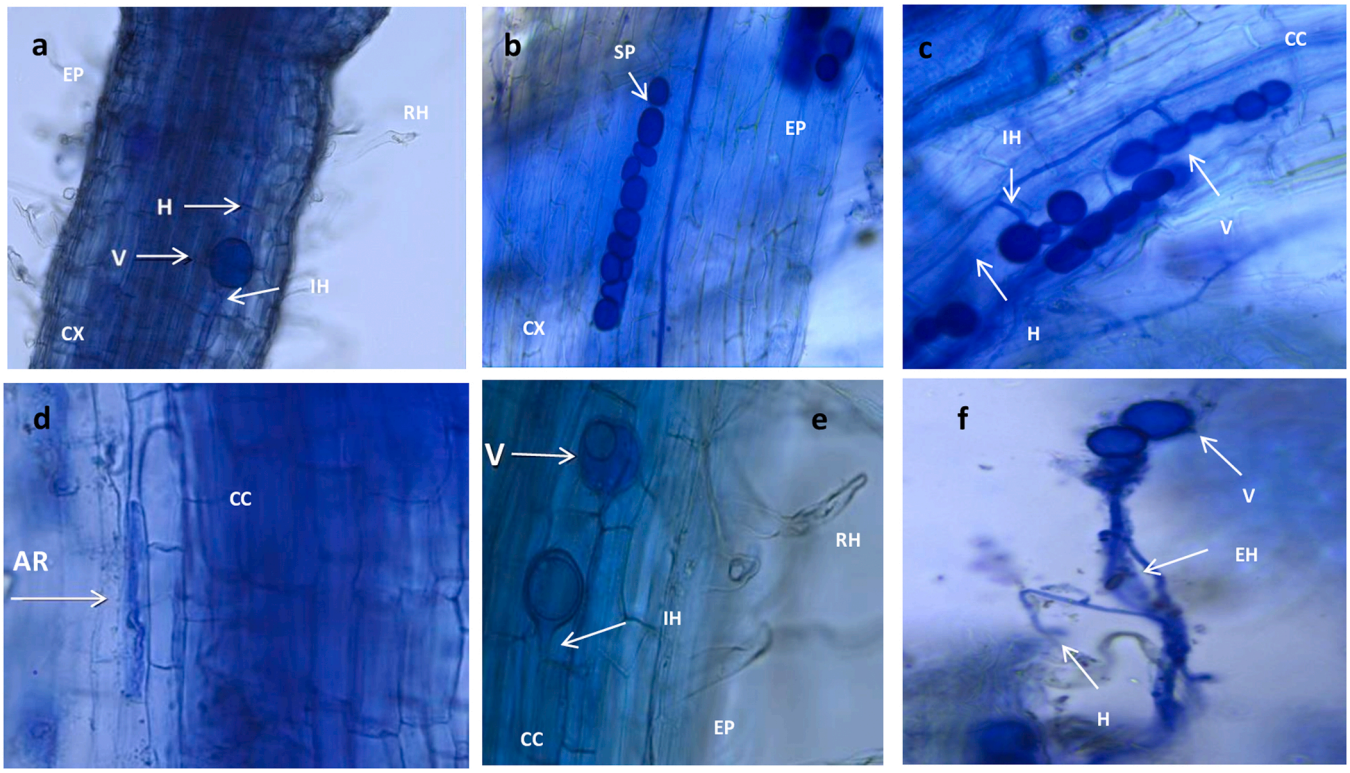


Fig. 6. The photomicrographs of AMF-inoculated sorghum roots demonstrating AMF colonization, abundance, and their typical fungal structures found under microscope: (a) AMF vesicles (V) attached with interadical hyphae (IH), fungal hyphae (H) on the cortex (CX) of roots, root hairs (RH) and epidermis (EP) of sorghum roots were also been observed; (b) AMF spores on the cortex (CX) of sorghum roots were observed; (c) Fungal hyphae (H) developing into interadical hyphae (IH) with vesicles (V) attached on the cortical cells (CC) of sorghum roots; (d) Arbuscules inside the cortical cell (CC) of sorghum roots; (e) vesicles (V) of AMF protruding from interadical hyphae (IH) inside the cortical cell (CC) of sorghum roots, root hairs (RH) and epidermis of sorghum roots (EP) were also been observed; (f) Fungal hyphae (H) and extraradical hyphae (EH) with vesicles (V) attached.

maintain 60% of the water holding capacity. Any phyto–sanitary measure was not required during crop growth. The crop was sown on 25th June 2019 and harvested at 50 % flowering stage after 70 days of sowing for biomass production.

2.5.1. Plant analysis

After harvesting the above-ground biomass was washed with deionized water and their height and fresh weight were measured. The roots were removed carefully and washed with a waterjet on a sieve to remove adhered soil particles followed by 4–5 rinsing with deionized water. The belowground and aboveground plant parts were oven-dried to record their dry matter and kept for further analysis. The oven–-dried shoot samples were digested using di–acid (Jackson, 1967) and phosphorus was estimated spectrophotometrically using the ascorbic acid method (Murphy and Riley, 1962). Sodium and potassium content in digest was determined with a flame photometer (Jackson, 1967). The ratio of K^{+}/ Na^{+} ratio was calculated subsequently based on the content of K^{+} and Na^{+}. Phosphorous (P) uptake was computed using dry biomass production and P concentration data.

2.5.2. Scanning electron microscopy (SEM) analysis

Colonization of AMF in roots was also examined under scanning electron microscopy (Padamsee et al., 2016). To visualize the colonization, clean roots were dried using soft tissue paper and treated for one h with glutaraldehyde solution (2.5 %). The samples were again treated with a fresh solution of glutaraldehyde for two h. Samples were washed five times with a 7 % sucrose solution. The washed samples were dehydrated using 30 %, 50 %, 70 %, and 80 % ethanol for 15 min each followed by 90 % and 100 % ethanol for 20 and 30 min, respectively. After dehydration samples were subjected to critical point drying and

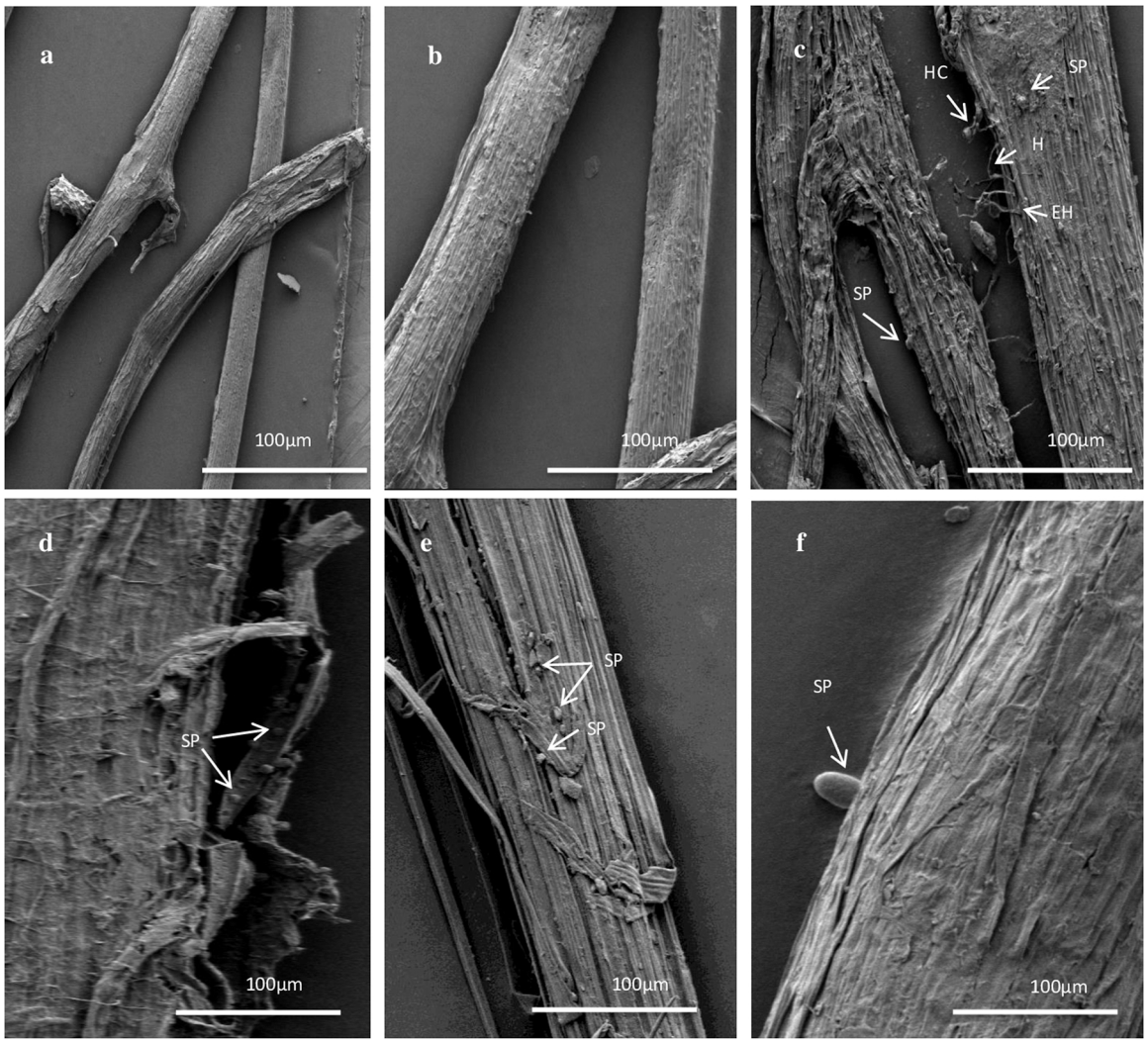


Fig. 7. Scanning Electron Micrograph of sorghum roots surface: (a–b) non inoculated control roots of sorghum demonstrating no AMF colonization; (c) mycorrhizal inoculated roots showing AMF colonization in the form of hyphae (H) (pointed white arrows) forming extraradical hyphae (EH) and hyphal coils (HC) in superficies of lateral roots of sorghum, AMF spores (SP) were also observed attached (pointed white arrows) on the roots of sorghum; (d) AMF spores (SP) attached to the cortical cells (pointed white arrows); (e–f) spores (SP) on the root surface (pointed white arrows).

mounted on stubs using double–stick tape. The mounted samples were sputtered with a film of gold and visualized under JOEL JSM–7610 F Plus Scanning Electron Microscope.

2.5.3. Soil analysis

The rhizosphere soils were collected aseptically and stored in refrigerated conditions for further analysis. Besides, the bulk soil samples were also collected for analysis of pH, EC_2 (Jackson, 1967), and Olsen's–P (Jackson, 1967). The dehydrogenase (Dick et al., 1997), alkaline (AlP, pH 11.0) phosphatases activities (Dick et al., 1997), and glomalin-related soil proteins content which includes difficultly-extractable (DE) and easily extractable (EE) (Wright and Upadhyaya, 1996) were analyzed from rhizospheric samples. The sum of both the fractions (EE and DE) was equivalent to the total glomalin (TG).

2.5.4. Culturable microbial population

The serial dilution method was used for the enumeration of culturable microbial counts in the rhizosphere soils (Chandra et al., 2020). For bacterial, fungal, and actinobacterial counts nutrient agar, Potato Dextrose Agar, and actinobacterial media of Himedia® were used, respectively (Supplementary Table 2). The soil suspension from 10^{-3} – 10^{-8} dilutions was poured on triplicate Petri plates containing respective media for bacteria, fungi, and actinobacteria. Bacterial, fungal, and actinobacterial colonies appearing after 1, 3–4, and 6–7 days after incubation at 28 ± 2 °C were counted, respectively.

2.6. AMF responsiveness

The responsiveness of different soil and plant parameters to AMF inoculation were computed separately using values of the response variable (X) under inoculated and uninoculated soils using the following equation:

$$\text{AMF } response\ (\%) = \left[\frac{X_{AMF\ inoculated\ soil} - X_{Uninoculated\ soil}}{X_{AMF\ inoculated\ soil}}\right] \times 100 \quad (3)$$

2.7. Statistical analysis

One-way analysis of variance (ANOVA) was used to analyze the data. The treatment means were compared using DUNCAN's Multiple Range Test ($P < 0.05$) using ICAR–IASRI, New Delhi portal (http://stat.iasri.res.in/sscnarsportal). Two–way repetitive ANOVA was employed with Greenhouse-Geisser correction to test the statistical significance of changes in colonization, arbuscules, and shoot-root traits at four time intervals and two crops (Sorghum and Maize). Data were analyzed using

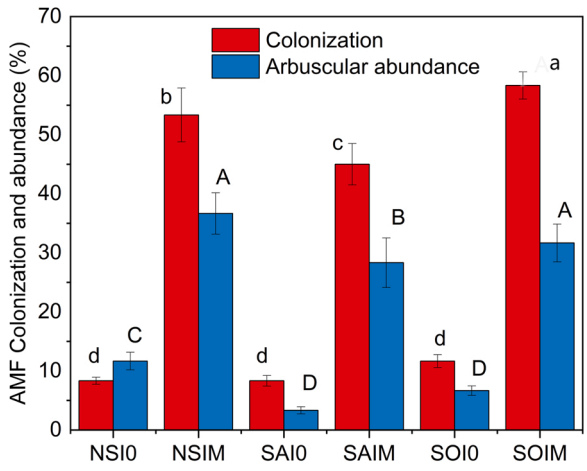


Fig. 8. Effect of inoculation with a mixed culture of *F. mosseae* and *F. geosporum on* colonization and arbuscules abundance in different soil types; capped lines on bars are standard deviation; $n = 5$; NSI0: normal soil uninoculated; NSIM: normal soil inoculated with AMF; SAI0: saline soil uninoculated; SAIM: saline soil inoculated with AMF; SOI0: sodic soil uninoculated; SOIM: sodic soil inoculated with AMF; bars with different letters within the same group are significantly different ($P < 0.05$) using DUNCAN's Multiple Range Test.

SPSS (20.0). Soil properties and AMF abundance data were analyzed using a non-parametric test. The saline and sodic soils were compared using the Man Whitney U test while cropping systems were compared using the Kruskal Wallis test ($P = 0.05$). The effect of soil properties on plant parameters and Olsen's P were visualized by redundancy analysis. A Monte Carlo permutation test was carried out for testing the model's significance. variation partitioning analysis (VPA) was also carried out using the vegan package in R (Dixon, 2003). The Corrplot package in R was used to develop the correlation plot (Wei and Simko, 2017).

3. Results

3.1. Native AMF abundance and soil properties

Soil samples collected for AMF abundance investigation vary with pH, EC, and available nutrients. The soil under the rice-wheat cropping system had greater pH and lower EC compared to other cropping systems sampled for studying the spore density (Table 2). The Olsen's–P, $KMnO_4$–N, and NH_4OAc–K were also greater under the rice–wheat system. The AMF spore density in the rice-wheat system was similar to pearl millet–mustard but greater than the sorghum-wheat and sorghum-mustard under saline and sodic soil. The spore density was greater under sodic compared to saline soils. The mycorrhizal colonization and arbuscular abundance in maize roots were relatively higher under sodic

Table 6
Effect of AMF inoculation on P nutrition and K^+/Na^+ ratio of sorghum grown under different soil types; NSI0: normal soil uninoculated; NSIM: normal soil inoculated with AMF; SAI0: saline soil uninoculated; SAIM: saline soil inoculated with AMF; SOI0: sodic soil uninoculated; SOIM: sodic soil inoculated with AMF; I0: uninoculated; IM: inoculated with AMF; means with different capital letters within column are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; *** $P < 0.001$.

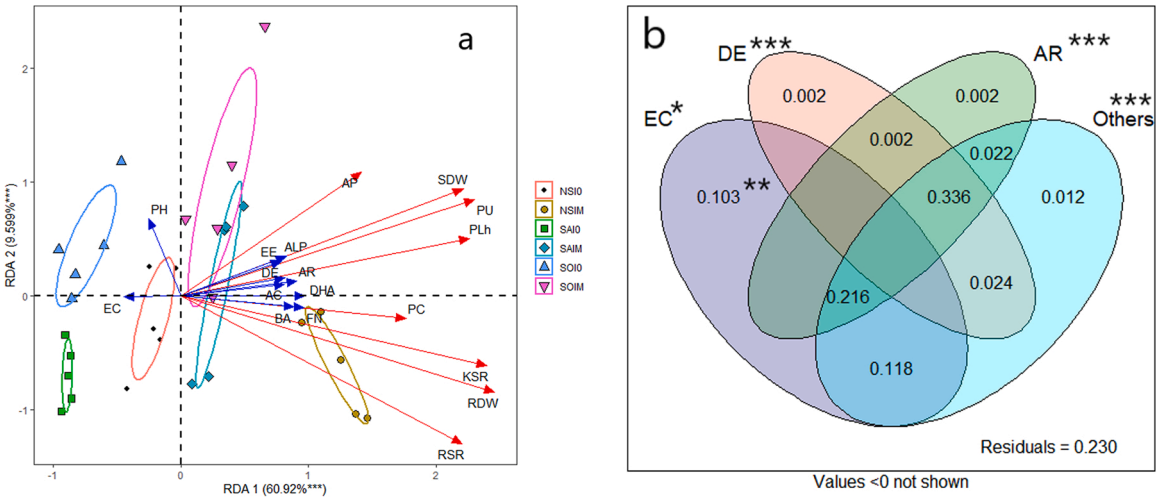
Treatment	P-concentration (mg kg^{-1})	P-uptake (mg pot^{-1})	K^+/Na^+ ratio
NSI0	0.11^{B}	0.03^{B}	1.55^{B}
NSIM	0.12^{A}	0.04^{A}	2.77^{A}
SAI0	0.11^{B}	0.02^{C}	0.60^{E}
SAIM	0.12^{A}	0.04^{A}	1.50^{C}
SOI0	0.10^{B}	0.02^{BC}	0.59^{E}
SOIM	0.12^{A}	0.04^{A}	1.18^{D}
I0 *vs* IM	***	***	***

Table 7
Effect of inoculation of arbuscular mycorrhizal fungi on soil properties; NSI0: normal soil uninoculated; NSIM: normal soil inoculated with AMF; SAI0: saline soil uninoculated; SAIM: saline soil inoculated with AMF; SOI0: sodic soil uninoculated; SOIM: sodic soil inoculated with AMF; I0: uninoculated; IM: inoculated with AMF; Means with different capital letters within column are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; ns $P > 0.05$; *** $P < 0.001$.

Treatment	EC_2 (dS m^{-1})	pH_2	Olsen's P (mg kg^{-1})	Glomalin related soil protein (mg g^{-1} dry soil)		
				Easily extractable (EE)	Difficultly extractable (DE)	Total (TG)
NSI0	0.20^{C}	8.22^{B}	13.5^{D}	0.04^{D}	0.02^{C}	0.06^{B}
NSIM	0.21^{C}	8.18^{B}	15.1^{A}	0.23^{B}	0.44^{AB}	0.67^{A}
SAI0	2.22^{A}	8.26^{B}	13.9^{C}	0.04^{D}	0.03^{C}	0.07^{B}
SAIM	2.20^{A}	8.22^{B}	14.4^{B}	0.19^{C}	0.46^{A}	0.65^{A}
SOI0	1.10^{B}	9.0^{A}	14.7^{B}	0.02^{D}	0.01^{C}	0.03^{B}
SOIM	1.09^{B}	8.94^{A}	15.22^{A}	0.30^{A}	0.35^{B}	0.65^{A}
I0 *vs* IM	ns	ns	***	***	***	***

Table 8
Effect of inoculation of AMF on soil associated microbiota and soil microbial enzymes; NSI0: normal soil uninoculated; NSIM: normal soil inoculated with AMF; SAI0: saline soil uninoculated; SAIM: saline soil inoculated with AMF; SOI0: sodic soil uninoculated; SOIM: sodic soil inoculated with AMF; I0: uninoculated; IM: inoculated with AMF; Means with different capital letters within column are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; *** $P < 0.001$.

Treatment	Bacteria (CFU g^{-1} $\times 10^5$)	Actinobacteria (CFU g^{-1} $\times 10^4$)	Fungi (CFU g^{-1} $\times 10^3$)	Dehydrogenase (μg TPF g^{-1} 24 h^{-1})	Alkaline phosphatase (mg p–nitrophenol kg^{-1} h^{-1})
NSI0	76.4^{C}	32.6^{BC}	26.8^{C}	207.7^{D}	76.4^{B}
NSIM	91.6^{A}	45.8^{A}	43.0^{A}	285.4^{A}	97.1^{A}
SAI0	63.8^{D}	27.8^{CD}	21.0^{D}	175.5^{F}	61.5^{C}
SAIM	83.8^{B}	43.8^{A}	33.0^{B}	229.3^{C}	78.2^{B}
SOI0	66.2^{D}	26.8^{D}	22.0^{D}	186.2^{E}	74.6^{B}
SOIM	75.8^{C}	37.4^{B}	34.0^{B}	245.7^{B}	97.0^{A}
I0 *vs* IM	***	***	***	***	***



c

Partitioning of correlations:

	Inertia	Proportion
Total	8	1
Constrained	6.646	0.8307
Unconstrained	1.354	0.1693

Monte Carlo permutation test for RDA model

AMF effects ~ EC + PH + EE + DE + AR + DHA + ALP + BA + FN + AC, scale = TRUE)

	Df	Variance	F	Adj. R^2	Pr(>F)[$]
Model	10	6.6457	9.3237	0.77	0.001
Residual	19	1.3543			

[$]Monte Carlo permutation test

Most parsimonious RDA model

Dependent variable	Response variable	Adjusted R^2	Pr(>F)
AMF effects (Soil and plants parameters)	EC	0.37	*
	EC + DE	0.73	**
	EC+DE+AR	0.76	*

Test for the simple and marginal effects of term

	Df	Simple effect		Marginal effect	
		Variance	Pr(>F)	Variance	Pr(>F)
EC	1	1.25	0.001	0.24	0.038
PH	1	0.83	0.001	0.16	0.106
EE	1	3.12	0.001	0.09	0.273
DE	1	0.35	0.011	0.09	0.281
AR	1	0.16	0.103	0.06	0.442
DHA	1	0.28	0.024	0.13	0.132
ALP	1	0.12	0.162	0.12	0.163
BA	1	0.07	0.345	0.06	0.489
FN	1	0.21	0.068	0.27	0.027
AC	1	0.27	0.028	0.27	0.027
Residual	19	1.35		1.35	

Fig. 9. Effect of soil properties on plant performance and Olsen's P (a) redundancy analyses (RDA) showing the relationship between soil properties (blue arrows) and plant response parameters and Olsen's P (red arrows); (b) RDA–based variance partitioning analysis demonstrating the contribution of EC, DE AR and other soil properties (pH+EE+DHA+ALP+BA+FN+AC) to plant response to AMF inoculation, and Olsen's P (c) RDA summary; missing values indicate non-significant interaction; significant soil properties were identified by the Monte Carlo permutation test; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; EC: Electrical conductivity (EC_2 dS m^{-1}); pH: soil pH_2; EE: easily extractable glomalin related soil protein; DE: difficultly extractable glomalin related soil protein; AR: Arbuscular abundance; DHA: dehydrogenase activity; ALP; alkaline phosphatase; BA: bacterial counts; FN: fungal counts; AC: actinobacterial counts.

soils with rice-wheat cropping systems (Supplementary Table 1, Table 2). Soil pH and $KMnO_4$–N showed a strong positive correlation with spore density while EC_2 showed a negative correlation. Soil P and K availability were also affecting the AMF spore density in the soil under different cropping systems. Amongst the soil variable studied $KMnO_4$–N had a significant positive correlation with AMF colonization (Table 3).

3.2. AMF preferential response to host

At all stages, AMF colonization was greater in maize compared to sorghum in both cycles of inoculation (Fig. 3). The mycorrhizal colonization and arbuscular abundance significantly ($P < 0.05$) increased with time in both the host plants. The rate of colonization in both the crops was more in the initial stage, about 61–81 % colonization and arbuscular abundance were achieved within 30 days of growth. The remaining 19–39 % VAM colonization and arbuscular abundance were attained in the next 30 days. The rate of colonization was more in the second cycle of inoculation compared to the first cycle. The shoot and-root traits of sorghum and maize were also significantly ($P < 0.05$) influenced by AMF colonization. The root and shoot biomass of the sorghum was relatively greater compared to maize in both the inoculation cycle (Table 4). The root to shoot ratio was also relatively more in for sorghum compared to maize.

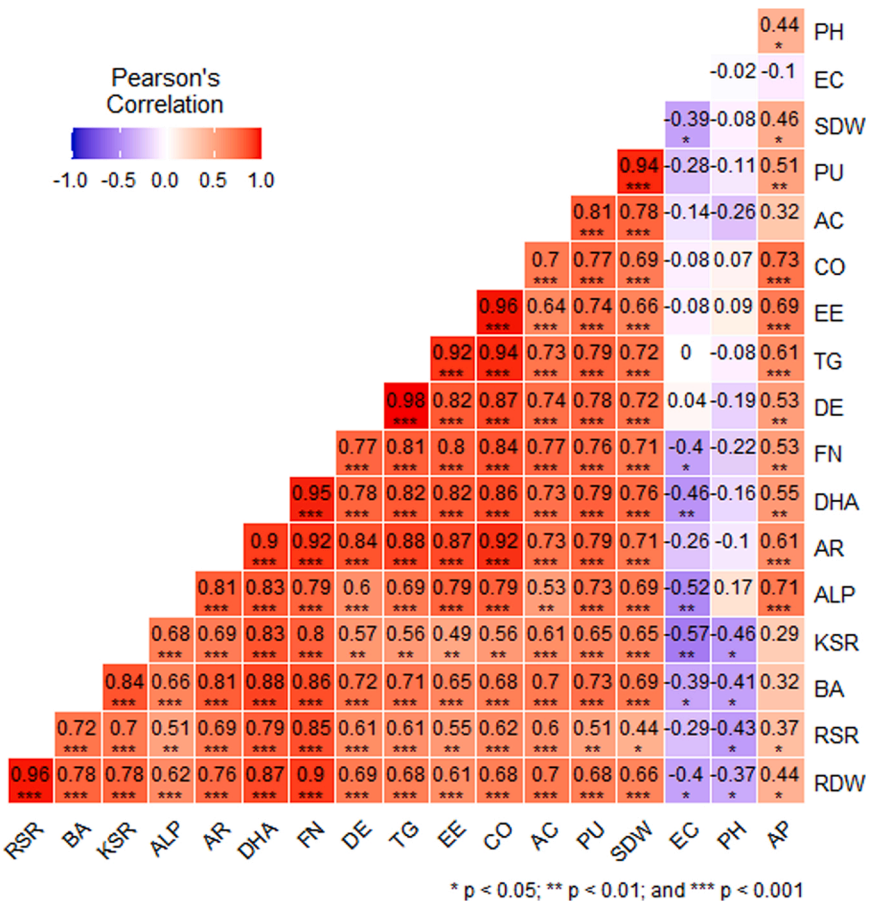


Fig. 10. Correlation matrix for plant parameters, soil properties, and AMF colonization; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. pH: soil pH_2; EC: electrical conductivity (EC_2 dS m^{-1}); SDW: Shoot dry biomass (g pot^{-1}); PU: P-uptake (mg pot^{-1}); CO: Mycorrhizal colonization (%); EE: easily extractable glomalin related soil protein; DE: difficultly extractable glomalin related soil protein; TG: total glomalin related soil protein; KSR: K^+/ Na^+ ratio; RSR: Root: shoot ratio; RDW: root dry biomass (g pot^{-1}); AR: Arbuscular abundance; DHA: dehydrogenase activity; ALP; alkaline phosphatase; BA: bacterial counts; FN: fungal counts; AC: actinobacterial counts.

Table 9
Mycorrhizal responsiveness in different types of soil; NSIM: normal soil inoculated with AMF; SAIM: saline soil inoculated with AMF; SOIM: sodic soil inoculated with AMF; Means with different capital letters within column are significantly different ($P < 0.05$) using Duncan's Multiple Range Test; EE: easily extractable glomalin related soil protein; DE: Difficultly extractable glomalin related soil protein; TG: total glomalin related soil protein.

	Mycorrhizal colonization	Arbuscules abundance	EE	DE	TG	Root shoot ratio	K^+ / Na^+ ratio	P-uptake	P–concentration	Olsen's–P
NSIM	84.3^{A}	67.0^{B}	84.34^{AB}	94.2^{A}	90.9^{A}	56.1^{A}	42.4^{B}	26.2^{C}	9.7^{B}	10.5^{A}
SAIM	81.3^{A}	90.0^{A}	79.3^{B}	93.1^{A}	89.1^{A}	39.5^{AB}	57.6^{A}	37.0^{A}	7.8^{B}	3.3^{B}
SOIM	80.0^{A}	80.0^{AB}	91.9^{A}	97.1^{A}	95.7^{A}	26.3^{B}	41.3^{B}	31.4^{B}	13.1^{A}	3.5^{B}

3.3. Characterization of AMFs

The two morphological sets named (i) type 1 AMF spore, and (ii) type 2 AMF spore were trapped from sodic soil under rice-wheat cropping (Supplementary material). The sequence of the amplified DNA of the 18 S region of the fungal ribosomal DNA suggested the *Funneliformis mosseae* and *Funneliformis geosporum* as the closest neighbour from the Glomeraceae family (Fig. 4). Sequences were registered in National Center for Biotechnology Information (NCBI). The NCBI GenBank accession number for *Funneliformis mosseae* and *Funneliformis geosporum* are OM510280 and OM510281, respectively.

The spores of *Funneliformis mosseae* were yellowish-brown and globose to subglobose shape. The spore size varied in the range of 150–210 μm (Fig. 5a). The shape of subtending hypha attached to spores was straight to somewhat recurved. The spores of the *Funneliformis geosporum* were yellowish-brown with a globose to subglobose shape (Fig. 5b). The spore size varied in the range of 80–170 μm. The spore wall layer of both the AMF consists of three layers (L1, L2, and L3). Similarly, the shape of subtending hypha of *F. geosporum* was also straight to somewhat recurved.

3.4. Response of sorghum to Funneliformis mosseae and Funneliformis geosporum inoculation

The AMF inoculation caused a significant ($P < 0.05$) improvement in growth in comparison to uninoculated control (Table 5). The mycorrhizal colonization and arbuscular abundance increased significantly because of AMF inoculation. Microscopic observations revealed the presence of different growth stages of mycorrhizal development in the roots of plants, such as intra and extra–radical hyphae, arbuscules, and vesicles (Fig. 6). The SEM analysis study also revealed the mycorrhizal colonization as well as the presence of spores on the root surface of plants inoculated with AMF in comparison to non-inoculated controls (Fig. 7). The AMF colonization and arbuscular abundance were greater for sodic and normal soil, respectively (Fig. 8). Among the salt–affected soils the impact of inoculation on plant height, fresh and dry biomass was greater in sodic followed by saline soils. The inoculation effect on dry matter content in above-ground biomass was not evident. However, below-ground biomass responded to inoculation, and saline soils showed a maximum increase (51 %) followed by normal (44.5 %) and sodic (28.8 %) soils. The root and shoot ratio also increased because of AMF inoculation. Sodic soil showed a greater increase in root to shoot

ratio compared to saline soils. The P content in sorghum biomass and P uptake was greater in AMF inoculated soils (Table 6). Although different soils showed varied P uptake under uninoculated conditions. The AMF inoculation effect of soil type was not evident in P nutrition. The AMF inoculation affected the drastic reduction in the Na^+/K^+ ratio in saline and sodic soil.

3.5. Effect on soil properties

The AMF inoculation caused a significant increase in soil Olsen's–P content compared to the un-inoculated control (Table 7). The increase in Olsen's–P was greater in sodic compared to saline soils. The contents of the GRSPs were greater in AMF inoculated soils. Saline and sodic soils recorded greater values for DE–GRSP and EE–GRSP, respectively. Sodic soils showed a maximum 15–35 fold increase in the EE–GRSP and DE–GRSP because of AMF inoculation ($P \leq 0.05$). The AMF inoculated soils had greater ($P \leq 0.05$) bacteria, actinomycetes, and fungi count in all the soil types (Table 8). Out of the studied soil microbiota, the bacterial population was significantly ($P \leq 0.05$) highest in normal soils. Mycorrhiza favored the growth in normal soils for the bacterial and fungal populations while the actinomycetes population in saline soils. Similarly, mycorrhiza caused a significant ($P < 0.05$) increase in microbial enzymes. Dehydrogenase and phosphatase enzymes varied with soil types. Dehydrogenase activity was highest in AMF inoculated normal soils. The alkaline phosphatases activity was highest ($P < 0.05$) in AMF inoculated normal soils following AMF inoculated sodic soils (Table 8).

3.6. Relationship between plant and soil parameters

Different soil attributes had a significant effect on the plant parameters, and P nutrition of the sorghum (Monte Carlo permutation test, $P = 0.001$). The AMF inoculated soils were distributed in the opposite quadrant from the uninoculated counterparts (Fig. 9a). The RDA model fitted with different soil properties explained about 83 % variability in growth and P nutrition of the sorghum under three different soils (Fig. 9b). The EC, pH, EE, DE, DHA, and AC showed a significant simple effect on the overall variability in the growth, P nutrition, and soil P availability ($P < 0.05$). However, the marginal effect was only apparent for EC, FN, and AC. The EC, DE, and AR were identified as the response variable for the most parsimonious RDA model (adj. R^2 0.76; $P < 0.05$). The variance partitioning analysis also highlighted the importance of the EC and its interaction effect with other soil parameters on the model predictability (Fig. 9c). Soil Olsen's–P formed acute angle with AR, CO, EE, DE and ALP ($r = 0.53$–0.73; $P < 0.01$), while P uptake (PU) formed acute angle with EE, DE, AC and BA and ALP ($r = 0.72$–0.81; $P < 0.001$). The EC and pH formed obtuse angles with P availability, P uptake, and plant growth parameters (Figs. 9a, 10).

3.7. Mycorrhizal responsiveness

Sorghum crops responded positively to AMF inoculation (Table 9). Mycorrhizal responsiveness for arbuscular abundance, K^+/Na^+ ratio, and P uptake was greater for saline compared to sodic soils. While, EE, TG, and P concentrations were greater for sodic soils ($P \leq 0.05$). Mycorrhizal responsiveness for Olsen's–P and root: shoot ratio were significantly ($P \leq 0.05$) greater in normal soil.

4. Discussion

The growth and development of the crop plants are challenged by the multiple stresses operating in the salt-affected soils (Abrol et al., 2019, 1988; Rai et al., 2021a; Soni et al., 2021). Water stress because of high osmotic/ matric stress and deficiency and /or toxicity of the specific ions, poor aeration and transport of water, and nutrients in the tortuous capillary paths are among the major factors limiting crop performance (Akhter et al., 2004; Rai et al., 2022; Sheldon et al., 2017). In these stressed soil environments, plants adapt by forging a mutualistic association with specific beneficial microorganisms to acquire tolerance against the dominant stresses (Chandra et al., 2020; Rai et al., 2020, 2021b; Zhao et al., 2020). This study showed the dominance of *Funneliformis mosseae,* and *F. geosporum* owing to Glomeraceae family in the rice-wheat cropping system of sodic soils. Both the species are reported to adapt to deleterious growing conditions such as water deficit, saline, and sodic ecosystems (Krishnamoorthy et al., 2014; Landwehr et al., 2002).

The observed change in spore density with change in soil pH, salinity level (EC_2), and nitrogen availability also indicated the development of strategic partnership by the crop plant with AMF in these soils to overcome the unfavourable growth conditions in salt–affected soils. Variation in spore density in different cropping systems was mainly related to the differential response of various crops in forging a mutualistic partnership with AMF in saline and sodic conditions. There are conflicting reports related to AMF abundance and soil properties (Abbott and Robson, 1991; Entry et al., 2002; Landwehr et al., 2002). Our study showed an increase in spore density with greater pH and nutrient availability while a decrease in spore density with increasing salinity. An increase in multiple stresses in sodic soil during the summer season (sampling time) was responsible for higher spore density with increasing pH ($r = 0.83$; $P < 0.001$). Similarly, higher nutrient availability was also associated with greater spore density ($r = 0.59$–0.72; $P < 0.05$). This was mainly because of the increased surface area available for forming a partnership as evident from higher AMF colonization in maize plants in different soils with increased available nitrogen ($r = –0.64$; $P < 0.05$). A greater AMF colonization with increased nitrogen availability is also favoured for sporulation to survive in desiccating summer. Lower spore density associated with higher soil salinity ($r = –0.61$; $P < 0.05$) was because of poor germination of spore and hyphal formation under high osmotic stress (Bencherif et al., 2015). Poor root growth under high salinity was also responsible for the reduction of symbiotic capacity because of the limited surface area available for forging partnerships (Table 5). All these factors culminated in lower AMF abundance and reduced spore formation in soils of higher salinity during summer.

Greater arbuscular abundance and spore density in rice-wheat compared to sorghum and pearl millet-based cropping systems were associated with the varied capabilities of the component crops in forming a mutualistic association with native AMF to mitigate the negative impact of sodicity. Earlier reports also showed the differential impact of the salinity and sodicity on the symbiosis of the AMF with grasses and legumes (García and Mendoza, 2008). Crop specific response to AMF symbiosis was mainly attributed to the difference in composition of root exudates secreted that attract mycorrhizal spores and favors its colonization in their roots (Fakhech et al., 2021). This was also evident from the greater ability of maize to form an association with AMF than sorghum (Fig. 3). Higher colonization in the second crop cycle also highlights the role of inoculum density and adaptability of AMF with the host plants for improving root colonization (Sivakumar, 2013).

The sorghum plants inoculated with a mixed culture of *F. mosseae* and *F. geosporum* grew better and produced greater plant height and biomass under saline and sodic soils than the uninoculated plants were because of the alleviation of salt stress through greater root biomass and root to shoot ratio and improved K^+/ Na^+ ratio compared to non-mycorrhizal plants. Wang et al. (2020) also reported the change in root plasticity under the influence of mycorrhizal association. Alleviation of salinity stress using AMF had been reported in many crop plants (Klinsukon et al., 2021; Kumar et al., 2015). The effect of mycorrhiza in different soil types was also evident from the increased Olsen's–P in soil and P uptake in the inoculated plants compared to uninoculated. The increased secretion of the organic acids and other chelating compounds in the rhizosphere of the mycorrhizal plants facilitated the solubilization of Al, Fe, and Ca bound P, and adsorbed P (Magallón–Servin et al., 2020). Increased competition for adsorption sites between conjugate

bases of organic acids secreted in the rhizosphere and phosphate ions also increased the soluble P content (Hinsinger et al., 2003). Apart from producing organic acids to solubilize P for plants, mycorrhizal fungi possess specific and high-affinity P transporters which facilitate the phosphorus movement under salinity and low P availability. The poor rate of P diffusion in the root depletion zone was compensated by hyphal P uptake and the transport was also responsible for the observed improvement in P nutrition. Besides increasing the availability of growth-limiting nutrients, AMF also imparted the salinity tolerance to plants by improving K^+/ Na^+ ratio in the plant in both saline and sodic soils. It was associated with the capability of AMF inoculated plants to sequester Na^+ in vacuoles or its exclusion from the cytosol (Evelin et al., 2012).

A higher microbial population observed in inoculated plants suggests the establishment of the tripartite mutualistic association between plants-AMF- microbes. After the establishment of the partnership, the flow of photo-assimilates across the symbiotic interface and root tip facilitated more establishment and persistence of soil-associated microbiota (Turrini et al., 2018). This created a niche for greater metabolic activity, as evident from the strong correlation between dehydrogenase and the number of bacteria ($r = 0.88$; $P < 0.001$), fungi ($r = 0.95$; $P < 0.001$), and actinobacteria ($r = 0.73$; $P < 0.001$). A higher concentration of phosphatases enzymes in mycorrhizal–treated soil improved the P uptake ($r = 0.51$; $P < 0.01$). This observation also supports the importance of VAM in plant phosphorus nutrition through the release of phosphatases enzymes and hyphal transport of P to the plant. Hyphae, and cortex of VAM inoculated roots release more phosphatases which are involved in the hydrolysis of P (Khade et al., 2010). The AMF effect on soil P availability and plant response varied with soil types. The RDA analysis also indicated the importance of salinity level contributing to ~37 % variability in AMF response in sorghum crop (Fig. 9c). Phosphorus uptake and soil P availability were highly correlated with glomalin content in the soil. The greater TG responsiveness of AMF inoculation in sodic soil indicated the adaptation of the AMF-plant partnership in sodic soil through the release of more glomalin in the rhizosphere. The mycorrhizal colonization significantly increased the concentrations of EE, DE, and TG. Previous studies also noted the increased glomalin production by AMF-plant under stress conditions (Jia et al., 2016; Wu et al., 2014). The P uptake, glomalin production, colonization, and arbuscular abundance were highly correlated with each other ($r = 0.77$–0.88; $P < 0.001$). This showed the positive role of glomalin production in salt-affected soils in establishing the mycorrhizal association. Further, the higher ratio of EE to DE in the mycorrhizosphere suggests slow stabilization of the EE glomalin produced by the mycorrhizal association into DE fraction with time.

The development and function of mycorrhizal partnership are affected by several edaphic factors (Entry et al., 2002). Colonization seemed to be sensitive in salt–affected soils because of the reduced germination of fungal spores. While the development of arbuscular vesicles might be stimulated by the host symbiosis-signaling pathway under less favorable conditions for root growth. The high responsiveness of arbuscules abundance observed in saline and sodic soil supports the hypothesis of the increased absorptive surface area of root because of the structural relationship between the partners. Under stress conditions, plants shrink their roots and compensate them with AMF partnership (Lee et al., 2015). Glomalin production is also related to stress response hence higher responsiveness of glomalin was found in sodic soils. It is involved in reducing the damage of cytosol because of protein misfolding induced by high Na^+ (Maathuis and Amtmann, 1999). It has been widely reported that responsiveness depends upon mycorrhizal colonization and is generally expressed in terms of improved growth and/or P nutrition over the uninoculated control and this also varied between soil types and crop cultivars (Treseder, 2013). The AMF inoculation was effective in increasing crop performance by manipulating the rhizospheric environment for providing better P nutrition and stress tolerance by enhancing the K^+/ Na^+ ratio under saline and sodic soils. Although AMF response for different parameters varied in different soils, the overall impact of AMF inoculation on plant growth and biomass production was at par in saline and sodic soils. This observation indicated the stress-specific response of partnership to mitigate stress and promote congenial growing conditions for macro-symbiont. These results are indicative and need further confirmation under salt-affected soils of different agro-ecology through field study.

5. Conclusions

Our study concludes that the abundance of native AMF depends upon the level of stress present in saline and sodic soils. The AMF spore density was positively affected by an increase in soil pH and nutrient availability and a decrease in soil salinity. The AMF abundance was also dependent upon the cropping systems. The rice–wheat cropping system under sodic soil supported greater AMF spore density of *Funneliformis sps.* Maize was the preferred host for the multiplication of *F. mosseae* and *F. geosporum* isolated from sodic soil with a rice–wheat cropping system. Application of mixed culture of *F. mosseae* and *F. geosporum* was found very effective in improving growth, yield, and P nutrition of sorghum under salt-affected soils. The AMF partnership was equally effective in saline as well as sodic soils. Therefore, the use of native AMF *F. mosseae* and *F. geosporum*, with mycotrophic plant species, might represent a convenient strategy to cope with abiotic stress in salt–affected soils.

CRediT authorship contribution statement

Priyanka Chandra: Conceptualization, Methodology, Investigation, Writing – original draft. **Awtar Singh**: Data curation, Formal analysis. **Kailash Prajapat**: Data curation, Formal analysis. **Arvind Kumar Rai**: Visualization, Formal analysis, Writing – review & editing. **R.K. Yadav**: Supervision, Writing – review & editing.

Data Availability

Data will be made available on request.

Acknowledgments

The authors would like to thank Indian Council of Agricultural Research (ICAR), New Delhi, India and the Director, ICAR-Central Soil Salinity Research Institute (CSSRI), Karnal, Haryana, India for providing financial assistance. The research finding is a part of the ICAR-CSSRI research project entitled “Development of endo-rhizospheric fungal consortia to increase salt tolerance in crops (NRMACSSRI-SIL201700600930). This research article was approved by Prioritization, Monitoring and Evaluation Cell (PME), ICAR-CSSRI (Research Article No. 37/2021).

Conflict of interest

The authors declare that they have no conflict of interest.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2022.104982.

References

Abbott, L.K., Robson, A.D., 1991. Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. Agric., Ecosyst. Environ. 35, 121–150. https://doi.org/10.1016/0167-8809(91)90048-3.

Abdelhalim, T., Jannoura, R., Joergensen, R.G., 2020. Arbuscular mycorrhizal dependency and phosphorus responsiveness of released, landrace and wild Sudanese sorghum genotypes. Arch. Agron. Soil Sci. 66, 706–716. https://doi.org/10.1080/03650340.2019.1633577.

Abrol, I., Yadav, J.S.P., Massoud, F.I., 2019. Salt Affected Soils and their Management.
Abrol, I.P., Yadav, J.S.P., Massoud, F.I., 1988. Salt-affected soils and their management. FAO Soils Bulletin No. 39. Food and Agriculture Organization of the United Nations, Rome.
Akhter, J., Murray, R., Mahmood, K., Malik, K.A., Ahmed, S., 2004. Improvement of degraded physical properties of a saline-sodic soil by reclamation with kallar grass (Leptochloa fusca). Plant Soil 258, 207–216. https://doi.org/10.1023/B:PLSO.0000016551.08880.6b.
AnonFAO, 2020. The state of food and agriculture 2020. Overcoming water challenges in agriculture. Rome. https://doi.org/https://doi.org/10.4060/cb1447en.
Basak, N., Barman, A., Sundha, P., Rai, A.K., 2020. In: Rakshit, A., Ghosh, S., Chakraborty, S., Philip, V., Datta, A. (Eds.), Recent Trends in Soil Salinity Appraisal and Management BT - Soil Analysis: Recent Trends and Applications. Springer, Singapore, Singapore, pp. 143–161. https://doi.org/10.1007/978-981-15-2039-6_9.
Bencherif, K., Boutekrabt, A., Fontaine, J., Laruelle, F., Dalpè, Y., Lounès-Hadj Sahraoui, A., 2015. Impact of soil salinity on arbuscular mycorrhizal fungi biodiversity and microflora biomass associated with Tamarix articulata Vahll rhizosphere in arid and semi-arid Algerian areas. Sci. Total Environ. 533, 488–494. https://doi.org/10.1016/j.scitotenv.2015.07.007.
Bindraban, P.S., Dimkpa, C.O., Pandey, R., 2020. Exploring phosphorus fertilizers and fertilization strategies for improved human and environmental health. Biol. Fertil. Soils 56, 299–317. https://doi.org/10.1007/s00374-019-01430-2.
Błaszkowski, J., Czerniawska, B., 2006. The occurrence of arbuscular mycorrhizal fungi of the phylum Glomeromycota in Israeli soils. Acta Soc. Bot. Pol. 75, 339–350. https://doi.org/10.5586/asbp.2006.041.
Briat, J.F., Gojon, A., Plassard, C., Rouached, H., Lemaire, G., 2020. Reappraisal of the central role of soil nutrient availability in nutrient management in light of recent advances in plant nutrition at crop and molecular levels. Eur. J. Agron. 116, 126069 https://doi.org/10.1016/j.eja.2020.126069.
Chandra, P., Dhuli, P., Verma, P., Singh, A., Choudhary, M., Prajapat, K., Rai, A.K., Yadav, R.K., 2020. Culturable microbial diversity in the rhizosphere of different biotypes under variable salinity. Trop. Ecol. 61, 291–300. https://doi.org/10.1007/s42965-020-00089-3.
Cobb, A.B., Wilson, G.W.T., Goad, C.L., Bean, S.R., Kaufman, R.C., Herald, T.J., Wilson, J.D., 2016. The role of arbuscular mycorrhizal fungi in grain production and nutrition of sorghum genotypes: enhancing sustainability through plant-microbial partnership. Agric., Ecosyst. Environ. 233, 432–440. https://doi.org/10.1016/j.agee.2016.09.024.
Dick, R.P., Breakwell, D.P., Turco, R.F., 1997. Soil Enzyme Activities and Biodiversity Measurements as Integrative Microbiological Indicators. Methods for Assessing Soil Quality. SSSA Special Publications. https://doi.org/10.2136/sssaspecpub49.c15.
Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14, 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x.
Dodd, J.C., Thomson, B.D., 1994. The screening and selection of inoculant arbuscular-mycorrhizal and ectomycorrhizal fungi. Plant Soil 159, 149–158. https://doi.org/10.1007/BF00000104.
Ellouze, W., Esmaeili Taheri, A., Bainard, L.D., Yang, C., Bazghaleh, N., Navarro-Borrell, A., Hanson, K., Hamel, C., 2014. Soil fungal resources in annual cropping systems and their potential for management. BioMed. Res. Int. 2014, 531824 https://doi.org/10.1155/2014/531824.
Entry, J., Rygiewicz, P., Watrud, L., Donnelly, P., 2002. Influence of adverse soil conditions on the formation and function of Arbuscular mycorrhizas. Adv. Environ. Res. 7, 123–138. https://doi.org/10.1016/S1093-0191(01)00109-5.
Evelin, H., Giri, B., Kapoor, R., 2012. Contribution of Glomus intraradices inoculation to nutrient acquisition and mitigation of ionic imbalance in NaCl-stressed Trigonella foenum-graecum. Mycorrhiza 22, 203–217. https://doi.org/10.1007/s00572-011-0392-0.
Fakhech, A., Jemo, M., Manaut, N., Ouahmane, L., Hafidi, M., 2021. Impact of mycorrhization on phosphorus utilization efficiency of Acacia gummifera and Retama monosperma under salt stress. Forests 12, 611.
García, I.V., Mendoza, R.E., 2008. Relationships among soil properties, plant nutrition and arbuscular mycorrhizal fungi-plant symbioses in a temperate grassland along hydrologic, saline and sodic gradients. FEMS Microbiol. Ecol. 63, 359–371. https://doi.org/10.1111/j.1574-6941.2008.00441.x.
Gerdemann, J.W., Nicolson, T.H., 1963. Spores of mycorrhizal Endogone species extracted from soil by wet sieving and decanting. Trans. Br. Mycol. Soc. 46, 235–244. https://doi.org/10.1016/S0007-1536(63)80079-0.
Ghollarata, M., Raiesi, F., 2007. The adverse effects of soil salinization on the growth of Trifolium alexandrinum L. and associated microbial and biochemical properties in a soil from Iran. Soil Biol. Biochem. 39, 1699–1702. https://doi.org/10.1016/j.soilbio.2007.01.024.
Giovannini, L., Palla, M., Agnolucci, M., Avio, L., Sbrana, C., Turrini, A., Giovannetti, M., 2020. Arbuscular mycorrhizal fungi and associated microbiota as plant biostimulants: research strategies for the selection of the best performing inocula. Agronomy. https://doi.org/10.3390/agronomy10010106.
Gopal, S., Kim, K., Walitang, D., Chanratana, M., Kang, Y., Chung, B., Sa, T., 2016. Trap culture technique for propagation of arbuscular mycorrhizal fungi using different host plants. Korean J. Soil Sci. Fertil. 49, 608–613. https://doi.org/10.7745/KJSSF.2016.49.5.608.
Gopal, S., Shagol, C., Kang, Y., Chung, B., Han, S., Tong-Min, S., 2018. Arbuscular mycorrhizal fungi spore propagation using single spore as starter inoculum and a plant host. J. Appl. Microbiol. 124, 1556–1565. https://doi.org/10.1111/jam.13714.
Gosling, P., Hodge, A., Goodlass, G., Bending, G.D., 2006. Arbuscular mycorrhizal fungi and organic farming. Agric., Ecosyst. Environ. 113, 17–35. https://doi.org/10.1016/j.agee.2005.09.009.
Hinsinger, P., Plassard, C., Tang, C., Jaillard, B., 2003. Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. Plant Soil 248, 43–59. https://doi.org/10.1023/A:1022371130939.
Jackson, M.L., 1967. Soil Chemical Analysis. Printice Hall of India Pvt. Ltd.,, New Delhi, p. 498.
Jalali, M., Kolahchi, Z., 2009. Effect of irrigation water quality on the leaching and desorption of phosphorous from soil. Soil Sediment Contam.: Int. J. 18, 576–589. https://doi.org/10.1080/15320380903113451.
Jia, X., Zhao, Y., Liu, T., Huang, S., Chang, Y., 2016. Elevated CO_2 increases glomalin-related soil protein (GRSP) in the rhizosphere of Robinia pseudoacacia L. seedlings in Pb- and Cd-contaminated soils. Environ. Pollut. 218, 349–357. https://doi.org/10.1016/j.envpol.2016.07.010.
Khade, S., Rodrigues, B., Sharma, P., 2010. Arbuscular mycorrhizal status and root phosphatase activities in vegetative Carica papaya L. varieties. Acta Physiol. Plant. 32, 565–574. https://doi.org/10.1007/s11738-009-0433-x.
Klinsukon, C., Lumyong, S., Kuyper, T.W., Boonlue, S., 2021. Colonization by arbuscular mycorrhizal fungi improves salinity tolerance of eucalyptus (Eucalyptus camaldulensis) seedlings. Sci. Rep. 11, 4362. https://doi.org/10.1038/s41598-021-84002-5.
Krishnamoorthy, R., Kim, K., Kim, C., Sa, T., 2014. Changes of arbuscular mycorrhizal traits and community structure with respect to soil salinity in a coastal reclamation land. Soil Biol. Biochem. 72, 1–10. https://doi.org/10.1016/j.soilbio.2014.01.017.
Kumar, A., Dames, J.F., Gupta, A., Sharma, S., Gilbert, J.A., Ahmad, P., 2015. Current developments in arbuscular mycorrhizal fungi research and its role in salinity stress alleviation: a biotechnological perspective. Crit. Rev. Biotechnol. 35, 461–474. https://doi.org/10.3109/07388551.2014.899964.
Kumar, S., Agrawal, R.K., Dixit, A.K., Rai, A.K., Singh, J.B., Rai, S.K., 2012. Forage production technology for arable lands. Indian Grassland and Fodder Research Institute, Jhansi 284 003, Uttar Pradesh, India.Technology Bulletin no.1/2012, pp 48.
Lambert, D.H., Cole Jr, H., Baker, D.E., 1980. Adaptation of vesicular-arbuscular mycorrhizae to edaphic factors. N. Phytol. 85, 513–520. https://doi.org/10.1111/j.1469-8137.1980.tb00766.x.
Landwehr, M., Hildebrandt, U., Wilde, P., Nawrath, K., Tóth, T., Biró, B., Bothe, H., 2002. The arbuscular mycorrhizal fungus Glomus geosporum in European saline, sodic and gypsum soils. Mycorrhiza 12, 199–211. https://doi.org/10.1007/s00572-002-0172-y.
Lee, J., Lee, S., Young, J.P.W., 2008. Improved PCR primers for the detection and identification of arbuscular mycorrhizal fungi. FEMS Microbiol. Ecol. 65, 339–349. https://doi.org/10.1111/j.1574-6941.2008.00531.x.
Lee, Y., Krishnamoorthy, R., Selvakumar, G., Kim, K., Sa, T., 2015. Alleviation of salt stress in maize plant by co-inoculation of arbuscular mycorrhizal fungi and Methylobacterium oryzae CBMB20. J. Korean Soc. Appl. Biol. Chem. 58, 533–540. https://doi.org/10.1007/s13765-015-0072-4.
Maathuis, F.J.M., Amtmann, A., 1999. K + nutrition and Na + toxicity: the basis of cellular K + /Na + Ratios. Ann. Bot. 84, 123–133. https://doi.org/10.1006/anbo.1999.0912.
Magallón-Servin, P., Antoun, H., Taktek, S., Bashan, Y., De-Bashan, L., 2020. The maize mycorrhizosphere as a source for isolation of arbuscular mycorrhizae-compatible phosphate rock-solubilizing bacteria. Plant Soil 451, 169–186. https://doi.org/10.1007/s11104-019-04226-3.
Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27, 31–36. https://doi.org/10.1016/S0003-2670(00)88444-5.
Omar, M.B., Bolland, L., Heather, W.A., 1978. A permanent mounting medium for fungi. Stain Technol. 53, 293–294.
Padamsee, M., Johansen, R.B., Stuckey, S.A., Williams, S.E., Hooker, J.E., Burns, B.R., Bellgard, S.E., 2016. The arbuscular mycorrhizal fungi colonising roots and root nodules of New Zealand kauri Agathis australis. Fungal Biol. 120, 807–817. https://doi.org/10.1016/j.funbio.2016.01.015.
Phillips, J.M., Hayman, D.S., 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection, 158-IN18 Trans. Br. Mycol. Soc. 55. https://doi.org/10.1016/S0007-1536(70)80110-3.
Querejeta, J.I., Allen, M.F., Caravaca, F., Roldán, A., 2006. Differential modulation of host plant delta13C and delta18O by native and nonnative arbuscular mycorrhizal fungi in a semiarid environment. N. Phytol. 169, 379–387. https://doi.org/10.1111/j.1469-8137.2005.01599.x.
Rai, A.K., Johri, S.N., Kaur, H., Basak, N., Sundha, P., 2020. Salinity and sodicity influence mutualistic association of beneficial microorganism in arid soils. J. Soil Salin. Water Qual. 12, 15–21.
Rai, A.K., Basak, N., Sundha, P., 2021a. In: Rakshit, A., Singh, S.K., Abhilash, P.C., Biswas, A. (Eds.), Saline and Sodic Ecosystems in the Changing World BT - Soil Science: Fundamentals to Recent Advances. Springer, Singapore, Singapore, pp. 175–190. https://doi.org/10.1007/978-981-16-0917-6_9.
Rai, A.K., Dinkar, A., Basak, N., Dixit, A.K., Das, S.K., Dev, I., Sundha, P., Chandra, P., Kumar, S., 2021b. Phosphorus nutrition of oats genotypes in acidic soils: Exploiting responsive plant-microbe partnership. Appl. Soil Ecol. 167, 104094 https://doi.org/10.1016/j.apsoil.2021.104094.
Rai, A.K., Basak, N., Soni, P.G., Kumar, S., Sundha, P., Narjary, B., Yadav, G., Patel, S., Kaur, H., Yadav, R.K., Sharma, P.C., 2022. Bioenergy sorghum as balancing feedback loop for intensification of cropping system in salt-affected soils of the semi–arid region: energetics, biomass quality and soil properties. Eur. J. Agron. 134, 126452 https://doi.org/10.1016/j.eja.2021.126452.
Rajeshkumar, P., Thomas, G., Gupta, A., Gopal, M., 2015. Diversity, richness and degree of colonization of arbuscular mycorrhizal fungi in coconut cultivated along with

intercrops in high productive zone of Kerala, India. Symbiosis 65, 125–141. https://doi.org/10.1007/s13199-015-0326-2.
Redecker, D., Schüßler, A., Stockinger, H., Stürmer, S.L., Morton, J.B., Walker, C., 2013. An evidence-based consensus for the classification of arbuscular mycorrhizal fungi (Glomeromycota). Mycorrhiza 23, 515–531. https://doi.org/10.1007/s00572-013-0486-y.
Rengasamy, P., 2016. Soil chemistry factors confounding crop salinity tolerance—a review. Agronomy. https://doi.org/10.3390/agronomy6040053.
Ruiz-Lozano, J.M., Porcel, R., Azcón, C., Aroca, R., 2012. Regulation by arbuscular mycorrhizae of the integrated physiological response to salinity in plants: new challenges in physiological and molecular studies. J. Exp. Bot. 63, 4033–4044. https://doi.org/10.1093/jxb/ers126.
Selvakumar, G., Shagol, C.C., Kim, K., Han, S., Sa, T., 2018. Spore associated bacteria regulates maize root K(+)/Na(+) ion homeostasis to promote salinity tolerance during arbuscular mycorrhizal symbiosis. BMC Plant Biol. 18, 109. https://doi.org/10.1186/s12870-018-1317-2.
Shariatmadari, H., Shirvani, M., Jafari, A., 2006. Phosphorus release kinetics and availability in calcareous soils of selected arid and semiarid toposequences. Geoderma 132, 261–272. https://doi.org/10.1016/j.geoderma.2005.05.011.
Sharpley, A.N., 1983. Effect of soil properties on the kinetics of phosphorus desorption. Soil Sci. Soc. Am. J. 47, 462–467. https://doi.org/10.2136/sssaj1983.03615995004700030013x.
Sheldon, A.R., Dalal, R.C., Kirchhof, G., Kopittke, P.M., Menzies, N.W., 2017. The effect of salinity on plant-available water. Plant Soil 418, 477–491. https://doi.org/10.1007/s11104-017-3309-7.
Singh, J., Singh, V., Dutt, V., Walia, N., Kumawat, G., Jakhar, M.L., Yadava, D.K., Sharma, P.C., 2022. Insights into salt tolerance of mustard (Brassica juncea L. Czern & Coss): A metabolomics perspective. Environ. Exp. Bot. 194, 104760 https://doi.org/10.1016/j.envexpbot.2021.104760.
Singh, S.B., Abrol, I.P., 1985. Effect of soil sodicity on the growth, yield and chemical composition of groundnut (Arachis hypogaea Linn.). Plant Soil 84, 123–127.
Singh, V., van Oosterom, E.J., Jordan, D.R., Messina, C.D., Cooper, M., Hammer, G.L., 2010. Morphological and architectural development of root systems in sorghum and maize. Plant Soil 333, 287–299. https://doi.org/10.1007/s11104-010-0343-0.
Sivakumar, N., 2013. Effect of edaphic factors and seasonal variation on spore density and root colonization of arbuscular mycorrhizal fungi in sugarcane fields. Ann. Microbiol. 63, 151–160. https://doi.org/10.1007/s13213-012-0455-2.
Smith, S.E., Jakobsen, I., Grønlund, M., Smith, F.A., 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiol. 156, 1050–1057. https://doi.org/10.1104/pp.111.174581.
Soni, P.G., Basak, N., Rai, A.K., Sundha, P., Narjary, B., Kumar, P., Yadav, G., Kumar, S., Yadav, R.K., 2021. Deficit saline water irrigation under reduced tillage and residue mulch improves soil health in sorghum-wheat cropping system in semi-arid region. Sci. Rep. 11, 1880. https://doi.org/10.1038/s41598-020-80364-4.
Sundha, P., Basak, N., Rai, A., Yadav, R., Sharma, D., Sharma, P., 2017. N and P release pattern in saline-sodic soil amended with gypsum and municipal solid waste compost. J. Soil Salin. Water Qual. 9, 145–155.
Sundha, P., Rai, A.K., Basak, N., Yadav, R.K., Sharma, P.C., 2022. P solubility and release kinetics in the leachate of saline–sodic soil: effect of reclamation strategies and water quality. Soil Tillage Res. 222, 105440 https://doi.org/10.1016/j.still.2022.105440.
Sylvia, D.M., Williams, S.E., 1992. Vesicular-Arbuscular Mycorrhizae and Environmental Stress. Mycorrhizae in Sustainable Agriculture, ASA Special Publications. https://doi.org/https://doi.org/10.2134/asaspecpub54.c5.
Teste, F.P., Jones, M.D., Dickie, I.A., 2020. Dual-mycorrhizal plants: their ecology and relevance. N. Phytol. 225, 1835–1851. https://doi.org/10.1111/nph.16190.
Treseder, K.K., 2013. The extent of mycorrhizal colonization of roots and its influence on plant growth and phosphorus content. Plant Soil 371, 1–13. https://doi.org/10.1007/s11104-013-1681-5.
Turrini, A., Avio, L., Giovannetti, M., Agnolucci, M., 2018. Functional complementarity of arbuscular mycorrhizal fungi and associated microbiota: the challenge of translational research. Front. Plant Sci.
Wang, X.-X., Li, H., Chu, Q., Feng, G., Kuyper, T.W., Rengel, Z., 2020. Mycorrhizal impacts on root trait plasticity of six maize varieties along a phosphorus supply gradient. Plant Soil 448, 71–86. https://doi.org/10.1007/s11104-019-04396-0.
Wei, T., Simko, V., 2017. R package "corrplot": Visualization of a Correlation Matrix.
Wilson, G.W.T., Rice, C.W., Rillig, M.C., Springer, A., Hartnett, D.C., 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. Ecol. Lett. 12, 452–461. https://doi.org/10.1111/j.1461-0248.2009.01303.x.
Wright, S.F., Upadhyaya, A., 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Sci. 161, 575–586.
Wu, Q.-S., Cao, M.-Q., Zou, Y.-N., He, X., 2014. Direct and indirect effects of glomalin, mycorrhizal hyphae and roots on aggregate stability in rhizosphere of trifoliate orange. Sci. Rep. 4, 5823. https://doi.org/10.1038/srep05823.
Wu, Y., Deng, M., Huang, J., Yang, S., Guo, L., Yang, L., Ahirwal, J., Peng, Z., Liu, W., Liu, L., 2022. Global patterns in mycorrhizal mediation of soil carbon storage, stability, and nitrogen demand: A meta-analysis. Soil Biol. Biochem., 108578 https://doi.org/10.1016/j.soilbio.2022.108578.
Yao, Q., Gao, J.-L., Zhu, H.-H., Long, L.-K., Xing, Q.-X., Chen, J.-Z., 2010. Evaluation of the potential of trap plants to detect arbuscular mycorrhizal fungi using polymerase chain reaction-denaturing gradient gel electrophoresis analysis. Soil Sci. Plant Nutr. 56, 205–211. https://doi.org/10.1111/j.1747-0765.2010.00444.x.
Zhao, C., Zhang, H., Song, C., Zhu, J.-K., Shabala, S., 2020. Mechanisms of plant responses and adaptation to soil salinity. Innovation 1, 100017. https://doi.org/10.1016/j.xinn.2020.100017.