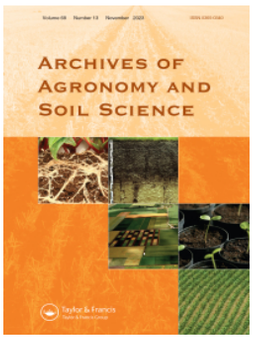

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Harnessing indigenous mycorrhizal symbiosis to boost sorghum productivity and phosphorus-use efficiency on contrasting Sudanese vertisols

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ABSTRACT

Sorghum productivity on vertisols is constrained by phosphate fixation, salinity, and nutrient limitations, undermining food security in semi-arid regions. We evaluated the impact of indigenous arbuscular mycorrhizal fungi (AMF) inoculation on growth, yield, and phosphorus (P) dynamics of four Sudanese sorghum cultivars across two vertisol sites: Abassyia (salinity – sodicity stress) and Medani (P deficiency). Field inoculation with indigenous AMF consortia (Rhizophagus, Glomus, Claroideoglomus, Funneliformis, Entrophospora, Scutellospora, and Acaulospora) improved sorghum performance, increasing biomass, panicle length, grain yield, root colonization, spore density, and phosphorus acquisition efficiency (PAE). Inoculated plants achieved colonization levels of 52–81% and spore densities up to 4894 spores per 100 g soil, with PAE increasing to 132 mg P plant^{-1}. Shoot P concentration and plant height were unaffected; no conclusion can be drawn regarding P allocation. Cultivar- and site-specific responses identified Tabat as the most productive cultivar (36.6 g grain yield plant^{-1}), while Tetron showed superior PAE. Multivariate analyses confirmed strong associations between AMF colonization, biomass, and yield, with clustering of inoculated and uninoculated plants. These findings provide robust field evidence that leveraging indigenous AMF biodiversity enhances P-use efficiency and sorghum productivity on vertisols, supporting sustainable biofertilization in low-input systems in sub-Saharan Africa under climate-stressed environments.

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Introduction

Vertisols occupy approximately 70 million hectares in Sudan, representing nearly 16% of the global vertisol area and making the country the third largest after India and Australia (Pal et al. 2012; Abdelhalim et al. 2021). These soils dominate the Central Clay Plain, which covers nearly 28% of Sudan's total area (Ayoub 2001). Despite their agricultural importance, vertisols present significant challenges, including strong phosphate fixation, high calcium carbonate content, and unfavorable physical properties that hinder water infiltration and root growth (Willcocks and Twomlow 1992). Consequently, phosphorus (P) deficiency remains a critical yield-limiting factor, particularly in staple crops such as sorghum.

Sorghum (*Sorghum bicolor* L. Moench), often referred to as the 'king of millets', is the most widely grown crop in Sudan, accounting for one-third of the cultivated land (Hossain et al. 2022). However, yields remain critically low (~0.4 t ha^{-1}) (FAOSTAT 2022), mainly due to nutrient depletion, recurrent droughts, reliance on unimproved landraces, and limited access to fertilizers. In addition, sorghum genotypes in Sudan exhibit substantial variation in their resistance to *Striga hermonthica*, a major parasitic weed that thrives in nutrient-poor vertisols and causes severe yield losses (Mohemed et al. 2018). Given that vertisols constitute the dominant production environment in the study region and are simultaneously characterized by low nutrient

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availability, strong P fixation, and high *Striga* pressure, there is an urgent need to develop strategies that sustainably enhance sorghum productivity in these challenging soils.

Arbuscular mycorrhizal fungi (AMF) are obligate symbionts belonging to the phylum Glomeromycota that colonize the roots of nearly 80% of land plants, facilitating mineral nutrient and water uptake in exchange for photosynthates (Meng et al. 2023). By extending the soil volume explored through external hyphae, AMF enhance access to immobile nutrients such as P, Fe, and Zn, thereby reducing the need for chemical fertilizers (Schüßler et al. 2001; Bello and Fabiyi 2024). Numerous studies have demonstrated the positive impact of AMF inoculation on plant growth, yield, and nutrient acquisition in a wide range of crops and environments. For instance, Ceballos et al. (2013) demonstrated that AMF significantly improved cassava yield under nutrient-limited conditions. Pellegrino et al. (2015) reported enhanced biomass and phosphorus (P) uptake in wheat at multiple field sites. Similarly, AMF inoculation has been shown to increase sunflower yield and oil content under low-input conditions (Arcidiacono et al. 2025), improve maize grain quality (Berta et al. 2014), and enhance nutrient-use efficiency in rice (Diedhiou et al. 2016). In addition, the syntheses highlight the ecological and functional diversity of AMF in agroecosystems (VAN Der Heijden et al. 2015). The effectiveness of AMF inoculation is strongly influenced by environmental conditions, with plant responses typically being greater under low nutrient availability (Johnson et al. 1997), a pattern confirmed by a global meta-analysis (Hoeksema et al. 2010). AMF responsiveness is also amplified under abiotic stress, including when pathogen pressure is initially high, before inoculation (Lutz et al. 2023). Furthermore, plants generally show superior growth and nutrient responses when inoculated with indigenous (sympatric) AMF communities compared to non-indigenous (allopatric) inocula (Johnson et al. 1955). Together, these studies highlight the broad agronomic value of AMF as a natural biofertilizer, particularly under low-input and nutrient-poor conditions in the tropics.

However, the effectiveness of AMF is not uniform across hosts or environments. This strongly depends on the genotype-specific responses of the plants. This principle has been demonstrated in diverse host species, where variations in root traits, exudates, and metabolic regulation influence colonization rates and yield benefits (Lekberg and Koide 2005; Turrini et al. 2018). Watts-Williams et al. (2022) and Kon et al. (2021) documented significant genotypic differences in the responsiveness of sorghum to AMF, suggesting that breeding for 'mycorrhizal responsiveness' could be a promising complementary strategy for genetic improvement under nutrient stress.

Despite these advances, studies on AMF – sorghum interactions under realistic field conditions remain scarce. Most existing research relies on pot experiments or sterilized substrates (Lendzemo et al. 2005; Cobb et al. 2018), which do not capture the complex soil-microbe interactions in farmers' fields. Given the low phosphate availability and high adsorption capacity of Sudanese vertisols (Yousif et al. 1988), and supported by recent evidence demonstrating that indigenous AMF adapted to local soil conditions can enhance plant performance across diverse cropping systems (John and Ray 2024; George and Ray 2025; Varghese and Ray 2025), a pressing need exists to evaluate whether indigenous AMF consortia, already adapted to local soil conditions, can enhance sorghum productivity under field environments.

Unlike most AMF studies, which rely on greenhouse conditions, sterilized substrates, or non-indigenous AMF isolates, this study provides one of the first field-based evaluations of indigenous AMF consortia under real-world vertisol constraints. By evaluating AMF performance across contrasting vertisols environments (salinity – sodicity vs. strong P-fixation) and integrating cultivar-specific responsiveness, our study generates new mechanistic and agronomic insights into AMF functioning in heavy clay soils. Such systems are overlooked in global AMF research, making this combination of field realism, sympatric inoculum, and genotype-specific responses a distinctive scientific and technical contribution.

Building on this knowledge gap, the present study evaluated the impact of indigenous AMF inoculation on the growth, yield, and P acquisition of four sorghum cultivars with contrasting agronomic and *Striga*-resistance backgrounds across two contrasting Vertisol environments (Abassyia and Medani, Sudan). By integrating field experimentation with physiological and symbiotic measurements, our objectives were to (i) determine the extent to which AMF improve sorghum performance under salinity – sodicity versus P-deficiency stress, (ii) assess cultivar-specific responsiveness to AMF, and (iii) evaluate the potential of indigenous AMF as a sustainable biofertilizer strategy for vertisol-dominated farming systems in Sudan.

Materials and methods

Study sites

Field experiments were conducted during the 2022–2023 primary growing season on vertisols at two Agricultural Research Corporation (ARC) research stations in Sudan: White Nile (Abassyia) and Gezira (Medani). Both sites are characterized by alkaline heavy clay soils with strong phosphate fixation; however, they differ in their chemical and physical properties (Abdelhalim et al. 2022; Elsafy et al. 2025). Abassyia soils exhibited higher salinity and sodicity, with an electrical conductivity (EC) of 2.8 dS m^{-1}, an exchangeable sodium percentage (ESP) of 11.7%, a sodium adsorption ratio (SAR) of 10.7%, and a sodium (Na^+) concentration of 18 meq L^{-1}. In contrast, Medani soils contained more organic carbon (1.06% vs. 0.50% in Abassyia) but less available phosphorus (1.4 mg kg^{-1} vs. 4.0 mg kg^{-1}). Textural differences were also evident, with Abassyia soils having more silt (41.3% vs. 23%) and less clay (52% vs. 61%), resulting in higher water infiltration (2.07 vs. 0.59 cm h^{-1}). These contrasting edaphic conditions enabled the evaluation of AMF performance under salinity-sodicity stress (Abassyia) and phosphorus deficiency (Medani).

Plant materials and AMF inoculum preparation

This study used four sorghum cultivars: Hakika, P954063, Tabat, and Tetron. Hakika and Tetron are widely cultivated in the rain-fed areas of the Central Clay Plain in Al-Gadareif State and are well known for their *resistance to Striga* (Cobb et al. 2018). P954063 is a Zera Zera-type sorghum with a low tannin content that is valued for its high grain quality and productivity in irrigated areas. Tabat is a widely grown white-seeded cultivar that thrives under irrigation. These cultivars were chosen to represent contrasting agronomic backgrounds and traits.

The AMF inoculum was prepared from indigenous AMF species collected from sorghum fields at the Gezira Research Station in January 2019. Gezira is located 190 km from the Abassyia site. The Gezira and Medani sites share highly similar vertisol characteristics because of their location within the central clay plain, whereas Abassyia represents a slightly more saline-sodic variant of vertisols. Spores were extracted using the wet sieving and decanting method described by Gerdemann and Nicolson (1963), and then multiplied in a greenhouse using Sudan grass (*Sorghum vulgare* Pers.) as the host plant. Pots with a 20 L capacity were filled with a sterilized sand – clay mixture (2:1 v/v) and maintained under controlled conditions for six months. At harvest, root fragments were chopped and mixed with the substrate to create a uniform inoculum of spores, hyphae, and colonized root segments. The inoculum was air-dried and stored in sealed bags for subsequent field application. The soils at the inoculum collection site (Gezira Research Station) were classified as typical vertisols with clay content > 55%, high exchangeable Ca^{2+}, moderate salinity (EC 1.6–2.3 dS m^{-1}), alkaline pH (7.8–8.3), and low available P (< 6 mg kg^{-1}), consistent with previously published characterizations (Elsafy et al. 2025). Morphological identification confirmed the presence of seven genera (*Rhizophagus, Glomus, Claroideoglomus, Funneliformis, Entrophospora, Scutellospora*, and *Acaulospora)*.

Experimental setup

A split-plot design with three replicates was used to create 24 plots. The main plots consisted of inoculation treatments, with AMF-inoculated (M^+) and non-inoculated (M^-) controls, whereas the subplots consisted of four sorghum cultivars. Each subplot measured 4 × 3.6 m. At sowing, because only spore abundance was quantified, 20 g of sand-based inoculum containing approximately 40 spores g^{-1} (≈800 spores per planting hole) was applied directly to the planting holes of the inoculated treatments. Sorghum seeds were sown manually at an inter-row spacing of 0.8 m and an intra-row spacing of 0.2 m, and later thinned to two seedlings per hole to maintain a uniform density. Irrigation was applied immediately after sowing and continued biweekly until the heading stage. To mimic farmer practices, irrigation was withheld for three weeks before harvest to facilitate the maturation of grains. Weeds were controlled manually by hoeing. Nitrogen fertilizer was applied at a rate of 43 kg N ha^{-1} as urea (46% N), broadcast evenly over the soil surface 28 days after sowing (DAS).

Measurements

At physiological maturity, sorghum panicles and aboveground biomass were used to assess the yield and plant performance. Panicles were manually threshed to determine grain yield, and fresh biomass samples were collected by cutting sorghum plants 5 cm above the soil surface for further analysis. To minimize edge effects, data on growth parameters, AMF colonization, and phosphorus uptake were recorded from two central rows within each plot. All measurements were taken from 10 randomly selected plants per subplot across three replicates to ensure reproducibility, following the standardized agronomic sampling procedures described by Gomez and Gomez (1984). Several yield-related traits were measured, including plant height, leaf number, leaf area, chlorophyll concentration, panicle length, panicle width, 1000-kernel weight, grain yield, and straw dry weight (D.W.).

The leaf number was counted manually for each selected plant using sorghum phenotyping guidelines (Reddy et al. 2004). The leaf area per plant was estimated using the standard length – width method, in which the length (L) and maximum width (W) of the uppermost fully expanded leaf were measured using a measuring tape. The product of these two values was then multiplied by 0.75, a correction factor widely used for sorghum leaf area estimation and initially validated by VAN Arkel (1978), to obtain the final leaf area estimate. Chlorophyll concentration was assessed using a SPAD-502 Plus chlorophyll meter (Uddling et al. 2007), and three readings from the middle portion of the youngest fully expanded leaf were averaged to obtain a single measurement.

Plant height was measured from the soil surface to the tip of the panicle, following established sorghum measurement procedures (Reddy et al. 2004). Shoot dry weight was determined by oven-drying the harvested aboveground biomass at 70°C for 72 hours and weighing the samples using a precision balance. Panicle length and width were measured using a measuring tape, grain yield per plant was obtained by threshing and weighing grains from each panicle, and 1000-kernel weight (TKW) was calculated by weighing 250 grains and multiplying the result by four. Straw dry weight (D.W.) was obtained from the dried biomass following the same drying protocol described above, and the harvest index (HI) was computed as the ratio of grain yield to total aboveground biomass, following Kemanian et al. (2007).

The phosphorus content in the shoots was analyzed using the vanadate/molybdate yellow method, as described by Olsen (1982).

To evaluate the effect of AMF inoculation on plant performance, the mycorrhizal inoculation effect (MIE) was calculated for each parameter and cultivar at both locations. MIE was determined using the following formula: MIE = (mean of inoculated – mean of non-infected plants)/mean of inoculated (Diedhiou et al. 2016). The values ranged from −1 to 1, with positive MIE values indicating the net benefit of AMF inoculation. In contrast, negative MIE values suggest that the cost of the AMF outweighs its benefits.

Staining and estimation of AMF root colonization

Fine root segments (~1.5 g) were randomly selected, cut into 10-mm sections, and cleared with 10% KOH (w/v) overnight at room temperature, followed by acidification with 10% HCl for 5 min. Roots were stained with Schaffer ink-vinegar solution (5 mL of Schaffer blue ink in 95 mL of vinegar containing 7% acetic acid), following the method described by Vierheilig et al. (1998). After rinsing with acidified tap water, AMF colonization was quantified under a dissecting microscope (40×) using the grid-line intersection method (Giovannetti and Mosse (1980).

Extraction and estimation of AMF spores

AMF spores were extracted and quantified using wet sieving and decanting (Gerdemann and Nicolson (1963). Briefly, 100 g of sieved soil was suspended in 1.5 L of water, stirred vigorously, and passed sequentially through sieves of 250, 180, 63, and 45 µm. This process was repeated three times as technical replicates. Spores were counted using the International Culture Collection of Vascular Arbuscular Mycorrhizal Fungi (INVAM) protocol (https://invam.wvu.edu/methods/spores). Morphological taxonomy of spores was performed following Pérez and Schenck (1990), and the most frequently occurring genera were *Glomus*, *Acaulospora*, and *Rhizophagus*, which constituted the dominant proportion of the identified AMF community.

Table 1. Plant growth attributes of four sorghum cultivars inoculated with (M^+) and without (M^-) arbuscular mycorrhizal fungi (AMF) across two vertisol locations (Abassyia and Medani).

Cultivars	Plant height (cm)	No. Leaves (n plant^{-1})	Leaf area (cm^2 plant^1)	SPAD Chlorophyll	Shoot dry weight (g^{-1})
Hakika	136.7C	11.0C	693.8B	53.7B	221.7B
P954063	163.4B	11.8BC	806.9A	59.3A	336.7A
Tabat	148.3C	12.6AB	686.8B	53.6B	224.2B
Tetron	298.6A	13.4A	588.6C	49.4C	380.8A
Mycorrhiza					
AMF-	188.5A	11.3B	576.6B	49.5B	226.9B
AMF+	185.0A	13.1A	811.4A	58.5A	354.8A
Locations					
Abassyia	196.2A	12.8A	690.8A	56.5A	332.5A
Medani	177.3B	11.6B	697.2A	51.5B	249.2B
Three-Way ANOVA					
Cultivars, C	577.5***	18.5***	29.8***	24.0***	31.5***
Mycorrhiza, M	1.2^{NS}	59.6***	206.1***	119.4***	79.6***
Locations, L	36.4***	28.3***	0.2 ^{NS}	35.3***	33.8***
C*M	1.4 ^{NS}	1.2 ^{NS}	8.6***	1.5 ^{NS}	13.1***
C*L	20.7***	9.5***	3.0*	21.0***	0.1 ^{NS}
M*L	6.0*	0.0 ^{NS}	1.2 ^{NS}	0.4 ^{NS}	0.2 ^{NS}
C*M*L	0.4 ^{NS}	1.2 ^{NS}	2.8 ^{NS}	5.1**	0.0 ^{NS}

Measured traits include plant height (cm), number of leaves per plant (No. leaves, n plant −1), leaf area (cm2 plant −1), SPAD chlorophyll content, and shoot dry weight (g plant −1). Values followed by different letters within each column indicate significant differences according to Tukey's HSD test (p < 0.05). Results of three-way ANOVA are presented for the main effects of cultivar (C), mycorrhiza (M), and location (L), as well as their interactions. ***p < 0.001; **p < 0.01; *p < 0.05; NS = not significant. Means followed by different letters within the same column indicate significant differences according to Tukey's HSD test (p < 0.05).

Statistical analysis

Data were tested for normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests ($p < 0.05$). The effects of sorghum cultivar, AMF inoculation, location, and their interactions were analyzed using a three-way ANOVA in XLSTAT software. AMF colonization and spore density percentages were root-transformed before analysis. Treatments showing significant differences were compared using Tukey's honest significant difference (HSD) post-hoc test. Multivariate analysis was conducted using HJ-Biplot PCA, as described by Vidal et al. (2020). Principal coordinate analysis (PCoA) and partial least squares regression (PLSR) were performed as described by Tenenhaus et al. (2005). Correlation plots and heatmaps were generated using the software.

Table 2. Yield attributes of four sorghum cultivars inoculated with (M^+) and without (M^-) arbuscular mycorrhizal fungi (AMF) at two research stations (White Nile/Abassyia and Gezira/Medani).

Cultivars	Panicle width (cm)	Panicle length (cm)	Grain yield/plant (g)	wt 1000 seed (g)	Harvest index (HI%)
Hakika	16.1A	31.3B	24.4B	40.3B	11.1B
P954063	17.2A	36.1A	28.2AB	39.0C	9.4BC
Tabat	17.0A	32.9B	33.6A	44.4A	14.8A
Tetron	16.8A	37.8A	26.8B	35.1D	7.2C
Mycorrhiza					
AMF-	16.1B	32.6B	26.1B	38.4B	9.4B
AMF+	17.5A	36.4A	30.4A	40.9A	11.8A
Locations					
Abassyia	18.0A	35.9A	38.2A	42.3A	12.5A
Medani	15.6B	33.2B	18.3B	37.0B	8.7B
Three-Way ANOVA					
Cultivars, C	2.5 ^{NS}	25.5***	5.4**	200.3***	13.1***
Mycorrhiza, M	19.2***	41.6***	6.5*	86.6***	7.0*
Locations, L	60.0***	21.8***	141.3***	378.8***	18.6***
C*M	3.3*	12.3***	2.6 ^{NS}	1.2 ^{NS}	3.1*
C*L	0.6 ^{NS}	31.5***	1.3 ^{NS}	17.0***	0.7 ^{NS}
M*L	2.1 ^{NS}	0.3 ^{NS}	0.8 ^{NS}	4.3*	0.7 ^{NS}
C*M*L	1.6 ^{NS}	4.4*	0.6 ^{NS}	3.2*	0.2 ^{NS}

Measured traits include panicle width (cm), panicle length (cm), grain yield per plant (g), thousand-kernel weight (g), and harvest index (HI, %). Values followed by different letters within each column indicate significant differences according to Tukey's HSD test (P < 0.05). Results of three-way ANOVA are shown for the main effects of cultivar (C), mycorrhiza (M), and location (L), as well as their interactions. ***p < 0.001; **p < 0.01; *p < 0.05; NS = not significant. Means followed by different letters within the same column indicate significant differences according to Tukey's HSD test (p < 0.05).

Results

Sorghum growth attributes

Significant variations were observed among sorghum cultivars, AMF inoculation treatments, and locations for most of the growth traits (Table 1). AMF inoculation significantly increased leaf number, leaf area, chlorophyll content (as measured by SPAD), and shoot dry weight but had no significant effect on plant height. The location effects were also pronounced, with plants grown in Abassyia generally being taller, with more leaves, higher chlorophyll content, and greater shoot biomass than those grown in Medani. Among the cultivars, Tetron exhibited the tallest plants and highest shoot dry weight, whereas P954063 exhibited the largest leaf area and highest chlorophyll content. Hakika consistently recorded the lowest values for most growth traits. Significant cultivar × AMF interactions were observed for leaf area and shoot dry weight, whereas cultivar × location interactions influenced nearly all traits, except for shoot dry weight.

Yield attributes

AMF inoculation significantly enhanced the yield components, including panicle length, grain yield, thousand-kernel weight, and harvest index (Table 2). Inoculated plants produced longer panicles, heavier

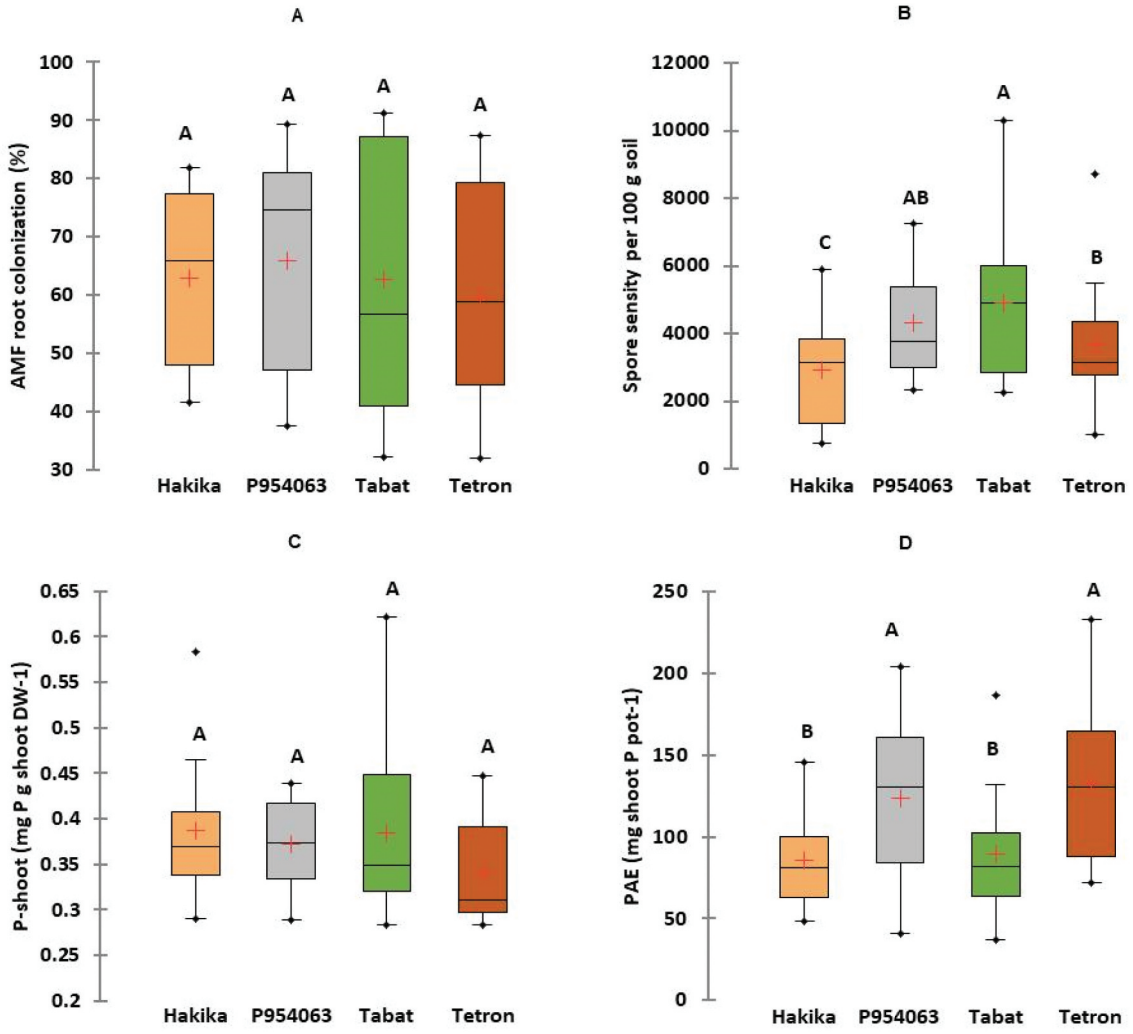

Figure 1. Boxplots showing the effects of sorghum cultivars on (A) AMF root colonization (%), (B) spore density (number of spores per 100 g soil), (C) shoot phosphorus content (mg P g^{-1} shoot dry weight, DW), and (D) phosphorus acquisition efficiency (PAE; mg shoot P $plant^{-1}$). Different letters above the boxplots indicate significant differences among the cultivars according to Tukey's HSD test ($p < 0.05$). Red crosses represent the mean values; box boundaries denote the interquartile range; whiskers indicate the minimum and maximum values.

grains, and higher grain yields per plant than uninoculated controls. Location effects were also substantial; plants at Abassyia outperformed those at Medani in all measured yield parameters. Cultivar differences were evident, with Tabat recording the highest grain yield per plant (36.6 g), thousand-kernel weight (44.4 g), and harvest index (14.8). In contrast, Tetron produced the longest panicles but the lowest thousand-kernel weight. Significant cultivar × AMF interactions were detected for panicle width, panicle length, and harvest index, whereas cultivar × location interactions influenced panicle length and grain weight.

AMF colonization, spore density, and phosphorus-related traits

Successful AMF colonization was confirmed in the inoculated plants, with colonization rates ranging from 52% to 81% (Figures 1A, 2A, and 3A). Inoculation markedly increased root colonization (Figure 2A), spore density (Figure 1B–3B), and phosphorus acquisition efficiency (PAE) (Figure 1D–3D), but did not alter shoot phosphorus content (Figure 1C–3C). Location effects were also significant, with Abassyia soils supporting higher spore densities (Figure 3B), whereas Medani soils promoted higher root colonization (Figure 3A). Cultivar differences were evident, with Tabat showing

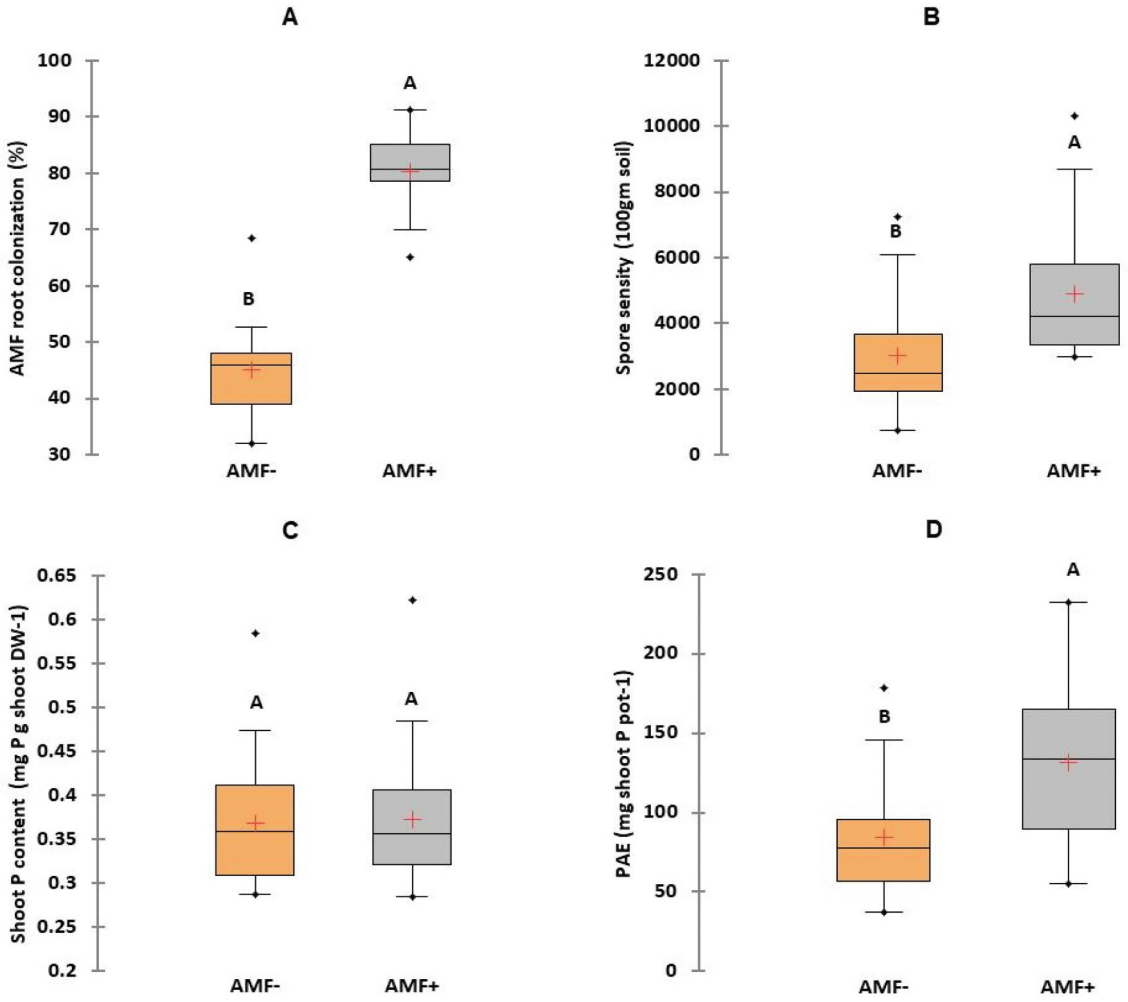

Figure 2. Boxplots showing the effects of field inoculation with AMF on (A) AMF root colonization (%), (B) spore density (number of spores per 100 g soil), (C) shoot phosphorus content (mg P g^{-1} shoot dry weight, DW), and (D) phosphorus acquisition efficiency (PAE; mg shoot P $plant^{-1}$). The treatments included non-inoculated (AMF^{-}) and inoculated (AMF^{+}). Different letters above the boxplots indicate significant differences, as determined by Tukey's HSD test ($p < 0.05$). Red crosses denote mean values, boxes represent the interquartile range, and whiskers indicate the minimum and maximum values.

the highest spore density (4,894 spores/100 g soil; Figure 1B) and Tetron exhibiting the highest PAE (132 mg shoot P/plant; Figure 1D). A significant cultivar × AMF interaction was observed for PAE (Figure 4A), and a substantial cultivar × location interaction was observed for spore density (Figure 4B).

Multivariate analyses

Principal component analysis (PCA) revealed that the first two components explained 69.8% of the variation in traits (Figure 5). Growth traits, including leaf number, chlorophyll content, shoot dry weight, panicle traits, root colonization, spore density, and PAE, clustered strongly with AMF-inoculated treatments along the positive F1 axis. In contrast, uninoculated plants were positioned on the negative side of the biplot, reflecting reduced values for most traits. Partial least squares regression (PLSR) confirmed strong positive associations between shoot biomass, PAE, panicle traits, and grain yield (Figure 6). In contrast, plant height and thousand-kernel weight contributed less to the overall variation in yield. Principal coordinate analysis (PCoA) further highlighted the separation of inoculated (M^+) and uninoculated (M^-) plants, with cultivar-specific clustering indicating a differential responsiveness to AMF (Figure 7).

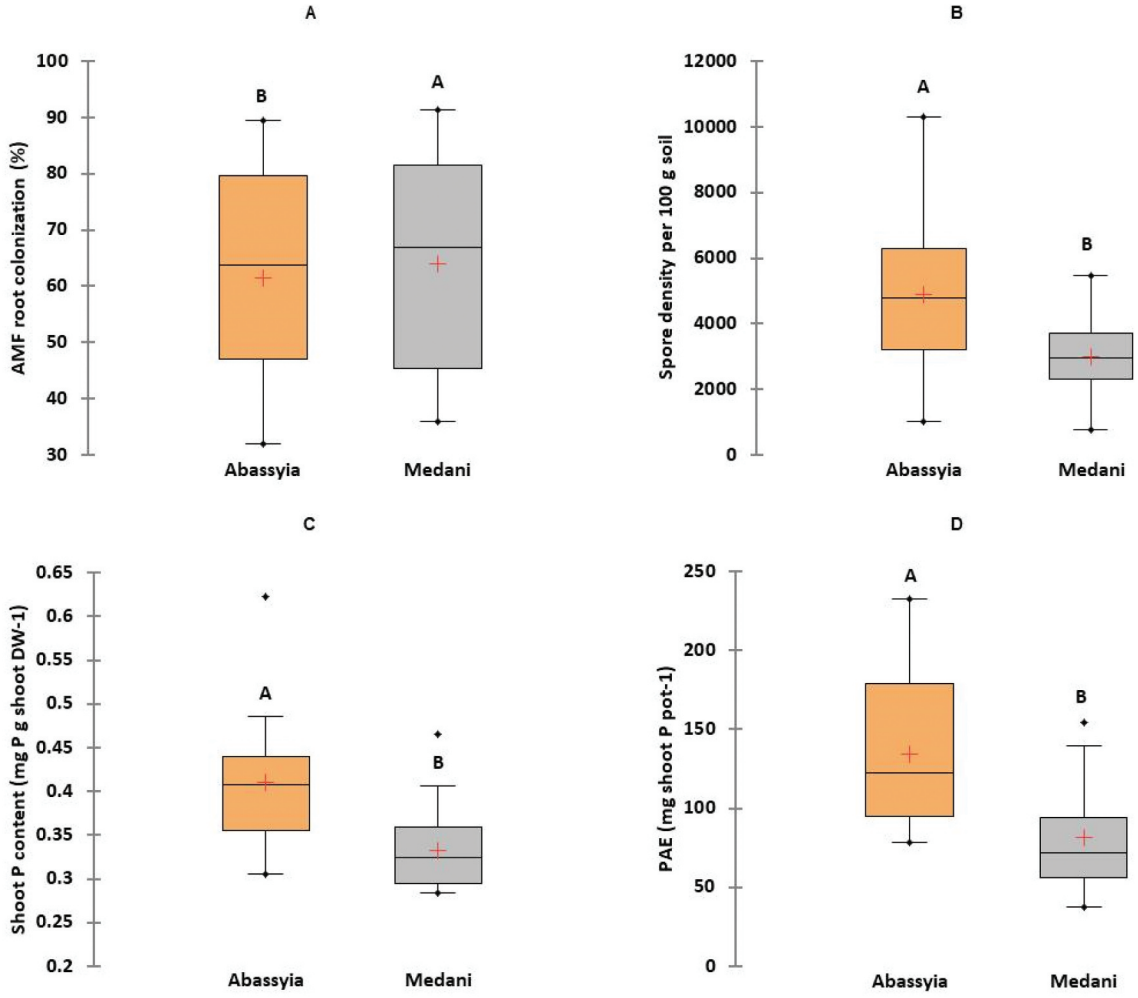

Figure 3. Boxplots showing the effects of location-specific on (A) arbuscular mycorrhizal fungi (AMF) root colonization (%), (B) spore density (number of spores per 100 g soil), (C) shoot phosphorus content (mg P g^{-1} shoot dry weight, DW), and (D) phosphorus acquisition efficiency (PAE; mg shoot P $plant^{-1}$). The locations represent Abassyia (salinity – sodicity stress) and Medani (phosphorus-deficient soils). Different letters above the boxplots indicate significant differences between sites, as determined by Tukey's HSD test ($p < 0.05$). Red crosses denote mean values; boxes represent the interquartile range; whiskers indicate minimum and maximum values.

Mycorrhizal inoculation effect (MIE)

The heatmap of MIE values (Figure 8) illustrated the consistent positive effects of AMF inoculation on shoot dry weight, PAE, root colonization, and spore density across all cultivars and locations. Grain yield also increased markedly in Tabat at both sites and in Tetron at Medani. In contrast, plant height, panicle width, and thousand-kernel weight were either negatively or weakly affected by the inoculation.

Correlations among traits

Correlation analysis (Figure 9) demonstrated strong positive relationships between AMF colonization and leaf area ($R^2 = 0.78$), chlorophyll content ($R^2 = 0.68$), and leaf number ($R^2 = 0.52$). Spore density was positively correlated with panicle traits, grain yield, and thousand-kernel weight ($R^2 = 0.55–0.72$). PAE showed the strongest correlations with shoot dry weight ($R^2 = 0.93$), total biomass ($R^2 = 0.93$), grain yield ($R^2 = 0.64$), and panicle width ($R^2 = 0.82$), confirming its central role in determining plant productivity. Notably, shoot phosphorus content correlated with yield-related traits but did not differ significantly between the inoculated and uninoculated treatments, indicating that AMF effects were primarily mediated through enhanced PAE rather than an increase in shoot P concentration.

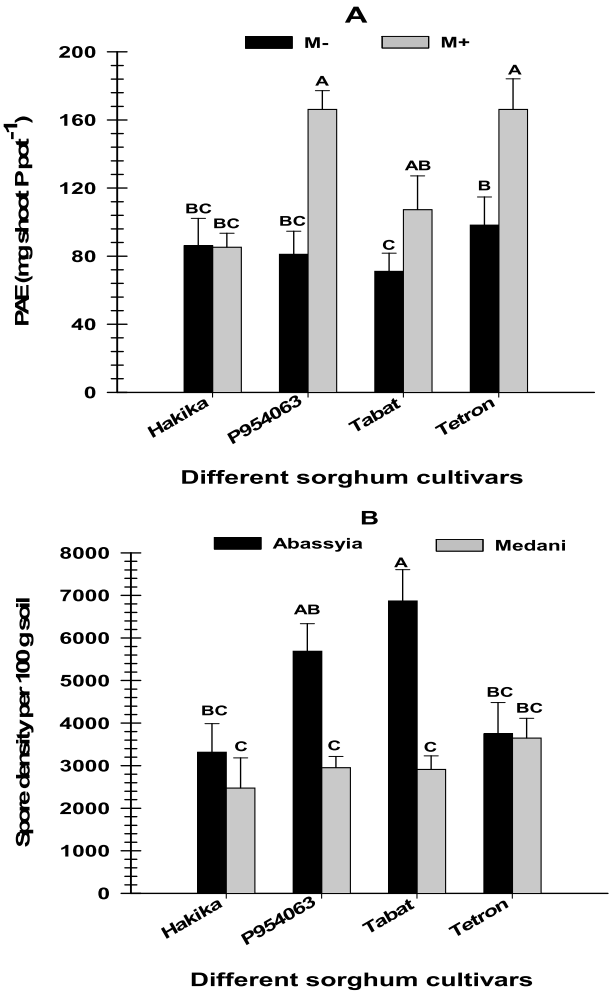

Figure 4. Two-way ANOVA interactions showing (A) the effects of sorghum cultivars and AMF inoculation (M^- = non-inoculated, M^+ = inoculated) on phosphorus acquisition efficiency (PAE; mg shoot P plant^{-1}), and (B) the effects of sorghum cultivars and experimental locations (Abassyia = salinity – sodicity stress; Medani = phosphorus-deficient soils) on spore density (number of spores per 100 g soil). Different letters above the bars indicate significant differences among treatments, as determined by Tukey's HSD test ($p < 0.05$). Error bars represent the standard error of the mean (±SE).

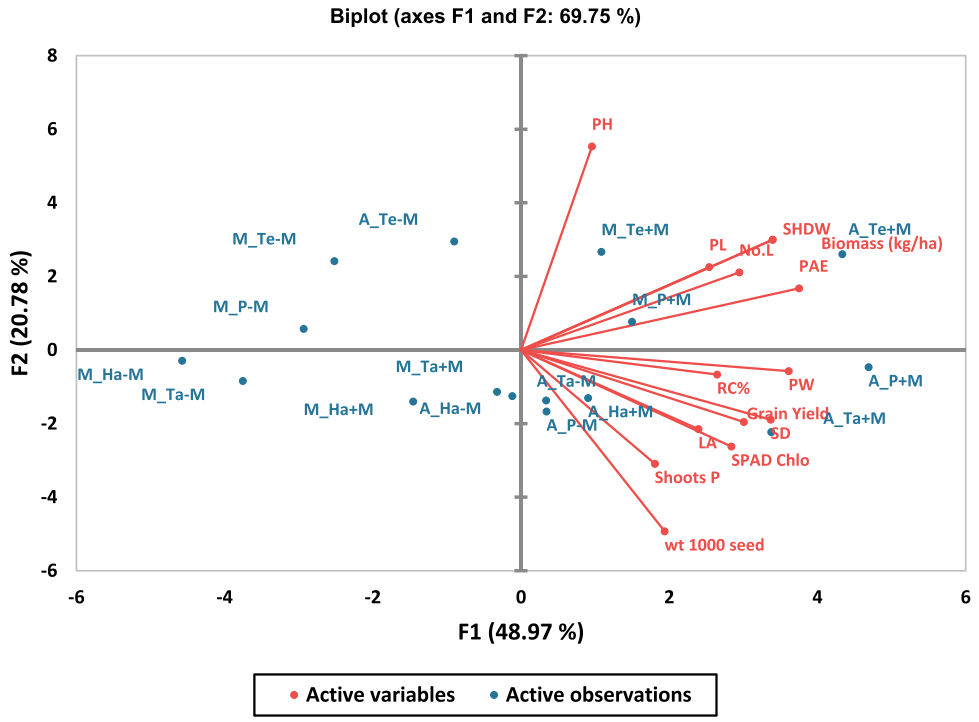

Figure 5. Principal component analysis (PCA) biplot of sorghum performance traits across four cultivars grown with (+M) and without (−M) AMF inoculation at Abassyia and Medani. The parameters included plant height (PH), number of leaves (No. L), leaf area (LA), aboveground biomass (kg ha^{-1}), SPAD chlorophyll content (SPAD Chlo), shoot dry weight (SHDW), panicle length (PL), panicle width (PW), thousand-kernel weight (wt 1000 seeds), grain yield, AMF root colonization (RC%), spore density (SD; number of spores per 100 g soil), shoot phosphorus content (shoot P; mg g^{-1} shoot DW), and phosphorus acquisition efficiency (PAE; mg shoot P $plant^{-1}$). The red vectors indicate trait loadings, and the blue points represent cultivar – treatment – location combinations.

Discussion

This study provides field-based evidence that indigenous AMF inoculation enhances sorghum growth, yield, and phosphorus acquisition efficiency (PAE) in Sudanese vertisols. While the positive effects of AMF on crops are well documented, most reports rely on pot trials or on sterilized substrates (Pellegrino et al. 2015; Peng et al. 2024), making the results of the present field study particularly valuable for practical applications in low-input agriculture.

AMF inoculation significantly improved leaf area, chlorophyll content, shoot dry weight, and yield components but did not affect plant height. Similar findings have been reported in other cereals, where biomass and chlorophyll content respond more strongly to AMF than to vertical growth (Akbar et al. 2024; Arcidiacono et al. 2025). Therefore, the lack of height response in sorghum is consistent with field evidence from sunflowers and maize, where AMF altered root and physiological traits without significantly affecting stem elongation (Berta et al. 2014; Arcidiacono et al. 2025). Rather than reflecting carbon 'drainage' to the fungus, as sometimes hypothesized (Campos et al. 2018) this response most likely results from genotype- and organ-specific allocation dynamics, wherein assimilates are preferentially allocated to photosynthetic tissues and reproductive sinks.

Yield improvements in inoculated sorghum are consistent with meta-analyses and field studies in wheat, maize, sunflower, cassava, and rice, all of which reported substantial AMF-mediated increases in biomass and grain production (Ceballos et al. 2013; Pellegrino et al. 2015; Diedhiou et al. 2016; Zhang et al. 2020; Marrassini et al. 2024; Arcidiacono et al. 2025). Notably, Tabat and Tetron displayed strong yield responses to AMF, confirming that cultivar × AMF interactions are critical determinants of sorghum productivity. Genotype-specific responsiveness is well established in cereals and legumes (Lekberg and Koide 2005; Turrini et al. 2018), and our results reinforce the need to consider mycorrhizal efficiency as a target trait in crop improvement and breeding programs (Kon et al. 2021; Watts-Williams et al. 2022).

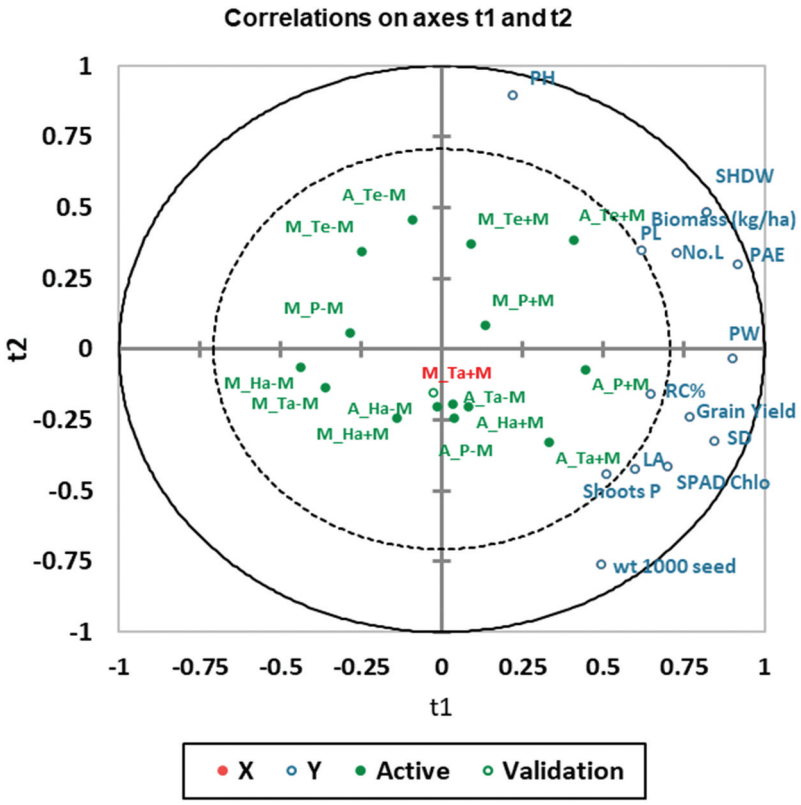

Figure 6. Partial least squares regression (PLSR) correlation plot showing associations between sorghum growth, yield, and mycorrhizal traits across four sorghum cultivars grown with (+M) and without (−M) **AMF** inoculation at two contrasting vertisol locations (Abassyia and Medani, Sudan). The traits included plant height (PH), number of leaves (No. L), leaf area (LA), aboveground biomass (kg ha^{-1}), SPAD chlorophyll content (SPAD chlo), shoot dry weight (SHDW), panicle length (PL), panicle width (PW), thousand-kernel weight (wt 1000 seeds), grain yield, AMF root colonization (RC%), spore density (SD; number of spores per 100 g soil), shoot phosphorus content (shoot P; mg g^{-1} DW), and phosphorus acquisition efficiency (PAE; mg shoot P $plant^{1}$).

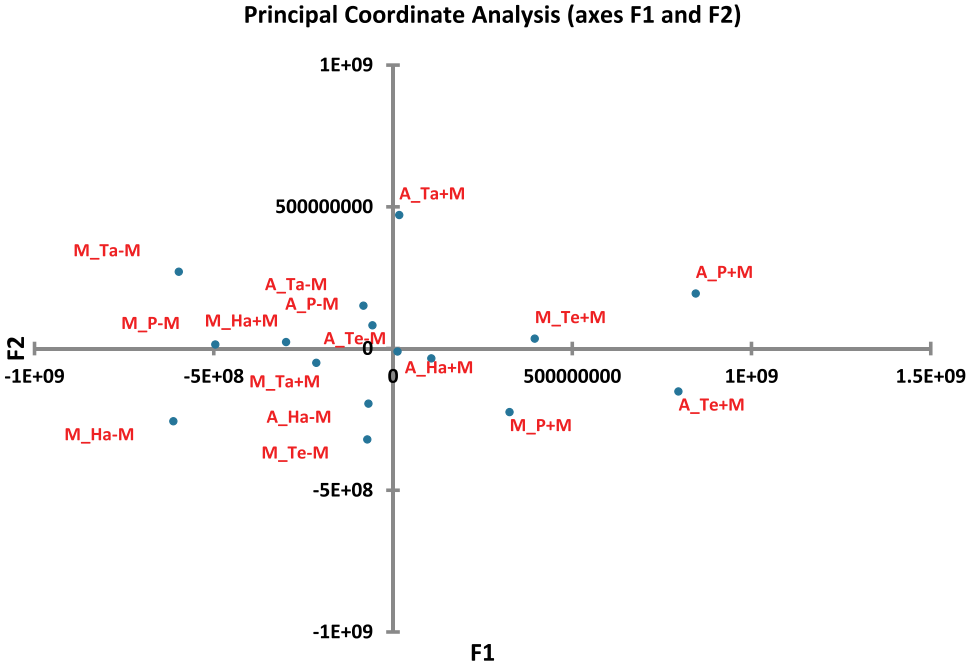

Figure 7. Principal coordinate analysis (PCoA) biplot illustrating the separation of sorghum cultivars under **AMF** inoculation (+M) and non-inoculated controls (−M) across two vertisol locations (Abassyia and Medani, Sudan). Cultivars included Tabat (ta), Tetron (te), P954063 (P), and Hakika (Ha).

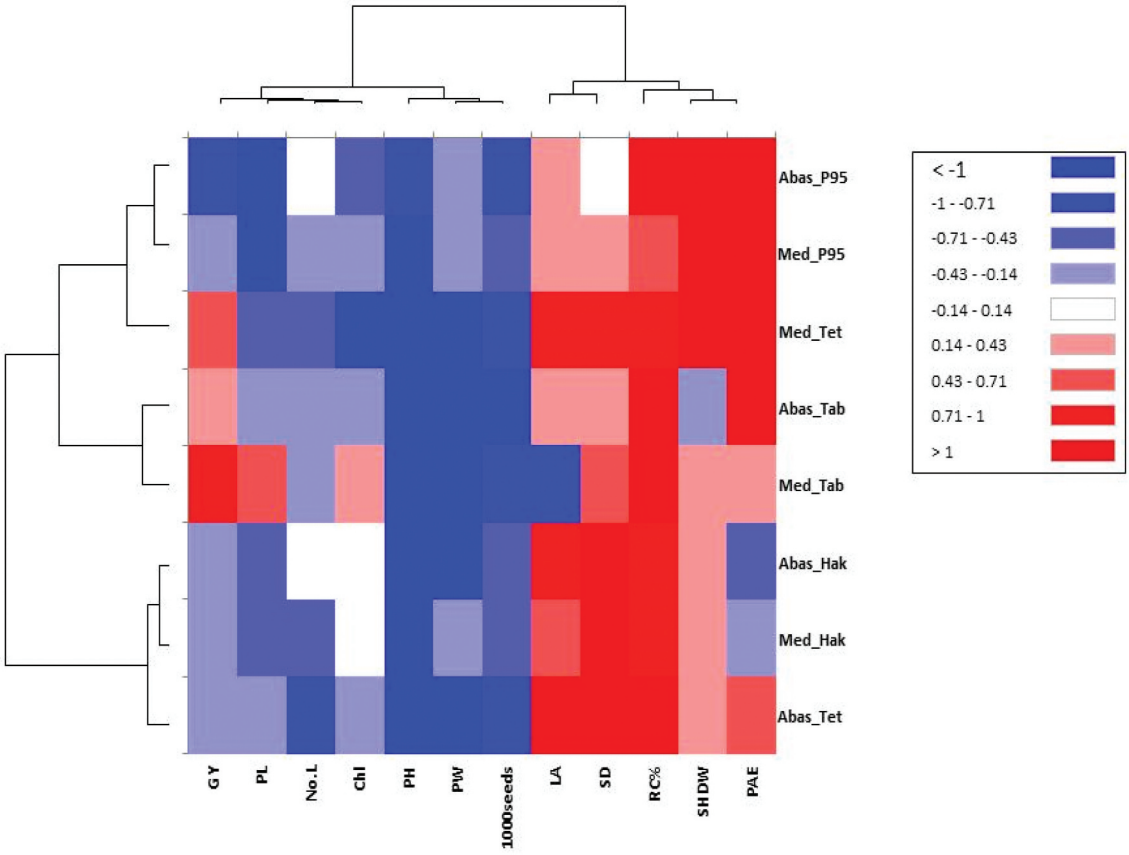

Figure 8. Heatmap of the mycorrhizal inoculation effect (MIE) on growth, yield, and symbiotic traits of four sorghum cultivars grown at two vertisol locations. Locations are abbreviated as Abas = Abassyia and med = Medani, respectively. The traits included grain yield (GY), panicle length (PL), number of leaves (No. L), chlorophyll content (chl), plant height (PH), panicle width (PW), thousand-kernel weight (1000 seeds), leaf area (LA), spore density (SD; spores per 100 g soil), AMF root colonization (RC%), shoot dry weight (SHDW), and phosphorus acquisition efficiency (PAE). The color scale represents the correlation strength, ranging from strong negative (blue) to strong positive (red).

Inoculation consistently increased root colonization, spore density, and PAE but not shoot P. This indicates that additional P uptake facilitated by AMF was allocated to shoot P concentration. A similar decoupling of total uptake from tissue concentration has been reported in sunflowers (Arcidiacono et al. 2025), wheat (Pellegrino et al. 2015) and maize (Berta et al. 2014). From a physiological perspective, AMF extend the root exploration zone through hyphal networks, enhancing PAE (Schnepf et al. 2008; Smith and Read 2010), but the partitioning of absorbed P depends on the plant developmental stage and sink demand. Thus, increases in grain yield without changes in shoot P concentration are consistent with preferential allocation of P to reproductive sinks.

The contrasting responses between Abassyia and Medani highlight the strong influence of soil properties on AMF effectiveness. Higher salinity and sodicity in Abassyia favored spore production but limited root colonization, likely reflecting the stress-induced reproductive strategy of AMF under saline conditions (Séry et al. 2016). Conversely, higher organic matter and clay content at Medani supported more extensive colonization, in agreement with reports that soil fertility and texture shape AMF establishment (Lekberg and Koide 2005; Rodriguez and Sanders 2015). These findings emphasize that AMF inoculation strategies must be tailored to specific soil conditions.

Correlation and multivariate analyses further demonstrated that PAE, shoot biomass, and panicle traits were the strongest predictors of sorghum yield. These associations mirror observations in wheat (Marrassini et al. 2024), rice (Diedhiou et al. 2016), and maize (Zhang et al. 2020), where AMF-driven improvements in P efficiency are directly translated into yield gains. Together, these findings suggest that PAE may serve as a robust proxy for selecting AMF-responsive sorghum genotypes under field conditions.

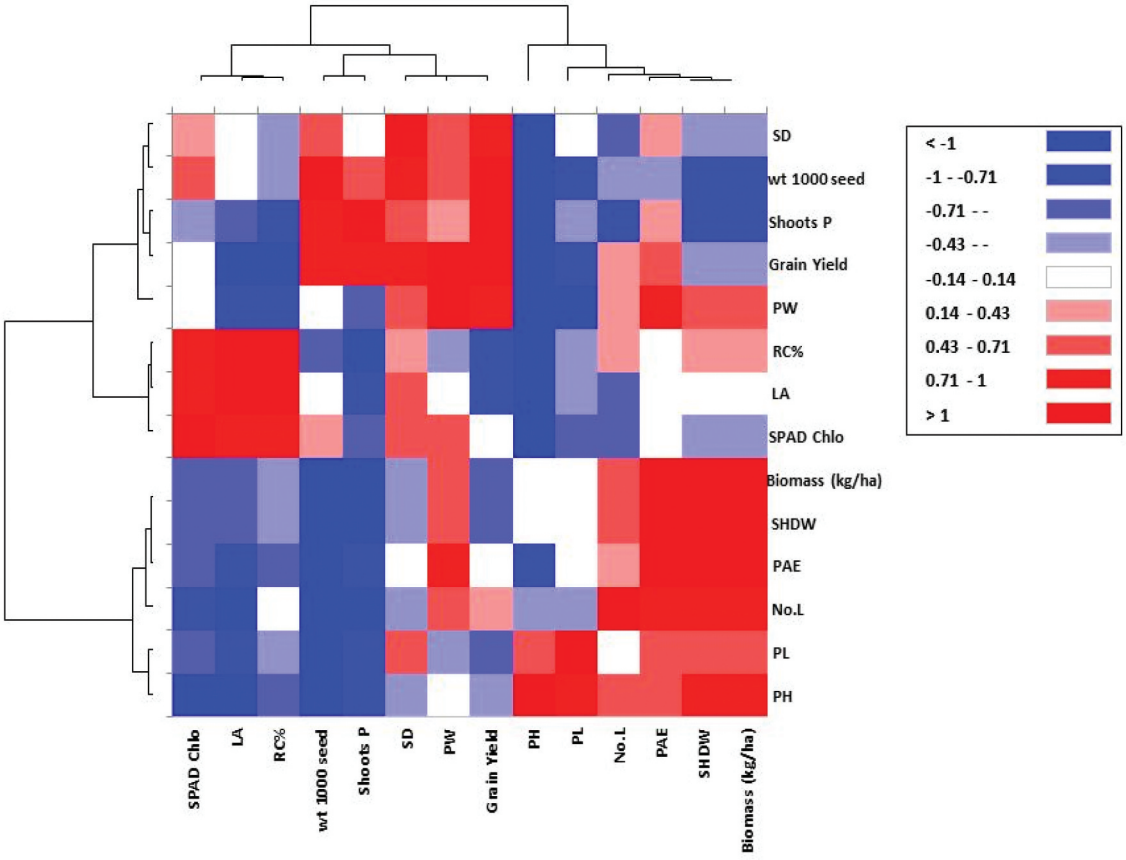

Figure 9. Correlation heatmap illustrating the relationships among sorghum growth, yield, and mycorrhizal traits. The traits included plant height (PH), number of leaves (No. L), leaf area (LA), aboveground biomass (kg ha^{-1}), SPAD chlorophyll content (SPAD Chlo), shoot dry weight (SHDW), panicle length (PL), panicle width (PW), thousand-kernel weight (wt 1000 seeds), grain yield, AMF root colonization (RC%), spore density (SD; spores per 100 g soil), shoot phosphorus content (shoot P; mg g^{-1} DW), and phosphorus acquisition efficiency (PAE; mg shoot P $plant^{-1}$). The color gradient represents the strength of the correlations, ranging from strong negative (blue) to strong positive (red).

Our study confirmed that indigenous AMF consortia can improve sorghum performance in vertisol-based systems under real field conditions. By demonstrating clear benefits for yield and PAE while highlighting genotype- and soil-specific responses, our findings provide evidence for the potential of *indigenous*, sympatric AMF rather than commercial inoculants, whose effectiveness is increasingly questioned in global assessments (Boussageon et al. 2025). However, limitations remain: only P-related traits were measured, and other nutrients such as N, Fe, and Zn should be assessed in future studies (Delavaux et al. 2017; Marro et al. 2022). Moreover, given the documented inconsistency and poor quality of many commercial AMF bio-inoculant products, direct comparisons between indigenous and commercial sources are necessary, along with long-term monitoring of rhizosphere microbiome dynamics, to refine and validate AMF inoculation practices.

Conclusions

This field study demonstrated that inoculating sorghum with indigenous arbuscular mycorrhizal fungi (AMF) significantly improved growth, yield, and phosphorus acquisition efficiency (PAE) in Sudanese vertisols. Across the two contrasting soil environments (Abassyia: more saline-sodic vertisols; Medani: typical high-clay, low-P vertisols), AMF inoculation consistently enhanced leaf area, chlorophyll content, shoot biomass, panicle traits, grain yield, root colonization, spore density, and PAE. However, the shoot phosphorus concentration was not altered. These findings indicate that AMF-mediated improvements in P uptake were preferentially allocated to reproductive sinks, resulting in higher yields rather than an increased vegetative shoot P concentration. Genotypic differences in responsiveness confirmed that host cultivar

selection is crucial for maximizing AMF benefits and that soil properties significantly influence colonization and sporulation. Taken together, these results provide clear field-based evidence that indigenous AMF consortia represent an effective biofertilizer option for enhancing nutrient-use efficiency and productivity in low-input vertisol systems. Future research should broaden the scope to include multi-nutrient responses, explore the long-term stability of AMF benefits, and integrate AMF responsiveness as a selection criterion in sorghum breeding programs aimed at promoting resilient and sustainable agriculture in sub-Saharan Africa.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Data availability statement

The data supporting this study's findings are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

All methods were performed in accordance with the relevant guidelines and regulations.

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