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Research article

Leveraging the complex interplay between arbuscular mycorrhizal fungi, seasonal dynamics, and genotypic diversity to optimize maize productivity in semi-arid agroecosystems

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ABSTRACT

Maize production under low-input agricultural systems in semi-arid areas of Sub-Saharan Africa faces significant challenges, primarily stemming from the synergistic impacts of climate variability and suboptimal agronomic practices. Harnessing soil microbiota, particularly arbuscular mycorrhizal fungi (AMF), represents a pivotal strategy for bolstering low-input systems. However, their functional utility is contingent upon their compatibility with the prevailing environmental conditions and biotic interactions. This study examines the influence of two distinct AMF inoculants on the growth and yield attributes of diverse maize genotypes across varying seasons within semi-arid regions of Kenya. We hypothesized that AMF inoculants exhibit differential adaptability to varying environmental sites and seasons, and their interaction will enhance the provision of key ecosystem services important for maize production. Field experiments were conducted in three semi-arid Counties (Tharaka-Nithi, Embu, and Kitui) during the 2019/2020 cropping seasons. A randomized complete block design with three replications and three treatments was adopted. Treatments consisted of Rhizatech (a commercial AMF inoculant), a consortium of AMF isolates (*Rhizophagus irregularis* and *Funneliformis mosseae*), and a non-inoculated control. In season one, notable interaction effects were observed for both site × maize genotype ($p = 0.0007$) and site × AMF inoculation ($p < 0.0001$), whereby Duma 43 genotype had the highest yield in Embu (11.93 t ha^{-1}) and Kitui (11.76 t ha^{-1}) counties, and Rhizatech and consortium inoculation consistently led to elevated grain yields across all three genotypes in Kitui, surpassing non-inoculated controls. AMF inoculation notably augmented phosphorus (P) uptake, with Rhizatech demonstrating a 79.7 % increase and consortium showing a 38.7 % increase in shoot P content compared to control plants in season 1. These findings highlight the complex interplay between AMF effectiveness, seasonal variations, and maize diversity. Further research is needed to elucidate the underlying mechanisms driving these seasonal shifts, allowing for optimized AMF inoculation strategies for improved maize performance under diverse conditions.

1. Introduction

Maize (*Zea mays* L.), a native crop of Central America, is currently a staple food in many parts of sub-Saharan Africa (SSA). It is a

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food source for humans, animals, and income, with a land usage of about 48.5 % of the cultivatable land in Kenya [1]. Undoubtedly, maize stands out as a crucial source of nutrition for millions of people and livestock [2]. Maize contains approximately 72 % starch and 10 % protein and supplies about 365 kcal/100 g of energy [3]. It has also been reported that maize has 71.88 g/100 g carbohydrate, 4.57 g/100 g fats, 0.12 mg/100 g Vitamin C, and 348 mg/100 g phosphorous [4]. This nutritional richness underscores maize's significant role in promoting health and well-being, making it a vital dietary component for diverse communities and animal populations, especially in SSA, where nutrition and food security are often limited.

Maize cultivation in Kenya faces substantial challenges, particularly concerning soil fertility depletion and water stress, exacerbated by the impacts of climate change. Kenya, located within SSA, has more than 80 % of its land classified as arid and semi-arid lands (ASALs), characterized by frequent and prolonged droughts, inconsistent rainfall patterns, and soil health degradation [5]. The compounding effects of climate change intensify water stress and contribute to the complexity of sustaining maize production in ASAL areas, underscoring the urgent need for adaptive strategies in this vital agricultural sector [6]. Notably, drought significantly impacts maize physiology, yield, and its components, presenting a critical challenge for maize production globally. Physiologically, drought stress leads to a reduction in photosynthesis primarily due to stomatal closure, which limits CO_2 uptake [7,8]. Additionally, drought can damage the photosynthetic apparatus, further decreasing photosynthetic efficiency [9,10]. It can also reduce vegetative growth, leading to reduced plant height, leaf number, and stem girth [11,12] and subsequently lowered grain quality and yield.

In addition to climate change, smallholder farmers have limited resources to purchase farm inputs such as inorganic fertilizers [13] and lack of access to better-yielding maize genotypes [14] that can boost crop production under ASAL environments. In light of these challenges, beneficial soil microbiota, including arbuscular mycorrhizal fungi (AMF) and Agaricomycetes fungus *Piriformospora indica*, are gaining, popularity in low-input agriculture due to their ability to boost crop production [15,16] and enhance water stress tolerance in crops [17], therefore, can offer an alternative cheap and sustainable way of boosting production in a resource-constrained environment.

AMF forms vesicles, arbuscules, and hyphae in the plant roots, spores, and mycelium hyphal networks in the rhizosphere [18]. The intricate AMF hyphal network significantly increases the plant roots' surface area interfacing with the soil, thus conferring biological advantages and heightening the plant's capacity for nutrient uptake [19]. A study by Boilard [20] has demonstrated that extra-radical hyphae can enhance the decomposition of organic matter in the soil, increasing the nutrient availability in the soil for plants. In addition, colonization of plant roots by AMF increases plant drought tolerance by effectively expanding the surface area for water absorption [18,21]. Furthermore, AMF provides essential agroecosystem services, including carbon sequestration and soil structure and texture stabilization, directly influencing the soil's potential to boost plant growth and production [22]. Glomalin-related soil protein, which is associated with AMF, plays a critical role in soil particle binding that enhances soil stability [23]. In addition, AMF confers drought tolerance [24], which could largely contribute to mitigating climate change perturbations in ASAL agroecosystems.

AMF inoculation has been regarded as a cost-effective and sustainable method that improves maize growth and production [25,26]. Numerous studies have reported that AMF inoculation improves phosphorus (P), nitrogen (N), and water uptake, which subsequently improves plant growth and boosts grain production [27–29]. However, inoculation with commercially proven AMF inoculants has, in some instances, failed to show any significant improvement in plant growth and production [30,31]. In maize, poor response to commercial AMF inoculants has been associated with the variation in plant genotypic interaction with the fungi, high competition by the native AMF strains in the soil, and environmental factors such as poor soil nutrition and water stress [32,33]. Indeed, the abundance and competitiveness of these native AMF species create a complex ecological scenario, hindering the successful establishment and efficacy of introduced AMF inoculants. However, amidst this challenge, there is a reported potential solution. AMF inoculants containing a consortium of AMF species that can develop synergistic associations with either native AMF species or amongst themselves can offer a promising alternative that can be strategically exploited to enhance plant growth and production [34]. In this study, we targeted the use of mycorrhizal inoculants containing a consortium of AMF strains so as to increase the chances of developing mycorrhizal associations with different maize genotypes grown in different agroecological zones in ASAL areas. We strongly believe that this collective approach can effectively address the limitations encountered by single strains, particularly in establishing associations with specific genotypes within distinct geo-ecological conditions. The exploration of diverse strain interactions not only overcomes challenges presented by individual strains struggling in certain contexts but also provides a valuable avenue for optimizing the overall effectiveness of AMF inoculants in enhancing maize cultivation practices.

In this study, we hypothesized that different maize genotypes and AMF inoculants exhibit differential adaptability to varying environmental sites and seasons, and their interaction will enhance the provision of key ecosystem services important for maize growth, production, and resilience in semi-arid agroecosystems. The specific objectives were (1) to assess the agronomic performance of three maize genotypes (Duma 43, KDV 4, and DH 02) in three agroecological zones (upper midlands, lower midlands, and inner lowlands) and two contrasting seasons (short-rain and long-rain), (2) to assess the effectiveness of AMF inoculants (Rhizatech and consortium) in promoting maize agronomic traits (plant height, stover dry weight and yield components), physiological traits (root mycorrhizal colonization, chlorophyll content and water status) and nutritional traits (shoot phosphorus) across different agroecological zones and seasonal variations, and lastly, (3) to explore the interaction between maize genotypes and AMF inoculation treatments in influencing maize growth and productivity across different agroecological zones and seasons.

2. Materials and Methodology

2.1. Experimental site

Field experiments were conducted in two growing seasons in 2019/2020 at three locations in smallholder farms in Embu County (S

0°30′3″ E 37°39'; S 0°30′12″ E 37°39′33''; S 0°30′2″ E 37°39′14″), Tharaka Nithi county (S 0°10′20″ E 37°49′21''; S 0°10′10″ E 37°49′12''; N 0°11′13″ E 37°49′3″), and Kitui county (S 1°11′11″ E 37°51′38'; S 1°12′15″ E 37°51′24''; S 1°12′28″ E 37°51′16″) as shown in Fig. 1. The fields selected are within lower midland (LM) and inner lowland (IL) agroecological zones (AEZs) with differing soil type, climatic conditions, elevation, and maize production capacities (Fig. 1, Table 1). The study's sites are typically semi-arid areas, with a mean rainfall of 256 mm in Embu County, 305 mm in Tharaka Nithi County, and 138 mm in Kitui County for season one and 237 mm in Embu County, 198 mm in Tharaka Nithi County, and 125 mm in Kitui County for season two. The study sites received a total of 3470 mm during the first growing season (October–February) and 2780 mm in the second season (March–July). Kitui County had the lowest total precipitations across the two seasons (Fig. 2). The first season started on 10th October 2019 to 14th February 2020, while the second season commenced on 23rd March 2020 to 25th July 2020.

Smallholder farming is practiced in these zones, with most of them engaging in rain-fed subsistence mixed farming, dominated by the cultivation of maize, cowpeas, common beans, green grams, sorghum, and finger millet, and keeping of livestock such as cattle, goats, sheep, poultry, pigs, and fish farming [35]. Although smallholder farmers prefer maize cultivation over other crops, its success is highly limited by climatic, soil and biotic conditions. All the experimental farms selected in this study have no history of AMF inoculation, as the farmers in these areas have limited knowledge about these eco-friendly methods [13].

2.2. Soil characteristics

Fig. 1 Monthly rainfall and temperature at the study sites during 2019/2020 cropping seasons in Tharaka- Nithi, Embu and Kitui counties, Kenya.

2.3. Experimental design, treatments, and planting

The first season began on 10th October 2019 to 14th February 2020, while the second season commenced on 23rd March 2020 to 25th July 2020. In each farm, the experiments were laid out in a randomized complete block design with three blocks (replicates). Plots consisted of three maize genotypes, namely Duma 43, KDV 4, and DH 02, sourced from Simlaw Seeds Kenya. The selected genotypes were chosen after a scoping survey was conducted and revealed that these genotypes are mostly grown by the farmers and are best adapted to the semi-arid regions of Eastern Kenya (Embu, Tharaka Nithi, and Kitui counties). They are short-seasoned genotypes and take 90–105 days to mature. The planted seeds were subjected to three treatments: (i) inoculation with a commercial arbuscular mycorrhizal inoculum (Rhizatech), (ii) a consortium of arbuscular mycorrhizal isolates (BEG 12 - *Funneliformis mosseae* and BEG 44 - *Rhizophagus irregularis*), and (iii) a control without AMF inoculation.

The experimental trial comprised 243 plots, each measuring 3 × 3 m, and were maintained under rain-fed conditions throughout the growing season. No inorganic fertilizers were used. Conventional tillage (25 cm depth) and shallow harrowing (5 cm depth) were carried out during field preparation as the first line of controlling weeds. After that, minimum tillage was used to control post-emergence weeds. Season two experiments were carried out within the same farms but on different sites to avoid cross-contamination between seasons. A single maize seed was mechanically planted in each hole (5 cm depth) following the maize seed

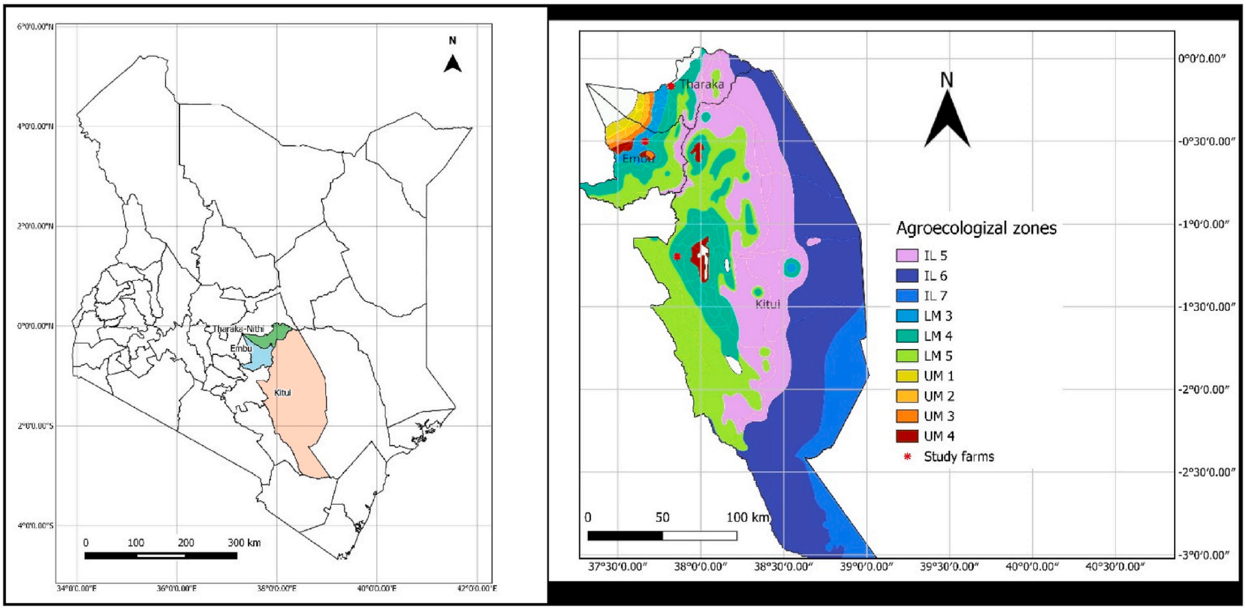

Fig. 1. A map of Kenya showing the study sites in Embu, Tharaka-Nithi, and Kitui Counties. inner lowland (IL), lower midland (LM) and upper midland (UM) agroecological zones. The red stars are the study farms (3 farms, close to each other (<300 m distance) in each County).

Table 1
Soil physiochemical properties (0–30 cm) at Tharaka-Nithi, Embu and Kitui counties.

Location	pH (1:2H_2O)	Total Organic C (%)	Clay (%)	Silt (%)	Sand (%)	Total N (%)	P (ppm, Mehlich III)
Tharaka- Nithi county	5.66–6.22	0.39–0.78	20–22	2–10	66–76	0.05–0.09	235–250
Embu county	5.38–5.85	1.33–1.67	22–26	12–14	62–64	0.12–0.15	20–25
Kitui county	5.7–6.9	0.89–1.9	12–44	8–12	48–76	0.1–0.17	30–120

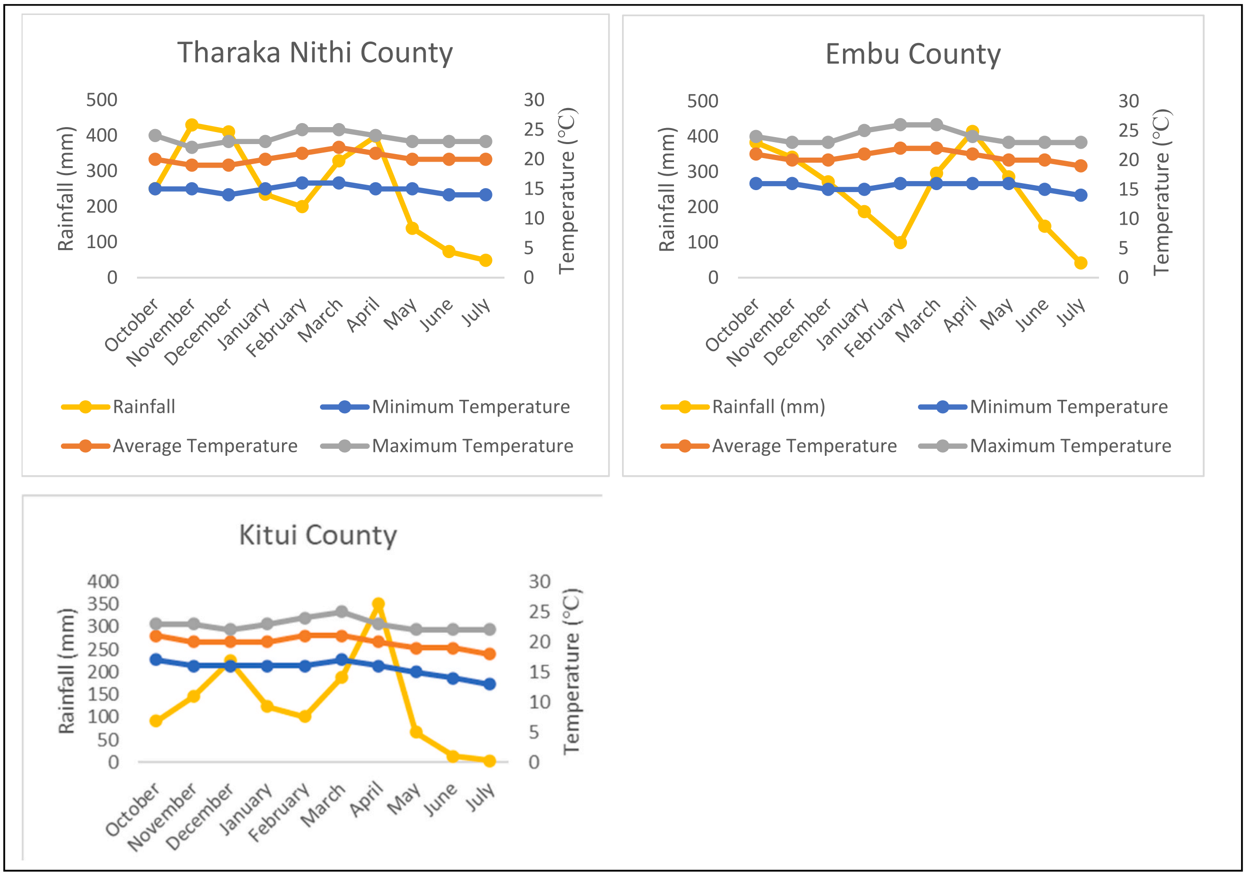

Fig. 2. Mean monthly rainfall and maximum and minimum temperature at the three study sites. The first season started on 10th October 2019 to 14th February 2020, while the second season commenced on 23rd March 2020 to 25th July 2020.

breeder's recommended row spacing of 75 × 25 cm. Each plot had a total of five rows and 70 plants. A buffer zone space measuring 2 m was left to separate the plots. For treatments requiring inoculation, AMF inoculum was applied at 0.7 g per planting hole, equivalent of 38 propagules (spores, extra-radical mycelium and colonized roots) and thoroughly mixed with the soil before the seeds were placed. All inoculation treatments received the same number of propagules. One spraying regime involving the insecticide Pyrinex Quick (Aceprid 200 WSP), Profen (active ingredient pyriproxyfen), and Chlorantraniliprole was done at vegetative stage V4 and V6 to control fall armyworms and aphids with formulations applied as per the manufacturer's instructions.

2.4. Source of AMF inoculum

The commercial Rhizatech inoculum was obtained packaged in 2 kg packets from Dudutech, Kenya. Rhizatech is a mixed commercial mycorrhizal fungal inoculum containing *Funneliformis mosseae, Glomus etunicatum,* and *G. intraradices*, and is supplied by Dudutech, Kenya [36], while the consortium consisted of *Rhizophagus irregularis* (BEG 44) and *Funneliformis mosseae* (BEG 12) that were acquired from the International Bank of the Glomeromycota in INRAE, Dijon France and maintained in the Department of Biochemistry, Microbiology, and Biotechnology, Kenyatta University (Nairobi) in pot cultures using Bermuda grass (*Cynodon dactylon*) as the host plant [37]. The consortium inoculum comprising *F. mosseae* and *R. irregularis* isolates was prepared in the greenhouse as follows. Twelve 4-L pots containing a mixture (1:1 v/v) of sterilized soil and sand were prepared. The sterilization was achieved by autoclaving the sand-soil mixture at 121 °C for 15 min for three consecutive days to kill AMF spores and extra-radical mycelium occurring in the soil [38]. The soil and sand were collected at Kenyatta University Agriculture Farm. Six pots were inoculated with crude (160 g of soil consisting of AMF spores) inoculum of *R. irregularis* and the rest with *F. mosseae* isolates. Bermuda grass seeds were planted in each pot and maintained in the greenhouse from March 2019 to August 2019 for season one, and another batch was planted in September 2019 and maintained up to January 2020 for season two. Bermuda grass shoots were excised and discarded during harvesting, and the roots were cut into fragments and mixed with the soil to form a homogenous mixture. The mixture of roots and soil containing AMF spores was used as a crude source of inoculum. A consortium of inoculum was obtained by mixing substrates from *R. irregularis* and *F. mosseae* in the ratio of 1:1 v/v of individual isolate inoculum.

2.5. Agronomic and mycorrhizal assessments

2.5.1. Maize crop height

Three plants per plot were randomly selected at the V4 stage, and their height was determined. Plant height was measured in centimeters, using a tape measure, from the plant base to the highest point of the arch of the top leaf, which had emerged to over 50 %. Plants in the inner rows were considered in the selection to avoid biases due to the border effect.

2.5.2. Leaf chlorophyll content

Leaf chlorophyll content was measured using a non-destructive estimation, using SPAD-502 plus chlorophyll meter (Soil Plant Analysis Development Konica, Japan) [39]. Chlorophyll content was measured on three young, fully expanded leaves in three different plants located in the inner rows of each plot. Measurements were taken in triplicates, and readings were recorded as SPAD values.

2.5.3. Plant sampling

Plant sampling for water status and phosphorus (P) analysis in the shoots was done at V4. Three maize plants from each plot were harvested by carefully uprooting the entire plant. Subsequently, the shoots and roots were separated, and the fresh weight of the shoots was recorded and then oven-dried to a constant weight. Plant roots were carefully cleaned, packaged in small khaki bags, and transported to the laboratory for percentage AMF root colonization analysis. Staining of the roots was achieved using a Trypan blue stain [37]. The roots were washed in running water, and 100 segments were cut into small pieces of 1 cm each. Using 15 ml falcon tubes, the roots were cleared using 10 % potassium hydroxide in a hot water bath of about 80 °C for 15 min. The cleared roots were neutralized using a 2 % hydrochloric acid solution and stained using 0.05 % Trypan blue in lactic acid. AMF root colonization using a dissecting microscope at × 40 magnification, and the colonization percentage was determined following the gridline intersect method outlined by Giovannetti and Mosse [40]. To obtain the water status of the harvested plants, the dry shoot weight was subtracted from the fresh weight, and the percentage water status was calculated with reference to the fresh weight [41]. 100 g of dried shoots were used for P analysis employing the wet digestion method and spectrophotometry [42].

2.5.4. Maize yield

Maize harvesting was done on 14th February 2020 and 25th July 2020 at maturity for seasons one and two, respectively. Three plants in the middle of each plot were randomly selected and harvested in each season, and the number of harvested cobs was counted per plant. The cobs were threshed, and the grains were oven-dried for seven days until they maintained 13 % moisture content and were weighed. To calculate maize yield per hectare, the spacing between and within rows of 75 cm by 25 cm, as recommended by the maize breeder, was considered. A 3 m by 3 m plot hosted 70 plants, which was used to compute the number of plants per hectare. The following formula was used to calculate the theoretical maize yield per hectare [43]. Harvest index (HI) was calculated from the grain yield and total biomass at harvesting (harvested yield/total plant shoot dry weight at maturity).

$$\text{Plants per hectare} = \frac{70\ plants\ (in\ 9\ \text{m2}) \times 10000\ \text{m2}}{9\ \text{m2}}$$

$$\text{Maize yield (tons)} = \frac{Yield\ obtained\ from\ three\ sampled\ plants\ (kg) \times numberof\ plants\ per\ hectare}{1000\ kg}$$

2.6. Statistical analysis

All data were subjected to a Bartlett test to check for homogeneity of variance. Data on percent water status were arcsine ($\sqrt{x}$) transformed while the rest of the data were log (x+1) transformed where possible to fulfill the assumptions of analysis of variance (ANOVA). Data on plant height, AMF colonization, water status, stover dry weight, 100-grain weights, yield per hectare, and shoot P content were analyzed using a three-way ANOVA based on a randomized complete block design. Whenever feasible, a post hoc test was carried out using Tukey's HSD test ($p < 0.05$) [44]. All the data were analyzed using SAS software (Version 9.0). Principal component analysis (PCA), based on a standardized correlation matrix, was used to examine the variation of agronomic traits (plant height, plant diameter, stover dry weight, 100-seed weight, and grain yield), physiological traits (AMF root colonization percentage, chlorophyll content, and water status), and a nutritional trait (shoot phosphorus content). PCA was performed separately for each season.

3. Results

3.1. Soil chemical and physical parameters

Tharaka Nithi County had a pH ranging between 5.66 and 6.22, and thus, the soil is averagely acidic to neutral. The pH for soils sampled from Embu County was slightly acidic, with a pH range of 5.38–5.85. On the other hand, the soil pH for soils sampled from Kitui County ranged from slightly acidic to neutral, with a pH range of 5.7–6.9. Kitui County soils recorded the highest total organic carbon, 1.9 %, followed by Embu County, while Tharaka Nithi County recorded the lowest total organic carbon. The total available N in the soil samples was also highest in Kitui County, followed by Embu County, and lowest in Tharaka-Nithi counties. Contrary to other soil chemical parameters, soil P was highest in Tharaka-Nithi county with up to 250 ppm compared with Kitui, with soil P ranging between 30 and 120 and Embu County with a range of 20–25. Kitui county registered the highest % clay, registering the highest value of 44 % compared to the highest values of 26 % and 22 % in the Embu and Tharaka-Nithi counties, respectively. Silt percentages were highest in Embu County, followed by Kitui County and Tharaka Nithi, which registered the lowest percentage of silt. Sand percentage composition was highest in soils sampled from Kitui and Tharaka Nithi counties, registering up to 76 % sand in a sample and Embu County registering up to 64 %.

3.2. Effects of AMF inoculation, maize genotype, and site on plant height in two contrasting seasons

The plant height of Duma 43, DH 02 and KDV 4 maize genotypes significantly differed ($p < 0.05$) across the two seasons. Averaged across the three genotypes, maize grown in season two exhibited a notable increase in plant height (129.44 cm plant^{-1}) compared to season one (82.03 cm plant^{-1}). Duma 43 was the tallest genotype, with mean values of 85.33 cm plant^{-1} and 134.09 cm plant^{-1} in the first and second seasons, respectively. Conversely, DH 02 and KDV 4 displayed the shortest stature, averaging 80.43 cm plant^{-1} and 80.30 cm plant^{-1} in the first season and 127.54 cm plant^{-1} and 126.68 cm plant^{-1} in the second season, respectively (Table 2).

In both seasons, plant height was also significantly affected ($p < 0.0001$) by the site. Tharaka-Nithi county recorded the highest plant height with a mean of 93.83 cm plant$^{-1,}$ whereas Kitui and Embu counties recorded the shortest plant heights of 76.43 cm plant^{-1} and 75.80 cm plant^{-1} in season one, respectively. In season two, Embu County recorded the highest plant height with a mean of 137.63 cm plant$^{-1,}$ whereas Kitui County recorded the shortest plant height of 121.09 cm plant^{-1} (Table 2).

Significant interactions were noted in season two between maize genotype × AMF inoculation ($p = 0.0277$) as well as between site × AMF inoculation ($p = 0.0013$) in relation to plant height (Table 2; Fig. S1). The application of consortium and Rhizatech AMF inoculants resulted in a significantly increased plant height of Duma 43 and KDV 4 genotypes compared to the non-inoculated control plants in Kitui (Duma 43; 125.67 cm plant^{-1} and 133.15 cm plant^{-1} vs. 108.07 cm plant^{-1}, respectively; KDV 4; 127.18 cm plant^{-1} and 127.04 cm plant^{-1} vs. 107.26 cm plant^{-1}, respectively) and Embu (Duma 43; 153.48 cm plant^{-1} and 154.04 cm plant^{-1} vs. 126.81 cm plant^{-1}, respectively; KDV 4; 146.48 cm plant^{-1} and 139.18 cm plant^{-1} vs. 119.07 cm plant^{-1}, respectively) counties (Table 2; Fig. S1).

Table 2
Effects of AMF inoculation, maize genotype and site on plant height and maize leaf chlorophyll content in two contrasting seasons.

Treatments	Season One		Season Two	
	Height (cm plant^{-1})	**Chlorophyll (SPAD values)**	**Height (cm plant^{-1})**	**Chlorophyll (SPAD values)**
Site				
Kitui	76.43 ± 1.17^{b}	37.62 ± 0.56b	121.09 ± 2.36^{c}	30.65 ± 0.78^{b}
Embu	75.80 ± 1.98^{b}	37.52 ± 0.56b	137.63 ± 2.20^{a}	39.07 ± 0.60^{a}
Tharaka-Nithi	93.83 ± 1.61^{a}	45.16 ± 1.34a	129.58 ± 1.72^{b}	39.08 ± 0.53^{a}
Maize Genotype				
Duma 43	85.33 ± 1.7^{a}	39.92 ± 0.66a	134.09 ± 2.47^{a}	34.79 ± 0.78^{b}
DH 02	80.43 ± 1.90^{b}	40.74 ± 1.40a	127.54 ± 2.03^{b}	38.05 ± 0.77^{a}
KDV 4	80.30 ± 1.88^{b}	39.65 ± 0.70a	126.68 ± 2.11^{b}	35.95 ± 0.75^{b}
AMF inoculation				
Rhizatech	83.49 ± 1.74^{a}	40.72 ± 0.73 ab	132.67 ± 2.20^{a}	37.07 ± 0.72^{a}
Consortium	82.69 ± 1.90^{a}	41.64 ± 1.36a	134.21 ± 2.22^{a}	37.43 ± 0.78^{a}
Control	79.88 ± 1.95^{a}	37.95 ± 0.65b	121.43 ± 2.02^{b}	34.31 ± 0.79^{b}
P-values of main factors and their interactions				
Maize Genotype (G)	**0.0461**	0.6665	**0.0134**	**0.0006**
Site	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**
AMF inoculation	0.2582	**0.0111**	< **0.0001**	**0.0004**
Site × Maize G	0.1257	0.1729	0.4951	0.9356
Maize G × AMF	0.9357	0.6677	**0.0277**	0.8661
Site × AMF	0.7998	0.3607	**0.0013**	**0.0001**
Site × Maize G × AMF	0.8356	0.9644	0.9442	0.7770

Values are presented as mean ± Standard Error of the Mean (SEM), and values followed by the same letters in a column within each major factor have no significant differences at $p < 0.05$ (Tukey's HSD test).

3.3. Effects of AMF inoculation, maize genotype, and site on maize leaves chlorophyll content in two contrasting seasons

Maize leaf chlorophyll content was significantly influenced by the site and AMF inoculation in both seasons. Maize leaves in season one exhibited the highest chlorophyll content in Tharaka-Nithi county (45.16 SPAD values) compared to Kitui (37.62 SPAD values) and Embu (37.52 SPAD values) counties, which produced maize leaves with the lowest chlorophyll content (Table 2). In season two, Tharaka-Nithi (39.08 SPAD values) and Embu counties (39.07 SPAD values) had maize leaves with the highest chlorophyll content, while Kitui County produced maize leaves with the lowest chlorophyll content, averaging 30.65 SPAD values (Table 2).

While the maize genotype exhibited no statistically significant effect on chlorophyll content during season one ($p = 0.6665$), a substantial influence emerged in season two ($p = 0.0006$). Notably, DH 02 displayed the highest chlorophyll content, recording 38.05 SPAD values, surpassing KDV 4 (35.95 SPAD values) and Duma 43 (34.79 SPAD values), which had the lowest chlorophyll content. In both seasons, chlorophyll content was significantly ($p < 0.05$) affected by AMF treatment, with the highest SPAD values (41.64) observed in maize inoculated with the consortium. In contrast, maize inoculated with Rhizatech and the non-inoculated controls produced the lowest SPAD values, averaging 40.72 and 37.95, respectively (Table 2). In season two, a significant ($p = 0.0001$) interaction effect between site × AMF inoculation was noted, whereby maize inoculated with consortium and Rhizatech in Embu County produced higher chlorophyll content, averaging 41.25 SPAD values compared to that of the non-inoculated controls (34.71 SPAD values) (Fig. S2).

3.4. Effects of AMF inoculation, site, and genotype on the percentage water status of maize at the V4 stage in two contrasting seasons

In both seasons, site and AMF inoculation significantly influenced the water status of maize shoots, while maize genotype did not have any effect (Table 3). In season one, maize shoots in Embu and Kitui counties had higher water status, averaging 44.8 % $plant^{-1}$ and 38.6 % $plant^{-1}$, respectively, while Tharaka Nithi county had the lowest values (20.1 % $plant^{-1}$). In season two, the maize shoots in Tharaka-Nithi and Embu counties had the highest water status, averaging 40.9 % $plant^{-1}$ and 40.2 % $plant^{-1}$, respectively. Unlike in season one, maize shoots in Kitui County had the lowest water status, averaging 33.2 % $plant^{-1}$ (Table 3). AMF inoculation differentially affected the maize water status in seasons one and two, with Rhizatech (38.0 % and 39.8 % $plant^{-1}$, respectively) and consortium (35.8 % and 42.8 % $plant^{-1}$, respectively) inoculated plants having the highest water status compared to non-inoculated controls (29.7 % and 31.7 % $plant^{-1}$, respectively). In season two, significant interactions between maize genotype × site ($p = 0.0387$) as well as between site × AMF inoculation ($p = 0.0003$) were noted (Table 3; Fig. S3). Duma 43 genotype that received Rhizatech AMF inoculant in Embu and Tharaka Nithi counties had the highest water status, averaging 55.69 % and 56.22 % $plant^{-1}$, respectively, while Duma 43 and KDV 4 genotypes that did not receive any AMF inoculant in Kitui and Embu counties, respectively, recorded the lowest values (15.77 % and 20.76 % $plant^{-1}$, respectively) (Fig. S3).

3.5. Effects of AMF inoculation, maize genotype, and site on percentage mycorrhiza root colonization in two contrasting seasons

Across both seasons, root colonization percentage was significantly influenced by site and AMF inoculation ($p < 0.0001$) (Table 3).

Table 3
The water status of maize at the V4 stage and AMF root colonization percentage (%) were influenced by site, genotype, and AMF treatments in two contrasting seasons.

Treatments	Season One		Season Two	
	Water Status (% $plant^{-1}$)	Percentage (%) Root Colonization	Water Status (% $plant^{-1}$)	Percentage (%) Root Colonization
Site				
Kitui	38.60 ± 1.69[b]	32.89 ± 1.65[c]	33.20 ± 2.56[b]	54.69 ± 2.19[b]
Embu	44.80 ± 2.81[a]	38.03 ± 1.79[b]	40.20 ± 2.39[a]	56.50 ± 2.48[b]
Tharaka-Nithi	20.10 ± 1.24[c]	54.71 ± 2.08[a]	40.90 ± 2.41[a]	65.93 ± 2.04[a]
Maize Genotype				
Duma 43	36.40 ± 2.48[a]	42.41 ± 2.15[a]	41.00 ± 2.85[a]	57.37 ± 2.31[a]
DH 02	35.60 ± 2.23[a]	39.30 ± 2.20[a]	36.80 ± 3.17[a]	60.70 ± 2.23[a]
KDV 4	31.50 ± 3.27[a]	43.90 ± 1.98[a]	36.40 ± 2.34[a]	59.10 ± 2.38[a]
AMF inoculation				
Rhizatech	38.00 ± 2.48[a]	51.61 ± 1.85[a]	39.80 ± 2.50[a]	73.37 ± 1.52[a]
Consortium	35.80 ± 2.08[a]	45.39 ± 1.92[b]	42.80 ± 2.45[a]	62.47 ± 1.72[b]
Control	29.70 ± 2.34[b]	28.63 ± 1.69[c]	31.70 ± 2.32[b]	41.28 ± 2.02[c]
P-values of main factors and their interactions				
Maize Genotype (G)	0.1975	0.0776	0.2506	0.5242
Site	< **0.0001**	< **0.0001**	**0.0208**	< **0.0001**
AMF inoculation	**0.0124**	< **0.0001**	**0.0008**	< **0.0001**
Site × Maize G	0.8653	0.1603	**0.0387**	0.2249
Maize G × AMF	0.4707	0.2667	0.0643	0.3165
Site × AMF	0.9745	0.6670	**0.0003**	**0.0068**
Site × Maize G × AMF	0.1037	0.2166	0.2538	0.2047

Values are presented as mean ± Standard Error of the Mean (SEM), and values followed by the same letters in a column within each major factor have no significant differences at $p < 0.05$ (Tukey's HSD test).

On average, maize in Tharaka-Nithi exhibited the highest root colonization at 54.71 % and 65.93 % in seasons one and two, respectively. Conversely, Kitui County displayed the lowest root colonization percentage, registering 32.89 % and 54.69 % in seasons one and two, respectively (Table 3). Notably, there was no significant difference in root colonization percentage among different maize genotypes across the two seasons. Inoculation with Rhizatech induced the highest root colonization percentage in season one (51.61 %) and season two (73.37 %), compared to the non-inoculated controls, which recorded the lowest values of 28.63 % and 41.28 %, respectively. With respect to control plots, the inoculation with consortium AMF led to significantly higher colonization, averaging 45.39 % in season one and 62.47 % in season two (Table 3). A significant interaction ($p = 0.0068$) effect between site × AMF inoculation was noted in season two (Table 3; Fig. S4). Rhizatech AMF inoculant induced higher root colonization in Tharaka Nithi and Embu counties (76.8 % and 74.4 %, respectively), surpassing that of the consortium inoculant (69.2 % and 57.5 %, respectively). In contrast, the performance of Rhizatech in Kitui county (68.8 %) was not significantly different from that of the consortium inoculant in Tharaka Nithi county (69.2 %) (Fig. S4).

3.6. *Effects of AMF inoculation, maize genotype, and site on maize stover dry weight*

Site and maize genotype significantly ($p < 0.0001$) influenced maize stover dry weight in both seasons (Table 4). Maize grown in Embu and Tharaka-Nithi counties had the highest stover dry weights, averaging 328.70 g plant^{-1} and 278.40 g plant$^{-1,}$ respectively, whereas Kitui county recorded the lowest maize stover dry weight with an average of 143.85 g plant^{-1} in season one (Table 4). Embu County recorded the highest stover dry weight with an average of 122.22 g plant^{-1} compared to that of Tharaka-Nithi County, which recorded the lowest stover dry weight (84.68 g plant^{-1}). Unfortunately, there was no harvest in season two from Kitui County due to the invasion of locusts and inadequate rainfall during crucial maize reproductive stages (Fig. 2). In season one, Duma 43 produced the highest stover dry weight, averaging 293.60 g plant$^{-1,}$ whereas DH 02 and KDV 4 recorded the lowest stover dry weights, averaging 218.10 g plant^{-1} and 239.21 g plant^{-1}, respectively. The pattern in maize genotype performance persisted in season two, albeit with a marginally reduced performance, with Duma 43 recording 123.81 g plant^{-1} while DH 02 (86.73 g plant-^{1}) and KDV 4 (99.82 g plant-^{1}) had the lowest stover dry weights (Table 4).

In season one, maize stover dry weight was significantly ($p < 0.0001$) affected by AMF inoculation, where Rhizatech produced the highest stover dry weight with a mean of 314.45 g plant^{-1} compared to that of the consortium (238.03 g plant^{-1}) and the non-inoculated controls (198.53 g plant^{-1}), which produced the lowest stover dry weights (Table 4). Notably, AMF inoculation in season two did not significantly ($p = 0.2728$) affect maize stover dry weight. Season one revealed a significant site × maize genotype interaction effect ($p < 0.0001$) (Table 4; Fig. S5). Rhizatech AMF inoculated maize, on average, had a higher stover dry weight in Tharaka Nithi county (495.5 g plant^{-1}), surpassing that of the consortium inoculant (255.2 g plant^{-1}). In contrast, the stover dry weight of maize inoculated with Rhizatech in Kitui county (167.5 g plant^{-1}) was not significantly different from that of the consortium inoculant (166.1 g plant^{-1}) (Fig. S5). Season two revealed a significant interaction effect between site × AMF inoculation ($p = 0.0012$) (Table 4; Fig. S6). Duma 43 genotype produced a higher stover dry weight in Embu County compared to KDV 4 and DH 02 genotypes. In contrast, no significant differences were observed in stover dry weights amongst the three genotypes in Tharaka Nithi county (Fig. S6).

Table 4
Stover dry weight (g plant^{-1}) and shoot phosphorus (P) (g 100 g^{-1}) of maize as influenced by site, genotype, and AMF treatments in two contrasting seasons.

Treatments	Season one		Season two	
	Stover Dry Weight (g plant^{-1})	Phosphorous (g 100g^{-1})	Stover Dry weight (g plant^{-1})	Phosphorous (g 100g^{-1})
Site				
Kitui	143.85 ± 7.95^{b}	0.2633 ± 0.0075^{a}	–	0.3395 ± 0.0149^{a}
Tharaka-Nithi	278.40 ± 18.87^{a}	0.2637 ± 0.0087$_{a}$	84.68 ± 2.78^{b}	0.1884 ± 0.0093^{c}
Embu	328.70 ± 21.70^{a}	0.1400 ± 0.0144^{b}	122.22 ± 4.63^{a}	0.2714 ± 0.0088^{b}
Maize Genotype				
Duma 43	293.60 ± 20.24^{a}	0.2704 ± 0.0128^{a}	123.81 ± 5.91^{a}	0.3200 ± 0.0129^{a}
DH 02	218.15 ± 17.11^{b}	0.2135 ± 0.0115^{b}	86.73 ± 4.02^{b}	0.2604 ± 0.0120^{b}
KDV 4	239.22 ± 19.45^{b}	0.1832 ± 0.0111^{c}	99.82 ± 4.64 ^{b}	0.2189 ± 0.0125^{c}
AMF inoculation				
Rhizatech	314.44 ± 22.77^{a}	0.2865 ± 0.0119^{a}	105.69 ± 5.43^{a}	0.3499 ± 0.0111^{a}
Consortium	238.03 ± 16.43^{b}	0.2211 ± 0.0118^{b}	106.55 ± 5.42^{a}	0.2723 ± 0.0115^{b}
Control	198.53 ± 15.59^{b}	0.1594 ± 0.0093^{c}	98.12 ± 5.13^{a}	0.1770 ± 0.0094^{c}
P-values of main factors and their interactions				
Maize genotype (G)	**0.0016**	< **0.0001**	< **0.0001**	< **0.0001**
Site	< **0.0001**	< **0.0001**	< **0.0001**	< **0.0001**
AMF inoculation	< **0.0001**	< **0.0001**	0.2728	< **0.0001**
Site × Maize G	0.7303	0.9234	**0.0012**	0.6250
Maize G × AMF	0.3018	0.4691	0.3329	0.5652
Site × AMF	< **0.0001**	0.6375	0.5593	0.0509
Site × Maize G × AMF	0.3808	0.3270	0.4739	0.9982

Values are presented as mean ± Standard Error of the Mean (SEM), and values followed by the same letters in a column within each major factor have no significant differences at $p < 0.05$ (Tukey's HSD test).

3.7. Effects of AMF inoculation, maize genotype, and site on shoot P content

In both seasons, shoot phosphorous content was significantly influenced ($p < 0.0001$) by site, maize genotype, and AMF inoculation (Table 4). In season one, maize grown in Kitui and Tharaka Nithi counties had higher shoot P values (0.2633 g 100 g^{-1} and 0.2637 g 100 g^{-1}, respectively) compared to that of Embu County (0.14 g 100 g^{-1}). In season two, maize in Kitui county consistently demonstrated elevated shoot P values (0.3395 g 100 g^{-1}) compared to that of Embu (0.2714 g 100 g^{-1}) and Tharaka Nithi (0.1884 g 100 g^{-1}) counties (Table 4).

In seasons one and two, Duma 43 consistently had the highest shoot P values, averaging 0.2704 g 100 g^{-1} and 0.3200 g 100 g^{-1}, respectively, surpassing that of DH 02 (0.2135 g 100 g^{-1} and 0.2604 g 100 g^{-1}) and KDV 4 (0.1832 g 100 g^{-1} and 0.2188 g 100 g^{-1}), respectively. The influence of AMF inoculation on maize shoot P content was evident across the two seasons. Rhizatech and consortium inoculations elicited a significant enhancement, yielding a 79.7 % and 38.7 % increase, respectively, compared to the non-inoculated control, which averaged 0.1594 g 100 g$^{-1\ 1}$ in season one (Table 4).

3.8. Effects of AMF inoculation, maize genotype, and site on 100 seed weight and maize grain yield

In season one, the 100-seed weight significantly varied depending on the site ($p < 0.0001$) and maize genotype ($p = 0.0001$), while in season two, maize genotype ($p = 0.0023$) and AMF inoculation ($p < 0.0001$) were the main determinants (Table 5). In season one, maize in Kitui county had the highest weights, averaging 34.75 g^{-1} plant$^{-1,}$ while that of Tharaka-Nithi county recorded the lowest values with a mean of 30.87 g^{-1} plant^{-1}. Duma 43 seeds had the highest weights with a mean of 34.47 g^{-1} plant^{-1} and 37.75 g^{-1} plant^{-1} in seasons one and two, respectively. Contrastingly, DH 02 and KDV 4 exhibited inferior performance in both seasons (Table 5). Rhizatech and consortium AMF inoculation in season two induced a higher 100-seed weight, averaging 37.84 g^{-1} plant^{-1} and 36.38 g^{-1} plant^{-1}, respectively, compared to non-inoculated controls, which recorded the lowest weight (33.54 g^{-1} plant^{-1}) (Table 5).

In both seasons, maize grain yield significantly ($p < 0.0001$) varied depending on the site and maize genotype (Table 5). In season one, Kitui county produced maize with the highest yield, averaging 10.72 t ha^{-1} compared to Embu (8.93 t ha^{-1}) and Tharaka-Nithi (8.57 t ha^{-1}) counties. In season two, Embu County yielded the highest at 7.64 t ha^{-1}, contrasting with Tharaka-Nithi County (5.18 t ha^{-1}), which had the lowest production. Notably, the overall yield was lower in season two compared to season one. Duma 43 consistently recorded the highest yield across the two seasons, averaging at 10.96 t ha^{-1} and 7.89 t ha^{-1} in seasons one and two, respectively (Table 5). In contrast, KDV 4 and DH 02 had the lowest yields of 8.97 t ha^{-1} and 8.29 t ha^{-1} in season one and 5.93 t ha^{-1} and 5.41 t ha^{-1} in season two, respectively. AMF inoculation influenced grain yield in season one ($p = 0.0003$), while in season two, no statistically significant difference was observed ($p = 0.958$). Rhizatech inoculation produced the highest grain yield in season one, averaging 10.09 t ha^{-1} compared to that of the consortium inoculant (9.64 t ha^{-1}) and non-inoculated control (8.47 t ha^{-1}). This represents a percentage increase in grain yield of 19.13 % and 13.81 % for Rhizatech and consortium inoculations, respectively.

In season one, notable interaction effects were observed for both site × maize genotype ($p = 0.0007$) and site × AMF inoculation ($p < 0.0001$) (Table 5; Fig. S7). Duma 43 genotype had the highest yield in Embu (11.93 t ha^{-1}) and Kitui (11.76 t ha^{-1}) counties. Unlike in other sites, the yield performance of KDV 4 and DH 02 did not significantly differ in Embu County, averaging 7.63 t ha^{-1} and 7.23 t ha^{-1}, respectively. Similarly, there was no significant difference in the yield performance of Duma 43 and KDV 4 genotypes in Tharaka

Table 5
100-seed weight (g plant^{-1}) and grain yield (t ha^{-1}) as influenced by site, genotype, and AMF treatments in two contrasting seasons.

Treatments	Season One		Season Two	
	100 seed weight (g plant^{-1})	Grain yield (t ha^{-1})	100 seed weight (g plant^{-1})	Grain yield (t ha^{-1})
Site				
Tharaka-Nithi	30.87 ± 0.61^{c}	8.57 ± 0.25^{b}	35.33 ± 0.66^{a}	5.18 ± 0.20^{b}
Kitui	34.75 ± 0.41^{a}	10.72 ± 0.32^{a}	–	–
Embu	32.71 ± 0.50^{b}	8.93 ± 0.43^{b}	36.51 ± 0.45^{a}	7.64 ± 0.30^{a}
Genotype				
Duma 43	34.47 ± 0.49^{a}	10.96 ± 0.39^{a}	37.75 ± 0.51^{a}	7.89 ± 0.40^{a}
DH 02	31.56 ± 0.51^{b}	8.29 ± 0.29^{b}	34.78 ± 0.72^{b}	5.41 ± 0.29^{b}
KDV 4	32.30 ± 0.57^{b}	8.97 ± 0.31^{b}	35.22 ± 0.78^{b}	5.93 ± 0.28^{b}
AMF inoculation				
Rhizatech	33.49 ± 0.52^{a}	10.09 ± 0.35^{a}	37.84 ± 0.05^{a}	6.47 ± 0.34^{a}
Consortium	32.73 ± 0.56^{a}	9.64 ± 0.39^{a}	36.38 ± 0.66^{a}	6.36 ± 0.32^{a}
Control	32.10 ± 0.53^{a}	8.47 ± 0.30^{b}	33.54 ± 0.78^{b}	6.39 ± 0.40^{a}
P-values of main factors and their interactions				
Maize genotype (G)	**0.0001**	< **0.0001**	**0.0023**	< **0.0001**
Site	< **0.0001**	< **0.0001**	0.1118	< **0.0001**
AMF inoculation	0.1426	**0.0003**	< **0.0001**	0.9580
Site × Maize G	0.5018	**0.0007**	0.5704	**0.0282**
Maize G × AMF	0.7898	0.7550	0.5544	0.7774
Site × AMF	0.1156	< **0.0001**	0.2661	0.4171
Site × Maize G × AMF	0.6913	0.0818	0.5787	0.7470

Values are presented as mean ± Standard Error of the Mean (SEM), and values followed by the same letters in a column within each major factor have no significant differences at $p < 0.05$ (Tukey's HSD test).

Nithi county, averaging 9.19 t ha^{-1} and 8.75 t ha^{-1}), respectively. Across the three maize genotypes, Rhizatech and consortium inoculation consistently manifested higher grain yields in Kitui county compared to non-inoculated genotypes (Fig. 3). However, this trend did not hold true in Embu County, whereby AMF inoculation did not significantly affect grain yield across the three genotypes (Fig. S7). In season two, a significant interaction effect between site × maize genotype ($p = 0.0282$) was observed (Table 5; Fig. S8). The yield performance of Duma 43 was 35 % lower in Tharaka Nithi County compared to that of Embu County. In both counties, KDV 4 and DH 02 exhibited comparable yield performances, averaging 5.96 t ha^{-1} and 5.41 t ha^{-1}, respectively, which was lower compared to Duma 43 (7.88 t ha^{-1}) (Fig. S8).

3.9. Effects of AMF inoculation, maize genotype, and site on harvest index (HI)

In the first season, the harvesting index (HI) varied significantly ($p < 0.0001$) among sites and AMF inoculations ($p < 0.0001$). Maize in Kitui County recorded the highest HI (0.535 ± 0.01), significantly exceeding the values observed in Tharaka Nithi (0.346 ± 0.01) and Embu (0.318 ± 0.02) Counties (Table 6). A significant interaction was observed between site × AMF ($p < 0.0001$). In Kitui County, the HI values of maize did not show significant differences across Rhizatech (0.518 ± 0.06), consortium (0.527 ± 0.03) and control (0.560 ± 0.04), treatments (Fig. S9). However, in Embu County, both consortium-inoculated plants (0.354 ± 0.01), and un-inoculated controls (0.387 ± 0.05) exhibited significantly higher HI values compared to maize inoculated with Rhizatech (0.212 ± 0.05) (Fig. S9). In the second season, maize plants in Kitui County failed to reach maturity due to prolonged drought. In Tharaka Nithi and Embu Counties, no significant differences in HI values were observed across different maize genotypes or AMF inoculations (Table 6, Fig. S9).

3.10. Principal component analysis (PCA) on the effect of AMF inoculation on maize agronomic, physiological, and nutrition traits

A PCA biplot was used to visualize correlations between maize agronomic traits (plant height, plant diameter, stover dry weight, 100-seed weight, and grain yield), physiological traits (AMF root colonization percentage, chlorophyll content, and water status), and a nutritional trait (shoot phosphorus content) as influenced by AMF inoculation and site (Fig. 4). In both seasons, PCA biplots showed variability of data across the three sites and three inoculation treatments. In the first season, the first two principal components (PCs) explained 51.6 % of the total variance (PC1: 29.9 %, PC2: 21.7 %). Growth and production traits (stover dry weight and plant diameter) positively correlated with PC1, while physiological (root AMF colonization) and nutritional (shoot P) traits correlated with PC2 (Fig. 4). Similarly, in the second season, the first two PCs explained 53.7 % of the total variance (PC1: 30.9 %, PC2: 22.8 %). Here, plant height and water status were associated with PC1, while production traits (100-seed weight, stover dry weight, and grain yield) and shoot P co-varied with PC2 (Fig. 4). Among the measured parameters, notable correlated traits in season one were shoot P and root AMF colonization, water status and grain yield, stover dry weight and plant diameter, root AMF colonization, and chlorophyll content. Season two displayed correlations between plant diameter and chlorophyll content, plant height and water status, and stover dry weight and grain yield. Interestingly, regarding AMF inoculation, the Rhizatech and consortium treatments clustered separately from

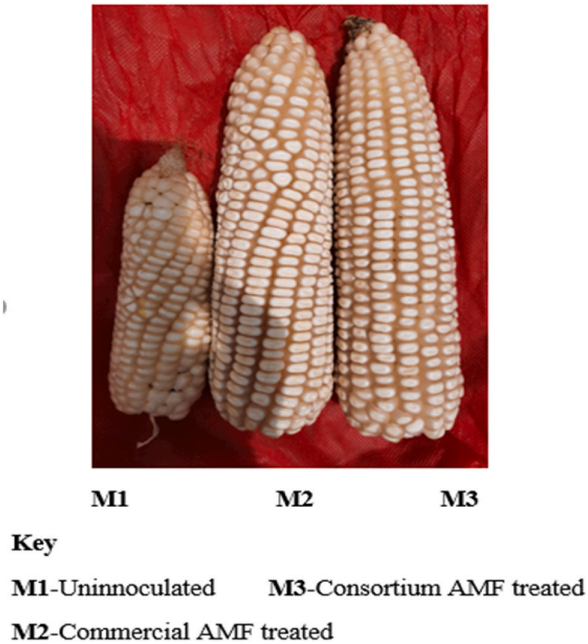

Fig. 3. Differences in maize cob (with seeds) sizes of Duma 43 genotype in Kitui county, season 1. M1, un-inoculated control; M2, consortium AMF inoculation and M3, Rhizatech AMF inoculation.

Table 6
Effects of site, genotype, and AMF inoculation on maize harvest index across two contrasting seasons.

Treatments	Season One	Season Two
Site	Harvesting Index	Harvesting Index
Tharaka-Nithi	0.346 ± 0.013[b]	0.461 ± 0.007[a]
Kitui	0.535 ± 0.010[a]	–
Embu	0.318 ± 0.015[b]	0.470 ± 0.008[a]
Genotype		
Duma 43	0.39 ± 0.015[a]	0.474 ± 0.009[a]
DH 02	0.408 ± 0.018[a]	0.465 ± 0.010[a]
KDV 4	0.402 ± 0.017[a]	0.457 ± 0.008[a]
AMF inoculation		
Rhizatech	0.366 ± 0.017[b]	0.464 ± 0.009[a]
Consortium	0.400 ± 0.016[ab]	0.459 ± 0.008[a]
Control	0.433 ± 0.016[a]	0.472 ± 0.010[a]
P-values of main factors and their interactions		
Maize genotype (G)	0.4946	0.3391
Site	< **0.0001**	0.3185
AMF inoculation	< **0.0001**	0.4928
Site × Maize G	0.1839	0.1122
Maize G × AMF	0.2220	0.4458
Site × AMF	< **0.0001**	0.0558
Site × Maize G × AMF	0.6913	0.7814

Values are presented as mean ± Standard Error of the Mean (SEM), and values followed by the same letters in a column within each major factor have no significant differences at $p < 0.05$ (Tukey's HSD test).

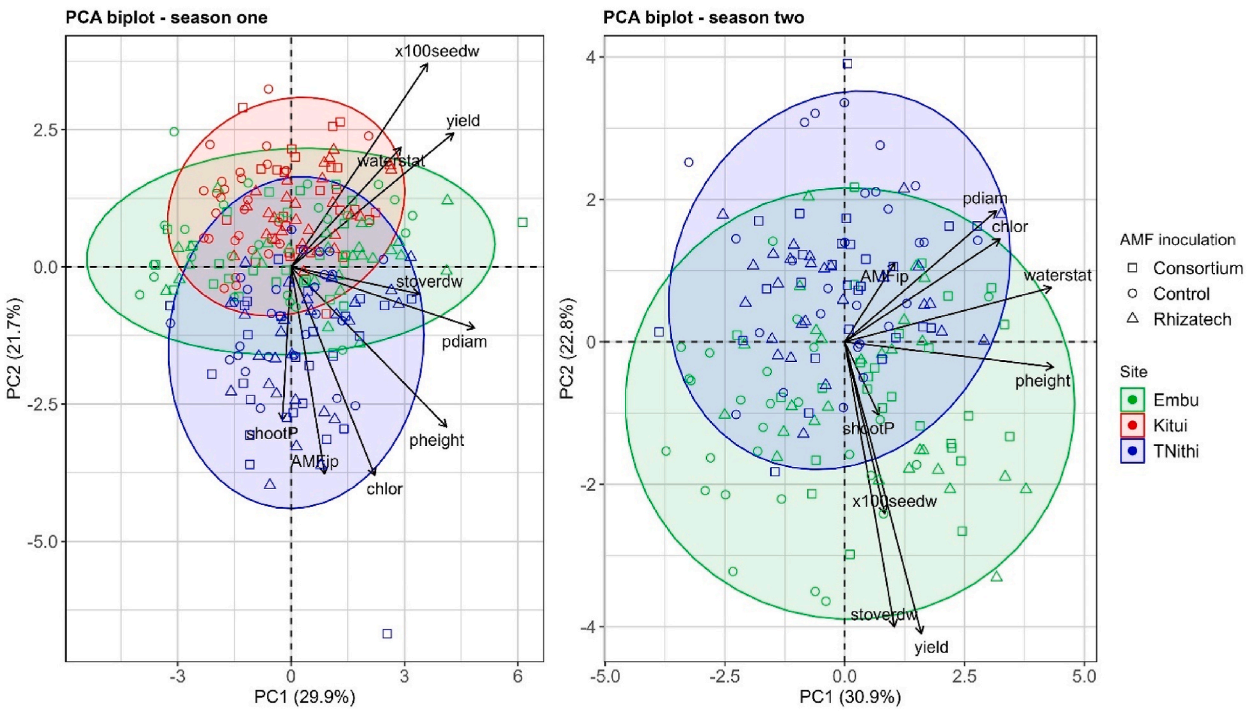

Fig. 4. Principal component analysis (PCA) showing the relationships among agronomic, physiological, nutritional, and mycorrhizal traits of maize as influenced by AMF inoculation, maize genotype, and site in seasons one and two. In season two, data from the Kitui site were not included because of the missing agronomic data. Extreme drought destroyed maize, and no data was collected beyond the V4 stage. AMFip; AMF root colonization, chlor; chlorophyll content, pdiam; plant shoot diameter, pheight; aboveground shoot height, shootP; shoot phosphorus content, stoverdw; stover dry weight, waterstat; aboveground shoot water status, ×100seedw; 100-seed weight, and yield; grain yield.

the controls in both seasons, with a more distinct separation evident in each site during the second season (Fig. 4).

4. Discussion

4.1. Differential influence of AMF inoculants on maize growth and yield parameters is dependent on agroecological zones and growing seasons

Generally, inoculation of maize with Rhizatech and consortium AMF inoculants exhibited the potential to enhance growth and yield parameters such as shoot height, stover dry weight, 100 seeds weight, and grain yield, compared to non-inoculated controls in at least one of the seasons (short-rain and long-rain) and agroecological zones (Upper midland, lower midland and inner lower midlands). Our study provides evidence of the selective nature of mycorrhizal symbiosis in three field-grown maize genotypes (Duma 43, KDV 4 and DH 02), where the benefits for the plant host depend on the responsiveness of the host genotype to AMF intrusion and the adaptability of both the host genotype and AMF to the environmental conditions including climatic and edaphic factors. Our results are consistent with the findings of Liang et al. [45], who demonstrated that mycorrhizal effect in maize is largely dependent on host genotypic identity and edaphic conditions.

AMF improves the mobilization and absorption of important minerals and organic carbon from the soil, which can translate to improved plant growth [17,46]. However, this outcome, in most cases, is dependent on plant host-AMF specificity, which determines the success or failure of the symbiosis [47,48]. Our field study revealed a fascinating interaction between AMF inoculants and maize genotype in relation to plant height during the second season. In Kitui county, which received the lowest mean seasonal precipitation (124.6 mm in season two) compared to Tharaka Nithi (197.66 mm) between March and July, maize genotypes Duma 43 and KDV 4 displayed a significant positive response to AMF inoculation compared to their non-inoculated counterparts. This differential response can be attributed to the varying water stress tolerance of the genotypes. Duma 43 and KDV 4, unlike DH 02, which was specifically bred for dryland regions, are less adapted to water scarcity. This water stress likely drove Duma 43 and KDV 4 to rely more heavily on AMF symbiosis for nutrient and water acquisition. This concept of genotype-specific responses to AMF under water stress is supported by Quiroga et al. [49], who found that AMF symbiosis improved maize development in drought-sensitive genotypes more than in drought-tolerant genotypes. The authors propose that in drought-sensitive plants, AMF down-regulates aquaporin genes and regulates involved in plant water transport.

Embu and Tharaka Nithi counties received nearly the same amounts of precipitation in the second season (305.14 mm and 256 mm, respectively), and the plants may not have experienced the same levels of water stress as in Kitui County. However, the two sites had contrasting soil properties. The study sites in Embu had higher soil organic carbon total nitrogen but with less available phosphorus (P) compared to the Tharaka Nithi sites. These geo-ecological differences can be attributed to the geographical location of the two counties as Embu County is on gentle slopes hence lesser risks of soil erosion [50]. In contrast, Tharaka-Nithi County has notably high phosphorus levels. The lower organic carbon and nitrogen levels in Tharaka-Nithi imply a potential need for additional soil amendments [51]. Soil texture further differentiates the counties: Tharaka-Nithi's sandy soils may require more frequent irrigation and nutrient management [52], while Embu's balanced clay and silt content supports better water and nutrient retention. The soil nutritional differences may also be attributed to the crop diversity used in the rotations, land use and management practices, considering that slopy topography may dictate or restrict the use of certain agricultural practices. The differential influence of AMF inoculants observed in this study emphasizes the need for region-specific strategies to optimize soil fertility and improve agricultural productivity across diverse landscapes.

Studies suggest that high soil P might even suppress the ability of AMF to contribute to plant growth. This could be through a decrease in nutrient exchange efficiency or downregulation of other beneficial effects AMF can have [53,54]. Thus, the contribution of AMF in inducing maize growth may have been more significant in Embu sites with less soil P than in Tharaka Nithi sites.

In addition, and consistent with our observation, a study by El-Fatta demonstrated that the use of a mixture of AMF inoculants can enhance water use efficiency (up to 34 %) in plants experiencing water stress compared to well-watered conditions [55]. According to the authors, this effect is attributed to the extensive development of the AMF hyphal network in conjunction with root hairs under water stress conditions. This enhanced network effectively increases the surface area for water and nutrient absorption, thereby mitigating the water deficit for the plant. The enhanced height in AMF-inoculated plants in our study is also consistent with what was reported by Vanitha et al. where treatment of *Osmium kilimandscharicum* with *Glomus fasciculatum* showed a significant improvement in the plant height and fresh weight parameters [56].

Stover dry weight is an important parameter to investigate in maize production because it is a food source for animals and can also be plowed back to the farm as crop residues to provide nutrients for subsequent crops [57,58]. Across all genotypes, biomass accumulation and grain yield were greater in the first season compared to the second season, with an average increase of 176 % and 146 %, respectively, under higher precipitation conditions (first season). Duma 43 consistently produced heavier stover dry weight and grain yield compared to DH 02 across both seasons in Embu County and in season one in Kitui County. The difference is likely due to inherent genetic characteristics and, to some extent, due to the responsiveness to specific environmental conditions. Data collection for stover dry weight and grain yield was unfortunately not possible in Kitui County during the second season due to severe drought and locust infestation. These factors resulted in complete crop failure after the V4 (fourth leaf) growth stage. This highlights the sensitivity of maize to water stress during critical reproductive and maturity stages, as evident by the minimal rainfall (<15 mm) recorded in June and July, which is insufficient to sustain maize growth during these crucial periods.

The selective effect of mycorrhizal inoculation on grain yield was more evident in Kitui County during the first season. Here, Rhizatech and consortium AMF inoculations significantly increased grain production compared to non-inoculated controls. However, this positive effect was not consistent across all locations and seasons. For instance, no significant effect of inoculation on yield was observed in Embu County during the first season or in any location during the second season. Several factors might explain this variation. This shows that Rhizatech and consortium inoculants typically contain specific AMF strains that are effective in promoting maize growth and yield under certain conditions. Optimal performance of AMF inoculants can only be achieved under a good set of conditions: a suitable environment (soil and climatic) and host that can allow the establishment, growth and proliferation of the AMF. In the absence of ideal conditions, the efficacy of AMF inoculants that have been proven effective under controlled conditions would be low. The effectiveness of the introduced inoculum can depend on the existing community composition [33], host genetics, environmental conditions and soil properties. If the native AMF population was already robust and compatible with the maize in Embu County or during the second season, the introduced inoculum might not have provided a significant benefit. Unfortunately, this study did not analyze the native AMF composition in the study sites. Again, grain yield, unlike other growth parameters, is regulated by many factors, including soil properties and environmental conditions such as water stress. Therefore, there could be other factors that strongly determine yield other than just mycorrhiza alone. Monitoring environmental factors like soil moisture and temperature might reveal their potential influence on mycorrhizal symbiosis effectiveness [59,60].

Harvest index (HI) is a crucial measure in agricultural research, as it represents the ratio of grain yield to aboveground biomass [61]. The findings of this study demonstrate a significant variation in the HI among different sites and AMF inoculations during the first season, with Kitui County showing the highest HI values compared to Tharaka Nithi and Embu Counties. The significant site × AMF interaction suggests that the impact of AMF treatments on HI is context-dependent, likely influenced by local environmental conditions such as soil or climate, which is in line with the findings of Ion et al. [62]. The observation that Kitui County, despite having lower aboveground biomass, produced a higher grain yield compared to Tharaka Nithi and Embu Counties can be attributed to several factors related to water availability and plant physiological responses to drought conditions. Kitui County experiences lower precipitation, which can lead to water stress. Under such conditions, plants often allocate more resources to reproductive growth (grain production) rather than vegetative growth (aboveground biomass) as a survival strategy. This allows the plant to maximize reproductive success when faced with limited water availability [61,62]. Conversely, in regions with more precipitation, like Tharaka Nithi and Embu, maize plants can sustain more vegetative growth, leading to higher aboveground biomass, but this does not necessarily translate into higher grain yield.

4.2. Mycorrhizal effect on maize physiological traits is driven by AMF inoculant type, ecological region, and genotype

A complex interplay exists between AMF inoculant type, ecological factors, and maize genotype in influencing the physiological traits of maize plants [63]. Understanding how different mycorrhizal strains influence specific physiological traits such as root colonization capacity, water status, and chlorophyll content allows researchers to develop targeted inoculation strategies ideal for specific genotypes and agroecological zones [64]. For instance, by identifying maize genotypes that are more responsive to mycorrhizal colonization, plant breeders can develop maize varieties that maximize the benefits of this symbiosis. This could lead to maize cultivars with improved nutrient uptake efficiency, photosynthetic activity, water stress tolerance, and overall yield potential.

The introduction of AMF spores and mycelium into the soil increases the chances of root colonization as the seeds germinate and form the first roots [37]. In our study, root colonization by AMF was significantly enhanced by inoculation, leading to positive effects on plant water status and leaf chlorophyll content. However, these positive responses displayed a complex dependence on three key factors: maize genotype, AMF inoculant type (Rhizatech or consortium), and the specific field site. The observed interaction effects highlight this complexity. For example, during the second season, the interaction between site and AMF inoculation (for root colonization, chlorophyll content, and water status) and between site and maize genotype (for water status) were statistically significant. In relation to the three physiological traits, Rhizatech inoculant performed differently compared to the consortium inoculant in some sites and in some genotypes. In other locations, however, there were no significant differences between the two inoculants. Notably, Kitui County, which experienced the lowest precipitation during the second season, had the lowest values in all the three physiological traits measured. These findings suggest that the effectiveness of each AMF type is contingent on the specific environmental conditions and maize genotype present at each field site [65].

Different maize genotypes exhibit diverse root structures, such as root length, density, and root hair presence, which affect their ability to form symbiotic relationships with AMF. Genotypes with more extensive root systems and higher root hair density are likely to support better AMF colonization, leading to more efficient nutrient uptake [59,62]. However, this may not be realized if the soil environment (pH, texture, nutrition) and climatic factors (precipitation and temperature) are unfavorable for the plant. Different agroecological zones experience varying seasonal patterns that can affect AMF growth cycles and maize development, hence affecting their symbiotic relationships [62]. Addressing this variability through targeted genotype selection, customized or blended inoculant application, and integrated soil and crop management practices can ensure more consistent and effective mycorrhizal benefits on maize.

In addition, the components of Rhizatech and consortium inoculants may partially explain the variation in their performances. Rhizatech inoculant, which is made up of a combination of four different AMF species (*Glomus mosseae, G. intraradices, G. etunicatum,* and *G. aggregatum*), may have higher chances to colonize the roots better than the consortium AMF inoculant, which consisted of two strains, namely *Rhizophagus irregularis* and *G. mosseae.* The difference in the rates of colonization could also be due to the different colonization strategies of each AMF strain, as reported by Klironomos and Hart [66]. It has also been speculated that the high infection rates in some inoculants could be due to a positive interaction of different AMF species present in that inoculant [67].

4.3. AMF inoculation enhances maize phosphorus (P) uptake, but genotype variability and site play a role

Phosphorous is an important macronutrient in plant growth and development but is usually available in small amounts in soil and in forms that cannot be readily used by plants [68]. In this study, maize shoot P was highest in AMF-treated plants, with Rhizatech showing the most increased P uptake followed by a consortium, which was higher than the non-inoculated plants. These results are consistent with the results reported by Battini, where mycorrhiza (*Rhizophagus irregularis*) and endomycorrhizosphere bacteria facilitated phosphorus uptake in AMF-inoculated maize [69]. AMF facilitates P uptake by plants by promoting the development of AMF extra-radical mycelium, which increases the surface area over which P can be absorbed by the plants [19]. In addition, AMF secrete chelating agents (organic acids) that help solubilize these bound forms of P, making them more readily available for plant uptake [70]. In other cases, AMF acquires P from the soil and transfers it to the plant root cells through specialized structures called arbuscules, which form a direct interface for P exchange between the fungal hyphae and plant root cells [71].

Maize genotypes showed a lot of variation in shoot P content. Duma 43 performed better compared to KDV 4 across the three counties. This is consistent with the findings of Chu, who demonstrated that different maize genotypes exhibit varying responses to AMF colonization [53]. Some maize genotypes might be more receptive to mycorrhizal symbiosis and benefit more significantly from enhanced P acquisition facilitated by AMF. Genetic differences in the expression of P transporters can influence how efficiently a plant takes up P from the soil and different AMF strains have different capacities in inducing the expression of P transporter genes [70]. Our study also revealed an interesting anomaly at the Tharaka Nithi sites. Despite having higher soil P content compared to other locations, the measured shoot P concentration in maize plants at the V4 stage was the lowest. This unexpected result warrants further investigation to elucidate the underlying mechanisms. Perhaps, while the total soil P content is high in Tharaka Nithi sites, the bioavailable P fraction for plant use might be limited. As a potential eco-friendly solution, AMF inoculation can be highly beneficial in such areas where bioavailable phosphorus P is limited. Based on the findings of this study, it is clear that the interplay between soil properties, maize genetic traits, and AMF inoculation is crucial for optimizing P uptake and improving maize performance. Understanding and leveraging these interactions can lead to more sustainable and productive agricultural systems.

4.4. Spatial variation influences the contribution of AMF in enhancing maize agronomic, physiological, and nutritional traits

PCA biplot analysis revealed significant variation in maize traits across sites and AMF inoculation treatments in both growing seasons (Fig. 4). This highlights the complex interplay between environmental factors, AMF inoculation strategy, and maize physiology [22]. The first two principal components explained over 50 % of the total variance, with distinct trait associations in each season. The first season exhibited positive correlations between physiological traits like chlorophyll content and shoot phosphorus content with root AMF colonization, suggesting coordinated responses to nutrient uptake [60]. Similarly, water status displayed positive correlations with yield parameters, highlighting the potential role of AMF in water acquisition during the first season. In contrast, the second season associated plant height and plant diameter with water status and chlorophyll content, respectively, and these traits showed weaker correlations with AMF root colonization. These findings suggest a potential shift in resource allocation by maize, prioritizing water management and structural development during the drier second season. Our results, showing a season-dependent association between AMF colonization and growth/production traits, align with the concept of dynamic resource allocation influenced by environmental factors and AMF interactions [63]. Interestingly, both Rhizatech and consortium inoculations displayed separation from controls in the biplots, with a more pronounced effect in the second season. This spatial variation in response to AMF inoculation warrants further investigation to understand underlying mechanisms and optimize inoculation strategies for specific locations. While this study demonstrates the potential contribution of AMF inoculants to enhance maize productivity in semi-arid agroecosystems, several limitations must be acknowledged. First, the influence of differences in soil types and nutrition, climate, and other environmental factors may have caused the high variability on the functionality of AMF and its interaction with different maize genotypes. To gain a more comprehensive understanding of such a complex interplay between microbes, plants and environment, long term trials should be conducted across diverse semi-arid locations with varying soil typologies and a broader range of maize genotypes and AMF individual strains or their specific combinations. Some microbial combinations can produce a synergistic or antagonistic effect and this needs to be explored. Additionally, this study did not explore variations in application methods and dosages. It is also important to consider investigating other factors such as overall soil health, long-term impacts on microbial communities, and additional ecosystem services, as these factors can significantly affect maize productivity. By addressing these limitations, future studies can better elucidate the complex interplay between AMF effectiveness, seasonal variations, and maize diversity.

5. Conclusion

This study primarily demonstrated that the use of Rhizatech, a commercial AMF, and consortium AMF, (BEG 12 - *Funneliformis mosseae* and BEG 44 - *Rhizophagus irregularis*), significantly improved agronomic, physiological, and nutritional parameters in maize across various genotypes (Duma 43, KDV 4, and DH 02), agroecological sites (Embu, Kitui, and Tharaka Nithi), and seasonal conditions (one-short rain and two-long rain). The benefits of these inoculations were selective, depending on both the responsiveness of the maize genotypes and the adaptability of the AMF to local environmental conditions. Notably, the mycorrhizal effects were most significant in Kitui County during the first season, where yield increases were markedly higher compared to non-inoculated controls. This variability highlights the complex interaction between environmental factors and AMF effectiveness, as previously discussed by Kennedy and Peay [55]. Additionally, our PCA biplot analysis identified distinct trait associations across different seasons, suggesting that maize resource allocation strategies may vary with seasonal conditions. Future research should aim to further elucidate these intricate interactions and optimize AMF inoculation strategies to better suit specific maize genotypes and local conditions. Moreover, there is need to conduct research aimed at isolating locally available AMF species, bulk them and apply into the soil as they may have better competitive advantage.

Data availability statement

The datasets generated and analyzed during this study can be availed upon request from the corresponding author.

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CRediT authorship contribution statement

Kipkorir Koech: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Gilbert Koskey:** Writing – review & editing, Visualization, Software, Data curation. **Ezekiel Mugendi Njeru:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **John Maingi:** Writing – review & editing, Validation, Supervision, Project administration, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:Ezekiel Mugendi Njeru reports financial support was provided by The Future Leaders African Independent Researchers. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2024.e37659.

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