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Arbuscular mycorrhizal fungi improve morphological and yield performance of *Eragrostis tef* genotypes in Tigray, Ethiopia

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Arbuscular mycorrhizal fungi (AMF) form beneficial partnerships with most plant species, helping to improve crop resilience in tough environmental conditions. This paper analyzed how different genotypes responded to AMF inoculation, focusing on root colonization percentage (RCP) and the impact of AMF on above-ground agronomic traits. However, RCP alone may not fully explain genotype variation, and AMF effects cannot be judged solely on above-ground traits. This research aims to explore the variation in ninety tef genotypes under AMF conditions and assess how AMF and genotypes affect root and shoot morphology traits. Genotypes were sorted into six cluster groups, showing varied responsiveness to AMF, with RCP ranging from 25.03 to 72.29%. Despite similar RCP, variations in morphological traits were observed, and groups with lower RCP exhibited important traits not found in those with higher RCP, indicating RCP alone cannot indicate genotype variability. Wider Mahalanobis distance (D^2) between clusters IV and VI, I and VI, and V and VI were crucial for developing different varieties and advancing root traits through hybridization. Among the tested genotypes, *Wehni* and *Tsaeda zezew*, followed by *Gureaza*, exhibited higher scores for plant height (PH), panicle length (PL), shoot biomass yield (SBY), root length (RL), and specific root length (SRL) compared to *Simada*. However, *Wehni*, *Tsaeda zezew*, and *Gureaza* showed similar results for days to maturity (DM), grain yield (GY), harvest index (HI), root dry weight (RDW), and root depth distribution (RDD) but differed from *Simada* genotype. Moreover, the inoculated *Wehni* genotype increased in days to panicle emergence (DPE) by 72%, DM by 84.11%, PH by 73.93%, PL by 73.68%, SBY by 144.17%, GY by 254.58%, HI by 133.33%, RL by 74.16%, RDW by 216.92%, SRL by 220%, and RDD by 93.28% as compared to the non-inoculated *Simada*. Improved performance of inoculated genotypes despite genotype variability could be because AMF enhances nutrient and water uptake by increasing root and shoot growth and the inherent growth strategy of the genotypes. Small-seeded crops planted shallowly benefit from AMF, which promotes deeper root growth for better nutrient and water uptake.

Keywords Below-ground, Inter-cluster distance, Root colonization, Shallow-rooted, Tef genotypes

Eragrostis tef, commonly known as tef, is a staple food for over 85 million people in Ethiopia[1]. It is a gluten-free crop, making it suitable for individuals with celiac disease[2]. Tef productivity remains low compared to wheat and maize due to limited adoption of advanced technologies, susceptibility to lodging, poor soil fertility, and unpredictable rainfall[3–7]. Efforts to improve tef productivity include developing high-yielding varieties, tailored agronomic practices, location-specific soil test-based fertilizer recommendations, and implementing irrigation to address climate effects on rainfall patterns[8–12].

In rainfed systems, tef seeds are planted on the soil surface because tef seeds are small and won't emerge if buried with any depth unless seedlings are used[13]. Surface seeding leads to weak and shallow root development, resulting in poor performance and low yields[14]. The colonization of shallow-rooted crops by arbuscular

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mycorrhizal fungi (AMF) can enhance the morphological and agronomic traits[15–17]. This symbiotic relationship is important for crops with shallow roots, such as tef, when planted at the surface of the soil[13].

The benefits derived from the symbiotic association between crops and AMF are contingent upon the level of root colonization percentage[18]. Higher levels of root colonization increased nutrient and water uptake, leading to improved morphological growth, and crop performance in nutrient and moisture-stressed environments[19–21]. The higher root colonization percentages by AMF can improve the tolerance to disease and insect pests in crops[22,23]. Crops with higher root colonization levels perform better in soils with acidic and saline environments and heavy metal toxicity than those with lower levels of root colonization[24–27]. Inoculating crops with AMF can change root and shoot morphology, influencing crop yield[16,28]. Soil conditions, land management practices, microbial diversity, AMF species, crop management, agrochemical use, and related factors, can influence the effectiveness and root colonization levels of crops by AMF[18,29–32]. Similarly, the compatibility and effectiveness of AMF in field crops can vary across different family levels, crop types, cultivars, and genotypes[33–35].

AMF symbiosis enhances nutrient and water uptake in crops and makes them more resilient to various stresses[36,37]. However, the level of root colonization and the mechanisms of growth strategies (morphological, biochemical process, and physiological changes) can vary depending on the differences in crop types, cultivars, and genotypes[38–40]. The combined effects of biotic and abiotic stresses, AMF species, and crop varieties on root colonization levels and the mechanisms derived from symbiosis require further exploration. Crops responded differently to the combination of growth-limiting factors when colonized by AMF. Maize exhibited higher root colonization levels and effectively utilizes limited moisture during drought stress[41,42]. Sorghum exhibited a higher root colonization percentage and benefits from symbiosis by regulating hydraulic conductivity and minimizing water losses through air pores[43,44]. Similarly, wheat crops with higher root colonization withstand drought through improved osmotic potential[45]. Barley had high root colonization and withstood the drought stress through increased root volume[46]. There is significant variability in root colonization levels across different species. For example, Lehnert et al.[47] found genotypic differences in wheat root colonization levels due to genetic variability specific to AMF. Diedhiou et al.[48] reported that upland rice genotypes displayed a more positive response and higher root colonization levels than lowland rice varieties. Additionally, Li et al.[49] reported genetic variability in maize's genotypes response to root colonization by AMF.

The root colonization percentage of crops to AMF at the gene level is determined using genome-wide association analysis (GWAs)[50]. Root colonization percentage only cannot determine genotype variation[51]. Genotypes with different levels of root colonization showed different morphological characteristics. Rice genotypes colonized by AMF exhibited different root colonization levels, which resulted in varying responses in their morphological traits[35]. Genotypes with similar root colonization levels may vary on morphological and agronomic traits under different stress types. For instance, in a study by Rani et al.[52], wheat genotypes with similar root colonization by AMF showed varied strategies for adapting to drought stress. Similarly, a study by Qiao et al.[53] found that different maize genotypes with similar root colonization percentages had variations in root morphology. Similar root colonization by AMF exhibits variations in morphological traits at the genotype level[51–53]. Root colonization alone cannot fully demonstrate the genotypic variability of the crop[54,55].

The Ethiopian crop varietal development programs prioritize agronomic traits linked to yield[56]. The belowground traits are equally important. Tef is a mycorrhizal plant that forms a symbiotic relationship with AMF[57]. There is a research gap in how different tef genotypes respond to AMF, their variability in above and below-ground morphological traits, and which groups of genotypes may be important for hybridization to improve crop yield and root traits when colonized by AMF. Furthermore, previous research has mainly focused on the genetic variability of genotypes and their response to AMF in colonizing roots[34,55,58,59]. The benefits of this symbiotic relationship have been assessed based on above-ground traits related to yield[60–63], but the equally crucial below-ground traits contributing to genotype variability have not been documented. The above and below-ground traits evaluation of tef genotype response to AMF is crucial for varietal development.

We conducted two consecutive experiments to address these identified gaps. The first experiment involved a study to evaluate ninety different tef genotypes based on above and below-ground morphological traits under AMF inoculation. The second experiment was on the interaction effects of AMF and selected genotypes on above and below-ground morphological and agronomic traits. This study aims to answer the following research questions: (1) Do the different tef genotypes have cluster variations when tested under AMF conditions based on above and below-ground morphological and agronomic traits? (2) Do all the genotypes have similar responsiveness to AMF? (3) Are there possibilities for genotype selection with higher yield under existing environmental conditions and options for further hybridization programs based on yield and belowground traits? (4) What are the interaction effects of AMF and selected tef genotypes on above and below-ground morphological and agronomic traits of tef? The first objective discussed in this study was to cluster the tef genotypes based on the above- and below-ground morphological and agronomic traits under AMF and assess the level of responsiveness of tef genotypes to AMF. The second objective was to identify potential cluster groups for selection and future breeding programs for yield and root traits. Finally, the study determined the interaction effects of AMF and the genotypes on above and below-ground morphological and agronomic traits.

Materials and methods

Two consecutive experiments: Experiments 1 and 2 were conducted in a greenhouse at Axum Agricultural Research Center, located in Tigray's Axum City, Ethiopia, at an altitude of 2000 m above sea level with a latitude and longitude of 13° 29′ N and 39° 28′ E, respectively. The greenhouse had an average temperature of 25 °C during the day and 21 °C at night, with a mean daily relative humidity of 50%. Experiment 1 was conducted from July 2020 to January 2021, and Experiment 2 from February to August 2021.

Planting material and experimental designs

Experiment 1

Experiment one was conducted to cluster the genotypes and to assess possible inter-clusters for better yield and root traits among 90 tef genotypes. The genotypes included 30 improved varieties when subjected to AMF inoculation according to the above and below-ground morphological and agronomic traits performance. The sources of these genotypes are detailed in Table S1 in the Supplementary material. Following the procedure outlined by Birhane et al.[64], each genotype was inoculated with soil containing 400 spores of AMF. The experiment included 90 genotypes with five replications in 450 pots using a completely randomized design (CRD).

Experiment 2

In this experiment, two AMF groups and four tef genotypes were used. The inoculated groups received AMF inoculum containing 400 spores per pot and the non-inoculated groups were without AMF inoculum. The four local tef genotypes were *Wehni, Gureaza*, *Tsaeda zezew*, and *Simada* selected from Experiment 1 based on their AMF root colonization level. *Wehni*, *Gureaza*, and *Tsaeda zezew* genotypes had higher root colonization percentages, while *Simada* showed lower root colonization levels. The experiment had eight treatment combinations with two levels of AMF and four genotypes. The eight treatment combinations were replicated five times, resulting in 40 treatment pots arranged in a factorial completely randomized design (CRD) experiment in a greenhouse.

Soil and AMF inoculum preparation

Soil samples for both experiments were collected from areas where tef was cultivated. AMF spores were collected from the tef rhizosphere[65]. The spore density of non-autoclaved soils was estimated using the method of Brundrett et al.[66]. The soil was mixed with water and shaken, and the spores were counted under a dissecting microscope with × 400 magnification to estimate the number of spores per 100 g of soil. The spore density inoculated for Experiment 1 was 178 spores per 100 g of soil and 176 spores per 100 g for Experiment 2. This estimation was used to cultivate and multiply AMF in the greenhouse by planting *Sorghum bicolor* (Linn.) Moench. Ten cylindrical plastic pots, each containing 15 kg autoclaved soil, following the procedure Birhane et al.[64] (Fig. 1a,c) were used to multiply the spores. Accordingly, 400 spores (178 spores × 224.7 g 100 g^{-1} of soil) for Experiment 1, and (176 spores × 227.27 g 100 g^{-1}) for Experiment 2 were inoculated and maintained for two months in the greenhouse. During inoculation, 300 mL of microbial wash was added to the center of each pot using the

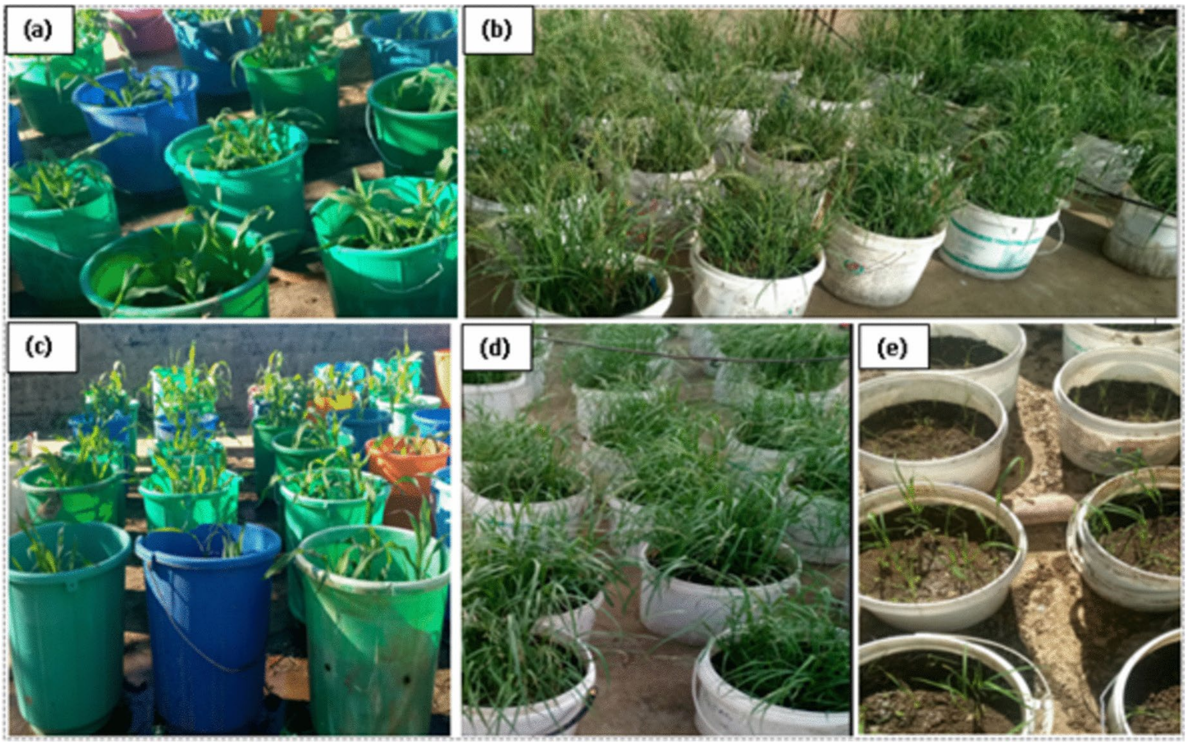

Fig. 1. Shows two separate experiments: Experiment 1, arbuscular mycorrhizal fungi (AMF) were cultivated with Sorghum bicolor (**a**). 400 spores were added to each pot during sorghum planting, and stayed for 60 days, after that, 181.8 g of cultivated AMF inoculum was added to all 90 tef genotypes during planting, and their performance was measured under AMF conditions (**b**). In Experiment 2, the AMF cultivation followed the same procedure as in Experiment 1 (**c**), but 182.7 g of cultivated AMF inoculum was only added to treatment groups (**d**) at the planting of tef, while the remaining groups (**e**) grew without AMF, all under greenhouse conditions.

extraneous extraction solution (without spores) to mimic the optimum rhizosphere ecosystem and increase AMF performance[67]. After two months, soil and sorghum roots in each pot were sampled to determine AMF root colonization and spore density. According to Birhane et al.[68], Experiment 1 had 220 spores per 100 g of soil and a root colonization of 98.96%, while Experiment 2 had 219 spores per 100 g of soil and a root colonization of 98.80%. These values were used to determine the weight of the AMF inoculum added to the two experiments. As a result of AMF cultivation, 181.8 g of soil was inoculated, including roots, in Experiment 1 for each pot and 182.7 g of AMF inoculum for Experiment 2 for the inoculated group (Fig. 1b,d) respectively.

Crop management and data collections

In both experiments, cylindrical plastic pots with 0.8 m in height, 0.6 m in diameter, and an area of 0.283 m^2 were used to plant forty seeds. For optimal growth, 92 kg ha^{-1} urea and 69 kg ha^{-1} triple superphosphate (TSP) were used as sources of nitrogen and phosphorous fertilizers, respectively. In addition, 80 kg ha^{-1} potassium chloride, 30 kg ha^{-1} calcium sulfate (gypsum), and 10 kg ha^{-1} Zinc oxide were applied as sources of potassium, sulfur, and zinc fertilizers, respectively, during planting, based on optimal recommendations for rain-fed tef cultivation in the study area[69]. Watering was done based on the field capacity of the soil, which is 39.63%, corresponding to the bulk water content retained at a hydraulic head or suction pressure of 0.33 bar[70]. The collected morphological and agronomic traits includes: (1) Days to panicle emergence (DPE): was determined by counting the number of days from sowing to the time when 50% of the plants started to emerge the tip of panicles through visual observation; (2) Day to maturity (DM): was determined as the number of days from sowing to the time when the plants reached maturity based on visual observation; (3) Plant height (PH): was measured at physiological maturity from the ground level to the tip of panicle from ten randomly selected plants in each plot; (4) Panicle length (PL): the length of the panicle from the node where the first panicle branches emerge to the tip of the panicle that was determined from an average of ten selected plants per plot; (5) Shoot biomass yield (SBY): At maturity, the whole plant parts, including leaves and stems, and seeds from the pot were harvested and after drying, the biomass was measured (g/pot); (6) Grain yield (GY): was measured by harvesting the crop from the whole pots and measured weight of grains per pot (g/pot); (7) Harvest index (HI) which refer to the ratio of grain yield to the total biomass; (8) Root Colonization Percentage (RCP) which was calculated by collecting live fine roots of inoculated tef live fine roots following the procedure of Giovannetti and Mosse[71]; (9) Root length (RL) which was measured at physiological maturity from the ground level to the tip of roots in cm for ten randomly selected plants in each pot; (10) Root dry weight (RDW) which was expressed as the oven-dry mass (mg) of sampled roots by its water-saturated fresh mass (g), expressed in mg /g; (11) Specific root length (SRL) which was expressed as the ratio of root length to mass, usually expressed as cm/g[72], and (12) Root depth distribution (RDD) which was expressed as dry root mass per volume of soil g/m^3[73]. Out of the twelve listed traits: DPE, DM, PH, PL, SBY, GY, and HI are agronomic traits for tef, and the rest are morphological.

Data analysis

Data collected from both experiments were analyzed with R-statistical software version 4.2.3[74] after checking the ANOVA assumptions using the global variability of linear model assumptions (GVLMA). For Experiment 1, one-way ANOVA was used to test the differences between the 90 genotypes. Cluster analysis of the genotypes was conducted based on Ward Jr[75] and squared Euclidean distance of the distance metric, with standardized variables performed using Minitab[76]. The genetic variability of tef genotypes under AMF conditions was measured by group distance based on multiple characters given as generalized Mahalanobis distance (D^2) statistics[77] and analyzed using the procedure of discrimination analysis by Minitab software. The average inter-cluster distance was computed according to the procedure by Singh and Chaudhary[78]. Principal components analysis (PCA) was employed to evaluate the interdependence of correlated traits and determine the optimal number of PCs using the[79] procedures. A Pearson correlation coefficient analysis was used to test the relationship between character traits[74]. In Experiment 2, a two-way ANOVA test was used, and the mean comparisons using the least significance difference test at the 5% significance level, following the procedure by Gomez and Gomez[80] in R-statistical software version 4.2.3.

Results

Cluster analysis of genotypes under AMF conditions

All the morphological and agronomic traits were significantly affected by the difference in genotypes ($P < 0.05$) under AMF inoculation (Table S2). The cluster analysis sorted 90 tef genotypes into six clusters (Table 1) in which Cluster I, II, and IV are the largest clusters, each consisting of 19 genotypes (21.11%). Cluster II and V comprised 18 (20%) and 11 (12.22%) genotypes, respectively. Cluster VI is the smallest cluster with only four genotypes (4.4%). Cluster mean values demonstrated considerable differences among the clusters for various above and below-ground traits (Table 2).

Cluster I exhibited relatively moderate plant height, panicle length, shoot biomass yield, and grain yield after clusters VI, II, and V. The genotypes in cluster I had a relatively higher root dry weight next to clusters V and IV but exhibited the least specific root length and root depth distribution among all clusters. Cluster II contained genotypes that were late in days to panicle emergence and days to maturity and had the highest shoot biomass yield, grain yield, and root colonization percentage. Cluster III exhibited the highest root depth distribution next to clusters VI and V. The specific root length and harvest index for cluster III were the least next to clusters I and V, and VI and IV respectively.

Genotypes in cluster IV had the earliest days to panicle emergence and days to maturity and the shortest plant height, panicle length, root length, and the lowest shoot biomass yield, grain yield, root dry weight, and root colonization percentage than the remaining clusters. Cluster V contained genotypes that were relatively late days to panicle emergence and days to maturity and had the tallest plant height, panicle length, root length,

Cluster	Genotype (number)	Genotype (%)	Name of genotypes (Tigrigna and Amharic languages)
I	19	21.11	Sergen Taf, Zezew, Tsaeda Taf, Gerima, Keyih Taf, Kudam, Accession_54, Tsedey, Amarach, Boset, Flagot, Tesfa, Key Tena, Zobel, Mechare, Etsub, Enatit, Gimbichu, Workiyu,
II	19	21.11	Barikay, Kuaday, Taf hagay, Tsaeda Taf Hagay, Keyih knfu, Tsaeda knfu, Kumelay, Accession_41, Accession_42, Accession_43, Accession_44, Accession_45, Accession_46, Accession_47, Quncho, Dagm, Genete, Dukom, Dega Tef
III	18	20.00	Gurade, Naeya, Eleni, Mussie, Wafey, Zagurae, Abagerima, Sergegna Taf, Mezbir, Danya, Finjal, Bkofu, Accession_57, Kebe, Lakech, Abola, Hibir, Gerado
IV	19	21.11	Taf Tsdiya, Keyihwafey, Lemlem, Adibelia, Bni, Adibelew, Accession_48, Accession_49, Accession_50, Accession_51, Accession_52, Accession_53, Accession_55, Accession_56, Accession_58, Accession_59, Accession_60, Ziquala, Simada
V	11	12.22	Shumolay, Tsaeda Fenkel, Gobezay, Tsaeda zezew, Murie, Kora, Nigus, areka_1, Dima, Ajora, Koye
VI	4	4.44	Wehni, Agam, Taftafo, Gureaza

Table 1. Distribution of tested genotypes across the six clusters based on cluster analysis.

Morphological and agronomic traits	Clusters					
	C-I	C-II	C-III	C-IV	C-V	C-VI
DPE (days)	51.34	55.36	47.53	43.68	53.84	62.41
DM (days)	110.32	114.61	106.22	102.68	112.36	121.25
PH (cm)	56.74	75.68	50.00	39.74	72.82	98.53
PL (cm)	26.67	35.57	23.50	18.68	33.22	50.44
SBY (g)	244.69	312.55	212.41	168.09	303.31	448.19
GY (g)	81.47	102.00	67.50	52.84	99.27	135.56
HI	0.33	0.33	0.32	0.31	0.33	0.30
RCP (%)	44.96	55.08	34.32	25.03	54.42	72.29
RL (cm)	32.85	44.64	28.95	23.01	42.16	55.15
RDW (g)	70.40	67.23	44.42	35.30	98.08	84.61
SRL (cm g^{-1})	0.006	0.009	0.008	0.010	0.007	0.012
RDD (g m^{-3})	207.98	210.75	314.22	221.17	331.15	334.56

Table 2. Mean values of clusters based on above and belowground morphological and agronomic character traits. DPE, days to panicle emergence (days); DM, days to maturity (days); PH, plant height (cm); PL, panicle length (cm); SBY, shoot biomass yield (g); GY, grain yield (g); HI, harvest index; RCP, root colonization percentage (%); RL, root length (cm); RDW, root dry weight (g); SRL, specific root length (cm g^{-1}), and RDD, root depth distribution (g m^{-3}). Values in each cluster represent the mean of morphological and agronomic traits based on the cluster analysis (Squared Euclidean Distance).

and higher shoot biomass yield, grain yield, and root colonization percentage next to clusters VI and II. The genotypes in Cluster VI display exceptional values in above and below-ground character traits. These genotypes boost remarkable yielding character traits, with late genotypes for days to panicle emergence and days to maturity. They had the tallest plant height, panicle length, root length, higher shoot biomass yield, grain yield, and root colonization percentage. The clusters had different AMF root colonization percentages (RCP). Clusters V, II, and VI had 54.42%, 55.08%, and 72.29% RCP, while clusters IV, III, and I had 25.03%, 34.32%, and 44.96% RCP values respectively (Table 2).

Tef genetic variability under AMF conditions

The study has identified some clusters with a high potential for heterosis. The inter-cluster divergence values (D^2) for the six clusters, were highly significant among the tef genotypes (Table 3). The largest inter-cluster distance was observed between clusters IV and VI, while the smallest was between clusters I and II. This finding suggests crossbreeding and advanced generation breeding programs may be beneficial for developing high-yielding tef varieties using AMF.

The Principal Component (PC) conducted using 12 quantitative traits revealed that in PC1, variables such as DPE, DM, HI, RL, RCP, and RDD, and in PC2, variables SRL and RDD played a major role in contributing to the total variations and were responsible for the differentiation of the six clusters. Additionally, SRL, RDD, and HI significantly contributed to the total variation from both PCs (Fig. 2).

Relationship of traits under AMF inoculations

Days to panicle emergence, maturity, plant height, panicle length, shoot biomass yield, grain yield, root colonization, root length, and root dry weight, had significant and positive correlations with most traits (Table 4). Plant height, panicle length, shoot biomass yield, and grain yield had strong positive correlations with root length and root dry weight (r = 0.99, 0.89, 0.93, 0.90, and 0.99, respectively).

Cluster	I	II	III	IV	V	VI
I	0.00	71.76**	129.74**	107.74**	127.95**	234.66**
II		0.00	165.94**	176.85**	111.84**	171.27**
III			0.00	119.16**	104.79**	259.02**
IV				0.00	190.16**	327.85**
V					0.00	155.13**
VI						0.00

Table 3. Mean average inter-cluster-squared distance (D^2) among clusters. **represent highly significant differences at the 0.01% probability level, and the critical tabular chi-square ($\chi2$) value is 24.72 at the degree of freedom of the number of traits (11, 0.01%).

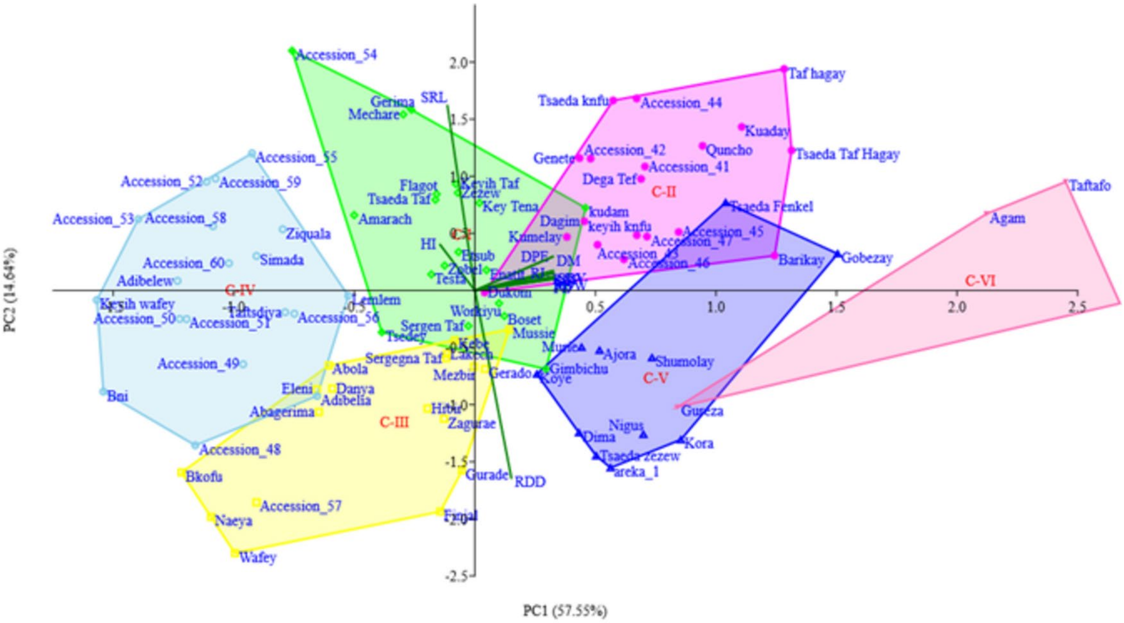

Fig. 2. Displays the results of the principal component analysis based on twelve above- and below-ground morphological and agronomic traits. The shaded boxes with different colors represent clusters, while the blue boxes with other symbols represent genotypes across various dimensions. Values with a higher vertex indicate a higher contribution, and PC1 and PC2 dimension1 and 2 respectively.

Effects of AMF and genotypes on above and below-ground traits

The main and interaction effects of arbuscular mycorrhizal fungi (AMF) and genotypes had a significant impact ($P < 0.05$) on all the morphological and agronomic traits measured (Table 5).

Above-ground morphological and agronomic traits

Shoot growth traits

AMF had a significant impact on days to panicle emergence (DPE) and days to maturity (DM). AMF inoculation delayed DPE and DM. Among the four tef genotypes, the delay in DPE and DM was pronounced in the *Wehni* genotype followed by the *Tsaeda zezew* genotype (Table S3).

The application of AMF significantly increased the plant height (PH) and panicle length (PL) of tef genotypes. *Wehni* genotype exhibited the highest PH and PL and was comparable to the *Tsaeda zezew* genotype. The lowest PH and PL were recorded for the *Simada* genotype. The non-inoculated *Wehni* and *Tsaeda zezew* genotypes had similar PH and PL. All the non-inoculated genotypes had higher PH and PL than the inoculated *Simada*. The inoculated and non-inoculated *Simada* genotypes had comparable PH and PL (Fig. 4, Table S3).

Biomass and grain yield

AMF-inoculated *Wehni*, *Tsaeda zezew*, and *Gureaza* genotypes had significantly higher shoot biomass yield (SBY), grain yield (GY), and harvest index (HI) compared to the non-inoculated *Simada* (Fig. 5a–c). All non-inoculated genotypes outperformed the inoculated *Simada* genotype on SBY except for non-inoculated *Simada* (Fig. 5a). The inoculated *Gureaza* genotype had similar GY with non-inoculated *Wehni* genotype, and the inoculated *Wehni* genotype had similar GY with the inoculated *Tsaeda zezew* genotype (Fig. 5b). The inoculated *Wehni*, *Tsaeda zezew*, and *Gureaza* genotypes had similar HI (Fig. 5c). The inoculated *Wehni* genotype showed

r	DPE	DM	PH	PL	SBY	GY	HI	RC%	RL	RDW	SRL	RDD
DPE	1.00	–	–	–	–	–	–	–	–	–	–	–
DM	0.89***	1.00	–	–	–	–	–	–	–	–	–	–
PH	0.67**	0.66**	1.00	–	–	–	–	–	–	–	–	–
PL	0.51*	0.70**	0.87***	1.00	–	–	–	–	–	–	–	–
SBY	0.63*	0.59*	0.95***	0.85***	1.00	–	–	–	–	–	–	–
GY	0.65*	0.69*	0.90***	0.84**	0.86***	1.00	–	–	–	–	–	–
HI	0.23 ns	− 0.14 ns	0.01 ns	− 0.34 ns	0.01	0.18 ns	1.00	–	–	–	–	–
RC%	0.57*	0.57*	0.69*	0.67*	0.72**	0.81**	0.20 ns	1.00	–	–	–	–
RL	0.65*	0.69*	0.98***	0.90***	0.91***	0.87***	− 0.02	0.68*	1.00	–	–	–
RDW	0.67*	0.68*	0.99***	0.89***	0.93***	0.90***	0.00 ns	0.68*	0.99***	1.00	–	–
SRL	− 0.11 ns	0.00 ns	− 0.12 ns	− 0.02 ns	− 0.09 ns	0.00 ns	− 0.09 ns	− 0.06 ns	− 0.07 ns	− 0.10 ns	1.00	–
RDD	0.00 ns	− 0.01 ns	0.12 ns	0.11 ns	0.15 ns	0.07 ns	− 0.07 ns	0.06 ns	0.09 ns	0.11 ns	− 0.41 ns	1.00

Table 4. Pearson correlation of 12 morphological and agronomic tef traits under greenhouse conditions. r (Pearson's correlation coefficient), ***,**, and *significance levels at 0.001, 0.01, and 0.05% probability level respectively, r value from 0.5 to 1.0 = positive correlation, r value from − 0.5 to − 1.0 = negatively correlated, r value from − 0.4 to 0.4 not significant correlation (ns). Morphological and agronomic traits measured: DPE (days to panicle emergence), DM (days to maturity, PH (plant height), PL (panicle length), SBY (shoot biomass yield), and GY (grain yield), and HI (harvest index), and RCP (root colonization percentage), RL (root length), RDW (root dry weight), SRL (specific root length), and RDD (root depth distribution).

Variables	Units	AMF		G		AMF *G		SEM
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value	
DPE	Days	295.64	< 0.001	257.52	< 0.001	89.454	< 0.001	2.8
DM	Days	138.54	< 0.001	100.04	< 0.001	427.78	< 0.001	6
PH	cm	112.84	< 0.001	210.66	< 0.001	43.23	< 0.001	23.5
PL	cm	102.51	< 0.001	202.71	< 0.001	36.69	< 0.001	10.7
SBY	G	266.19	< 0.001	748.89	< 0.001	153.74	< 0.001	120
GY	G	294.60	< 0.001	69.381	< 0.001	77.03	< 0.001	192
HI	%	181.24	< 0.001	31.231	< 0.001	43.14	< 0.001	0.001
RCP	%	164.63	< 0.001	10.221	< 0.001	4229.24	< 0.001	4
RL	Cm	115.43	< 0.001	214.75	< 0.001	44.18	< 0.001	18.3
RDW	G	56.666	< 0.001	25.166	< 0.001	13.83	< 0.001	296
SRL	cm g^{-1}	391.99	< 0.001	540.87	< 0.001	95.24	< 0.001	0.023
RDD	G m^{-3}	89.69	< 0.001	44.68	< 0.001	23.06	< 0.001	597

Table 5. Analysis of variance for morphological and agronomic traits is influenced by both arbuscular mycorrhizal fungi (AMF) and tef genotypes (G) and their interactions, SEM (Square Error Mean). DPE (days to panicle emergence), DM (days to maturity, PH (plant height), PL (panicle length), and SBY (shoot biomass yield), and GY (grain yield), and HI (harvest index), and RCP (root colonization percentage), RL (root length), RDW (root dry weight), SRL (specific root length), and RDD (root depth distribution). *P* values < 0.05 are significant.

significant increases in SBY, GY, and HI by 144.16%, 254.58%, and 133.33% respectively than the non-inoculated *Simada* genotype despite variations in the rate of increments. *Tsaeda zezew* and *Gureaza* genotypes had 134.37%, 240.10%, and 125%, and 113.11%, 209.38%, and 108.33% higher SBY, GY, and HI respectively than the non-inoculated *Simada* (Table S3).

Below-ground morphological traits

Root growth traits

The AMF inoculation had a significant impact on root growth traits, including root length (RL), root colonization percentage (RCP), specific root length (SRL), and root depth distribution (RDD) (Fig. 6a–d**,** Table 5). Among the four tef genotypes, *Wehni* displayed the highest RCP, RL, SRL, and RDD, and were statistically similar to the *Tsaeda zezew* genotype for all the root growth traits compared to the *Simada* genotype (Table S3). The inoculated and non-inoculated *Wehni* and *Tsaeda zezew* genotypes had similar trends in RL, SRL, and RDD (Fig. 6a,b,d). The inoculated *Wehni* genotype exhibited a 74.16%, 180%, and 7% increase in RL, SRL, and RDD respectively compared to the non-inoculated *Simada* genotype (Table S3).

Root biomass trait
The interaction effects of AMF and genotypes had a significant impact ($P < 0.05$) on root dry weight (RDW), and the inoculated genotypes had 52.11% higher RDW compared to non-inoculated ones (Table 5 and Table S3). *Wehni*, *Tsaeda zezew*, and *Gureaza* genotypes had consistently higher RDW performance when inoculated compared to non-inoculated *Simada* (Fig. 5d, Table S3).

Discussion

Genotype variability under AMF condition

Studying plant genotype variability is crucial for optimizing and preserving genotypes, given the challenges of climate variability and genotype loss due to climate change[81,82]. In this study, different tef genotypes had significant morphological and agronomic responses (Table S2). The variability might be attributed to genotype AMF responsiveness, with more colonized genotypes demonstrating higher shoot and root morphological characteristics. The diverse origins of the genotypes led to inherent morphological traits developed by variation in resource utilization when colonized by AMF. These findings are consistent with Bayable et al.[83] and Ashagrie et al.[84], there is variability in tef genotypes from different agroecological regions based on agronomic trait measures. Root morphological traits are important for selecting tef genotypes. Understanding the variability in root traits is crucial for selecting genotypes, as different genotypes exhibit diverse root morphological variations when depth nutrient availability and utilization are limiting[85,86].

The variations in agroecology, including moisture availability and soil fertility are essential for studying genotype variability and identifying those that thrive and adapt in stress conditions. Analyzing genotype variability across various traits enables the selection of genotypes based on specific characteristics. For example, Cluster VI and V genotypes are suitable for sufficient moisture areas. Cluster I and III genotypes are better suited for moisture-deficient areas. Certain cluster groups had better below-ground traits. Cluster VI had higher below-ground traits and Cluster IV had low AMF colonization, promising for tef improvement through root system traits (Table 3). This finding agrees with W Kebede and K Assefa[87], who recommended a cluster of genotypes with higher yield and early maturity for moisture-deficient areas of Ethiopia. Similarly, Kebede et al.[88], identified a genotype with higher grain yield and late maturity suited for high-potential zones in Ethiopia. However, previous studies did not consider below-ground traits in cluster analysis or genotype evaluation under AMF conditions.

The RCP varies widely from 25.03 to 72.29% among different cluster genotype groups, indicating diverse responses to AMF symbiosis. Previous research has observed variations in the AMF responsiveness in rice cultivars and sorghum genotypes[35,89]. Cluster groups with higher RCP (Cluster-VI) exhibited higher performance for most traits except for HI. On the other hand, cluster groups with lower RCP showed important traits such as DPE and DM, which are linked to moisture availability, and HI, an important yield trait. These traits differed from those in clusters with higher RCP, indicating that RCP alone cannot indicate genotype variability. Root colonization percentage alone cannot be used as the sole factor in determining genotype variability[54,55]. Moreover, when comparing genotypes with similar RCP (Cluster V and II), genotypes displayed differences in root traits due to unique strategies in developing root structures after colonization, indicating diverse mechanisms driving their morphological changes. Genotypes with similar RCP affect above-ground traits similarly but have varying influences on below-ground traits, showing the importance of below-ground traits in contributing to genotype variability under AMF (Table 2). Selecting parental lines from clusters with a wider inter-cluster distance (D^2) could benefit hybridization programs by producing diverse offspring with strong hybrid vigor[90]. Accordingly, genotypes from clusters IV and VI ($D^2 = 327.85$) were recommended for developing high-yielding varieties with early maturity, while genotypes from clusters I and VI ($D^2 = 234.66$) were recommended for late maturity. Genotypes from clusters V and VI ($D^2 = 155.13$) were recommended for studying below-ground traits (Table 3). Similarly, Ashe et al.[91] and Kebede and Assefa[87] reported tef genotypes from a wider inter-cluster distance can result in higher-yielding varieties and would be an option for future tef improvement programs. However, no specific clusters have been suggested for improving root growth traits through hybridization.

AMF genotypes on above and belowground traits

The AMF-inoculated genotypes showed significant improvements in all traits compared to the non-inoculated ones (Table S3). The AMF inoculated tef genotypes had increased access to soil exploration, leading to better absorption of nutrients and water[62]. This, in turn, resulted in increased rates of photosynthesis and respiration, contributing to improved root and shoot structure compared to non-inoculated genotypes[93]. AMF increases the availability of essential nutrients such as phosphorus and maximizes the absorption of other vital nutrients for healthy shoot growth and development[92]. AMF can enhance root structure, optimizing shoot and agronomic traits[62]. For example, AMF improves root crown diameter, leading to better root anchorage and enabling crop plants to absorb nutrients and water more effectively[94]. This maintains the appropriate balance of shoot-to-root ratio, resulting in maximized shoot and root traits without lodging which increased yield compared to non-inoculated genotypes[92]. AMF increases nutrient availability and uptake, enhancing respiration and photosynthesis rates, and maximizing shoot and root morphological traits[62,92]. AMF improves the root crown diameter in cereal crops and improves the root anchorage, leading to a balanced shoot-to-root ratio, which enhances morphological and yield traits without any lodging effects[93]. The maturity time of the tef genotypes has a significant impact on crop productivity under dryland farming systems[94], whether inoculated or non-inoculated. Inoculated genotypes, benefiting from the symbiotic relationship with AMF had a delay in reaching physiological maturity (Table S3). This delay favors vegetative growth and grain yield and may present challenges in dryland areas with limited rainfall. On the other hand, non-inoculated genotypes mature earlier, making them better suited for rain-fed farming systems. It is important to emphasize the ecological role of AMF and its

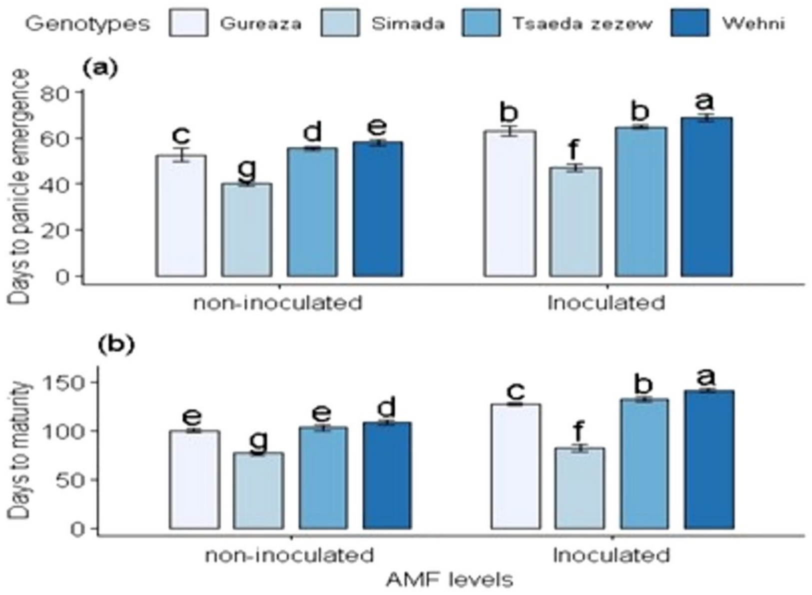

Fig. 3. Effects of AMF to days to panicle emergence (days) (**a**) and days to maturity (days) (**b**) of four tef genotypes. The bolded lower-case letters above the error bars are significantly different at the $P = 0.05$ probability level according to the least significant difference (LSD).

potential yield benefits, and integrating AMF into irrigation practices could enhance yields in moisture-deficient areas[95–98].

The interaction effects of AMF and different genotypes on both above and below-ground morphological and agronomic traits play a vital role in identifying the optimal combination of AMF and genotypes for specific agroecological settings and cultivation methods to maximize crop yields. In this study, the inoculated *Wehni* genotype exhibited superior performance in DPE, DM, SBY, and RCP compared to other inoculated genotypes. Conversely, the inoculated *Tsaeda zezew* genotype had similar performance in PH, PL, GY, HI, SRL, and RDD when compared to the inoculated *Wehni* genotype. The inoculated *Wehni* genotype had similar HI

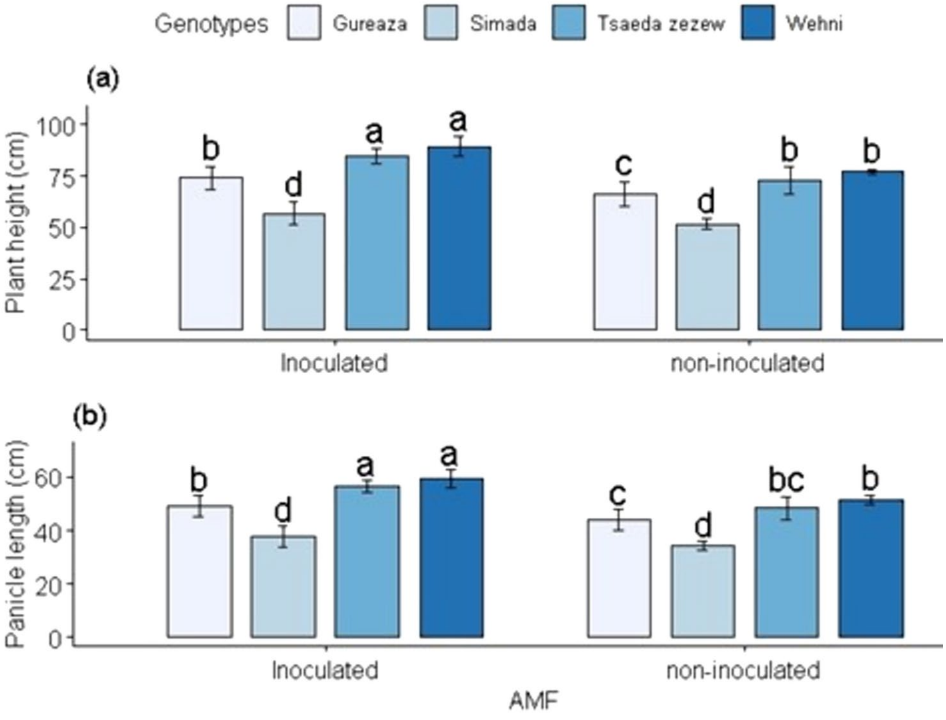

Fig. 4. Effect of AMF on (**a**) plant height, and (**b**) panicle length of four tef genotypes. Similar bolded lowercase letters above the error bar are not significantly different at the $P = 0.05$ probability level.

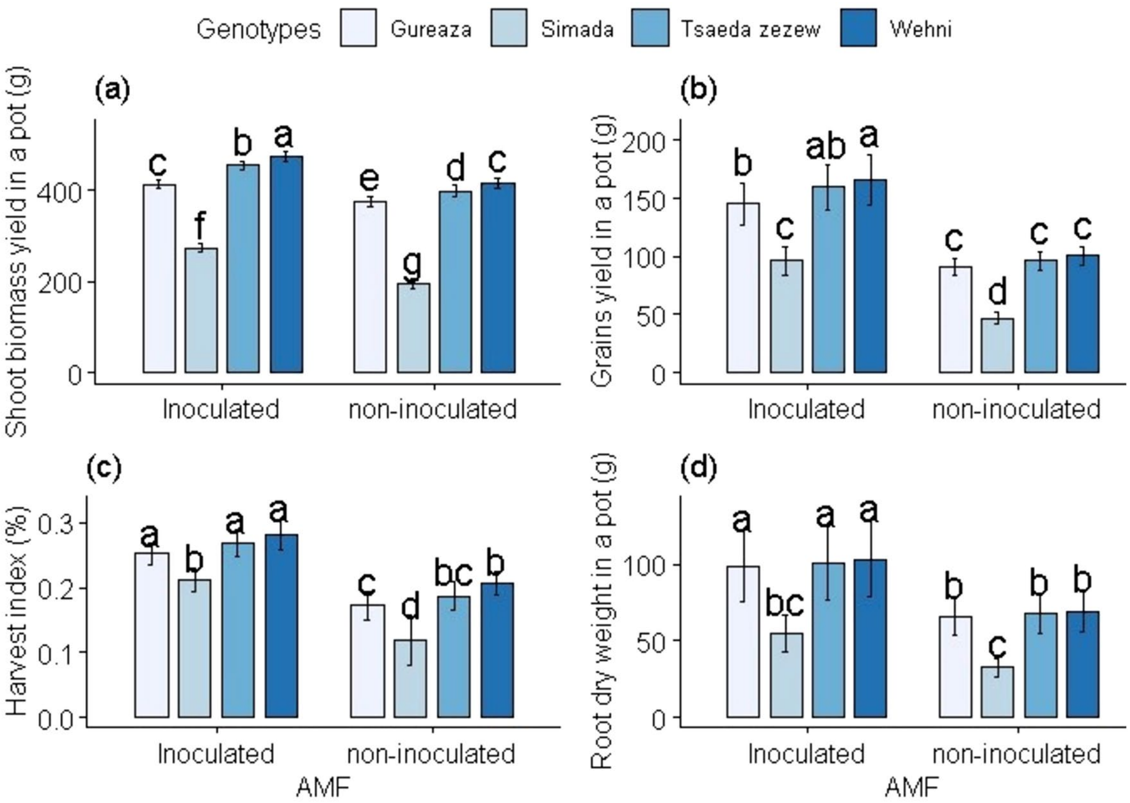

Fig. 5. Effects of AMF on (**a**) shoot biomass yield, (**b**) grain yield, (**c**) harvest index, and (**d**) root dry weight of four tef genotypes. A similar bolded lowercase letters above the error bar did not differ significantly at the $P = 0.05$ level, based on the least significant difference mean comparison (LSD).

and RDW to the inoculated *Tsaeda zezew* and inoculated *Gureaza* genotypes (Figs. 3, 4, 5, 6). These variations and inconsistency among the genotypes might be attributed to variations in AMF colonization[99], specific morphological growth characteristics of genotypes[100], root morphological changes after AMF colonization[101], and variations in nutrient uptake abilities among genotypes after roots colonized by AMF[102]. Inoculated *Wehni, Tsaeda zezew*, and *Gureaza* genotypes had higher yield traits and were well-suited for irrigation despite their delayed maturity. Conversely, non-inoculated *Wehni, Tsaeda zezew*, and *Gureaza* genotypes were better suited for areas with sufficient rainfall in the rainfed agricultural system, where a delay in days to maturity does not affect yield. The inoculated *Wehni* and *Tsaeda zezew* genotypes had better RL, SRL, and RDD, which might improve immobile nutrient management beyond the root zone. This suggests that AMF not only influences root morphology but also has the potential to enhance nutrient management and reduce production costs while offering environmental benefits. The non-inoculated *Simada* genotype matures earlier than the other genotypes, making it better suited for moisture-deficit areas where the adaptability of late-maturing genotypes is affected.

Conclusion

The assessment of genotype variability under AMF conditions revealed significant diversity, with genotypes falling into six distinct clusters based on their traits. Variations in RCP among different cluster groups indicate differences in AMF colonization. Higher RCP genotypes exhibited higher values for most traits, while genotypes with lower RCP showed important DPE, DM, and HI. Suggestions for crop improvement through hybridization were made based on genotype inter-cluster distance. Furthermore, inconsistencies were observed among inoculated genotypes, indicating different genotypes follow specific strategies in changing morphological traits after root colonization by AMF. AMF enhances shoot and root traits; however, AMF-inoculated genotypes may exhibit delayed maturity, which is more significant in irrigated areas than in rain-fed. RL, SRL, and RDD traits in AMF-inoculated genotypes are important for nutrient uptake and can reduce the need for synthetic fertilizers. These traits are crucial for crops with shallow roots, such as tef, as they help to improve root morphology and extend root systems. This study emphasizes the importance of understanding genotype responsiveness to AMF and evaluating below-ground traits under field conditions with additional genotypes and AMF types.

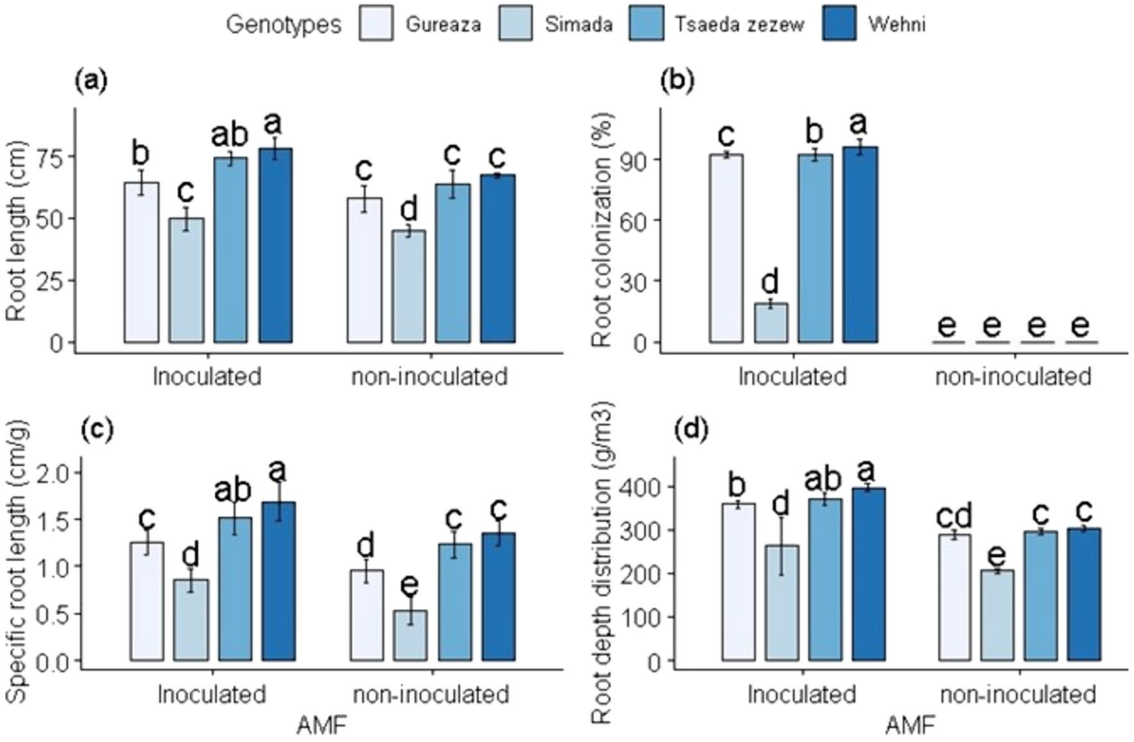

Fig. 6. Effects of AMF on root-growth traits of four tef genotypes (**a**) Root length, (**b**) Root colonization percentage, (**c**) Specific root length, and (**d**) Root depth distribution. Similar bolded lowercase letters above the error bar did not differ significantly at the $P = 0.05$ level, based on the least significant difference mean comparison (LSD).

Data availability

All data generated or analyzed during this study are included in this published article [and its supplementary material files].

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Kidu Gebremeskel: Conceptualization, Investigation, Data collection, Formal analysis, Visualization, Writing—original draft, manuscript editing. Emiru Birhane: Conceptualization, Investigation, Data collection, Formal analysis, Writing and manuscript editing, Supervision. Solomon Habtu: Investigation, Formal analysis, manuscript editing. Mitiku Haile: Investigation, manuscript editing, Supervision. Solomon Chanyalew: Investigation, Formal analysis, manuscript editing. Zerihun Tadele: Investigation, Formal analysis, manuscript editing, Supervision. Kbebew Assefa: Investigation, Formal analysis, manuscript editing. Informed consent was not required for this study because no content requires informed consent.

Declarations

Competing interests

The authors declare no financial, and non-financial competing interests.

Additional information

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