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RESEARCH

Profiling Ethiopian finger millet (*Eleusine coracana*) accessions for major agronomic traits and nutrient composition under varying drought stress

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Abstract Finger millet (*Eleusine coracana* L. Gaertn) is a drought-resilient cereal with notable agronomic and nutritional value, yet remains underutilized due to limited research and product development. The objective of this study was to profile genetically diverse Ethiopian finger millet accessions for major agronomic traits, drought response, and nutritional compositions under contrasting drought stress conditions to select genotypes for breeding or production. This study evaluated 448 Ethiopian accessions (landraces and improved varieties) for agronomic performance, drought responses and nutrient composition across three moisture regimes: non-stressed (Arsinegelle: AN), moderately drought-prone (Maitsebri: SH), and severely drought-stressed (Meiso: MI). Field trials employed a row-column design (64 × 7 with two replications). Significant ($P < 0.001$) effects of genotype, environment, and genotype × environment interaction were detected for all traits. Grain yield (GY) declined by ~ 60% at MI site. The test genotypes varied considerably at MI for key traits: days to 50% flowering (DF) (78.5–107.5 days), days to maturity (DM) (101.0–149.5 days), grain yield (GY) (0.5–3.2 t/ha), grain iron (53.6–81.0 ppm) and grain zinc (67.8–83.1 ppm) suggesting conisderable genetic varaition for selection. Black-seeded genotypes maintained higher GY and Fe/Zn under drought, while red-seeded types flowered and matured earlier and produced larger seed size. Broad-sense heritability exceeded 60% for drought tolerance (Drt) score, DF, and DM, but remained below 30% for plant height,

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starch content and GY. GY was negatively correlated with DF, DM, Drt and stay-green traits, but positively correlated with seed weight across environments. Principal component analysis explained > 67% of the variance in key traits across test sites, and hierarchical clustering grouped genotypes into four clusters. Eight accessions (G141, G423, G297, G247, G171, G204, G294, and G46) were identified as promising candidates for direct use or breeding for improved yield, nutrient density and drought resilience.

Keywords Agronomic traits · Cluster analysis · Drought tolerance · Finger millet · Grain colour · Nutritional composition · Principal component analysis

Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn.; 2n = 2x = 18) is an underutilized but high-potential cereal crop valued for its resilience to climate stress and superior nutritional profile. It is naturally gluten-free and rich in calcium, iron, dietary fibre, essential amino acids, and phytochemicals, including polyphenols, flavonoids, and antioxidants (Devi et al. 2014; Chandra et al. 2016; Gebreyohannes et al. 2021, 2024; Kaur et al. 2024). The crop is well-adapted to arid and semi-arid regions, tolerating heat and drought stress (Ceasar et al. 2018; Kudapa et al. 2023).

Globally, finger millet is cultivated on approximately 2.1 million hectares, producing an estimated annual yield of 3.7 million tons (FAOSTAT 2022; Indiastat 2022). It accounts for around 20% of the global millet cultivation area and 26% of total production (Gebreyohannes et al. 2024). In East Africa, it serves as a multipurpose crop for food, feed, and beverage production (Hilu et al. 1979; Tesfaye & Mengistu 2017). In Ethiopia, its grains are used to make traditional alcoholic and non-alcoholic drinks, as well as unleavened bread. The straw is also valued for animal feed and roofing material (Tsehaye et al. 2006; Lule et al. 2012). In Tanzania and Uganda, finger millet flour is used to prepare a staple food such as porridge and traditional beverages including 'togwa', 'obushera', and 'obutoko' (Mugula et al. 2003; Mukisa et al. 2010, 2012). These diverse uses underscore its relevance for food security, health, and economic development (Hawaz et al. 2025).

The market potential of finger millet is rapidly increasing due to its exceptional food value and superior nutritional profile, which provides valuable human health benefits (Devi et al. 2014; Chandra et al. 2016). Lifestyle changes and consumer preference for healthy and alternative nutrient-dense crops drive a shift from traditional staple crops to economical and nutritious food and feed sources, such as finger millet. The demand for finger millet products highlights the need for product diversification, strategic marketing, and commercialisation (Mugula et al. 2003; Tsehaye et al. 2006; Lule et al. 2012; Mukisa et al. 2012). Designing value-added products would leverage the crop's benefits, with the potential of amplifying its market value and stimulating economic growth. Therefore, there is a need for targeted research and development on finger millet that would include the design of market-preferred varieties integrating both climate resilience and superior nutritional profiles.

Finger millet grain productivity remains below 1 ton/ha in Africa and Asia, far less than the attainable yields reaching 6–8 tons/ha (Gebreyohannes et al. 2021; 2024). This yield gap arises from a complex interplay of biotic, abiotic, and socio-economic factors (Sasmal 2018; Mukami et al. 2019; Mahapatra et al. 2021; Mbinda et al. 2021). Lack of high yielding varieties, severe recurrent drought, fungal disease (e.g. blast caused by *Magnaporthe grisea* [Barr] and insect pests (e.g. grasshoppers, shoot flies [*Atherigona soccata* [Rondani]]), pink stem borer (*Sesamia inferens* [Walker]), root aphid (*Tetraneura nigriabdominalis* [Sasaki]) and aphids (*Aphidoidea*)) are the major constraints to sustainable production and yield gains (Sasmal 2018; Mbinda, & Masaki 2021; Mbinda, & Mukami 2021; Mahapatra et al. 2021; Mbinda et al. 2021).

Recurrent and severe drought conditions are the major production constraint of dryland millets, curtailing yield and quality (Maqsood and Ali 2007; Mukami et al. 2019). For example, yield losses ranging from 40 to 77% were reported in finger millet due to drought stress (Maqsood & Ali 2007; Khatoom & Singh 2016). Drought stress disrupts key physiological processes such as photosynthesis, stomatal regulation, and nutrient uptake, leading to premature senescence and impaired growth. Its agronomic consequences include delayed flowering, shortening grain filling, reduced biomass, and poor yield stability with

the severity depending on whether stress occurs at pre- or post-flowering stages (Maqsood and Ali 2007; Ceasar et al. 2018; Mukami et al. 2019; Sood et al. 2019). These adverse effects highlight the need to evaluate finger millet across diverse environments to identify genotypes with adaptive resilience and stable productivity under varying water stress conditions.

A lack of and poor adoption of improved finger millet varieties with desirable product profiles, including enhanced climate resilience, high-yielding capacity and superior nutritional profiles, limits sustainable crop production. Also, poor access to agricultural inputs and inadequate infrastructure contribute to the persistent yield disparities (Owere et al. 2014; Jerop et al. 2018). Therefore, to mitigate the above multifaceted constraints, there is a need for strengthening research and development investment, multi-institutional collaboration, and an inclusive innovation system that integrates breeding, agronomy, and socio-economic interventions. A strategic approach that leverages the rich genetic diversity of finger millet genetic resources is critical to mitigate production constraints and bridge the yield gap.

Finger millet is believed to have originated in the East African highlands, with both Ethiopia and Uganda recognised as primary centres of genetic diversity (Harlan 1971; Hilu et al. 1979; Tsehaye et al. 2006; Tesfaye & Mengistu 2017). The Ethiopian Institute of Biodiversity maintains an estimated 2200 collections of finger millet genetic resources, which were collected from the diverse agro-ecologies (i.e., Tigray, Amhara, Oromia, Benishangul & Gumuz and the Southern Nations, Nationalities and Peoples' Region) of the country. Also, the Ethiopian Institute of Agricultural Research (EIAR)-Melkassa Agricultural Research Centre maintains an additional set composed of 400 accessions (EBI 2024; Gebreyohannes et al. 2024). These collections are composed mainly of landraces, crop-wild relatives (i.e., *E. coracana* subsp. Africana) and released varieties offering a vital genetic reservoir for enhancing yield, drought tolerance, and nutritional quality. Hence, the diverse genotypes should be systematically characterised for breeding climate-resilient and nutritious cultivars (Tsehaye et al. 2006; Assefa et al. 2013; Brhane et al. 2017; Dida et al. 2021).

Previous studies evaluated a limited set of finger millet genetic resources of Ethiopia (Chemeda & Gemechu 2010; Bezaweletaw 2011; Tesfaye, & Mengistu 2017; Lule et al. 2018; Anteneh et al. 2019). The earlier findings provided a modest understanding of the extent of phenotypic diversity for economic traits. A more comprehensive assessment involving a larger and diverse germplasm of finger millet genetic resources across representative growing environments is required to appraise useful genetic variants for economic traits and diverse market segments.

The objective of this study was to profile genetically diverse Ethiopian finger millet accessions for major agronomic traits, drought response, and nutritional compositions under drought conditions to select contrasting and superior genotypes for breeding or production. The research seeks to appraise unique genetic resources and vital data for developing drought-resilient and nutritionally enhanced varieties.

Materials and methods

Plant materials and the study sites

The study used a collection of 448 finger millet accessions, purposefully selected to represent the genetic and agro-ecological diversity of Ethiopia for the evaluation of key agronomic traits such as yield potential, drought tolerance, and nutritional quality. Of the total collection, 425 accessions were sourced from the Ethiopian Biodiversity Institute (EBI). The 425 from EBI were previously collected from Tigray (168), Amhara (145), Oromia (86), the Southern Nations, Nationalities, and Peoples' Region (SNNPR) (17), and Benishangul & Gumuz (9). A targeted selection that comprised 23 improved varieties was acquired from various key regional and national research centres of Ethiopia. The names, region of collection and grain colour of the finger millet accessions used in the study are presented in Table S1.

Three sites were selected for the study, namely: Arsinegelle (designated as AN), Maitsebri (SH) and Meiso (MI) (Table 1). The specific sowing and harvesting months for each location during the 2019 growing season are provided to define the experimental timeline. Soil analyses were conducted following the standardized procedures according to Estefan et al. (2013). The analysis revealed that the AN site was characterized by loam soil with moderate fertility, including 2.10% total organic carbon, 0.16% total nitrogen, and a soil pH of 6.5. The MI site has

Table 1 Description of the study locations

Parameter	Location		
	Arsinegelle (AN)	Maitsebri (SH)*	Meiso (MI)
Soil texture	Loam	Clay	Clay loam
pH	6.5	6.1	7.0
Total organic carbon (%)	2.1	1.1	1.2
Total nitrogen (%)	0.2	0.1	0.1
Clay (wt/wt) (%)	26.0	42.0	36.0
Sand (wt/wt) (%)	37.0	25.0	27.0
Silt (wt/wt) (%)	37.0	33.0	37.0
Latitude	N07°19.541′	N13°41.303′	N09°13.713′
Longitude	E038°39.494′	E038°10.329′	E040°45.442′
Altitude (masl)	1933.0	1445.0	1326.0
Mean temperature (°C)	20.3	21.7	22.5
Maximum temperature (°C)	32.9	34.9	35.7
Minimum temperature (°C)	7.7	8.6	9.3
Annual rainfall (mm/year)	1223.4	632.8	394.2
Relative humidity (%)	67.0	56.0	61.0
Distance from Addis Ababa (km)	240.0	939.0	296.0
Sowing month	May/2019	July/2019	July/2019
Harvesting month	November/2019	November/2019	December/2019

Note: wt/wt = weight by weight, masl = meter above sea level,* source: Redda and Abay (2015)

clay loam soil with low organic carbon (1.20%) and nitrogen content (0.08%), and a pH of 7.03, indicating slightly alkaline soil. MI had higher clay content (36%) compared to AN (26%). The SH site, as reported by Redda and Abay (2015), possesses Vertisols with clay-texture, moderate acidity (pH of 6.1), low organic carbon (1.1%), and total nitrogen (0.1%). AN received the highest annual rainfall (1223.45 mm) and had the lowest mean (20.34 °C), minimum (7.73 °C), and maximum (32.94 °C) temperatures. Conversely, MI exhibited the highest mean (22.47 °C) and maximum (35.67 °C) temperatures, with the lowest rainfall (394.20 mm), which is characteristic of an arid environment. MI, was notably warmer, recording an average temperature of 21.72 °C and moderately dry (with 632.81 mm annual rainfall). Overall, the sites represented a diverse range of agro-ecological conditions, which are crucial for agronomic evaluation and stability tests.

Experimental design and field management

The 448 finger millet genotypes were evaluated using a 64 × 7 row-column experimental design, replicated twice at each site. The field study was conducted in 2019/20 growing season. Individual plots comprised of a single 3 m row with an inter-row spacing of 0.4 m and an intra-row spacing of 10 cm. To optimize early growth, a basal application of di-ammonium phosphate (DAP, 18% N, 46% P_2O_5) fertilizer was administered at a rate of 100 kg/ha during sowing. Urea (46% N) was not applied to facilitate natural expression and prevent lodging.

Data collection

Agronomic data

Data on agronomic traits were collected following the protocols described by the International Board for Plant Genetic Resources (IBPGR) (1985), with some minor modifications. Plant height (PH) was determined in cm by measuring five randomly selected and tagged plants per plot from ground level to the inflorescence apex at the dough developmental stage. Days to 50% flowering (DF) and maturity (DM) were quantified as the number of days from sowing until 50% of the main tillers within each plot exhibited emerged ears and fully mature ears, respectively. Grain yield (GY) was determined by harvesting the total grain from a 1.2 m^2 plot, and then adjusting the

weight to a standard moisture content of 12.5% and converting the result to tons per hectare. Thousand seed weight (TW) was determined gravimetrically (g) for a random sample of 1000 seeds.

Drought tolerance

Standardize phenotypic scoring approaches are essential for reliable characterization of drought tolerance. In this study, stay-green (SG) and drought tolerance (Drt) scores were assessed at the post-flowering stage using visual scales widely applied in finger millet and related cereals (Jordan et al. 2012; Borrell et al. 2014; Hoang et al. 2019; Kamal et al. 2019; Shin et al. 2020). The SG was visually scored on a scale of 1–5 at maturity as follows: a score of 1 indicates excellent SG and denotes strong drought tolerance, as the canopy remains fully green; a score of 2 represents good SG and reflects moderate to high drought tolerance characterized by a largely green canopy with slight yellowing; a score of 3 indicates an intermediate drought response, where noticeable yellowing occurs but partial upper-canopy greenness remains; a score of 4 signifies poor SG and indicates low drought tolerance evidenced by substantial canopy senescence; a score of 5 denotes very poor SG and high drought sensitivity, as the canopy is completely senescent. Furthermore, Drt is a composite measure of key morphological and physiological indicators, including SG ability, earliness, leaf wilting, and plant canopy vigour. It was visually assessed at maturity on a standardised scale of 1–5; where a score of 1 indicates high tolerance, where plants remain green with minimal wilting or leaf rolling, exhibit early maturity and retain good biomass; a score of 2 reflects tolerance with a largely green canopy and only mild yellowing or wilting; a score of 3 denotes moderate tolerance, characterized by partial canopy senescence, moderate leaf wilting, and delayed maturity; a score of 4 represents susceptibility, with widespread yellowing, poor canopy maintenance, and reduced vigour; a score of 5 denotes high susceptibility, marked by severe wilting, complete canopy senescence, stunted growth, or plant death.

Nutrient composition

Post-harvest nutritional composition analysis was performed at the Melkassa Agricultural Research Centre (MARC) food and nutrition laboratory in Ethiopia. Representative grain samples (150–200 g) were collected per accession from replicated plots across test sites. Samples were subjected to rigorous cleaning to eliminate extraneous materials. Moisture loss and contamination were minimized by storing cleaned samples in hermetically sealed containers. Prior to non-destructive Near-Infrared Reflectance Spectroscopy (NIRS) analysis, instrument calibration was conducted using a polystyrene reference plate with a known spectral signature. NIRS analysis was performed using a Perten IM 9500 analyser (Perten Instruments AB, Sweden) by placing the subsamples in the sample hopper. Duplicate spectral acquisitions were performed per sample, for iron and zinc contents in percent and amylose and starch content in parts per million (ppm), the mean values were used to enhance data reliability. Finally, grain colour of the test genotypes was categorized as follows: 1 = white, 2 = light brown, 3 = brown, 4 = dark brown, 5 = red, and 6 = black.

Data analysis

Diagnostic Bartlett's test of homogeneity of variance (Bartlett 1937) was conducted in each test environment, followed by a combined analysis of variance using a linear mixed model in SAS 9.4 (SAS Institute, Inc.). The mixed model treated environment as a fixed effect, and genotypes and genotypes by environment interaction as random effects to partition the phenotypic variation into its constituent components: environmental, genotypic, and their interaction effects (SAS 2013). The linear mixed model across multiple test environments was defined as follows:

$$Y_{IJKLM} = \mu + g_I + s_J + (gs)_{IJ} + b_{JK} + r_{JKL} + c_{JKM} + \epsilon_{IJKLM}.$$

Where:

- Y_{IJKLM} is the value of the variable measured from the I^{th} genotype in K^{th} replicate in L^{th} row and M^{th} column nested in the J^{th} environment.
- μ is the overall mean.
- g_I is the random effect of genotype I, $N(0, \sigma^2_g)$.
- s_J is the fixed effect of environment J.
- $(gs)_{IJ}$ is the effect of the interaction between genotype i and environment J, $N(0, \sigma^2 gs)$.

- b_{JK} is the random effect of replicate K within environment J, N(0, σ^2b).
- r_{JKL} is the random effect of row L within replicate K within environment J, N(0, σ^2r).
- c_{JKM} is the random effect of column M within replicate K within environment J, N(0, σ^2c).
- ϵ_{IJKLM} is the residual effect, N(0, σ^2_e).

Genetic parameters

Variance components, broad-sense heritability and genetic advance were computed to assess the magnitude of genetic variability and the potential for selection among finger millet accessions across three environments.

Variance components

The variance components, namely phenotypic, genotypic, and environmental variances, were computed using the expected mean squares from ANOVA summary results by following the procedure outlined by Holland et al. (2003) from the linear mixed model. To estimate the total phenotypic variance, the model integrates contributions from genotypic effects, genotype-by-location interactions, and residual errors, structured differently for multi-location and single-location analyses as follows: the Phenotypic variance (σ^2_p) was computed following the procedure described by Gebreyohannes et al. (2018) as follows: $\sigma_p^2 = \sigma_g^2 + \frac{\sigma_{gs}^2}{J} + \frac{\sigma_e^2}{KJ}$, where: σ^2_g, σ^2_{gs}, and σ^2_e represent variance due to genotype, genotype x environment interaction, and residual error, respectively; J, and K denote the number of environments and replications in that order. The genotypic variance (σ^2_g) was calculated as $\sigma^2 g = \frac{MS_g - \mathrm{MS}_{gs}}{\mathrm{JK}}$, where MS_g, and MS_{gs} denote mean square due to genotypes, and genotypes x environment interaction; J, and K are the number of environments, and replications in that order. The environmental variance (σ^2_E) was computed as $\sigma_E^2 = \frac{\sigma_{gs}^2}{J} + \frac{\sigma_e^2}{JK}$, where σ^2_{gs}, and σ^2_e are the variance due to genotype x environment interaction and residual error, respectively; J, and K represent the number of environments and replications, in the same order.

Genetic parameters, correlation, principal component and cluster analyses

Genetic parameters, including broad-sense heritability (H^2), genetic advance (GA) and genetic advance as percent of mean (GA%) were computed according to Johnson et al. (1955) and Holland et al. (2003). The (H^2) was calculated across and single locations: $H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{gs}^2}{K} + \frac{\sigma_e^2}{KJ}}$ (multi-locations), and $H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{K}}$ (single-location), where: σ^2_g, σ^2_{gs}, and σ^2_e represent variance due to genotype, genotype x environment interaction, and residual error; J, and K denote the number of environments and replications, respectively. The GA and GA% were estimated following the procedure described by Johnson et al. (1955). GA was computed using the formula: GA = K x $H^2\sqrt{\sigma^2_p}$, where K is the selection intensity at 5% (2.06), σ^2_p = Phenotypic variance, while GA% was computed as GA% = $\frac{\mathrm{GA}}{\mu}$x100, where GA = genetic advance and μ = the overall mean.

Multivariate analysis

Phenotypic correlation analysis was determined to discern the pattern and magnitude of association for assessed agronomic, nutritional traits and drought-tolerant traits for each environment using the corrplot package (Wei and Simko 2024). Hierarchical clustering and a red-blue diverging scale facilitated the interpretation of positive and negative associations, enabling the identification of key trait combinations relevant for breeding (Kassambara 2017).

Principal component analysis (PCA) was done to dissect interrelationships of the finger millet genotypes within the agronomic and nutritional traits, and drought tolerance characteristics using the FactoMineR (Lê et al. 2008) and factoextra (Kassambara & Mundt 2016) packages in R version 4.1.2 (R Core Team 2021). Eigenvalues and eigenvectors were computed to derive the percent variation explained by the respective principal components (PC's) and variable loading scores, which assorts individual trait contributions. Subsequently, PC biplots were constructed to visualize genotype-trait associations.

Hierarchical clustering with complete linkage was applied to the standardised trait data, and genotypes were assigned to four clusters. Cluster membership was extracted using the cutree function, and genotype names within each cluster were listed to characterise group composition. To further describe cluster properties, mean values of traits were calculated for each cluster using the aggregate function (Kaufman & Rousseeuw 2009; Kassambara 2017).

Results

The effect of genotypes, environments, and their interaction on agronomic traits, drought response and nutritional profiles

Table 2 summarises the results of the combined analysis of variance for agronomic traits. Highly significant ($P < 0.001$) differences were observed among the main effects of genotypes, environments, and their interactions for all the agronomic traits. The coefficient of variation (CV) ranged from 2.3% for days to 50% flowering to 13.5% for grain yield, while the proportion of explained variance (R^2) varied from 88.5% for thousand seed weight to 99.0% for days to 50% flowering. Further, genotypes, environment, and their interactions significantly affected SG score (SG) and drought tolerance (Drt) score (Table 2). The CVs ranged from 16.0% for Drt to 21.8% for SG, while the R^2 values varied from 90 (SG) to 92% (Drt). The nutritional parameters, such as amylose (Am), starch (Stc), iron (Fe), and zinc (Zn) concentrations, were significantly ($p < 0.01$) affected by genotypes, environments, and genotype by environment interaction. The CV values were low 2.3% (for AM) to 10.9% (Fe), while the R^2 values ranged from 71% (Stc) to 92% (Zn) (Table 2).

Mean performance of test genotypes for the assessed traits

Agronomic traits Figure 1 and Supplemental Table S2 summarise agronomic traits across three locations, namely: Arsinegelle (denoted as AN, non-stressed environment), Maitsebri (SH, moderately drought-stressed), and Meiso (MI, highly drought-stressed). Drought significantly impacted agronomic traits at the MI site compared to the non-stressed environment (AN) and moderate stress environment (SH). At MI, drought stress led to a 17.4% reduction in thousand-grain weight (Fig. 1 and Supplemental Table S2). Furthermore, grain yield at MI was significantly affected by drought stress. Overall, yield reductions varied from 33.0% (SH) to 60.0% (MI) relative to AN.

The top ten best-performing and bottom five poor-performing were selected based on grain yield response under stressed conditions (MI) (Supplemental Table S2). The top performers were G141, G423, G297, G247, G18, G432, G195, G223, G435, and G171 with higher grain yield of > 2.5 t/ha, and early flowering (< 90 days) and maturity (< 122 days). The mean grain yield of the best-performing genotypes was 2.69 t/ha at MI and 3.46 t/ha at AN, corresponding to an average yield loss of approximately 22.25% due to drought stress (Table 3). Of the test genotypes, G141, G423, G297, and G247 were high yielding at 3.2, 2.9, 2.8, and 2.7 tons/ha, respectively, at MI. The genotypes G257, G198, G361, G296, and G333 were high-yielding and recorded grain yields of 6.6, 6.4, 6.2, 6.0, and 6.0 tons/ha, in the same order, at AN. None of the released finger millet varieties were ranked among the top ten performers at the non-stressed environment, AN. However, in a stressed environment, MI, genotypes G432 and G435, officially released as cultivar Mecha (229,371) and Meba (GBK011119A), demonstrated superior performance for grain yield at 2.6 t/ha and 2.5 t/ha, respectively (Fig. 1). These high-yielding genotypes at MI were early flowering, with 85–96 days to 50% flowering and 113–133 days to maturity. These genotypes were moderately tall (122.5–149.0 cm) with moderate to higher seed weight (1.5–2.8 g/1000 seed). The grain colour was predominantly dark brown (38.8%), black (37.1%), and brown (12.7%) accounting for the total assessed finger millet genotypes. In contrast, the bottom five performing genotypes at MI, including G239, G49, G128, G37, and G50, displayed consistently low yields with a mean of 0.56 tons/ha compared to 1.68 t/ha at AN, which resulted in a yield penalty of 66.7%. Furthermore, the genotypes showed slightly delayed flowering (94–101 days) and maturity (128–142 days).

Table 3 presents the variation in agronomic traits in grain colour groups across three environments. The common grain colours of the finger millet accessions were dark brown, black, brown, white, and red.

Table 2 Combined analysis of variance showing mean square values and level of significance for the studied agronomic traits, drought parameters and nutritional profiles of 448 finger millet accessions evaluated at Arsinegelle, Maitsebri and Meiso sites in Ethiopia

Sources of variation	Degree of freedom	Agronomic traits					Drought parameters			Nutrition profiles		
		DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Fe	Zn
		Mean squares and significant tests										
Genotypes	447	119.4**	469.5**	330.6**	1.9**	0.3**	2.6**	5.1**	0.7**	71.7**	253.1**	38.5**
Environments	2	250,327.8**	581,367.3**	202,375.9**	768.7**	33.5**	205.2**	56.0**	98.3**	2760.0**	43,789.8**	2708.7**
GEI	894	17.5**	314.7**	46.7**	1.0**	0.1**	1.1**	0.7**	0.4**	47.1**	105.9**	15.9**
Columns(Rep)	12	36.0^{NS}	415.6**	92.6^{NS}	0.1^{NS}	0.02^{NS}	0.5*	0.4*	0.4**	41.2^{NS}	187.9**	18.8**
Rows(Rep)	126	5.7^{NS}	120.1^{NS}	15.8^{NS}	0.1^{NS}	0.04*	0.2^{NS}	0.2^{NS}	0.2^{NS}	2476^{NS}	38.4^{NS}	5.4^{NS}
Rep(E)	2	94.4**	805.0**	266.5**	0.7**	0.2*	3.0**	3.1**	1.0**	12.7**	167.8*	37.0
Error	1116	5.5	99.2	14.8	0.1	0.03	0.3	0.2	0.2	29.8	46.1	5.4
Trial statistics												
CV(%)		2.3	9.2	2.8	13.5	8.9	21.8	16.0	2.3	10.9	10.8	3.1
R^2 (%)		99.0	93.2	97.1	97.3	88.5	90.1	92.2	80.3	71.4	85.2	86.1
LSD (5%)		2.7	11.3	4.4	0.3	0.2	0.6	0.5	0.5	6.2	7.7	2.6

Note: ^{NS}, * & ** denotes non-significant, significance at the 5, and 1% probability levels, respectively, GEI = Genotypes by environment interactions, Columns(Rep) = columns nested in replication, Rows(Rep) = rows nested in replication, Rep(E), replication nested in environment, CV% = coefficient of variation, R^2(%) = coefficient of determination, LSD = least significant difference at 5% level of significance, DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn = zinc content (%)

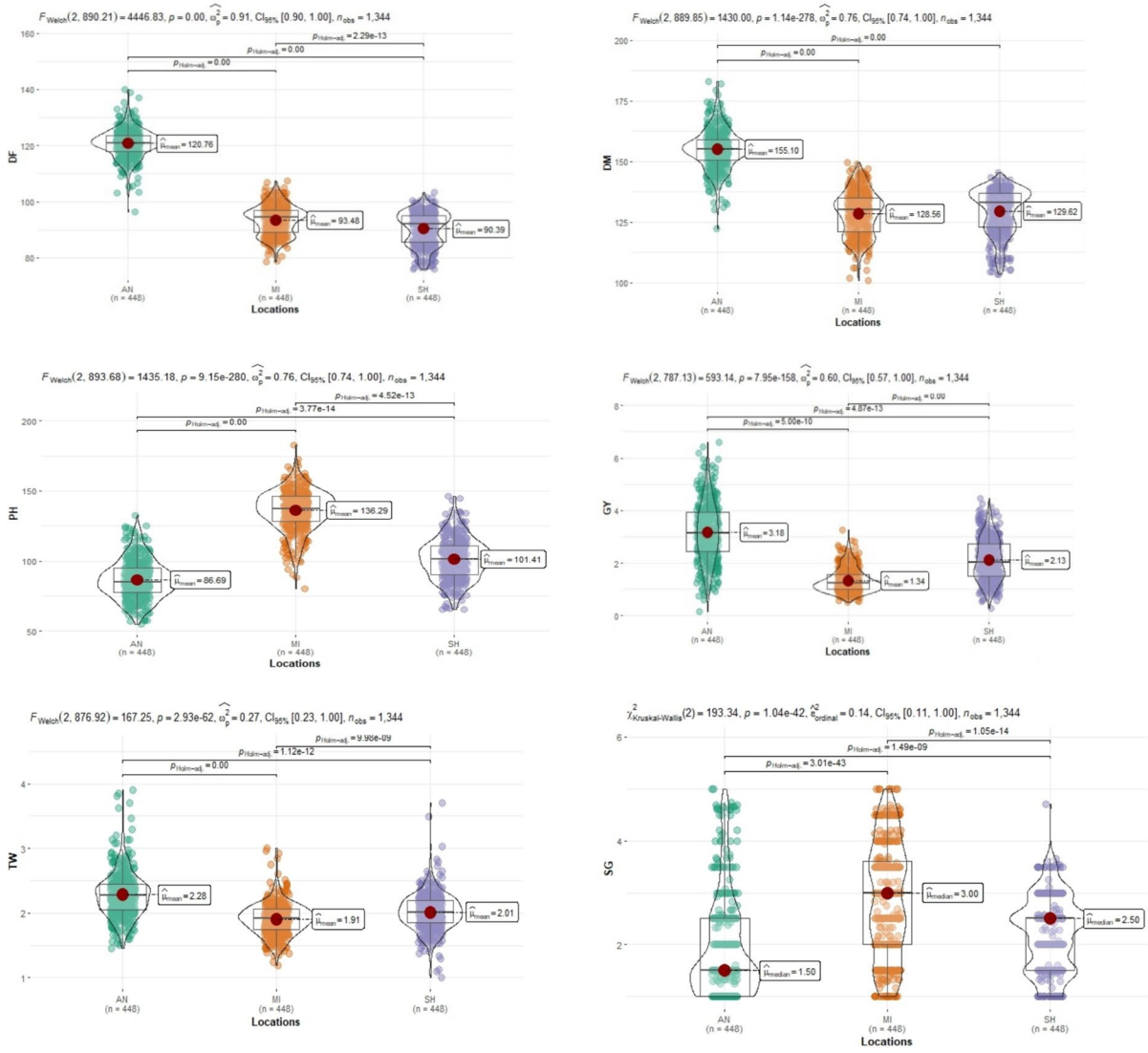


Fig. 1 Distribution of agronomic, drought-responsive, and nutritional traits of 448 finger millet genotypes across three locations in Ethiopia. Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn = zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri

There were variations in grain colour, panicle and nodal pigmentations (Fig. 2A–E). Across locations, black and dark brown grain colour groups consistently demonstrated superior agronomic performance, notably associated with higher grain yield. Furthermore, genotypes with red grains displayed the shortest time to flowering (89–111 days), and maturity (115–141 days) across the test environments. At AN, black seeded types achieved the highest grain yield (3.4 t/ha), while red types matured earlier (141.3 days), and had higher thousand seed weight (2.7 g). In SH, grain yields across grain colour groups were relatively moderate (2 tons/ha). However, genotypes with black and dark brown grain colours exhibited relatively better performance, particularly in terms of grain yield (2.1–2.2 tons/ha). Overall, the lowest grain yield was observed in the MI site; however, the black and red types demonstrated

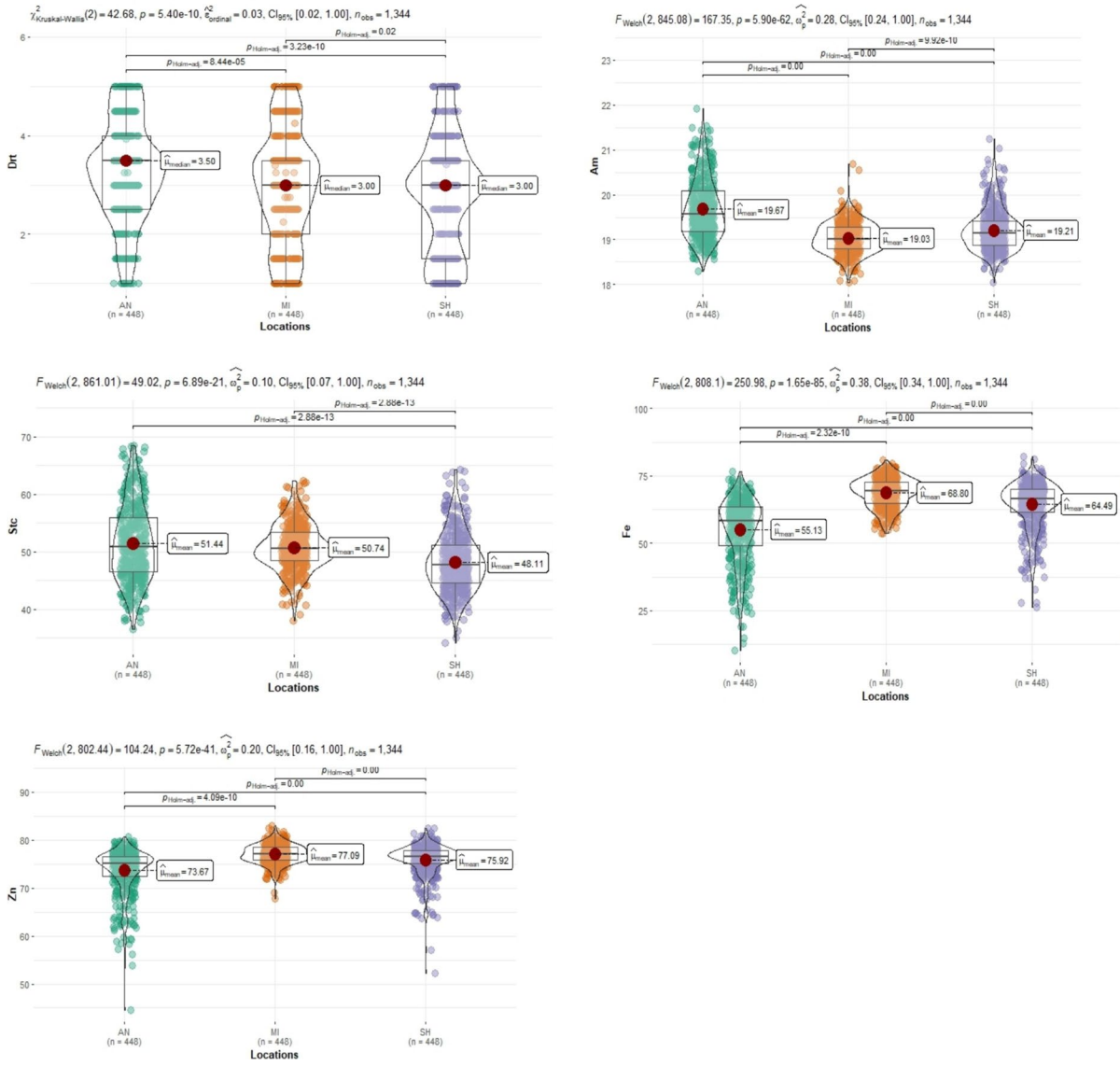


Fig. 1 (continued)

comparatively better performance, maintaining slightly higher grain yield (1.4–1.6 tons/ha) compared to other groups.

Nutritional profiles

Figure 1 displays the mean performance of finger millet genotypes for the nutritional profiles across the contrasting test sites. Unlike most agronomic and drought-related traits that were affected by drought stress, certain nutritional traits, such as iron and zinc concentrations were unaffected under drought conditions at MI compared to the other environments. While the stressed environment, MI, maintained relatively higher levels of iron and zinc, which declined more significantly under the potential environment, AN. However, the concentrations of the amylose and starch contents appeared to remain relatively stable across the test environments (Fig. 1).

The top ten best grain yield performing genotypes displayed higher amylose content, which varied between 18.3 and 19.2%, starch content of

Table 3 Mean values for agronomic traits, drought parameters, and nutritional profiles of 448 finger millet genotypes evaluated across three test environments in Ethiopia based on seed coat colours

Grain colour	Locations	Agronomic traits					Drought parameters		Nutrition profiles			
		DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Iron	Zinc
Black	AN	121.4	88.1	156	3.4	2.3	2.0	3.4	19.4	49.0	59.9	75.7
Red	AN	111.2	74.4	141.3	3.2	2.7	1.0	1.8	20.6	58.4	37.3	66.9
Dark brown	AN	119.9	85.8	153.8	3.3	2.3	1.9	3.1	19.6	50.1	57.8	75.2
Brown	AN	121.8	86.3	156.9	2.9	2.4	2.0	3.5	20.3	56.6	41.9	69.1
Light brown	AN	124.6	88.9	161.5	2.1	2.3	2.3	4.1	20.5	59.9	38.4	65.5
White	AN	120.4	86.2	154.3	2.9	2.2	1.7	3.2	19.9	57.5	49.5	67.4
Mean	AN	119.9	85.0	154	3.0	2.4	1.8	3.2	20.1	55.3	47.5	70.0
Black	SH	90.6	101.7	130.1	2.1	2.0	2.3	2.8	19.0	46.2	67.9	77.2
Red	SH	82.1	99.0	115.3	1.8	2.3	1.7	1.6	19.5	52.0	58.9	73.7
Dark brown	SH	89.4	99.8	128	2.2	2.0	2.3	2.6	19.1	47.2	67.3	76.9
Brown	SH	92.0	102.2	131.9	2.3	2.2	1.9	3.1	19.7	51.4	54.9	73.1
Light brown	SH	94.6	100.6	135.3	1.8	2.0	2.1	3.6	19.8	53.2	53.1	71.8
White	SH	91.8	108.2	132.3	1.8	1.9	2.1	3.0	19.7	54.4	54.7	70.7
Mean	SH	90.1	101.9	128.8	2.0	2.1	2.1	2.8	19.5	50.7	59.5	73.9
Black	MI	93.3	138.4	128.3	1.4	1.9	2.9	3.0	19.0	51.0	69.7	77.4
Red	MI	88.7	130.9	120.4	1.6	2.2	1.7	1.4	18.9	51.2	68.6	77.3
Dark brown	MI	92.6	136.3	127.1	1.3	1.9	2.8	2.9	19.0	50.3	69.2	77.3
Brown	MI	95.5	133.4	132.2	1.3	2.0	2.8	3.1	19.1	51.0	67.1	76.5
Light brown	MI	97.7	128.3	135.5	1.2	1.9	2.9	3.4	19.2	50.7	65.4	76.1
White	MI	94.4	134.6	130.1	1.3	1.8	3.1	3.3	19.2	51.4	66.3	76.0
Mean	MI	93.7	133.7	128.9	1.4	2.0	2.7	2.9	19.1	50.9	67.7	76.8

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn = zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri

45.0–55.1%, iron concentration of 62.0–74.7 ppm, and zinc concentration of 75.4 and 80.2 ppm at MI (Fig. 1). Genotypes G163, G16, G259, G106, and G340 recorded higher amylose content of 20.7, 20.5, 20.1, and 19.9% in MI, respectively. Similarly, genotypes G431, G166, G240, G49, and G173 expressed higher amylose content at AN with values of 21.9, 21.5, 21.5, 21.4%, respectively. Genotypes G106 and G163 displayed superior performance for both amylose and starch contents at MI recording values of 19.9 and 20.7%, and 62.1 and 59.3%, in that order. The bottom five performing genotypes at MI did not consistently rank as the lowest performing across all traits and environments. For instance, the iron concentration of genotype G37 showed marked variation across environments, ranging from 24.7 ppm at AN to 57.1 ppm in MI, and peaking at 64.9 ppm in SH. Likewise, G37 recorded the lowest zinc values in AN (58.9 ppm), MI (72.8 ppm), and SH (75.3 ppm). In contrast, some of the lowest-yielding genotypes for grain yield, such as G49, demonstrated relatively higher iron content (56.9 ppm) in MI. For starch content, G423 consistently showed lower values (AN: 42.6%, MI: 51.5%, SH: 46.8%). Amylose content remained relatively stable across the least performing genotypes for grain yield, with slight variations, for example, G49 (AN: 21.4%, MI: 19.6% and SH: 19.3%).

Grain colour had distinct patterns in nutritional trait expression across environments. Table 3 presents the differential responses in carbohydrate stability and micronutrient accumulation under varying moisture conditions. Amylose content exhibited remarkable environmental and phenotypic stability, consistently ranging from 18.9 to 20.6% across diverse environments and grain colours. In contrast, starch content showed greater variability, with notably elevated levels exceeding 58% in light brown and red seeds at AN. Dark-seed genotypes exhibited relatively higher micronutrient levels in low moisture environments. At MI, black seeds recorded the highest values, reaching 69.7 ppm iron and 77.4 ppm of

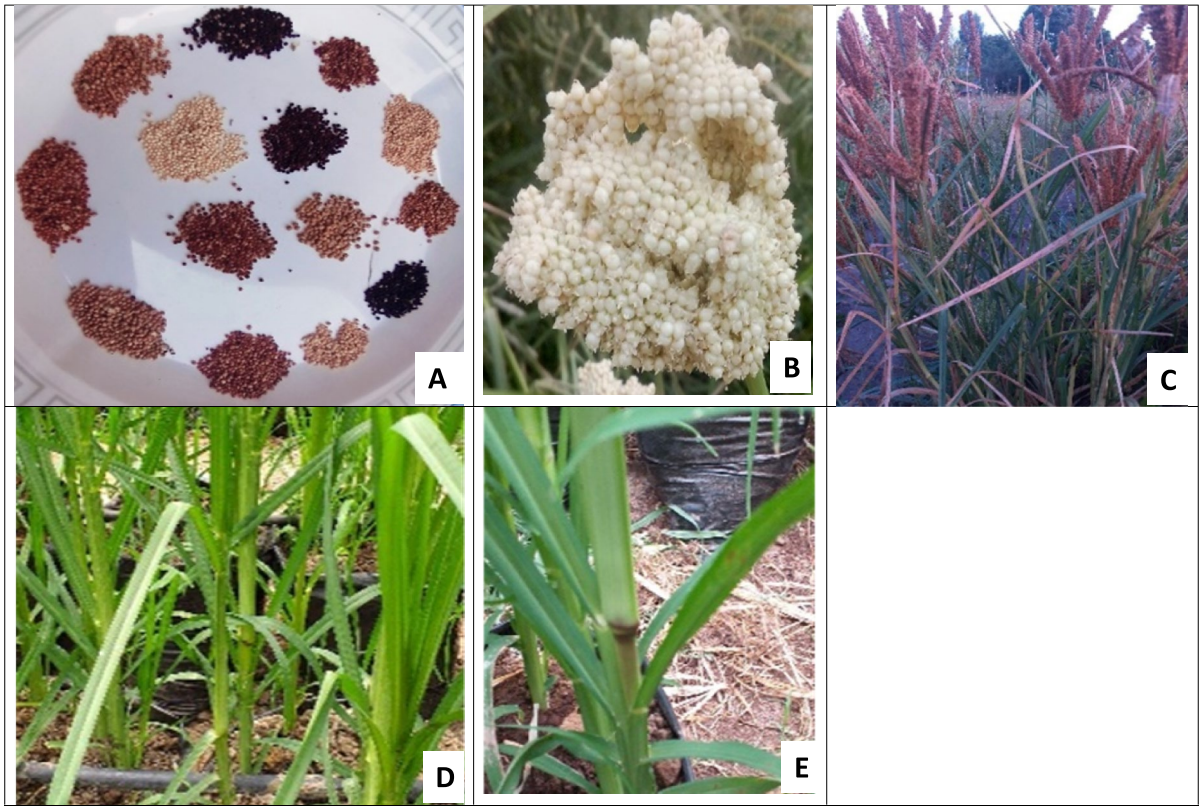


Fig. 2 Variations among the evaluated finger millet genotypes for grain colour **A**, panicle types **B** and **C**, and stem pigmentation **D** and **E**

zinc, signalling the influence of test environments on geneotype performance.

Response to stay-green and drought

Drought tolerance (Drt) score and the stay-green (SG) traits were essential parameters for discriminating finger millet genotypes under water-limited conditions (Fig. 1). The top 10 genotypes, selected based on better grain yield under the drought-prone condition, MI, displayed lower drought scores and more favourable SG scores compared to the bottom five performers. For instance, high-yielding genotype G141 scored a drought score of 2.5 and a SG score of 2.0 at MI, while genotype G239 from the lower-performing group had a significantly higher drought score (5.0) and SG score (4.5). This trend was consistent across environments, with superior genotypes maintaining lower average drought scores (e.g., 3.0 at AN, 2.8 at SH) and better chlorophyll retention.

Grain colour groups showed notable variation in drought-related traits across environments (Table 3), providing additional insight into the genotypic plasticity under stress. Black and dark brown-seeded genotypes consistently recorded higher SG and drought scores, averaging 2.0 and 3.4 at AN and 2.9 and 3.0 at MI, in that order, compared to light brown and red groups, which tended to score higher on both scales. In particular, light brown genotypes, despite having higher starch content, displayed poor drought responses with mean drought scores of 4.1 and 3.4 and SG scores of 2.3 and 2.9 at AN and MI locations, respectively. White-seeded types performed moderately, maintaining relatively balanced SG and drought scores across sites.

Genetic parameters for the assessed traits

Agronomic traits

Genetic parameter estimates for agronomic traits are summarised in Table 4. At AN, phenotypic variance was notably high for plant height (184.54 cm), and days to maturity (59.84), with genotypic variance following a similar trend, particularly for plant height (114.86 cm), and days to maturity (47.49). Heritability estimates were relatively high ($H^2 > 0.6$) across traits, especially for grain yield (0.90), days to 50% flowering (0.79) and days to maturity (0.79). Genetic advance (GA) was the highest for plant height (17.42), and days to maturity (12.65). Likewise, genetic advance as a percent of mean (GA%) was remarkably high for grain yield (59.95%) (Table 4). In SH, a comparable pattern was observed, where the largest phenotypic variances were recorded for plant height (160.05) and days to maturity (75.05), and genotypic variances were higher for days to maturity (68.90) and plant height (113.52). Environmental variances remained comparatively low for most traits, further supporting the genetic basis of observed variability. Heritability estimates were consistently high, ranging from 0.71 for plant height to 0.93 for grain yield. GA was the highest for days to maturity (16.38), and plant height (18.48), while GA% was highest for grain yield (65.81%). At MI, phenotypic variation was most pronounced in plant height (165.87), and days to maturity (68.25), and this was closely mirrored by genotypic variance, with notable values in plant height (112.67), and days to maturity (59.16). Despite moderate contributions from environmental variance such as for plant height (53.20), heritability estimates remained high for most traits, including days to maturity (0.87), and grain yield (0.82). GA was the highest for days to maturity (14.75), and plant height (18.02), while GA% reached higher for grain yield (52.20%). In the combined analysis across environments, phenotypic variance remained high for plant height (150.08), and days to maturity (65.73), whereas genotypic variances were comparatively lower across most traits (Table 4). Heritability was high (> 0.6) only for days to 50% flowering (0.71), and days to maturity (0.72), while moderate values (0.3 to 0.6) were observed for thousand seed weight. Traits such as plant height, and grain yield exhibited low heritability (< 0.3). The GA for key agronomic traits varied from 0.25 for thousand seed weight to 12.02 for days to maturity, while GA% spanned from a low 4.02% for plant height to moderate 17.89% for grain yield (Table 4).

Nutritional composition

The summary of genetic parameters for nutritional traits is presented in Table 4. Unlike agronomic traits, nutritional profiles presented variable trends. At AN, phenotypic variance was high for iron (164.27), and starch concentrations (60.98), with genotypic variance showing a similar pattern, especially for iron (83.01). Environmental variance surpassed genotypic variance for amylose concentration and was remarkably more pronounced for starch concentration at 41.60%. In contrast, zinc, and iron contents displayed higher genotypic variance, though environmental influence was relatively more evident in iron concentration (Table 4). Broad sense heritability estimates were moderate (0.3–0.6) for the majority of nutritional traits except for zinc concentration (0.67). The GA for nutritional traits varied from 0.66 in Am to 13.34 in iron content, while the GA% ranged from a low of 3.37% for amylose content to a moderate value of 24.20% for iron concentration. In SH, genetic influence was notably high for the two nutritional traits, except for starch concentration, which was the highest due to the environment (Table 4). Broad-sense heritability varied from 0.45 (starch content) to (0.45) to 0.75 (iron concentration. The estimates of GA and GA% followed a similar pattern to that observed in Arsinegelle. In Meiso, both amylose, and starch contents were more strongly influenced by the environment, as evidenced by their respective variance components. Notably, starch was affected by the environment (10.28) with its genetic variance (5.22), leading to a reduced heritability (0.34). In contrast, iron, and zinc contents showed more stable genetic expression, reflected in relatively high heritability estimates of 0.71, and 0.61, respectively. When pooled across environments, nutritional traits revealed a more complex interaction. Starch content was more influenced by environmental effect (13.62 vs. genotypic 4.10), resulting in a very low heritability (0.23), and a marginal genetic advance of 4.01%. Amylose content showed low heritability (0.27). However, micronutrients retained some breeding potential: iron ($H^2 = 0.39$), and zinc ($H^2 = 0.38$) presented moderate to low genetic control, with respective GA of 10.21%, and 3.26%.

Table 4 Genetic parameters for agronomic and drought parameters, and nutritional traits for finger millet accessions tested across three environments in Ethiopia during the 2019 /2020 main rainy season

Genetic parameters	Locations	Agronomic traits					Drought parameters		Nutritional traits			
		DF	PH	DM	GY	TW	SG	Drt	Am	Stc	Fe	Zn
Phenotypic variance	AN	24.44	184.54	59.84	1.07	0.13	0.93	0.96	0.51	60.98	164.27	23.52
Genotypic variance	AN	19.38	114.86	47.49	0.96	0.10	0.69	0.75	0.23	19.38	83.01	15.81
Environmental variance	AN	5.06	69.68	12.35	0.11	0.03	0.24	0.21	0.28	41.60	81.26	7.71
Heritability in broad sense (H^2)	AN	0.79	0.62	0.79	0.90	0.76	0.74	0.78	0.45	0.32	0.51	0.67
Genetic advance	AN	8.07	17.42	12.65	1.91	0.55	1.47	1.57	0.66	5.11	13.34	6.71
Genetic advance as a % of mean	AN	6.69	20.09	8.15	59.95	24.17	75.63	47.73	3.37	9.94	24.20	9.11
Mean	AN	120.76	86.70	155.10	3.18	2.29	1.94	3.29	19.67	51.43	55.13	73.67
Phenotypic variance	SH	30.95	160.05	75.05	0.54	0.08	0.42	1.13	0.20	23.14	66.05	9.38
Genotypic variance	SH	28.34	113.52	68.90	0.50	0.06	0.28	1.04	0.13	10.32	49.83	6.86
Environmental variance	SH	2.61	46.53	6.16	0.04	0.02	0.14	0.09	0.07	12.82	16.22	2.52
Heritability in broad sense (H^2)	SH	0.92	0.71	0.92	0.93	0.73	0.67	0.92	0.64	0.45	0.75	0.73
Genetic advance	SH	10.49	18.48	16.38	1.40	0.41	0.90	2.02	0.58	4.42	12.63	4.62
Genetic advance as a % of mean	SH	11.61	18.23	12.64	65.81	20.38	40.33	71.98	3.04	9.19	19.59	6.08
Mean	SH	90.39	101.41	129.62	2.13	2.03	2.22	2.80	19.21	48.11	64.49	75.92
Phenotypic variance	MI	22.38	165.87	68.25	0.17	0.06	1.02	1.00	0.11	15.50	26.04	3.70
Genotypic variance	MI	19.44	112.67	59.16	0.14	0.05	0.89	0.86	0.05	5.22	18.60	2.27
Environmental variance	MI	2.94	53.20	9.10	0.03	0.01	0.13	0.14	0.07	10.28	7.44	1.43
Heritability in broad sense (H^2)	MI	0.87	0.68	0.87	0.82	0.82	0.88	0.86	0.41	0.34	0.71	0.61
Genetic advance	MI	8.47	18.02	14.75	0.70	0.40	1.82	1.77	0.28	2.73	7.51	2.43
Genetic advance as a % of mean	MI	9.06	13.22	11.47	52.20	20.69	63.41	59.45	1.47	5.38	10.91	3.15
Mean	MI	93.48	136.29	128.56	1.34	1.91	2.87	2.98	19.04	50.74	68.80	77.09
Phenotypic variance	Combined	23.90	150.08	65.73	0.62	0.07	0.70	1.02	0.18	17.72	62.12	9.92
Genotypic variance	Combined	16.98	25.80	47.32	0.15	0.03	0.25	0.73	0.05	4.10	24.53	3.77
Environmental variance	Combined	6.92	124.28	18.42	0.47	0.04	0.45	0.28	0.13	13.62	37.58	6.15
Heritability in broad sense (H^2)	Combined	0.71	0.17	0.72	0.24	0.45	0.36	0.72	0.27	0.23	0.39	0.38
Genetic advance	Combined	7.16	4.34	12.02	0.39	0.25	0.62	1.50	0.24	2.01	6. 41	2.46
Genetic advance as a % of mean	Combined	7.04	4.02	8.71	17.89	12.25	26.42	49.45	1.25	4.01	10.21	3.26
Grand mean	Combined	101.63	107.90	138.00	2.20	2.07	2.33	3.03	19.30	50.07	62.80	75.57

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), and Zn = zinc content (%), AN = Arsinegelle, MI = Meiso, and SH = Maitsebri

Drought parameters

At the AN test site, stay-green (SG) and drought tolerance (Drt) scores displayed a strong genetic basis with genotypic variances of 0.69 and 0.75, markedly exceeding environmental variance of 0.24, and 0.21, in that order (Table 4). Heritability in the broad sense was remarkably high for both traits (0.74 for stay-green, and 0.78 for drought score). This was supported by high GA% (75.63% for stay-green, and 47.73% for drought score). In contrast, genotypes at the MI site displayed remarkably high heritability values for SG (0.88) and drought score (0.86), supported by higher genotypic variances (0.89, and 0.86, in that order). However, the genetic advance values (1.82 for stay-green, and 1.77 for drought score) and their GA% (63.41% and 59.45%), respectively, were somewhat lower than those observed in AN. At SH, the variance components for SG and drought score showed a clear contribution of the genetic effect, with genotypic variances (stay-green: 0.28, and drought score: 1.04), far greater than their corresponding environmental variances (stay-green: 0.14 and drought score: 0.09), in that order. This strong genetic influence was further substantiated by high heritability estimates (SG score: 0.67, and drought score: 0.92). The GA values (SG score: 0.90, and drought score: 2.02), coupled with considerable GA% (SG score: 40.33%, and drought score: 71.98%) recorded for these traits. In the combined analysis across environments, both SG and drought scores showed a decline in genotypic variance at 0.25 and 0.73 in comparison with the increased environmental variability 0.45 and 0.28, in that order, resulting to high heritability for drought score (0.72) while moderate heritability was recorded for SG score (0.36). Notwithstanding this, the genetic advance for both traits remained high for drought score (GA:1.50, GA%: 49.45%), and SG score (GA: 0.62, GA%: 26.42%).

Correlations among phenotypic and nutritional traits

Associations among agronomic traits under drought

The correlation heatmap (Fig. 3) revealed variable trends and magnitudes of associations among agronomic traits. A strong and positive association was computed between days to 50% flowering and days to maturity across all environments. However, days to 50% flowering, and days to maturity revealed consistent negative correlations with grain yield ($r=-0.35$ at MI, while -0.47, and -0.46 at the SH sites), in that order. Moreover, thousand seed weight displayed substantial and negative associations with days to 50% flowering ($r=-0.13$) and days to maturity ($r=-0.13$) at MI. In contrast, there existed a positive correlation between thousand seed weight and grain yield ($r=0.13$ to 0.24) across locations. Conversely, plant height had poor associations with most traits, including grain yield, and days to 50% flowering in MI, except for a positive and strong correlation with days to 50% flowering ($r=0.27$) in AN. Furthermore, grain colour revealed a weak and negative correlation with phenological traits in some environments. For instance, grain colour was negatively associated with days to 50% flowering and days to maturity at MI ($r=-0.11$), and at SH ($r=-0.08$ and -0.07), in that order (Fig. 3).

Association between nutritional composition

The nutritional traits, namely, amylose, starch, iron, and zinc contents, presented uniform pattern of association across all environments, although the magnitude of these correlations varied (Fig. 3). Amylose content was strongly and positively related to starch content at all sites ($r=0.32$ to 0.80), but exhibited a marked negative interaction with both iron ($r=-0.92$ to -60) and zinc ($r=-0.75$ to -0.56) contents. Similarly, starch content was negatively associated with iron ($r=-0.75$ to -0.03) and zinc ($r=-0.74$ to -0.09). Remarkably, iron and zinc were highly and positively correlated at all sites ($r=0.63$ to 0.83). Moreover, among agronomic and drought-related traits, grain yield highlighted a modest but remarkable positive connection with both iron and zinc content at AN and MI ($r=0.16$ to 0.33). Drought tolerance score displayed a consistent and noteworthy positive association with amylose content, specifically at AN ($r=0.19$), MI ($r=0.25$), and SH ($r=0.21$). In contrary, stay-green had variable correlations with amylose and starch contents, with weak and inconsistent associations ($r=0.17$) at MI and ($r=-0.13$) at SH for amylose, and mildly negative with starch content at both MI ($r=-0.08$) and SH ($r=-0.15$) (Fig. 3). Grain colour was positively correlated with iron and

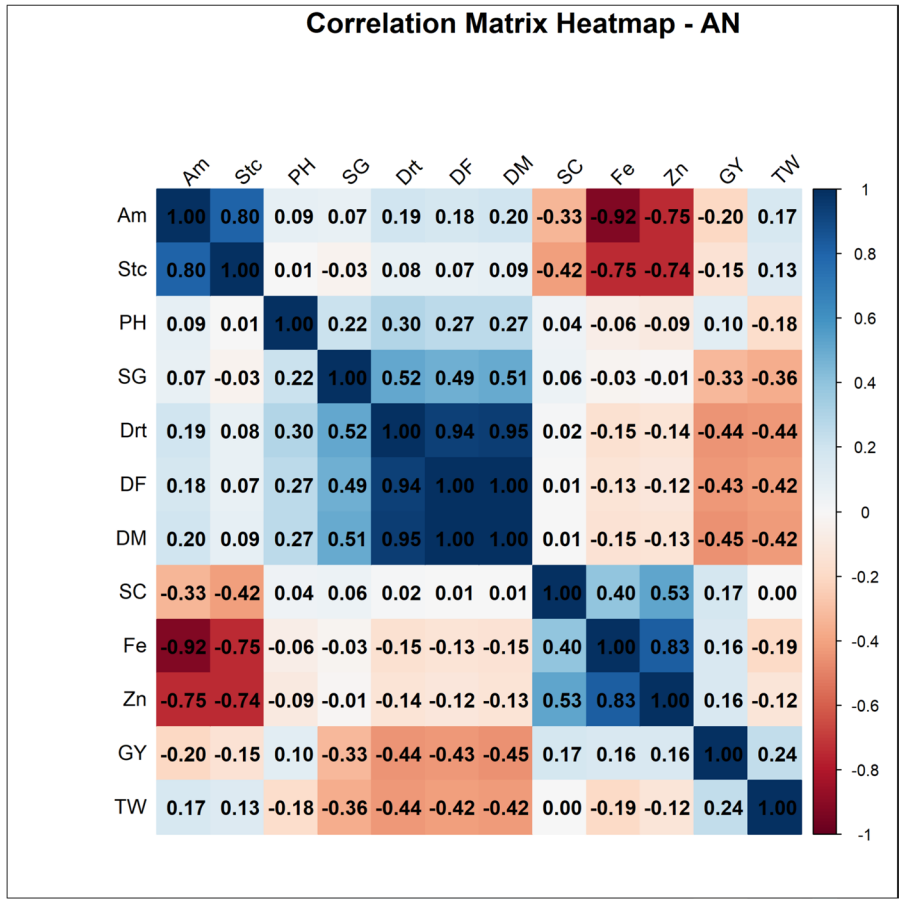


Fig. 3 Correlation matrix heatmap of the various agronomic, drought parameters and nutritional profiles of finger millet accessions evaluated at Arsinegelle (AN) and Meiso (MI), and Maitsebri (SH) in Ethiopia. Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), Zn = zinc content (%), and SC = grain colour

zinc content, making it a good morphological marker for indirectly selecting for these traits. The correlation was also significantly lower for MI.

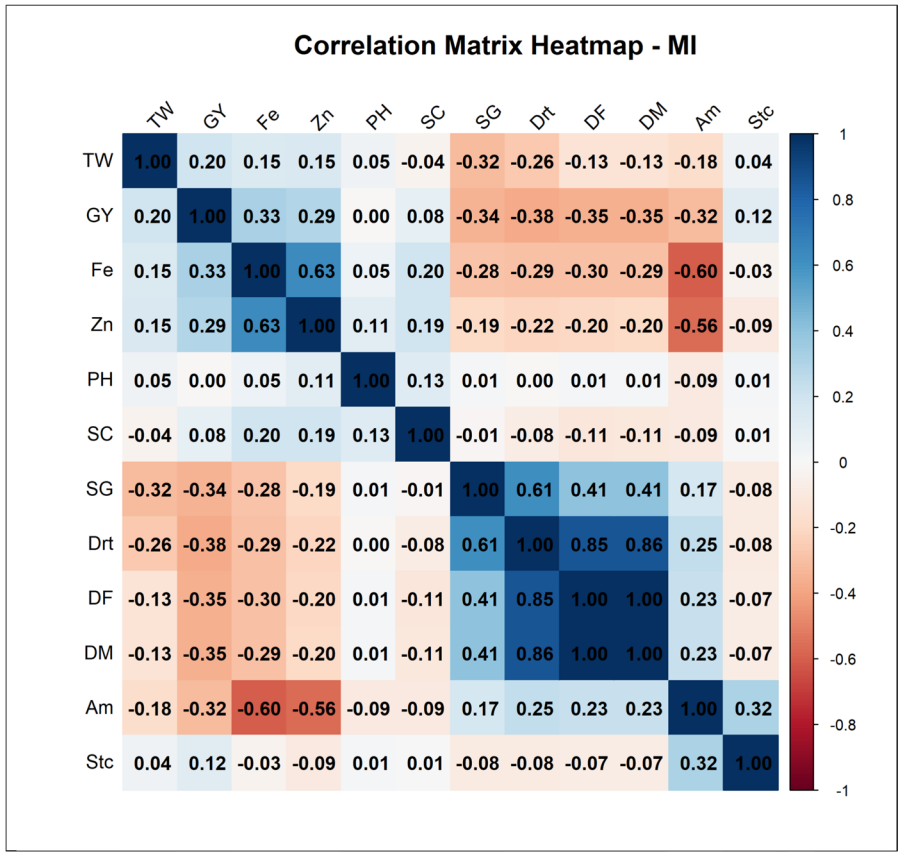
Associations of drought parameters

The association heatmap across the three test locations displayed consistent relationships among drought parameters and key agronomic traits in finger millet. Stay-green (SG) score showed a strong and positive association with drought tolerance score across all environments, with (r = 0.52 at AN, r = 0.61 at MI, and r = 0.35 at SH). Additionally, SG score showed marked positive correlation with days to 50% flowering (r = 0.49 at AN, r = 0.41 at MI, and r = 0.36 at SH), and days to maturity (r = 0.51 at AN, r = 0.41 at MI, r = 0.36 at SH). Likewise, drought tolerance score was strongly and positively associated with days to 50% flowering (r = 0.94 at AN, r = 0.85 at MI, r = 0.95 at SH) and days to maturity (r = 0.95 at AN, r = 0.86 at MI, and r = 0.93 at SH). Contrarily, both SG and drought tolerance score revealed significant negative correlations with grain yield (stay-green: r = −0.33 at AN, r = −0.34 at MI, r = −0.37 at SH; drought tolerance: r = −0.44 at AN, r = −0.38 at MI, and r = −0.47). Additionally, both drought-related parameters were inversely correlated with thousand seed weight and grain colour at several locations, though the strength and significance of the associations varied (Fig. 3).

Principal component and biplot analyses

Principal component analysis showing eigenvalues (> 1.0), percent and cumulative variation for agronomic, nutritional traits, and drought response parameters is presented in Table 5. In the potential environment, Arsinegelle (AN), three principal components were partitioned by the PCA, which

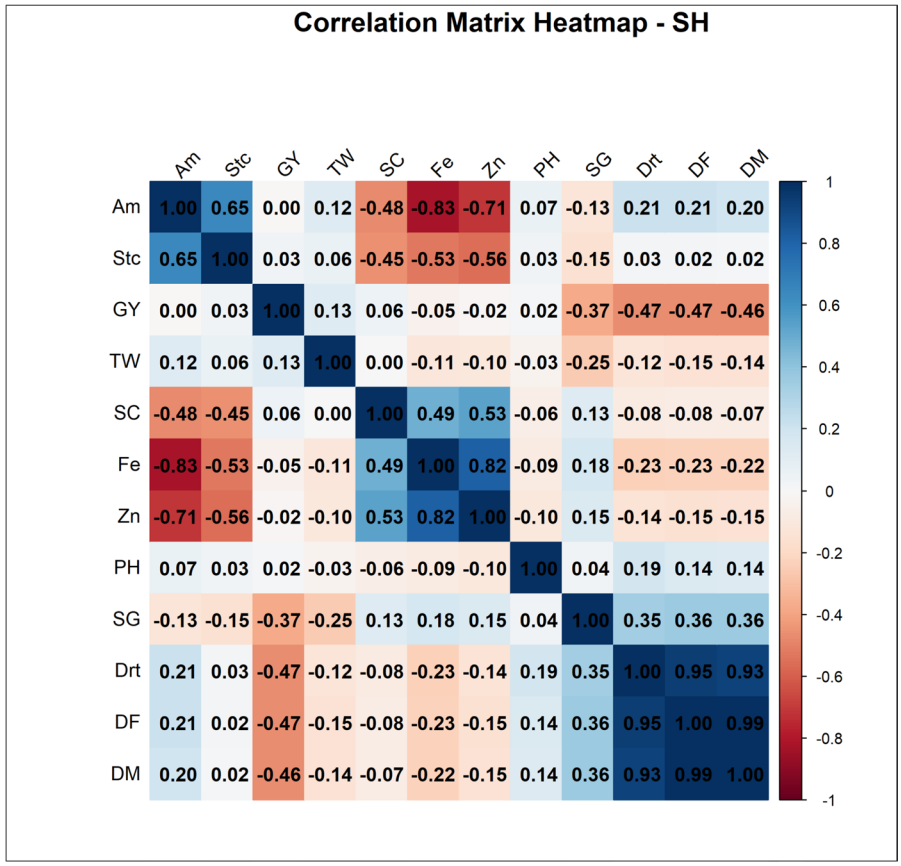
Fig. 3 (continued)



cumulatively contributed 73.1% of the total variance. Notably, days to 50% flowering and days to maturity were strong contributors to PC-1, while plant height and grain yield contributed to PC-3. Uniquely, grain colour (SC) was moderately loaded across PC-3 and PC-2, contributing to genotype differentiation. At AN (Fig. 4A), genotypes sourced from Amhara region and released varieties were closely clustered with grain yield, plant height and thousand seed weight, while genotypes from Tigray region were more linked with days to flowering, and grain colour, and genotypes from Oromiya region showed proximity with days to maturity. In the intermediate stress environment (Maitsebri-SH), a similar pattern to AN was observed where PC-1, PC-2 and PC-3 cumulatively accounted for 67.7% of the total variation. PC-1 captured days to 50% flowering (14.2%) and days to maturity (13.8%) effects alongside grain colour (6.7%), while thousand seed weight and plant height dominated PC-3 with 39.6% and 23.4% contributions, respectively (Table 5). At SH, genotypes obtained from Amhara region showed close association with grain yield and thousand seed weight, while released genotypes were linked with plant height, and SNNP and Tigray regions genotypes were positioned towards grain colour (Fig. 4B). Four PCs were identified in the stressed environment (Meiso-MI), cumulatively explaining 68.0% of the total variation. Starch significantly contributed to PC-4, while plant height and grain colour were prominent traits across two groups of principal components (PC-3 and PC-4). Notably, grain colour also showed strong associations with PC-3 and PC-4, and plant height contributed to PC-4. Under the stress condition, MI (Fig. 4C), genotypes from Amhara region were associated with thousand seed weight and days to maturity. Released genotypes-maintained association with plant height, and SNNP region continued to link with grain colour (Fig. 4C).

Nutritional traits revealed distinct differentiation across environments, particularly under moderate and severe stress. At AN, PC-2 captured most variation for iron (13.3%), starch (13.2%), zinc (12.6%), and amylose (11.5%) (Table 5). The biplot for AN showed that Benishangul & Gumz and SNNP regions

Fig. 3 (continued)



genotypes clustered near starch and iron contents, while accessions from Oromiya region were associated with amylose concentrations (Fig. 4A). At SH, although the trait loadings differed, nutritional traits remained influential where iron (14.0%), amylose (13.6%), and zinc (12.0%) were co-expressed in PC-1, while starch was also moderately involved in PC-2 (9.6%) (Table 5). In SH, genotypes obtained from Benishangul & Gumz region maintained a strong association with iron contents, while those genotypes from SNNP region remained near starch content, and released accessions were relatively close to Zinc contents (Fig. 4B). Under the MI environment, starch had a strong contribution to PC-4 (40.9%), while zinc (21.0%), amylose (22.2%), and iron (15.7%) dominated PC-2. Figure 4C confirms these trends, where genotypes from Benishangul & Gumz, SNNP, and Oromiya regions clustered around high concentrations of amylose, iron and zinc contents.

Traits related to drought response, namely stay-green (SG) and drought tolerance (Drt) scores, played a prominent role in genotype discrimination across environments. At AN, drought response contributed strongly to PC-1 (14.4%), with SG trait loading moderately across PC-1 and PC-2. at AN, SG and drought response scores showed weaker associations across genotypes under the favourable conditions (Fig. 3A). Similarly, at SH, drought response (13.7%) was again a key contributor to PC-1, co-loading with SG score (11.4%) in PC-2. At SH, genotypes sourced from Oromiya and Tigray regions were closely aligned with SG and Drt traits (Fig. 3B). In MI, drought response remained influential in PC-1 (18.4%), while SG was significantly associated with PC-3 (11.4%). Figure 3C further illustrates the spatial separation of drought-resilient genotypes, where accessions with higher SG and drought response scores aligned away from yield-related traits. The genotype sources that showed strong drought associations at SH exhibited similar patterns at MI (Fig. 3C).

Table 5 Trait loadings of agronomic traits, drought parameters, and nutritional profiles on principal component axes, showing eigenvalues, percentage and cumulative variation for 448 finger millet genotypes evaluated at three diverse environments in Ethiopia

Traits	Trait category	Arsinegelle (AN)			Maitsebri (SH)			Meiso (MI)			
		PC-1	PC-2	PC-3	PC-1	PC-2	PC-3	PC-1	PC-2	PC-3	PC-4
DF	Agronomic	14.2	8.7	0.0	14.2	11.7	2.0	17.5	8.3	6.4	1.6
DM		14.8	8.5	0.0	13.8	11.7	2.0	17.5	8.4	6.4	1.7
PH		1.8	1.2	55.7	1.0	0.1	23.4	0.1	2.4	3.3	27.6
GY		6.7	1.1	32.8	3.4	8.6	7.3	8.5	0.2	4.3	2.5
TW		2.1	9.1	1.1	0.0	3.1	39.6	2.9	0.0	39.0	3.0
SC		2.6	6.3	8.2	6.7	6.0	7.1	0.9	2.6	27.7	16.2
SG	Drought response	5.5	6.1	0.0	0.7	11.4	11.1	9.9	2.1	11.0	0.5
Drt		14.4	8.4	0.2	13.7	11.1	2.9	18.4	7.5	0.2	0.5
Am	Nutritional composition	10.9	11.5	1.0	13.6	8.5	0.1	7.4	22.2	0.2	4.6
Stc		7.7	13.2	0.0	6.8	9.6	4.1	0.0	9.6	1.7	40.9
Fe		10.0	13.3	0.8	14.0	8.6	0.2	9.7	15.7	0.0	0.3
Zn		9.3	12.6	0.2	12.0	9.6	0.1	7.1	21.0	0.0	0.5
Explained variance (eigenvalue)		4.2	3.4	1.1	3.9	3.2	1.0	4.0	1.9	1.1	1.1
Proportion of total variance (%)		35.3	28.4	9.4	32.6	26.4	8.7	33.4	15.7	9.6	9.3
Cumulative variance (%)		35.3	63.6	73.1	32.6	59.0	67.7	33.4	49.1	58.7	68.0

Note: DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Am = amylose content (ppm), Stc = starch content (ppm), Fe = iron content (%), Zn = zinc content (%), and SC = grain colour. PC-1 = principal component 1; PC-2 = principal component 2; PC-3 = principal component 3; and PC-4 = principal component 4

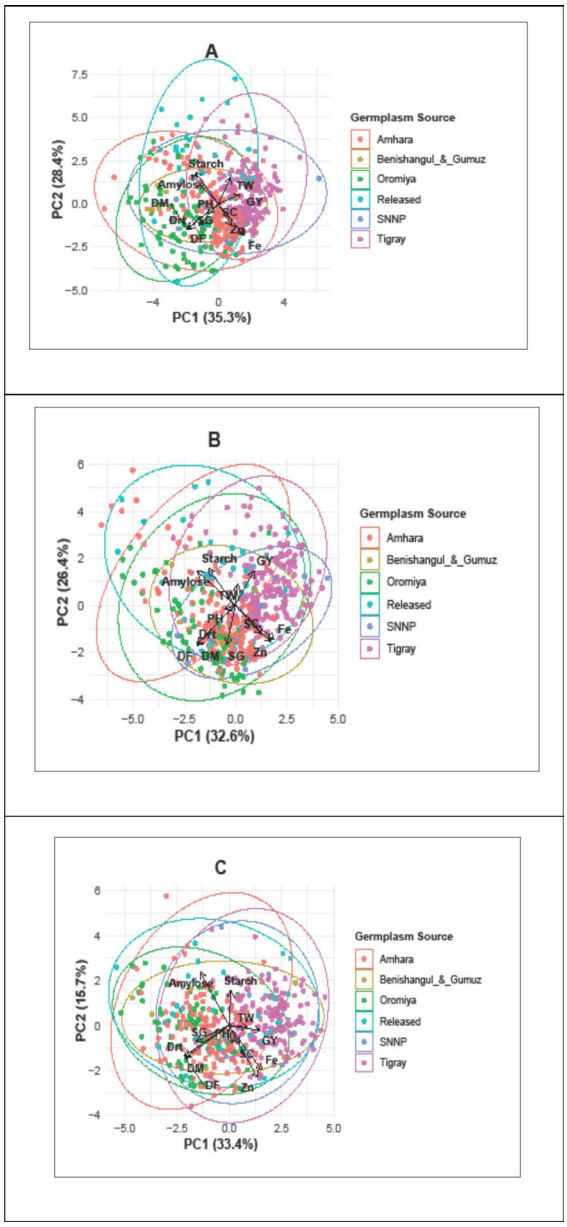


Fig. 4 Principal component biplot showing the distribution of 448 finger millet genotypes and 12 traits at A: Arsinegelle, B: Maitsebri, and C: Meiso locations in Ethiopia. Note DF = days to 50% flowering, PH = plant height (cm), DM = days to maturity, GY = grain yield (t/ha), TW = thousand seed weight (g), SG = stay-green score, Drt = drought response score, Fe = iron content (%), Zn = zinc content (%), and SC = grain colour

Clustering finger millet genotypes for simultaneous selection

Cluster analysis revealed unique pattern for some key genotypes (Table 6). Cluster 1 encompassed the majority of genotypes in all three locations, including those from regions such as Benishangul & Gumuz, Amhara, Oromia, Tigray, and SNNP. This cluster grouped genotypes such as G1–G5, G14, G21–G25, G34, G48, G58, G83, G91–G92, G100, G110–G112, and G125–G135. Cluster 2 grouped the genotypes G6, G11, G13, G41, G52, G84, G107, G164, and G240, across the test environments. Genetically differentiated genotypes including G10, G16–G18, G26–G31, G60, G73–G75, G95–G99, G149–G159 were grouped in Cluster 3. A small subset formed cluster 4, comprising G143, G235, G303, and G418 (Table 6).

Discussion

Finger millet is an important drought-resilient cereal with exceptional nutritional value and adaptability across diverse agro-ecological zones of sub-Saharan African, particularly in Ethiopia, where it is cultivated across diverse agro-ecological zones. Ethiopia's diverse finger millet germplasm comprising landraces, wild relatives, and improved varieties represents a rich genetic reservoir for developing high-yielding, climate-resilient, and nutrient-dense cultivars. In this study, Ethiopian finger millet accessions were systematically evaluated under drought condition to profile genetically diverse finger millet accessions for major agronomic traits, drought response, and nutritional compositions in relation to adaptation under contrasting drought stress conditions to select genotypes for breeding or production. In the current study, there were pronounced effects of genotype (G), environment (E), and their interaction (GEI) observed in this study for agronomic, drought response, and nutritional traits (Table 2). The extensive genotypic diversity has previously been reported in finger millet, concurring with present findings (Tesfaye & Mengistu 2017; Kumari et al. 2018; Singh et al. 2024). The genotypes were varied for grain yield, and genotypes such as G141, G423, G247, G171, G46, G294, and G204 were identified with high yield potential, with grain yield exceeding 3.0 tons per hectare. Further, these genotypes were high-yielders compared to the widely cultivated genotypes in the country, including Tadesse (G441), Tesema (G442), Necho (G433), and Diga-2 (G446). These genotypes

Table 6 Clustering of 448 Ethiopian finger millet genotypes for agronomic and nutritional traits at three testing environments with variable rainfall

Clusters	Arsinegelle (AN)	Maitsebri (SH)	Meiso (MI)
1	G1, G2, G3, G4, G5, G7, G8, G9, G14, G20, G21, G22, G23, G24, G25, G32, G34, G36, G37, G38, G39, G40, G48, G49, G50, G51, G58, G64, G67, G80, G83, G85, G90, G91, G92, G100, G106, G108, G109, G110, G111, G112, G114, G115, G116, G117, G118, G119, G120, G121, G122, G123, G124, G125, G126, G127, G128, G129, G130, G131, G132, G133, G134, G135, G137, G152, G153, G161, G162, G163, G167, G168, G170, G173, G179, G182, G183, G184, G185, G202, G227, G228, G236, G239, G243, G264, G266, G268, G269, G270, G307, G312, G320, G325, G329, G331, G335, G336, G337, G342, G373, G374, G375, G376, G377, G378, G379, G380, G381, G383, G384, G385, G436, G437, and G446	G1, G2, G3, G4, G10, G11, G12, G14, G15, G17, G20, G21, G22, G23, G24, G25, G26, G27, G28, G29, G30, G31, G32, G34, G35, G38, G40, G43, G44, G48, G50, G53, G54, G55, G56, G57, G58, G60, G62, G63, G64, G65, G66, G71, G72, G74, G75, G77, G78, G79, G80, G81, G82, G83, G85, G86, G87, G88, G89, G91, G92, G93, G94, G95, G96, G97, G98, G99, G100, G101, G102, G103, G104, G105, G110, G111, G112, G113, G114, G115, G116, G117, G118, G119, G121, G123, G124, G125, G126, G128, G129, G130, G131, G132, G135, G136, G137, G138, G141, G148, G149, G150, G151, G152, G154, G155, G157, G158, G159, G160, G161, G165, G166, G167, G169, G172, G175, G176, G177, G178, G179, G180, G181, G183, G184, G185, G187, G191, G192, G193, G194, G198, G199, G200, G201, G202, G203, G205, G207, G213, G215, G217, G218, G219, G228, G230, G232, G237, G238, G239, G241, G242, G243, G246, G250, G253, G254, G255, G256, G258, G262, G263, G265, G266, G267, G272, G274, G275, G279, G281, G282, G283, G284, G286, G292, G295, G296, G297, G299, G300, G306, G307, G308, G309, G310, G311, G312, G318, G319, G320, G321, G322, G324, G326, G327, G328, G329, G331, G332, G333, G334, G335, G336, G337, G338, G339, G341, G342, G344, G351, G355, G366, G368, G369, G371, G372, G373, G375, G376, G378, G379, G380, G381, G384, G385, G391, G400, G426, and G446	G1, G2, G3, G4, G5, G7, G8, G12, G13, G14, G15, G16, G21, G23, G24, G33, G34, G35, G38, G39, G43, G44, G48, G51, G52, G53, G55, G56, G57, G58, G62, G65, G66, G68, G71, G72, G73, G75, G77, G78, G80, G82, G83, G84, G89, G90, G91, G92, G94, G95, G96, G97, G98, G100, G102, G103, G106, G107, G108, G109, G110, G111, G112, G113, G114, G115, G117, G118, G120, G121, G122, G125, G126, G127, G128, G129, G130, G132, G133, G134, G135, G137, G140, G149, G150, G151, G152, G153, G157, G160, G161, G162, G165, G167, G168, G170, G175, G177, G178, G181, G183, G184, G185, G189, G191, G193, G194, G205, G207, G214, G216, G217, G218, G236, G237, G239, G243, G254, G257, G262, G263, G265, G266, G267, G268, G271, G277, G295, G299, G305, G306, G307, G309, G310, G311, G312, G313, G318, G319, G320, G321, G322, G323, G324, G325, G328, G330, G331, G332, G333, G335, G336, G337, G338, G339, G340, G341, G342, G364, G367, G368, G369, G370, G372, G373, G374, G375, G378, G379, G380, G381, G382, G383, G384, G385, G386, G391, G404, G407, G426, G436, G437, and G446

Table 6 (continued)

Clusters	Arsinegelle (AN)	Maitsebri (SH)	Meiso (MI)
2	G6, G11, G13, G19, G41, G42, G46, G52, G61, G70, G79, G84, G107, G113, G139, G142, G160, G164, G165, G166, G188, G195, G197, G211, G229, G230, G240, G241, G246, G247, G252, G257, G261, G282, G296, G299, G300, G305, G313, G315, G317, G323, G324, G330, G338, G340, G356, G359, G361, G362, G364, G365, G370, G372, G382, G386, G387, G394, G396, G399, G402, G407, G408, G412, G414, G421, G422, G424, G427, G428, G429, G431, G432, G433, G434, G435, G438, G439, G440, G441, G442, G443, G444, G447, and G448	G5, G7, G8, G9, G13, G33, G37, G39, G41, G49, G51, G52, G67, G70, G76, G84, G90, G106, G107, G109, G120, G122, G127, G133, G134, G139, G143, G144, G153, G163, G164, G168, G170, G173, G174, G182, G186, G229, G236, G240, G257, G264, G268, G269, G270, G277, G305, G313, G315, G323, G325, G330, G340, G362, G364, G365, G370, G374, G377, G382, G383, G386, G427, G428, G430, G431, G433, G436, G437, G438, and G439	G6, G10, G11, G17, G18, G19, G20, G22, G25, G26, G27, G28, G29, G30, G31, G32, G40, G42, G45, G46, G47, G50, G54, G59, G60, G61, G63, G64, G67, G70, G74, G76, G79, G81, G85, G86, G87, G88, G93, G99, G101, G104, G105, G116, G119, G123, G124, G131, G136, G138, G139, G141, G143, G144, G145, G146, G147, G148, G154, G155, G156, G158, G159, G164, G166, G169, G171, G172, G176, G179, G180, G182, G186, G187, G188, G190, G192, G195, G196, G197, G198, G199, G200, G201, G202, G203, G204, G206, G208, G209, G210, G211, G212, G213, G215, G219, G220, G221, G222, G223, G224, G225, G226, G227, G228, G230, G232, G233, G234, G238, G240, G241, G242, G244, G245, G246, G247, G248, G250, G251, G252, G253, G255, G256, G258, G261, G272, G273, G274, G275, G276, G278, G279, G280, G281, G282, G283, G284, G285, G286, G287, G288, G289, G290, G291, G292, G293, G294, G296, G297, G298, G300, G301, G302, G303, G308, G314, G316, G317, G326, G327, G329, G334, G343, G344, G345, G346, G347, G348, G349, G350, G351, G352, G354, G355, G356, G357, G358, G360, G361, G362, G363, G365, G366, G371, G376, G387, G388, G389, G390, G392, G393, G394, G395, G396, G397, G398, G399, G400, G401, G402, G403, G405, G406, G408, G409, G410, G411, G412, G413, G414, G415, G416, G417, G418, G419, G420, G421, G422, G423, G424, G425, G429, G431, G432, G434, G435, G439, G440, G441, G442, G443, G444, G447, and G448

Table 6 (continued)

Clusters	Arsinegelle (AN)	Maitsebri (SH)	Meiso (MI)
3	G10, G12, G15, G16, G17, G18, G26, G27, G28, G29, G30, G31, G33, G35, G43, G44, G45, G47, G53, G54, G55, G56, G57, G59, G60, G62, G63, G65, G66, G68, G69, G71, G72, G73, G74, G75, G76, G77, G78, G81, G82, G86, G87, G88, G89, G93, G94, G95, G96, G97, G98, G99, G101, G102, G103, G104, G105, G136, G138, G140, G141, G144, G145, G146, G147, G148, G149, G150, G151, G154, G155, G156, G157, G158, G159, G169, G171, G172, G174, G175, G176, G177, G178, G180, G181, G186, G187, G189, G190, G191, G192, G193, G194, G196, G198, G199, G200, G201, G203, G204, G205, G206, G207, G208, G209, G210, G212, G213, G214, G215, G216, G217, G218, G219, G220, G221, G222, G223, G224, G225, G226, G231, G232, G233, G234, G237, G238, G242, G244, G245, G248, G249, G250, G251, G253, G254, G255, G256, G258, G259, G260, G262, G263, G265, G267, G271, G272, G273, G274, G275, G276, G277, G278, G279, G280, G281, G283, G284, G285, G286, G287, G288, G289, G290, G291, G292, G293, G294, G295, G297, G298, G301, G302, G304, G306, G308, G309, G310, G311, G314, G316, G318, G319, G321, G322, G326, G327, G328, G332, G333, G334, G339, G341, G343, G344, G345, G346, G347, G348, G349, G350, G351, G352, G353, G354, G355, G357, G358, G360, G363, G366, G367, G368, G369, G371, G388, G389, G390, G391, G392, G393, G395, G397, G398, G400, G401, G403, G404, G405, G406, G410, G411, G413, G415, G416, G417, G419, G420, G423, G425, G426, G430, and G445	G6, G16, G18, G19, G36, G42, G45, G46, G47, G59, G61, G68, G69, G73, G108, G140, G142, G145, G146, G147, G156, G162, G171, G188, G189, G190, G195, G196, G197, G204, G206, G208, G209, G210, G211, G212, G214, G216, G220, G221, G222, G223, G224, G225, G226, G227, G231, G233, G234, G235, G244, G245, G247, G248, G249, G251, G252, G259, G260, G261, G271, G273, G276, G278, G280, G285, G287, G288, G289, G290, G291, G293, G294, G298, G301, G302, G303, G304, G314, G316, G317, G343, G345, G346, G347, G348, G349, G350, G352, G353, G354, G356, G357, G358, G359, G360, G361, G363, G367, G387, G388, G389, G390, G392, G393, G394, G395, G396, G397, G398, G399, G401, G402, G403, G404, G405, G406, G407, G408, G409, G410, G411, G412, G413, G414, G415, G416, G417, G418, G419, G420, G421, G422, G423, G424, G425, G429, G434, G435, G441, G442, G443, G444, G445, G447, and G448	G9, G36, G37, G41, G49, G69, G163, G173, G174, G229, G259, G264, G269, G270, G315, G359, G377, G427, G428, G430, G433, G438, and G445
4	G143, G235, G303, G409, and G418	G432, and G440	G142, G231, G235, G249, G260, G304, and G353

Note: See Table S1 for descriptions of genotypes

also showed superior performance for major agronomic traits, including early flowering, heavier seed, stay-green (SG) trait. The SG trait is particularly valuable for drought avoidance and biomass retention under moisture-limited conditions (Jordan et al. 2012; Borrel et al. 2014; Danful et al. 2019; Shin et al. 2020; Gebreyohannes et al. 2025). These are valuable genetic resources for immediate release and for future breeding programs.

The significant effects of environment on the studied agronomic and nutritional traits in finger millet revealed that genotype performance is strongly shaped by contrasting agro-ecological conditions. Specifically, environments like Arsinegelle (AN), characterized by higher rainfall and moderate temperatures (Table 1) tend to favour genotypes with high yield development and late maturity, while Meiso (MI), with its arid climate and heat stress, amplifies the expression of drought tolerance and early flowering. Maitsebri (SH), representing an intermediate zone, balances both stress resilience and productivity traits. This environmental heterogeneity particularly in rainfall patterns, temperature regimes, and soil characteristics plays a vital role in trait expression of genotypes and supports earlier observations by Anuradha et al. (2022), and Lanjewar et al. (2025), who emphasized that stress gradients across test sites can trigger significant GEI. The observed significant GEI for most traits indicates that genotype performance varied widely across locations, reflecting differential and spatial adaptability. This necessitates the identification of location-specific superior genotypes, enabling breeders to recommend best-performing accessions for specific environments. For instance, genotypes excelling in MI may be drought-resilient but less suitable for high-potential areas like AN. Recognizing and exploiting such patterns is vital for designing targeted breeding and deployment strategies, ultimately enhancing genetic gains and production stability across diverse growing regions (Mulualem 2022; Gangashetty et al. 2023; Tesfaye et al. 2023). GEI on the assessed genotypes is yet to be conducted to explore specific and wide adaptation.

Heritability is a useful measure of the degree of association between an individual's breeding value and its observable phenotypic traits, whereas genetic advance predicts the effectiveness of selection for specific traits in crop breeding programs (Falconer and Markey 1996). The observed high broad-sense heritability estimates (> 60%) for days to 50% flowering, days to maturity, and drought tolerance is consistent with reports by Ketema et al. (2025) and Kannababu et al. (2025). This indicats that these traits are largely under additive genetic control and minimally affected by the environment, making them ideal candidates for early-generation phenotypic selection. Drought tolerance exhibited high genetic advance as percent of the mean, making it highly responsive to direct selection. However, days to 50% flowering and days to maturity showed low genetic advance as a percent of mean (GA%) despite their high heritability, suggesting constrained genetic variability or non-additive effects, which necessitates later-generation selection (Sharma et al. 2018; Nagaraja et al. 2024; Brhane et al. 2024). In contrast, traits like plant height, and grain yield, amylose, and starch concentrations showed low heritability and low genetic advance and GA%, underscoring strong environmental influence and polygenic inheritance, as alluded by Naveen et al. (2024). The NIR-based estimates of nutritional composition exhibited an acceptable level of accuracy, mainly given the high cost and labor-intensive nature of the wet chemistry procedure. However, there is a need to validate the current results through conventional wet chemistry analysis. Sood et al. (2019) highlighted that the integration of advanced plant phenomics and genomics has meaningfully enhanced genetic gains and strengthened the understanding of key agronomic, adaptive, and nutritional traits in finger millet. Furthermore, the recent multi-omics studies in finger millet provide complementary insights into Fe and Zn homeostasis, highlighting the potential of integrating omics-driven biofortification with modern breeding strategies (Chandra et al. 2020). Moderate heritability and GA% values for thousand seed weight (TW), SG, and micronutrients (Fe, Zn) point to the potential for steady genetic improvement via recurrent selection. Despite moderate heritability, the low genetic advance for micronutrients indicates limited short-term gains, emphasizing the need for biofortification breeding strategies such as genomic selection and hybridization to exploit heterosis to enhance nutritional traits (Fred et al. 2021; Teklu et al. 2023a, b). In addition, this study corroborates earlier reports in finger millet (Marefia et al. 2022; Mulualem 2022) that emphasize high heritability for phenological traits but limited selection efficiency for yield and quality traits. Therefore, to optimize

genetic gains in finger millet across Ethiopia's variable climates, a stratified breeding strategy is essential-combining direct selection for high-heritability traits, recurrent breeding for moderately complex traits, and genomic-assisted or hybrid approaches for low-heritability traits. This approach ensures both selection precision and adaptability of genotypes across diverse agro-ecological zones.

Breeding for drought tolerance is crucial to improve yield stability, ensure food and nutritional security under variable and water-limited conditions of Ethiopia and similar agroecologies in sub-Saharan Africa. Environmental effects were pronounced at MI, where intense drought stress during critical growth stages especially flowering accelerated phenological progression and caused a substantial reduction in grain yield, reaching nearly 60%, relative to the more favorable conditions observed at AN. This outcome is consistent with earlier reports in cereals, where drought stress at flowering resulted in 40–70% yield loss in tef, finger millet, and pearl millet (Maqsood and Ali 2007; Tadele 2018; Numan et al. 2021). Consistent with the current result, early flowering and maturity finger millet genotypes such as G141, G423, G297, G247, and G171 performed better under severe drought (MI site), reflecting a drought-escape strategy that enables completion of their life cycle before peak water stress (Tadelle 2018; Panda et al. 2023). Remarkably, several genotypes exhibited consistence performance across these contrasting environments, indicating inherent adaptability and potential for breeding heat and drought-resilient cultivars. These genotypes G141, G423, G297, G247, and G171, which exhibited excellent drought-adaptation, can be used as parents in hybridization programs to introgress early maturity and stress-resilient traits into diverse and cultivated backgrounds, or as donor lines in recurrent selection to enhance population performance. The genotypes' consistency makes them ideal candidates for multi-environment trials and release for broad cultivation in Ethiopia and similar environments. A notable pattern emerged in relation to seed pigmentation such that genotypes with black or dark brown grains consistently exhibited superior performance for grain yield, drought resistance, and SG ability, particularly under stress-prone conditions (Table 3). This observation suggests a possible adaptive advantage of darker pigmentation, which may be linked to pleiotropic effects or tight genetic linkage with stress-resilience loci (Vadivoo et al. 1998; Singh et al. 2024). Black or red seeds generally show superior drought because their pigmentated seed-coats are rich in phenolics and flavonoids that enhance antioxidant protection, regulate water uptake, and improve seedling vigor under stress (Radchuk & Borisjuk 2014; Dabravolski & Isayenkov 2023; Li & Ahammed 2023; Zhang et al. 2023). Genotypes with darker pigmentation such as G141, G423, G297, G247, G171, G204, G294, and G46 were noted as top performers under the harsh conditions of MI, combining several desirable traits, including early flowering and maturity, high yield potential, large seed size, SG characteristics, and strong drought tolerance. Notably, they also exhibit superior nutritional quality, with high zinc and iron content. Their multi-trait excellence and proven stability make them valuable assets for breeding climate-resilient and nutrient-rich cultivars.

Tait correlation analyses resolved interesting associations for finger millet improvement (Fig. 3). Negative association was detected between grain yield and stress adaptive traits across the test locations, suggesting targeted selection under stress-prone environments. High-yielding finger millet genotypes tend to mature early and show reduced drought sensitivity, aligning with previous findings in finger millet (Manyasa et al. 2016; Kumari et al. 2018; Mulualem 2022) and other cereals such as sorghum (Haussmann et al. 2012), pearl millet (Yadav et al. 2021), and maize (Talabi, et al. 2017). Early maturity linked with drought escape is a proxy trait for drought tolerance breeding. Furthermore, the negative association between stay-green and grain yield is beneficial, as lower SG scores (1–2) were linked to higher productivity under drought, highlighting their value in selecting drought-tolerant genotypes. Therefore, breeding strategies should prioritise early flowering and drought resilience. Additionally, integrating location-specific selection indices that consider local drought scenarios, maturity, and nutritional goals will be instrumental in developing climate-smart and nutritionally superior finger millet cultivars (Sharma et al. 2022; Pramanick et al. 2024).

Principal component analysis (PCA) clearly revealed how key traits drive the adaptation and differentiation of finger millet genotypes across Ethiopia's contrasting environments. PCs with eigenvalues > 1.0 were retained, and the number of

components varied across environments depending on their eigenvalues (Table 5). At AN, a high-potential site, three PCs accounted for > 70% of the total variation, with genotypes primarily differentiated by grain yield, plant height (PH), and nutritional traits, including Fe, Zn and amylose contents. In MI, a drought-prone environment, four PCs were retained, due to the fourth component captured additional meaningful variation in starch content, plant height and grain colour. At MI, early flowering (DF), and maturity (DM), and drought tolerance were the most defining traits, with the four PCs collectively explaining 68.0% of the total variation. At SH, an intermediate environment, three PCs explained 67.7% of the variation, with both resilience-related and grain nutritional quality contributing substantially to genotype separation. This spatially explicit trait clustering highlights distinct adaptation strategies, with genotypes excelling either in stress avoidance and early maturity or in high productivity and nutritional quality. Such patterns, consistent with previous studies in finger millet and other cereals (Admas & Tesfaye 2017; Kumari et al. 2018; Negash et al. 2019; Kumar et al. 2020), underscore the need for environment-specific breeding pipelines. Prioritizing early-maturing, drought-tolerant lines in harsh zones and yield- and nutrient-rich lines in favorable areas offers a strategic, resource-efficient path to maximize genetic gains and climate resilience.

Cluster analysis of 448 Ethiopian finger millet genotypes evaluated under contrasting environments revealed consistent genotype groupings that show underlying trait synergies and adaptive patterns across variable agroclimatic conditions. The majority of genotypes, originating from diverse regions such as Amhara, Oromia, Tigray, SNNP, and Benishangul-Gumuz, were grouped in Cluster 1 across all locations, suggesting shared trait combinations favoring broad adaptation and general agronomic stability. Cluster 2 comprised moderately distinct genotypes that showed some degree of environmental adaptability across sites. In contrast, Cluster 3 contained highly divergent genotypes with unique trait combinations, making them valuable candidates for targeted trait-specific breeding. A small, unique subset formed Cluster 4, representing rare or extreme trait expressions. This pattern aligns with prior findings in finger millet by Kumari et al. (2018), who reported distinct clustering patterns based on genotype origin and trait divergence, and is echoed in multi-trait clustering studies of pearl and foxtail millet (Backiyalakshmi et al. 2021; Rao et al. 2024). This clustering validates the genetic structure and trait composition of Ethiopian finger millet genotypes. It also highlights the value of cluster-based selection for developing ideotypes that optimize yield, stress resilience, and nutritional quality tailored to specific environments (Singhal et al. 2024; Naveen et al. 2024).

Conclusions and recommendations

The study profiled the 448 Ethiopian finger millet accessions under varying drought stress conditions for agronomic, drought-responsive, and nutritional traits. The findings revealed marked genotype by environment interactions and substantial yield reduction (60%) under a severe stress growing condition, highlighting the need for drought tolerance breeding. Drought adaptive traits such as early flowering, stay-green score (SG), and drought tolerance scores (Drt), were significantly associated with yield gains. Notably, days to flowering, days to maturity, and drought tolerance score exhibited relatively high broad-sense heritability ($H^2 > 60\%$), suggesting their reliability and potential for genetic improvement under drought stress. Black-seeded finger millet genotypes had high yield and elevated micronutrient content (iron and zinc), while red-seeded, early maturing and heavier grain weight was related to drought tolerance. Significant associations of SG and Drt with grain yield across environments indicated that genotypes with lower scores, early flowering, delayed senescence, and reduced stress symptoms were more productive under drought-prone conditions. The trait associations were further supported by principal component analysis (PCA), where DF, DM, and Drt accounted for the largest explained variance across environments. Also, cluster analysis delineated four distinct genotype groups based on agronomic performance, drought response parameters and nutritional profiles. In this context, the NIR-based analyses of nutritional content offered a rapid and cost-effective option with acceptable accuracy; yet, validation through conventional wet chemistry remains recommended for ensuring data accuracy. Integrating agronomic, drought-responsive, and nutritional traits with PCA and clustering analyses provided a robust data set for the identification of unique genotypes such as G141,

G423, G297, G247, G171, G204, G294, and G46, for direct cultivation or as donors in breeding programs targeting drought-prone regions.

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Declarations

Conflict of interest The authors declare no competing interests.

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