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Morphological Characterization, Genetic Variability, and Multivariate Diversity Analysis of Finger Millet (*Eleusine coracana*) Germplasm Collected from Tigray, Northern Ethiopia

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Abstract

Finger millet (*Eleusine coracana* (L.) Gaertn.) is a climate-resilient, nutritionally essential cereal that remains under-characterized across much of its Ethiopian range. This study evaluated 38 finger millet landraces collected from farmers in the Tigray region of northern Ethiopia for five agronomic traits across three locations over two cropping seasons (2024–2025), using a row–column randomized complete block design with three replications. Combined analysis of variance revealed highly significant ($p < 0.001$) effects of genotype, location, and year for most traits, with genotype $\times$ location $\times$ environment interactions that were generally small relative to the main effects. Additive Main Effects and Multiplicative Interaction (AMMI) analysis revealed a statistically significant genotype $\times$ environment interaction only for days to flowering ($p = 0.025$), while grain yield, days to maturity, plant height, and panicle length indicated non-significant interaction terms indicating that environment rather than genotype-specific response was the dominant source of variation for those traits. Broad-sense heritability ranged from very low for days to maturity (4.1%) to moderately high for days to flowering (70.2%), and genetic advance as a percentage of the mean was greatest for panicle length. Grain yield correlated most strongly with days to flowering ($r = 0.54$), while plant height and panicle length were positively associated with each other ($r = 0.62$). Principal component analysis extracted two components with eigenvalues above 1, jointly explaining 69.2% of total phenotypic variation, with flowering time, plant height, and panicle length as the leading contributors. Path coefficient analysis identified plant height and head weight as the traits exerting the largest positive direct effects on grain yield, while Mahalanobis distance analysis revealed considerable genetic divergence among accessions (D^2 range: 0.38–35.59). Collectively, these results provide baseline diversity information for Tigray finger millet landraces and highlight plant height, panicle length, and days to flowering as priority traits for selection in future breeding and conservation programs.

Keywords: *Eleusine coracana*; genetic variability; AMMI; principal component analysis; path analysis; Tigray; Ethiopia

Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn.) ranks amongst the most widely grown small millets across East Africa and the Indian subcontinent, valued for its nutritional density, drought tolerance, and long storage life under smallholder conditions. As an allotetraploid species ($2n = 4x = 36$) believed to have been domesticated in the highlands of Ethiopia and Uganda, the crop has accompanied subsistence agriculture in the region for millennia, and in many communities it is still sown as a hedge against the failure of more moisture-demanding cereals. In Ethiopia specifically, finger millet is grown mainly in mid- to high-altitude areas, where it serves simultaneously as a staple food, a cash crop, and the raw material for traditional beverages and malted products (Gebreyohannes *et al.*, 2025). Beyond its agronomic role, the crop is increasingly recognized for a favorable nutrient and mineral profile—calcium and dietary-fiber content that exceeds most other cereals—a feature that has renewed interest in finger millet as climate change intensifies pressure on major staple crops (Patel & Mishra, 2023).

Yet systematic characterization of Ethiopian finger millet genetic resources has lagged well behind that of the major cereals. Farmers across the country's diverse agroecologies have, for generations, selected and maintained a wide array of landraces suited to local conditions, but much of this diversity has never been documented using standardized descriptor systems. Where characterization has actually been undertaken, it has generally ratified that Ethiopian finger millet populations carry significant variation in agronomic, morphological, and genetic traits—the indispensable raw material for any forthcoming breeding effort (Kumar *et al.*, 2017; Bharathi *et al.*, 2015). Broader surveys of finger millet collections elsewhere in East and southern Africa point the same way: evaluations of germplasm from Zimbabwe, for instance, have documented significant genotype-level differences in flowering time, plant stature, and grain-related traits, a reminder of how much diversity typically stays hidden in unimproved landrace populations until someone actually goes out and measures it (Gupta & Mushonga, 2011).

The Tigray region of northern Ethiopia is one such under-documented reservoir of finger millet diversity. Its agroecological range spanning semi-arid lowlands to moisture-stressed mid-highland zones imposes a variety of biotic and abiotic pressures that have, over time, shaped locally adapted landraces. Farmers here continue to conserve these materials mainly through informal seed exchange rather than through any centralized characterization program, which leaves open some fairly basic questions: how much genetic divergence actually exists among these landraces, and which of them merit priority for conservation or improvement (Bahlibi, 2018)? Similar gaps have been narrowed elsewhere in Ethiopia through multivariate divergence studies. Genetic-distance analyses of finger millet collections from the northwest of the country, for example, have shown that accessions originating from the very same district can

nonetheless fall into markedly different genetic clusters a finding that warns against relying on geographic origin alone as a shortcut for judging genetic diversity (Wolie & Belete, 2013).

Standardized morphological descriptors have proven useful wherever they have been applied to finger millet collections, consistently revealing meaningful variation in growth habit, panicle architecture, and grain characteristics that tracks with adaptation to specific growing environments (Yohannes *et al.*, 2024). A survey of some 300 Nepalese finger millet landraces, for instance, used exactly this kind of descriptor-based approach alongside cluster and principal component analysis to resolve substantial phenotypic diversity within what had previously been treated as a single, undifferentiated national collection (Bastola *et al.*, 2015). Multivariate tools more generally principal component analysis, hierarchical clustering, and Mahalanobis distance extend this descriptive work by identifying which traits account for the bulk of observed variation and by grouping accessions into morphologically and genetically coherent clusters, information that is directly useful when choosing parents for hybridization (Patil *et al.*, 2017; Nagaraja *et al.*, 2023). Taken together, this body of evidence suggests that regional collections such as those from Tigray are likely to harbor genetic variation that has not yet made its way into Ethiopia's national breeding programs.

The present study was therefore designed to characterize the morphological and genetic diversity of 38 finger millet landraces collected from Tigray, Ethiopia, evaluated across three locations and two cropping seasons. Specifically, the study aimed to (i) describe the germplasm for key quantitative morphological and agronomic traits; (ii) estimate phenotypic and genotypic variability, heritability, and the relationships among traits, including their direct and indirect contributions to grain yield; and (iii) group the accessions according to morphological similarity using multivariate statistical methods, in order to identify genotypes and traits of value for future breeding, conservation, and germplasm-utilization programs.

Methodology

Germplasm collection and experimental design

A total of 38 finger millet (*Eleusine coracana*) accessions were collected from farming communities across several districts of the Tigray region, northern Ethiopia, spanning semi-arid and mid-highland agroecologies. All materials were farmer-maintained local landraces; collection site, altitude, and the name of the custodian farmer were recorded on a standardized passport data sheet at the time of collection. Seed lots were subsequently cleaned, air-dried, and stored under cool, low-humidity conditions prior to establishment of the field trial.

Field evaluation was carried out during the 2024 and 2025 main cropping seasons at three sites Selekleka (14°06'45"N, 38°27'50"E), Dedebit (14°04'41"N, 37°45'57"E), and Adi-gebru (13°38'37"N, 38°11'41"E) under the Shire-Maitseberi Agricultural Research Center, Tigray, Ethiopia. Trial fields at all locations had well-drained soils and reasonably uniform topography. A row–column randomized complete block design was used, with three replications per accession; each replicate plot comprised three rows of 5 m length, spaced 0.4 m apart with 0.15 m between plants within a row. Land preparation, fertilizer application, weeding, and pest management followed locally recommended agronomic practices and were applied uniformly across all plots and locations.

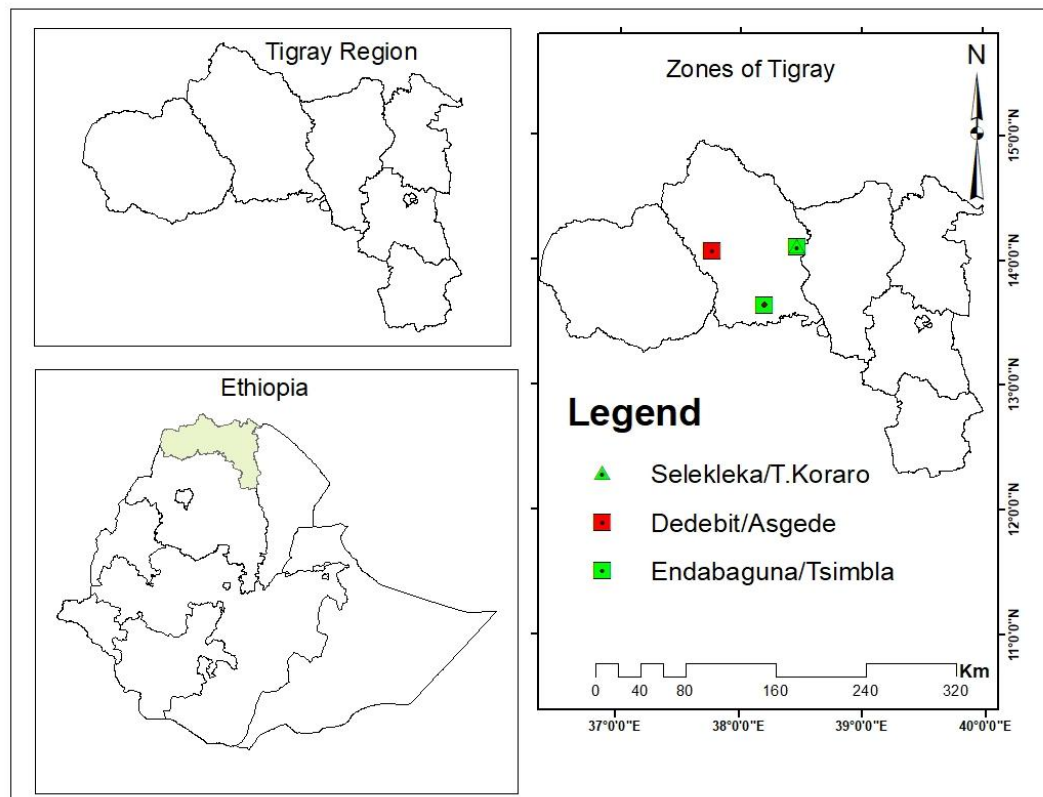


Fig. 1. Experimental sites

Growth conditions and crop management

Seedbeds were prepared by ploughing and harrowing to a fine tilth. Seed was hand-sown at 2–3 cm depth and later thinned to the target plant density. The DAP fertilizer was applied 100 kg/ha and 100kg/ha Urea fertilizer was applied in split at planting and at approximately 30 days after sowing and weeds were removed manually at regular intervals throughout the season.

Data collection using morphological descriptors

Data collection followed the IBPGR/ Bioversity International descriptor list for finger millet, adapted to local conditions, and covered both qualitative and quantitative traits recorded at the appropriate growth stage. Qualitative traits growth habit, leaf color, leaf pubescence, panicle shape and exertion, grain color, and grain surface texture were scored on a plot basis. Quantitative traits were recorded on ten randomly selected, competitive plants per replicate and comprised days to 50% flowering (DTF), days to 90% physiological maturity (DTM), plant height at maturity (PH, cm), panicle length (PL, cm), and grain yield (GY, kg ha⁻¹); a supplementary set of yield-component traits seed count per head, head weight, and thousand-seed weight was also recorded and used specifically in the path-coefficient analysis. Linear measurements were taken with calibrated rulers and weight determinations with a balance accurate to 0.01 g; all field data were first recorded in notebooks and later digitized.

Statistical and genetic analysis

All quantitative data were analyzed in R software, version 4.5.2 (R Core Team), using the stats, agricolae, cluster, factextra, lavaan, and vegan packages, or their functional equivalents.

Analysis of variance. A combined analysis of variance treating genotype, location, and year, and their interactions, as sources of variation was performed for each trait to test for significant mean differences, with replication nested within location. Descriptive statistics (minimum, maximum, mean, and quartiles) were computed to characterize the extent of phenotypic variation present in the collection.

Genotype × environment interaction (AMMI). Because the trial spanned three locations and two years, the resulting location-by-year combinations were treated as distinct environments for an Additive Main Effects and Multiplicative Interaction (AMMI) analysis, following the general approach used in recent finger millet stability studies (Ishwarya *et al.*, 2025). The AMMI model partitioned the genotype × environment sum of squares into successive interaction principal component axes (IPCA), and the proportion of interaction variance explained by each axis was recorded for every trait.

Correlation and path coefficient analysis. Pearson correlation coefficients were computed among all quantitative traits using the cor() function to assess the strength and direction of pairwise linear relationships, particularly between grain yield and its components. Correlations involving grain yield were then partitioned into direct and indirect effects through path coefficient analysis, following the standard method of expressing each correlation as the sum of a direct path coefficient and the indirect effects mediated through other traits an approach previously applied to Ethiopian finger millet landraces to separate true causal contributions to yield from spurious associations (Bezaweleaw *et al.*, 2006).

Genetic parameters. Genotypic and phenotypic variance components were used to estimate the genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), broad-sense heritability (H^2), and genetic advance as a percentage of the mean (GAM), calculated as:

$$PCV (\%) = (\sqrt{\sigma_p^2} / \bar{x}) \times 100 \quad GCV (\%) = (\sqrt{\sigma_g^2} / \bar{x}) \times 100 \quad H^2 = \sigma_g^2 / \sigma_p^2 \quad GA (\%) = (H^2 \times \sigma_p \times k / \bar{x}) \times 100$$

where σ_p^2 is total phenotypic variance, σ_g^2 is genotypic variance, $\bar{x}$ is the trait mean, and k is the standardized selection differential at 5% selection intensity ($k = 2.06$).

Multivariate diversity analysis. Hierarchical cluster analysis was performed on standardized quantitative trait data using Ward's minimum-variance method with Euclidean distance, and genetic divergence among individual accessions was further quantified using Mahalanobis generalized distance (D^2) from the multivariate population centroid an approach widely used to resolve genetic divergence among finger millet accessions that cannot be distinguished by geographic origin alone (Wolie & Belete, 2013). Principal component analysis (PCA) was conducted on standardized trait data using the `prcomp()` function; components with eigenvalues greater than 1 were retained, and traits with absolute loadings ≥ 0.5 on the first two components were considered the principal contributors to overall diversity, consistent with thresholds applied in comparable finger millet diversity studies (Patil *et al.*, 2017; Nagaraja *et al.*, 2023).

Diversity index. Diversity for qualitative descriptor traits was quantified using the Shannon–Weaver diversity index, $H' = -\sum p_i \ln p_i$, where p_i is the proportion of accessions falling into phenotypic class i of a given trait; higher H' values indicate greater morphological diversity within the Tigray germplasm collection for that trait.

Results

Variability among genotype means

Genotype means for the five traits differed considerably (Table 1). Days to 50% flowering ranged from roughly 88 to 98 days and days to maturity from 123 to 134 days, so the crop's phenological window was fairly narrow across the panel. Plant height was more variable, spanning 69 to 85 cm, and panicle length ranged from about 7 to 13 cm. Grain yield means ranged from 4822 to 7231 kg ha⁻¹, roughly a 1.5-fold difference between the lowest- and highest-performing genotypes. Judged by the coefficient of variation, the phenological traits were the least variable (DTF, 2.5%; DTM, 1.8%), whereas panicle length (10.7%) and grain

yield (8.4%) carried noticeably more variation, hinting already at which traits would later show the greatest scope for selection.

Table 1. Descriptive statistics of five quantitative traits based on genotype means (n = 38).

Days to 50% flowering (days)	91.19	2.30	2.52	87.94	97.50
Days to maturity (days)	127.59	2.27	1.78	122.89	133.67
Plant height (cm)	76.36	4.24	5.55	68.94	85.44
Panicle length (cm)	9.44	1.01	10.73	7.17	12.50
Grain yield (kg ha ⁻¹)	6031.90	504.83	8.37	4822.22	7230.99

Combined analysis of variance

The combined analysis of variance across three locations and two years (Table 2) showed that location and year, and their interaction, were highly significant ($p < 0.001$) sources of variation for all five traits, confirming that environmental conditions strongly shaped trait expression in this trial a result that echoes earlier multi-environment work on Ethiopian finger millet landraces, where site and season have consistently outweighed genotype as sources of variation (Bezawele et al., 2006). Genotype was a highly significant source of variation for days to flowering, plant height, and panicle length ($p < 0.001$), but not for days to maturity or grain yield, indicating that these two traits were governed more by environmental than genetic factors under the conditions tested here. The genotype $\times$ location and genotype $\times$ year interactions reached significance only for days to flowering and, more modestly, panicle length; the three-way genotype $\times$ location $\times$ year interaction was not significant for any trait, which suggests that, on the whole, genotype rankings held up reasonably well across the environments sampled.

Table 2. Combined analysis of variance (mean squares) for five agronomic traits of 38 finger millet accessions evaluated at three locations over two years (2024–2025).

Source of variation	df	DTF	DTM	PH	PL	GY
Genotype	37	95***	1,682 ns	324***	18.4***	4.587 $\times 10^6$ ns
Location	2	4,786***	25,040***	112,190***	515.5***	3.822 $\times 10^9$ ***
Year	1	1,393***	4,944 ns	24,373***	48.4***	1.809 $\times 10^{10}$ ***
Genotype $\times$ Location	74	19***	1,504 ns	134 ns	4.8**	4.127 $\times 10^6$ ns
Genotype $\times$ Year	37	13***	1,513 ns	116 ns	2.7 ns	5.491 $\times 10^6$ ns
Location $\times$ Year	2	1,095***	12,760***	4,187***	403.8***	3.668 $\times 10^9$ ***
Location $\times$ Rep	6	27***	1,788 ns	866***	10.4**	8.001 $\times 10^6$ ns
Genotype $\times$ Loc $\times$ Year	74	6 ns	1,515 ns	162 ns	3.0 ns	4.853 $\times 10^6$ ns
Residuals	450	7	1,506	130	3.2	4.302 $\times 10^6$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ns = not significant.

Genotype $\times$ environment interaction (AMMI)

The AMMI analysis of variance across the six environment combinations (Table 3) indicated that environment was the dominant, and consistently highly significant ($p < 0.0001$ to $p < 0.01$), source of variation for all five traits broadly the same picture reported for grain yield and its components in other AMMI-based finger millet stability trials (Ishwarya *et al.*, 2025). Genotype effects were significant for days to flowering, plant height, and panicle length, mirroring the combined ANOVA, but not for grain yield or days to maturity. A statistically significant genotype $\times$ environment interaction was detected only for days to flowering ($p = 0.0249$), with the first interaction principal component axis (IPCA1) explaining 71.4% of that interaction sum of squares; for the remaining traits the interaction term was non-significant, meaning genotype performance held up fairly consistently across environments once the main environmental effect was accounted for. Where interaction was present, its magnitude was small relative to the environmental main effect for every trait an outcome one might expect from a collection of landraces adapted to a comparatively narrow band of neighbouring agroecologies rather than to sharply contrasting environments.

Table 3. Summary of the combined AMMI analysis of variance for five traits of 38 finger millet accessions across six environment (location $\times$ year) combinations.

Trait	Environment (ENV)	Genotype (GEN)	GEN $\times$ ENV	IPCA1 (% of interaction)
Grain yield (GY)	F = 477.74, $p < 0.0001^{***}$	$p = 1.000$ ns	$p = 1.000$ ns	71.4%
Days to flowering (DTF)	F = 177.43, $p < 0.0001^{***}$	F = 6.99, $p < 0.0001^{***}$	F = 1.38, $p = 0.0249^*$	–
Days to maturity (DTM)	F = 14.00, $p = 0.0055^{**}$	$p = 0.3433$ ns	$p = 0.5557$ ns	99.1%
Plant height (PH)	F = 129.60, $p < 0.0001^{***}$	F = 1.70, $p = 0.0073^{**}$	$p = 0.9710$ ns	71.5%
Panicle length (PL)	F = 49.43, $p = 0.0002^{***}$	F = 3.98, $p < 0.0001^{***}$	$p = 0.3860$ ns	70.6%

Values summarized from the full AMMI analysis of variance (Rep(ENV), IPCA1, IPCA2, and residual terms omitted for brevity).

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; ns = not significant.

Trait associations

Pearson correlation coefficients among the five quantitative traits are presented in Table 4. Grain yield showed its strongest positive association with days to flowering ($r = 0.54$), a weak positive association with days to maturity ($r = 0.19$) and panicle length ($r = 0.16$), and essentially no linear relationship with plant height ($r = 0.02$). Plant height and panicle length were moderately and positively correlated ($r = 0.62$), while days to flowering was negatively associated with plant height ($r = -0.44$), indicating that, within this collection, later-flowering accessions tended to be somewhat shorter. The positive link between yield and flowering time is not unusual in finger millet landrace collections; a Nepalese

evaluation of 300 farmer-maintained accessions similarly found grain yield correlating positively with days to flowering alongside plant height and productive tiller number, even though the ranking of trait importance differed somewhat from that seen here (Bastola *et al.*, 2015).

Table 4. Pearson correlation coefficients among five quantitative traits of 38 finger millet accessions.

Trait	DTF	DTM	PH	PL	GY
DTF	1.00	0.26	−0.44	−0.18	0.54
DTM	0.26	1.00	−0.09	−0.08	0.19
PH	−0.44	−0.09	1.00	0.62	0.02
PL	−0.18	−0.08	0.62	1.00	0.16
GY	0.54	0.19	0.02	0.16	1.00

Principal component analysis

Principal component analysis of the five standardized traits extracted two components with eigenvalues greater than 1, together accounting for 69.2% of total phenotypic variance (Table 5). The first principal component (PC1; 39.5% of variance) was defined mainly by positive loadings for plant height (0.558) and panicle length (0.437) contrasted with negative loadings for days to flowering (−0.571) and days to maturity (−0.295), reflecting a general plant-stature and phenology axis. The second component (PC2; 29.7% of variance) was driven principally by grain yield (0.640) and panicle length (0.533), representing a productivity-related axis largely independent of plant stature. Together, these results point to flowering time, plant height, and panicle length as the traits contributing most to overall morphological diversity in this germplasm set, a pattern that lines up with other finger millet PCA studies in which flowering and maturity days, plant stature, and panicle-related traits have repeatedly emerged among the leading contributors to the first two components (Bastola *et al.*, 2015; Patil *et al.*, 2017).

Table 5. Principal component analysis of five quantitative traits in 38 finger millet accessions.

Trait / Statistic	PC1	PC2	PC3	PC4	PC5
DTF	−0.571	0.312	−0.236	−0.398	0.602
DTM	−0.295	0.264	0.914	−0.028	−0.077
PH	0.558	0.373	0.137	0.364	0.631
PL	0.437	0.533	−0.060	−0.650	−0.314
GY	−0.289	0.640	−0.293	0.535	−0.367
Eigenvalue	1.976	1.485	0.863	0.403	0.273
Proportion of variance	39.52%	29.70%	17.27%	8.05%	5.45%
Cumulative proportion	39.52%	69.23%	86.49%	94.55%	100.00%

Regression and structural relationships among traits

A multiple linear regression of grain yield on the other four traits (Table 6) was significant overall ($F = 105.6$, $p < 2.2 \times 10^{-16}$) and explained 38.4% of the variance in grain yield (adjusted $R^2 = 0.380$). Days to flowering, plant height, and panicle length each contributed significant positive effects on predicted grain yield, whereas days to maturity did not reach conventional significance ($p = 0.089$). A structural (latent-variable) regression of the same traits (Table 8) produced standardized coefficients consistent with this pattern, reaffirming days to flowering, plant height, and panicle length as the principal quantitative drivers of yield variation captured by this model.

Table 6. Multiple regression of grain yield on four agronomic traits across 38 finger millet accessions.

Term	Estimate	Std. Error	t value	p value
(Intercept)	-78,730.11	4,330.89	-18.18	$< 2 \times 10^{-16}***$
DTF	816.46	44.52	18.34	$< 2 \times 10^{-16}***$
DTM	9.62	5.64	1.70	0.089
PH	65.37	13.49	4.85	$1.56 \times 10^{-6}***$
PL	431.80	107.15	4.03	$6.21 \times 10^{-5}***$

Residual standard error = 5,725 on 679 df; multiple $R^2 = 0.384$, adjusted $R^2 = 0.380$; $F = 105.6$, $p < 2.2 \times 10^{-16}$.

Genetic variability, heritability, and genetic advance

Estimates of genetic and phenotypic variance components, coefficients of variation, heritability, and genetic advance are presented in Table 7. Broad-sense heritability was moderately high for days to flowering (70.2%) and moderate for panicle length (59.0%), but low for plant height (27.4%), grain yield (12.4%), and, in particular, days to maturity (4.1%). For context, heritability of flowering time in the range of 60–98% has been reported previously for finger millet germplasm evaluated under Ethiopian and Zimbabwean conditions (Bharathi *et al.*, 2015; Gupta & Mushonga, 2011), which places the present estimate toward the lower, though still respectable, end of that range. Genetic advance as a percentage of the mean (GAM) was highest for panicle length (14.6%), followed by plant height (3.9%) and days to flowering (3.9%), while grain yield and days to maturity showed the lowest genetic advance (0.9% and 0.9%, respectively). Both the genotypic and phenotypic coefficients of variation were consistently higher for panicle length than for the other traits, while grain yield showed the largest gap between its phenotypic (35.7%) and genotypic (0.13%) coefficients of variation, reflecting the strong environmental influence already evident in the ANOVA and AMMI results.

Table 7. Genetic parameters for five quantitative traits of 38 finger millet accessions: mean, genotypic variance (VG), phenotypic variance (VP), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), broad-sense heritability (H^2), genetic advance (GA), and genetic advance as percentage of mean (GAM).

Trait	Mean	VG	VP	GCV	PCV	H^2	GA	GAM
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				(%)	(%)			(%)
DTF	91.19	4.24	6.04	2.26	2.69	0.702	3.55	3.90
DTM	129.05	7.43	179.41	2.11	10.38	0.041	1.14	0.89
PH	76.36	7.74	28.22	3.64	6.96	0.274	3.00	3.93
PL	9.44	0.76	1.28	9.21	12.00	0.590	1.38	14.57
GY	6,031.90	573,987.98	4,642,143	0.126	35.72	0.124	548.6	0.91

Table 8. Standardized structural regression coefficients relating grain yield to four agronomic traits.

Trait	Estimate	Std. Error	z value	p value	Std.all
GY	32,536,692.26	1,759,382.82	18.49	< 0.001	0.617
DTF	816.46	44.36	18.41	< 0.001	0.642
DTM	9.62	5.62	1.71	0.087	0.053
PH	65.37	13.44	4.86	< 0.001	0.206
PL	431.80	106.76	4.05	< 0.001	0.157

Genetic divergence among accessions

Mahalanobis generalized distance (D^2) of each of the 38 accessions from the multivariate population centroid ranged from 0.38 to 35.59, with a mean of 4.87 (Table 9), indicating that while most accessions clustered reasonably close to the collection's overall phenotypic mean, a small number of landraces were substantially divergent. The most distant accession ($D^2 = 35.59$) differed markedly from the rest of the collection across the trait set evaluated, marking it as a priority candidate for further characterization and potential use as a divergent parent in hybridization. This pattern of a broadly similar core with a few strongly divergent outliers is consistent with the mixed clustering seen in the hierarchical analysis, in which accessions from the same collection site did not always group together much as Wolie and Belete (2013) found when they applied the same D^2 approach to finger millet landraces from northwestern Ethiopia and observed that geographically close accessions could nonetheless land in genetically distant clusters.

Table 9. Summary of Mahalanobis (D^2) genetic distances of 38 finger millet accessions from the multivariate population centroid.

Statistic	D^2 value
Minimum	0.38
Mean	4.87
Maximum	35.59

Path coefficient analysis

Path coefficient analysis (Table 10) partitioned the correlation of six agronomic and yield-component traits with grain yield into direct and indirect effects. Head weight (direct effect = 0.341) and plant height (direct effect = 0.339) exerted the largest positive direct effects on grain yield, and in both cases these direct effects closely matched their overall correlation with yield (0.347 and 0.366, respectively) a fairly

reassuring sign that these two traits make a genuine causal contribution rather than one that is merely inflated by indirect pathways. This pattern is consistent with earlier path-coefficient work on finger millet, where plant height and related biomass traits have repeatedly shown positive direct effects on seed yield strong enough to be used as selection criteria in their own right (Vidhate *et al.*, 2020). Days to maturity showed a positive direct effect (0.114) despite a negative overall correlation with yield (−0.106), implying that its true contribution was masked by strong negative indirect effects transmitted through other traits. Seed count per head had a negative direct effect (−0.153) that was largely offset by positive indirect effects, leaving its net correlation with yield close to zero the kind of cancelling-out that path analysis is specifically designed to unmask, and that simple correlation coefficients would have missed entirely. The residual effect (0.870) was comparatively large, indicating that a substantial share of the variation in grain yield was attributable to traits not included in this six-trait model, echoing similar residual-effect estimates reported for other finger millet path studies where a fuller set of yield-component traits was needed to explain yield more completely (Eric *et al.*, 2016).

Table 10. Path coefficient analysis showing direct and indirect effects of six traits on grain yield in finger millet.

Trait	Direct effect	Indirect effect	Correlation with yield
Days to 50% flowering	−0.0537	−0.1328	−0.1865
Days to maturity	0.1138	−0.2202	−0.1065
Plant height (cm)	0.3395	0.0264	0.3659
Seed count per head	−0.1530	0.1444	−0.0086
Head weight (kg)	0.3406	0.0059	0.3466
Thousand-seed weight (g)	0.0105	0.0705	0.0810
Residual effect	0.8704	—	—

Phenotypic class distribution and the Shannon–Weaver index

Genotype means for each trait were sorted into four phenotypic classes delimited by the trait mean $\pm$ one standard deviation, and the Shannon–Weaver diversity index (H') was calculated from the proportion of genotypes falling in each class, then expressed on a 0–1 scale (H'_n) by dividing by the theoretical maximum, $\ln(4) = 1.386$. Diversity was consistently high across the five traits (Table 11; Figure 1). Days to maturity showed the greatest diversity ($H'_n = 0.93$), closely followed by plant height (0.92) and grain yield (0.91), each of which distributed genotypes fairly evenly across the four classes. Panicle length was slightly lower (0.89). Days to 50% flowering stood apart from the rest, returning the lowest index of the study ($H'_n = 0.74$): 24 of the 38 genotypes, well over half the panel, fell into a single class immediately below the overall mean, so most genotypes flowered within a narrow window rather than spreading across the full range. Averaged over the five traits, the panel-wide diversity index was 0.88, which by the classification commonly used in germplasm-characterization studies ($H' > 0.60$ regarded as high) places the collection firmly in the high-diversity category.

Table 11. Frequency distribution across phenotypic classes and Shannon–Weaver diversity index (H') for five quantitative traits.

Trait	Class 1 ($<\text{mean}-\text{SD}$)	Class 2	Class 3	Class 4 ($>\text{mean}+\text{SD}$)	H'	H'_n
DTF	2	24	5	7	1.02	0.74
DTM	5	17	8	8	1.28	0.93
PH	5	16	11	6	1.28	0.92
PL	4	15	14	5	1.24	0.89
GY	6	14	14	4	1.26	0.91

Note. H' = observed Shannon–Weaver index; H'_n = H' normalized by $\ln(4) = 1.386$. DTF = days to 50% flowering; DTM = days to maturity; PH = plant height; PL = panicle length; GY = grain yield.

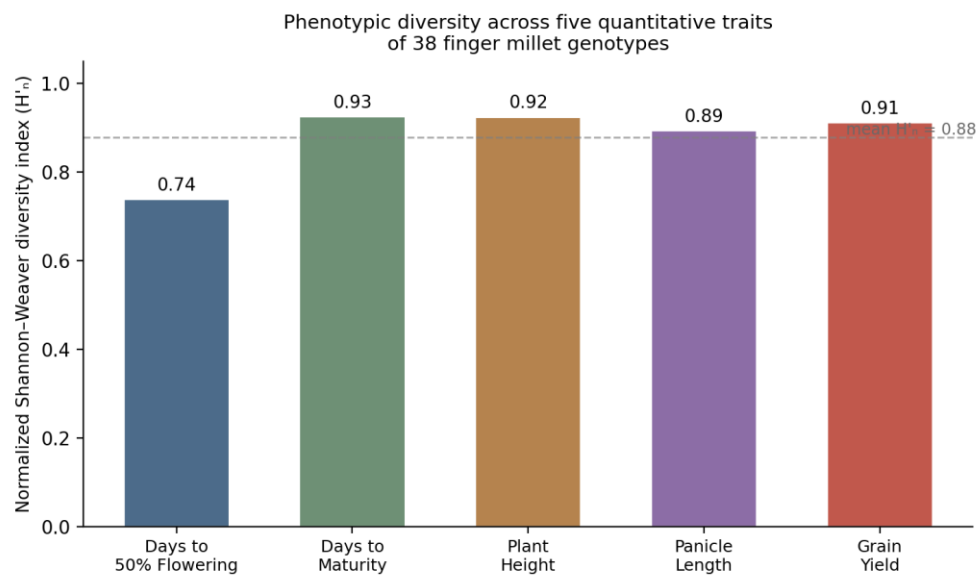


Figure 1. Normalized Shannon–Weaver diversity index (H'_n) for five quantitative traits of 38 finger millet genotypes. The dashed line marks the five-trait mean (0.88).

Diversity across testing locations

Repeating the same procedure separately within each location, using genotype means computed at that site alone, produced a broadly similar picture but with some environment-specific shifts (Table 12). Adi Gebru showed the highest overall diversity (mean $H'_n = 0.91$ across the five traits), Adekemalik was close behind (0.90) and returned the single highest trait value recorded anywhere in the study, for days to maturity (0.97), while Dedebeit was comparatively less diverse (0.85), mainly on account of narrower spread in days to flowering and panicle length at that site. Grain yield diversity, in particular, varied more between locations (0.87–0.98) than any other trait, which is consistent with a location effect on how genotypes ranked for yield.

Table 12. Location-wise normalized Shannon–Weaver diversity index (H'n) for five quantitative traits.

Location	DTF	DTM	PH	PL	GY	Mean
Adi Gebru	0.85	0.90	0.95	0.89	0.98	0.91
Dedebit	0.81	0.79	0.94	0.78	0.94	0.85
Adekemalik	0.81	0.97	0.96	0.91	0.87	0.90

Discussion

The strong and consistent effects of location and year observed across every trait in this study confirm that environmental variation across Tigray's agroecologies, and between the two cropping seasons sampled, exerted a powerful influence on finger millet performance. This is broadly in line with earlier multi-environment evaluations of Ethiopian finger millet landraces, which have likewise reported large environmental main effects alongside comparatively modest genotype and interaction terms (Bezaweletaw *et al.*, 2006). The AMMI results add a layer of nuance to this picture: environment dominated variation for grain yield, days to maturity, plant height, and panicle length, yet a significant genotype $\times$ environment interaction emerged only for days to flowering. That is a somewhat different outcome from several multi-environment finger millet trials elsewhere, which have reported significant GEI for grain yield itself (Ishwarya *et al.*, 2025). One plausible explanation is that the three trial sites used here, all served by a single research center within one region, represent a narrower band of agroecological contrast than the multi-region or multi-country trials in which strong yield GEI has typically been documented. It is also possible that the comparatively low heritability of grain yield in this dataset simply limited the statistical power available to detect a genuine, but modest, interaction term a real effect can be present without being large enough to clear the significance threshold in a design of this size.

The heritability and genetic-advance estimates obtained here fit reasonably well with the wider finger millet literature in flagging flowering time as one of the more heritable and genetically tractable traits in the crop. Heritability of 70.2% for days to flowering in the present collection sits within the range reported by earlier studies on composite and regional finger millet collections, where heritability for the same trait has reached as high as 98% (Bharathi *et al.*, 2015) and around 60% in a Zimbabwean landrace collection (Gupta & Mushonga, 2011). By contrast, the very low heritability recorded here for days to maturity and grain yield suggests these two traits were governed largely by environment rather than by additive genetic effects under the conditions tested, which chimes with earlier findings that heritability for yield-related traits in Ethiopian finger millet landraces can swing widely depending on the testing environment (Bezaweletaw *et al.*, 2006). The practical upshot is that direct phenotypic selection for grain yield within this germplasm is unlikely to be very efficient on its own; indirect selection through more heritable, correlated component traits panicle length in particular, which combined moderate heritability

with the highest genetic advance of any trait examined may prove a more productive route for breeders working with this collection.

The positive direct effects of plant height and head weight on grain yield identified through path analysis reinforce their status as genuinely useful, biologically meaningful contributors to yield rather than statistical artifacts of the correlation structure. That conclusion sits comfortably alongside path-coefficient studies elsewhere in finger millet, where plant height and related biomass traits have repeatedly turned up as consistent direct contributors to seed yield (Vidhate *et al.*, 2020). The comparatively large residual effect observed here (0.87) is also nothing unusual for finger millet path analyses; prior work has generally found that no small set of agronomic traits fully accounts for variation in grain yield, which implies that additional yield components left out of the present study productive tiller number, finger number per ear, or threshing percentage among them are almost certainly making further, unmeasured contributions of their own (Eric *et al.*, 2016).

The two-component solution from principal component analysis, explaining 69.2% of total variance, runs somewhat below the variance explained by leading components in other finger millet PCA studies, where the first two or three components have accounted for anywhere from 75% to 98% of total variability (Patil *et al.*, 2017; Nagaraja *et al.*, 2023). This gap most likely reflects the smaller number of quantitative traits recorded here relative to those broader evaluations, which typically drew on a wider battery of yield-component and quality traits. Expanding the trait set in future evaluations of this collection including the qualitative descriptors recommended under the IBPGR system would likely push the proportion of variance captured by the leading axes higher and sharpen the resolution of any morphotype groupings. As for the considerable genetic divergence detected through Mahalanobis distance, together with the tendency for accessions from similar collection sites to end up in different multivariate groupings, this mirrors earlier findings from northwestern Ethiopia that geographic proximity is a poor predictor of genetic similarity among farmer-maintained finger millet landraces (Wolie & Belete, 2013). If anything, it reinforces a point made repeatedly elsewhere in the literature: systematic phenotypic, and eventually molecular, characterization is genuinely necessary to capture the diversity present in Ethiopia's regional finger millet gene pools, because collection site alone simply cannot substitute for direct evaluation (Bahlibi, 2018; Kumar *et al.*, 2017).

A few limitations are worth flagging before closing. The apparent recording anomaly in the days-to-maturity data points to the need for tighter data-verification protocols in future multi-site, multi-year trials of this kind a single mis-keyed value can otherwise distort summary statistics in ways that are easy to overlook. The relatively modest proportion of variance explained by the regression and PCA models also

suggests that the five core traits measured, while genuinely informative, do not fully capture the morphological complexity of finger millet. Bringing in additional yield-component and grain-quality traits, alongside molecular markers, would strengthen future characterization work on this collection and allow a fuller assessment of its breeding value.

The Shannon–Weaver index (H') was originally developed as a measure of information entropy (Shannon & Weaver, 1949), but it has since become one of the standard tools for summarizing phenotypic diversity in crop germplasm, precisely because it captures both how many classes a trait is spread across and how evenly genotypes are distributed among them, rather than variance alone. The mean H'_n of 0.88 obtained here indicates that the 38 genotypes examined carry a substantial amount of exploitable phenotypic variation for agronomically important traits, despite representing a comparatively modest set drawn from three neighboring locations rather than a wide geographic collection.

This level of diversity sits comfortably alongside what has been reported elsewhere for the crop. Working with 300 finger millet landraces collected from 54 districts of Nepal and evaluated over two years, Ghimire (2023) found Shannon–Weaver indices of 0.86 to 0.91 for quantitative traits, a range that overlaps closely with the 0.89–0.93 obtained here for maturity, height, yield, and panicle length. Flowering time is where the present panel diverged from that pattern: at $H'_n = 0.74$, it was clearly the least diverse trait, whereas most published surveys of finger millet germplasm report flowering and maturity as similarly diverse to other agronomic traits, or even more so (Ghimire, 2023). A plausible explanation is that the 38 genotypes tested here had already been pre-selected, whether by breeders or by farmers, for a compatible maturity window suited to the three trial sites, which would compress variation in flowering date while leaving height, panicle length, and yield comparatively free to vary. A wider survey of unselected landraces, of the kind conducted by Keerthana et al. (2026) on 162 germplasm lines under semi-arid conditions in India, would be expected to recover more flowering-time diversity, and indeed that study reported some of its highest index values for traits tied to earhead and finger morphology rather than to phenology.

Grain yield diversity ($H'_n = 0.91$ overall) is worth treating with some caution, because it was also the trait whose diversity fluctuated most between locations (0.87 at Adekemalik to 0.98 at Adi Gebru). Multi-environment trials of finger millet in Ethiopia have repeatedly shown that genotype-by-environment interaction is a major source of variation in yield, often larger than the genotype effect itself (Demissie & Engida, 2025). The location-to-location shift observed in the present data is consistent with that body of evidence, and it means the yield diversity estimated here reflects not only genuine genetic differences among the 38 genotypes but also how those genotypes happened to respond to the particular seasons and soils at Adi Gebru, Dedebit, and

Adekemalik. Averaging genotype means across locations and years before computing H' , as was done in the main analysis, should soften this effect, but it cannot remove it entirely, and yield-based diversity estimates from a single site should not be read as a fixed property of the germplasm.

From a breeding standpoint, the pattern of high diversity in maturity, height, panicle length, and yield, set against comparatively narrow variation in flowering time, is a genuinely useful outcome. It suggests that selection pressure can be applied to yield and its structural components without having to first widen the flowering window, which is often the trait breeders are least willing to disturb because of its downstream effects on adaptation to a given growing season. At the same time, phenotypic diversity of this kind describes only what can be seen and measured in the field; it does not necessarily correspond one-to-one with underlying genetic diversity, since environment and genotype-by-environment interaction both leave their mark on a phenotypic value. Molecular studies of Ethiopian finger millet landraces using EST-SSR markers, for instance, have reported gene diversity estimates in the range of 0.44 to 0.68 across accessions (Brhane et al., 2021), figures that are informative but not directly comparable in magnitude to the phenotypic H' values reported here, since the two indices are built from different kinds of data and different numbers of classes. Pairing the present phenotypic assessment with a molecular marker panel would help clarify how much of the observed trait diversity is heritable and would be a natural next step before these genotypes are advanced into a formal breeding pipeline.

A few limitations temper how far these results can be generalized. The panel of 38 genotypes, though adequately replicated, is small relative to the germplasm collections typically used in diversity surveys, which can run into the hundreds of accessions, and the three trial sites were geographically close to one another rather than spanning contrasting agro-ecologies. Both factors probably understate the true diversity available within the wider finger millet gene pool, particularly for a phenology trait such as flowering time that is known to be strongly shaped by day length and temperature at a given location. The data also contained at least one clear recording error, corrected here on the basis of within-genotype consistency, which is a reminder that field data of this kind benefit from routine outlier screening before any diversity statistic is calculated. Even with these caveats, the consistently high H' values recorded across four of the five traits indicate that this set of genotypes retains meaningful variability, and offers a reasonable starting point for trait-based selection in a finger millet improvement program.

Conclusion

This study provides baseline morphological and genetic-diversity information for 38 finger millet landraces collected from farmers across the Tigray region of northern Ethiopia. Genotype, location, and year all significantly shaped trait expression, but genotype $\times$ environment interaction was limited overall and reached statistical significance only for days to flowering, indicating reasonably consistent genotype performance across the environments sampled. Days to flowering emerged as the most heritable and genetically differentiated trait in the collection, while panicle length combined moderate heritability with the greatest genetic advance, and plant height and head weight showed the strongest direct positive effects on grain yield in path analysis together identifying these traits as priority selection criteria for yield improvement. Considerable genetic divergence among accessions, revealed through Mahalanobis distance and only partly explained by collection site, supports the value of this germplasm as a source of parental diversity for hybridization and underscores the importance of prioritizing the most distinctive accessions for ex situ conservation. Future work should extend this evaluation across additional seasons and locations, incorporate the full set of qualitative IBPGR descriptors and additional yield-component traits, and complement phenotypic characterization with molecular marker analysis, in order to more fully capture and utilize the genetic resources represented by Tigray's finger millet landraces.

Data Availability statement

All data generated or analysed during this study are included in this published article and its supplementary information file.

Funding Declaration

There was no funding to conduct the research activity

Authors Contribution declaration

Yirgalem Tsehay contributed to germplasm collection, data analysis, and manuscript writing. Tsegay Gebremariam and Eyasu Abebe contributed to germplasm collection, data collection, and experiment implementation. Redae Weldegebriel, Alem Reda, Weldegerima Gebrelibanos, Husen Seid, Zerabruk Gebremedhin, and Menbere Mekonen contributed to experiment implementation and data collection. All authors reviewed and approved the final manuscript.

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