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Qualitative and Quantitative Trait Diversity, Correlation and Path Analysis in Finger Millet [Eleusine coracana (L.) Gaertn.]

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Research Article

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Qualitative and Quantitative Trait Diversity, Correlation and Path Analysis in Finger Millet *[Eleusine coracana (L.) Gaertn.*]

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Abstract

Thirty finger millet [*Eleusine coracana* (L.) Gaertn.] genotypes were evaluated in a randomized block design (three replications, *kharif 2020*) for qualitative characterization and genetic variability, character association, path and divergence analysis of fifteen quantitative yield traits. DUS descriptors revealed wide diversity for growth habit, branching, ear shape and seed colour, with erect growth habit and copper-brown seed colour predominating. Genotypic differences were highly significant for all quantitative traits, and the phenotypic coefficient of variation exceeded the genotypic coefficient of variation for every trait, both highest for harvest index, productive tillers per plant and grain yield per plant. High heritability coupled with high genetic advance was recorded for harvest index, grain yield per plant and productive tillers per plant, among other traits, indicating additive gene action. Grain yield per plant correlated positively with harvest index (rp=0.8474), 1000-grain weight (rp=0.5744) and days to 50% flowering (rp=0.5644). Path analysis identified harvest index (direct effect=1.1403) and biological yield per plant (direct effect=0.5985) as the principal direct contributors to yield. Mahalanobis D^2 analysis grouped genotypes into five clusters, with grain yield (14.54%), biological yield (11.32%) and 1000-grain weight (8.50%) contributing most to divergence, indicating that hybridization between genetically distant genotypes could generate superior recombinants. A Smith–Hazel selection index combining grain yield per plant with six component traits was 9.51% more efficient than direct selection on yield alone, ranking KMR 656 and GPU 104 as the top two genotypes, matching their rank by grain yield alone.

Keywords- Eleusine coracana · Genetic variability · Heritability · Correlation · Path coefficient · Genetic divergence

Introduction

Finger millet (*Eleusine coracana* (L.) Gaertn.) is one of the oldest cultivated cereal crops belonging to the family Poaceae and subfamily Chloridoideae. Finger millet is predominantly a self-pollinated, allotetraploid species with chromosome number 2n = 4x = 36 and possesses a genome size of approximately 1.5–1.6 Gb (Goron and Raizada 2015; Hittalmani et al. 2017). It is an important small millet cultivated mainly in the semi-arid tropics of Asia and Africa, where it serves as a staple food for millions of people. The crop is believed to have originated in the Ethiopian highlands and was domesticated from its wild progenitor, Eleusine africana, before spreading to the Indian subcontinent approximately 3,000–5,000 years ago (de Wet et al. 1984; Hittalmani et al. 2017). Owing to its remarkable adaptability to drought, low soil fertility, and erratic rainfall, finger millet has emerged as one of the most climate-resilient cereal crops and is increasingly recognized for its role in sustainable agriculture and food security under changing climatic conditions (Gebreyohannes et al. 2024).

In recent years, the global importance of finger millet has increased considerably because of growing awareness regarding its nutritional superiority over major cereals. The designation of 2023 as the International Year of Millets by the United Nations General Assembly, following India's proposal, significantly enhanced global attention towards millet research, production, and consumption. This initiative highlighted the contribution of millets to sustainable agriculture, climate resilience, nutritional security, and achievement of the Sustainable Development Goals (SDGs). Consequently, finger millet has gained recognition not merely as a traditional cereal but also as a "smart food" capable of addressing the dual challenges of malnutrition and climate change (FAO 2023; Kaur et al. 2024).

Despite its immense nutritional and ecological importance, the productivity of finger millet remains relatively low compared with major cereals. This is primarily attributed to limited genetic improvement, narrow utilization of available germplasm, inadequate characterization of genetic resources, and comparatively fewer investments in breeding programmes. Therefore, systematic evaluation of germplasm for variability, yield-contributing traits is indispensable for developing superior cultivars suitable for diverse agro-climatic conditions (Gebreyohannes et al. 2024). Efficient improvement of grain yield, a complex polygenic trait governed by the cumulative expression of several component characters, requires prior knowledge of the nature and magnitude of variability present in the available germplasm. Equally, qualitative or morphological descriptors scored as per Distinctiveness, Uniformity and Stability (DUS) guidelines are indispensable for varietal identification, registration and intellectual property protection, besides offering breeders simple visual markers for tracking diversity in segregating and germplasm populations.

While correlation coefficients largely reveal how different characters relate to one another, path analysis makes it possible to separate the cause-and-effect relationships among those interrelated traits (Wright 1921). A correlation coefficient measures

both the strength and the direction of the link between two characters, and this information can be exploited to improve several correlated traits at once through selection. In effect, such estimates capture how plant characters influence each other and point to the component traits that selection should target for genetically improving yield. Because of this, understanding which yield components exist and how they associate with one another is a necessary first step before any real gain in yield can be made. Path analysis goes further by showing whether a character's association with yield reflects its own direct contribution or arises indirectly through other component traits. Studying the links between yield and its contributing characters in this way helps identify the traits that act directly on grain yield, which in turn guides the development of improved lines.

Estimates of genotypic and phenotypic coefficients of variation, heritability and genetic advance partition the observable variability into its heritable and non-heritable components and indicate the relative efficiency of direct selection for individual traits. Because grain yield is rarely improved by selecting for yield alone, correlation and path coefficient analyses are required to identify component traits that influence yield directly as well as those that act indirectly through other characters, thereby refining the selection criteria used in a breeding programme. Genetic divergence analysis through Mahalanobis' D^2 statistic further assists in choosing genetically dissimilar parents whose hybridization is likely to yield desirable transgressive segregants. Because grain yield is governed by several interacting component traits, a multi-trait selection (discriminant function) index combining these components can outperform direct selection on yield alone, and constructing and validating such an index for this germplasm complements the correlation, path and divergence analyses described above.

The present investigation was undertaken with the following objectives: to characterize a set of finger millet genotypes for both qualitative (DUS) and quantitative traits; to assess the extent of genetic divergence among these genotypes; and to construct a Smith–Hazel selection index combining grain yield per plant with its principal component traits, thereby evaluating its efficiency relative to direct selection based on yield alone.

Materials and Methods

Experimental Site and Plant Material

The experiment comprised thirty genotypes of finger millet, including released varieties and a local check, evaluated in a randomized block design with three replications during kharif 2020 at the Instructional Farm, AICRP on Small Millets, College of Agriculture, Rewa (Madhya Pradesh). Each genotype was raised in a 3.0 m plot with a spacing of 22.5 cm (row to row) × 10 cm (plant to plant). Recommended agronomic practices were followed uniformly across all plots.

Qualitative (DUS) Traits

Seven morphological descriptors were recorded as per DUS guidelines through visual assessment of a group of plants/seeds in each genotype: plant growth habit (erect, decumbent, prostrate), stem culm branching (absent, present), finger branching (absent, present), finger branching position (in thumb finger, in all fingers), finger multiple whorl (absent, present), ear shape (fist, compact, semi-compact, open, droopy) and seed colour (white, light brown, copper brown, dark brown).

Quantitative Traits

Days to 50% flowering and days to maturity were recorded on a whole-plot basis. Observations on the remaining thirteen traits-plant height (cm), number of productive tillers per plant, flag leaf length (cm), flag leaf width (cm), peduncle length (cm), ear length (cm), finger length (cm), finger width (cm), number of fingers per ear 1000-grain weight (g), biological yield per plant (g), harvest index (%) and grain yield per plant (g) were recorded on five randomly tagged plants per plot in each replication and averaged.

Statistical Analysis

Analysis of variance was carried out following the standard randomized block design procedure (Panse and Sukhatme 1967) to test the significance of genotypic differences. Genotypic and phenotypic coefficients of variation were estimated according to Burton (1952), broad-sense heritability following Burton and Devane (1953), and genetic advance as percentage of mean following Johnson et al. (1955). Genotypic and phenotypic correlation coefficients among the fifteen quantitative traits were computed from the respective variance–covariance components (Hanson et al. 1956; Miller et al. 1958), and path coefficient analysis following Wright (1921) and Dewey and Lu (1959) was used to partition the phenotypic correlation of each component trait with grain yield per plant into direct and indirect effects. Genetic divergence among genotypes was assessed using Mahalanobis' D^2 statistic (Mahalanobis 1936), genotypes were grouped into clusters by Tocher's method (Rao 1952), and average intra- and inter-cluster distances were calculated following Singh and Chaudhary (1977). Phenotypic diversity for each of the seven qualitative traits was further quantified using the Shannon–Weaver diversity index (Shannon and Weaver 1949), computed as $H' = -\Sigma pi \ln(pi)$, where pi is the proportion of genotypes in the i-th phenotypic class of a trait; H' was normalized by its maximum possible value ($H_{max} = \ln k$, where k is the number of classes defined for that trait) to give an evenness index

(H′/Hmax) ranging from 0 (all genotypes in one class) to 1 (genotypes spread equally across all classes). The association of each qualitative trait with grain yield per plant and harvest index was tested by one-way analysis of variance (traits with more than two classes) or Welch's t-test (binary traits), and the observed class frequency of each qualitative trait was tested against an equal-frequency null hypothesis by a chi-square goodness-of-fit test (Panse and Sukhatme 1967).

Selection Index

A Smith-Hazel discriminant function (selection) index (Smith 1936; Hazel 1943) was constructed for grain yield per plant together with six component traits identified by the correlation and path analyses as principal contributors to yield-harvest index, biological yield per plant 1000-grain weight, ear length, flag leaf width and number of fingers per ear. Traits showing strong collinearity with these (e.g. days to maturity with days to flowering, finger length with ear length) were excluded to avoid an ill-conditioned variance–covariance matrix. Phenotypic (P) and genotypic (G) variance–covariance matrices for the seven traits were derived from their coefficients of variation and pairwise correlation coefficients. Relative economic weights of 10, 8, 5, 3, 2, 2 and 2 were assigned to grain yield per plant, harvest index, biological yield per plant 1000-grain weight, ear length, flag leaf width and number of fingers per ear, respectively, reflecting their relative direct effect on yield and conventional economic importance; discriminant function coefficients were then computed as $b = P^{-1}Ga$, where a is the vector of economic weights. Genotypes were ranked by their resulting index score, and the expected genetic advance and efficiency of index-based selection were compared with those expected from direct selection on grain yield phenotype alone.

Results and Discussion

Characterization for Qualitative Traits

The thirty genotypes exhibited considerable diversity for all seven DUS descriptors scored (Table S1, Figs. 1, 2). For plant growth habit, the majority of genotypes (80.00%) were erect, while 16.66% were decumbent and a single genotype (UM) was prostrate. Stem culm branching and finger branching were each present in 43.33% of the genotypes and absent in the remainder; among the thirteen genotypes showing finger branching, branching originated from the thumb finger in eight genotypes and from all fingers in five. Finger multiple whorl was present in a large majority (83.33%) of genotypes. Compact ear shape was the most frequent class (40.00%), followed by fist (23.33%), semi-compact (20.00%) and open (16.66%) types, while the droopy class was not represented in this set. At the seed level, copper-brown seed colour predominated (86.67%), with light brown and dark brown seed colour each restricted to two genotypes; white-seeded genotypes were absent.

The presence of clearly distinguishable classes for growth habit, branching pattern, ear shape and seed colour indicates that these morphological descriptors can be profitably used for rapid varietal identification, distinctness testing and seed-purity assessment in finger millet improvement and seed-production programmes, in agreement with similar morphological diversity reported for global finger millet germplasm (Bharathi 2011). Similar findings were reported by Karishma et al. 2025; Dasanayaka and Kaluthanthri 2017; Lule et al. 2012 and Reddy et al. 2009.

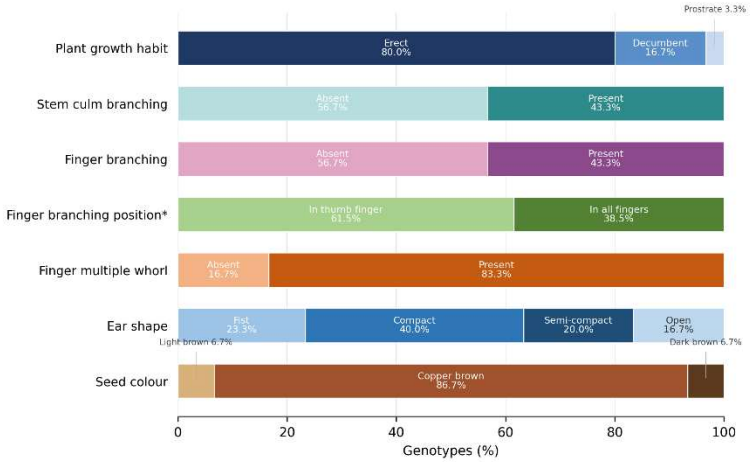


Fig. 1 Percentage distribution of 30 finger millet genotypes across classes of seven qualitative (DUS) traits

**Finger branching position is expressed as a percentage of the 13 genotypes showing finger branching, not of all 30 genotypes*

Fig. 2 Morphological characterization of finger millet (*Eleusine coracana*) genotypes showing variation in plant, stem, ear, and seed traits. ***Stem culm branching***: (a) absent, (b) present. ***Plant growth habit*****:** (c) erect, (d) decumbent. ***Finger branching:*** (e) absent, (f) present. ***Finger branching position:*** (g) restricted to the thumb finger, (h) present in all fingers. ***Ear shape:*** (i) fist, (j) compact, (k) semi-compact, (l) open, (m) droopy. ***Seed colour:*** (n) light brown, (o) copper brown, (p) dark brown. ***Finger multiple whorls:*** (q) absent, (r) present

Phenotypic diversity within each qualitative trait was further quantified using the Shannon–Weaver diversity index (Table 1, Fig. 3). The evenness index (H′/Hmax) was highest for stem culm branching and finger branching (0.99 each) and finger branching position (0.96), indicating that genotypes were almost evenly split between the two respective classes of these traits. Ear shape also showed fairly high evenness (0.82), reflecting its spread across four of the five defined classes. In contrast,

evenness was low for seed colour (0.35) and plant growth habit (0.54), and moderate for finger multiple whorl (0.65), reflecting the strong dominance of a single class (copper-brown seed colour and erect growth habit, respectively) in this germplasm set. These results indicate that branching-related traits and ear shape offer the most discriminating power for distinguishing genotypes morphologically, whereas seed colour and growth habit, despite being useful descriptors, are dominated by one predominant class in the present collection.

Table 1 Shannon–Weaver diversity index (H′) and evenness for seven qualitative (DUS) traits in finger millet

Trait	H′	Hmax	Evenness (H′/Hmax)
Plant growth habit	0.5905	1.0986	0.5375
Stem culm branching	0.6842	0.6931	0.9871
Finger branching	0.6842	0.6931	0.9871
Finger branching position*	0.6663	0.6931	0.9612
Finger multiple whorl	0.4506	0.6931	0.6500
Ear shape	1.3266	1.6094	0.8243
Seed colour	0.4851	1.3863	0.3499

*Hmax = ln(k), where k is the number of phenotypic classes defined for the trait (3 for plant growth habit, 5 for ear shape, 4 for seed colour, 2 for all other traits). *Computed among the 13 genotypes showing finger branching*

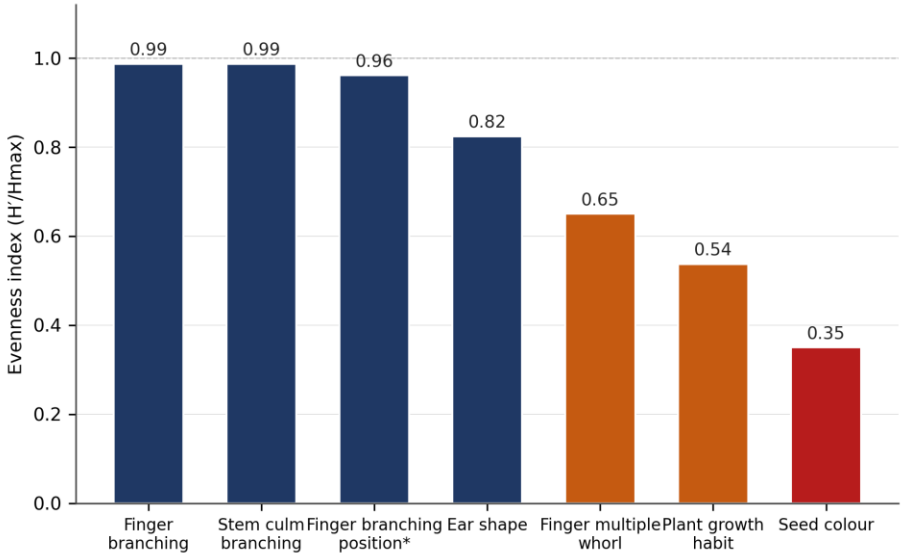


Fig. 3 Shannon–Weaver evenness index (H′/Hmax) for seven qualitative traits in finger millet, ranked in descending order

To examine whether qualitative trait classes were associated with yield, mean grain yield per plant and harvest index were compared across classes of each qualitative trait (Table 2, Fig. 4). Plant growth habit showed a significant association with grain yield per plant ($P<0.05$), erect genotypes (7.32 g) out-yielding decumbent (6.40 g) and the single prostrate genotype (4.04 g). Finger branching showed the strongest association of all seven traits: genotypes with finger branching averaged 7.88 g grain yield per plant and 28.05% harvest index, significantly higher than non-branched genotypes (6.42 g, $P<0.01$; 22.63%, $P<0.05$). Ear shape was also significantly associated with grain yield per plant ($P<0.05$), with compact- and fist-eared genotypes (7.59 and 7.55 g) outperforming open-eared genotypes (5.54 g). Seed colour was not significantly associated with grain yield per plant, but was associated with harvest index ($P<0.05$), although this comparison rests on only two genotypes each for the light- and dark-brown classes and should be interpreted with caution. Stem culm branching, finger multiple whorl and finger branching position showed no significant association with either trait. These results suggest that finger branching and, to a lesser extent, plant growth habit and ear shape, could serve as simple visual markers for preliminarily screening genotypes for yield potential in the field, in addition to their established role in morphological characterization.

Table 2 Association of qualitative trait classes with grain yield per plant (GYP) and harvest index (HI) in finger millet

Trait	Class means – grain yield/plant (g)	Test	Stat.	P (GYP)	Class means – harvest index (%)	Stat.	P (HI)

Plant growth habit	Erect (n=24) 7.32; Decumbent (n=5) 6.40; Prostrate (n=1) 4.04	ANOVA	3.70	0.038*	26.13 / 21.52 / 14.72	2.76	0.081
Stem culm branching	Absent (n=17) 7.47; Present (n=13) 6.51	t-test	1.88	0.072	26.77 / 22.64	1.81	0.082
Finger branching	Absent (n=17) 6.42; Present (n=13) 7.88	t-test	-3.23	0.003**	22.63 / 28.05	-2.62	0.014*
Finger branching position*	In thumb finger (n=8) 8.12; In all fingers (n=5) 7.50	t-test	0.85	0.435	28.31 / 27.63	0.19	0.857
Finger multiple whorl	Present (n=25) 7.23; Absent (n=5) 6.16	t-test	1.40	0.218	25.80 / 20.87	1.80	0.119
Ear shape	Compact (n=12) 7.59; Fist (n=7) 7.55; Semi-compact (n=6) 6.67; Open (n=5) 5.54	ANOVA	3.62	0.026*	26.51 / 26.46 / 24.18 / 20.20	1.41	0.264
Seed colour	Copper brown (n=26) 6.90; Light brown (n=2) 7.62; Dark brown (n=2) 8.45	ANOVA	1.26	0.299	24.20 / 24.59 / 35.52	3.50	0.045*

**P<0.05, **P<0.01. Test = one-way ANOVA (traits with >2 classes) or Welch's t-test (binary traits); Stat. = F-value (ANOVA) or t-value (t-test). *Finger branching position computed among the 13 genotypes showing finger branching*

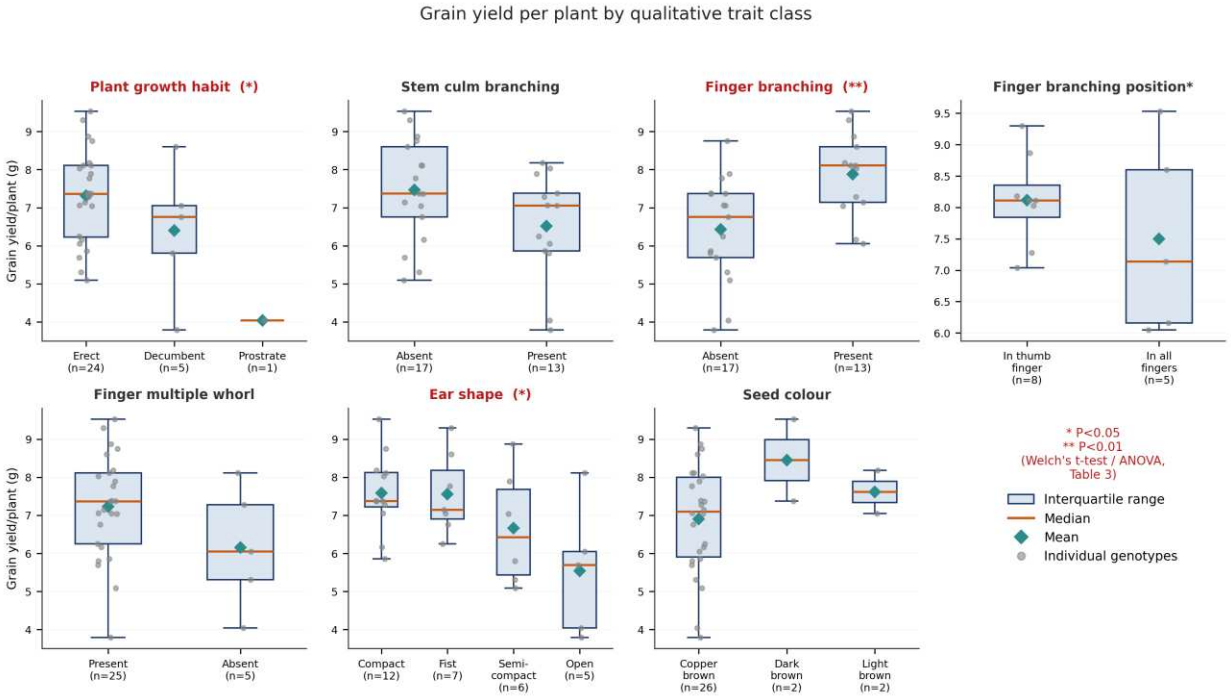


Fig. 4 Grain yield per plant by qualitative trait class, showing individual genotypes, the interquartile range, median and mean for each class; asterisks denote significant class differences (Table 2)

A chi-square goodness-of-fit test was used to determine whether the observed class frequencies of each qualitative trait departed from an equal-frequency expectation (Table 3, Fig. 5). Plant growth habit ($\chi2$=30.20, P<0.0001), finger multiple whorl ($\chi2$=13.33, P<0.001) and seed colour ($\chi2$=38.40, P<0.0001) deviated highly significantly from an equal distribution, consistent with their low Shannon-Weaver evenness values (Table 1) and reflecting the strong dominance of the erect, multiple-whorl-present and copper-brown-seeded classes, respectively, in this germplasm. Stem culm branching, finger branching, finger branching position and ear shape did not deviate significantly from an equal-frequency distribution, again mirroring their comparatively high evenness values. The close correspondence between the chi-square outcomes and the Shannon-Weaver evenness index cross-validates both measures of qualitative trait distribution in this germplasm set.

Table 3 Chi-square goodness-of-fit test for class frequencies of seven qualitative traits in finger millet

Trait	**Observed class frequencies**	**df**	**χ^2**	**P-value**

Plant growth habit	Erect 24, Decumbent 5, Prostrate 1	2	30.20	<0.0001***
Stem culm branching	Absent 17, Present 13	1	0.53	0.465
Finger branching	Absent 17, Present 13	1	0.53	0.465
Finger branching position*	In thumb finger 8, In all fingers 5	1	0.69	0.405
Finger multiple whorl	Present 25, Absent 5	1	13.33	0.0003***
Ear shape	Compact 12, Fist 7, Semi-compact 6, Open 5	3	3.87	0.276
Seed colour	Copper brown 26, Dark brown 2, Light brown 2	2	38.40	<0.0001***

****P<0.001 (deviates highly significantly from an equal-frequency null hypothesis); ns = not significant. *Finger branching position computed among the 13 genotypes showing finger branching*

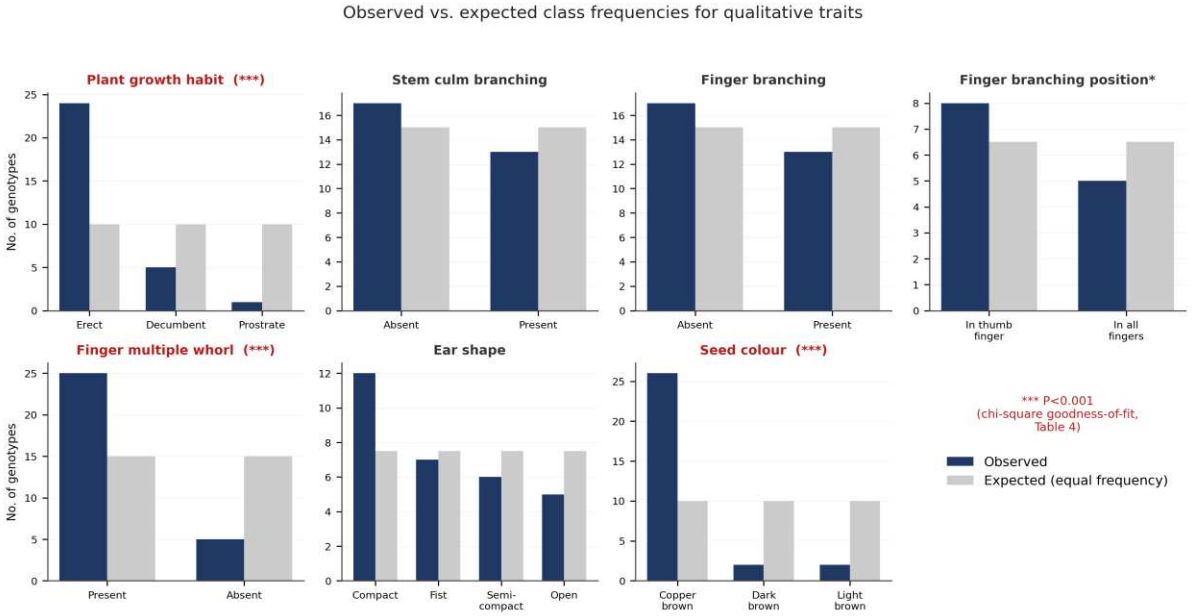
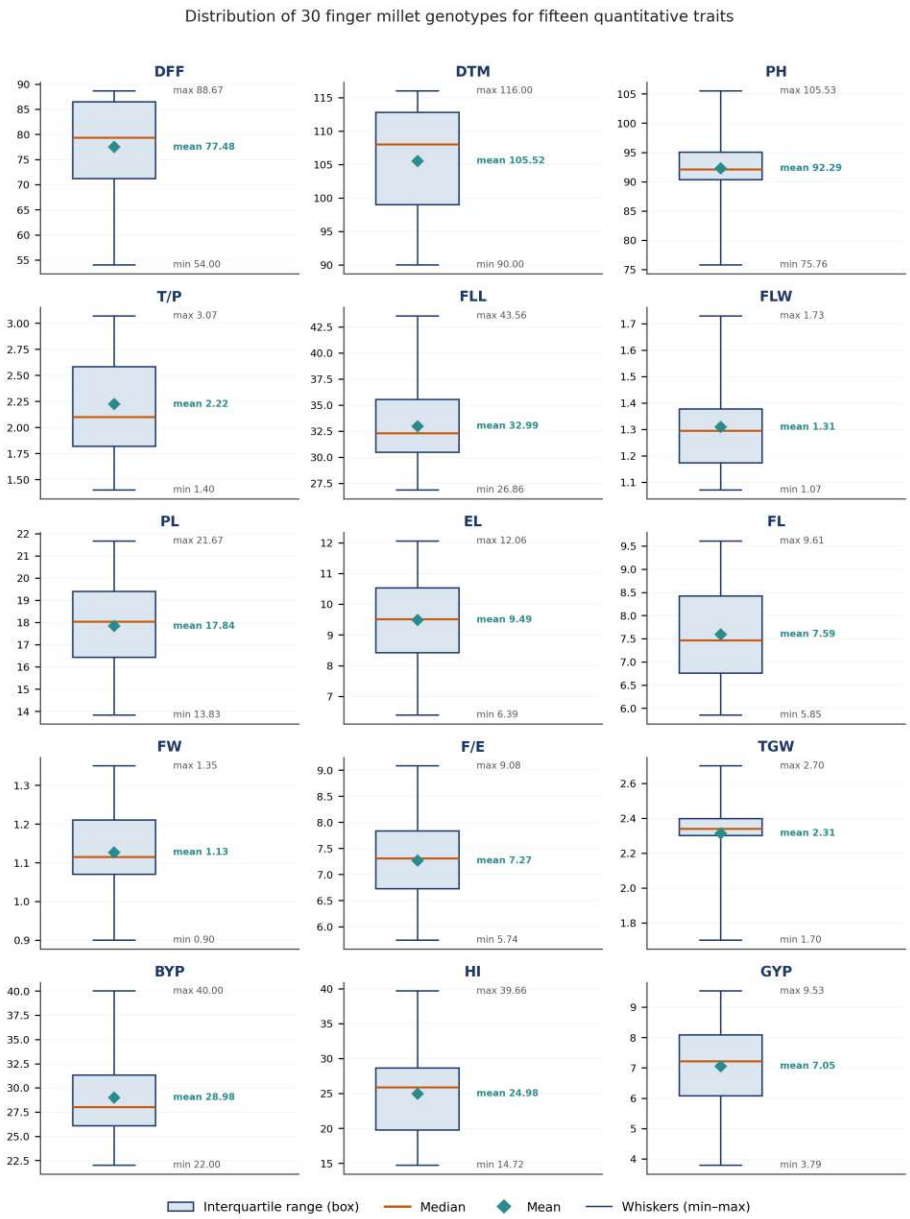


Fig. 5 Observed versus expected (equal-frequency) class counts for seven qualitative traits in finger millet, with chi-square goodness-of-fit significance (Table 3)

Mean Performance of Quantitative Traits

Wide variation in mean performance was recorded for all fifteen quantitative traits (Table S2, Fig. 6). Days to 50% flowering ranged from 54.00 (Local check) to 88.67 days (GPU 104 and PR 1731), and days to maturity from 90.00 (PR 202) to 116.00 days (PR 1731). Plant height varied from 75.76 cm (GPU 104) to 105.53 cm (PR 202), while the number of productive tillers per plant ranged from 1.40 (VL 407) to 3.07 (PR 202). Among traits directly related to the ear, finger length ranged from 5.85 cm (Local check) to 9.61 cm (GPU 104, BR-IAR 6), and the number of fingers per ear from 5.74 (IIMR-FM-3003) to 9.08 (KMR 656). 1000-grain weight varied from 1.70 g (UM) to 2.70 g (GPU 104), biological yield per plant from 22.00 g (PR 1731, Local check) to 40.00 g (PR 202), and harvest index from 14.72% (UM) to 39.66% (KMR 656). Grain yield per plant, the principal trait of economic interest, ranged from 3.79 g (Local check) to 9.53 g (KMR 656), with genotypes KMR 656, GPU 104, GPU 103, PPR 1096 and VR 1130 emerging as the highest yielding entries. The wide range observed for every character, and the spread of values evident from the box plots in Fig. 6, confirms the presence of substantial exploitable variability in the germplasm under study.



Trait abbreviations used throughout the Results: DFF = Days to 50% flowering; DTM = Days to maturity; PH = Plant height (cm); T/P = No. of productive tillers/plant; FLL = Flag leaf length (cm); FLW = Flag leaf width (cm); PL = Peduncle length (cm); EL = Ear length (cm); FL = Finger length (cm); FW = Finger width (cm); F/E = No. of fingers/ear; TGW = 1000-grain weight (g); BYP = Biological yield/plant (g); HI = Harvest index (%); GYP = Grain yield/plant (g).

Fig. 6 Box plots of fifteen quantitative traits across 30 finger millet genotypes; the box spans the interquartile range, the orange line marks the median, the teal diamond marks the mean, and whiskers extend to the observed minimum and maximum

Analysis of Variance

The mean sum of squares due to genotypes was highly significant (P<0.01) for all fifteen quantitative traits (Table 4), confirming the existence of substantial genetic variability among the genotypes for days to 50% flowering, days to maturity, plant height, number of productive tillers per plant, flag leaf length, flag leaf width, peduncle length, ear length, finger length, finger width, number of fingers per ear 1000-grain weight, biological yield per plant, harvest index and grain yield per plant. This confirms that the genotypes constitute a suitable base population for further genetic analysis and selection.

Table 4 Analysis of variance (mean sum of squares) for fifteen quantitative traits in finger millet

Character	Replication (df=2)	Treatment (df=29)	Error (df=58)
DFF	31.811	279.464**	21.662
DTM	39.878	210.292**	27.384
PH	23.893	117.040**	34.501
T/P	0.029	0.663**	0.038
FLL	8.905	43.801**	6.323
FLW	0.002	0.085**	0.008
PL	2.150	13.968**	2.830
EL	0.986	5.785**	0.549
FL	0.494	3.280**	0.471
FW	0.006	0.032**	0.007
F/E	0.791	1.830**	0.661
TGW	0.017	0.129**	0.021
BYP	6.444	64.529**	5.004
HI	1.326	119.840**	3.704
GYP	0.039	6.190**	0.226

***Significant at 1% level of probability*

Genetic Variability, Heritability and Genetic Advance

The phenotypic coefficient of variation (PCV) exceeded the corresponding genotypic coefficient of variation (GCV) for every trait studied (Table 5, Fig. 7), indicating some environmental influence on trait expression; however, the relatively small gap between PCV and GCV for most traits suggests that this environmental contribution was modest and that observed variability was predominantly genetic in origin. High PCV and GCV were recorded for harvest index (26.07, 24.91), number of productive tillers per plant (22.31, 20.52) and grain yield per plant (21.09, 19.99), followed by moderate estimates for biological yield per plant, ear length, finger length, peduncle length, number of fingers per ear, flag leaf width, days to 50% flowering, flag leaf length, finger width and 1000-grain weight. The lowest PCV and GCV were observed for days to maturity and plant height, reflecting comparatively conserved expression of these traits across the genotypes.

Table 5 Mean, range, phenotypic and genotypic coefficients of variation, heritability and genetic advance for fifteen quantitative traits in finger millet

Character	Mean	Min.	Max.	PCV (%)	GCV (%)	h^2(bs) (%)	GA (% mean)
DFF	77.48	54.00	88.67	13.39	11.97	79.87	22.03
DTM	105.52	90.00	116.00	8.91	7.40	69.01	12.66
PH	92.28	75.76	105.53	8.53	5.68	44.37	7.80
T/P	2.22	1.40	3.07	22.31	20.52	84.66	38.90
FLL	32.99	26.86	43.56	13.15	10.71	66.40	17.98
FLW	1.31	1.07	1.73	14.02	12.18	75.39	21.78
PL	17.84	13.83	21.67	14.34	10.80	56.75	16.77
EL	9.49	6.39	12.06	15.97	13.93	76.06	25.02
FL	7.59	5.85	9.61	15.63	12.74	66.52	21.41
FW	1.13	0.90	1.35	11.11	8.06	52.67	12.05
F/E	7.27	5.74	9.08	14.11	8.59	37.10	10.78
TGW	2.31	1.70	2.70	10.35	8.20	62.70	13.37
BYP	28.98	22.00	40.00	17.20	15.37	79.86	28.29
HI	24.98	14.72	39.66	26.07	24.91	91.27	49.02
GYP	7.05	3.79	9.53	21.09	19.99	89.80	39.02

h²(bs) = broad-sense heritability; GA = genetic advance. Abbreviations as above

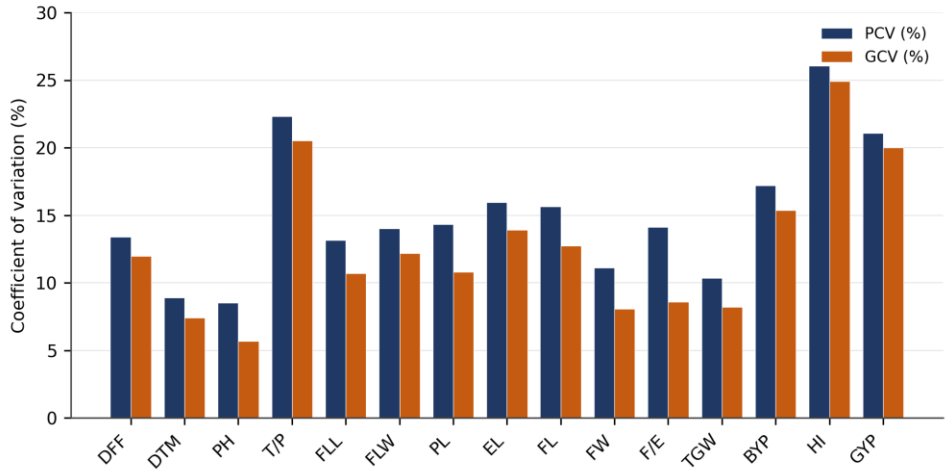


Fig. 7 Phenotypic (PCV) and genotypic (GCV) coefficients of variation for fifteen quantitative traits in finger millet

Broad-sense heritability was high (>60%) for eleven of the fifteen traits, the highest being recorded for harvest index (91.27%), grain yield per plant (89.80%), number of productive tillers per plant (84.66%), days to 50% flowering (79.87%) and biological yield per plant (79.86%); moderate heritability (37–57%) was observed for peduncle length, finger width, plant height and number of fingers per ear, and no trait showed low heritability. Genetic advance as percentage of mean was likewise highest for harvest index (49.02%), grain yield per plant (39.02%) and number of productive tillers per plant (38.90%) (Fig. 8).

High heritability coupled with high genetic advance as percentage of mean – the combination considered most reliable for predicting selection response, since it reflects the action of additive gene effects (Johnson et al. 1955) – was recorded for harvest index, grain yield per plant, number of productive tillers per plant, days to 50% flowering, biological yield per plant, ear length, flag leaf width and finger length. Direct phenotypic selection based on these traits is therefore expected to be effective for improving grain yield in finger millet, corroborating earlier reports of predominantly additive genetic control for yield-component traits in this crop (Anuradha and Patro 2019; Sao et al. 2016).

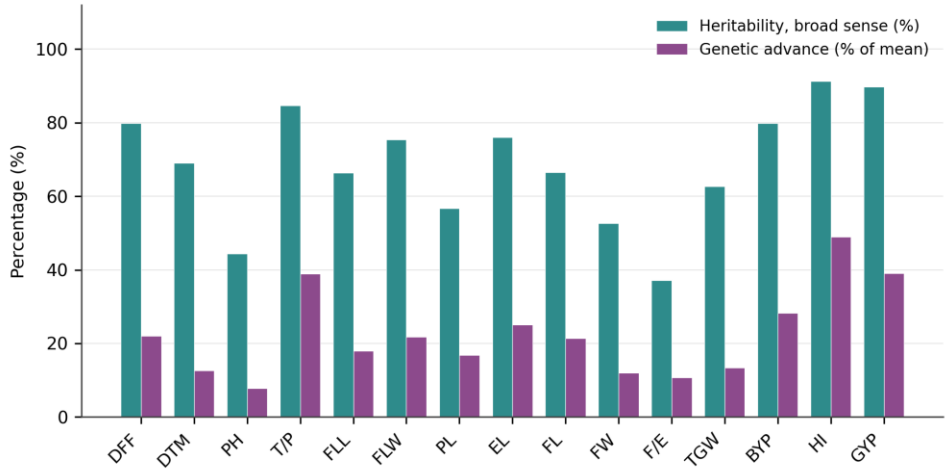


Fig. 8 Broad-sense heritability and genetic advance (as percentage of mean) for fifteen quantitative traits in finger millet

Correlation Coefficient Analysis

Genotypic and phenotypic correlation coefficients among the fifteen quantitative traits are presented in Table S3 and visualized as a heat map in Fig. 9. Genotypic correlations were generally higher in magnitude than the corresponding phenotypic correlations, suggesting that the phenotypic association was attenuated by environmental factors and that a true genetic relationship between most trait pairs is somewhat stronger than indicated by phenotypic values alone, a pattern also reported in other genetic-diversity studies on finger millet (Ganapathy et al. 2011; Rawat et al. 2018).

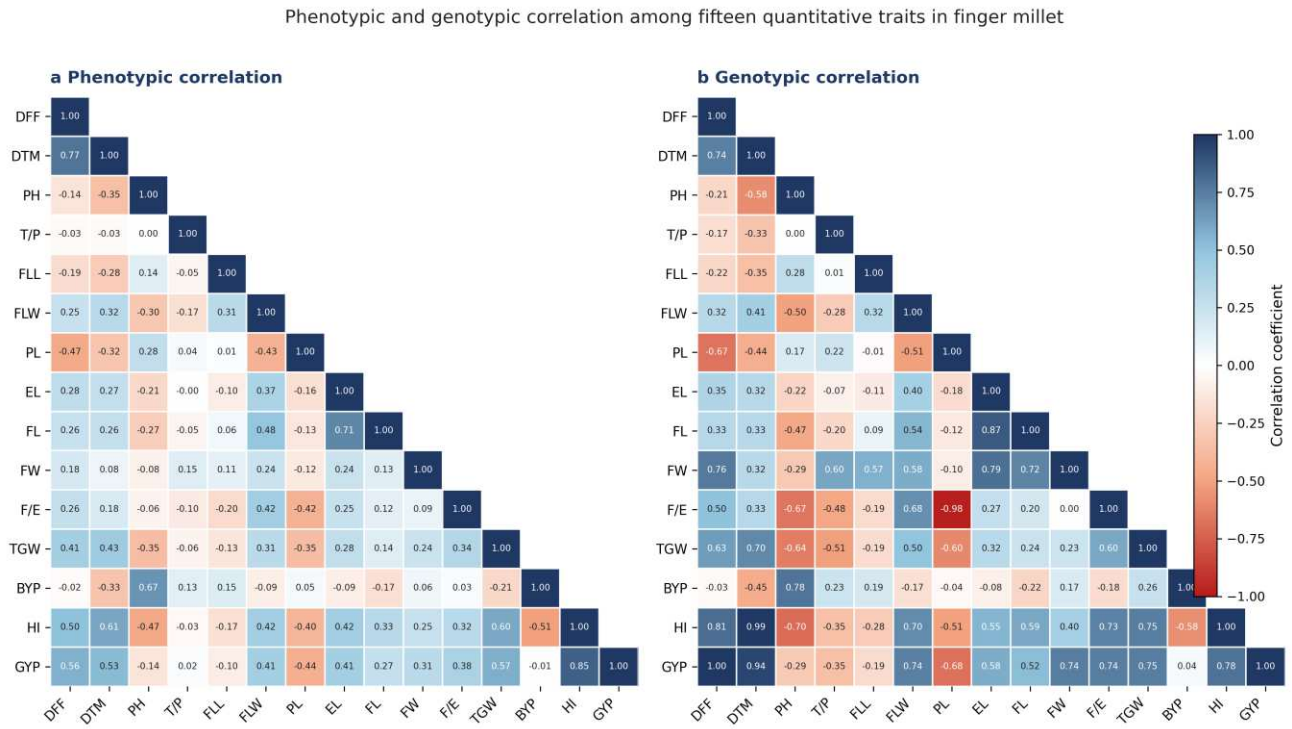


Fig. 9 Heat map of (a) phenotypic and (b) genotypic correlation coefficients among fifteen quantitative traits in finger millet; cell colour and shade indicate the sign and magnitude of the correlation

Grain yield per plant showed highly significant positive correlation, at both genotypic and phenotypic levels, with harvest index (r^p=0.8474, r^g=0.7824), 1000-grain weight (r^p=0.5744, r^g=0.7478), days to 50% flowering (r^p=0.5644, r^g=1.0023), days to maturity (r^p=0.5278, r^g=0.9412), flag leaf width (r^p=0.4075, r^g=0.7353) and ear length (r^p=0.4064, r^g=0.5825), and significant positive correlation with number of fingers per ear, finger width and finger length. In contrast, grain yield per plant was significantly and negatively correlated with peduncle length (r^p=-0.4356, r^g=-0.6845) and showed a small negative association with biological yield per plant at the phenotypic level. Among component traits, days to 50% flowering and days to maturity were strongly positively inter-correlated (r^p=0.7749), as were ear length and finger length (r^p=0.7144); peduncle length, conversely, was negatively associated with most other yield-contributing traits. These associations indicate that simultaneous improvement of harvest index 1000-grain weight, ear length, flag leaf width and number of fingers per ear, together with a reduction in peduncle length, is likely to enhance grain yield per plant in finger millet, consistent with earlier correlation studies in the crop (Anuradha et al. 2017; Bharathi 2011). Wolie and Dessalegn (2011), working with germplasm in northwest Ethiopia, likewise reported that biological yield per plant, productive tillers per plant, number of fingers per ear, finger length and harvest index were positively associated with grain yield per plant. Jadhav et al. (2015) similarly found 1000-grain weight, number of fingers per ear, days to maturity, ear weight per plant, finger length and days to 50% flowering to be significantly and positively correlated with grain yield per plant.

Path Coefficient Analysis

Because correlation coefficients reflect only the net mutual association between two traits without distinguishing cause from effect, path coefficient analysis was used to partition the phenotypic correlation of each component trait with grain yield per plant into direct and indirect effects (Table S4, Fig. 10). Harvest index exerted the maximum positive direct effect on grain yield per plant (1.1403), followed by biological yield per plant (0.5985) and days to maturity (0.1079); positive but comparatively small direct effects were also recorded for flag leaf length, finger length, number of fingers per ear 1000-grain weight and plant height. Substantial negative direct effects were exerted by days to 50% flowering (-0.0786), flag leaf width (-0.0783) and ear length (-0.0416), among others.

Several traits showing a positive phenotypic correlation with grain yield per plant nevertheless exerted a negative direct effect, indicating that their apparent association with yield was largely mediated indirectly through other traits rather than reflecting a direct causal contribution. Days to 50% flowering, for instance, registered a significant positive correlation with grain yield (0.5644) but a negative direct effect (-0.0786); its positive correlation was instead built up indirectly, principally through peduncle length, flag leaf length and plant height. Flag leaf width behaved similarly, its sizeable positive correlation with yield (0.4075) being generated largely through harvest index, finger length and number of fingers per ear rather than through a direct

effect. By contrast, harvest index and biological yield per plant combined a strong positive correlation with a strong positive direct effect, confirming them as the most dependable single-trait selection criteria for improving grain yield in this material. The residual effect of 0.186 was relatively low, indicating that the fifteen traits considered accounted for the major part of the variation in grain yield per plant and that few additional unmeasured traits would be needed to explain yield variation in this germplasm, a conclusion broadly similar to that reached for finger millet yield (Ganapathy et al. 2011).

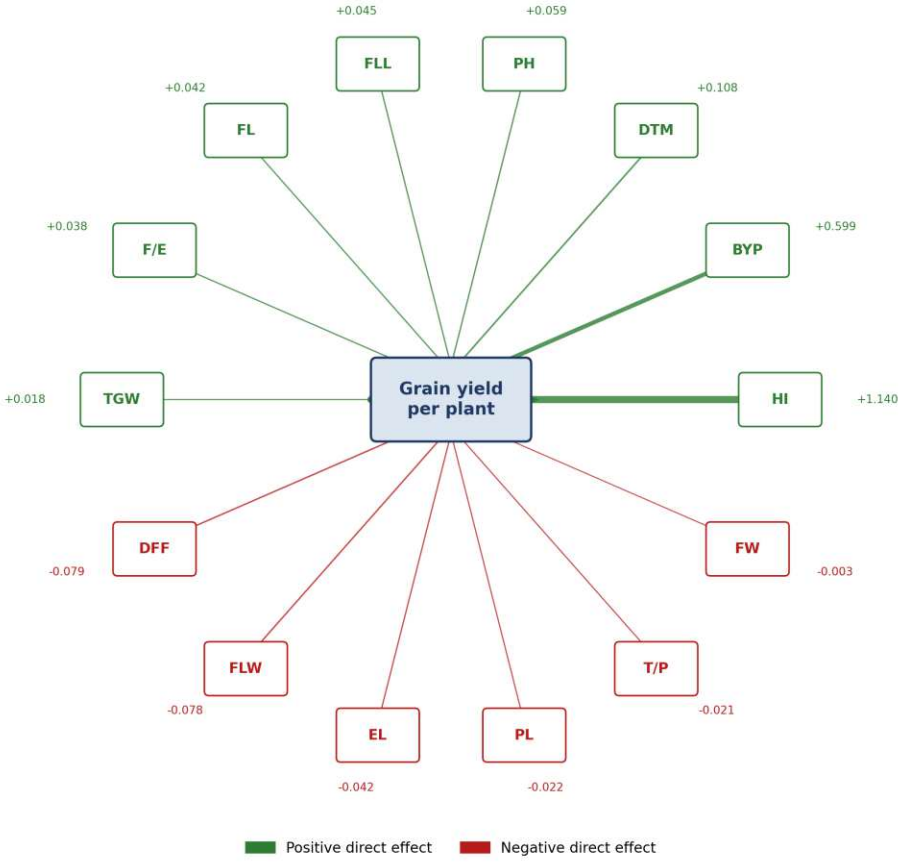


Fig. 10 Path diagram showing the direct effects of component traits on grain yield per plant in finger millet (arrow thickness proportional to the magnitude of the direct effect)

The primacy of harvest index and biological yield per plant as direct contributors to grain yield in the present study is corroborated by Negi et al. (2017), who likewise reported harvest index (0.8345), 100-seed weight (0.6044), biological yield (0.6044) and number of fingers per ear (0.3973) as the traits with the highest positive direct effects on grain yield per plant across 35 finger millet genotypes. Dubey and Rangaiah (2026) similarly found ear weight per plant to exert the largest direct effect on grain yield in F4 and F5 generations, alongside significant correlations with total and productive tillers per plant and number of fingers per ear, reinforcing biomass- and ear-related traits as recurrent direct determinants of yield in this crop.

Genetic Divergence

Mahalanobis' D^2 analysis based on fifteen quantitative traits grouped the thirty genotypes into five non-overlapping clusters (Table 6), of which two (Cluster I with 21 genotypes and Cluster II with 6 genotypes) were polygenic while Clusters III, IV and V were each represented by a single genotype (KMR 656, VL 376 and PR 202, respectively). The distribution of a large majority of genotypes within Cluster I, despite their diverse geographic and pedigree origin, suggests that factors other than geographic origin – such as natural and human selection pressure, exchange of breeding material among centres, and genotype × environment interaction – have shaped genetic divergence in this set of germplasm, consistent with similar observations in other finger millet diversity studies (Patel et al. 2020).

Table 6 Distribution of 30 finger millet genotypes into five D^2 clusters (Tocher's method)

Cluster	No. of genotypes	Genotypes included

I	21	TNEc 1326, IIMR-FM-3001, VR 1130, PPR 1096, OEB 610, OEB 633, GPU 103, VL 408, GPU 45, KMR 702, TNEc 1323, GPU 67, PR 1731, IIMR-FM-3126, BR-IAR 5, GPU 104, OEB 644, IIMR-FM-3002, BR-IAR 6, PR 1433, VL 407
II	6	BR-14-1, PR 1433, VR 1131, IIMR-FM-3003, RAUF 25, UM
III	1	KMR 656
IV	1	VL 376
V	1	PR 202

Average intra- and inter-cluster D^2 distances are presented in Table S5 and Fig. 11. Intra-cluster distance was low for Cluster I (27.62) and Cluster II (34.32), the two polygenic clusters, while it was zero for the solitary Clusters III, IV and V, as expected. Inter-cluster distance was maximum between Cluster IV and Cluster V (211.31), followed by Cluster III and Cluster V (167.86), Cluster II and Cluster III (157.87), Cluster II and Cluster V (108.81) and Cluster I and Cluster V (103.70), whereas the minimum inter-cluster distance occurred between Cluster I and Cluster III (62.96). The wide genetic distance separating Clusters IV and V, and Clusters III and V, indicates that hybridization between genotypes from these cluster pairs – namely VL 376 or KMR 656 with PR 202 – holds the greatest promise for generating desirable transgressive segregants in future breeding programmes for finger millet.

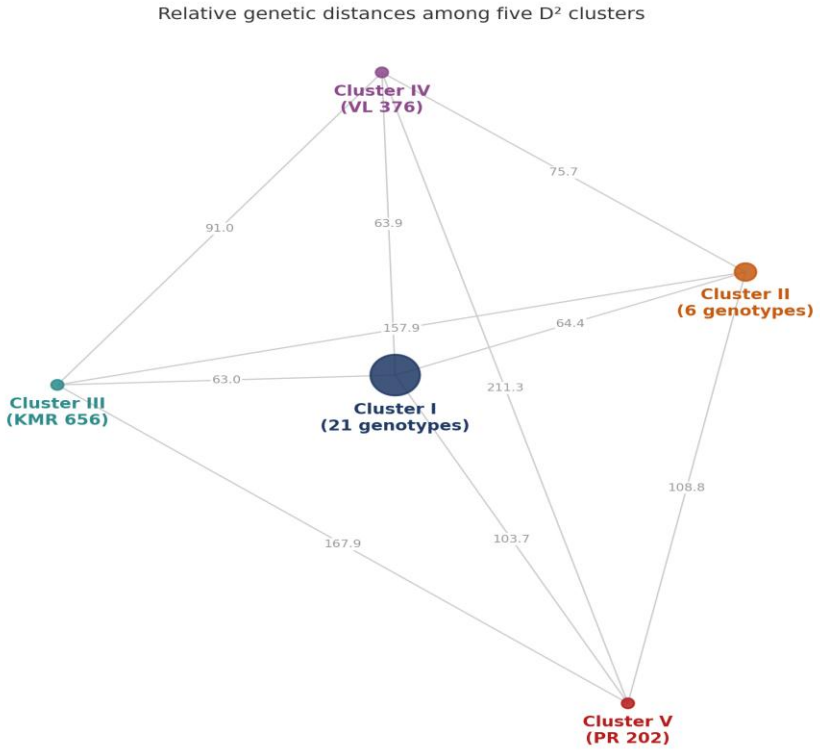


Fig. 11 Two-dimensional ordination (multidimensional scaling) of five D^2 clusters of finger millet genotypes; circle size is proportional to the number of genotypes per cluster and edge labels show inter-cluster D^2 values

Cluster mean values (Table S6) revealed that the solitary Cluster III (KMR 656) combined the highest mean grain yield per plant (9.53 g), harvest index (39.66%), 1000-grain weight (2.63 g), ear length (12.06 cm) and number of fingers per ear (9.08), while the solitary Cluster V (PR 202) recorded the tallest plants (105.53 cm), the highest number of productive tillers per plant (3.07) and the highest biological yield per plant (40.00 g) but a comparatively low harvest index (17.64%). Cluster II, comprising six genotypes including RAUF 25 and UM, had the lowest mean grain yield per plant (4.98 g) and harvest index (16.93%) among all clusters. These contrasting cluster profiles further support KMR 656 (Cluster III) and PR 202 (Cluster V), or KMR 656 and VL 376 (Cluster IV), as promising and genetically divergent parental combinations for hybridization aimed at combining high harvest index with high biological yield potential.

The percentage contribution of individual traits towards total genetic divergence (Table S7, Fig. 12) was highest for grain yield per plant (14.54%, ranked first in 63 of the pairwise comparisons), followed by biological yield per plant (11.32%), 1000-grain weight (8.50%), harvest index (6.19%), and ear length and flag leaf length (5.98% each). Number of productive tillers per plant, days to maturity, plant height, number of fingers per ear, flag leaf width and peduncle length each contributed modestly, while the remaining traits contributed negligibly. Grain yield per plant and its closely associated component traits being the principal

drivers of divergence implies that selection of genetically distant parents on the basis of these traits would be the most effective strategy for designing crosses in a finger millet hybridization programme.

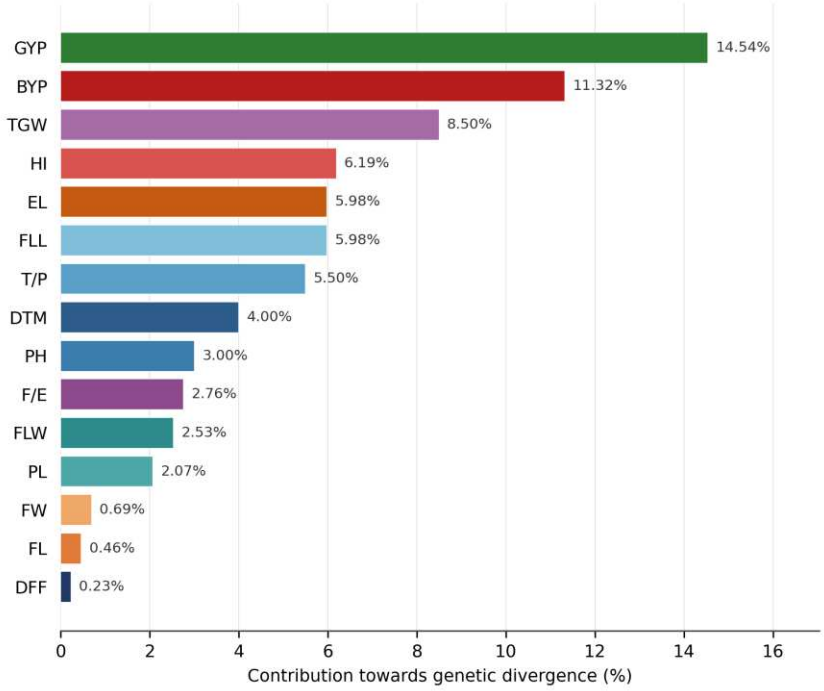


Fig. 12 Percentage contribution of fifteen quantitative traits towards genetic divergence in finger millet, ranked in descending order

Selection Index

A Smith–Hazel discriminant function index combining grain yield per plant with harvest index, biological yield per plant 1000-grain weight, ear length, flag leaf width and number of fingers per ear was constructed to evaluate whether multi-trait selection could outperform direct selection on yield alone (Table 7). Although harvest index and biological yield per plant were each assigned high positive economic weight, their discriminant function coefficients were negative (-3.07 and -1.91, respectively), while 1000-grain weight and flag leaf width received unexpectedly large positive coefficients (74.03 and 89.79). This pattern is a recognized feature of the Smith–Hazel procedure rather than an anomaly: because biological yield per plant and harvest index are themselves strongly negatively correlated (r^p=-0.51, r^g=-0.58) and both correlate strongly with grain yield, the index partials out this redundancy so that the coefficients reflect each trait's *marginal* contribution once the others are accounted for, rather than reproducing the input economic weights directly.

Table 7 Economic weights and Smith–Hazel discriminant function coefficients for grain yield per plant and six component traits in finger millet

Component trait	Economic weight (a)	Discriminant function coefficient (b)
GYP	10	34.02
HI	8	-3.07
BYP	5	-1.91
TGW	3	74.03
EL	2	5.57
FLW	2	89.79
F/E	2	-0.08

Abbreviations as above; $b = P^{-1}Ga$, where P and G are the phenotypic and genotypic variance–covariance matrices and a is the economic weight vector

The selection index was more efficient than direct selection on grain yield phenotype alone, with a relative efficiency of 109.51% (Table 8); that is, selecting on the seven-trait index is expected to give approximately 9.5% greater progress towards the breeding objective than selecting on yield phenotype alone. The correlation between the index and the aggregate genotype, r(H,I), was estimated at 1.01, marginally above its theoretical maximum of 1.00; such estimates occasionally exceed unity

when genotypic variance–covariance components are estimated from a trial with a limited number of replications (three, in this study), a well-recognized limitation of small-sample genotypic covariance estimation that should be borne in mind when interpreting the precise magnitude, though not the direction, of the efficiency gain.

Table 8 Expected genetic advance and relative efficiency of selection index over direct selection for grain yield per plant in finger millet

Parameter	Value
Variance of selection index, Var(I) = b′Pb	3495.65
Variance of aggregate genotype, Var(H) = a′Ga	3400.83
Correlation between index and aggregate genotype, r(H,I)	1.01*
Expected genetic advance – index selection	121.80
Expected genetic advance – direct selection on grain yield alone	111.22
Relative efficiency of index over direct selection (%)	109.51

**Marginally exceeds the theoretical maximum of 1.00, attributable to small-sample estimation of genotypic variance–covariance components (see text)*

Ranking the thirty genotypes by selection index score (Table 9) placed KMR 656 and GPU 104 first and second, matching their ranking by grain yield alone, confirming them as outstanding selections by either criterion. Beyond the top two, however, the index reshuffled the ranking: VR 1130 rose to third on the index despite being only the fifth-highest yielder, reflecting its more balanced profile across the component traits, whereas GPU 103 – the third-highest yielder – fell outside the index top ten, indicating that its high yield was not matched by an equally favourable profile for 1000-grain weight, ear length and flag leaf width. This reordering illustrates the practical value of the index over single-trait selection: it identifies genotypes with balanced genetic merit across yield and its principal components, rather than genotypes that are exceptional for yield alone but comparatively weaker in the traits underlying it.

Table 9 Top ten finger millet genotypes ranked by Smith–Hazel selection index score, compared with their rank by grain yield per plant alone

Index rank	Genotype	Index score	Grain yield/plant (g)	Yield-alone rank
1	KMR 656	124.39	9.53	1
2	GPU 104	108.69	9.30	2
3	VR 1130	69.61	8.60	5
4	PPR 1096	53.35	8.75	4
5	IIMR-FM-3001	47.16	8.11	8
6	OEB 633	43.72	8.11	7
7	VL 407	39.32	7.36	14
8	TNEc 1326	38.66	8.03	9
9	PR 1731	37.51	7.89	10
10	VL 408	36.96	8.18	6

Index score expressed as deviation from the trial mean across the seven traits in the index (see Materials and Methods, Selection Index)

Conclusion

The present study confirmed substantial qualitative and quantitative diversity among thirty finger millet genotypes. High heritability coupled with high genetic advance as percentage of mean for harvest index, grain yield per plant, number of productive tillers per plant, days to 50% flowering, biological yield per plant, ear length, flag leaf width and finger length indicates that these traits are governed predominantly by additive gene action and can be improved through straightforward phenotypic selection. Correlation and path analyses jointly identify harvest index and biological yield per plant as the most reliable single-trait selection criteria for raising grain yield, while a seven-trait Smith–Hazel selection index combining these with 1000-grain weight, ear length, flag leaf width and number of fingers per ear achieved about 9.5% greater expected efficiency than direct selection on yield alone, and identified KMR 656, GPU 104 and VR 1130 as genotypes with the most balanced overall merit. Genetic divergence analysis grouped the genotypes into five clusters and identified grain yield per plant, biological yield per plant 1000-grain weight, harvest index and ear length as the principal contributors to divergence; hybridization between genetically distant genotypes such as KMR 656, VL 376 and PR 202 is recommended to generate superior segregants. The high-yielding genotypes identified in this study – KMR 656, GPU 104, GPU 103, PPR 1096 and VR 1130 – warrant multi-location evaluation to confirm their stability before release or use as donor parents, and the morphological descriptors characterized here may be used for rapid varietal identification in seed-production programmes. Continued

collection, conservation and molecular characterization of finger millet germplasm is recommended to widen the genetic base available for future breeding. Finger millet is a climate-resilient, nutrient-dense cereal of importance to food security in rainfed and tribal farming systems, yet remains genetically under-improved. This study quantifies exploitable variability, identifies harvest index and biological yield per plant as the most reliable yield-selection criteria, and pinpoints genetically divergent parents for hybridization, providing breeders with concrete, data-based criteria for accelerating varietal improvement of this nutri-cereal.

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Statements and Declarations

Competing Interests The authors declare that they have no competing interests relevant to the content of this article.

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Data Availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics Approval Not applicable. This study did not involve human participants, human data or animal experimentation.

Author Contributions R.B. conducted the field experiment, recorded observations, analysed the data and drafted manuscript; R.P.J. conceived and supervised the study; A.K.J. supervised the study; A.C. helped in data collection; R.K.Y. helped in data collection. All authors drafted, read and approved the final manuscript.

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