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ESTIMATION OF GENETIC VARIABILITY AND GENE ACTION FOR GRAIN YIELD IN FINGER MILLET

ESTIMATION DE LA VARIABILITÉ GÉNÉTIQUE ET DE L'ACTION DES GÈNES POUR LE RENDEMENT EN GRAINS DU MIL FINGER

O.S. MAPAKO and M. MAPHOSA

Department of Agronomy and Horticulture, Faculty of Agriculture, Environment and Natural Resources Management, Midlands State University, Gweru, Zimbabwe
Corresponding author: mapakoo@staff.msu.ac.zw

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ABSTRACT

Finger millet (*Eleusine coracana* (L.)) is a climate resilient crop, with an elevated nutritional profile; cultivated mainly in semi-arid and arid regions of Africa and Asia. Despite its importance as a climate smart and nutrient dense crop, its production has not reached full potential partly due to limited availability of improved varieties. The objective of this study was to assess yield and related traits genetic variability, heritability and number of genes in finger millet (FM). The field study comprising of ten FM genotypes, was carried out during the 2023-2024 summer cropping season at Lupane State University Farm in the Northwestern Zimbabwe. There were significant ($P<0.05$) genetic variations among the genotypes for all traits studied. Several grain yield traits (grain yield per plant, number of productive tillers, ear head weight, and thousand grain weight) showed high broad sense heritability (estimated at 0.97, 0.90, 0.88 and 0.86, respectively). Moreover, the narrow difference between trait phenotypic and genotypic coefficients of variation, suggests a predominance of additive gene action. High genetic advance, as a percentage of mean for these traits, suggests that direct selection would be effective for achieving early genetic gains. A combination of high broad sense heritability with high genetic advance as a percentage, coupled with preponderance of additive gene action, suggests that these traits can respond to selection within this population. Grain yield per plant was significantly and positively correlated with ear head weight ($r = 0.72$), number of productive tillers ($r = 0.70$) and thousand grain weight ($r = 0.66$); but showed a negative correlation with plant height ($r = -0.62$). Path analysis further revealed that these traits exert a positive direct effect on grain yield, suggesting that selecting these specific traits would be effective in increasing yield. This study noted that despite the intricate inheritance of some quantitative traits, strategic selection can still lead to significant genetic improvement.

Key Words: *Eleusine coracana*, genetic advance, path analysis

RÉSUMÉ

Le millet doigt (*Eleusine coracana* (L.)) est une culture résiliente au climat, avec un profil nutritionnel élevé, cultivée principalement dans les régions semi-arides et arides d'Afrique et d'Asie. Malgré son importance en tant que culture intelligente face au climat et riche en nutriments, sa production n'a pas atteint son plein potentiel en raison de la disponibilité limitée de variétés améliorées. L'objectif de cette étude était d'évaluer la variabilité génétique du rendement et des traits associés, l'héritabilité et le nombre de gènes chez le millet doigt (FM). Une étude comprenant dix génotypes de FM a été réalisée pendant la saison de culture estivale 2023-2024 à la ferme de l'Université d'État de Lupane, dans le nordouest du Zimbabwe. Il y avait une variation génétique significative (P<0,05) entre les génotypes pour tous les traits étudiés. Plusieurs traits de rendement en grains (rendement en grains par plante, nombre de talles productives, poids de l'épi et poids de mille grains) ont montré une héritabilité au sens large élevée (estimée à 0,97, 0,90, 0,88 et 0,86, respectivement). De plus, la faible différence entre les coefficients de variation phénotypiques et génotypiques des traits suggère une prédominance de l'action additive des gènes. Une avancée génétique élevée, en pourcentage de la moyenne pour ces traits, suggère qu'une sélection directe serait efficace pour obtenir des gains génétiques précoces. La combinaison d'une héritabilité au sens large élevée avec une avancée génétique élevée en pourcentage, associée à une prédominance de l'action additive des gènes, suggère que ces traits peuvent répondre à la sélection dans cette population. Le rendement en grains par plante était significativement et positivement corrélé avec le poids de l'épi (r = 0,72), le nombre de talles productives (r = 0,70) et le poids de mille grains (r = 0,66); mais il montrait une corrélation négative avec la hauteur de la plante (r = -0,62). L'analyse de chemin a en outre révélé que ces traits exercent un effet direct positif sur le rendement en grains, suggérant que la sélection de ces traits spécifiques serait efficace pour augmenter le rendement. Cette étude a noté que malgré l'héritage complexe de certains traits quantitatifs, une sélection stratégique peut encore conduire à une amélioration génétique significative.

Mots Clés : *Eleusine coracana*, avancée génétique, analyse de chemin

INTRODUCTION

Finger millet (*Eleusine coracana* L.) has generated a lot of research and development interest, particularly with respect to breeding for improved yield due to its resilience in the face of climate change and variability. The crops' status is shifting from an underutilised crop to an opportunity crop that has a high nutritional profile and adaptation to harsh climatic conditions (Udamala *et al*., 2020). Furthermore, crop yield potential on-station is significantly greater than on-farm due to; limited availability of improved varieties on the formal markets; poor agronomic practices; biotic pressure from pests and diseases and limited marketing platforms (Chavan *et al*., 2019; Madhavilatha *et al*., 2019; Prajwala *et al*., 2025).

Yield represents cumulative effects of many genes expressed through yield-contributing traits (Schmidt and Hallauer, 1995; Hadi *et al*., 2019). A holistic understanding of genetic variance, heritability of yield and yield components cannot be overemphasised; it is a critical step for advancing crop improvement strategies (El-Hashash, 2017; El-Hashash and Yehia, 2021). To realise meaningful finger millet genetic improvement, requires that breeders evaluate populations from an extensively diverse genetic background and targeting traits with high heritability that respond favourably to selection intensity.

Estimates of heritability gauge the extent to which genotype and environment exert influence on the phenotype; these estimates are propitious in hereditary studies of quantitative traits. Evaluation of heritability

estimates enables breeders to infer whether to consider the phenotypic value as the breeding value of a genotype (Falconer and Mackay, 1996); predict how genes interact in succeeding generations; provide insight on the mechanisms by which morphogenetic traits are inherited; as well as provide a barometer for selection pressure in segregating populations (El-Hashash and Yehia, 2021). Parameters estimating heritability are paramount for decision making in connection with the choice of breeding method and prediction of response to selection (Schmidt and Hallauer, 1995; Schmidt *et al*., 2019); for these reasons heritability is a practical and effective tool in breeding programmes.

Broad sense heritability is a comparative ratio of genetic variance and phenotypic variance; it incorporates environmental effects; while narrow sense heritability is a ratio of additive gene variance and phenotypic variance (Fasahat *et al*., 2016). Heritability estimates are classified as low (0-0.30), moderate (0.31-0.60) and high (0.61-1.0). Traits with low heritability do not respond to selection and least likely to be transmitted to succeeding generation, especially when they are coupled with low genetic advance as a percentage of mean (GAM). These traits are governed by non-additive gene action and selection based on these traits should be delayed to later generations when the alleles are fixed (Fischer and Rebetzke, 2018; Al-Naggar *et al*., 2022). Conversely, traits exhibiting moderate to high heritability and high GAM are under the control of additive gene action and are expected to respond favourably to selection (Udamala *et al*., 2020; Patel *et al*., 2023).

Gene number estimation is essential in the study of inheritance and evolution of quantitatively inherited traits (Lande, 1981). According to Lande (1981), about 5-10 genes controlling a quantitative are the minimum required to effect pronounced variation between population. Most quantitative traits are polygenic; meaning that multiple genes contribute to their expression, which can significantly diminish the effects of environmental variables (Hadi *et al*., 2019).

This study was guided by the hypothesis that significant genetic variability exists among finger millet genotypes for yield and yield-related traits and that traits exhibiting high heritability and genetic advance are predominantly governed by additive gene action and can, therefore, respond effectively to phenotypic selection. The objective of this study was to: (i) determine the genetic variability in finger millet genotypes for yield and related traits, (ii) estimate heritability and genetic advance for these traits, (iii) evaluate the relationship between traits through correlation and path analysis, and (iv) estimate the effective number of genes controlling important traits.

MATERIALS AND METHODS

Study area description. This study was carried out over two summer cropping seasons in 2023 and 2024, at Lupane State University Farm in the northwestern region of Zimbabwe. The experimental site lies at approximately 18°112 S latitude and 27°452 E longitude, with an elevation of about 1,080 meters above sea level. The climate is subtropical, characterised by wet summers and dry winters, with mean annual precipitation between 350 - 450 mm; and temperature range of 28 to 40 °C. The soils of the farm are predominately classified as sandy Aeronosls with pockets of Luvisols and Lixisols characterised by low organic matter due to high leaching.

Source and type of plant materials. The FM germplasm used in the study were sourced from the National Gene Bank of Zimbabwe. Hybridisation was done in the first season using a Line x Tester mating design, where the improved varieties (FMV1 and FMV2) served as testers; and selected landrace accessions served as lines (Table 1).

TABLE 1. Characteristic features of evaluated finger millet parents and their hybrids

Entry no.	Genotype	Characteristics	Biological status
1	FMV1	Purple stigma, dark brown seeds, compact ears	Improved variety
2	FMV2	Purple stigma, dark brown seeds, compact ears	Improved variety
3	2307	Yellow stigma, light brown seeds, incurved ears	Landrace
4	5045	Yellow stigma, light brown seeds, open ears	Landrace
5	5327	Yellow stigma, light brown seeds, incurved ears	Landrace
6	5244	Yellow stigma, dark brown seeds, incurved ears	Landrace
7	5154	Purple stigma, light brown seeds, incurved ears	Landrace
8	2307*FMV1	Purple stigma, light brown seeds, compact ears	F_1 hybrid
9	2307*FMV2	Purple stigma, dark brown grain seeds, compact ears	F_1 hybrid
10	5045*FMV1	Purple stigma, light brown seeds, incurved ears	F_1 hybrid
11	5045*FMV2	Purple stigma, dark brown seeds, open ears	F_1 hybrid
12	5327*FMV1	Purple stigma, light brown seeds, compact ears	F_1 hybrid
13	5327*FMV2	Purple stigma, dark brown seeds, fisty ears	F_1 hybrid
14	5244*FMV1	Purple stigma, light brown seeds, incurved ears	F_1 hybrid
15	5244*FMV2	Purple stigma, dark brown seeds, incurved ears	F_1 hybrid
16	5154*FMV1	Purple stigma, light brown seeds, incurved ears	F_1 hybrid
17	5154*FMV2	Purple stigma, dark brown seeds, incurved ears	F_1 hybrid

Controlled pollination was carried out by emasculating selected panicles, prior to anthesis; followed by manual pollination using pollen from the designated male parent. Ten F_1 FM hybrids from Line x Tester crossing, were planted in a randomised complete block design (RCBD), with three replications. Each experimental plot had five 4 metre rows, with the in-row spacing of 10 cm and inter-row spacing of 90 cm.

Data collection. Data were collected following the guides stipulated in the Descriptors List for finger millet. Five randomly selected plants per plot, to minimise sampling bias, were used for data collection. Plant height was measured from the soil surface to the tip of the main ear at physiological maturity. Peduncle length was measured from the flag leaf node to the base of the ear head. Ear head size and finger length were measured using a measuring ruler. Spikelet density was determined by counting spikelets per unit ear length.

The number of productive tillers was recorded as the number of tillers bearing mature ear heads per plant. Ear head weight and grain yield per plant were measured using a digital analytical balance, after harvesting and drying samples to constant moisture content. One thousand grain weight was determined by randomly counting and weighing 1000 grains from each plot.

Data analysis. R software's variability package version 4.4.1 was used to compute the following genetic estimates based on methods postulated by several researchers (Hallauer and Miranda, 1981; Singh and Chaudhary, 1979; Shukla *et al.,* (2006). The genotypic and phenotypic correlation; genotypic and phenotypic path analysis were computed in Agrianalyze (Popat *et al*., 2024). The gene numbers were estimated using Microsoft Excell 2016.

1. Genotypic variance $V_G = \frac{GMS-EMS}{r}$

Where:

GMS = Genotypic Mean Squares, EMS = Error Mean Square and r = Number of replication

2. Phenotypic variance (V_P)= $V_G + V_E$

Where:

V_G = Genotypic variance and V_E = Environmental variance

3. Genotypic coefficient of variation (GCV)

$= \sqrt{\frac{VG}{\bar{x}}}$ x 100

Where:

$\sqrt{V_G}$ = Genotypic standard deviation and $\bar{x}$ = population mean

4. Phenotypic coefficient of variation (PCV)

$= \sqrt{\frac{Vp}{\bar{x}}}$ x 100

Where:

$\sqrt{V_P}$= Phenotypic standard deviation and = population mean

The genetic coefficient of variation (GCV) and phenotypic coefficient (PCV) were categorised according to Siva Subramanian and Menon (1973); Low: 0 – 10, moderate; >10 - 20, high: >20.

5. Heritability (H^2) = $\frac{Vg}{Vp}$ x 100

Where:

V_G = genotypic variance, V_P = phenotypic variance

6. Genetic advance, GA = $H^2 \times K \times \sqrt{V_p}$

Where:

H^2 = Heritability in broad see, $\sqrt{V_p}$ = Phenotypic standard deviation, and K= selection differential, the value of which is 2.06 at 5% selection intensity.

7. Genetic Advance as percentage of the mean (GAM) (%) = $\sqrt{\frac{GA}{\bar{x}}}$ x 100 (Falconer, 1996)

Where:

GA= Genetic advance, = Population mean; Genetic advance as percentage of the mean were categorised according to Johnson *et al.* (1955); Low: 0 – 10, moderate: >10 – 20 and high: >20.

8. The genotypic (r_g) and phenotypic (r_p) correlation were determined using the variance and covariance components as suggested by Al-Jibouri *et al.* (1958);

$$rg = \frac{\text{covg(xy)}}{\sqrt{(\sigma 2\text{g(x)}.\sigma 2\text{gy})}}$$

$$rp = \frac{\text{covp(xy)}}{\sqrt{(\sigma 2\text{p(x)}.\sigma 2\text{py})}}$$

Where:

rg (xy) = genotypic correlation coefficients, rp (xy) = the phenotypic correlation coefficients, covg = genotypic covariance of xy, covp = phenotypic covariance of xy, σ2g = genotypic variance of x and y and σ2p = phenotypic variance of x and y.

The Wright and Weng estimators were used to calculate the number of effective genes;

9. Weng estimator: $\frac{(\bar{P}_1-\bar{P}_2)^2}{16(V_g)}$

10. Wright estimator: $\frac{(\bar{P}_1-\overline{P_2})^2}{8(\partial^2 g)}$

Where:

P_1 is mean of parent 1, P_2 is mean parent, V_g is genetic variance.

Statistical significance was evaluated at P< 0.05 and P<0.01 probability levels. The assumptions of analysis of variance, including normality and homogeneity of variance, were assessed prior to analysis. Pearson correlation analysis was used to determine relationships among traits; while path coefficient analysis was performed to partition correlation coefficients into direct and indirect effects. These analyses enabled identification of traits that contribute most strongly to grain yield.

RESULTS

Genetic variability in yield related traits. Analysis of variance (ANOVA) revealed highly significant F-value (P<0.01) for genotypes for plant height (318.72**), ear head weight (8.50**), number of productive tillers (4.12**), and most importantly, grain yield per plant (998.13**) (Table 2). Furthermore, the comparison between parents and their crosses revealed highly significant differences (P<0.01) for key traits including grain yield per plant (564.10**), plant height (872.67**) and number of productive tillers (27.11**).

Estimation of genetic variance and heritability. Phenotypic coefficient of variation (PCV) was greater than the genotypic coefficient of variation (GCV) for all traits; this is consistent with the phenotypic variance (VP) which was greater than the genotypic variance (VG) (Table 3). The difference between the genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) in traits such as peduncle length, finger length, and spikelet density is large; suggesting that environmental effects influence their phenotypic expression.

High genetic coefficient of variation (GCV) and genetic advance as percentage of the mean (GAM) were observed for number of productive tillers, ear head weight and grain yield per plant. Conversely, plant height and thousand grain weight showed moderate GCV and GAM; while peduncle length, and spikelet density exhibited low GCV and GAM.

High broad sense heritability was observed for grain yield per plant (0.97), number of productive tillers (0.90), ear head weight (0.88), thousand grain weight (0.86). Moderate heritability was recorded for plant height (0.49), ear head size (0.39) and finger length (0.32); while low heritability estimates

TABLE 2. Genetic variability of finger millet parents and hybrids for yield related traits

Trait	Replication	Genotypes	Parents vs Crosses	Error
Plant height	19.07	318.72**	872.67**	20.08
Peduncle length	20.15**	5.60*	20.26**	2.35
Ear head size	5.70**	1.72**	2.89*	0.59
Finger length	7.85**	2.29**	8.99**	0.52
Spikelet density	0.03	1.18*	0.52	0.28
Number of grain per spikelet	0.04	1.43**	10.51**	0.03
Number of productive tillers	0.10	4.12**	27.11**	0.37
Ear head weight	0.30	8.50**	0.70	0.36
1000 grain weight	0.005	0.33**	2.17**	0.03
Grain yield per plant	12.51	998.13**	56410**	7.66

TABLE 3. Genetic variance, heritability, genetic advance of selected traits in finger millet yield related traits

Trait	VE	VG	VP	ECV	GCV	PCV	H^2	GA	GAM
Plant height	84.76	80.92	165.68	12.10	11.83	16.92	0.49	12.95	17.02
Peduncle length	3.16	0.45	3.61	8.71	3.31	9.31	0.13	0.49	2.42
Ear head size	0.79	0.49	1.28	11.44	9.08	14.6	0.39	0.90	11.62
Finger length	0.66	0.30	0.96	12.78	8.68	15.45	0.32	0.64	10.04
Spikelet density	0.20	0.08	0.28	7.02	4.50	8.34	0.29	0.32	5.00
Number of productive tillers	0.35	3.26	3.61	6.60	20.11	21.16	0.90	3.53	39.36
Ear head weight	0.58	4.47	5.05	9.18	25.44	27.05	0.88	4.10	49.30
1000 grain weight	0.01	0.09	0.10	3.89	10.83	11.51	0.86	0.58	21.00
Grain yield/plant	9.79	319.44	329.23	4.77	27.27	27.69	0.97	36.27	55.34

were recorded for spikelet density (0.29) and peduncle length (0.13).

High heritability, coupled with high genetic advance as percentage of the mean (GAM) were observed for grain yield per plant, ear head weight, number of productive tillers and thousand grain weight. Conversely, moderate heritability and GAM was found for plant height, ear head size and finger length; while low heritability and GAM were recorded for spikelet density, and peduncle length.

Correlation analysis for yield and yield related traits. Pearson correlation analysis revealed several significant associations among traits (Fig. 1). A strong, positive correlation ($P<0.05$) was found between ear head weight and grain yield per plant ($r = 0.72$), number of productive tillers and grain yield per plant ($r = 0.70$), thousand grain weight and grain yield per plant ($r = 0.66$) and number of productive tillers per plant and ear head weight ($r = 0.62$). Moderate, positive correlations were also significant ($P<0.05$) for thousand grain weight and number of productive tillers ($r = 0.59$), and grain yield per plant ($r = 0.54$), and peduncle length and ear head size ($r = 0.50$). Conversely, weak statistically insignificant ($P>0.05$) positive correlations were observed between several trait pairs, including finger length and spikelet density ($r = 0.03$), plant height and finger length (0.14), and spikelet density and peduncle length (0.24).

A strong, significant negative correlation ($P<0.05$) was found between grain yield per plant and plant height ($r = -0.62$), and between number of productive tillers and spikelet density ($r = -0.60$). Significant negative correlation existed between number of productive tillers and ear head size ($r = -0.56$). Grain yield per plant exhibited moderate negative associations with finger length, ear head size, and spikelet density ($r = -0.47$). Other moderate negative correlations were noted between ear head weight and plant height as well as spikelet density ($r = -0.46$), and between thousand grain weight and plant height ($r = 0.41$).

Path analysis for yield and yield related traits. The genotypic path analysis revealed a significant positive correlation between grain yield per plant and several key traits, including number of productive tillers (0.77^{**}), ear head weight (0.80^{**}), and thousand grain weight (0.74^{**}); whereas finger length (-0.93**), ear head size (-0.91**), plant height (-0.84**) and spikelet density (-0.78**) had significant negative relationship with grain yield per plant (Table 4). However, a deeper analysis of the direct effects showed a more complex relationship. Despite the existence of a positive

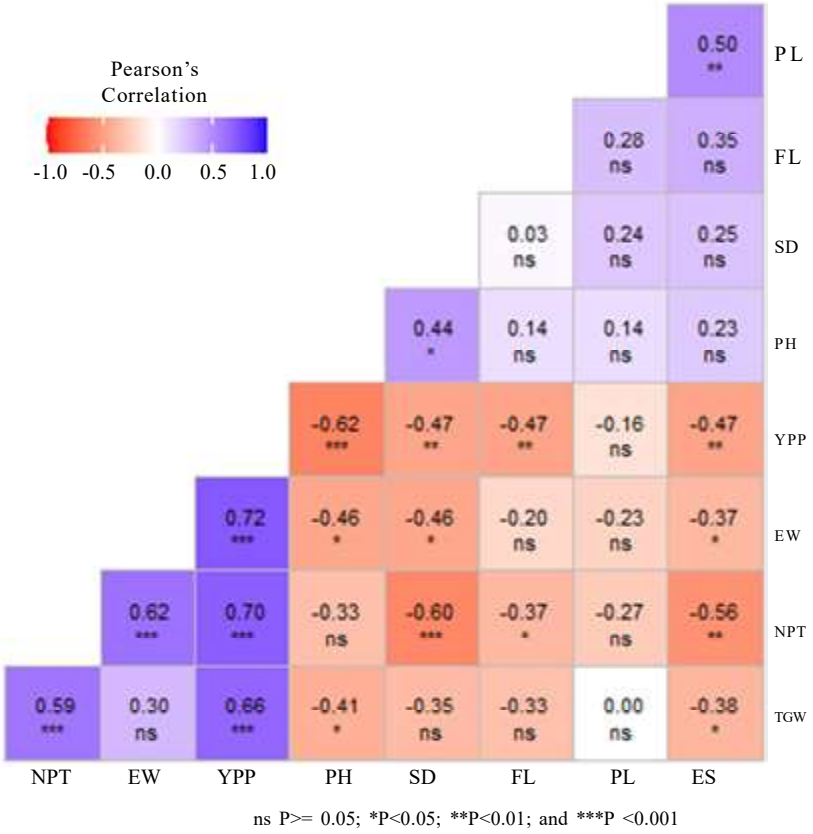

Figure 1. Pearson correlation matrix among finger millet yield and yield-related traits.

TABLE 4. Genotypic path analysis of finger millet yield and yield related traits

Trait	PH	PL	ES	FL	SD	NPT	EW	TGW	YPP
PH	**-0.41**	0.12	0.14	-0.29	0.17	0.12	-0.40	-0.16	-0.84 **
PL	0.11	**-0.45**	0.35	-0.18	0.11	0.13	-0.18	0.02	-0.19
ES	-0.17	-0.46	**0.34**	-0.41	0.24	0.22	-0.40	-0.16	-0.91 **
FL	-0.36	-0.24	0.41	**-0.33**	0.21	0.18	-0.25	-0.25	-0.93 **
SD	-0.33	-0.23	0.39	-0.33	**0.21**	0.21	-0.40	-0.12	-0.78 **
NPT	0.25	0.29	-0.37	0.31	-0.22	**-0.20**	0.36	0.16	0.77 **
EW	0.30	0.15	-0.24	0.15	-0.15	-0.13	**0.56**	0.08	0.80 **
TGW	0.28	-0.03	-0.23	0.36	-0.11	-0.13	0.19	**0.23**	**0.74** *

Bold figures indicate direct effects. Significant correlations are indicated at P< 0.05 (*) and P< 0.01 (**). PH = plant height, PL = peduncle length, ES = ear head size, FL = finger length, SD = spikelet density, NPT = number of productive tillers, EW = ear head weight, TGW = thousand grain weight, and GYP = grain yield per plant

correlation between grain yield per plant and number of productive tillers, the direct effects of this trait to grain yield were negative. Although the direct effects of spikelet density (0.21) and ear head size (0.20) to grain yield per plant were positive, these traits also exhibit significant negative correlation. Conversely, the most substantial positive and direct effects on grain yield per plant were attributed to ear head weight (0.56), ear head size (0.34) and thousand grain weight (0.23). This highlights these traits as the primary direct contributors to yield.

In contrast, the largest negative direct effects were exerted by peduncle length (-0.45), plant height (-0.41) and finger length (-0.33). The independent variables in the genotypic path analysis explained a substantial portion of the variation in grain yield per plant, with a coefficient of determination (R^2) of 88.35. Further analysis revealed that positive indirect effects to grain yield per plant were channelled through ear head size (0.97), number of productive tillers (0.84), and spikelet density (0.77). Conversely, the largest negative indirect effects were observed through finger length (-2.13), ear head weight (-1.21), plant height (-1.16), peduncle length (-0.92), and thousand grain weight (-0.83). The negative correlations are likely due to these strong negative indirect effects.

The phenotypic path analysis showed that the independent variables included in the model; explained significant portion of the variation in grain yield per plant, with a coefficient of determination (R2) of 88.69% (Table 5). Several key traits showed a significant and positive correlation with grain yield per plant and their direct contributions were also positive. Specifically, ear head weight (0.49), thousand grain weight (0.21), and all had a direct and positive impact on grain yield per plant. Conversely, finger length (-0.32), and plant height (-0.16) exerted negative direct effects on yield (Table 4). Notably, while the number of productive tillers had a strong positive correlation with grain yield per plant, its direct effect was negative. The greatest positive indirect effects on grain yield per plant was observed through the pathway of number of productive tillers via ear head weight (0.30) and finger length (0.20).

Effective gene numbers (N_e) for yield and yield related traits. Gene number estimation using Wright and Weng's estimators revealed consistent differences between the two methods, with the Weng estimator invariably yielding higher gene number estimates for all traits and crosses (Table 6). The highest effective gene numbers were estimated for complex traits like ear head size, with

TABLE 5. Phenotypic path analysis of finger millet yield and yield related traits

Trait	PH	PL	ES	FL	SD	NPT	EW	TGW	YPP
PH	**-0.16**	0.02	-0.01	-0.10	0.01	0.05	-0.23	-0.09	-0.64 **
PL	-0.04	**0.07**	-0.02	-0.03	0.01	0.05	-0.12	-0.01	-0.13
ES	-0.04	0.03	**-0.04**	-0.07	0.01	0.09	-0.19	-0.09	-0.49 **
FL	-0.05	0.01	-0.01	**-0.32**	0.00	0.09	-0.14	-0.11	-0.61 **
SD	-0.07	0.02	-0.01	-0.09	**0.02**	0.08	-0.23	-0.07	-0.49 **
NPT	0.05	-0.02	0.02	0.20	-0.01	**-0.14**	0.30	0.13	0.71 **
EW	0.07	-0.02	0.02	0.09	-0.01	-0.09	**0.49**	0.06	0.72 **
TGW	0.06	0.00	0.02	0.17	-0.01	-0.08	0.15	**0.21**	**0.67****

Bold figures indicate direct effects. *, ** Significant t-test at probability levels of 0.05, and 0.01 respectively. PH = plant height, PL = peduncle length, ES = ear head size, SD = spikelet density, NPT = number of productive tillers, EW = ear head weight, , GYP = Grain yield per plant, TGW = thousand grain weight

TABLE 6. Effective gene numbers for finger millet yield and yield related trait in crosses.

Cross	Plant height		Peduncle length		Ear head size		Finger length		Spikelet density	
	Wright	Weng	Wright	Weng	Wright	Weng	Wright	Weng	Wright	Weng
2307*FMV1	0.08	0.12	0.34	0.51	23.44	35.16	1.45	2.18	0.22	0.34
2307*FMV2	1.07	1.61	0.06	0.10	28.02	42.03	0.13	0.20	0.76	1.13
5045*FMV1	1.74	2.61	1.89	2.84	0.15	0.23	0.00	0.00	0.16	0.23
5045*FMV2	4.31	6.46	0.29	0.44	0.00	0.01	0.69	1.04	0.00	0.00
5327*FMV1	0.01	0.02	0.92	1.38	2.50	3.75	0.27	0.40	0.31	0.46
5327*FMV2	0.75	1.12	0.01	0.02	1.28	1.91	0.11	0.16	0.90	1.35
5244*FMV1	1.23	1.84	0.46	0.69	6.83	10.25	1.13	1.70	0.00	0.00
5244*FMV2	3.48	5.22	0.02	0.04	9.40	14.10	0.05	0.07	0.12	0.18
5154*FMV1	0.183	0.27	0.51	0.76	0.13	0.19	0.05	0.07	0.10	0.15
5154*FMV2	0.11	0.16	0.01	0.02	0.65	0.98	0.39	0.59	0.47	0.70

Cross	Productive tillers		Ear head weight		Grain yield per plant		1000 grain weight	
	Wright	Weng	Wright	Weng	Wright	Weng	Wright	Weng
2307*FMV1	8.29	12.43	0.62	0.93	0.00	0.00	0.05	0.08
2307*FMV2	13.00	19.50	0.06	0.08	0.00	0.00	0.07	0.10
5045*FMV1	0.90	1.35	0.04	0.07	4.03	6.05	1.43	2.14
5045*FMV2	2.81	4.22	0.58	0.87	3.74	5.61	1.35	2.03
5327*FMV1	0.25	0.38	2.65	3.97	0.01	0.02	0.55	0.83
5327*FMV2	1.51	2.27	1.15	1.73	0.03	0.05	0.50	0.76
5244*FMV1	0.23	0.34	0.09	0.13	1.06	1.59	0.07	0.10
5244*FMV2	1.44	2.17	0.07	0.10	0.91	1.37	0.05	0.08
5154*FMV1	1.80	2.70	1.49	2.23	0.43	0.65	0.13	0.19
5154*FMV2	4.28	6.42	0.45	0.67	0.34	0.51	0.10	0.16

maximum estimates of 42.03 (Weng) and 28.02 (Wright) genes in hybrid cross 2307*FMV2. High gene numbers were also estimated for number of productive tillers (19.5 and 13.00) in 2307*FMV2. In contrast, a low number of effective genes were estimated for other traits. Both estimators recorded less than three genes controlling a 1000 grain weight (2.14 and 1.43 genes) and a low number for grain yield per plant (6.05 and 4.03 genes) in hybrid cross 5045*FMV1. Interestingly, for some specific traits and crosses, including spikelet density, ear head size, and finger length, both estimators reported an effective gene number of zero, indicating simple inheritance.

DISCUSSION

Genetic variance and heritability yield related traits. Analysis of the genotypic and phenotypic coefficients provided deeper insights into the genetic architecture and inheritance patterns governing the studied traits. The genotypic and lowest phenotypic coefficients provided further insights into the inheritance of the studied traits. The highest genotypic variation (GCV) was recorded for the number of productive tillers; while the lowest phenotypic coefficient of variation (PCV) was found for peduncle length. The results conform to the findings from Divya *et al* (2022) and suggest the relative importance of

additive gene action for productive tillers. Traits exhibiting moderate heritability and moderate genetic advance as a percentage of mean (GAM), such as plant height, ear head size and both additive and non-additive gene effects were significant in their inheritance. As established by Panse (1957), a trait governed by additive gene action and displaying high heritability can show a high genetic gain. Conversely, traits with low heritability and low genetic gain are typically influenced more by non-additive gene action and environmental.

High broad-sense heritability, combined with high genetic advance as a percentage of mean (GAM), was observed for key traits including the number of productive tillers, ear head weight, and thousand grain weight, and grain yield per plant. These findings suggest that these traits are governed by additive gene action, making them highly amenable to improvement through direct phenotypic selection (Mackay, 1996; Priya *et al.,* 2023; Patel *et al.,* 2024). This aligns with the results of Chavan *et al* (2019), Patel *et al* (2024) and Udamala *et al* (2020), who similarly concluded that these traits are under control of genes with cumulative effects. Low heritability and genetic advance (GA), along with a significant disparity between the phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV), were observed for peduncle length, and spikelet density. These findings suggest that the genetic contribution to the variation to these traits is relatively small, with their expression being largely influenced by environmental factors (Anuradha *et al.,* 2023). Consequently, direct selection based solely on the phenotype of these traits would be ineffective. For their effectual improvement, alternative breeding strategies are recommended. These include indirect selection for traits that exhibit high heritability, genetically correlated with these traits, or the use of marker-assisted selection (MAS) to circumvent the limitations of environmental influence (Acquaah, 2012; Ketema *et al.,* 2025).

Correlation analysis for yield and yield related traits. Significant positive strong correlations were recorded between grain yield and the following traits, thousand grain weight, ear head weight and number of productive tillers. Similar results were reported by Patel *et al.* (2023) Lad *et al.* (2020). The positive and significant correlations observed between grain yield and traits such as ear head weight, number of productive tillers, and thousand grain weight suggest that these traits may serve as reliable indirect selection criteria in finger millet breeding programmes aimed at improving grain yield. Indirect selection for these traits would significantly improve finger millet yield.

The negative and significant correlation between grain yield per plant and the traits plant height and finger length imply that taller finger millet with longer fingers plants tend to produce lower yields in comparison shorter genotypes therefore selection against plants with a shorter stature and shorter fingers is likely to increase yield.

Path analysis for yield and yield related traits. The traits, number of productive tillers, ear head weight, thousand grain weight showed strong correlations with grain yield per plant. The negative direct effects of number of productive tillers to yield reveal that they reduce yield, but contribute indirectly to yield through traits such as ear head size, and spikelet density. Thousand grain weight, ear head size and ear head weight exhibit positive direct effects to grain yield per plant, suggesting that they are the primary drivers to grain yield, thus they are ideal candidates for selection in targeted finger millet breeding programmes.

Caution must be exercised when selecting for traits like peduncle length and plant height; these may have a reductive effect on finger millet yield. Residual effects of 11.65% at the genotypic level and 11.31% at the phenotype level indicate that 88.35% and 88.70% of the

variation in grain yield per plant, respectively, was explained by the traits understudy.

Effective number of genes (Ne) controlling yield and yield related traits. The high gene numbers estimated in the number of productive tillers and ear head size indicate polygenic inheritance of these traits in finger millet (Hadi *et al.,* 2019). Selection in these traits must be delayed to later generation to achieve significant improvement because they have more genetic complexity and environmental sensitivity which has a negative effect on selection efficiency.

The 1000 grain weight and grain yield per plant recorded very low gene numbers, suggesting that they are governed a few major genes with additive effects, making them more amenable to direct selection leading to quick genetic gains under stable environments (Rana *et al.,* 2019). The low gene number estimates can also be attributed to the estimators' limitations and the independence to use of markers leading to inefficiencies in accurately estimate gene numbers.

Wright estimators assumes that all loci are homozygous, preponderance of additive gene action and the absence of linkage (Jones, 2001). These assumptions make the estimator ideal the purpose under researched inbreeding crops like finger millet; however, often result in gene number underestimating (Zeng, 1992).

Interpretation of gene numbers in the crosses. The hybrid 5045*FMV2 is genetically diverse offering greater recombination potential; while 5045*FMV1 has a simpler genetic architecture as revealed by low gene numbers for the traits that were studied. This suggests that the traits are under the influence of a single major gene; thus they are highly heritable. Hybrids 2307*FMV1 and 2307*FMV2 show variability in productive tillers, reflecting difference in parental contributions or interaction effects. Cross 2307*FMV2 exhibited higher gene number estimates than 2307*FMV1 in both models; which suggests that there is a higher genetic diversity between accession 2307 and FMV2 and complex gene interactions in FMV2 influencing ear head size.

Disparities in gene numbers are mathematically generated by computational differences in the variance terms (numerator) and the segregating genetic variance term (denominator). Weng estimator variance term is three time larger, and the genetic variance is twice that Wright that explains why the estimates are greater than Wright estimates. The existence of variability and differential phenotypic performance that create a large variance and lower mean will compute a larger gene number estimation (El-Hashash, 2021). The higher the number of genes controlling a trait the slower the genetic gain and more stable it is.

Study limitations. This research provides valuable clues for the genetic architecture of the traits for yield and related traits in finger millet, although a few limitations are to be acknowledged. The research was conducted in one environment and the evaluation of F1 hybrids was done in one season, which might limit the general applicability of the results to varying environments. Gene number estimation was based on biometrical methods, which assume the action of genes to be additive with no linkage between the genes. The results for the number of genes might not be precise, as there was no use of molecular marker techniques. Future studies can focus on the use of multi-environments and molecular markers, to gain a better insight into the genetic control of the traits for yield in finger millet.

CONCLUSION

This study provides insights into the genetic variability, heritability, and gene action governing important yield-related traits in finger millet. Yield contributing traits in finger millet are largely controlled by polygenes however, traits such as number of productive tillers, ear head weight and thousand-grain weight did exhibit additive gene and were shown to be

positively correlated to grain yield per plant and also contributed directly to grain yield. Thus, simple selection strategies for these are likely to lead to early genetic gains as shown by their high genetic advance as a percentage of mean and high broad sense heritability.

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