



RESEARCH ARTICLE

Genetic variability, trait associations and path analysis of yield and downy mildew resistance in pearl millet (*Pennisetum glaucum* (L.) R. Br.)

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Abstract

The present study was conducted during the kharif season of 2025 at Jaipur, Rajasthan, to assess the extent of genetic variability, heritability and interrelationships among 51 genotypes of *Pennisetum glaucum* (L.) R. Br. (pearl millet) for yield and associated traits. The experiment was laid out in a randomized block design (RBD) with 2 replications. Analysis of variance revealed highly significant differences among genotypes for most of the traits, indicating substantial genetic variability and potential for selection and improvement. The estimates of genotypic and phenotypic coefficients of variation were highest for downy mildew intensity and severity, suggesting wide genetic diversity for disease resistance. High heritability coupled with high genetic advance was observed for plant height, panicle girth and disease-related traits, implying the predominance of additive gene action. Correlation analysis indicated that yield per plot was positively and significantly associated with panicle length and girth, identifying these as key yield-contributing traits along with panicle density and productive tillers. Path coefficient analysis further revealed that panicle length exerted the highest positive direct effect on grain yield, while disease-related traits showed negative associations. Overall, the study highlights considerable genetic variability and identifies panicle traits and downy mildew resistance as crucial determinants of yield performance in pearl millet, providing valuable insights for the development of high-yielding, disease-resistant cultivars suited to semi-arid environments.

Keywords: correlation; downy mildew; genetic advance; genetic variability; heritability; path coefficient analysis; panicle morphology; pearl millet

Introduction

Pennisetum glaucum (L.) R. Br. (Pearl millet), one of the most climate-resilient cereal crops, occupies a pivotal position in global food and nutritional security, particularly in the arid and semi-arid regions of Asia and Africa (1, 2). It is widely cultivated in India, where it serves as both a staple food and a source of fodder for livestock, accounting for almost half of the global millet production (3, 4). The crop's exceptional tolerance to drought, high temperatures and low soil fertility makes it indispensable for sustainable dryland agriculture (5, 6). Furthermore, pearl millet grains are highly nutritious, rich in essential micronutrients such as iron and zinc, as well as dietary fiber and antioxidants, which contribute significantly to human health and nutritional security programs (7). Owing to these attributes, the crop is increasingly recognised not only for its role in food systems but also for its potential in combating hidden hunger and enhancing dietary diversity (8).

Despite these advantages, the productivity of pearl millet has remained relatively stagnant compared to other major cereals. This limitation is primarily due to a combination of abiotic stresses such as drought, heat and poor soil fertility, along with biotic pressures including downy mildew and blast diseases.

Additionally, limited utilisation of available genetic diversity and inadequate germplasm characterisation have constrained genetic improvement efforts (9, 10). To overcome these challenges, a detailed understanding of the extent of genetic variability among genotypes is essential for identifying superior parental lines and formulating effective breeding strategies (11). The estimation of genetic parameters such as the genotypic and phenotypic coefficients of variation (GCV and PCV), heritability (h^2) in broad sense and genetic advance provides valuable insight into the magnitude of inherent genetic differences and the potential response to selection. These parameters help breeders identify the most promising traits that contribute to yield improvement under both normal and stress-prone environments (12, 13). The study of association among yield and its component traits through correlation and path coefficient analysis further enables breeders to discern the direct and indirect effects of various characters on yield. While correlation analysis reveals the degree and direction of association among traits (14), path coefficient analysis partitions these correlations into direct and indirect effects, thereby identifying the most influential yield components (15, 16). Such insights are crucial in designing effective selection strategies for complex quantitative traits like yield, where interdependence among characters often obscures true relationships.

Despite several reports on genetic variability and trait association in pearl millet, most studies have primarily focused on yield components under normal conditions, with limited emphasis on the simultaneous evaluation of downy mildew resistance and its relationship with yield-determining traits. Information on the relative contribution of panicle architecture and disease parameters to grain yield, particularly under semi-arid production environments, remains inadequate. Moreover, the identification of traits governed predominantly by additive gene action is essential for formulating effective selection strategies in breeding programs. The experimental site at Jaipur represents a semi-arid agro-ecology characterised by sandy loam soils with medium fertility and high temperature regimes during the rainy (kharif) season. During the crop growth period (June–September 2025), the crop experienced 32 rainy days with moderate to high rainfall distribution and mean maximum temperatures ranging from 33.8–35.5 °C, conditions typical for pearl millet cultivation in this region. In this context, the present investigation was undertaken to assess the genetic variability, inter-trait relationships and contribution of various yield and disease-resistance traits through correlation and path coefficient analysis in 51 genotypes of pearl millet evaluated under field conditions.

Materials and Methods

The field investigation was conducted during the kharif season of 2025 at Jaipur, Rajasthan, to evaluate genetic variability among 51 inbreds of pearl millet (Table 1). The experimental field had sandy loam soil with medium fertility status. The crop was grown under rainfed conditions and received 32 rainy days with moderate to high rainfall distributed from sowing to harvest. The temperature during the crop growth period ranged from 33.8–35.5 °C (maximum day temperature) and 28.2–31.0 °C (minimum day temperature), while night temperatures ranged from 25.6–27.2 °C (maximum) and 22.1–24.4 °C (minimum) from June to September 2025. The inbreds lines were acquired from the rasi seeds. The experiment was laid out in a randomized block design (RBD) with 2 replications. Each genotype was sown in a single row of 4 m length, with inter-row spacing of 50 cm and intra-row spacing of 15 cm. All recommended agronomic

and plant protection practices were followed to ensure optimal crop growth and uniform stand establishment. Observations were recorded on 5 randomly selected plants per genotype in each replication for 9 quantitative traits: days to 50 % flowering (DFF), plant height (PH (cm)), panicle length (PL (cm)), panicle girth (PG (cm)), panicle density (PD), panicle exertion (PE), number of productive tillers per plant (NPT), thousand-seed weight (TSW (g)) and yield per plot (YPP (g)). The YPP was recorded by harvesting all productive panicles of each genotype at physiological maturity, sun-drying, manual threshing and weighing the cleaned grains from each plot. Additionally, 2 disease-related parameters—downy mildew intensity (DMI) and downy mildew severity (DMS) were assessed.

The DMI was assessed as the percentage of infected plants in each plot and the genotypes were classified into reaction groups: highly resistant (0–5 % incidence), resistant (>5–10 %), moderately resistant (>10–20 %), susceptible (>20–50 %) and highly susceptible (>50 % incidence). Mean data were subjected to statistical analysis to estimate variability, heritability and trait associations. Analysis of variance (ANOVA) was performed using R software (version 4.3.0) (17). The GCV, PCV, heritability (h^2) and genetic advance was calculated (18). Correlation coefficients were determined and path coefficient analysis was performed (19).

The DMS was recorded on an individual plant basis at crop maturity using a 1–5 disease rating scale where 1 = no infection; 2 = up to 20 % productive tillers infected; 3 = up to 50 % productive tillers infected; 4 = up to 80 % productive tillers infected; and 5 = all tillers infected or complete plant mortality.

Results

Analysis of variance

The ANOVA revealed highly significant differences among the 51 pearl millet genotypes for DFF, PH, PL, PG, TSW, YPP, DMI and DMS (Table 2). Significant replication effects were observed for DFF, PL, PG and PD, indicating minor environmental influences. The predominance of genotypic variance over error variance confirmed substantial genetic variability among the genotypes.

Table 1. Panel of 51 pearl millet genotypes used in the present study

Sl. No	Genotype	Sl. No	Genotype
1	RDMR25K1	27	RDMR25K27
2	RDMR25K2	28	RDMR25K28
3	RDMR25K3	29	RDMR25K29
4	RDMR25K4	30	RDMR25K30
5	RDMR25K5	31	RDMR25K31
6	RDMR25K6	32	RDMR25K32
7	RDMR25K7	33	RDMR25K33
8	RDMR25K8	34	RDMR25K34
9	RDMR25K9	35	RDMR25K35
10	RDMR25K10	36	RDMR25K36
11	RDMR25K11	37	RDMR25K37
12	RDMR25K12	38	RDMR25K38
13	RDMR25K13	39	RDMR25K39
14	RDMR25K14	40	RDMR25K40
15	RDMR25K15	41	RDMR25K41
16	RDMR25K16	42	RDMR25K42
17	RDMR25K17	43	RDMR25K43
18	RDMR25K18	44	RDMR25K44
19	RDMR25K19	45	RDMR25K45
20	RDMR25K20	46	RDMR25K46
21	RDMR25K21	47	RDMR25K47
22	RDMR25K22	48	RDMR25K48
23	RDMR25K23	49	RDMR25K49
24	RDMR25K24	50	RDMR25K50
25	RDMR25K25	51	RDMR25K51
26	RDMR25K26		

Table 2. Analysis of variance for yield and yield attributing traits in 51 pearl millet genotypes

Mean sum of squares												
Source of variation	d.f.	DFF	PH	PL	PG	PD	PE	NPT	TSW	YPP	DMI	DMS
Replication	1	214.75***	0.79	81.19***	0.37**	6.62**	3.54	0.19	0.51	25	0.79	2.77
Genotype	50	69.53***	572.02***	14.02***	0.23***	1.03*	0.61	0.84	4.88***	34610**	710.61**	1103.66***
Residuals	50	4.83	88.79	4.12	0.04	0.59	1.10	0.76	1.32	16951	35.99	64.84

*** : Significant at 0.1 %, ** : Significant at 1 % and * : Significant at 5 %. Note: DFF: Days to 50 % flowering; PH: plant height (cm); PL: panicle length (cm); PG: panicle girth (cm); PD: panicle density (cm); PE: panicle exertion; NPT: No. of productive tillers; TSW: thousand seed weight; YPP: yield plot⁻¹; DMI: DM intensity and DMS: DM severity.

Genetic variability parameters

The PCV was slightly higher than GCV for all traits, indicating limited environmental influence on trait expression (Table 3, Fig. 1). The highest GCV and PCV were recorded for DMI and DMS, followed by moderate values for PH, PL, PG and TSW. Low GCV and PCV were observed for DFF, PD, PE, NPT and YPP. High heritability coupled with high genetic advance as percent of mean (GAM) was observed for PH, PG, DMI and DMS. Moderate heritability with moderate GAM was recorded for PL and TSW, whereas low heritability and low GAM were noted for PD, PE and NPT.

Association studies

The YPP showed highly significant positive correlation with PL and PG (Table 4, Fig. 2). The PH exhibited significant positive correlations with DFF, PE and NPT but a weak negative association with YPP. The PL was positively correlated with PG and PG showed positive association with PE. The DMI and severity (DMS) exhibited a very strong positive correlation with each other and non-significant negative association with YPP. The NPT showed significant negative correlations with both DMI and DMS.

Path coefficient analysis

Path analysis partitioned the correlation coefficients into direct and indirect effects and indicated that PL exerted the highest positive direct influence on grain yield (Table 5). The PG had low direct effect but a very high positive indirect effect through PL, confirming earlier reports that identified panicle architecture as the primary yield-determining complex (20). The TSW contributed moderate, positive indirect effects. In contrast, the negative direct effects of PH and productive tillers differ from studies where these traits showed positive contributions to yield (21, 5), suggesting that under semi-arid conditions, excessive vegetative growth may limit assimilate partitioning to the developing sink. Downy mildew intensity and severity exhibited low direct effects on grain yield along with negative indirect effects through major yield components, resulting in an overall negative association with yield. The PE displayed contrasting effects at genotypic and phenotypic levels, indicating environmental sensitivity.

Table 3. Estimates of mean and genetic parameters for yield and yield attributing traits in 51 pearl millet genotypes

Traits	Mean	Range		CD	CV (%)	GCV (%)	PCV (%)	h ² broad sense (%)	GAM
		Min	Max						
DFF	64.76	50.00	77.00	4.41	9.63	8.78	9.41	87.02	16.88
PH (cm)	94.87	60.00	156.00	18.93	19.06	16.38	19.16	73.13	28.87
PL (cm)	19.97	13.00	29.00	4.08	15.66	11.14	15.08	54.60	16.95
PG (cm)	2.62	1.60	3.60	0.39	14.15	11.86	14.03	71.45	20.65
PD	8.16	5.00	9.00	1.54	11.41	5.77	11.02	27.35	6.21
PE	8.25	6.00	9.00	2.11	11.38	6.01	11.20	28.82	6.65
NPT	3.25	1.00	5.00	1.75	27.36	5.96	27.46	4.72	2.67
TSW	7.50	1.20	12.50	2.30	23.37	17.80	23.46	57.53	27.81
YPP (g)	1205.98	780.00	1740.00	261.50	13.25	7.79	13.31	34.25	9.39
DMI	10.78	0.00	121.66	12.05	178.36	170.39	179.25	90.36	333.64
DMS	15.13	0.00	130.00	16.17	158.94	150.61	159.73	88.90	292.53

Note: CD- Critical difference; CV- coefficient of variation; PCV- phenotypic coefficient of variation; GCV- genotypic coefficient of variation; h²- heritability; GAM- genetic advance as per cent of mean; DFF- days to 50 % flowering; PH- plant height (cm); PL- panicle length (cm); PG- panicle girth (cm); PD- panicle density (cm); PE- panicle exertion; NPT- No. of productive tillers; TSW- thousand seed weight; YPP- yield plot⁻¹; DMI- DM intensity, DMS- DM severity.

Table 4. Estimates of correlation coefficient for yield attributing traits in 51 pearl millet genotypes

Trait	DFF	PH	PL	PG	PD	PE	NPT	TSW	YPP	DMI	DMS
DFF	1.00	0.25*	0.08	-0.17	-0.07	0.02	-0.03	0.00	-0.07	-0.05	-0.04
PH		1.00	0.05	-0.12	-0.09	0.24*	0.23*	-0.02	-0.15	-0.18*	-0.19*
PL			1.00	0.31*	-0.12	0.10	0.11	-0.24*	0.60***	-0.14	-0.12
PG				1.00	0.12	0.23*	-0.16	0.08	0.46**	-0.03	-0.05
PD					1.00	-0.11	0.03	0.11	0.06	-0.15	-0.16
PE						1.00	0.10	-0.19*	0.14	0.06	0.05
NPT							1.00	0.14	0.06	-0.32**	-0.31**
TSW								1.00	-0.04	0.19*	0.22*
YPP									1.00	-0.06	-0.05
DMI										1.00	0.99***
DMS											1.00

*** -Significant at 0.1 %, ** - Significant at 1 % and * - Significant at 5 %. Note: DFF- days to 50 % flowering; PH- plant height (cm); PL- panicle length (cm); PG- panicle girth (cm); PD- panicle density (cm); PE- panicle exertion; NPT- No. of productive tillers; TSW- thousand seed weight; YPP- yield plot⁻¹; DMI- DM intensity; DMS- DM severity.

Table 5. Estimates of genotypic and phenotypic path coefficients for yield attributing traits in 51 pearl millet genotypes

Trait		DFF	PH	PL	PG	PD	PE	NPT	TSW	DMI	DMS	YPP
DFF	G	-0.20	0.00	0.15	0.00	-0.03	-0.07	-0.03	0.02	-0.07	0.13	-0.09
	P	-0.06	-0.02	0.04	-0.02	0.00	0.01	0.00	0.00	-0.05	0.05	-0.07
PH	G	-0.04	-0.01	-0.04	0.00	-0.05	0.11	-0.22	-0.04	0.01	0.01	-0.26
	P	-0.01	-0.15	0.03	-0.02	0.00	0.03	0.00	0.00	0.00	0.01	-0.15
PL	G	-0.03	0.00	1.08	0.00	-0.08	0.02	-0.04	-0.11	-0.05	0.11	0.89**
	P	-0.01	-0.01	0.45	0.04	0.00	0.01	0.00	-0.03	-0.03	0.03	0.60***
PG	G	0.03	0.00	0.45	0.01	0.07	0.13	0.06	-0.04	-0.02	0.06	0.75**
	P	0.01	0.02	0.11	0.18	0.00	0.01	0.00	-0.01	-0.02	0.02	0.46**
PD	G	0.02	0.00	-0.34	0.00	0.27	-0.21	0.32	0.16	-0.03	0.10	0.28
	P	0.00	0.01	-0.02	0.01	-0.03	0.01	0.00	0.00	-0.02	0.03	0.06
PE	G	0.04	0.00	0.05	0.00	-0.15	-0.38	0.40	-0.04	0.05	-0.11	0.00
	P	0.00	-0.02	0.02	0.01	0.00	0.15	0.00	-0.02	0.01	-0.01	0.14
NPT	G	-0.02	-0.01	0.16	0.00	-0.27	-0.49	-0.31	0.46	-0.31	0.76	-0.04
	P	0.00	-0.02	0.06	-0.03	0.00	0.04	0.01	0.01	-0.04	0.05	0.06
TSW	G	-0.01	0.00	-0.27	0.00	0.10	-0.03	-0.31	0.46	0.01	-0.06	-0.12
	P	0.00	0.00	-0.10	-0.01	0.00	-0.03	0.00	0.15	0.01	-0.03	-0.04
DMI	G	0.05	0.00	-0.23	0.00	-0.04	0.08	0.40	0.02	0.24	-0.57	-0.03
	P	0.02	0.00	-0.07	-0.02	0.00	0.02	0.00	0.01	0.19	-0.23	-0.06
DMS	G	0.05	0.00	-0.21	0.00	-0.04	0.07	0.40	0.05	0.24	-0.58	-0.02
	P	0.01	0.00	-0.06	-0.02	0.00	0.02	0.00	0.02	0.19	-0.23	-0.05

*** -Significant at 0.1 % and ** - Significant at 1 %. Note: DFF- days to 50 % flowering; PH- plant height (cm); PL- panicle length (cm); PG- panicle girth (cm); PD- panicle density (cm); PE- panicle exertion; NPT- No. of productive tillers; TSW- thousand seed weight; YPP- yield plot⁻¹; DMI- DM intensity; DMS- DM severity.

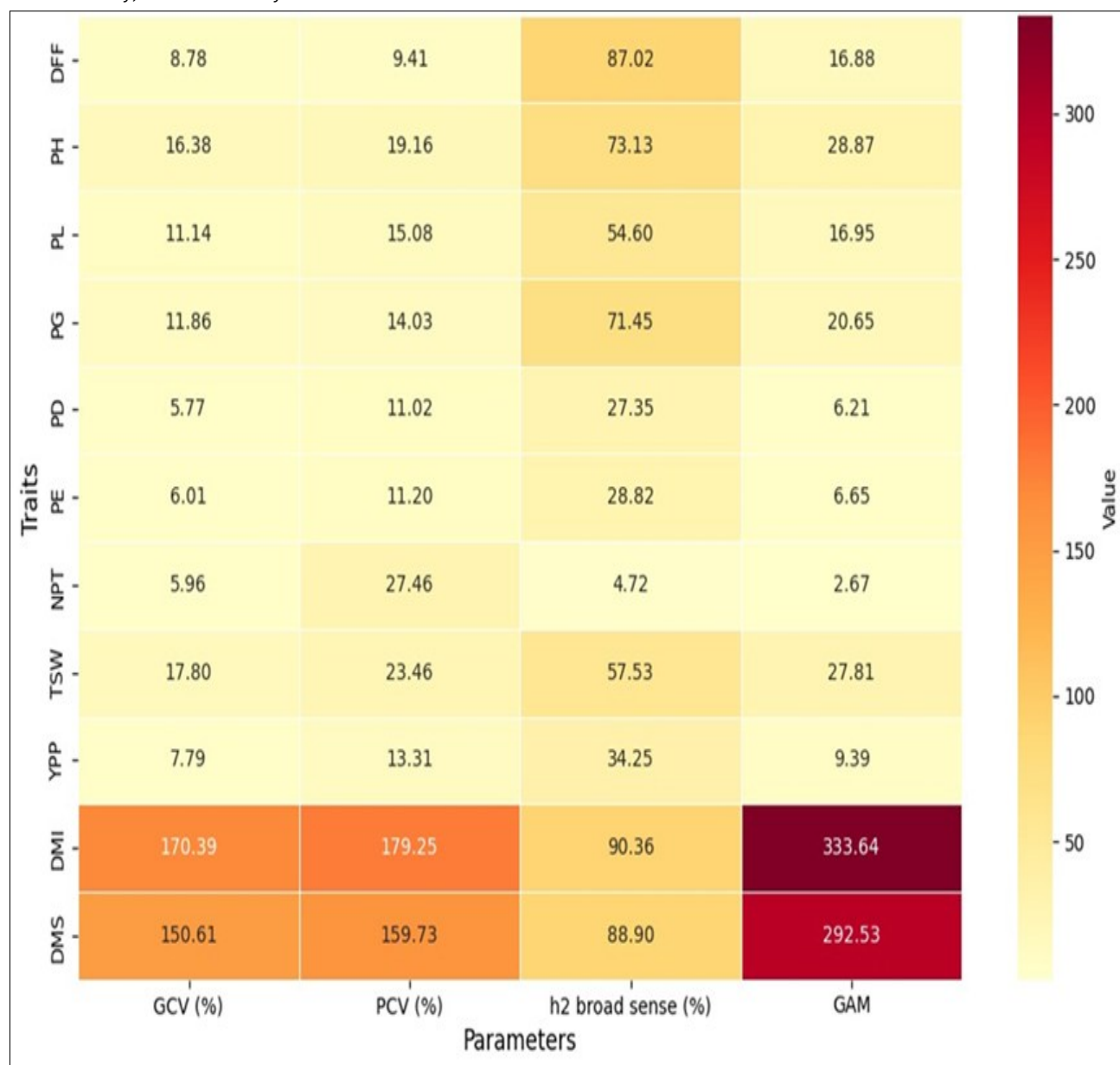


Fig. 1. Heatmap depicting genetic variability parameters across traits in 51 pearl millet genotypes. Note: DFF- days to 50 % flowering; PH- plant height (cm); PL- panicle length (cm); PG- panicle girth (cm); PD- panicle density (cm); PE- panicle exertion; NPT- No. of productive tillers; TSW- thousand seed weight; YPP- yield plot⁻¹; DMI- DM intensity; DMS- DM severity.

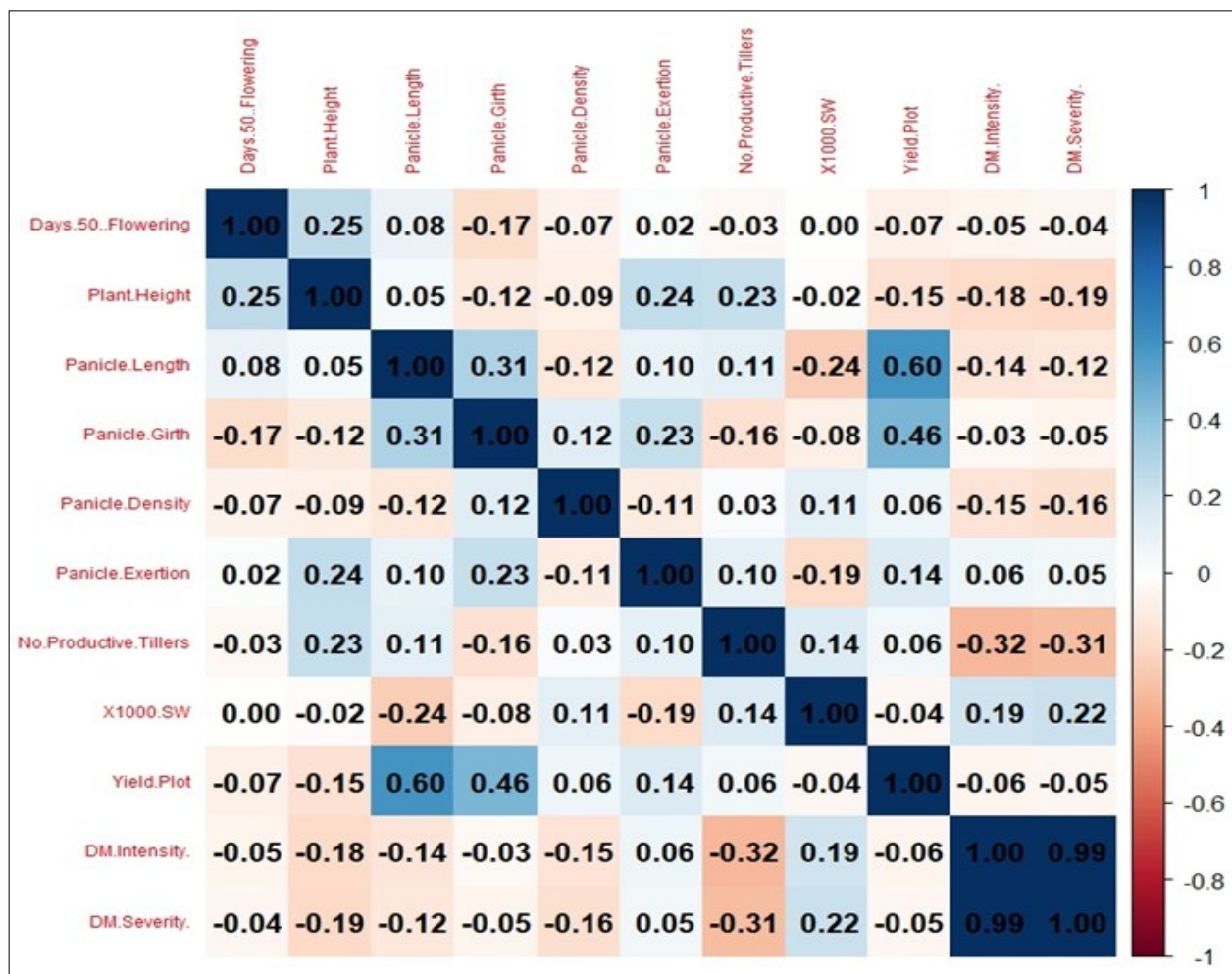


Fig. 2. Correlogram depicting the association of grain yield with other traits in 51 pearl millet genotypes.

Discussion

The highly significant differences among the 51 pearl millet genotypes for DFF, PH, PL, PG, TSW, YPP, DMI and DMS confirmed substantial genetic variability, offering ample scope for selection and genetic improvement. Significant replication effects for DFF, PL, PG and PD reflect minor environmental influences, but the predominance of genotypic variance indicates a strong underlying genetic basis. Similar findings of wide genetic variability for yield and component traits were also reported earlier (22). Significant differences in yield and disease-related traits (DMI and DMS) underscore the potential to identify genotypes with both high yield and downy mildew resistance. These results agree with the reports of the authors, who emphasised that genetic diversity and heritable variation are essential for effective selection and breeding of high-yielding, disease-resistant pearl millet cultivars (23, 24).

The higher PCV than GCV for all traits suggests minor environmental influence on trait expression. The highest GCV and PCV for DMI and DMS indicate wide genetic variability and strong potential for selection for downy mildew resistance. Moderate GCV and PCV for PH, PL, PG and TSW suggest these traits are mainly governed by genetic factors, whereas low values for DFF, PD, PE, NPT and YPP indicate higher environmental influence. The relatively low heritability observed for grain yield per plot (34.25 %) despite a large genotypic mean square in the ANOVA indicates the substantial contribution of environmental variance to the total phenotypic expression of this trait. This suggests that grain yield is a highly complex character governed by several component traits and is strongly influenced by non-genetic factors under the

prevailing experimental conditions. Consequently, direct selection for yield per se would be less effective and greater emphasis should be placed on indirect selection through highly heritable component traits such as PL and PG, which showed strong positive association with yield, same findings also reported earlier with moderate to high variability for yield components and large genotypic variation for downy mildew resistance (25, 26).

High heritability coupled with high GAM for PH, PG, DMI and DMS indicates predominance of additive gene action, suggesting that effective improvement can be achieved through direct phenotypic selection in early generations. The wide variability observed for these traits further enhances the scope for identifying and fixing resistant genotypes. From a breeding standpoint, this enables efficient integration of disease resistance into high-yielding backgrounds through simple selection. Moderate heritability and GAM in PL and TSW indicate involvement of both additive and non-additive gene effects, while low values in PD, PE and NPT suggest strong environmental influence and limited response to selection. Findings that high heritability combined with high genetic advance indicates additive gene effects. Similar trends were reported earlier (10, 27).

The highly significant positive correlation of YPP with PL and PG suggests that longer and thicker panicles contribute effectively to higher grain productivity. The weak negative association of PH with yield indicates that excessive vegetative growth may not proportionally enhance grain production, as noted earlier (5, 28). Positive associations among panicle traits (PL, PG, PE) were also reported in previous studies (29, 30). The 1000-seed weight showed a

negative association with grain yield, indicating that selection for bold seeds alone may not enhance productivity. This suggests a trade-off between seed size and grain number per panicle. In contrast to reports of positive relationships under favourable environments, yield in the present semi-arid conditions was mainly governed by panicle size and grain number, as reflected by the strong positive association of yield with PL and girth. The strong positive correlation between DMI and DMS and their negative (though non-significant) association with yield, together with significant negative correlation of NPT with both disease parameters, imply that genotypes with higher tillering ability possess better tolerance or escape mechanisms against downy mildew. These observations align with earlier findings (31, 32).

Path coefficient analysis revealed that panicle-related traits are the primary yield determinants in pearl millet. The highest positive direct effect of PL and substantial indirect effect of PG through PL, coupled with moderate contribution from TSW, highlight the principal yield-determining complex. Negative direct effects of DFF, PH and NPT suggest that early-maturing, moderately tall plants with fewer but efficient tillers are more productive. The overall predominance of panicle morphology agrees with authors, who identified PL and girth as major yield determinants across environments (33–35). The negative contribution of delayed flowering and excessive height corroborates with earlier study (36), better resource utilisation by early, moderately tall genotypes under stress conditions. Low to negative effects of DMI and DMS confirm that resistance stabilises rather than directly increases yield.

A comparison of genotype performance revealed that several lines combined complete absence of downy mildew incidence with high grain yield. Among these, RDMR25K44 recorded the highest mean yield per plot (1585 g), followed by RDMR25K21 (1400 g) and RDMR25K3 (1355 g). The simultaneous expression of high yield and disease resistance in these genotypes indicates the presence of favourable gene combinations for both productivity and stability under semi-arid conditions. These genotypes represent valuable genetic resources for developing high-yielding, downy mildew-resistant hybrids and for use in resistance introgression programmes. The study reveals that panicle architecture influences yield through an integrated interaction with tillering ability, seed weight and disease tolerance rather than acting as an isolated structural trait.

This study was conducted at a single location in a single season with 2 replications; therefore, genotype $\times$ environment interaction could not be assessed and the precision of the error variance is limited. The significant replication effects for some traits indicate environmental influence on trait expression. Hence, the genetic parameters and trait associations reported here are environment-specific and should be considered as preliminary. Multi-location and multi-season evaluation with more replications is required to confirm the stability of these relationships.

Conclusion

The study demonstrated significant genetic variability among 51 pearl millet genotypes for yield and related traits. The PL and girth were the primary determinants of grain yield. Downy mildew intensity and severity ranged widely, highlighting opportunities for breeding disease-resistant varieties. High heritability and genetic

advance for select traits point to strong additive gene effects and suggest that selection will be effective. Correlation and path analysis reinforced the key role of panicle morphology in yield determination. Traits such as flowering time, PH and tiller number provided limited positive effects, indicating that a balanced approach to selection is warranted. Favorable panicle traits combined with low disease incidence can improve yield stability in semi-arid environments and the findings provide actionable guidance for breeding programs targeting high-yielding, disease-resistant cultivars.

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Authors' contributions

KBR carried out field experiments, collection, noting, recorded data and wrote drafts for research work. KS participated in the design of the study, supervised the whole research and helped in compiling the manuscript. ASH and GM contributed to analysis of samples data, technical manuscript writing and M contributed to editing the manuscript. All authors read and approved of the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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