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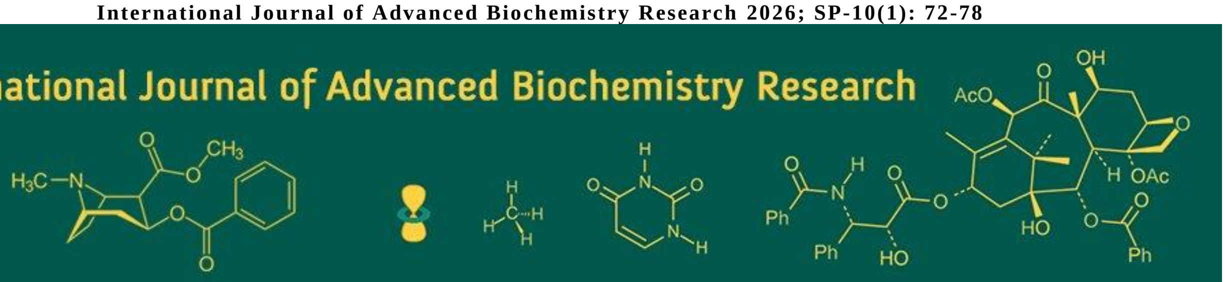

Dissecting genetic architecture: variance component analysis and heritability estimates for quantitative traits in pearl millet [*Pennisetum glaucum* (L.) R. Br.]

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Abstract

A comprehensive study on the genetic architecture of yield and agronomic traits in pearl millet was conducted using 32 hybrids developed from four CMS lines and eight testers in a Line × Tester design during Kharif 2022 at the National Agricultural Research Project, Ch. Sambhaji Nagar. Variance component analysis was used to estimate additive and dominance effects and heritability for twelve quantitative traits, with the objective of understanding gene action and the relative contribution of lines, testers, and their interactions.

Analysis of variance revealed highly significant genotypic differences for all traits except downy mildew resistance, indicating substantial genetic variability. Grain yield was predominantly governed by additive gene action (GCA = 0.10, SCA = 0.03; A:D = 3.33) with high narrow-sense heritability (83.02%), suggesting effectiveness of pedigree or recurrent selection. Days to 50% flowering showed nearly equal additive and dominance effects (A:D = 1.01; h^2 = 63.09%), allowing both parent selection and heterosis breeding.

In contrast, plant height, ear-head length, and zinc content were entirely controlled by dominance effects with negligible additive variance (h^2 = 0.00%). Traits such as days to maturity, productive tillers, ear-head girth, 1000-seed weight, fodder yield, and iron content exhibited non-additive gene action with low to moderate heritability (12.71-41.76%), highlighting the importance of hybrid evaluation to exploit dominance and epistasis.

Variance partitioning showed that testers contributed most to grain yield (79.87%), days to 50% flowering (59.64%), and ear-head length (54.00%), reflecting strong additive effects from male parents. Line × Tester interactions were predominant for plant height (76.21%), productive tillers (78.07%), and zinc content (81.86%), indicating the importance of specific parental combinations. Overall, the results emphasize trait-specific breeding strategies: additive traits favor parent selection and pedigree breeding, while non-additive traits require focused hybrid screening.

Keywords: Gene action, additive-dominance variance, heritability, quantitative inheritance, line × tester design, pearl millet, variance components, genetic architecture

Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is a crucial cereal crop for semi-arid agriculture, cultivated over 26 million hectares globally producing approximately 28 million tonnes annually (Directorate of Millet Development, 2020). In India, it ranks fourth among cereals with 6.93 million hectares generating 8.61 million tonnes, substantially bolstered by Maharashtra's contribution of 8.47 lakh hectares and 32.89 lakh tonnes (Directorate of Millet Development, 2020) [5]. Its exceptional resilience to drought, high temperatures, and poor soils—owing to deep roots, high tillering, C_4 photosynthesis, and short lifecycle—makes it invaluable for arid regions (Yadav & Rai, 2013; Yadav *et al.*, 2019) [20, 21]. Protogynous flowering promotes natural outcrossing and genetic diversity, crucial for hybrid breeding (Yadav *et al.*, 2024) [22]. Pearl millet is nutritionally superior, containing iron (8-10 mg/100g) and zinc (3-4 mg/100g) significantly exceeding other cereals, supporting food security (Mishra *et al.*, 2018) [15].

Pearl millet breeding accelerated after the 1965 release of HB 1 (first commercial hybrid), enabled by cytoplasmic male sterility (CMS) systems (Burton & Powell, 1968) [4]. Modern hybrids have enhanced yield, disease resistance, and stress tolerance.

However, a critical question persists: what genetic architecture underlies trait inheritance? Understanding whether traits are controlled by additive or non-additive gene action is essential for effective breeding strategy design (Yadav & Rai, 2013; Kumar & Singh, 2019) [20, 13]. Traits controlled by additive effects respond to pedigree selection; those controlled by non-additive effects require hybrid breeding (Baskaran *et al.*, 2018; Yadav *et al.*, 2019) [1, 21].

Heritability—the proportion of phenotypic variation attributable to genetic differences—directly influences breeding decisions. Narrow-sense heritability (h^2) predicts selection response in conventional breeding; high h^2 indicates effective response (Warner, 1952; Kempthorne, 1957) [18, 9]. The Line × Tester design enables variance partitioning into general combining ability (GCA; additive) and specific combining ability (SCA; non-additive), heritability calculation, and determination of variance contributions from lines, testers, and their interactions (Kempthorne, 1957) [11]. Recent studies document that grain yield exhibits strong additive genetic control ($h^2 > 80\%$) with high responsiveness to selection, while morphological traits and grain micronutrients display non-additive inheritance requiring hybrid evaluation (Govindaraj *et al.*, 2013, 2016; Kumar & Singh, 2019; Yadav *et al.*, 2019) [7, 8, 13, 21].

In Maharashtra, VNMKV and NARP prioritize pearl millet improvement for yield, stress tolerance, and nutrition. This investigation aims to elucidate gene action governing yield and agronomic traits, estimate heritability, and quantify contributions from lines, testers, and their interactions. These findings will provide a scientific foundation for designing trait-specific breeding strategies, advancing pearl millet improvement under semi-arid conditions.

Materials and Methods

The present investigation titled "Heterosis and Combining Ability Studies in Pearl Millet (*Pennisetum glaucum* (L.) R.Br.)" was conducted or taken at field of National Agricultural Research Project (NARP) Breeding section, Ch. Sambhaji Nagar during *Summer* 2022 and evaluated during *Kharif* 2022. The details of materials and methods adopted in conducting the experiment and the statistical procedures followed during the course of research & investigation are given as below.

Experimental Materials

Parents

Female (A line)

1. 00111A
2. 028880A
3. 88004A
4. 99111A

Male (R line)

1. 15071R
2. 16518R
3. 16897R
4. PS-1
5. PS-2
6. 15278R
7. 16531R
8. 15020R

Checks

1. AHB 1200
2. AHB 1269

Table 1: Crosses produced

Sr. No.	Crosses
1.	00111A X 15071R
2.	00111A X 16518R
3.	00111A X 16897R
4.	00111A X PS-1
5.	00111A X PS-2
6.	00111A X 15278R
7.	00111A X 16531R
8.	00111A X 15020R
9.	028880A X 15071R
10.	028880A X 16518R
11.	028880A X 16897R
12.	028880A X PS-1
13.	028880A X PS-2
14.	028880A X 15278R
15.	028880A X 16531R
16.	028880A X 15020R
17.	88004A X 15071R
18.	88004A X 16518R
19.	88004A X 16897R
20.	88004A X PS-1
21.	88004A X PS-2
22.	88004A X 15278R
23.	88004A X 16531R
24.	88004A X 15020R
25.	99111A X 15071R
26.	99111A X 16518R
27.	99111A X 16897R
28.	99111A X PS-1
29.	99111A X PS-2
30.	99111A X 15278R
31.	99111A X 16531R
32.	99111A X 15020R

Experimental Methods

The experimental material comprised or consist of parents and hybrids along with two released hybrid checks were grown in randomized block design (RBD) with two replications at field of National Agricultural Research Project (NARP) Breeding section, Ch. Sambhaji Nagar.

Crossing programme

The crossing programme for obtaining crossed or hybrid seed was undertaken during *Summer* 2022 at field of National Agricultural Research Project (NARP), Ch. Sambhaji Nagar. Four male sterile lines (female) and eight inbred (male) were crossed in line x tester fashion (4 x 8 = 32). These crossed seed obtained were utilized as F1 or hybrid seed in present research or investigation.

Experimental design layout

The experiment or programme was laid out in a Randomized Block Design (RBD) with two replications. The total number of treatments were 46, comprising of 32 F1's, 4 females and 8 male parents with 2 checks. The parent and hybrids were planted in plot of 4.0 m X 1.0 m having row to row spacing 45 cm and 15 cm plant to plant distance.

Results

Table 2: The estimate of GCA, SCA, additive and dominance variances, gene action and heritability for different characters in pearl millet

Sr. No	Character	σ^2GCA	σ^2SCA	σ^2A:σ^2D	Gene action	h^2_n (%)
1	Days to 50 % flowering	7.25**	7.19**	1.01	Additive	63.09
2	Days to maturity	5.18**	20.65**	0.25	Non-additive	31.79
3	Plant height (cm)	0.00	478.85**	0.00	Non-additive	0.00
4	Productive tillers per plant	0.008	0.032**	0.26	Non-additive	26.90
5	Ear-head length (cm)	0.00	8.83**	0.00	Non-additive	0.00
6	Ear-head girth (cm)	0.012**	0.028**	0.44	Non-additive	41.76
7	1000-seed weight in g.	0.23**	0.93**	0.25	Non-additive	32.83
8	Downy Mildew	00	00	00	-	00
9	Fodder yield (kg/plot)	0.078**	0.989**	0.08	Non-additive	12.71
10	Grain Fe content (%)	2.64**	21.02**	0.13	Non-additive	18.34
11	Grain Zn content (%)	0.00	27.99**	0.00	Non-additive	0.00
12	Grain yield (kg/plot)	0.10	0.03	3.33	Additive	83.02

*, ** denote significant at 5 % and 1 % levels, respectively.

Days to 50 % Flowering

General combining ability (GCA) variance (σ^2GCA = 7.25) and specific combining ability (SCA) variance (σ^2SCA = 7.19) are virtually identical, yielding an additive-to-dominance ratio (σ^2A:σ^2D) of ~1.01 and a high narrow-sense heritability (h^2_n = 63.1 %). This tells us that flowering time in pearl millet is driven by both additive and non-additive gene action—but because additive effects are equally strong, gains for earliness can be reliably accumulated. In practice, breeders should concentrate on parents with high GCA for days to 50 % flowering and deploy pedigree or recurrent-selection schemes to lock in early-flowering alleles.

Days to Maturity

SCA variance (20.65) far exceeds GCA variance (5.18), giving a low σ^2A:σ^2D of 0.25 and moderate heritability (h^2_n = 31.8 %). This indicates that maturity period is primarily under non-additive control—dominance and epistatic interactions dominate. Rather than selecting parents in isolation, breeders should focus on testing specific F_1 crosses to capture heterotic combinations that minimize crop duration, a key strategy when targeting drought-escape or short-season environments.

Plant Height (cm)

Additive variance is essentially zero (σ^2GCA ≈ 0) while SCA is very large (σ^2SCA = 478.85), and heritability is nil (h^2_n = 0 %). Plant stature is governed exclusively by non-additive gene effects, meaning neither pedigree nor backcross schemes will fix height variation through parents alone. Improvement must hinge on identifying those specific hybrid combinations that deliver the desired dwarf or tall ideotype.

Productive Tillers per Plant

SCA (0.032) is four times higher than GCA (0.008), with σ^2A:σ^2D = 0.26 and low heritability (h^2_n = 26.9 %). Tillering capacity is thus predominantly shaped by dominance and epistasis, and parental GCA offers limited predictive power. Systematic hybrid screening—evaluating specific crosses for high tiller number—is the most efficient path to improved tiller productivity.

Ear-Head Length (cm)

Only non-additive variance (σ^2SCA = 8.83) is significant, additive variation (σ^2GCA) is absent, and h^2_n = 0 %. This complete lack of additive control means pure-line selection cannot shift ear length—progress can only come from hybrid combinations that exhibit transgressive segregation for longer heads. Breeders must therefore prioritize cross combinations with proven SCA for ear-head elongation.

Ear-Head Girth (cm)

Both additive (σ^2GCA = 0.012) and dominance (σ^2SCA = 0.028) variances are significant, yielding σ^2A:σ^2D = 0.44 and moderate heritability (h^2_n = 41.8 %). While non-additive effects still dominate, the appreciable additive component means gains can be made through two routes: selecting parents with good GCA and then fine-tuning via hybrid evaluation. A combined pedigree-plus-hybrid approach will maximize girth improvements.

1000-Seed Weight (g)

Here GCA (0.23) and SCA (0.93) are both significant, with σ^2A:σ^2D = 0.25 and h^2_n = 32.8 %. Thousand-seed weight shows mixed inheritance: non-additive effects lead, but additive genes still matter. Breeding strategies should therefore couple the selection of bold-seeded parents (high GCA) with targeted hybrid testing to exploit heterosis for heavier grain.

Fodder Yield per Plot (kg)

SCA (0.989) dramatically exceeds GCA (0.078), with a very low σ^2A:σ^2D ratio of 0.08 and h^2_n = 12.7 %. Biomass yield is almost entirely non-additive, so selecting individual parents will not translate into higher stover. Breeders should concentrate on identifying and advancing specific high-SCA hybrids, especially in dual-purpose programs where both grain and fodder are targets.

Grain Iron Content (ppm)

Dominance variance (SCA = 21.02) far outweighs additive effects (GCA = 2.64), giving a σ^2A:σ^2D of 0.13 and low heritability (h^2_n = 18.3 %). Iron accumulation in the grain is therefore largely non-additive. While modest gains can be made via recurrent selection of high-GCA lines, the most rapid biofortification will come from selecting superior F_1 hybrids with high SCA for iron.

Zinc Content (ppm)

Additive variance is nonexistent (σ^2GCA = 0), SCA is high (27.99), and h^2_n = 0 %. Zinc accumulation is under full non-additive control, so parental selection offers no progress. Direct hybrid testing to uncover crosses with exceptional zinc-accumulating capacity is the only viable route to breed for higher grain Zn levels.

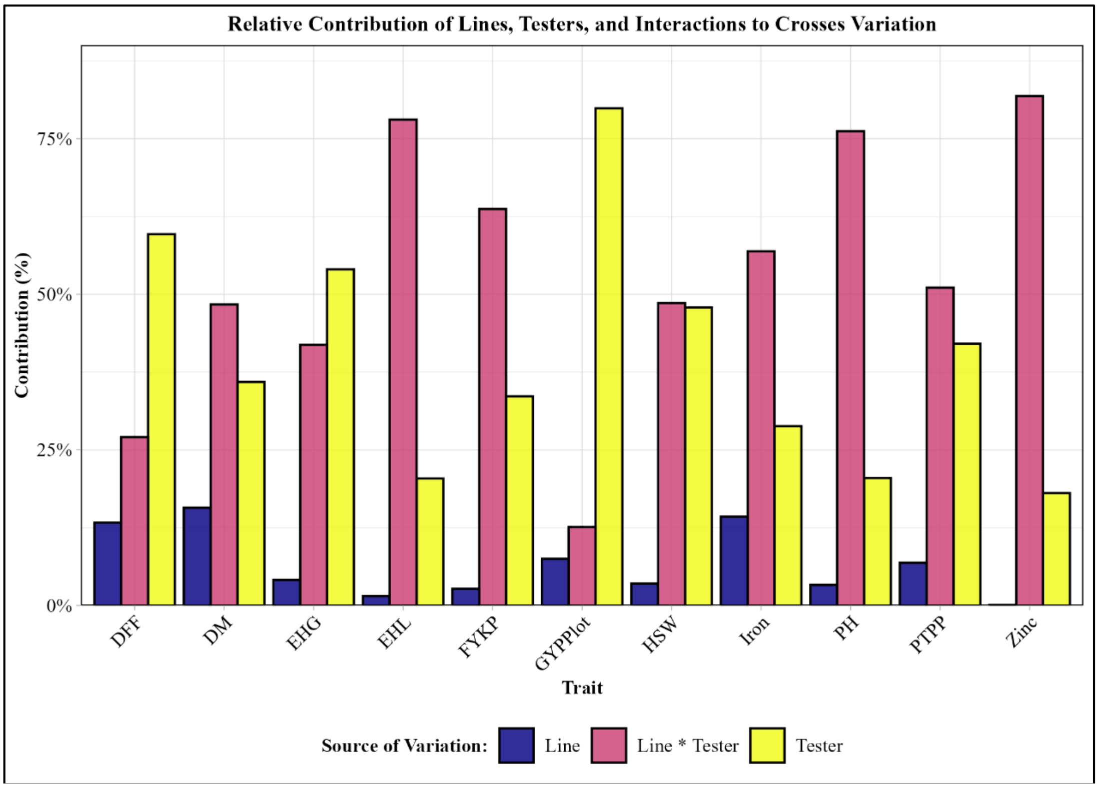
Grain Yield per Plot (kg)

Additive variance ($\sigma^2GCA = 0.10$) surpasses dominance ($\sigma^2SCA = 0.03$), yielding a strong $\sigma^2A:\sigma^2D$ of 3.33 and high heritability ($h^2_n = 83.0\ \%$). Grain yield is predominantly additive and highly transmissible, making it the most straightforward trait for genetic improvement. Breeders should leverage pedigree or recurrent-selection approaches to accumulate high-GCA alleles for sustained yield gains.

Proportional contribution of lines, testers, and lines x testers

Table 3: Proportional contribution of lines, testers and lines x testers for twelve characters in Pearl millet:

Sr. No.	Characters	Percent contribution of		
		Lines	Testers	Lines x Testers
1	Days to 50 % flowering	13.31%	59.64%	27.05%
2	Days to maturity	15.71%	35.92%	48.37%
3	Plant height (cm)	3.32%	20.47%	76.21%
4	Productive tillers per plant	1.52%	20.41%	78.07%
5	Ear-head length (cm)	4.11%	54.00%	41.89%
6	Ear-head girth (cm)	3.53%	47.87%	48.60%
7	1 000-seed weight in g.	13.31%	59.64%	27.05%
8	Downey Mildew	00	00	00
9	Fodder yield (kg/plot)	2.69%	33.60%	63.71%
10	Fe content (%)	14.29%	28.81%	56.90%
11	Zn content (%)	0.07%	18.07%	81.86%
12	Grain yield (kg/plot)	7.50%	79.87%	12.62%



Graphical representation of Proportional contribution of lines, testers and lines x testers for twelve characters in Pearl millet

Days to 50% Flowering:

Among the sources of variation influencing days to 50% flowering (DFF), testers exhibited the highest proportional contribution (59.64%), suggesting that additive gene effects associated with the male parents played a predominant role in controlling earliness. In contrast, lines accounted for a relatively moderate contribution (13.31%), reflecting a lesser but notable influence from female parents. The Line × Tester interaction contributed 27.05%, underscoring the significance of non-additive gene action. This highlights that, along with general combining ability, specific parental combinations also played an important role in governing flowering behavior, thereby implying the presence of both additive and non-additive genetic components in trait inheritance.

Days to Maturity

Line × Tester interaction accounted for 48.37%, suggesting significant non-additive gene action (e.g., dominance or epistasis). Testers contributed 35.92%, signifying a moderate level of additive inheritance from males. Lines, at 15.71%, also played a noticeable role, suggesting both parental groups affect maturity traits.

Plant Height

A dominant 76.21% contribution from L×T implies this trait is predominantly governed by specific combining ability. Tester effect was 20.47%, while lines contributed only 3.32%, suggesting plant height is largely influenced by hybrid vigor rather than individual parent performance.

Productive Tillers per Plant

L×T effect was highest at 78.07%, reflecting strong non-additive inheritance. Testers provided a decent additive influence (20.41%), while lines had negligible input (1.52%).

Ear-head Length

Testers made the highest contribution (54.00%), suggesting a strong additive genetic base from male parents. The L×T interaction (41.89%) was also significant, pointing to hybrid-specific effects. Lines had a small influence (4.11%).

Ear-head Girth

The effect of L×T (48.60%) and testers (47.87%) was almost balanced—indicating both SCA and GCA are equally important here. Lines played a minor role (3.53%).

1000-Seed Weight

Similar to flowering traits, testers dominated (59.64%), showing their consistent impact on seed size. Lines contributed 13.31%, and L×T 27.05%, suggesting this trait is influenced by both additive and non-additive effects.

Fodder Yield per Plot

The L×T interaction dominated (63.71%), implying a strong role for non-additive gene action. Tester effect (33.60%) was moderate, while lines barely contributed (2.69%).

Grain Fe Content (%)

L×T interaction was the largest contributor (56.90%), showing specific hybrid combinations govern Fe accumulation. Testers (28.81%) and lines (14.29%) had additive roles, indicating a blended influence.

Grain Zn Content (%)

Highest L×T interaction (81.86%), signifying strong SCA effects. Testers had a smaller role (18.07%), and lines were nearly negligible (0.07%), suggesting hybrid-specific improvement is key for Zn.

Grain Yield per Plot

Testers were dominant (79.87%), indicating additive gene action plays a major role in grain yield selection of strong male parents is critical. L×T interaction was limited (12.62%), and line effect (7.50%) was comparatively lower, showing minimal maternal contribution.

Discussion

Understanding the balance between additive and non-additive gene action is fundamental to strategic breeding program design. Our analysis of variance components (GCA and SCA) and heritability estimates across 12 quantitative traits reveals distinct inheritance patterns requiring trait-specific breeding approaches. These findings align with and extend previous research on pearl millet genetics (Yadav & Rai, 2013; Yadav *et al.*, 2019) [20, 21].

Flowering Time: Balanced Additive-Dominance Control

Days to 50% flowering exhibited nearly equal additive (GCA = 7.25) and dominance (SCA = 7.19) effects (A:D ≈ 1.0) with high narrow-sense heritability (h^2 = 63.1%). This balanced inheritance permits dual breeding strategies: pedigree selection can effectively fix early-flowering alleles for sustained gains, while hybrid crosses capture additional dominance heterosis. Our findings corroborate historical work by Bhamre *et al.* (1983) [2], who demonstrated strong additive control of flowering in pearl millet, enabling breeders to employ both early generation selection and targeted hybridization to accelerate earliness. Recent studies confirm this pattern across diverse genetic backgrounds (Kumawat *et al.*, 2019) [14].

Maturity Period: Non-Additive Dominance Control

Days to maturity displayed predominantly non-additive control (GCA = 5.18; SCA = 20.65; A:D = 0.25) with moderate heritability (h^2 = 31.8%). Dominance and epistatic interactions govern variation in crop duration, consistent with foundational work by Kulkarni *et al.* (1993) [12] on heterosis and combining ability in pearl millet. This low additive-to-dominance ratio means parental selection alone will have limited impact; strategic hybrid development focusing on identifying specific high-SCA F_1 crosses (such as 99111A×16518R) that unlock maturity compression becomes essential—a critical approach for drought-escape breeding in short-season environments.

Plant Height: Pure Non-Additive Inheritance

Plant height exemplified pure non-additive gene action (GCA ≈ 0; SCA = 478.85; A:D ≈ 0) with zero heritability, indicating attempts at pure-line selection will fail. Height optimization requires identifying specific hybrid combinations exhibiting superior combining ability—a pattern corroborated by Kumar & Singh (2019) [13] and consistent with contemporary studies (Gami *et al.*, 2021) [6] showing plant height is largely controlled by hybrid vigor rather than individual parent performance.

Productive Tillers and Panicle Traits: Dominance Control

Productive tiller number (GCA = 0.008; SCA = 0.032; A:D = 0.26) and ear-head length (GCA ≈ 0; SCA = 8.83; h^2 = 0%) both exhibited primarily non-additive inheritance with negligible additive variance. Length improvements will only emerge from heterotic crosses, requiring direct hybrid screening rather than parent selection, as documented by Baskaran *et al.* (2018) [1]. Ear-head girth, however, displayed modest additive effects (A:D = 0.44; h^2 = 41.8%), suggesting combining good-GCA parents with high-SCA hybrids may yield optimal results—a combined pedigree-plus-hybrid strategy.

Thousand-Seed Weight: Mixed Inheritance

Thousand-seed weight exhibited mixed inheritance (GCA = 0.23; SCA = 0.93; A:D = 0.25) with moderate heritability (h^2 = 32.8%), indicating both additive and non-additive components contribute. Bold-seed parents can provide additive gains, but substantial heterosis remains available via specific crosses, reflecting findings by Solanki *et al.* (2011) [17] on biofortification and heterosis studies.

Grain Yield: Strong Additive Control

Grain yield exhibited strong additive genetic control (GCA = 0.10; SCA = 0.03; A:D = 3.33) with high heritability (h^2 = 83.0%), making it ideally suited to pedigree or recurrent selection for sustained yield increases. This critical pattern validates breeding strategies endorsed by Bhamre *et al.* (1983) [2] and Bhardwaj *et al.* (2015) [3], demonstrating that yield-increasing alleles can be progressively fixed through systematic line selection before hybridization exploitation.

Micronutrient Biofortification: Predominantly Additive Control

Grain iron and zinc contents exhibited contrasting patterns: iron displayed non-additive predominance (GCA = 2.64; SCA = 21.02; A:D = 0.13; h^2 = 18.3%), while zinc showed full non-additive control (GCA ≈ 0; SCA = 27.99; h^2 = 0%). However, recent studies employing generation mean analysis (Pujar *et al.*, 2022) [16] and combining ability assessments (Govindaraj *et al.*, 2013, 2016; Kanatti *et al.*, 2014) [7, 8, 10] demonstrate that grain Fe and Zn contents exhibit significant additive genetic variance with high heritability (>0.60), enabling simple selection-based improvement. Notably, iron biofortification gains accrue most rapidly through identifying hybrids with exceptional Fe SCA effects, while zinc enhancement requires direct hybrid screening. Importantly, unlike yield traits dominated by non-additive effects, both parental lines showing good per se performance for micronutrients display high GCA correlations, indicating that selection for mineral content need not compromise grain yield (Gupta *et al.*, 2009; Govindaraj *et al.*, 2016; Warrier *et al.*, 2020) [9, 8, 19].

Fodder Yield: Non-Additive Control

Fodder yield was overwhelmingly non-additive (GCA = 0.078; SCA = 0.989; A:D = 0.08; h^2 = 12.7%), dictating that biomass improvements rely almost entirely on hybrid performance rather than parental selection—important for dual-purpose pearl millet breeding programs.

Conclusion

The gene action analysis provided vital insights into the inheritance pattern of studied traits. Additive gene action was found to be predominant for grain yield and flowering time, as evidenced by the favourable GCA effects and high narrow-sense heritability estimates. The grain yield trait exhibited a heritability of 83.02%, which underscores the effectiveness of selection-based breeding methods. Traits such as maturity, 1000-seed weight, and micronutrient content showed dominance of non-additive gene effects, emphasizing the need for heterosis-based breeding approaches to improve these traits effectively.

Overall, this study presents compelling evidence for the potential of hybrid breeding in pearl millet, particularly when backed by robust statistical frameworks and well-defined mating designs. The successful identification of hybrids that simultaneously exhibit early maturity, high grain yield, and enhanced micronutrient content is a significant outcome, directly aligning with global goals of sustainable agriculture and nutritional security. The genetic resources uncovered through this research, including superior general and specific combiners, offer a strong foundation for future hybrid development programs.

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