



Combining ability and heterosis studies for yield, grain iron and zinc content in pearl millet (*Pennisetum glaucum*)

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ABSTRACT

Pearl millet (*Pennisetum glaucum* L.) is a vital food crop in semi-arid regions of Asia and Africa. The present study was carried out during summer and rainy (*khari*) season of 2023 at Rajasthan Agricultural Research Institute (Sri Karan Narendra Agriculture University, Jobner, Jaipur, Rajasthan), Durgapura, Jaipur, Rajasthan to enhance iron (Fe) and zinc (Zn) content in pearl millet. The experimental material included 127 entries, comprising 105 crosses, 15 male-sterile lines, and 7 testers. The experiment was laid out in a randomized block design (RBD) with three replications across the two environments. The study revealed significant genetic diversity among parents and hybrids, particularly for Fe and Zn. The analysis of general combining ability (GCA) revealed significant differences among lines and testers across environments. Key general combiners for grain yield were P4 and P11, while P5, P11, P12, and P13 contributed significantly to fodder yield. For Fe and Zn enhancement, P1 and P3 emerged as effective combiners. Among 105 hybrids, 30 exhibited significantly positive specific combining ability (SCA) for grain yield, while four and five hybrids showed positive SCA for Fe and Zn, respectively. Notably, 89 hybrids displayed positive heterosis for grain yield. Fe content ranged from 20.83–83.50 ppm, with two hybrids showing significant positive heterosis, whereas Zn content varied from 20.00–57.17 ppm, with five hybrids performing well. Limited positive mid-parent and better-parent heterosis for Fe and Zn suggested heterosis has restricted potential for micronutrient improvement. The study underscores the need to incorporate Fe and Zn into parental lines for effective hybrid development. Hybrids P1 × P19 and P14 × P18 were promising for micronutrient enhancement, supporting strategic breeding for yield, fodder, and nutritional quality.

Keywords: Pearl millet, Combining ability, Genotype × Environment interactions, Iron, Zinc

Pearl millet (*Pennisetum glaucum* L.) is a resilient cereal crop critical for food security in arid and semi-arid regions of the world. It thrives in harsh climates, withstanding drought, high temperatures, and low soil fertility, making it indispensable for subsistence farming. Besides being a dietary staple, it holds considerable economic and nutritional value, especially in regions where iron (Fe) and zinc (Zn) deficiencies are prevalent. These micronutrients are essential for health, as deficiencies can cause issues like anemia and compromised immune function. Research highlights

biofortification's potential in staple crops to address micronutrient deficiencies cost-effectively in Asia and Africa (Meenakshi *et al.* 2010). In India and parts of sub-Saharan Africa, pearl millet serves as a vital energy source, contributing significantly to cereal consumption. Recent studies indicate that pearl millet comprises approximately 20–63% of total cereal intake in key growing states such as Maharashtra, Gujarat, and Rajasthan (Sharma *et al.* 2024). Furthermore, it is a staple food for over 90 million people in the Sahelian region of Africa and north-western India, highlighting its critical role in food security (Kumar *et al.* 2023). In these regions, it significantly contributes to Fe and Zn intake, surpassing other cereals in some cases. India cultivates pearl millet on 7.36 million hectares, half of which is planted with improved cultivars, predominantly hybrids (Department of Agriculture 2024).

Despite its resilience and nutritional advantages, enhancing pearl millet's grain yield and nutrient content remains a challenge. Genetic improvement in pearl millet involves understanding combining ability and heterosis.

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Table 1 List of the parental lines and their pedigree

Parents	Name	Pedigree	Parents	Name	Pedigree
		Lines	P12	ICMB-89111	{843B × (GNS × SS-48-40-4)-1-9-8}-30-B-B-1
P1	IICMB-99444	(SPF3/S91-327 × SPF3/S91-5)-6-2-2	P13	ICMB-94333	((843B × Togo plot#26-1)-27-B
P2	IICMB-02333	((BSECBPT/91-39 × SPF3/S91-116)-15-2-1-2	P14	ICMB-92777	{(843B × (ICMPS 500-4-4-3 × ICMPS 1800-3-1-2-C3-4))-7-1-3
P3	IICMB-843-22	(SPF3/S90-412 × SPF3/S91-6)-4-1-3	P15	ICMB-04999	((EBC-Gen-S1-40-2-2-1 × B-line bulk)-25-B-B
P4	IICMB-96666	(SPF3/S91-327 × SPF3/S91-5)-6-2-3			Testers
P5	IICMB-93333	((843B × ICMPS 900-9-3-8-2)-21-8-4	P16	RIB-3135-18	RIB-237-91 × RIB-2131
P6	IICMB-00444	(SPF3/S91-544 × SPF3/S91-5)-5-1-2-1	P17	RIB-192	RIB-50 × RIB-120
P7	IICMB-97111	(HTBC-48-B-1-1-1-1	P18	RIB-15176	(MC 94 C2-S1-3-2-2-2-1-3-B-BxSDMV 90031 S1-93-3-1-1-3-1-1-3-2-B-2)-B-23-2-1-B-B
P8	IICMB-98222	(ARD-288-1-10-1-2(RM)-5	P19	RIB-494	RIB-100 × RIB-205
P9	IICMB-98444	((BSECBPT/91-40 × SPF3/S91-529)-12-1-1-5	P20	RIB-15177	(IPC 1617 × SDMV 90031-S1-84-1-1-1-1) × (AIMP92901 S1-296-2-1-1-3-B-1)-44-4-3-2
P10	IICMB-88004	(Togo-11-5-2 selection	P21	RIB-57	RIB-40 × RIB-110
P11	IICMB-94444	((843B × 405B)-4-B	P22	RIB-335/74	RIB-80 × RIB-250

Combining ability assesses the potential of parent lines to enhance progeny performance, while heterosis denotes the superior traits of hybrids over parents. Line × Tester analysis is a breeding tool that evaluates these factors by crossing inbred lines with testers, helping identify hybrids with promising yield and nutritional traits. This research aims to examine combining ability and heterosis in pearl millet for grain yield and nutrient content, specifically focusing on zinc and iron. By assessing various parental lines and hybrids in diverse environments, the study seeks to pinpoint high-yielding, nutrient-dense genotypes. Insights gained will support the development of nutritionally fortified pearl millet varieties, enhancing food security and public health in regions where the crop is crucial.

MATERIALS AND METHODS

The present study was carried out during summer and rainy (*kharif*) season of 2023 at Rajasthan Agricultural Research Institute (Sri Karan Narendra Agriculture University, Jobner, Jaipur, Rajasthan), Durgapura, Jaipur, Rajasthan. The experimental material included 127 entries, comprising 105 crosses, 15 male-sterile lines, and 7 testers (Table 1). The crosses were generated using a line × tester mating design in an off-season nursery programme at the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, during the summer of 2023. The experiment was laid out in a randomized block design (RBD) with three replications across the two environments. Each plot consisted of two rows, each 4 m in length, with a row spacing of 60 cm and a plant spacing of 15 cm. Standard cultural practices were applied to ensure optimal crop growth. Observations were recorded for grain yield/plant (g), dry fodder yield/plant (g), Fe content (ppm),

and Zn content (ppm). Iron (Fe) and Zinc (Zn) levels were measured using an atomic absorption spectrophotometer (AAS) following the tri-acid mixture method outlined by Sahrawat *et al.* (2002) at the Central Analytical Services Laboratory, ICRISAT, Patancheru, Hyderabad. The replication-wise mean values of each genotype for various traits were used in statistical and genetic analyses. Analysis of variance (ANOVA) for the design was conducted following the fixed-effects model by Panse and Sukhatme (1954). The line × tester design analysis for combining ability followed Kempthorne's (1957) method, partitioning the variance among hybrids into general combining ability (GCA) and specific combining ability (SCA) components. Heterosis was evaluated as a percentage change in the F1 hybrid over the mid-parental value (Briggle 1963), with heterobeltiosis and standard heterosis representing heterosis over the better parent (BP) and standard check (SC), respectively.

RESULTS AND DISCUSSION

The pooled analysis of variance revealed that the genotypes were significantly different for all four traits taken under the investigation. Among the parents females and males were recorded for significant difference for all the traits studied. Significant mean sum of squares for females vs males revealed that the female and male parent differed significantly from each other for grain yield, Fe content and Zn content, except for dry fodder yield/plant. The 105 crosses showed significant difference for all the characters and also differed significantly from 22 parents (Table 2). The mean sum of squares for genotype × environment interactions was significant for most traits, except for Fe and Zn content. Specific subcomponents (parents × environments, females × environments, males ×

Table 2 Pooled analysis of variance for yield and micronutrients in pearl millet

Source of variance	DF	Grain yield/plant (g)	Dry fodder yield/plant (g)	Fe content (ppm)	Zn Content (ppm)
Environment (E)	1	0.77**	128.69**	211.02**	230.4**
Rep/env	4	0.02	0.22	0.48	16.62
Genotypes (G)	126	0.77**	3.76**	470.4**	1157.52**
Parents (P)	21	0.42**	1.15**	854.51**	1652.78**
Female (F)	14	0.45**	1.42**	932.83**	1556.47**
Males (M)	6	0.28**	0.7**	324.87**	1582.44**
F vs M	1	0.77**	0.01	2935.9**	3423.13**
P vs C	1	25.96**	154**	11004.76**	37513.81**
Crosses (C)	104	0.6**	2.84**	291.55**	707.94**
G × E	126	0.57**	1.44**	7.6	9.98
P × E	21	0.34**	0.77**	8.33	13.79
Female × E	14	0.38**	0.93**	7.54	17.42*
Males × E	6	0.13**	0.43**	10.54	6.65
F vs M × E	1	0.98**	0.52*	6.03	5.74
P vs C × E	1	12.47**	5.98**	9.11	2.52
C × E	104	0.5**	1.54**	7.44	9.28
Pooled error	504	0.01	0.1	7.61	9.68

* and **, Significant at the $P < 0.05$ and 0.01 probability level, respectively.

environments, etc.) also showed significant mean sum of squares for dry fodder yield, while Fe and Zn content exhibited non-significant results, except for Zn content in females across environments. The box plots illustrate the variability among the pooled environments of lines, testers, and crosses. Each box plot represents the distribution of performance metrics, highlighting differences in stability and performance across these breeding groups. The inter quartile ranges and medians demonstrate the variability within these groups, offering insights into their relative adaptability and response to environmental conditions. This analysis is essential for understanding genetic potential and establishing selection criteria to enhance breeding strategies (Fig. 1). Studies by Govindaraj *et al.* (2013, 2020) emphasize the importance of genetic diversity in enhancing agronomic traits, particularly nutrient content. The observed variability in essential nutrients like Fe and Zn is crucial for breeding programme aimed at developing nutrient-rich varieties, ultimately contributing to improved food security and health outcomes. The analysis of

combining ability for grain yield/plant showed significant mean square for lines in the E2 environment and on a pooled basis (Table 3). The interaction between lines and testers ($L \times T$) was also significant in both environments and pooled data, indicating that specific line-tester combinations can significantly enhance grain yield. These finding aligns with previous studies that highlight the importance of specific hybrids in maximizing yield potential (Yadav *et al.* 2022, Gavali *et al.* 2024). Conversely, the mean squares for lines in the E1 environment and testers were non-significant,

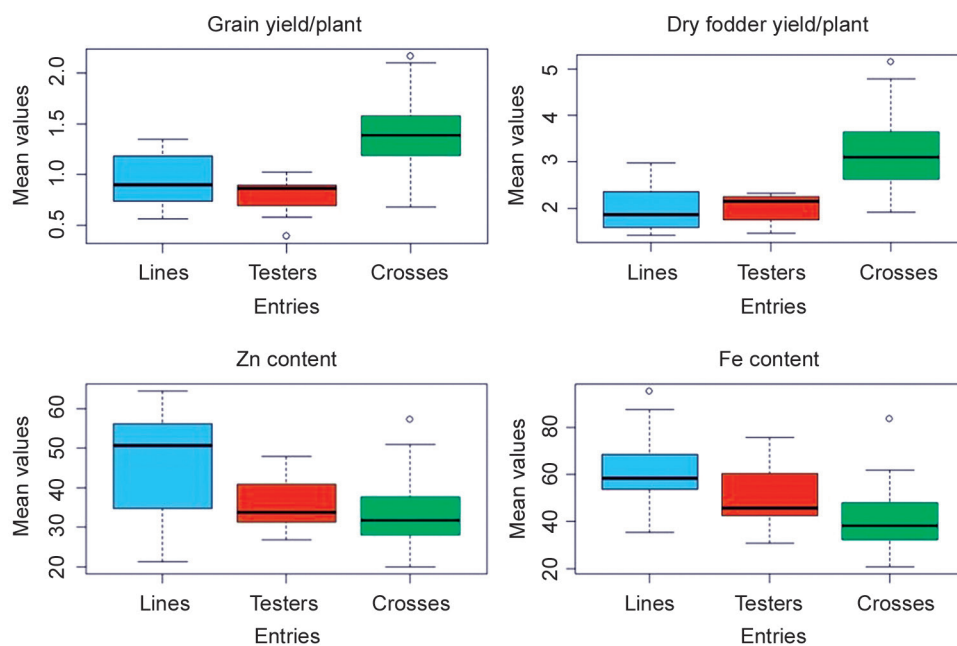


Fig. 1 Box plots representing the variability within pooled environment of lines, testers and crosses.

suggesting that environmental factors may uniquely influence certain lines' performance. The pooled analysis of variance further revealed significant variance due to line $\times$ environment ($L \times E$) and line $\times$ tester $\times$ environment ($L \times T \times E$) interactions, while the tester $\times$ environment ($T \times E$) interaction was non-significant. This outcome supports previous findings indicating that the stability of genotypes can vary across environments, a crucial consideration for breeding programmes (Surendhar *et al.* 2023). For dry fodder yield/plant, the mean squares for lines and $L \times T$ were highly significant across both environment and the pooled analysis. This reflects the potential for selecting high-yielding lines that contribute positively to dry fodder production, crucial for livestock feed (Kapoor and Singh 2017). The significant contribution of lines emphasizes the necessity of evaluating multiple environments to identify superior genetic materials in pearl millet. In the context of micronutrient content, the analysis showed highly significant mean squares for iron (Fe) and zinc (Zn) content across both environments and pooled data for lines, testers, and their interactions. The non-significant variance for line $\times$ environment ($L \times E$), tester $\times$ environment ($T \times E$), and line $\times$ tester $\times$ environment ($L \times T \times E$) suggests that the potential for improving micronutrient content in pearl millet may be stable across varying environmental conditions (Yadav *et al.* 2014, Kumar *et al.* 2020). This stability is essential for developing biofortified pearl millet varieties, particularly in regions where micronutrient deficiencies are prevalent. The analysis of general combining ability (GCA) revealed significant differences among lines and testers across environments (Supplementary Table 1). Female parents such as P4 and P11 emerged as strong general combiners for grain yield/plant, with P11 exhibiting the highest GCA. This is consistent with previous studies that emphasize the role of certain parent lines as superior combiners for yield traits in pearl millet (Sumathi and Revathi 2017, Solanki *et al.* 2017). In terms of dry fodder yield, females P5, P11, P12, and P13 showed significant and desirable GCA effects, suggesting their potential for improving fodder yield in breeding programs. For Fe and

Zn content, significant positive GCA effects were observed among female parents P1, P3, P4, P5, P6, and P9, indicating their potential to enhance micronutrient content in pearl millet (Rani *et al.* 2019). Among male testers, P18, P19, and P20 consistently demonstrated positive GCA effects across environments, reaffirming their contributions to improving iron and zinc content. Significant positive and negative SCA effects were observed for all the traits of interest among the crosses in both the environments (Supplementary Table 2). For grain Fe concentration, only the hybrids P1 $\times$ P19, P3 $\times$ P18, P6 $\times$ P20 and P9 $\times$ P19 exhibited positive significant specific combining ability. As for grain Zn concentration, positive significant SCA effects were observed for the hybrids P1 $\times$ P18, P1 $\times$ P19, P6 $\times$ P22, P14 $\times$ P18 and P15 $\times$ P20. Positive significant SCA effects for grain yield were observed for 30 crosses. These crosses originated from high and high or low and high GCA effects parents and had good performance per se across sites. This is in line with Gaoh *et al.* (2023), who reported that hybrids that generally perform well exhibit significant SCA effects. Hybrid evaluations demonstrated a wide range of performance for grain yield/plant, with 89 out of 105 hybrids displaying significant positive heterosis. Top ranking hybrids are present in Supplementary Table 2. The hybrid P2 $\times$ P18 exhibited the highest specific combining ability (SCA) effect for grain yield. Such hybrid performance underscores the potential of heterosis in pearl millet, aligning with prior findings that emphasize the genetic potential of specific hybrid combinations (Bhatnagar *et al.* 2019, Kumar *et al.* 2022). For dry fodder yield, mean values ranged from 1.92–4.78 g, with 80 hybrids demonstrating significant positive heterosis, indicating the promising avenues for enhancing fodder production through hybridization. For Fe content, averages ranged from 20.83–83.50 ppm, with two hybrids exhibiting positive significant heterosis while 67 hybrids showed significant negative heterosis. In terms of Zn content, values ranged from 20.0–57.17 ppm, with hybrid performance demonstrating variability, essential for selecting genotypes with enhanced micronutrient profiles. The hybrid P1 $\times$ P19 was identified as the best specific combiner for

Table 3 Analysis of variance for combining ability under individual environments as well as pooled environments

Sources	DF	Grain yield/plant (g)			Dry fodder yield/plant (g)			Fe content (ppm)			Zn content (ppm)		
		E1	E2	Pooled	E1	E2	Pooled	E1	E2	Pooled	E1	E2	Pooled
Lines (L)	14	0.39	2.49**	1.57**	8.61**	9.29**	13.14**	381.64**	344.24**	717.91**	1033.25**	963.18**	1989.71**
Testers (T)	6	0.27	0.46	0.46	1.37	2.81*	1.9	339.61**	293.84*	625.18**	1166.8**	944.18**	2102.05**
$L \times T$	84	0.38**	0.46**	0.45**	1.04**	1.1**	1.19**	106.78**	97.17**	196.65**	205.01**	199.46**	394.73**
Error	252	0.01	0.01	-	0.07	0.13	-	7.37	7.85	-	8.63	10.74	-
$L \times E$	14	-	-	1.31**	-	-	4.76**	-	-	7.96	-	-	6.71
$T \times E$	6	-	--	0.28	-	--	2.29*	-	-	8.27	-	-	8.93
$L \times T \times E$	84	-	-	0.38**	-	-	0.95**	-	-	7.3	-	-	9.74
Pooled	504	-	-	0.01	-	-	0.1	-	-	7.61	--	--	9.68
Error													

* and **, Significant at the $P < 0.05$ and 0.01 probability level, respectively; E, Environment.

both grain Fe and Zn content, reflecting the importance of integrating nutritional quality into breeding objectives for pearl millet (Kapoor and Singh 2017, Gaoh *et al.* 2023). Fig. 2 illustrates the magnitude of heterosis observed for grain yield/plant, dry fodder yield/plant, iron (Fe) content, and zinc (Zn) content. The data indicate significant heterotic effects, highlighting the potential for enhanced yield through hybridization. The limited number of hybrids exhibited significant positive mid-parent and better-parent heterosis among the total hybrids for grain Fe and Zn, indicating that heterosis provides limited potential for improving these micronutrients in pearl millet. Similar findings have been reported in pearl millet by Govindaraj *et al.* (2013). Kanatti *et al.* (2014) emphasized that to effectively develop pearl millet hybrids with enhanced iron and zinc content, these micronutrients must first be incorporated into both parental lines. This study's findings, including the hybrid combinations $P2 \times P18$ and $P9 \times P21$, support the effectiveness of hybrid vigour in breeding, especially for enhancing productivity traits like grain and fodder yield. Such hybrids could be particularly valuable in meeting agricultural demands in varied and challenging growing environments. The stability of Fe and Zn content across environments, as observed in this study, suggests these traits have a strong genetic component with minimal environmental interaction a finding consistent with recent studies by Satyavathi *et al.* (2015), Rai *et al.* (2016) and Surendhar *et al.* (2023). These studies noted that certain micronutrient traits, once incorporated into breeding lines, are less influenced by environmental changes, making them reliable for developing nutrient-dense varieties.

Overall, this study supports recent research on the role of genetic and environmental factors in breeding high-yielding and nutrient-rich crops. The significant GCA and SCA effects observed among lines and hybrids, as well as the identified heterosis for yield traits, underscore the genetic potential available for targeted breeding efforts. The consistent GCA performance of lines like P11, P4, and P1, coupled with specific hybrid combinations such as $P2 \times P18$ for grain yield, provides clear guidance for future breeding programs. By focusing on genotypes with stable performance across environments, breeding strategies can enhance both productivity and nutritional quality. The observed stability of micronutrient content, particularly for Fe and Zn, reinforces the potential for developing varieties with predictable and enhanced nutritional benefits, which is increasingly important for sustainable agriculture and global food security initiatives.

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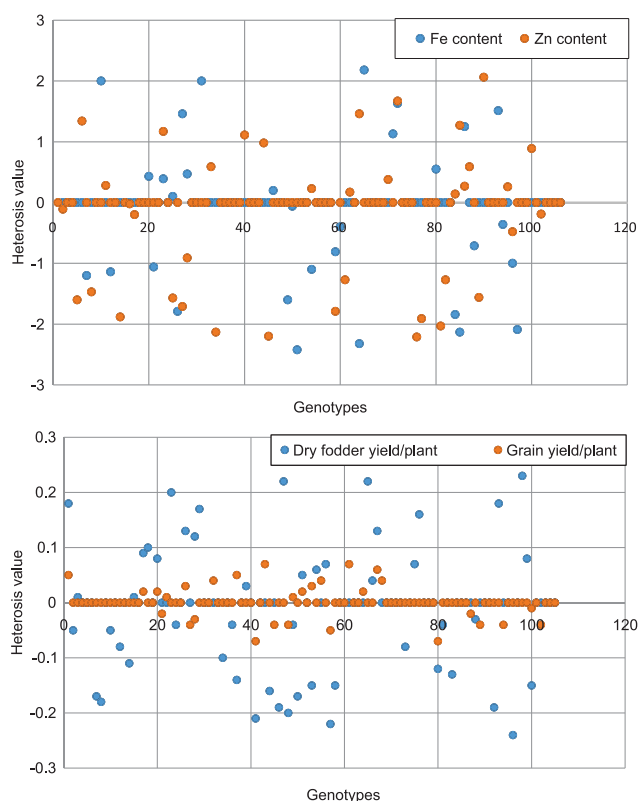


Fig. 2 Magnitude of heterosis for grain yield/plant, dry fodder yield/plant, Fe content and Zn content.

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